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**Vulnerability analysis and new tools for climate change adaptation of marine and
lagoon systems**

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Abstract

Climate change (CC), particularly sea warming, and marine heat waves (MHWs), are affecting coastal marine ecosystems around the world on different hierarchical levels of ecosystem organization. In this context, the Mediterranean Sea can be considered an "open-air laboratory", as it is universally recognized as a "miniature ocean" that, due to its geographical and geomorphological characteristics, it already exhibits the changes expected in the global ocean by 2050 and beyond.

Among its coastal marine environments, coastal lagoons play a crucial ecological role due to their strategical position between land and sea hosting biodiversity, facilitating nutrient recycling and decomposition of organic matter and nutrient removal. However, due to their characteristics, they are particularly vulnerable to climate change, considering them as "sentinel systems" (Eisenreich, 2005; Brito et al., 2012).

In this context, the aim of my thesis was to assess the impact of climate change hazards (including sea warming and marine heatwaves) on species, communities, and functions of Mediterranean marine-coastal ecosystems, with a particular focus on coastal lagoon environments.

I first focused on the impact of sea warming on species of ecological and economic interest along the coasts of Sardinia. The construction of monthly thermal habitat suitability maps for a reference period (1987-2019) and future sea warming scenarios up to 2050 (SSP2-4.5 and SSP5-8.5) for each species, allowed me to identify how the potential thermal habitat suitability could change for species identifying which ones may be most impacted and when.

I then investigated how marine heat waves can affect the quantity, composition and degradation rates of sedimentary organic matter in a Mediterranean coastal lagoon (Santa Gilla). Through simulation in benthocosms of marine heat waves of different intensities, I was able to highlight their impact on sedimentary organic matter of coastal lagoons, showing a possible alteration of resources for benthic consumers and the C storage capacities of lagoons.

I then deepened this knowledge by evaluating how sedimentary type, and consequently organic loads, can influence the impact of marine heat waves on benthic metabolism comparing two coastal lagoons located in different semi-enclosed seas (the Mediterranean and the Baltic) and at different latitudes (low and high). Through integration between mesocosm experiments and incubation techniques for the measurement of gas and nutrient fluxes, I highlighted how the intensity of heat

waves and the type of sediment, as well as the difference in organic loads, can influence the intensity and type of alteration of benthic metabolism ("oligotrophy" vs "eutrophy").

I then observed in the field the seasonal and spatial variability and the effects of a dystrophic crisis on a lagoon in Sardinia, events caused by nutrient enrichment but exacerbated by temperature increases, on the quantity, quality and composition of sedimentary organic matter as well as on the benthic communities of meiofauna. The field assessment helped me to understand the most vulnerable areas to the impact and cascading responses of the change in trophic status on environmental quality.

Finally, I integrated all the knowledge acquired in all the research activities within impact chains, logical-formal tools useful for climate change risk assessment. This allowed me to schematize the logical flow of cause and effect between hazards (surface water warming and heat waves) and vulnerability (elements of sensitivity and/or capacity of species and ecosystems) and possible impacts on species and ecosystems.

Although many aspects still need to be explored, my PhD thesis (through the use of various methodologies, including literature review, modeling approaches, experiments on the mesocosm and field investigations) has contributed to expanding the current knowledge on the assessment of the vulnerability and impacts of climate change.

Chapter 1: Introduction

1.1 Climate change as a driver of marine ecosystems' alteration

Climate change is defined by the Intergovernmental Panel on Climate Change (IPCC) as “*a statistically identifiable variation in the state of the climate, detected through changes in the mean or in the variability of its properties, that persists for an extended period, typically decades or longer.*” According to the IPCC report 2022, (IPCC, 2022: Annex I), such variations may result from either natural forcings (e.g., solar cycles or volcanic eruptions) or anthropogenic activities. The United Nations Framework Convention on Climate Change (UNFCCC, 1992) attributed climate change primarily to human causes, though considering natural variability as an additional primer.

Anthropogenic influence on climate is associated with emissions from fossil-fuel combustion, industrial processes, agricultural practices, and land-use modification: these have led to measurable alteration in atmospheric composition of heat-trapping greenhouse gases, including CO₂, CH₄, N₂O, tropospheric ozone, and chlorofluorocarbons (Doney et al., 2012). Human-driven increase of particularly CO₂ atmospheric concentrations has amplified the natural greenhouse effect, ultimately increasing heat retention in the Earth's atmosphere. Despite oceans have absorbed nearly 90% of the excess atmospheric heat generated by anthropogenic greenhouse gas emissions over the past five decades, global mean temperature has continuously increased (Venegas et al., 2023). The increased CO₂ absorption, however, caused a significant drop of oceans' pH (by ca. 0.1 pH units) namely known as ocean acidification or “the other CO₂ problem” (Doney et al., 2009; Doney et al., 2012).

Climate change, acting synergistically with other anthropogenic pressures like intensive use of fertilizers, coastal and benthic habitat degradation, overexploitation of fish stocks, rising aquaculture production, and biological invasions, is changing profoundly and rapidly marine ecosystems worldwide (Halpern et al. 2008; Hoegh-Guldberg & Bruno, 2010; Doney et al., 2012; Hewitt et al., 2016).

The profound implications of widespread and rapid oceans' alterations driven by climate, including effects on their structure, function and resilience, involve cascading effects across all levels of the ecological hierarchy, from individuals to populations, habitats and communities, and across ecological interactions (e.g., competition, predation), and ecosystem functions (e.g., nutrient cycling, primary production, carbon degradation) (Doney et al., 2012; He et al., 2019; Guild et al.,

2024). Altogether the impacts of climate change on marine ecosystems perpetrate not only their health and integrity, but their ability to produce goods and services, ultimately affecting human societies and the local and global economies (Harvey et al., 2014; Trégarot et al., 2024).

1.2. Vulnerability of marine ecosystems to the impacts of climate change

Understanding how climate change affects marine ecosystems and at which level of biological organization the impacts become tangible is essential to detect early signs of degradation, anticipate future trajectories of ecological change, and thus develop mitigation and adaptation strategies (Oliver et al. 2019; Capotondi et al., 2024).

Generally, when a system is prone to be *“unable to cope with injury, damage or harm”* to a certain stressor is defined vulnerable (De Lange et al, 2010). Vulnerability depends on sensitivity (which depends on potential impact) and resilience (or adaptability) of the system to stress (Turner et al., 2003; Schröter et al., 2005; De Lange et al., 2009 and 2010). When used in an ecological context, the term vulnerability can be addressed at different levels of the ecological organization (individual, population, community, ecosystem; Suter et al, 2002; De Lange et al., 2010). This concept has been also adopted by the IPCC which considers vulnerability as *“the propensity or predisposition of the system under consideration (e.g., an ecosystem or a species) to be adversely affected and includes either sensitivity and susceptibility to harm or lack of capacity to cope and adapt”* (IPCC, 2014; 2022; GIZ & EURAC., 2017). Nonetheless, the whole assessment of marine ecosystems’ vulnerability to the impacts generated by the various manifestations of climate change should be based on assessments carried out at each level of ecological complexity.

At the species level, climate change is expected to affect metabolic, physiological, morphological, and behavioral traits, ultimately influencing population dynamics, abundance, spatial distribution and temporal fluctuations (Doney et al., 2012; Harvey et al., 2014; Pörtner et al., 2021; Guild et al., 2024). Species vulnerability is well represented by organismal physiological performance, that is a proxy for species tolerance level to the abiotic environment. When environmental conditions change (e.g. increase in temperature), to counteract the change species (especially ectotherm invertebrates) may: i) reshape their physiology to the new environmental asset (acclimatation); ii) promote the perpetuation of more tolerant genotypes over generations (adaptation; Parmesan, 2006; Doney et al, 2012); iii) if intolerant to the change migrate whenever possible (Parmesan 2006; Doney et al, 2012). The thresholds of tolerance to the environmental change then determine “winners” or “losers” species (Doney et al., 2012). Species vulnerability

assessment may be carried out also by integrating trait-based approaches with mechanistic and demographic models, enabling to infer the impacts of climate change at species, population and habitat levels (Foden and Young, 2016).

The impacts of climate change on composition and functionality of marine communities have been documented by changes in species abundance and distribution, which, by cascading, depend cumulatively and synergistically (Jennings and Brader, 2010; Flanagan et al., 2018) on single species' physiological tolerance, dispersion capacity and biological interactions such as predation and competition (Doney et al., 2012).

Climate change may alter marine ecosystems' functionality impairing primary production, bottom-up or top-down energy transfers through the trophic web, organic matter microbe-mediated degradation and turnover, biogeochemical cycles (Hoegh-Guldberg and Bruno, 2010; Doney et al., 2012; Grimm et al., 2013; Arreguín-Sánchez and Ruiz-Barreiro, 2014). To assess or predict climate change impacts on marine ecosystems' functionality either field observations or remote sensing or manipulative laboratory experiments have been used (Payne et al., 2015; Grimm et al., 2013; Arreguín-Sánchez and Ruiz-Barreiro, 2014; Soru et al., 2022).

1.3 Climate change hazards in marine ecosystems: sea warming and marine heat waves

The different stressors through which climate change alters organisms, communities and ecosystems functionality, are defined as climate hazards (IPCC, 2014). Among these, sea water warming is one of the most evident consequences of the increased emissions of greenhouse gases. Sea warming, usually expressed as the thermal anomaly (the 30-year mean increase in sea surface temperature), is associated to oceans' alterations, such as sea level rise, water column stratification (deepening thermocline), reduction in marine ice extent, changes in oceanic circulation dynamics, changes in atmospheric precipitations and freshwater inputs, chemical (e.g. reduction in oxygen concentration) and biochemical (e.g. eutrophication) alterations (Doney et al., 2012; Venegas et al., 2023). Consequently, oceans' warming is causing severe impacts on either coastal (Wernberg et al., 2013; Halpern et al., 2015; Poloczanska et al., 2016; Pinsky et al., 2019; Wernberg et al., 2023; Trégarot et al., 2024) or deep-sea ecosystems (Danovaro et al., 2001; Danovaro et al., 2004; Pusceddu et al., 2013; Gambi et al., 2017)

Sea surface water warming can manifest both as a gradual, long-term increase in baseline temperatures and as short-term, extreme thermal anomalies. These anomalous warming events are

commonly referred to as *Marine Heat Waves* (MHWs) (Pearce et al., 2011) and are qualitatively defined as discrete periods of prolonged anomalously warm water occurring at a specific location (Hobday et al., 2016; Oliver et al., 2019).

The causes of marine heatwaves are complex and dependent on a combination of processes including, among the others, air-sea heat flux, being usually connected to atmospheric heat waves, and horizontal advection of warmer superficial waters (Doney et al., 2012; Holbrook et al., 2019, Pastor et al., 2024).

To characterize and compare different marine heatwaves, quantitative definitions have been based on measurable parameters, inspired by the atmospheric heat waves metrics (Perkins and Alexander, 2013). These include the temperature threshold, i.e. the value above which temperatures are considered anomalously warm (Hobday et al., 2016; Oliver et al., 2019). Other important criteria include the duration, i.e. the time interval during which the temperature is greater than the threshold, and the magnitude (intensity), i.e. the temperature anomaly (or the variation from the 30-years climatology referred to either the maximum or the mean value; Hobday et al., 2016; Oliver et al., 2019). The most widely adopted quantitative definition of marine heatwave is the one provided by Hobday et al. (2016) as the time interval during which sea temperature in a certain location and period of the year exceeds the 90th percentile of the local climatology (30-years mean) for at least five consecutive days, with no more than two days below this threshold.

The associated parameters (threshold, duration, intensity) are then used for heatwaves climatic characterization and for categorizing different marine heat waves (Hobday et al., 2018), depending on the scale and scope of the study (Capotondi et al., 2024; Kajtar et al., 2024). As marine heat waves are increasing in intensity, duration, and spatial extent at the global scale (Deser et al., 2024), the scientific community's interest in studying the single and cumulative effects of these events has grown.

1.4 The Mediterranean Sea as a climate change hotspot for marine coastal ecosystem

The Mediterranean Sea is considered a "miniature ocean" for its characteristics such as thermohaline circulation, multiple areas of deep-water formation and strong space-time variations, making it an excellent natural laboratory for the study of the effects of climate change on the oceans (Bethoux et al., 1999; Lejeusne et al., 2010).

Due to its bio-geophysical characteristics (e.g. semi-closed evaporitic basin, located between different continents), it is particularly sensitive to climate change and is therefore considered a "hot spot" of sea warming (Giorgi et al, 2006; Lionello et al., 2006; Diffenbaugh et al., 2007; Lejeusne et al., 2010). Its surface water temperature has increased by 0.034 to 0.041 °C/year, a much higher rate of change than that reported for the global oceans (Pisano et al., 2020; Pastor et al., 2020; EU Copernicus Marine Service Product, 2022; Darmaraki et al., 2024).

Furthermore, the significant rise in Mediterranean Sea surface temperature is expected to accelerate future MHW occurrence, frequency, duration and intensity (Darmaraki et al, 2019; Benedetti Cecchi, 2021; Pastor and Khodayar, 2023). Indeed, the Mediterranean Sea experienced several recent MHWs events including those in 2003 (Olita et al., 2007), 2007 (Mavrakis and Tsiros, 2018), 2020 (Dexana et al., 2020) and 2022, the latter being ranked as exceptional (Marullo et al., 2023; Bonino et al., 2025).

The Mediterranean coastal marine ecosystems most vulnerable to climate change include seagrass meadows, rocky and sandy shores, coastal lagoons, salt marshes, and coralligenous assemblages (Halpern et al., 2008; Varela et al., 2023; Hassoun et al., 2025). Such ecosystems are fundamental as they provide essential ecosystem services, like food provision (e.g., fisheries), coastal protection from storms and erosion, water purification, carbon sequestration, and cultural and recreational benefits that, altogether, support both human wellbeing and biodiversity (MEA, 2005; Borja et al., 2015).

Sea warming and marine heatwaves are both known to affect marine biodiversity in the Mediterranean Sea causing mass mortality events, reduced abundance, shifts in community structure (Cerrano et al., 2000; Garrabou et al., 2009; Coma et al., 2009; Smale and Moore., 2017; Stipcich et al., 2022; Garrabou et al., 2022; Galli et al., 2017; Gómez-Gras et al., 2021; La Manna et al., 2023). These, in turn, have generated at times several ecological and socio-economic implications as, for example, impacting commercial activities of fisheries and aquaculture (Sarà et al., 2012; Martinez et al., 2018; Sarà et al., 2021; Giacoletti et al., 2024).

Therefore, understanding whether and how hazards associated with sea warming and marine heatwaves affect individually or synergistically the different levels of biological organization is not only a global priority, but also a local one, since, even from a protection perspective, acting globally is quite difficult but acting local is possible" (Trégarot et al., 2024).

1.5 Coastal lagoons as sentinel systems of climate vulnerability

Coastal lagoons are aquatic transitional ecosystems, separated from the sea by physical barriers such as sandbanks, shingle, or rocks, and connected to it through one or more inlets (Pérez-Ruzafa et al., 2011; Cataudella et al., 2015; Newton et al., 2018). Due to their peculiar sensitivity to environmental change, they are widely known as “sentinel systems” for studying and detecting the impacts of current climate change (Eisenreich, 2005, Brito et al., 2012, Perez-Ruzafa et al., 2011, Newton et al., 2018). Mediterranean coastal lagoons are generally characterized by shallow waters with well irradiated bottoms, that, together with large inorganic nutrients availability, support primary production levels much higher than the facing marine waters (Levin et al., 2001; Danovaro & Pusceddu, 2007). They have different ranges of salinity depending on the width opening with the sea (Perez-Ruzafa et al., 2011) and are also shaped by other environmental gradients of temperature, oxygen and balance between respiration/primary productivity (Perez-Ruzafa et al., 2011). Many Mediterranean coastal lagoons are considered “detritus traps” and sinks for organic matter accumulation, thus representing important storage basins of blue carbon (Pusceddu et al., 1999, 2003; Manini et al., 2003; Palmas et al., 2025). Because of their characteristics they provide numerous services such as food production, regulating services like nutrient retention, carbon storage, water purification, and climate regulation (Inacio et al., 2018; Rodrigues-Filho, et al 2023).

Due to their transition position, coastal lagoons are prone to the impacts of sea level rise, heavy rainfall, evaporation, and storminess (Anthony et al., 2009; Kennish and Paerl, 2010; Perez-Ruzafa et al., 2011). Anomalous warming episodes defined either as heat waves or marine heat waves are reported for coastal lagoons worldwide (Barbosa et al., 2023) and, also, for the Mediterranean Sea (Bertolini and Pastres, 2021; Ferrarin et al., 2024). Here, however, the knowledge of climatic characteristics and the actual impacts of such episodes is much less consistent than for marine coastal ecosystems. Despite most studies follow the wide-used Hobday et al. (2016) definition of marine heatwave, the quantitative definition of the climatological baseline in coastal lagoons hampers often its use, as the historical data are much less abundant than for the open sea (Bilajac et al., 2024). Most of the scientific studies addressing the effects of heatwaves on coastal lagoons, especially because of the economical importance, are focused on species tolerance and, particularly, culturable bivalves (Bertolini et al., 2023). Moreover, although of considerable ecological and trophic importance, the possible consequences of heatwave events on

biogeochemical and nutrient cycles in coastal lagoons are understudied and, thus, poorly understood (Correira-Martins et al, 2022; Derolez et al., 2020).

Eutrophication, one of the most common problems faced by many Mediterranean coastal lagoons is caused by excess nutrient loads from agricultural and farming activities and is becoming progressively more frequent (Taylor et al., 1995). The detrimental effect of eutrophication may be catalyzed and exacerbated by increasing temperature, causing shifts in the ecological state of lagoons and priming the summer occurrence of dystrophic crises, ultimately leading to the loss of biodiversity and, by cascade, ecosystem functioning and ecosystem ability to produce goods and services (Lloret and Marin-Guirao, 2008; Viaroli et al., 2008).

1.6 Assessment of the vulnerability of marine and lagoon ecosystems to the impacts of climate change

Given their ecological and socio-economic importance, understanding how multiple climate-related stressors are affecting coastal marine and lagoon ecosystems is becoming an urgent priority. In this context, scientific-based information is needed to inform policymakers for planning mitigation and adaption strategies to climate change (Kirchhoff, et al., 2013; Scherhaufer, 2014). For this reason, a Climate Risk and Vulnerability Assessment (CRVA) protocol was developed by the Intergovernmental Panel on Climate Change (IPCC, 2014; 2022). This protocol has the main purpose to acquire new knowledge on present and future climate changes risks. In the Fifth Assessment Report (AR5) of the IPCC Working Group, climatic risk is considered something uncertain but also a potential specific consequence associated with climate change impacts (climate impacts) on a valued entity (i.e. species, ecosystem) (GIZ, & EURAC, 2017). It is expressed as the sum of the interaction of climatic hazards, the characterizes of the system (species, community, ecosystem) and which element are exposed to the damage. How all these elements relate together and contribute to the climatic risk can be integrated in a conceptual framework termed the Climate Impact Chain. Firstly, developed by Schneiderbauer et al. 2013, this logical tool describes the cause-and-effect sequences between elements to understand and prioritize the factors driving risk and vulnerability within specific systems and to identify the most relevant elements contributing to a specific risk (GIZ and EURAC 2017). Climate impact chains consider the relationships among the different components of climate risk, namely vulnerability, in terms of sensitivity and capacity, hazard, and exposure, where:

- **vulnerability** is *“the propensity or predisposition of the system under consideration (e.g., an ecosystem or a species) to be adversely affected and includes either sensitivity and susceptibility to harm or lack of capacity to cope and adapt”*. (IPCC, 2014; 2022; GIZ, & EURAC. (2017)
- **sensitivity** represents the attribute of the system factors that directly influence the consequences of a hazard
- **capacity** refers to the ability of the system to cope with and adapt to a hazard (IPCC, 2014; 2022; GIZ, & EURAC. (2017)
- **hazard** is *“the potential occurrence of a natural or anthropogenic physical event, climatic trend, or physical impact”* that could cause damage to the object of the exposure (e.g. ecosystems, environmental resources” (IPCC, 2014; 2022; GIZ, & EURAC. (2017)
- **exposure** refers to *“the presence of people, livelihoods, species or ecosystems, functions, services and environmental resources, infrastructure, or economic, social, or cultural assets in places and settings that may be adversely affected”* (IPCC, 2014; 2022; GIZ, & EURAC. (2017).

Climate Impact Chains are conceptual models of climate risks that have been developed to streamline the analysis of climate-related impacts and provide a structured framework for the comprehensive assessment of related risks following the comprehensive risk management framework (UNDRR 2023). The impact chains methodology helps elicit, conceptualize, represent, and share knowledge about multi-hazard risks within a given geographical and temporal scope. They describe in an intuitive, graphical, and logical manner the complex chain of cascaded impacts induced by possibly compounded climate hazard-related events and trends. The typical graphical output of Climate Impact Chains (Figure 1) can include also other relevant risk-related factors, e.g., exposed systems and vulnerabilities. Within the resulting conceptualization of hazard and impact cascades, adaptation or risk mitigation measures of different types can be identified, such as early warning systems, ecosystem-based adaptation, capacity building, and technical as well as socio-economic measures.

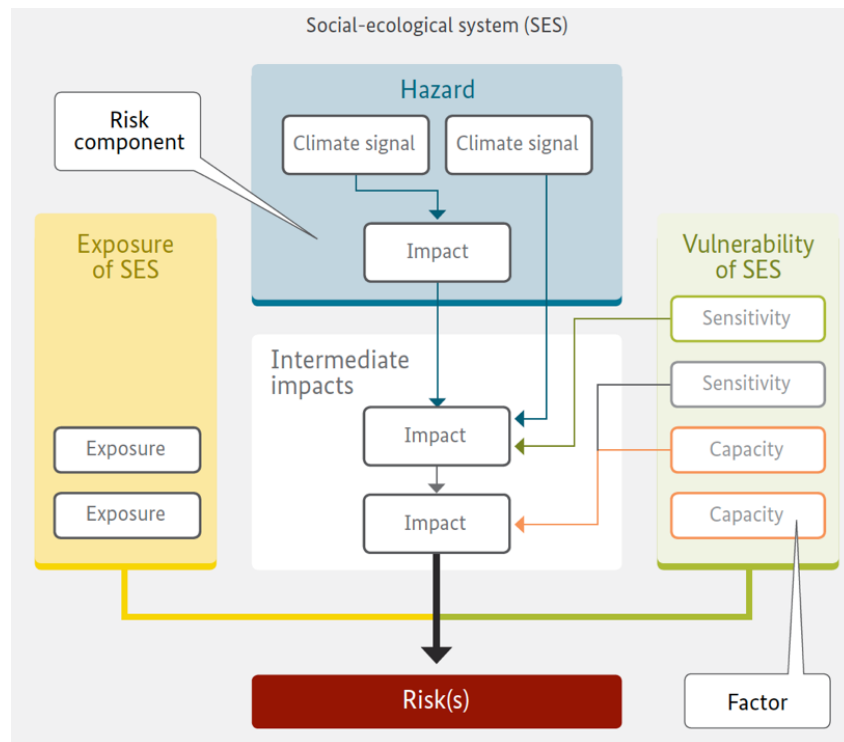


Figure 1. Example of Climate Impact Chain (GIZ, EURAC & UNU-EHS, 2018)

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Chapter 2: Thesis Outline

Based on the conceptual framework and the scientific background presented in Chapter 1, this thesis aims to assess the impact of climate change hazards (including sea warming and marine heatwaves) on species, communities, and functions of Mediterranean marine and coastal lagoon environments to identify possible risks. More in details, emphasis is placed on coastal lagoon ecosystems, evaluating their vulnerability to climate-driven stressors and identifying potential climate-related risks by studying their vulnerabilities.

Given the highlighted importance of assessing risks at the local level, the thesis focuses on Sardinia as a case study, applying complementary methodologies across multiple levels of biological organization.

In **Chapter 3**, to answer the question “*What is the impact of sea warming on commercial and/or protected species on the coast of Sardinia?*” the thermal suitability probability of the habitat of five marine and lagoon species of commercial interest (the mussel *Mytilus galloprovincialis*, the sea urchin *Paracentrotus lividus*, the sea cucumber *Holothuria tubulosa*, the seagrass *Posidonia oceanica*, and the fish *Mullus barbatus*) has been assessed for current (1987-2010) and projected (SSP2-4.5 and SSP5-8.5) scenarios for the period 2021-2050 based on their vulnerability to sea water warming.

In **Chapter 4**, to answer the questions “*Do marine heatwaves have an impact on the quantity, composition, and degradation rates of sedimentary organic matter in coastal lagoons?*” and “*Do such impacts differ among heatwaves with different intensities?*”, short-term marine heat waves (5 days) with different intensities (+4 °C and +8 °C) were simulated in benthocosms at on the sediments of a Mediterranean lagoon (Santa Gilla lagoon). This chapter has been already published as: “Palmas, F., Cariccia, F., Pasquini, V., Cabiddu, S., Addis, P., and Pusceddu, A. (2025). Marine heatwaves effects on quantity, composition, and turnover of sedimentary organic matter in a Mediterranean coastal lagoon: A benthocosm study. *Estuar.Coast. Shelf Sci.* 318, 109252. doi: 10.1016/j.ecss.2025.109252”.

In **Chapter 5**, the experiment whose results are reported in Chapter 4 was expanded to include the study of biogeochemical fluxes of gases (oxygen) and nutrients (ammonium) in two different lagoons to answer the questions: “*Does sediment type influence the impact of marine heatwaves on the quantity, composition, and degradation rates of sedimentary organic matter and*

on biogeochemical fluxes in coastal lagoons at different latitude? Do the impacts of marine heatwaves differ among heatwaves with different intensities?”, “Is there a variation in the effect of time on biogeochemical flows?” “Does the duration of heat waves cause significant changes in biogeochemical fluxes?” Here, marine heat waves (MHWs) of different intensity (+2°C and +6°C) were simulated in benthocosms on muddy and sandy sediments from two coastal lagoons characterized by different latitudes and, thus, background thermal regimes: the colder Curonian Lagoon (Baltic Sea) and the warmer Santa Gilla Lagoon (Mediterranean Sea).

In **Chapter 6**, I further explored knowledge about coastal lagoons by answering the question *“How do seasonality, the confinement gradient, and the occurrence of dystrophic events influence sedimentary organic matter features and meiobenthic communities?”* The aim was to assess the present ecological condition of a Mediterranean lagoon (S'Ena Arrubia Lagoon) and explore its potential susceptibility to future climate-driven stressors by interpreting current ecological patterns considering climate change related anomalous events.

Finally, in **Chapter 7**, I summarized the main results collected from the studies described in Chapters 3-6, articulating the results in the climate impact chains framework (divided into Climate Hazards, Exposure and Vulnerability) outlining the possible risks for the protected and commercial species analyzed and for the coastal lagoons.

Chapter 3: Effects of sea warming on marine and lagoon species of commercial or conservation interest in the Sardinia seas

3.1 Introduction

Ocean warming represents one of the most spread and studied manifestations of global climate change (IPCC, 2022). As a key component of the Earth system, the ocean has been capable of absorbing ~90% of the atmospheric heat due to the increase in greenhouse gas concentrations in the last 50 years (Venegas et al., 2023). Nonetheless, oversaturation of its heat absorption capacity is altering oceans' chemical and physical properties, causing severe changes in marine ecosystems worldwide (IPCC, 2022).

Marine ecosystems have been affected by warming at levels of ecological organization, with several implications for its functioning and the services they provide for human beings (Alter et al., 2024). Semi-enclosed basins like the Mediterranean Sea are more exposed to warming for their morphological characteristics, anticipating the future ocean changes (Lejeusne et al., 2010; Pastor et al., 2020). This phenomenon and its most extreme manifestations, such as marine heatwaves, are causing major consequences, including mass mortality events (Cerrano et al., 2000; Garrabou et al., 2009; Garrabou et al., 2022), local extinctions (Yeruham et al., 2015), and seagrass meadows regression (Telesca et al., 2015). Even marine ecosystems in Sardinia, Italy's second largest island and biodiversity hotspot, have been affected by sea warming and marine heatwaves in particular (Stipcich et al., 2024a).

At the species level, warming has significant impacts on physiology, abundance, distribution and interactions among marine organisms (Doney et al., 2012; Pörtner and Gutt, 2016; Assan et al., 2020; Pörtner, 2021). Ultimately, it may have cascading effects on community compositions and ecosystem functioning (Doney et al., 2012).

Species sensitivity and adaptation capacities to sea warming, a key component of vulnerability assessment to warming, depend on how their thermal performance responds to increasing temperatures (Foden and Young, 2016). Specifically, the ecological performance of an organism describes how it responds to environmental stimuli (e.g., rising temperature), assessed through one or more traits directly related to its physiology or fitness, such as organism's metabolic, growth, reproduction, and survival rates (Violle et al., 2007; Pörtner, 2021). Temperature is one of the

fundamental abiotic factors that naturally influence the biological processes of aquatic organisms (Bruno et al., 2015), especially for ectotherms that are unable to autonomously regulate their body temperature (Rohr et al., 2018). In fact, temperature has an important role in shaping the metabolic responses of aquatic ectotherms, influencing their energy assimilation, conversion, and expenditure (Sarà et al., 2013; Sokolova et al., 2013, 2021).

Understanding the sensitivity of species to changes of temperature is essential to assess their vulnerability to climate change, and allows identifying potential “winners”, more tolerant to warming, and potential “losers”, not tolerant or poorly tolerant to warming (O’Brien & Leichecho, 2008; Cavole et al., 2016).

The knowledge of the relationship between temperature and species thermal performance helps to determine their biogeographical range and, so, to predict their changes in future warming scenarios (Bosch-Belmar et al., 2022). Tools such as habitat suitability models (HSMs) can link environmental variables and species tolerance and their use helps predicting the likelihood that a particular area provides suitable environmental conditions for a species to occur, survive, and reproduce (Hirzel et al., 2008; Bosch-Belmar et al., 2022). HSMs are widely used in conservation and ecological research to inform decisions about species protection, habitat restoration, and spatial planning (Hirzel et al., 2008). The use of HSMs is also among the strategies identified by the IUCN for assessing climate change, providing useful information to policymakers at international, national or local level to undertake mitigation and/or adaptation measures (Foden and Young, 2016).

The aim of this chapter, developed as a contribution to the Regional Strategy of Adaptation to Climate Change of the Sardinia Region (SRACC), was to assess vulnerability and potential range shifts of selected species of commercial or conservation interest under projected sea temperature scenarios across Sardinian Seas. The analysis focused on five representative species.

Bivalves like *Mytilus galloprovincialis*, Lamarck, 1819, eurythermal species, inhabit intertidal and subtidal zones down to 40 m depth, occurring in marine-coastal and transitional environments such as estuaries and coastal lagoons (Kooijman, 2010; Pörtner, 2010; Michaelidis et al., 2014; Bonham et al., 2022). *M. galloprovincialis* is a keystone species of both ecological and commercial importance as harvested at both national and regional levels. In Sardinia, due to the different manifestations of climate change—particularly extreme events such as marine heat waves and “flash floods”—several mass mortality events of *M. galloprovincialis* have been reported by farmers (Addis et al., 2021).

Sea urchins like *Paracentrotus lividus* (Lamarck, 1816) inhabit subtidal environments, rocky substrates, seagrass meadows of the endemic seagrass *Posidonia oceanica* and intertidal rock pools (Boudouresque & Verlaque, 2020). Sea urchins in general are key species due to their ecological role, as grazers, as well as for their (local) commercial value. Their gonads are sold as high-value gourmet food in several European, national, and regional markets (Furesi et al., 2016). Excessive fishing pressure has led regional governments to implement temporary fishing bans, as occurred in the Sardinia Region (Law No. 17 of November 22, 2021). In addition to strong anthropogenic pressures, other factors threaten *P. lividus*, the many manifestations of climate change, such as sea warming and acidification (Collard et al., 2016; Byrne et al., 2011; Toso et al., 2025).

The fish *Mullus barbatus* (Linnaeus, 1758) (red mullet) is a widely distributed demersal fish in the Mediterranean Sea (Fiorentino et al., 1998; Maggio et al., 2009; Tüzün et al., 2019; Sieli et al., 2021; Geraci et al., 2023). Temperature and salinity are key factors in its distribution: the species prefers shallow waters with Mediterranean salinity and temperatures above 18°C, avoiding colder waters. Historical stock collapses have been reported, likely due to population shifts offshore, but temporary fishing closures have led to rapid stock recovery (Maravelias et al., 2007; García-Rodríguez et al., 2011).

Sea cucumbers like *Holothuria tubulosa* (Gmelin, 1791) are important components of the benthic macrofauna of the Mediterranean for their role as bioturbators (Mezali & Soualili, 2014). They inhabit rocky substrates, unconsolidated sediments, and *Posidonia oceanica* meadows (Ocaña and Sánchez, 2005; İşgören-Emiroğlu and Günay, 2007). Their overexploitation driven by increasing consumers' demand, particularly from the Asian markets, has led to a ban on collection in Italy, and consequently in Sardinia as well, although illegal fishing is still frequent (Meloni and Esposito, 2018; Pierrat et al., 2022). In addition to overfishing, other factors such as pollution and climate change are also likely threatening this species (Halpern et al., 2008; Purcell et al., 2013; Sadeghi-Nassaj et al., 2018; Sadoul et al., 2022; Pasquini et al., 2023, Ennas et al., 2023; Abyaba et al., 2025).

Posidonia oceanica (Linnaeus) Delile, 1813 (firstly known as *Zostera oceanica*, Linnaeus, 1767) Mediterranean endemic seagrass (Gobert et al., 2006), provides important ecosystem goods and services (Vassallo et al., 2013). It absorbs dissolved carbon dioxide and releases oxygen (Kennedy et al., 2022) and acts as a habitat-forming species (Vasarri et al., 2021). Due to its ecological importance and sensitivity to various abiotic and anthropogenic pressures, *P. oceanica* is subject to multiple protection measures at international, national, regional, and local levels including the Bern Convention (1996; Annex I), the Barcelona Convention (Annex II, 1995), several European directives

such as the Habitat Directive (Annex I, 1992), the Water Framework Directive (WFD, 2000), the Marine Strategy Framework Directive (MSFD, 2008), the Common Fisheries Policy (CFP, 2006). The regression of this important species, caused by multiple stressors (Blanco-Murillo et al., 2022), has cascading consequences on the ecosystem, leading to both chemical changes (e.g., alterations in water oxygenation and in the quantity and quality of nutrients) and biological ones (e.g., bottom-up effects on herbivorous species) (Pergent et al., 2014).

To assess vulnerability and potential range shifts of all the abovementioned species across Sardinian Seas, thermal habitat suitability maps were created, based on literature-reconstructed thermal performance curves (TPCs) for different functional traits for current (1987-2010) and projected sea temperature scenarios (SSP2-4.5 and SSP5-8.5) for the period 2021-2050.

3.2 Material and Methods

To create trait-based thermal suitability maps of the target species, I followed the methodology used in Bosch-Belmar et al., 2022. The main steps of this procedure include:

- constructing of thermal performance curves based on a functional and/or a selected metabolic trait for each species (Padfield et al., 2021);
- creating surface temperature distribution maps for a reference period 1987-2010 and the two future IPCC scenarios (at 2050) SSP2-4.5 and SSP5-8.5;
- integrating the thermal performance models of each target species with the surface temperature distribution maps into habitat suitability maps (HSMs, Habitat Suitability Models).

3.2.1 Thermal performance curves (TPCs)

3.2.1.1 Collection of information about the species and their functional and metabolic traits

The construction of the performance curves involved an initial exploratory literature review to gather information on the impacts of climate change hazards (e.g. Sea Warming, Extreme Events etc) on the selected species and on how their functional and metabolic traits respond to these stressors and particularly to temperature changes.

Although the review did not follow a fully systematic structure, it was conducted following some of the principles of PRISMA (Page et al., 2021). Indeed, the aim of the review was not to provide an

exhaustive extraction of all variables from all retrieved studies, but rather to identify and contextualize relevant trait-environment relationships to inform the subsequent reconstruction of the thermal performance curve.

The literature review was conducted using the SCOPUS database from November 2022 to June 2023. Despite the study is mainly focused on the Sardinia Island, the bibliographic search was extended to the entire Mediterranean basin due to the limited number of studies specifically focused on the coastal and marine environments of Sardinia.

Targeted search strings were designed to retrieve studies addressing the responses of marine species to key environmental drivers associated with climate change. The following separated combinations of keywords were used:

- "Species" AND "Extreme Events" AND "Mediterranean Sea"
- "Species" AND "Eutrophication" AND "Mediterranean Sea"
- "Species" AND "Climate Change" AND "Mediterranean Sea"
- "Species" AND "Sea Level Rise" AND "Mediterranean Sea"
- "Species" AND "Sea Warming" AND "Mediterranean Sea"
- "Species" AND "Temperature" AND "Mediterranean Sea"
- "Species" AND "Acidification" AND "Mediterranean Sea"
- "Species" AND "Hypoxia" AND "Mediterranean Sea"
- "Species" AND "Salinity" AND "Mediterranean Sea"
- "Species" AND "Thermal Tolerance" AND "Mediterranean Sea"
- "Species" AND "Flood" AND "Mediterranean Sea"

where "species" was the scientific name of the species.

For *Holothuria tubulosa* and *Mullus barbatus*, for which the available literature was negligible, additional simplified search strings were also used:

- "Species" AND "Mediterranean Sea"
- "Species" AND "Temperature".

After reading the full texts of the papers returned by these queries, articles were excluded if they did not i) specifically address the effects of climate change on the species; II) report the relationship between one or more functional and metabolic traits. The literature search resulted in the selection of studies for each target species from all above queries as follows:

- *Mytilus galloprovincialis*: 34 selected papers over 59 retrieved not repeated papers

- *Paracentrotus lividus*: 22 selected papers over 34 retrieved not repeated papers
- *Mullus barbatus*: 17 selected papers over 313 retrieved not repeated papers
- *Holothuria tubulosa*: 16 selected papers over 59 retrieved not repeated papers
- *Posidonia oceanica*: 44 selected papers over 93 retrieved not repeated papers

3.2.1.2 Trait selection and data collection

Based on the studies identified through the previous bibliographic search, an arbitrary selection was conducted with the aims of:

- identifying the most suitable traits for describing each species' sensitivity to temperature, with at least one representative response trait for each species
- collecting quantitative data capable of describing the relationship between the selected trait and temperature, thereby enabling the construction of performance curves along a thermal gradient.

For each of the five species, the selected traits were chosen based on their relevance to organismal fitness (maintenance, growth, or reproduction), their dependence on temperature, and the availability of sufficient quantitative data to allow curve fitting.

Quantitative data required for the construction of thermal performance curves (TPCs), namely the values of the selected trait and the temperature at which they were measured, were extracted from tables, supplementary materials, and figures published in the cited studies using WebPlotDigitizer software (Rohatgi, 2022). All temperature and trait observations extracted from the retained studies were combined into a single dataset for each selected species and trait, providing the empirical basis for reconstructing thermal performance curves. All available data points were retained for analysis; no averaging or aggregation was applied to observations at the same temperature. The data were organized into Microsoft Excel spreadsheets, converted into *.txt files separately for each species, and then imported into RStudio scripts (R version 4.5.1, June 13, 2025).

The traits selected for the construction of thermal performance curves for each species are summarized in Table 3.1, while the extracted data are reported in Table S3.1.

Table 3.1. Selected trait and data sources for thermal performance curves each species

Species	Selected trait	Sources
<i>Mytilus galloprovincialis</i>	Hourly respiration rate (RR, $\mu\text{mol O}_2 \text{ h}^{-1}$)	Anestis et al., 2010 Gazeau et al., 2014 Montalto et al., 2015 Montalto et al., 2016 Parisi et al., 2021
<i>Paracentrotus lividus</i>	Growth rate (mm 60 days^{-1})	Pagés et al., 2018
<i>Mullus barbatus</i>	Gonado-somatic index (%)	Sieli et al., 2011
<i>Holothuria tubulosa</i>	Gonado-somatic index (%)	Mezali et al., 2014 Tahri et al., 2019 Dereli et al., 2016
<i>Posidonia oceanica</i>	Daily biomass turnover (day^{-1})	Savva et al., 2018

3.2.1.3 Thermal performance curves model fitting

Then, data analysis was conducted in RStudio (R version 4.5.1 (2025-06-13) using the rTPC package (Padfield et al., 2021). This package implements 23 mathematical models describing different potential shapes of thermal performance curves.

Each trait-temperature observation is considered as a single point in the fitting of the TPC model. Through integration in a custom R script, this routine enables the comparison for all the trait and species, of all the models and then the selection of the model that provides the best fit to the empirical data of each species. The selection of the most suitable model included:

- the model with the lowest Akaike Informative Criterion (AIC) index
- the model among those with the lowest AIC index that best reflects the physiology of the species based on the literature (Padfield et al., 2021).

In details, Akaike Informative Criterion (AIC) is an information-theoretic metric used to assess how well a statistical model fits the data while penalizing unnecessary model complexity (Akaike, 1974; Burnham & Anderson, 2002). It has been used to compare the alternative models and identify the one that best balances goodness of fit and parsimony to infer which one best fits with the data,

identified by the lowest AIC values. Particularly, in this context, we used the corrected version (AICc), considered more appropriate for relatively small sample sizes.

3.2.2. Surface temperature distribution maps

The temperature data used to represent sea surface temperature (SST) distributions for the reference period (1987–2010) and for future projections (2021–2050) were obtained from the Copernicus platform (<http://copernicus.eu>). The mid-century target period (2021–2050) was selected to for intercepting the mid-term potential consequences of sea warming caused by current climate change, thus providing a possible decision-making basis for governance to identify and implement the most immediate mitigation and/or adaptation actions.

Data for the reference period (1987–2010) were obtained from Escudier et al. (2020), with monthly projections at a spatial resolution of $0.04166667^\circ \text{ lon} \times 0.04166667^\circ \text{ lat}$. Future projections were derived from a combination of Shared Socioeconomic Pathways (SSPs) and Representative Concentration Pathway (RCPs) scenarios, sourced from the CMIP6 multi-model ensemble (Coupled Model Intercomparison Project), with monthly projections at a coarser resolution of $1.00405^\circ \text{ lon} \times -0.03660934^\circ \text{ lat}$ (Copernicus Climate Change Service, Climate Data Store, 2021). The coarser spatial resolution of future projections should be considered when interpreting spatial patterns.

The SSPs, an extension of the RCPs, integrate possible socioeconomic pathways, land-use changes, and other human-driven climate factors that influence greenhouse gas emissions and radiative forcing (Meinshausen et al., 2020; Lee et al., 2021). These pathways consider the impact of societal adaptation measures and of different levels of climate change (Meinshausen et al., 2020; Lee et al., 2021). SSPs are grouped into five families based on challenges to mitigation and challenges to adaptation (Meinshausen et al., 2020; Lee et al., 2021).

Specifically, the scenarios used in this chapter are based on the CMCC-CM2-SR5 model (Italy), containing climate projection experiments that combined SSP–RCP pathways:

- SSP2-4.5, following SSP2, defined as “Middle of the road,” representing intermediate challenges to mitigation and adaptation, and RCP4.5, leading to a radiative forcing of 4.5 Wm^{-2} by 2100;
- SSP5-8.5, following SSP5, defined as “Fossil-fueled development,” representing high challenges to mitigation and adaptation, and RCP8.5, leading to a radiative forcing of 8.5 Wm^{-2} by 2100.

For each of the selected periods, maps of monthly mean temperature were generated using RStudio (R version 4.5.1 (2025-06-13)). The temperature data from the scenarios were rescaled to match the resolution of the reference period for improved visualization.

3.2.3. Trait-based thermal habitat suitability maps

For the last step, data on species thermal performance was transformed into probability of occurrence at different temperatures. Each value for the selected rates for each species was scaled to the value identified as optimal by the model. This can be expressed as:

$$OP = \frac{XR_t}{XR_{opt}}$$

where OP represents the probability of occurrence, XR_t is the value of each rate at each temperature t , and XR_{opt} is the value identified as optimal by each model (adapted by Bosch-Belmar et al., 2022).

In detail, to represent the probability of occurrence at the spatial level, it was calculated at the pixel scale using the temperature values reported in the raster layers respectively for the reference period (1987–2010) and for future projections SSP2-4.5 and SSP5-8.5 (2021–2050), as follows:

$$SOP_{im} = \frac{PXR_{im}}{XR_{opt}}$$

where SOP_{im} was the spatial occurrence probability in the spatial pixel “i” for the month “m,” PXR_{im} was the predicted X rate in the spatial pixel “i” and the month “m,” XR_{opt} is the value identified as optimal by each model (adapted by Bosch-Belmar et al., 2022).

Then, maps of estimated rank of thermal habitat suitability at each month of the year in both the reference period and the future scenarios were constructed for each species. This estimation didn’t consider any other abiotic (e.g salinity, oxygen, food availability etc) and biotic factors (e.g. competition). Therefore, the results deal merely with the physiological or metabolic trait selected for each species and do not allow predicting species presence/absence, density, or biomass.

The scale of habitat adequacy was ranged between 0 (almost completely unsuitable habitat) and 1 (optimal habitat), spitted in intervals of 0.2 units and color-coded as follows:

- **dark green** (1-0.8) for Optimal habitat: in this range from a metabolic point of view, the energy balance is positive, and the organism has maximum energy available for all vital processes (growth, development reproduction and accumulation)

- **light green** (0.8-0.6) and **yellow** (0.6-0.4) for upper and lower limits of *pejus*, respectively: when aerobic energy balance is positive but decreased due to the increased basal metabolic cost
- **orange** (0.4-0.2) for *pessimum*; in this case, aerobic metabolism is partially replaced by anaerobic metabolism, which is necessary to partially meet the cost of maintaining basal metabolism
- **red** (0.2-0.0) for “lethal” range: homeostatic balance is no longer maintained, and survival depends on the intervention of emergency metabolic mechanisms (Bosch-Belmar et al., 2022, Sokolova et al., 2012).

Additionally, maps of estimated percentage changes in thermal habitat suitability were realized for each month and future scenario (Bosch-Belmar et al., 2022). New raster files were realized through the subtractions between the SSP2-4.5 and SSP5-8.5 (2021-2050) and reference period (1987-2010, representing increasing or decreasing spatial occurrence probability of the species at pixel level. (Bosch-Belmar et al., 2022).

3.3 Results

3.3.1 Thermal performance curves (TPCs)

The mathematical model that, among the others (Table S3.2) best described the thermal performance of *M. galloprovincialis*, *P. lividus*, and *M. barbatus* is the gaussian one (gaussian_1987; Lynch et al., 1987). This nonlinear regression model is described by the following equation:

$$rate = r_{max} \times \exp \left(-0.5 \left(\frac{temp - t_{opt}}{a} \right)^2 \right)$$

where rate is the respiration rate (mmol O₂ h⁻¹) for *M. galloprovincialis*, the growth rate (mm 60 days⁻¹) for *P. lividus*, gonado-somatic index (%) for *M. barbatus*, temp is the temperature in centigrade degrees; r_{max} is the maximum respiration rate at the optimum temperature; t_{opt} is the optimum temperature (°C); “a” is the parameter related to the full curve width (°C)

For *M. galloprovincialis* (Figure 3.1A), hourly respiration rates (RR, μmol O₂ h⁻¹) were measured within the temperature range comprised between 5° C and 36 °C. The maximum respiration rate (r_{max}) was 30.30 μmol O₂ h⁻¹, observed at the optimal temperature of 21.80 °C. The value of the parameter “a” results in 8.52 °C

The best thermal performance curve of *P. lividus* (Figure 3.1B) shows a maximum growth rate ($r_{\max}$) of 0.51 mm in 60 days, occurring at an optimal temperature (t_{opt}) of 22.50 °C. The parameter “a” value is 4.97 °C

For *Mullus barbatus*, due to the known different biological performances of males and females, the thermal performance curves were constructed separately for the two sexes (Figure 3.1C and 3.1D). The curves covered a range of temperature from 14 °C to 27 °C. The maximum gonado-somatic index value for females (Figure 3.1C) was 3.47 %, observed at the optimal temperature of 19.41°C. For males it was 6.93 % (Figure 3.1D) at the optimal temperature of 17.61 °C. The values of the “a” parameter were 2.97 °C for females and 1.10 °C for males.

For *Holothuria tubulosa*, the best thermal performance among the others (Table S3.2) (Figure 3.1E) was described by the Flinn et al. (1991) nonlinear regression model, described by the following equation:

$$\text{Gonado – somatic index (\%)} = \frac{1}{1 + a + b \times \text{temp} + c \times \text{temp}^2}$$

where temp = temperature (°C); a = parameter related to the height of the curve; b = parameter that controls the slope of the initial increase of the curve; c = parameter that controls the position and steepness of the decline of the curve.

The values of resulted parameters were “a” = 7.49; “b” = -0.688; “c” = 0.014.

The mathematical model that best describes among the others (Table S3.2) the performance of *Posidonia oceanica* (Figure 3.1F) was represented by pawar_2018 (Kontopoulos et al., 2018), a modified version of sharpeschoolhigh_1981 that explicitly models the optimum temperature. Equation is described as followed:

$$\text{Biomass daily turnover}(\text{day}^{-1}) = \frac{r_{\text{tref}} * \exp\left(\frac{-e}{k}\left(\frac{1}{\text{temp} + 273.15} + \frac{1}{t_{\text{ref}} + 273.15}\right)\right)}{1 + \left(\frac{e}{e_h - e}\right) * \exp\left(\frac{e_h}{k}\left(\frac{1}{t_{\text{opt}} + 273.15} + \frac{1}{\text{temp} + 273.15}\right)\right)}$$

where k is the Boltzmann's constant (8.62×10^{-5}), temp = temperature (°C); r_{tref} = gonado-somatic index at the standardized temperature; e= activation energy (eV); e_h = high temperature de-activation energy (eV); t_{opt} = optimum temperature (°C); t_{ref} = standardization temperature (°C), at which rates are not inactivated by high temperatures. The thermal performance curve covered a

temperature range from 12 to 34°C. The values of the parameters were: $r_{\text{tref}} = 0.004$, $e = 0.445$, $e_h = 4.71$, $t_{\text{opt}} = 26.97$, $t_{\text{ref}} = 25.00$ (°C).

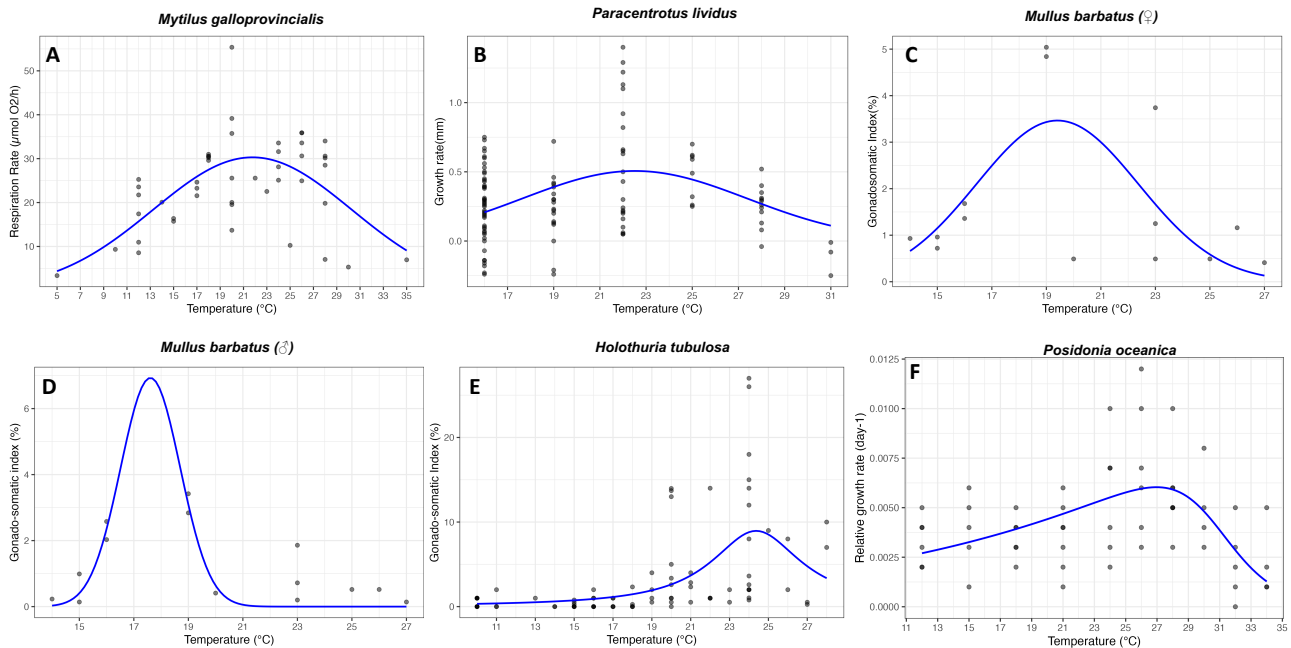


Figure 3.1. Thermal performance curves (TPC) of *Mytilus galloprovincialis* (A), *Paracentrotus lividus* (B), *Mullus barbatus* ♀ (C) and ♂ (D), *Holothuria tubulosa* (E) and *Posidonia oceanica* (F).

3.3.2 Sea surface temperatures in Sardinia in the reference period and the two projected scenarios

3.3.2.1 The reference period

In the reference period (1987-2010) (Figure S3.1), the coldest months are comprised between December (winter) and April (early spring). In more details, February and March show temperatures ranging 12-14 °C, slightly increasing in April to 14-16 °C and then in late spring (May, 16-18 °C). The warm season begins in June (20-22°C) and rises in July (on average 22-24 °C), and more evidently on the east coast (24-26°C). August is typically the hottest month with mean temperatures ranging 24-26 °C all around the Island, with the eastern coast peaking up to 26-28 °C. September shows a similar distribution of temperature as in July, whereas temperature distribution in October mirrors that in June. The temperatures typically cool down in Autumn (November), more evidently in the northern and western coasts (16-18°C).

3.3.2.2 The SSP2-4.5 scenario

In the SSP2-4.5 scenario (Figure S3.2 and Figure 3.2A), the temperature distribution between January and March is not different from that in the reference period. On the other hand, in April

temperatures are some like 2°C higher than those in the reference period, whereas in May such positive shift is ca. +4°C, especially in the northern, north-western and north-eastern coast. The positive shift is projected also from June to September (except for the eastern coast). In July, the temperature rise in the north-eastern and north-western coasts peaks up to +6°C, reaching temperatures between 26 and 28°C (typical of August in the reference period). Minor changes in mean temperatures in this scenario occur between October and December.

3.3.2.3 The SSP5-8.5 scenario

The same temperature rising pattern observed for the milder scenario is observed also in the SSP5-8.5 scenario (Figure S3.3 and Figure 3.2B), though with some minor exceptions. When compared with the reference period, wider extents of the areas characterized by a temperature rise of ca. +6°C are observed in July and areas characterized by a temperature rise of the ca. +4°C in August (with mean temperatures ranging 28-30°C).

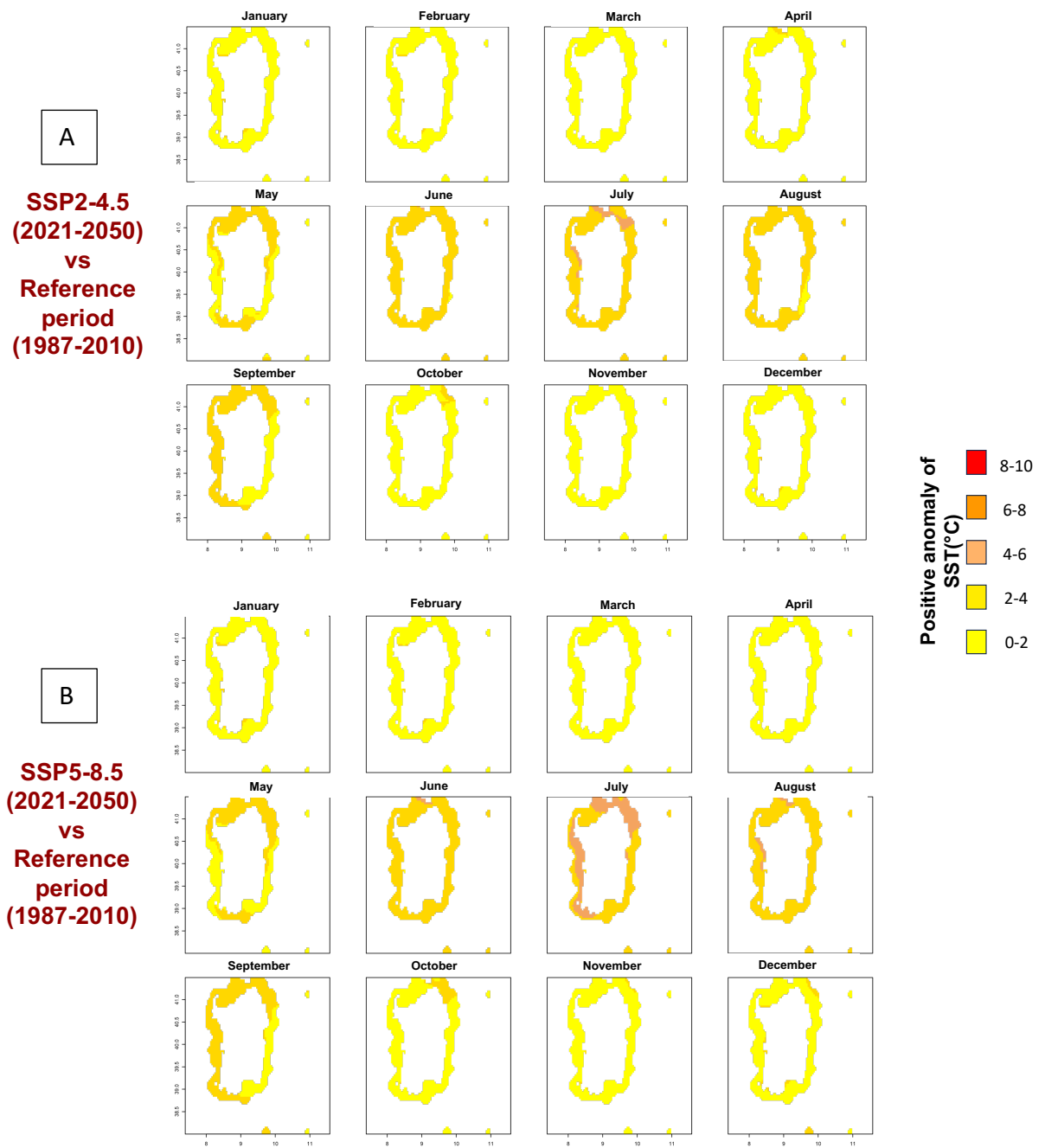


Figure 3.2. Projected temperature increases in sea surface temperatures in Sardinian coasts for SSP2-4.5 scenario (A) and in the SSP5-8.5 scenario (B) for 2021-2050.

3.3.3 Thermal habitat suitability (THS) probability maps

3.3.3.1 THS probability maps of *Mytilus galloprovincialis*

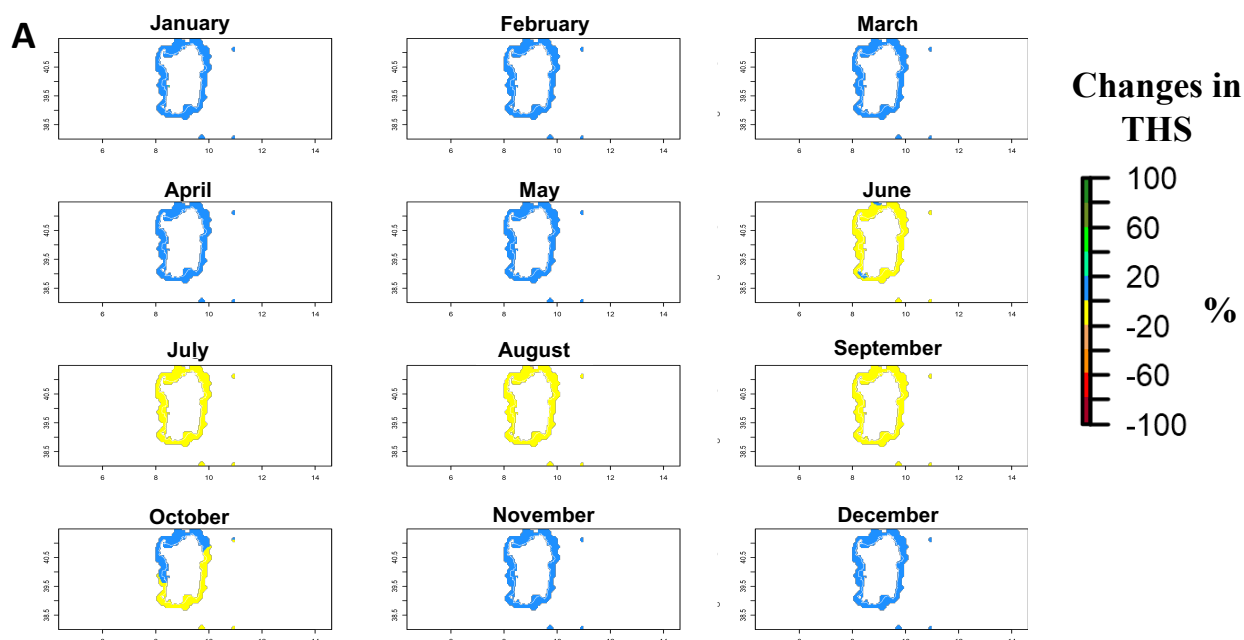
During the reference period (1987-2010) (Figure S3.4A), optimal habitat conditions for *Mytilus galloprovincialis* (based on respiration rates) are generally observed from May to November. Between December and April, the probability is lower (upper limit of *pejus*) than in other periods of the year, but still within the survival limits. Conditions were close to the lower critical temperature limit (*pejus*) in January, February, and March, especially in some areas on the central western (Gulf of Oristano and Montiferru coast) and northern coasts of Sardinia (Gulf of Asinara and Capo Testa).

In the SSP2-4.5 scenario (Figure S3.4B), when compared with the reference period, optimal conditions are anticipated in April-June. In July (in the north-eastern and eastern coast) and August, the probability of thermal habitat suitability approaches the upper limit of *pejus* conditions but improves again in December.

In the SSP5-8.5 scenario (Figure S3.4C), thermal habitat suitability probability remains optimal from April on, as in the SSP2-4.5 scenario, except for the northern part of the island. In July, THS probability approaches the upper limit of *pejus* conditions across all Sardinia Sea, but the south-western areas. Also in this scenario, THS probability improves in December.

The analysis of maps of percentage variation between the reference period and the two different scenarios of the *Mytilus galloprovincialis* THS probability reveals a possible deterioration of the habitat suitability in summer months (Figure 3.3A and 3.3B). Particularly, a possible decrease until -20% could occur from June to September along the entire coastline of the island and in October, limitedly to the southwestern, southern, central-eastern, and southeastern coasts. Such deteriorating conditions are even more pronounced in the SSP5-8.5 scenario, in which a possible decline until -40% could occur in in July and August (less marked) the northern-east coast and in August in the western one.

Mytilus galloprovincialis
SSP2-4.5(2021-2050) vs 1987-2010



Mytilus galloprovincialis
SSP5-8.5 (2021-2050) vs 1987-2010

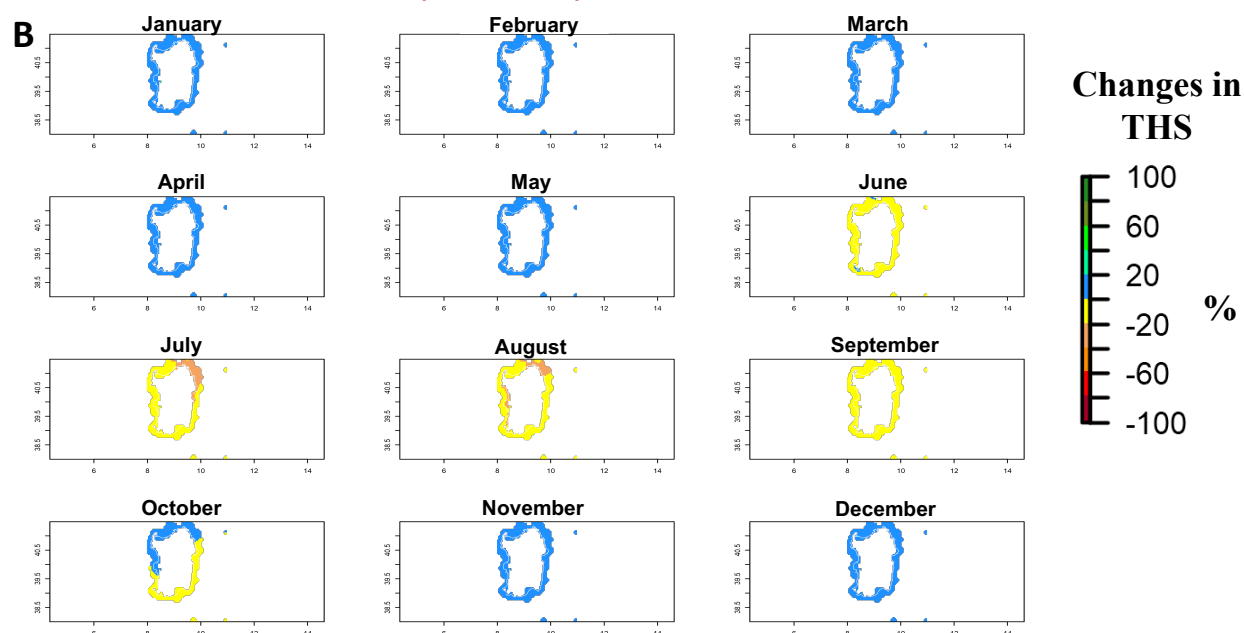


Figure 3.3. Change in thermal habitat suitability for *Mytilus galloprovincialis* in SSP2-4.5(A) and SSP5-8.5 (B) scenarios for 2021-2050 compared to reference period 1987-2010.

3.3.3.2 THS probability maps of *Paracentrotus lividus*

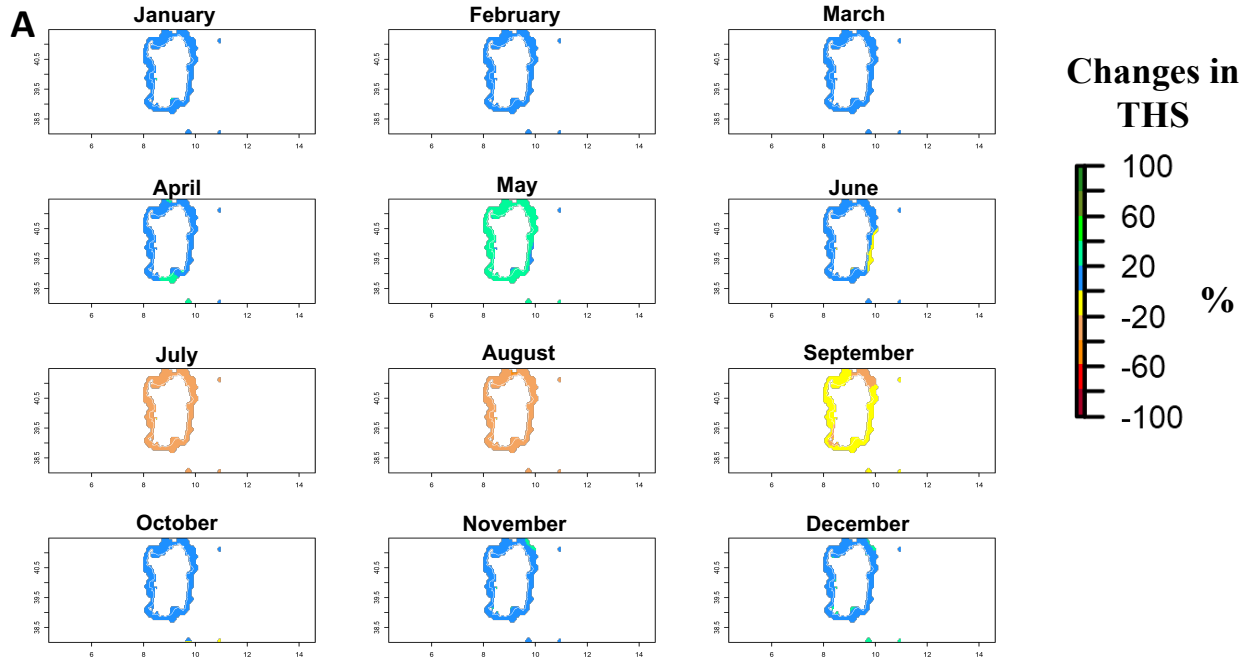
In the reference period 1987–2010 (Figure S3.5A), the THS probability of *Paracentrotus lividus* (based on growth rates) ranges from the worst conditions (lethal or *pessimum*) during winter and early spring (December to April) to the most favorable ones (optimum or upper limit of *pejus*) during summer and early autumn (June to October). In May, THS probability values approach the lower limit of *pejus* conditions, except for the south-eastern coast, where they approximate the upper *pejus* ones. In November, conditions are generally close to the upper *pejus* limit, except along the northeastern coast and within the Gulf of Oristano.

In the SSP2-4.5 scenario (Figure S3.5B), THS probability slightly improve in winter, when compared to the reference period, with no lethal conditions detected, though values are close to the *pessimum* conditions from January to March. In April, THS probability slightly improves to the lower limit of the *pejus* conditions and reaches the optimum ones in May. In July, August, and, to a lesser extent, in September, habitat THS probability could decrease, ranging within the upper and lower *pejus* thresholds. In November and December, THS probability could improve along the entire coastline, approaching the *optimum* threshold in November (all southern and central-eastern coasts) and the lower *pejus* one in December.

In the SSP5-8.5 scenario (Figure S3.5C), patterns of THS probability resemble those obtained for the SSP2-4.5 scenario. The only exception is a visible expansion of the area at the lower limit of *pejus* conditions in July, excluding the southwestern area.

Maps of percentage changes for *Paracentrotus lividus* reveal a possible increase of THS probability in May (+40%) for both future scenarios (Figure 3.4A and 3.4B) for 2021-2050. On the contrary, a possible marked decrease of THS probability could occur along the western and north-eastern coasts from July to September, with milder changes for July and August in the SSP2-4.5 scenario (-40%) and more pronounced ones (-60%) in the SSP5-8.5 scenario.

Paracentrotus lividus
SSP2-4.5 (2021-2050) vs 1987-2010



Paracentrotus lividus
SSP5-8.5 (2021-2050) vs 1987-2010

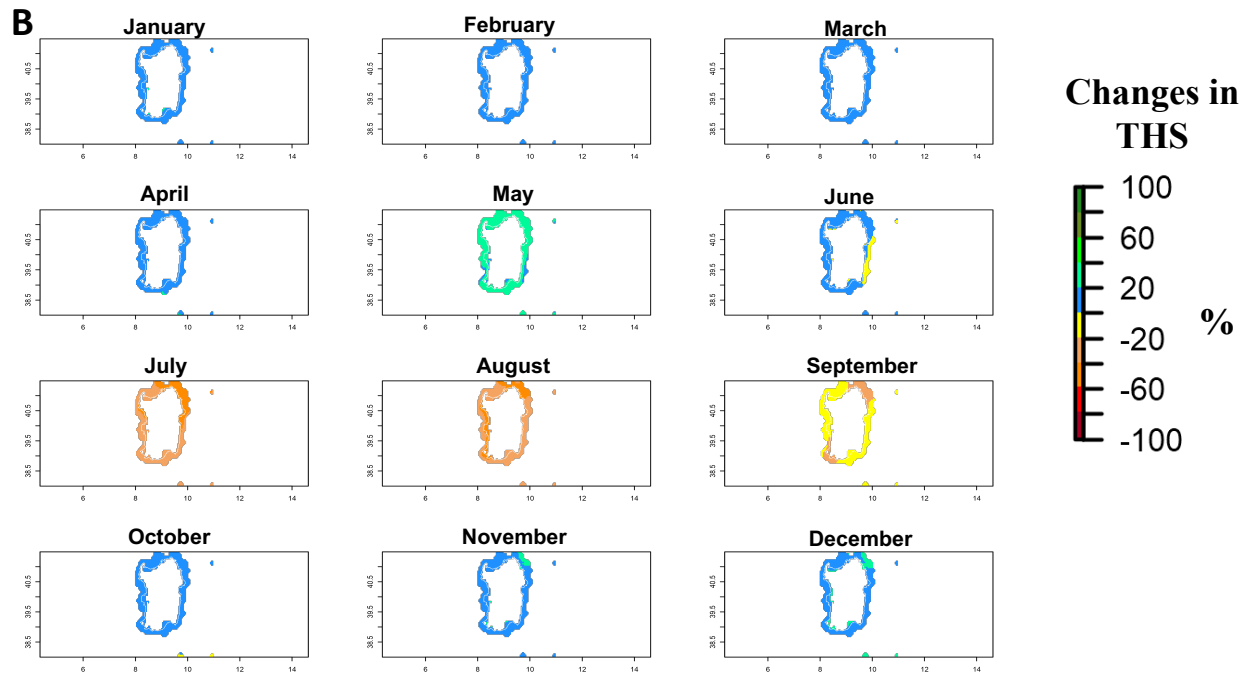


Figure 3.4. Change in thermal habitat suitability for *Paracentrotus lividus* in SSP2-4.5(A) and SSP5-8.5 (B) scenarios for 2021-2050 compared to reference period 1987-2010.

3.3.3.3 THS probability maps of *Mullus barbatus*

In the reference period 1987-2010 (Figure S3.6 A,D), optimal conditions for *Mullus barbatus* (based on the gonado-somatic index) are typically observed for females in May-June and October-November and for males in May and November for males. The 'lethal' conditions appear for females in January (northern coast), February and March (eastern coast), and for males in all months except the optimum months and along the south-eastern coast in December.

In the SSP2-4.5 scenario, THS probability for females (Figure S3.6B) could improve in April, reaching the upper limit of *pejus* conditions in the south and the lower one in the north, and the optimum in May. THS probability could drastically be worse from June (till the *pessimum* conditions) to October (upper limit of the *pejus* in the north, lower one in the south), with lethal condition from July to September. It improves again in December (upper limit of the *pejus*). As far as the males are concerned (Figure S3.6E), the THS probability could improve in April, although the northern area could experience *pessimum* conditions. In May, the THS probability could downgrade to *pessimum* conditions. Similar declines could occur in November, when "lethal" conditions could be reached in the southern area. In December, a significant improvement to *optimum* conditions could occur in the southern and southeastern areas.

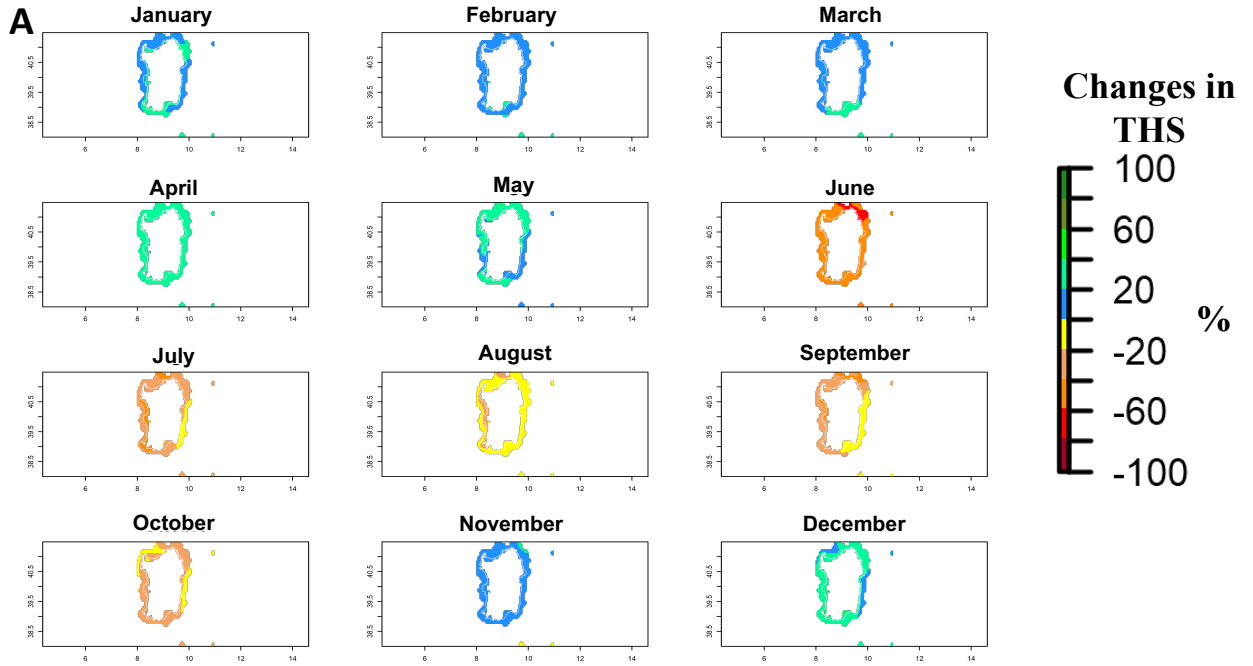
In the SSP5-8.5 scenario (Figure S3.6C,F), compared to the reference period, THS probability for females (Figure S3.6C) might deteriorate from June to October, especially in July, August and September, when "lethal" conditions could be reached. THS probability might improve from December to May, reaching even the optimum conditions in the latter month. THS probability for *M. barbatus* males (Figure S3.6F) could improve in April, reaching the upper limit of *pejus* conditions in the south, while deteriorate in May (*pessimum*) and November ("lethal" in the southern area). THS probability might ameliorate in December, when optimal conditions could occur in either the southern or eastern coasts.

The analysis of maps of THS probability changes for *Mullus barbatus* reveal that females (Figure 3.5A,B) might undergo a severe deterioration of conditions (from -20% to -80%) from June to October in both scenarios. These declines might be more pronounced in the north-eastern area in June, particularly in the SSP5-8.5 scenarios. On the contrary, an increase (+40%) in THS probability is expected in April and in May in the northern and south-western coasts of Sardinia, and during the winter months (December and January).

For males of *M. barbatus* (Figure 3.5C,D) loss in THS probability might occur from May to November. More, the strongest declines could occur in May (-80%) and November (-60%). As for females, more suitable conditions might occur for males in April, especially in the south-east area including the Gulf of Cagliari, and in December, in north-eastern and south-western coasts, when increases up to +80% could occur.

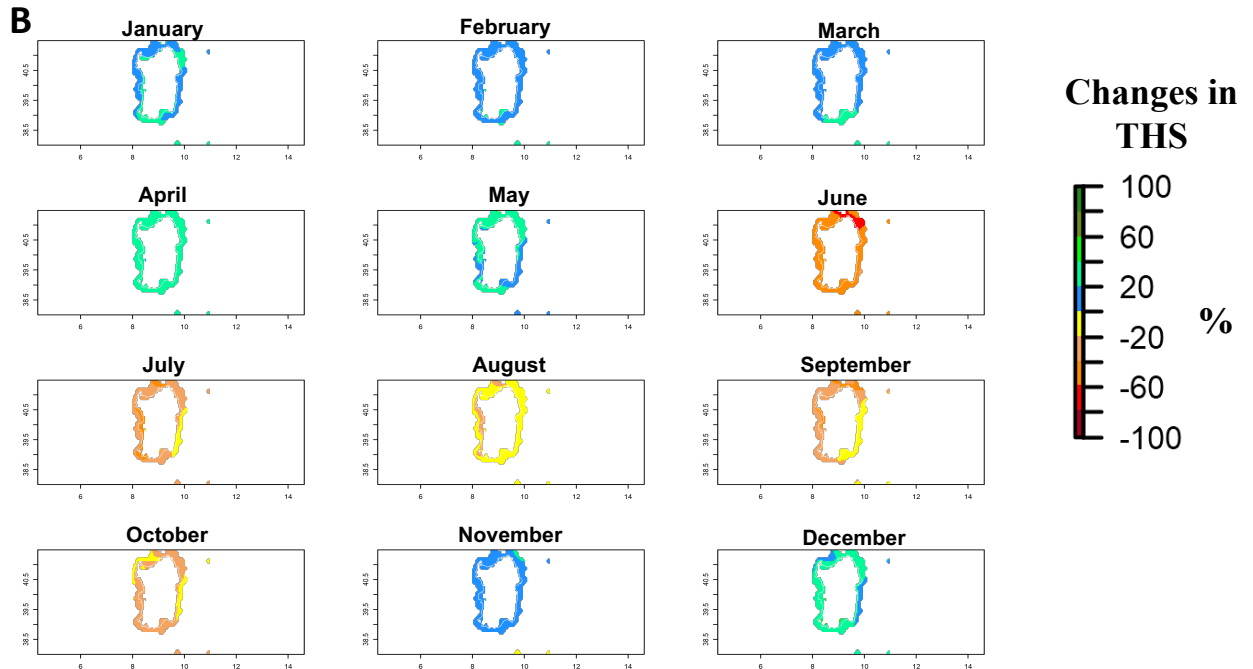
Mullus barbatus ♀

SSP2-4.5 (2021-2050) vs 1987-2010



Mullus barbatus ♀

SSP5-8.5 (2021-2050) vs 1987-2010



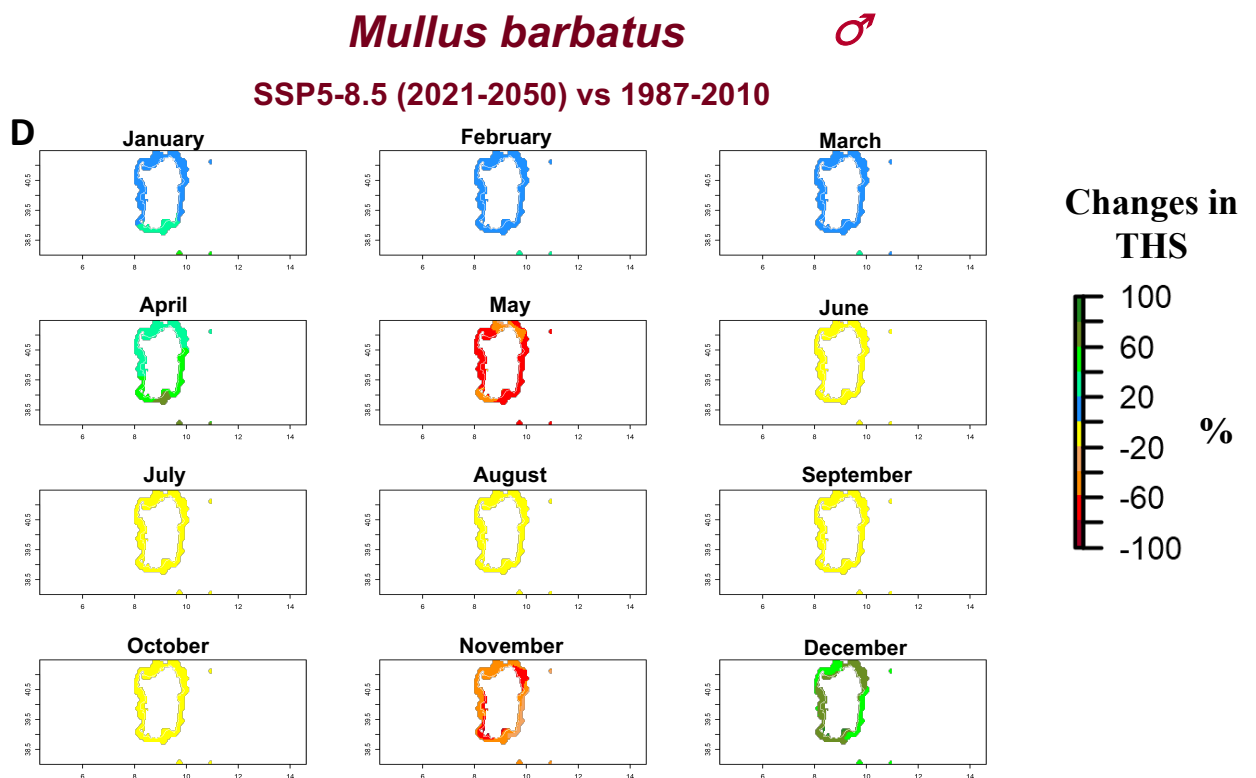
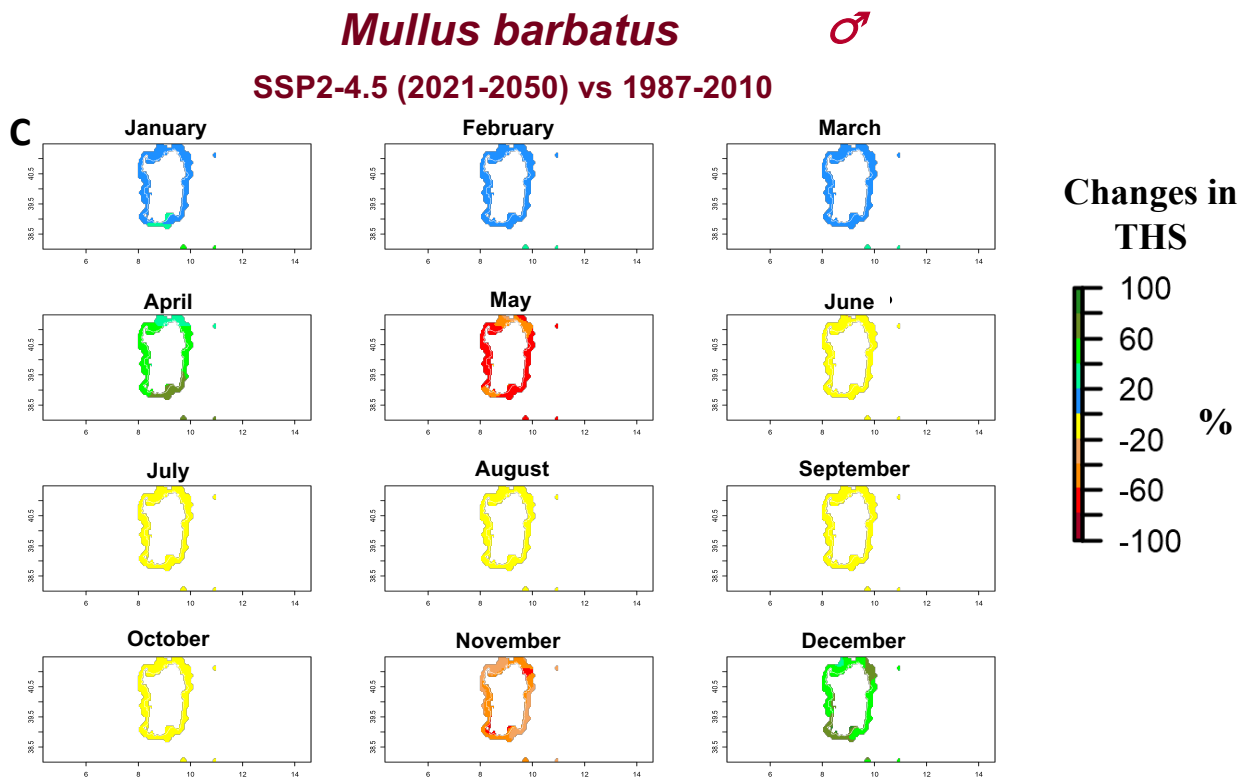


Figure 3.5. Change in thermal habitat suitability for *Mullus barbatus* for female (left) and male (right) in SSP2-4.5 (A,D) and SSP5-8.5 (B for females and D for males) scenarios for 2021-2050 compared to reference period 1987-2010.

3.3.3.4. THS probability maps of *Holothuria tubulosa*

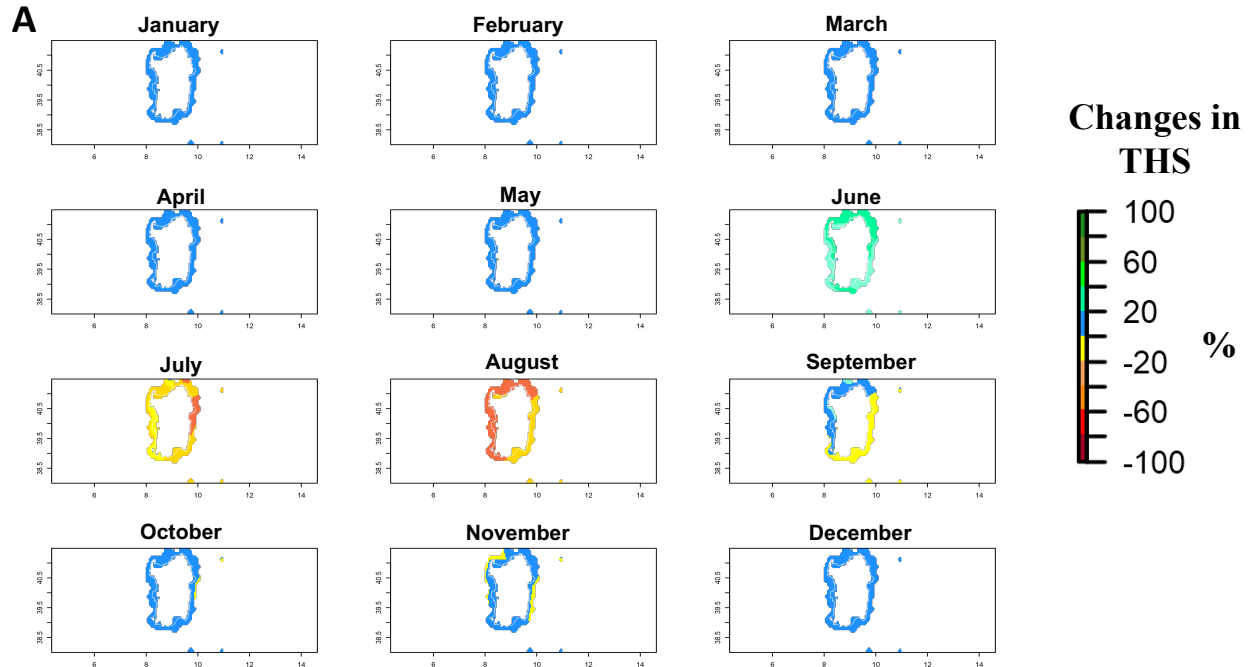
In the reference period 1987-2010 (Figure S3.7A), lethal conditions for *Holothuria tubulosa* (based on gonado-somatic index) are observed from November to May. THS probability gradually improves to *pessimum* conditions in June (lower *pejus* limit along the east coast) and reach their optimum between July and September. In October, the conditions are closer to the lower *pejus* limits in the southern coasts, while they approach the *pessimum* ones along the northern coasts.

In the SSP2-4.5 (Figure S3.7B), THS probability improves, when compared to the reference period, while remains close to the *pessimum* conditions in May. *Optimum* conditions are anticipated in June on the east coast and worsen from July (east coast) to August (all the coasts). THS probability improves in October and November, especially in the south and remains unchanged in September and December.

Also, in the SSP5-8.5 scenario (Figure S3.7C), THS probability could improve from “lethal” to *pessimum* conditions in May, though more relevantly than in the SSP2-4.5 scenario. The improvement may persist in June with optimal condition occurring along the entire coastline, beside the south-western area. In July, a more marked deterioration than in the SSP2-4.5 scenario could occur, reaching *pessimum* conditions in the eastern coast. Conversely, in August the conditions could slightly improve but may be worse than those in both the reference period and the SSP2-4.5 scenario. THS probability, compared to the reference period, may improve in September, October, and November, when larger areas might approach the potentially lethal conditions.

Analysis of changes in the probability of THS for *Holothuria tubulosa* (Figures 3.6 A and 3.6B) reveals an increase in June of 40% in both scenarios and +60% in the northeast area in the SSP5-8.5 scenario. The pattern of change reverses from July to September, with a decrease in the SSP5-8.5 scenario of up to 80% in July on the central-eastern coast and in August on the western and northeastern coasts. In October, a potential increase was observed only in the SSP5-8.5 scenario (+40%).

Holothuria tubulosa
SSP2-4.5 (2021-2050) vs 1987-2010



Holothuria tubulosa
SSP5-8.5 (2021-2050) vs 1987-2010

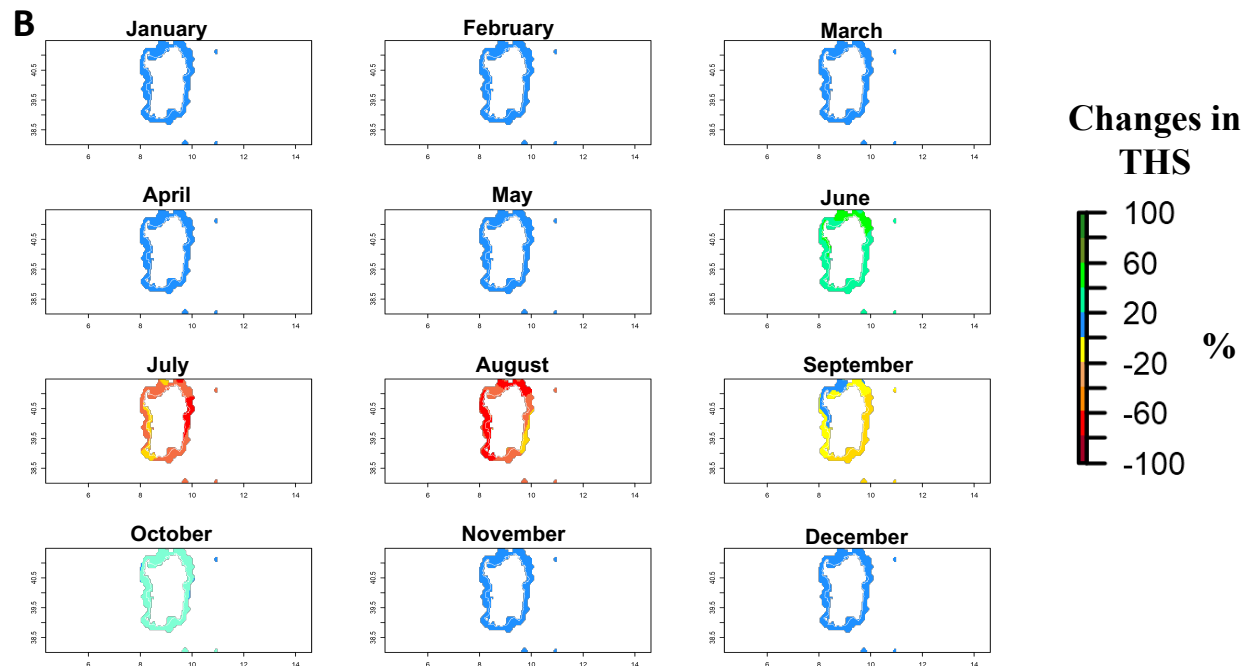


Figure 3.6. Change in thermal habitat suitability for *Holothuria tubulosa* in SSP2-4.5(A) and SSP5-8.5 (B) scenarios for 2021-2050 compared to reference period 1987-2010.

3.3.3.5 THS probability maps of *Posidonia oceanica*

In the reference period 1987-2010 (Figure S3.8A), THS probability for *Posidonia oceanica* (based on growth rate) are at the lower limit of *pejus* from December to April, and at the upper one in May, June, October and November. Optimal conditions occur from July to September and, in the south-eastern coast only, in October.

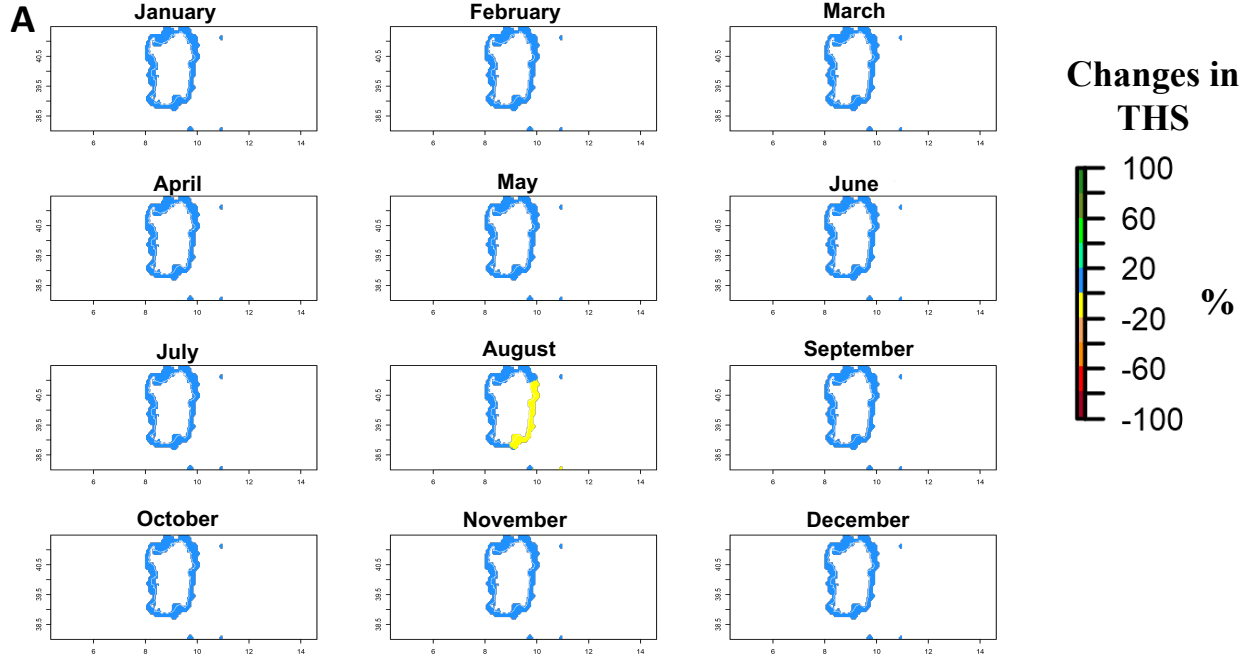
In the SSP2-4.5 scenario (Figure S3.8B), optimal conditions are anticipated in June and May and persist till October. An improvement could also occur in December, when conditions may upgrade from the lower to the upper limits of *pejus* conditions.

In the SSP5-8.5 scenario (Figure S3.8C), a similar improvement of THS probability can occur as in the milder scenario, but more pronounced in December, when conditions reach the upper limit of *pejus* along the almost entire coastline of the island.

Maps of changes in THS probability between the reference period and the two projected scenarios for *Posidonia oceanica* (Figure 3.7 A and B) reveal a slight decrease (-20%) only in August and along the eastern coast of Sardinia, spatially more extended in the SSP5-8.5 scenario than in the SSP2-4.5 one.

Posidonia oceanica

SSP2-4.5 (2021-2050) vs 1987-2010



Posidonia oceanica

SSP5-8.5 (2021-2050) vs 1987-2010

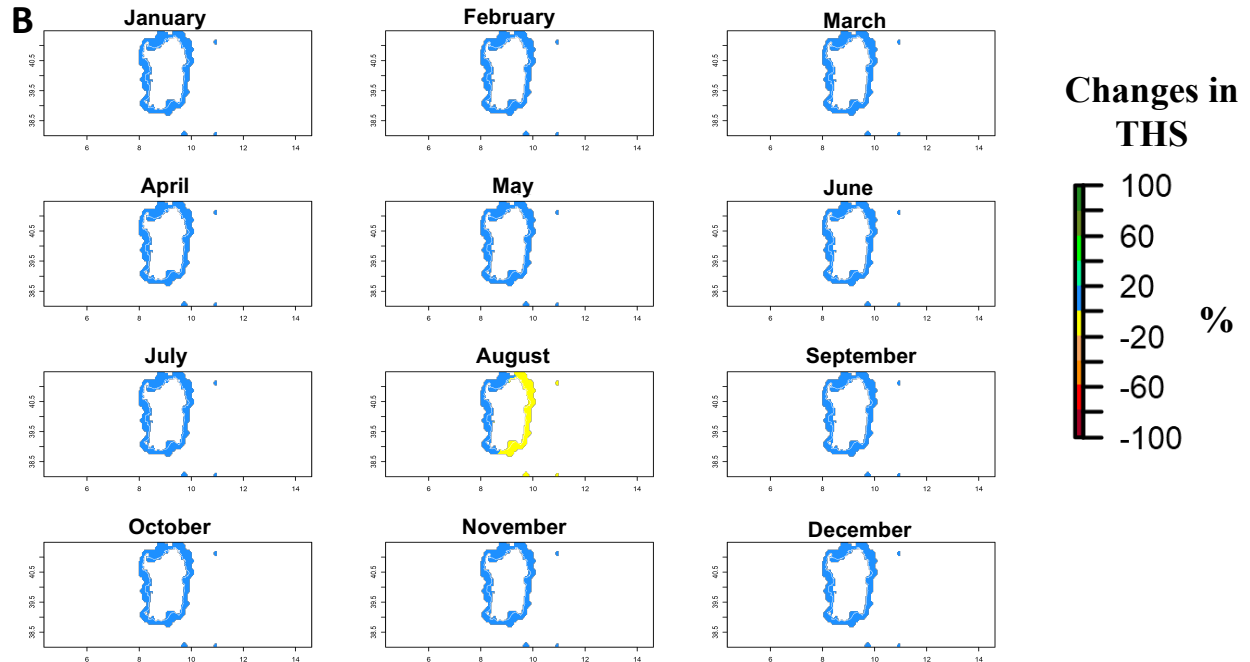


Figure 3.7. Change in thermal habitat suitability for *Posidonia oceanica* in SSP2-4.5(A) and SSP5-8.5 (B) scenarios for 2021-2050 compared to reference period 1987-2010.

3.4 Discussion

This chapter provides the results of an exploratory analysis carried out to assess the potential changes in the thermal habitat suitability probability of five marine species in response to Sardinia seas warming caused by climate change.

Trait-based habitat suitability models are recognized as a profitable tool for assessing species vulnerability in the context of climate change (Foden and Young, 2016). Prior to this study, habitat suitability models have been already used either in Sardinia, in both terrestrial (Isola et al., 2022) and marine contexts (Lauria et al., 2021; Bittau et al., 2025) or other regions (Marras et al., 2015; Bertolini and Pastres, 2021; Bertolini et al., 2023).

Here, by comparing present and future habitat suitability maps based on different metabolic traits of a selection of marine species of commercial or conservation interest, the results shed light on how projected temperature increases in Sardinia seas could affect the extent of the suitable habitats of the scrutinized species across seasons and climatic scenarios. Indeed, according to the SSP2-4.5 and SSP5-8.5 scenarios, the coasts of Sardinia might mirror the future sea warming trends projected for the entire Mediterranean Sea (Cos et al., 2022).

The set of scrutinized species includes the commercial bivalve *Mytilus galloprovincialis*, two echinoderms (namely *Paracentrotus lividus* and *Holothuria tubulosa*), the seagrass *Posidonia oceanica* and the bony fish *Mullus barbatus*. All these species are ectothermic organisms so that water temperature directly affects their body temperature, their physiological and, thus, their energy budget for maintenance, growth and reproduction (Sarà et al., 2013; Yeruham et al., 2019).

3.4.1 *Mytilus galloprovincialis*

The literature-based best thermal performance curve of *Mytilus galloprovincialis* confirms its eurythermal nature, already observed for other species of the genus *Mytilus* that have found survival ranges between 3 and 30°C (Kamermans and Saurel, 2022).

Respiratory rate is an indicator of aerobic metabolic performance (Sarà et al., 2011, 2013). While increased respiration is associated with metabolic stress at high temperatures, an increase in respiration reflects enhanced aerobic capacity rather than stress within the ascending and peak portion of the thermal performance curve described by the Gaussian model based on literature data. Within this suboptimal and optimal thermal range, higher respiratory rates correspond to increased oxygen uptake and ATP production. This allows energy to be allocated not only to

maintenance, but also to fitness-related processes, such as growth and reproduction (Sokolova, 2013).

Thermal habitat suitability maps realized for the future scenario suggest that the potential habitat suitability may remain within the *pejus* range, within which the metabolic energy demand increases, but the aerobic energy balance remains positive (Sokolova et al., 2012). The results of the comparison of THS probability maps between the reference and the two future climate scenarios show that the habitat suitability for the mussels may decrease during summer months in both future scenarios. The worst deterioration is projected in July in the SSP5-8.5 scenario, when temperature may reach 30°C in the northeastern coast, one of the biggest mussel farming areas in Sardinia. A similar decline in habitat suitability is also observed in August in the SSP5-8.5 scenario, affecting the western coasts, where other important farming areas are located.

The temperature between 21 and 22 °C, here considered as optimal based on the constructed curve, corresponds for some studies to the temperature at which stress response mechanisms begin to be established (Andrade et al., 2019). Differences may be due to factors such as food concentration, increased exposure to air and previous exposure to high temperatures, oxygen concentration which can contribute together with temperature to changes in respiration rates (Andrade et al., 2019; Parisi et al., 2021; Georgoulis et al., 2021 and 2022).

At moderate warming (up to 24 °C), the mussel may start to close its valves, thus reducing filtration, oxygen uptake, and metabolism. Prolonged exposure to this temperature can impair food assimilation and energy availability. At higher temperatures (26–28 °C), as projected in future summers, mussels may activate some protection strategies such as activating anaerobic pathways and antioxidant defenses to limit the energetic stress and reactive oxygen species (ROS) production. If these compensatory responses are kept for several days, mortality rises sharply, especially up to 30°C (Anestis et al., 2007; Bejaoui-Omri et al., 2014; Gazeau et al., 2014). Moreover, sea warming has been also observed to induce sub-lethal alterations of mussels' morphometric traits, growth rates, and condition indexes, altering the food product for the market (Martinez et al., 2018).

Mass mortality events of mussels have already been recorded along the coasts of northern Sardinia coasts during the summers of 2009, 2015, and 2018. These events have been triggered by extreme events like “flash floods” (Addis et al., 2021) and marine heat waves. The combination of high temperatures and concurrent hypoxia can activate compensatory mechanisms with a high energetic cost, which are not sustainable over long periods (Parisi et al., 2021). Additionally, extreme

warming events may promote higher deposition rates of particulate organic matter, abating the food availability for the mussels and, at the same time, stimulating the growth of sulfur-producing sedimentary bacteria, which concur in abating oxygen levels and prompt mussels mass mortality (Bejaoui-Omri et al., 2014).

Based on the above evidence, the results of my projections highlight, on the one hand, a significant worsening of the mussels' thermal habitat suitability in summer under both future climate scenarios (2021-2050), possibly impairing their metabolism and adaptation capabilities. Moreover, since these consequences will most likely occur in areas with the highest density of mussels' farms, the predicted summer warming trends will severely impact mussels' production during months of highest market demand, with unpredictable to date but surely severe negative consequences on the local and regional economy. Based on these scenarios, a possible reduction of up to 40% in the thermal habitat suitability of *Mytilus galloprovincialis* is forecast for the aquaculture farming areas of Northeast Sardinia in July and for the areas on the West Coast in August.

Furthermore, although this study does not explicitly address reproductive dynamics, the projected deterioration of thermal habitat suitability during the summer may indirectly affect the reproduction and population persistence of *Mytilus galloprovincialis*.

In the Mediterranean Sea, gametogenesis of *M. galloprovincialis* occurs typically in the fall, followed by spawning throughout the winter and in late spring. The summer season is crucial for nutrient storage due to the consistent and optimal levels of chlorophyll a, which is necessary for rebuilding energy reserves (Bressan & Marin, 1985; Boni et al., 2015). Higher metabolic costs due to thermal stress from the observed projected increase in summer temperature may reduce the energy budget allocated to somatic and gonadal development (Sarà et al., 2011, 2013). Thus, the reproductive potential of the species may decrease in the following season. Since patterns of spawning and bioenergetics linked to reproduction are key factors in determining how populations of these species respond to warming, the populations may decline (Thomas and Bacher, 2018). However, these effects remain speculative and would need further studies integrating thermal stress, reproductive phenology, and recruitment dynamics to understand implications at population level.

3.4.2 *Paracentrotus lividus*

Thermal habitat suitability maps based on growth rates reveal patterns consistent with those observed in nature. Specifically, in the reference period, unsuitable habitat conditions ensuring the

growth of *Paracentrotus lividus* occur from December to April, when temperature generally ranges 12 °C-16 °C. This result agrees with the almost negligible somatic growth observed at 12°C (Spirlet et al., 2000; Santos et al., 2020) and matches the close-to-lethal conditions occurring in February and March during the reference period. Such negative conditions in winter are projected to shorten to from January to March in both scenarios, suggesting the possibility of an anticipated favorable condition. This hypothesis is also corroborated by the actual anticipation of the optimal conditions, characterized by a temperature range of 20-22 °C (Le Gall et al., 1990; Santos et al., 2020). Other environmental factors such as photoperiod and food availability may also influence growth rate (Yeruham et al., 2019)

Indeed, in both future scenarios such optimal conditions may anticipate in May, when the *P. lividus* habitat suitability may increase by >40% when compared with the reference period. The habitat suitability may then downgrade to the *pejus* range (-40/-60%) in July and August, especially on the eastern coast and under the worst scenario (SSP5-8.5). Such a downgrade of habitat suitability could depend upon the physiological stress of sea urchins exposed to temperatures exceeding 22 °C and resulting in raised feeding rates to meet higher metabolic demands, thus lowering the energy allocated for growth and reproduction (Pagès et al., 2013; 2018; Sartori et al., 2015; Yeruham et al., 2019). The possible resulting reduction in sea urchins' reproductive capacity could then have auto-ecological implications, threatening the persistence of the species, which is, unfortunately, already under strong pressure due to intense the regional human harvesting even within protected areas (Ceccherelli et al., 2022; Farina et al., 2022). Worsening conditions of the habitat, causing reduced reproduction outcomes of the sea urchin *P. lividus*, could also have severe economic consequences due to the reduced quantity and quality of the fishery product. Impaired metabolic capacity coupled with other environmental stressors like diseases, per se stimulated by sea warming and heatwaves (Meher et al., 2025) might also contribute to the occurrence of sea urchins' mass mortality events (Yeruham et al., 2015; Grech et al., 2022).

Despite thermal stress is not (and will not be) the sole cause of disrupted populations of the edible sea urchin *Paracentrotus lividus* in Sardinia, my results suggest that sea warming will be a negative factor along with overexploitation concurring to the overall decreased habitat suitability especially in summer, when the species accumulates energy for the following reproduction period.

3.4.3 *Mullus barbatus*

Thermal suitability maps based on gonadosomatic-index, proxy of reproductive capacity, showed different results for males and females, aligned with the observed differences in their gonadal development. For females, January, February and March were unsuitable months for reproduction. Better condition started from April, recognized as the start of the spawning season in Sardinia (Follesa et al., 2019) but also in the Aegean Sea and Sicily (Kokokiris et al., 2013; Carbonara et al., 2015) till June and again in October and November (Kokokiris et al., 2013; Carbonara et al., 2015; Follesa et al., 2019). For males, optimum period is highlighted in May and November.

This differs from some studies that identify the spawning period as occurring also in February and June (Carbonara et al., 2015; Melinkova & Kuzminova, 2020). This mismatch could be due to the limited amount of data available for this species, but also to the fact that, unlike the curves for the previous species—mostly derived from experimental extrapolations—the environmental factor with different constraints may influence the gonadal development.

Despite the differences, the reproductive periods of the two sexes appear to be aligned in reference period but show potential mismatches under future scenarios. Both sexes and future scenarios show an improvement in habitat conditions in April, particularly along the southern coast of Sardinia, there is a marked reduction in habitat quality during the period considered optimal. In fact, stronger declines in habitat quality are observed especially for the female in summer (-80% in north-easter coast in June). In May, on the one hand, females experience an increase in optimal habitat quality (+40%), while males undergo a sharp decrease (-80%). Similar pattern is projected in November.

My results suggest that sea warming may anticipate the spawning in spring but causing different distribution of the optimal temperature for reproduction for females and males of *Mullus barbatus*, with possible consequences on recruitment. In fact, seasonality is an important factor for gamete release, since species fertility is synchronized with zooplankton abundance peaks (the natural food source for larvae) (Kokokiris et al., 2013). Shift in spawning time and zooplankton abundance peaks driven by ocean warming may have cascade effect on population preservation.

3.4.4 *Holothuria tubulosa*

The analysis of the THS maps for *Holothuria tubulosa* based on the gonado-somatic index show that the suitability of its habitat is characterized by clear seasonal fluctuations and agree with previous findings based on gonadal growth and maturation (Kazanidis et al., 2014; Pasquini et al., 2022). Gonadal development of holothuroids is typically classified into 5 stages: recovery stage (I), growing stage (II), mature stage (III), spawning stage (IV) and post-spawning stage (V) (Desplatovic et al., 2004).

During the reference period, lethal conditions occurring from November to May correspond with the gonadal recovery (stage I) and growing stage (stage II) described in Desplatovic et al. (2004). This result, firstly, shows that the model used here, though based on real data and an accurate statistical choice of the best model, is not free of biases. *H. tubulosa* gamete release from mature gonads is typically stimulated at temperatures ranging between 22 and 27 °C, with upper limits varying between 24.5 °C and 27 °C (Desplatovic et al., 2004; Kazanidis et al., 2014; Dereli et al., 2016). During the reference period such thermal window occurs from June to October, when the habitat condition shift from *pessimum* (June) to *optimum* (July, August and September). The optimum conditions in particular correspond with gonadal maturation (stage III) and gamete release (stage IV) (Bulteel et al., 1991; Pasquini et al., 2021), also in Sardinia seas (Pasquini et al., 2023).

Under the SSP2-4.5 and SSP5-8.5 future scenarios, the analysis of THS maps highlight anticipated optimal condition in June, with the strongest positive shift under the most severe scenario (SSP5-8.5). This result suggests that under future warmer conditions the spawning season could anticipate. However, in both scenarios the duration of the optimum period is projected to shorten drastically but also to deteriorate from optimum to *pejus* in July and August, even reaching the *pessimum* conditions on the east coast under the SSP5-8.5 scenario.

The scientific literature supports the hypothesis that episodic and/or prolonged warming events (including marine heatwaves) can induce spawning and so, have cascading effects on the sequence and duration of the reproductive and maturation phases of *Holothuria tubulosa* (Rajak et al., 2017). An impaired reproduction capacity at species level may result in local reductions in population abundance (Dereli et al., 2016). Beside representing a potential component of the seafood market (though its harvesting is prohibited in Italy), it is noticeable that *Holothuria tubulosa*, one of the most common sea cucumbers in the Mediterranean Sea, is generally associated with organically enriched coastal sediments and seagrass beds (Pasquini et al., 2021). Being a deposit-feeder, it is

also responsible for strong bioturbation processes and plays a putative key role in sedimentary carbon cycling and benthic trophodynamics (Pasquini et al., 2021). Recent manipulation experiments demonstrated that the sea cucumber *H. tubulosa* can resist to a certain extent to marine heatwaves (Ennas et al., 2023), but also that its bioturbation activity could be affected by marine heatwaves, thus modifying its role in benthic bioturbation and, more generally, sedimentary biogeochemistry (Abyaba et al., 2025).

Based on this evidence, the projected warming-related deterioration of the habitat suitability for the sea cucumber *Holothuria tubulosa* in Sardinia seas in both future climatic scenarios, causing plausible shifts in its metabolic and reproduction rates, will most likely also alter or even impair sedimentary biogeochemistry, ultimately altering benthic food webs and the coastal ability of coastal seas to store blue C (Abyaba et al., 2025).

3.4.5 *Posidonia oceanica*

The analysis of the THS maps of *Posidonia oceanica* suggests it will likely experience only minimal reductions in habitat suitability probability, and that these will likely to be limited to the summer months. These results differ from previous findings (Jordà et al., 2012; Olsen et al., 2012) including the one in Chefaoui et al. (2021), which projected a possible loss of 75 % of suitable habitat for *Posidonia oceanica* by 2050 to the RCP8.5 scenario. This difference in results between the various models could be explained by the difference in parameters used and types of modeling and considering that although the survival ranges of *Posidonia* may stay to 29°C (or optimal growth rate as observed in this study; Savva et al., 2018), prolonged exposures to these temperatures may still indicate a suboptimal functioning of metabolic processes. When thermal thresholds are exceeded, these variations can induce sub-lethal or even lethal effects, such as morphological damage including reduced growth rates, in leaf density and lower survival (Garcia et al., 2012; Marbà & Duarte, 1997 and 2010; Diaz-Almela et al., 2009; Bennett et al., 2022a). Above 30°C, severe tissue degradation and the collapse of entire populations may occur (Traboni et al., 2018; Savva et al., 2018; Bennett et al., 2022b). Furthermore, it should be emphasized that our results relate to the potential effects of a projected long-term sea warming and not those of marine heat waves MHWs). In this regard, it must indeed notice that MHWs effects could be more deleterious due to the relatively short-term but intense thermal anomalies that can abruptly exceed the physiological

thresholds of the seagrass, potentially leading to more severe and rapid impacts on *Posidonia oceanica* (Stipcich et al., 2022c).

Results from Ozkiper et al. (2024) evaluating suitability parameters related to growth and survival, very suitable conditions around the coasts of Sardinia in present time highlighted high suitability of this area for growing. Studies such as that of Pansini et al. (2021) have shown how the thermal habitat can influence the leaf density of *Posidonia* plants along the coasts of Sardinia, which would respond to temperature by increasing meadow density and reducing in the number of leaves. Although with possible effects on the associated biodiversity and storage capacities of C, this could be an adaptive response of the plant to the rise in temperature. Other mechanisms such as increased flowering frequency could allow their survival in warming conditions (here also predicted) and associated with the wide adaptive capacity and phenotypic plasticity of this species (Elkalay et al., 2003; Savva et al., 2018). These may enhance genetic variation and thus resilience to disturbances (Díaz-Almela et al., 2007; Díaz-Almela et al., 2009; Ruiz et al., 2018; Stipcich et al., 2024a and b). Overall, factors as increased reproductive effort, genetic diversity, and physiological flexibility may increase the plasticity of *Posidonia oceanica* in response to climate change. Additionally, *P. oceanica* meadows exposed to higher thermal fluctuations due to geographical location and/or depth display higher tolerance, and greater resilience to warming and heatwaves (Traboni et al., 2018; Bennett et al., 2022a; Bennett et al., 2022b; Pazzaglia et al., 2022; Stipcich et al., 2022a; Stipcich et al., 2022b).

Overall, the results show us a reduction in thermal habitat limited to 20% only in August in both scenarios for 2024. Although the results are positive, it is necessary to consider the possible effects of even small changes on the metabolic functioning of the plant and further investigate their adaptive responses.

3.4.6 Further applications and limitations

Although my work aims to provide a valuable tool for assessing species' vulnerability to sea warming, it should still be interpreted with caution when informing adaptation and mitigation strategies. Indeed, the thermal performance curves constructed for each species are based on literature data and are therefore limited by real data availability. Moreover, as these curves are derived from studies carried out in the Mediterranean but in regions other than Sardinia, they may not fully capture the potential differences in sensitivity or adaptive capacity at the population level in the Sardinian Sea. Experiments designed to generate thermal performance curves that reflect

local variability could help fill these knowledge gaps. When this is not feasible, local sampling, at least on a seasonal basis, could provide useful supplementary information.

The predictive model I used projects potential spatial distributions based on variations in a single climatic factor: sea surface temperature. While isolating the effect of one stressor is important, climate change effects often occur synergistically in nature, for example, sea warming combined with hypoxia, which may exacerbate impacts. This approach could also be applied to assess other climate change manifestations, such as marine heatwaves and, possibly, investigate cross effects of multiple stressors.

Nonetheless, the analyses carried out here highlight apparent spatial differences along the Sardinian coast, including east–west variations. However, the coarse resolution of future temperature datasets, due to the lack of finer-scale data for the Sardinian Sea, limits the precision of these predictions. Consequently, these interpretations should be regarded as indicative trends rather than definitive and fully quantitative site-specific outcomes.

3.5 Conclusions

The study presented in this chapter aimed to evaluate the impact of sea surface warming on the thermal habitat suitability probability along the coasts of Sardinia for five species considered ecologically and commercially important.

To achieve this goal, habitat suitability maps were constructed based on the thermal performance of an arbitrarily selected key functional and metabolic trait (respiration, growth, or reproductive potential) for each species, considering a reference period (1987–2010) and two future projection scenarios for 2021–2050, SSP2-4.5 and SSP5-8.5.

Although several habitat suitability models have been applied for research and conservation purposes in Sardinia, this study represents the first attempt conducted at this scale for most of the species considered.

Overall, all organisms appeared to be affected by sea warming showing vulnerability to sea surface warming, showing different degrees of sensitivity, a key vulnerability property. The only apparent exception was the seagrass *Posidonia oceanica*, which showed a comparatively higher thermal tolerance and thus a potential positive response to future sea warming.

In more details, the results for the 2021–2050 period indicated a reduction of suitable habitats during the summer months, particularly under the more severe SSP5-8.5 scenario, for benthic species such as the bivalve mollusk *Mytilus galloprovincialis* and the echinoderm *Paracentrotus lividus*. Due their crucial ecological roles as filter feeders and grazers, respectively, their physiological impairment or, in the worst cases, mortality could have cascading effects on trophic status and webs as well as on the benthic habitat complexity (Bracchetti et al., 2024; Melis et al., 2019). Moreover, due to their high commercial value, their decline could also negatively affect the local economies.

Potential shifts in the reproductive period for the sea cucumber *Holothuria tubulosa* and the red mullet *Mullus barbatus* may lead to local population declines.

Considering their roles as bioturbators and bioreactors, a decrease in *Holothuria tubulosa* abundance could alter key ecological processes such as sediment and nutrient cycling, leading to reduced productivity and biodiversity loss. On the contrary, the anticipation of the breeding season could compensate for the possible negative effects on reproduction and population maintenance.

Similarly, *Mullus barbatus* has often been used as an indicator of environmental change, and its reduction or potential disappearance could disrupt trophic networks and cause economic losses in the fisheries sector.

The seagrass *Posidonia oceanica* may have minor contractions concerning the species growth rate. Despite this, further investigations on species acclimation and adaptation mechanisms may be needed as noted by previous studies (Pansini et al, 2021).

Despite some limitations, primarily related to the coarse spatial resolution of the future climate datasets, the approach presented here provides a valuable scientific tool to evaluate the impact of sea warming on species. Habitat suitability maps and better knowledge on species tolerance to warming and other climate change stressors may be the basis for supporting decision-makers in developing effective mitigation and adaptation strategies to address the impacts of climate change.

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3.8 Supplementary materials

Table S3.1. Extracted values from the selected papers for temperature and rate, represented by hourly respiration rates (RR, $\mu\text{mol O}_2 \text{ h}^{-1}$) for *Mytilus galloprovincialis*, maximum growth rate (rmax) in 60 days for *Paracentrotus lividus*, gonado-somatic index % for *Mullus barbatus* (♀ and ♂) and *Holothuria tubulosa*, daily biomass turnover (day^{-1}) for *Posidonia oceanica* respectively.

<i>Mytilus galloprovincialis</i>		<i>Paracentrotus lividus</i>		<i>Mullus barbatus</i> ♀		<i>Mullus barbatus</i> ♂		<i>Holothuria tubulosa</i>		<i>Posidonia oceanica</i>	
T (°C)	Rate	T (°C)	Rate	T (°C)	Rate	T (°C)	Rate	T (°C)	Rate	T (°C)	Rate
5	3.36	16	0.75	14	0.93	14	0.23	10	1.00	12	0.002
10	9.34	16	0.73	15	0.72	15	0.14	10	1.00	12	0.002
12	8.56	16	0.67	15	0.96	15	0.99	10	1.00	12	0.003
12	10.97	16	0.65	16	1.36	16	2.58	10	0.00	12	0.004
12	17.42	16	0.61	16	1.68	16	2.03	10	1.00	12	0.004
12	21.74	16	0.6	19	5.04	19	2.84	10	1.00	12	0.005
12	23.56	16	0.56	19	4.84	19	3.42	10	0.00	15	0.006
12	25.27	16	0.53	20	0.49	20	0.41	10	0.00	15	0.005
14	20.08	16	0.5	23	1.25	23	0.72	10	0.00	15	0.004
15	15.73	16	0.49	23	0.49	23	0.2	10	0.00	15	0.003
15	16.37	16	0.45	23	3.74	23	1.86	11	2.00	15	0.001
17	21.56	16	0.44	25	0.49	25	0.52	11	0.00	18	0.005
17	23.26	16	0.43	26	1.16	26	0.52	11	0.00	18	0.004
17	24.64	16	0.4	27	0.41	27	0.14	13	1.00	18	0.004
18	29.6	16	0.39					14	0.00	18	0.003
18	30.2	16	0.39					14	0.00	18	0.003
18	30.51	16	0.38					15	0.52	18	0.002
18	30.57	16	0.31					15	0.78	21	0.006
18	30.99	16	0.3					15	0.00	21	0.005
20	13.69	16	0.3					15	0.26	21	0.004
20	19.53	16	0.29					15	0.00	21	0.004
20	20.03	16	0.28					15	0.00	21	0.003
20	25.57	16	0.27					15	0.00	21	0.002
20	35.74	16	0.26					16	2.00	21	0.001
20	39.16	16	0.25					16	0.00	24	0.010
20	55.37	16	0.22					16	1.00	24	0.007
22	25.57	16	0.21					16	1.00	24	0.007
23	22.53	16	0.2					16	0.00	24	0.004
24	25.1	16	0.19					16	0.00	24	0.003
24	28.13	16	0.18					16	0.00	24	0.002
24	31.6	16	0.17					17	0.00	26	0.012
24	33.57	16	0.11					17	0.00	26	0.010
25	10.25	16	0.1					17	0.00	26	0.007

26	24.95	16	0.09			17	1.00	26	0.006
26	30.62	16	0.07			17	1.00	26	0.004
26	33.58	16	0.06			18	0.26	26	0.003
26	35.88	16	0.05			18	2.33	28	0.010
26	35.88	16	0.02			18	0.00	28	0.006
28	7.05	16	0			18	0.00	28	0.006
28	19.83	16	-0.07			18	0.00	28	0.005
28	28.51	16	-0.14			19	0.52	28	0.005
28	30.15	16	-0.14			19	4.00	28	0.005
28	30.59	16	-0.16			19	2.00	28	0.003
28	34.02	16	-0.18			19	1.00	30	0.008
30	5.31	16	-0.23			20	2.59	30	0.005
35	6.96	16	-0.24			20	13.71	30	0.004
		19	0.72			20	3.36	30	0.003
		19	0.46			20	0.52	32	0.005
		19	0.42			20	13.97	32	0.003
		19	0.41			20	0.00	32	0.002
		19	0.39			20	13.00	32	0.001
		19	0.34			20	1.00	32	0.000
		19	0.3			20	1.00	34	0.005
		19	0.3			20	5.00	34	0.002
		19	0.28			21	2.33	34	0.001
		19	0.23			21	0.52	34	0.001
		19	0.22			21	2.84		
		19	0.2			21	4.00		
		19	0.14			22	14.00		
		19	0.13			22	1.00		
		19	0.12			22	1.00		
		19	0			22	1.00		
		19	-0.21			23	0.52		
		19	-0.24			23	2.00		
		22	1.4			24	0.78		
		22	1.29			24	1.03		
		22	1.22			24	3.62		
		22	1.13			24	2.59		
		22	1.1			24	2.00		
		22	0.92			24	8.00		
		22	0.82			24	12.00		
		22	0.66			24	18.00		
		22	0.65			24	14.00		
		22	0.63			24	2.00		
		22	0.5			24	26.00		
		22	0.43			24	27.00		
		22	0.3			24	15.00		

22	0.24			24	2.00
22	0.22			25	9.00
22	0.21			26	2.00
22	0.2			26	8.00
22	0.16			27	0.26
22	0.1			27	0.52
22	0.06			28	10.00
22	0.05			28	7.00
22	0.05				
25	0.7				
25	0.62				
25	0.61				
25	0.59				
25	0.49				
25	0.32				
25	0.26				
25	0.25				
28	0.52				
28	0.4				
28	0.35				
28	0.31				
28	0.3				
28	0.29				
28	0.26				
28	0.24				
28	0.21				
28	0.13				
28	0.08				
28	-0.04				
31	-0.01				
31	-0.08				
31	-0.25				

Table S3.2. List of the fitted 23 models for thermal performance curves and the corresponding AICc values for the fitting of the trait-based data collected in Table S3.1 for *Mytilus galloprovincialis*, *Paracentrotus lividus*, *Mullus barbatus* (♀ and ♂), *Holothuria tubulosa* and *Posidonia oceanica* respectively.

model name		AICc					
		<i>Mytilus galloprovincialis</i>	<i>Paracentrotus lividus</i>	<i>Mullus barbatus</i> ♀	<i>Mullus barbatus</i> ♂	<i>Holothuria tubulosa</i>	<i>Posidonia oceanica</i>
1	beta	337.29	52.97	67.87	50.4469144	518.055757	-515.3618
2	boatman	337.30	59.47	67.95	64.9941928	518.081396	-515.27218
3	briere2	345.04	53.34	63.00	51.4539524	521.713222	-515.86808
4	flinn	333.53	50.11	53.91	36.5201026	512.367324	-511.20189
5	gaussian	332.55	51.78	57.31	38.8625814	513.526038	-515.0871
6	hinshelwood	339.83	59.86	66.88	56.169874	569.584753	-517.5081
7	joehnk	338.19	66.64	74.08	63.2969101	520.68085	-515.15863
8	johnson_lewin	337.35	54.17	80.46	70.5837268	569.584753	-520.89957
9	kamykowski	338.41	54.20	70.16	55.9580982	525.807907	-514.27417
10	lactin2	368.00	51.75	66.41	55.9023938	519.95402	-516.76257
11	modifiedgaussian	334.82	50.12	56.71	43.6143906	512.650286	-520.3644
12	oneill	334.72	50.39	61.75	58.195807	515.736622	-517.89098
13	pawar	335.40	50.09	65.33	54.2227034	515.00382	-521.04662
14	quadratic	333.88	51.96	59.36	48.5332913	520.184046	-514.12837
15	ratkowsky	333.95	50.97	62.90	50.7240511	516.64392	-522.0585
16	rezende	338.87	51.60	66.40	55.6773557	518.286366	-519.28364
17	sharpeschoolfull	Not working	Not working	Not working	Not working	Not working	Not working
18	sharpeschoolhigh	335.40	50.09	65.33	54.2227034	515.00382	-521.04662
19	sharpeschoollow	Not working	Not working	Not working	Not working	Not working	Not working
20	spain	340.07	53.04	66.77	56.0938085	518.726061	-517.50707
21	thomas1	337.60	49.84	60.86	44.5301274	522.839613	-517.74145
22	thomas2	338.53	53.99	71.37	60.710216	520.68077	-515.15589
23	weibull	334.73	50.58	60.89	43.5974236	531.594255	-517.11237

**Reference
Period
(1987-2010)**

SST (°C)

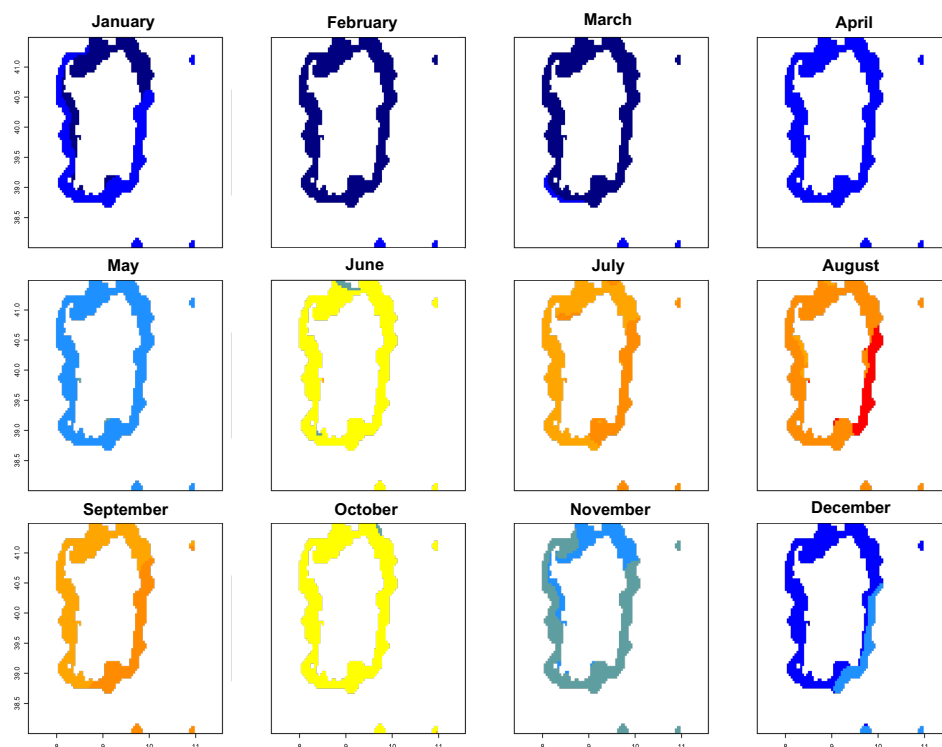
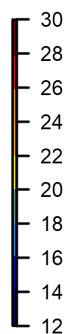


Figure S3.1. Projected Sea surface temperatures in Sardinian coasts for reference period (1987-2010).

**SSP2-4.5
(2021-2050)**

SST (°C)

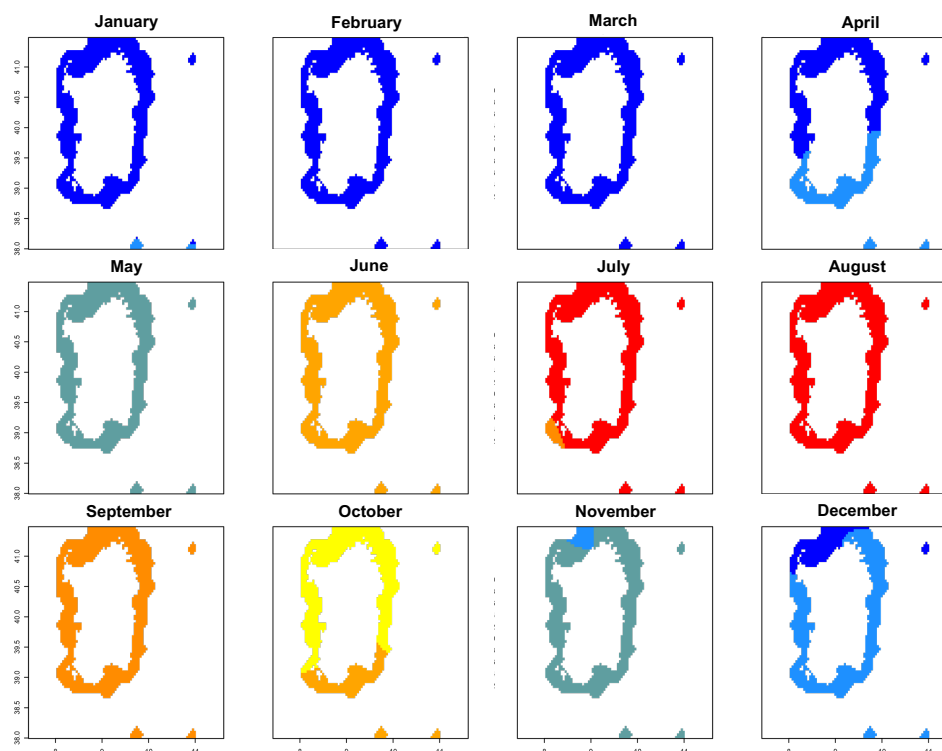
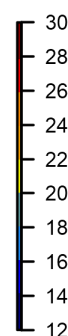


Figure S3.2. Projected Sea surface temperatures in Sardinian coasts for SSP2-4.5 scenario for 2021-2050.

**SSP5-8.5
(2021-2050)**

SST (°C)

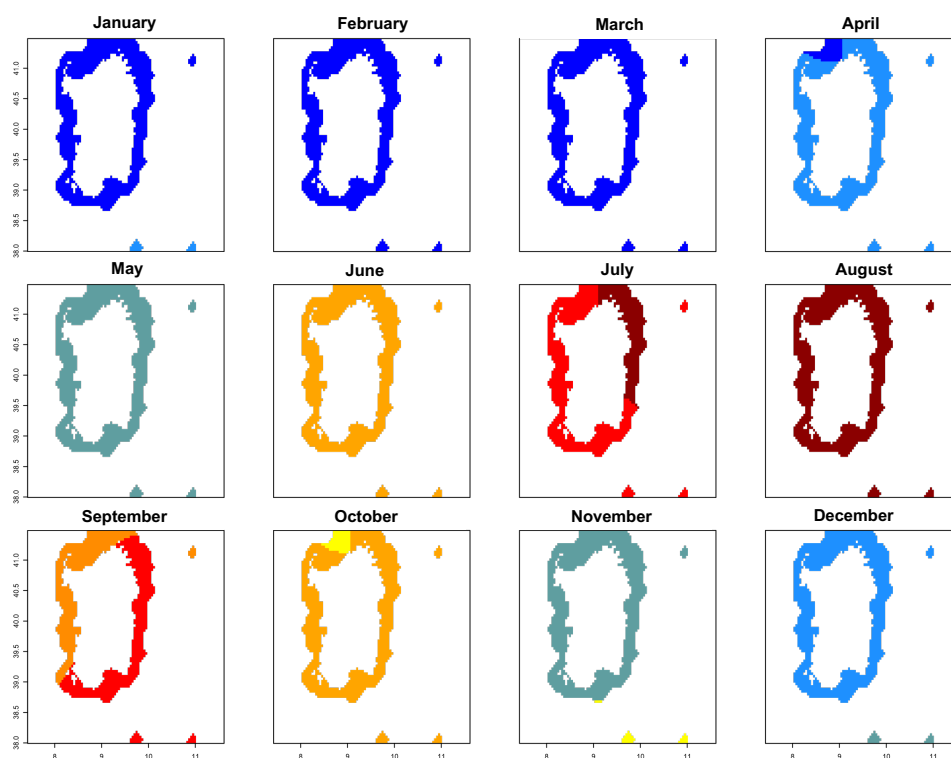
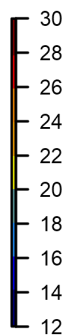
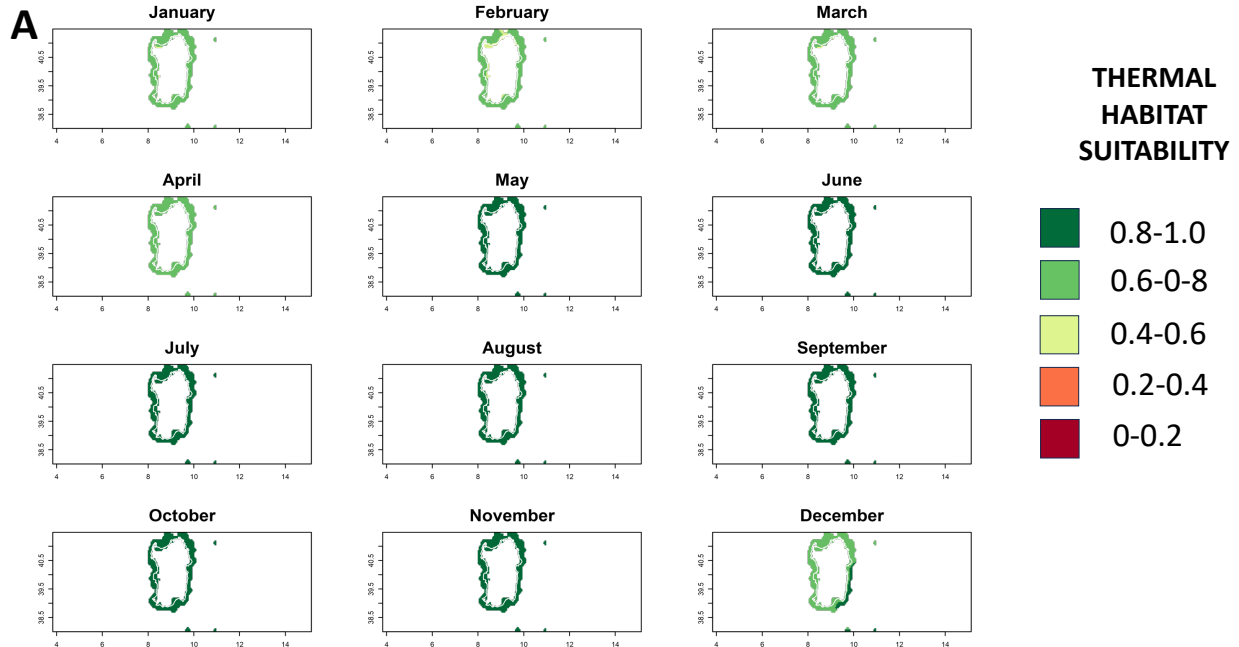


Figure S3.3. Projected Sea surface temperatures in Sardinian coasts for SSP5-8.5 scenario (C) for 2021-2050.

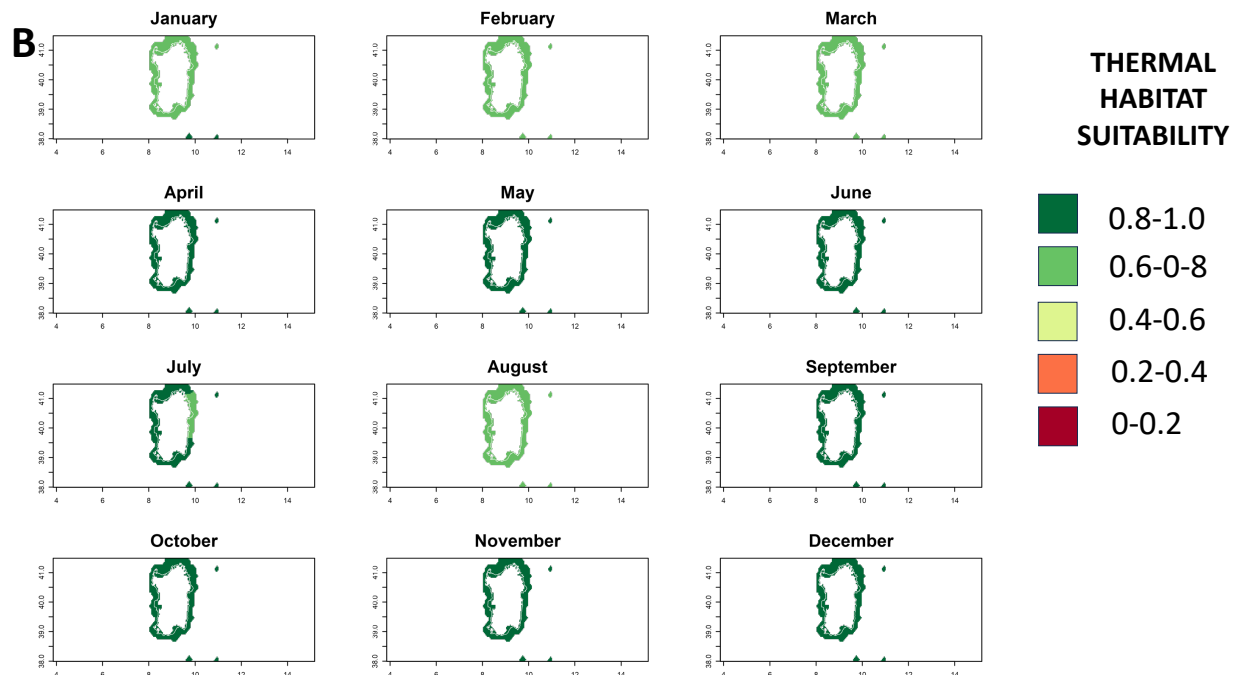
Mytilus galloprovincialis

Reference Period (1987-2010)



Mytilus galloprovincialis

SSP2-4.5 (2021-2050)



Mytilus galloprovincialis

SSP5-8.5 (2021-2050)

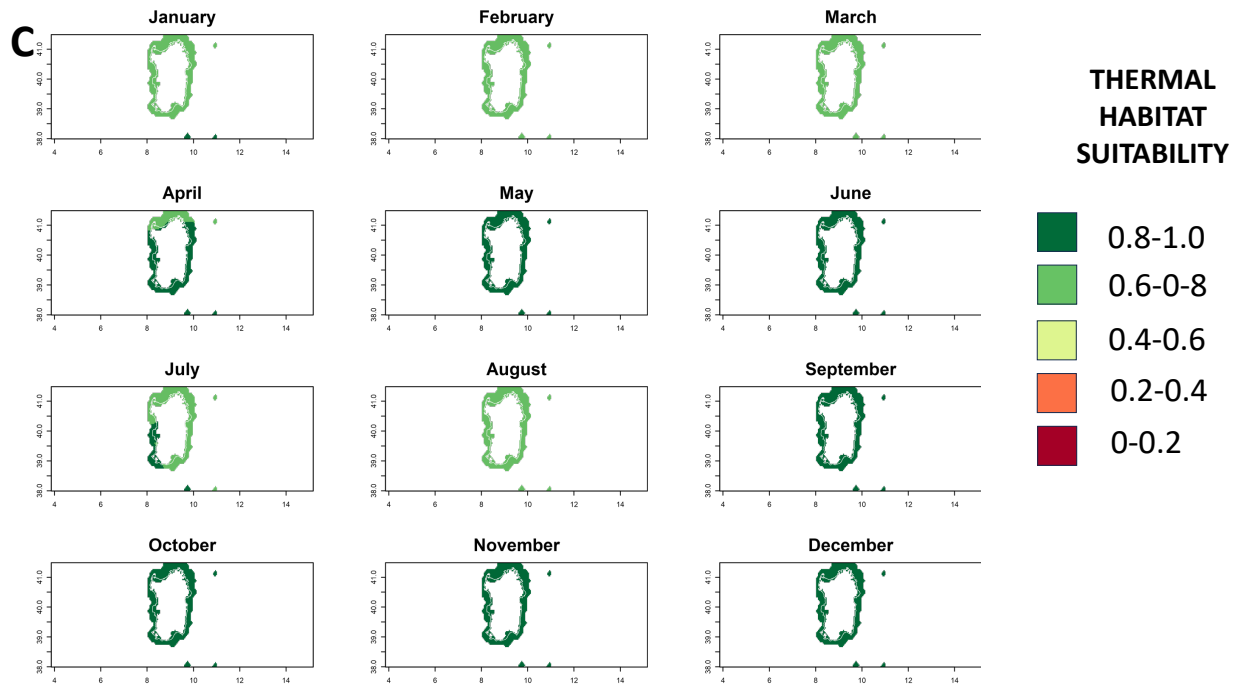
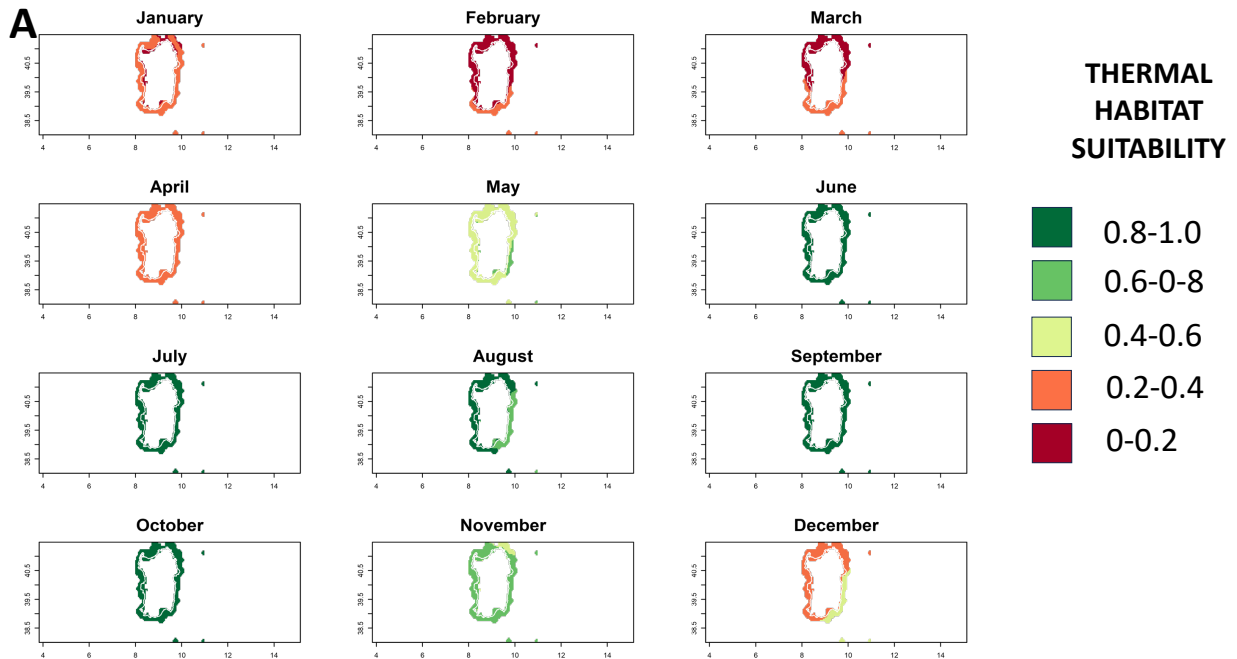


Figure S3.4 Thermal habitat suitability for *Mytilus galloprovincialis* in reference period 1987-2010 (A), in SSP2-4.5 (2021-2050) (B) and SSP5-8.5 (2021-2050) (C) for 2021-2050.

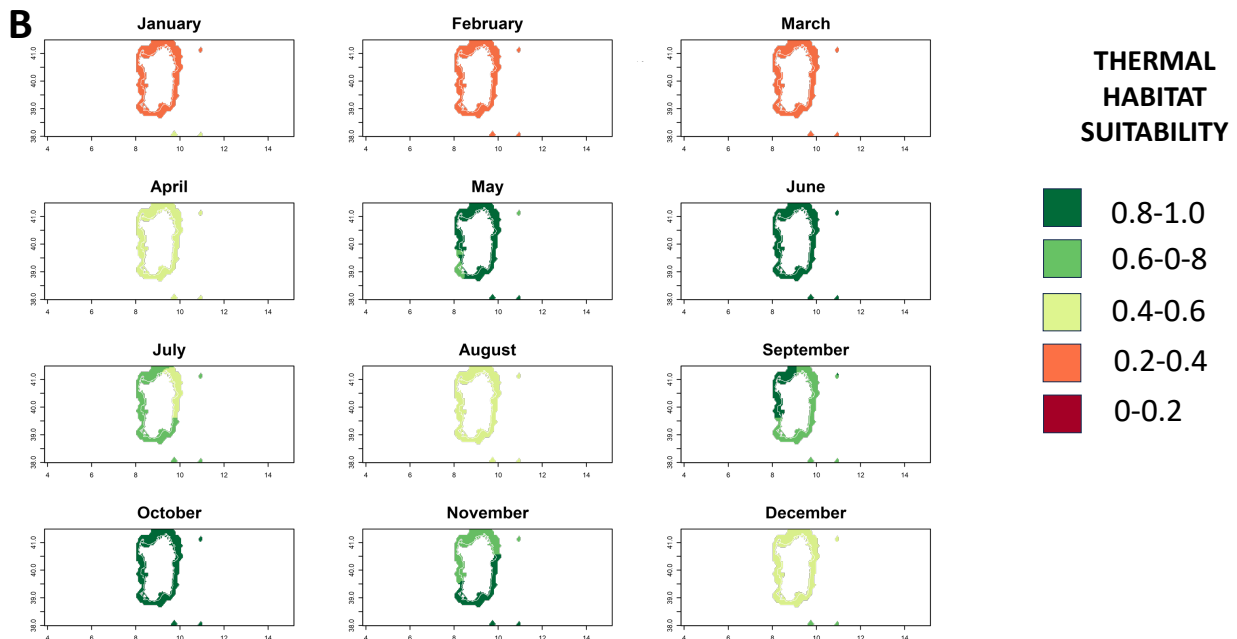
Paracentrotus lividus

Reference Period (1987-2010)



Paracentrotus lividus

SSP2-4.5 (2021-2050)



Paracentrotus lividus SSP5-8.5 (2021-2050)

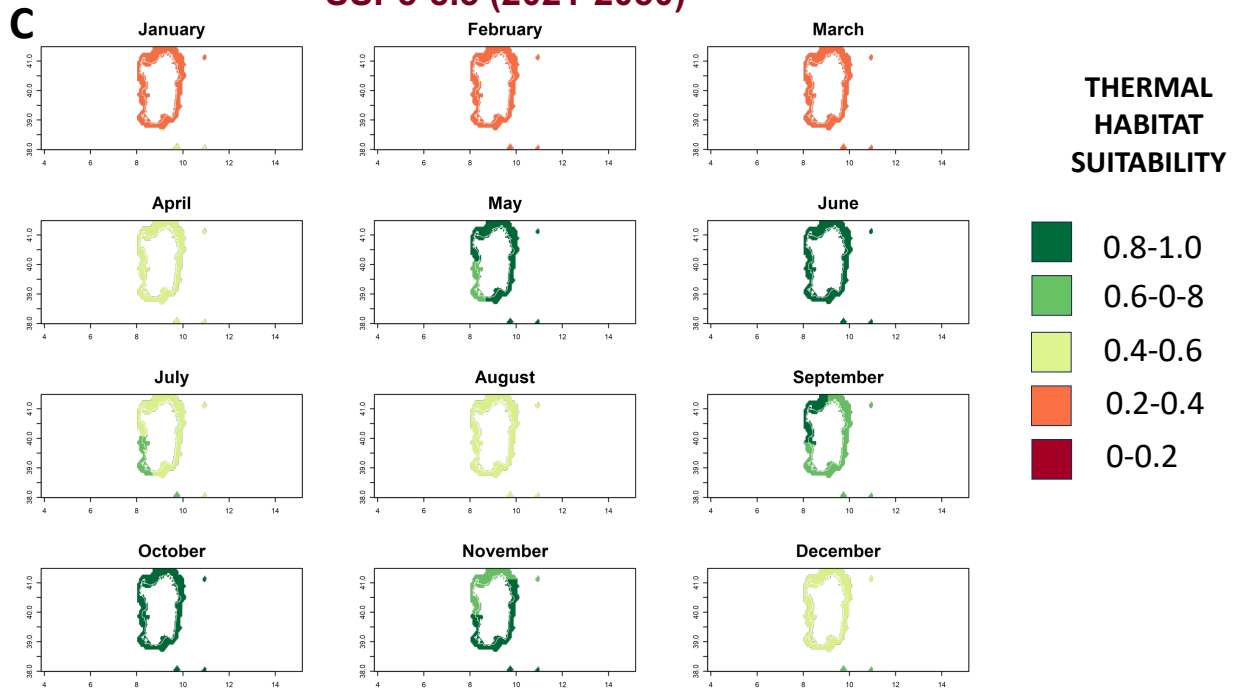
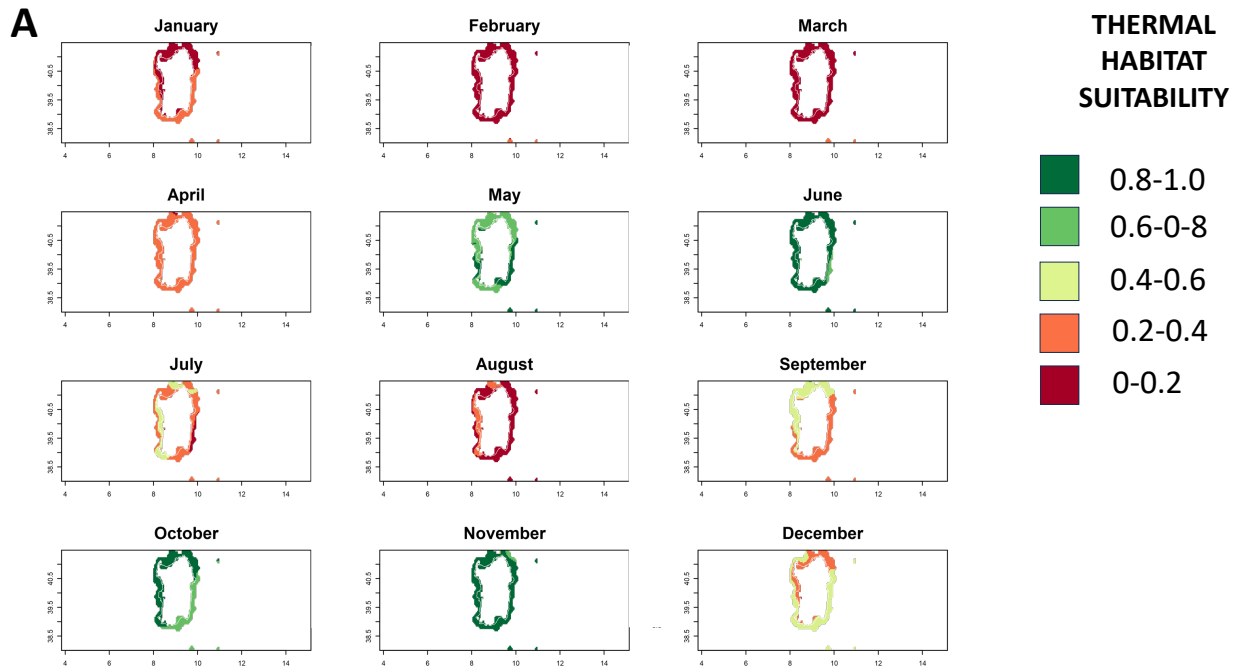


Figure S3.5. Thermal habitat suitability for *Paracentrotus lividus* in reference period 1987-2010 (A), in SSP2-4.5 (2021-2050) (B) and SSP5-8.5 (2021-2050) (C) for 2021-2050.

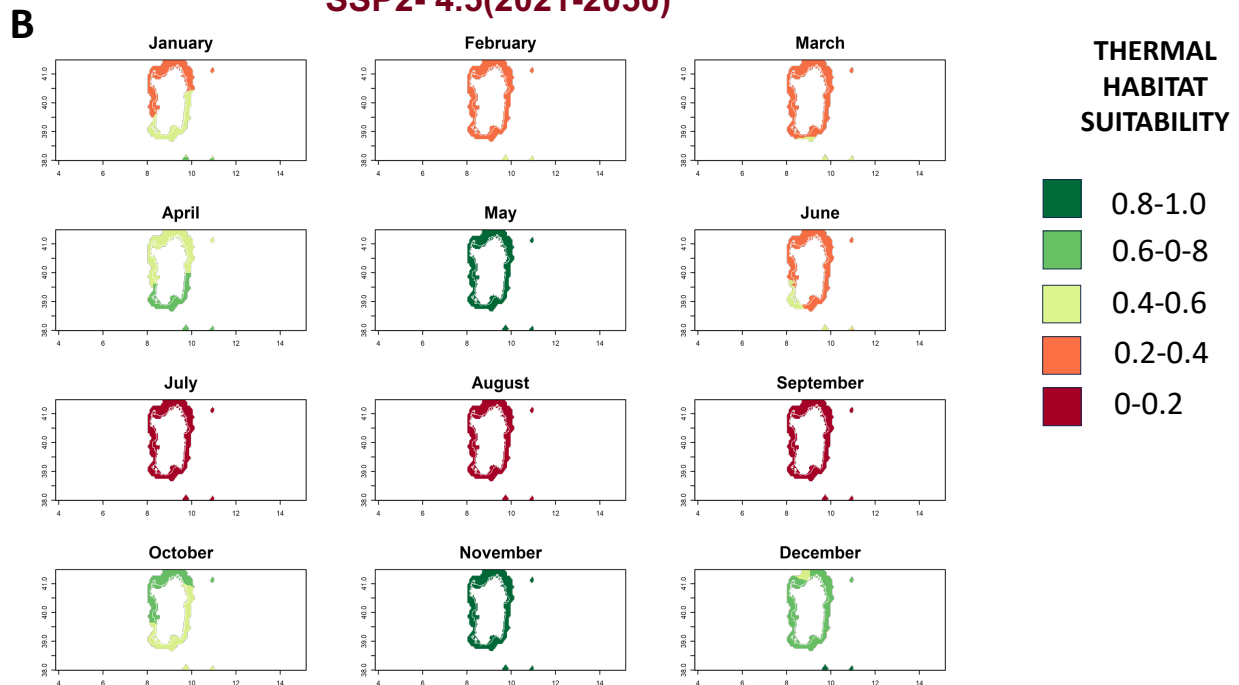
Mullus barbatus ♀

Reference Period (1987-2010)



Mullus barbatus ♀

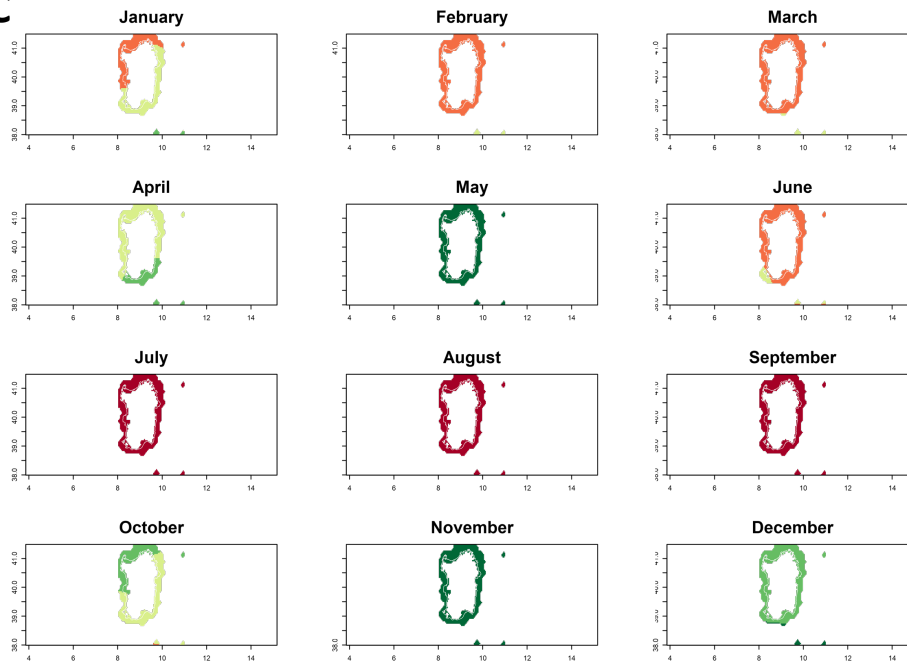
SSP2- 4.5(2021-2050)



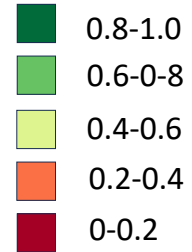
Mullus barbatus ♀

SSP5-8.5 (2021-2050)

C



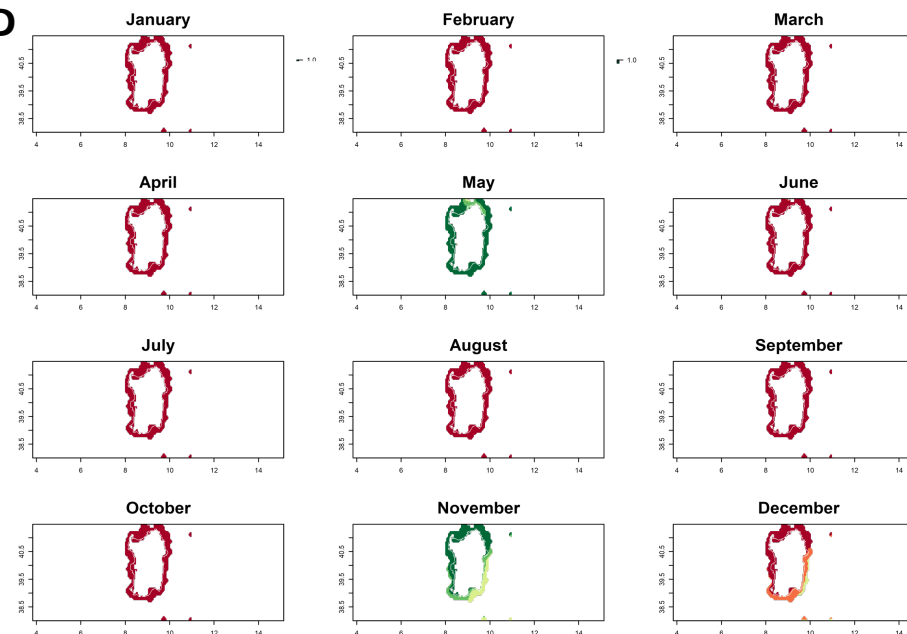
THERMAL
HABITAT
SUITABILITY



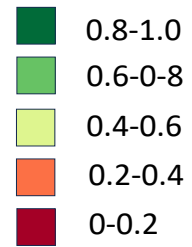
Mullus barbatus

Reference Period (1987-2010)

D

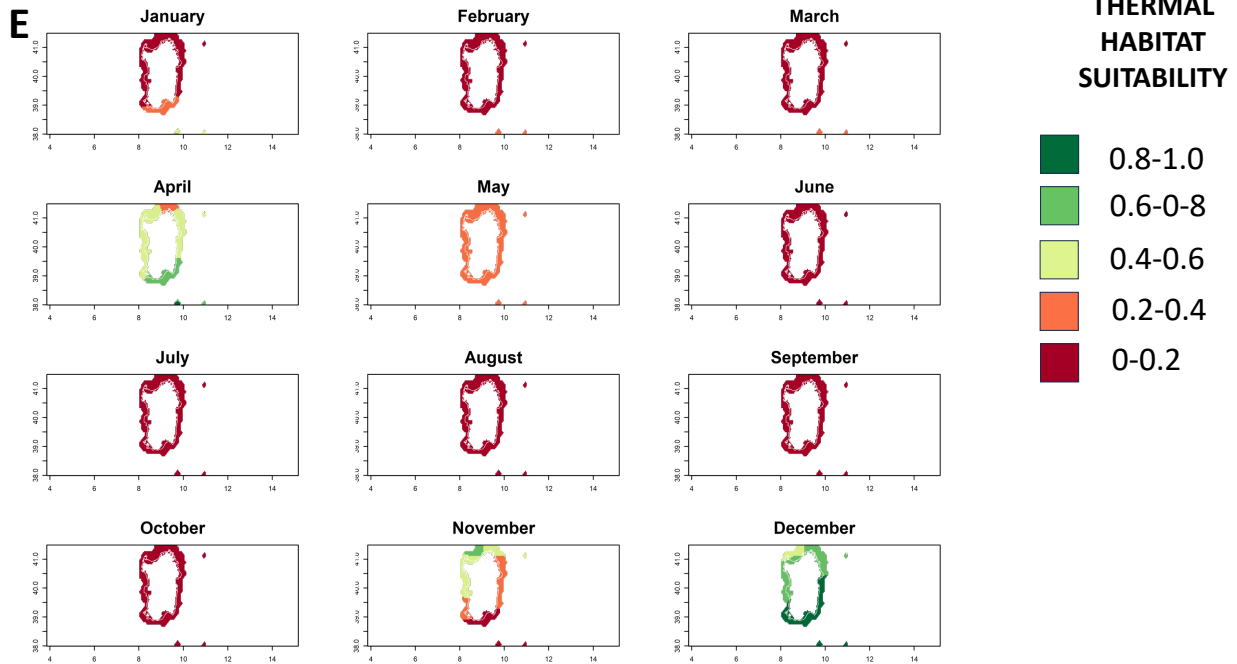


THERMAL
HABITAT
SUITABILITY



Mullus barbatus ♂

SSP2-4.5 (2021-2050)



Mullus barbatus ♂

SSP5-8.5 (2021-2050)

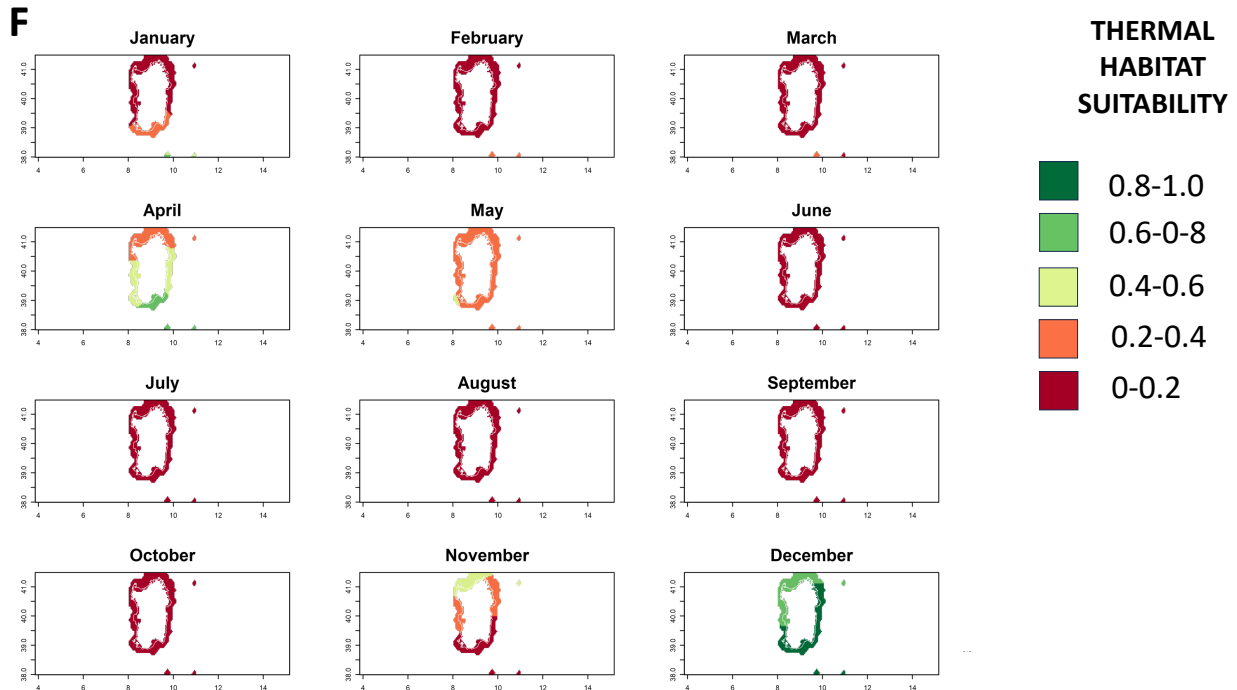
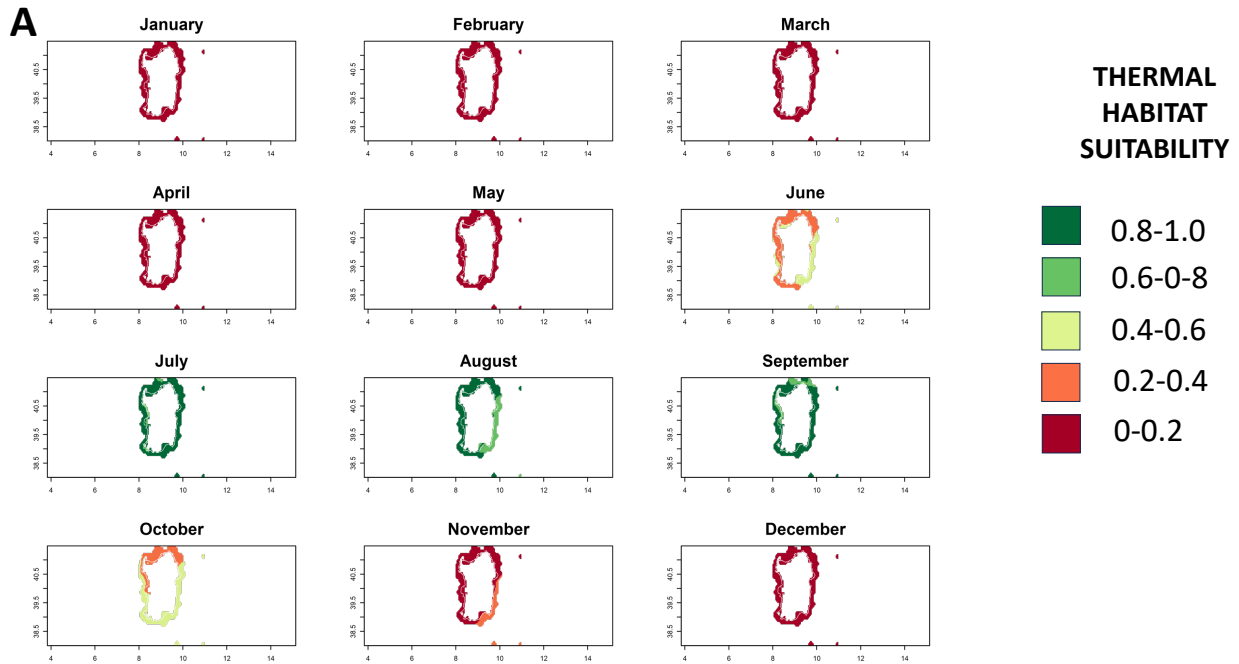


Figure S3.6 Thermal habitat suitability for *Mullus barbatus* for female (left) and male (right) in reference period 1987-2010 (A,D), in SSP2-4.5 (2021-2050) (B,E) and SSP5-8.5 (2021-2050)(C,F)

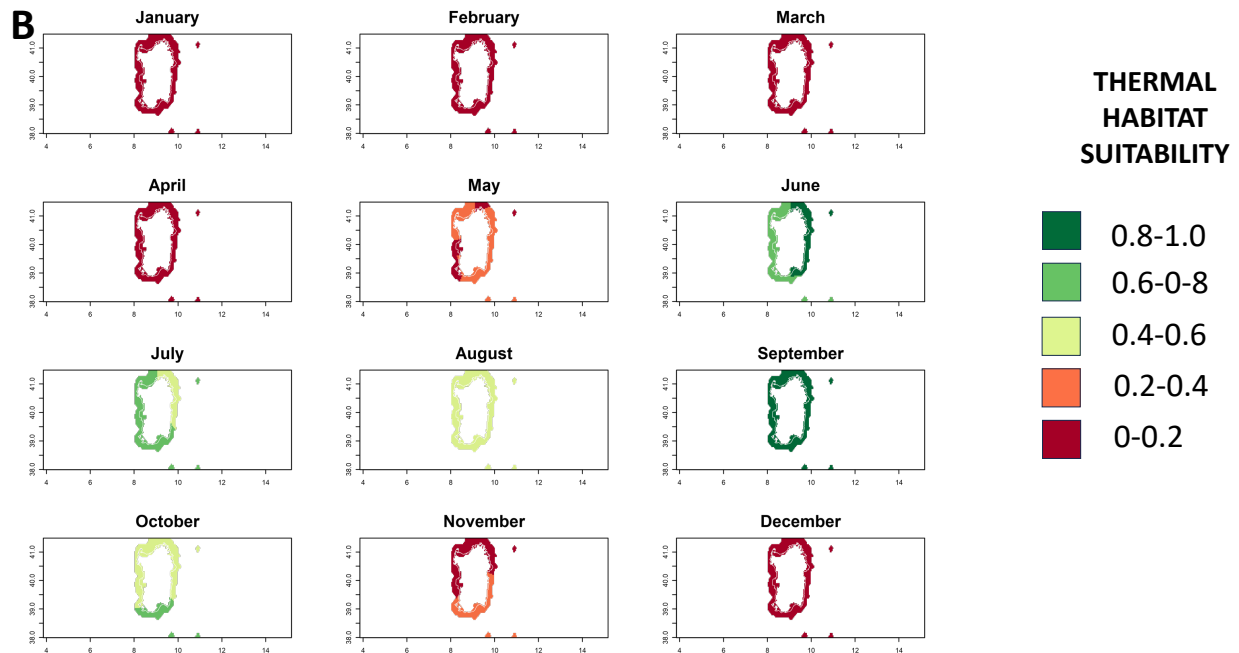
Holothuria tubulosa

Reference Period (1987-2010)



Holothuria tubulosa

SSP2-4.5(2021-2050)



Holothuria tubulosa

SSP5-8.5 (2021-2050)

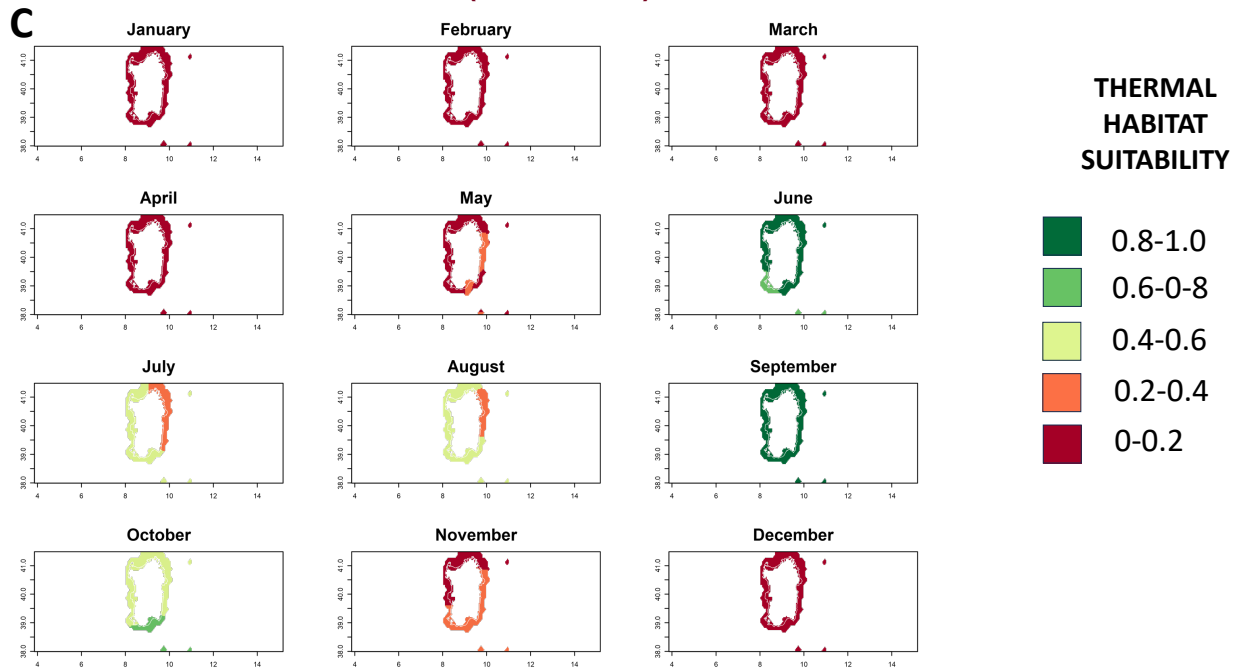
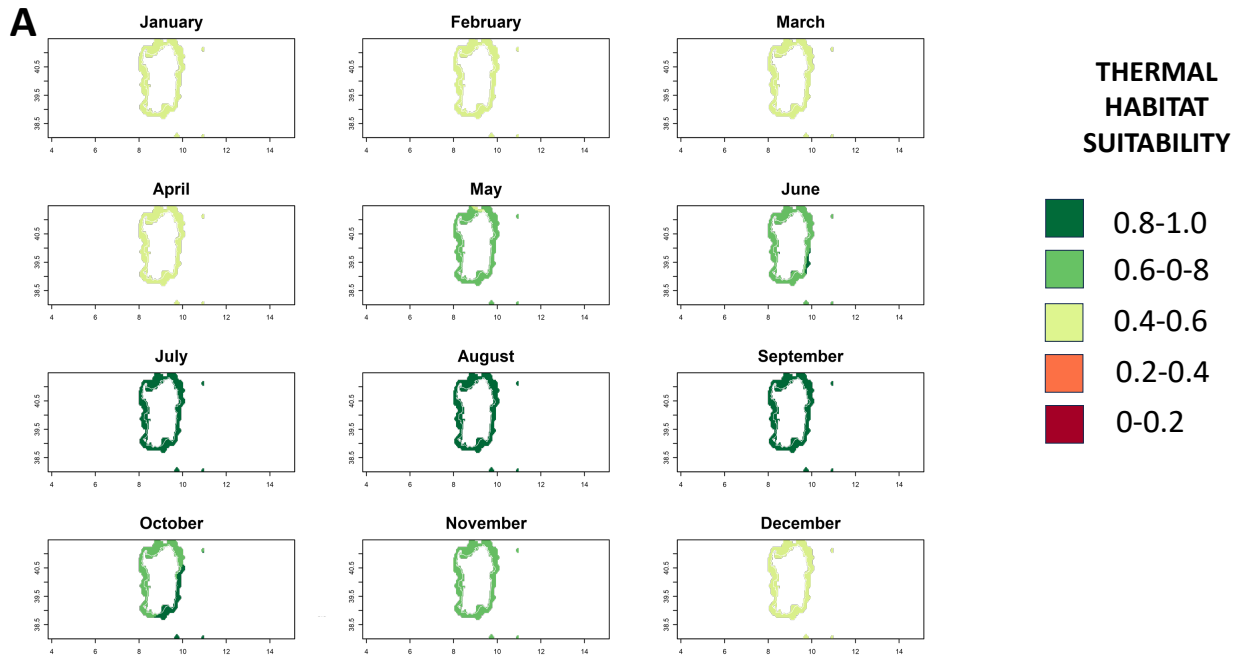


Figure S3.7. Thermal habitat suitability for *Holothuria tubulosa* in reference period 1987-2010 (A), in SSP2-4.5 (2021-2050) (B) and SSP5-8.5 (2021-2050) (C) for 2021-2050.

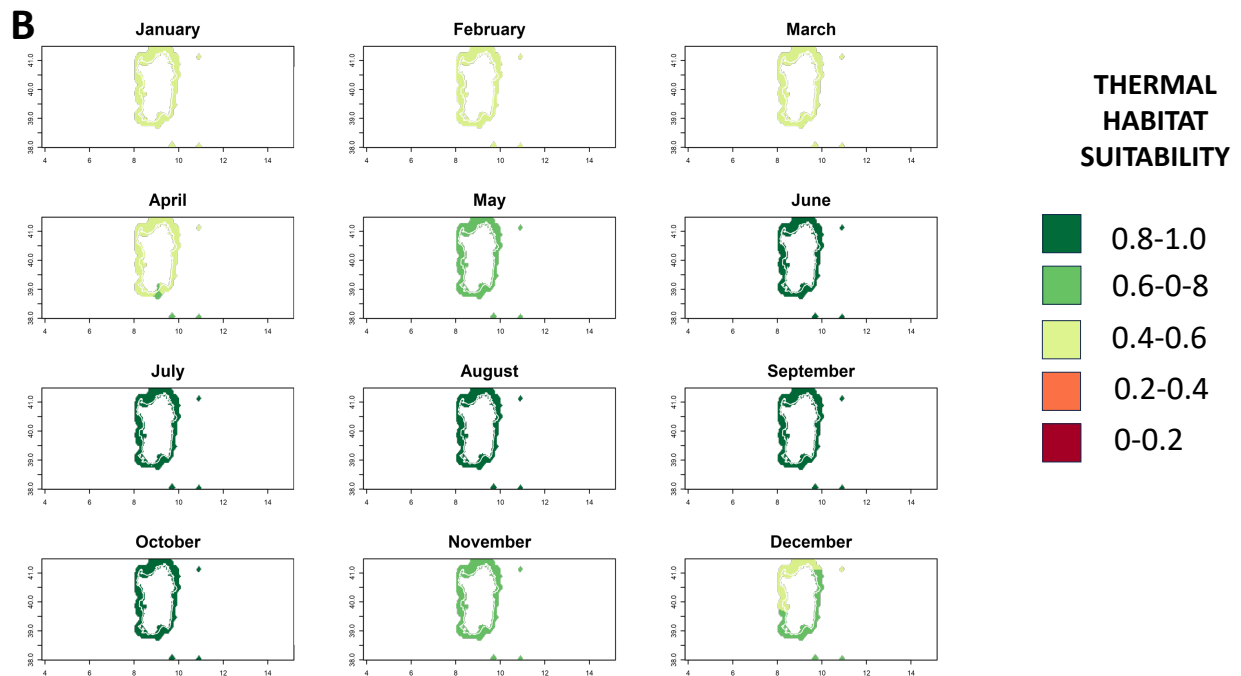
Posidonia oceanica

Reference Period (1987-2010)



Posidonia oceanica

SSP2-4.5 (2021-2050)



Posidonia oceanica SSP5-8.5 (2021-2050)

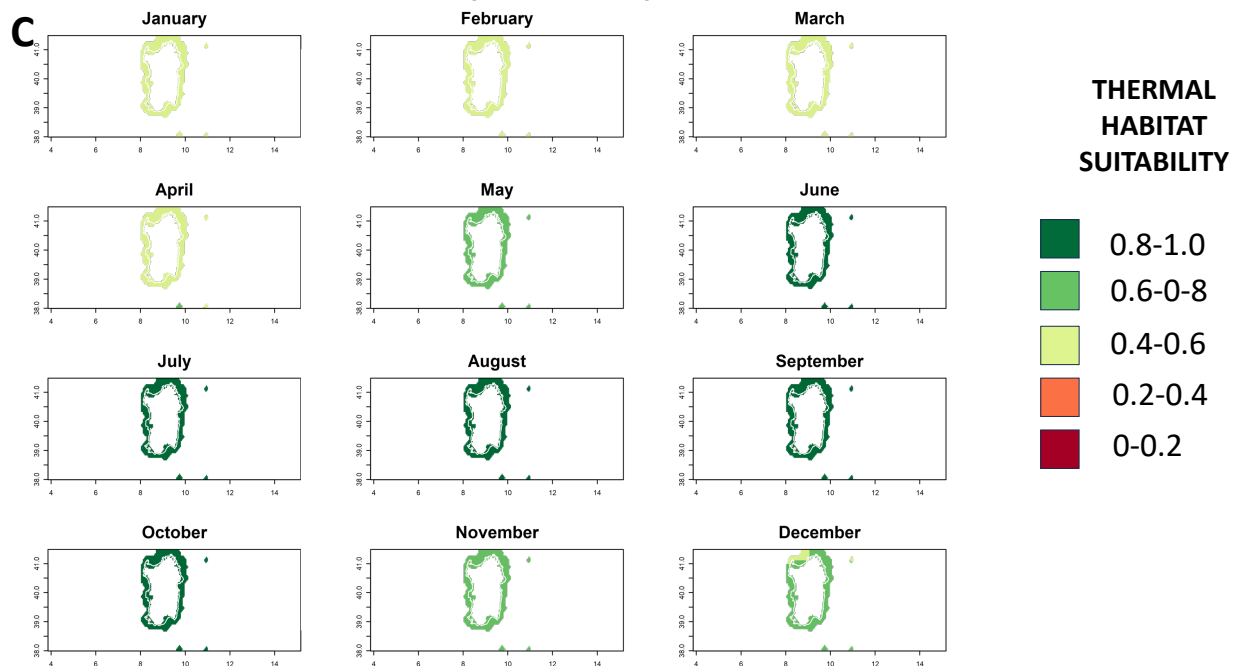


Figure S3.8. Thermal habitat suitability for *Posidonia oceanica* in reference period 1987-2010 (a), in SSP2-4.5 (2021-2050) (b) and SSP5-8.5 (2021-2050) (c)

Chapter 4: Marine heatwaves effects on quantity, composition, and turnover of sedimentary organic matter in a Mediterranean coastal lagoon: a benthocosm study

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4.1. Introduction

The Mediterranean region is among the most vulnerable areas to global warming (Cramer et al., 2018; MedECC, 2020; Seneviratne et al., 2016). Besides increasing mean global temperature, other changes in the climate system include increased frequency, intensity, and/or amount of heavy and convective precipitation events, along with a heightened risk of drought (Giorgi and Lionello, 2008; IPCC, 2023; MedECC, 2020; Taylor et al., 2021). Of particular concern is also the escalation in the occurrence of more frequent and intense heatwaves affecting both land and sea surface temperatures (Benedetti-Cecchi, 2021; Holbrook et al., 2019; Marx et al., 2021; Oliver et al., 2019). A terrestrial heatwave event can be identified as three or more consecutive days where the maximum temperature is over the 90th percentile (Perkins and Alexander, 2013), whereas a marine heatwave (hereafter MHW) can be usually defined as a discrete, prolonged (minimum 5 days), anomalously warm water event ($>2^{\circ}\text{C}$) in a particular location (Hobday et al., 2016).

MHWs can exert on marine ecosystems severe impacts (Smith et al., 2023), that include mass mortality events among invertebrates and fish (Garrahou et al., 2022; Gómez-Gras et al., 2021), declines in the abundance of seagrass meadows and alteration in plant performances (Marbà and Duarte, 2010; Stipcich et al., 2022ab), increased spread of invasive species and pathogens (Bosch-Belmar et al., 2022; Danovaro et al., 2009), and several negative indirect effects on the benthos mediated by altered nutritional quality of the available food sources (Soru et al., 2022; Stipcich et al., 2022b). Some of the MHWs impacts have been also documented with manipulative experiments showing severe consequences on from individuals to communities (Ennas et al., 2023; Samuels et al., 2021; Smale et al., 2011; Smale et al., 2015; Sorte et al., 2010). Nonetheless, studies addressing the effects of MHWs on sediment biogeochemistry are very limited (Alsterberg et al., 2012; Sanz-Lázaro et al., 2011; Soru et al., 2022).

Transitional aquatic systems, including coastal lagoons, are characterized by high biodiversity and productivity, offering distinct socio-economic services and ecosystem functions, such as water purification, flood reduction, microclimate regulation, soil erosion prevention, water and biodiversity conservation, C storage (Cataudella et al., 2015; Danovaro and Pusceddu, 2007; IPCC, 2023; Mitsch et al., 2015; Pusceddu et al., 2003; Trombetti et al., 2022; Yang et al., 2021).

In the Mediterranean basin, coastal lagoons are areas of shallow water, partially separated (semi-enclosed systems) from the sea by physical barriers (sandbanks, shingle or, less frequently, rocks) connected at least intermittently to the sea by one or more restricted inlets (Cataudella et al., 2015; Newton et al., 2018). Such ecosystems, due to their transitional location at the land-sea interface, experience large fluctuations of environmental variables over ample ranges of spatial and temporal scales (Lacoste et al., 2023; McLusky and Elliott, 2007).

Coastal lagoons, through complex biogeochemical processes, can mitigate the eutrophication processes of the adjacent sea by controlling and reducing mixtures of different pollutants, total phosphorus, and nitrogen riverine loads entering the sea from the agricultural catchments (Domingues et al., 2017; Sousa et al., 2016; Tanner and Sukias, 2011). Furthermore, coastal lagoons can actively contribute to carbon sequestration and accumulation as plant biomass (mainly macrophytes) or detrital organic matter (OM) in soil and sediments (Davidson et al., 2019; de Vicente, 2021; Laiho, 2006; Pusceddu et al., 2003), representing hot spots of blue C storage (Boadella et al., 2021; Newton et al., 2018; Sousa et al., 2016). They, thus, ultimately provide an important contribution to the global carbon budget (Geertz-Hansen et al., 2011; Laiho, 2006). Because of the mainly refractory composition of lagoon sediment OM, only a minor fraction of it is directly available to the consumers, whereas the largest fraction needs to be fragmented and processed through prokaryotes and meiofauna to enter the higher levels (Manini et al., 2003).

In all aquatic environments, the relationships between organic matter and the members of the benthic communities are influenced by multiple, often interacting, environmental variables, like water currents and the substrate composition, which, in turn, enhance the levels and variance of natural disturbance, as well as shape habitat-specific conditions (Danovaro and Pusceddu, 2007; Pusceddu et al., 2007, 2003). For instance, organic matter degradation processes are temperature-dependent, and rising temperatures may alter the global balances of carbon (C) and nutrients, potentially influencing biological productivity and the food web process (Kirwan et al., 2014; Sanz-Lázaro et al., 2011).

While the effects of extreme temperatures triggered by heatwaves on biodiversity and trophic webs of transitional aquatic environments have received some attention (Couboulès et al., 2022; Martínez-Megías and Rico, 2022; Pulina et al., 2016; Pansch et al., 2018; Pulina et al., 2020; Pitacco et al., 2018; Vidussi et al., 2011; Vilas-Boas et al., 2021) information on the effects of MHWs on lagoon sedimentary biogeochemistry is, at the best of our knowledge, not existent or if any, cross-investigated in conjunction with the effects of combined climatic stressors (i.e., hypoxia, Sarà et al., 2021).

To partially fulfill such a gap of knowledge, we investigated changes in quantity, biochemical composition, and degradation rates of sedimentary organic matter from a Mediterranean coastal lagoon in response to heatwaves of different intensity (+4 and +8 °C) in benthocosm. Specifically, we tested the (null) hypothesis by which the quantity, biochemical composition, nutritional quality for benthic consumers and extracellular enzyme-mediated turnover of sedimentary organic matter do not vary under heatwaves characterized by temperature anomalies of different magnitude. To test this hypothesis, we carried out a manipulation experiment in benthocosms by which we exposed lagoon sediments to different water temperatures simulating 5-day lasting heatwaves.

4.2. Material and Methods

4.2.1 Study area and sediment sampling

The study was conducted using surficial (top 2-cm) sediments collected from the Santa Gilla Lagoon, one of the largest coastal lagoons of Sardinia (Italy). Spanning an area of 1300 hectares, this lagoon holds international importance under the Ramsar Convention (D.M. 03/09/1980) and is designed as a Site of Community Importance (Directive 92/43 CEE) (Cabiddu et al., 2014). Besides its significance for habitat and biodiversity conservation purposes, the Santa Gilla Lagoon hosts facilities for culturing and harvesting of several commercial species like mussels, clams, and oysters (Culurgioni et al., 2015).

An indoor manipulation experiment was conducted in benthocosm at the Experimental Aquaculture Laboratory of the University of Cagliari located close to the Santa Gilla lagoon (Sardinia, Italy). Surficial sediments were collected using plexiglass corers (3.7 cm internal diameter) operated manually in May 2023, in an area (1.5 m depth) proximal to the marine pole of the lagoon (Figure 4.1). This area is characterized by generally well oxygenated sandy sediments (Atzori et al., 2018). To ensure that the sediments represented the widest natural variability of the sampling area, the

top 2 cm of each of ca. 100 corers, collected within a 10x10 m square, were pooled together, sieved (1 cm mesh size) to remove largest benthic organisms and debris, and then gently homogenized. This procedure most likely minimized the risk of any hypoxic patch within the sediment, thus isolating, at least initially, the possible covarying effect of oxygen availability. Seawater was collected from the same area at the sediment-water interface using a 10-L Niskin bottle operated horizontally and immediately filtered through a 200- μ m mesh to remove larger plankton organisms. During pre-treatment operations, both sediments and seawater were maintained at in-situ temperature (21°C) and salinity (28-32 PSU).

The homogenized sediment was then distributed into 15 individual benthocosms, each consisting of a 250 mL glass beaker, creating a 2.5 cm-thick layer of sediment within each beaker. These benthocosms were then placed in a 100-L tank filled with filtered seawater for a 2-day acclimation. The tanks were maintained indoor at the in-situ temperature recorded at the time of sampling (21°C). To avoid a lateral parasite light exposure of the whole sediment within the beakers, these were equipped with adhesive tape applied to darken the sides below the water-sediment interface line, thus allowing the light to penetrate the sediment only from above, as in the field. The light rhythm followed the one in the field at the time of the experiment, with a light:dark ratio of ca. 14:10 hours. The temperature was controlled using a thermostat (230 V, 10 A). Considering the small volume of the benthocosms, we assumed that the sediments attained the same temperature as the surrounding bath water. To ensure that this expectation was correct, we performed another experiment with the same architecture as the manipulative one, in which we monitored sediment temperature twice a day in each benthocosm throughout the five-day experimental period and compared them with the corresponding water bath temperatures. As expected, no significant differences were observed between sediment and water temperatures (Wilcoxon-Mann-Whitney test; $p > 0.05$; Figure S4.2).

To ensure an adequate oxygenation and prevent the establishment of anoxic conditions in the water, eventually propagating to the sediment, each benthocosm was equipped with a single, gently operating, tap aerator that allowed maintaining oxygen concentrations in the water at similar levels of those in the lagoon at the time of sediment sampling (6.182 ± 0.004 mg L⁻¹).

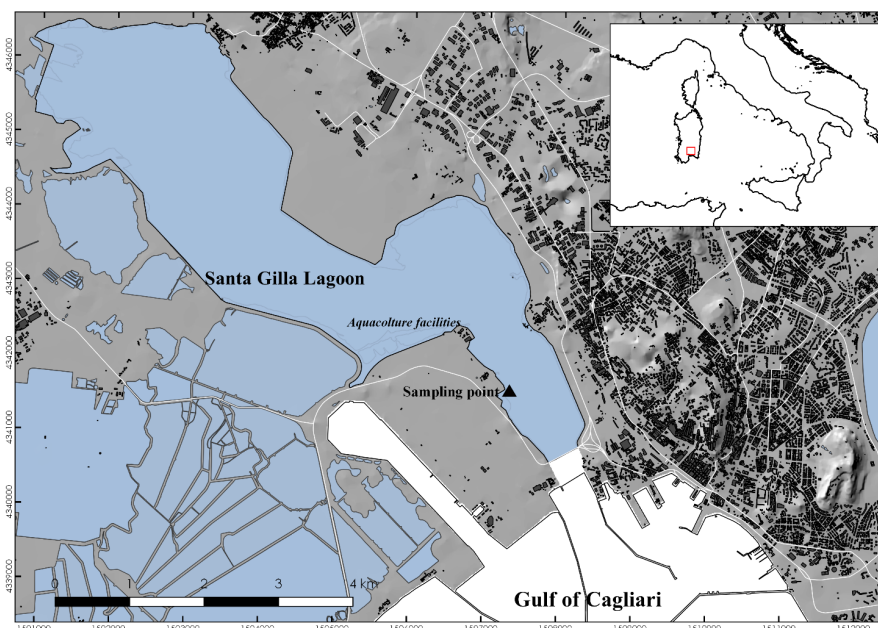


Figure 4.1. Study area and sediment sampling location. Coordinate reference system (EPSG: 3003).

4.2.2 Experimental design and set-up

After the 2 days acclimation period, three of the 15 replicate benthocosms were retained as a reference and maintained at the in-situ temperature (hereafter 21°C, Before), to assess any potential effect during the experiment (Figure 4.2). Subsequently, another set of benthocosms was divided into four 15-L tanks, each of which was heated over a five-day period (representing the minimum duration of marine heatwaves; Hobday et al., 2016) at the temperatures of 21°C, 25°C and 29°C, resulting in final temperature anomalies of +0°C (reference, 21°C, After), +4 °C, and +8°C. The reference temperature of 21°C represents the in-situ water temperature measured during sediment collection. The +4°C and +8 °C increases (corresponding to 25 and 29 °C, respectively) reflect longer-term projections for temperature in the Mediterranean region (Darmaraki et al., 2019; Giorgi and Lionello, 2008; Martínez et al., 2023) and were selected to simulate moderate and strong heatwaves, respectively. Our simulation of moderate and strong heatwaves magnitude has been used also in previous mesocosm experiments (Bilajac et al., 2024; Pulina et al., 2020; Soulié et al., 2022).

Upon completion of the manipulation phase, the sediments were transferred and stored in Petri dishes at -20°C for the subsequent analyses.

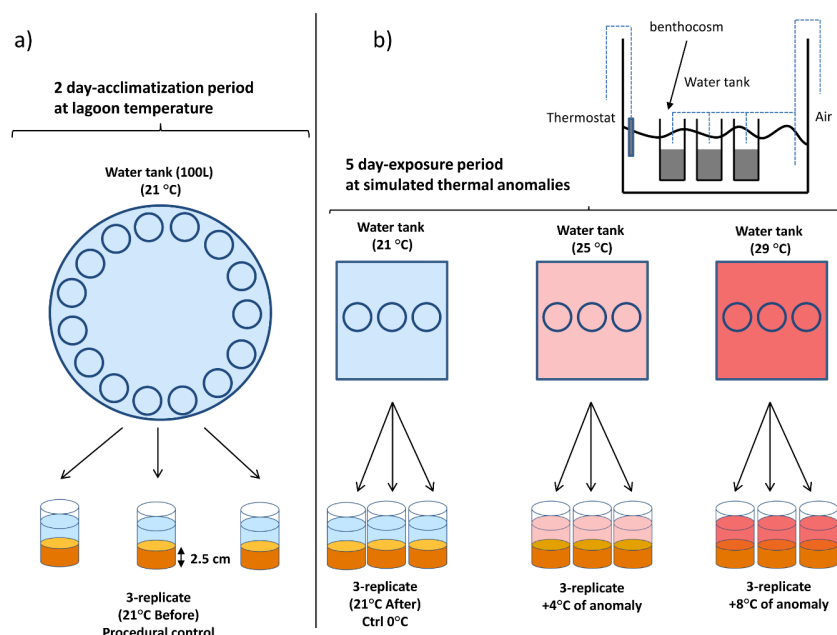


Figure 4.2. Twelve replicate benthocosms, each consisting of a 250mL glass beaker filled with a 2.5 cm-thick layer of sediment and ca. 200 mL of water were placed in a 100L water tank at 21°C (the *in-situ* temperature at the time of sampling) for a 2-day acclimatization period (a). After this period, three replicate benthocosms were removed, stored at -20°C, and used as procedural control (21°C, Before) until analyses, while the remaining 9 benthocosms were submerged in three separate tanks (15L each; three replicates per tank) with water temperature gradually reaching set points over 5 days (b).

4.2.3 Quantity, biochemical Composition, nutritional quality and degradation of Sedimentary Organic Matter

Protein, carbohydrate, and lipid contents were determined spectrophotometrically (Danovaro, 2010). For each biochemical assay, blanks were obtained using pre-calcinated sediments (450 °C for 4 h). Protein, carbohydrate, and lipid concentrations were converted into C equivalents using the conversion factors 0.49, 0.40, and 0.75 mg C mg⁻¹, respectively, obtained from the C contents of the respective standard molecules (albumin, glucose, and tripalmitin, respectively), and their sum was reported as biopolymeric C (BPC) (Fabiano et al., 1995).

Chlorophyll-a contents and phaeopigment (after acidification with 200 µL 0.1N HCl) sedimentary contents, after extraction overnight at 4°C in the dark with 5 mL of 90% acetone, were determined fluorometrically (Danovaro, 2010). The algal fraction of BPC was estimated as the percentage of total phytopigment (as the sum of chlorophyll-a and phaeopigment) to BPC concentrations, after converting the total phytopigment concentrations into C equivalents using a 40 mgC mg⁻¹ as a conversion factor (Pusceddu et al., 2010).

C degradation rates were estimated from aminopeptidase and β -glucosidase activities, determined by the cleavage of fluorogenic substrates (L-leucine-4-methylcoumarinyl-7-amide and 4-methylumbelliferone-D-glucopyranoside, respectively) at saturating concentrations (Bianchelli et al., 2020). Prefiltered (0.2 μ m) and autoclaved seawater containing the specific substrate up to the final volume of 5 mL were added to 2.5 mL aliquots of the sediment (Danovaro, 2010). Substrate incubations were performed in the dark at the in-situ temperature for 1 h. After incubation, the samples were centrifuged (3000 rpm, 5 min) and supernatants were analyzed fluorometrically (at 380 nm excitation and 440 nm emission for aminopeptidase and at 365 nm excitation and 455 nm emission for β -glucosidase) (Bianchelli et al., 2020). Data were normalized to sediment dry weight (60 °C, 24 h) and reported as nanomoles of substrate released per g of sediment dry weight h⁻¹. Protease and glucosidase activities were converted into C equivalents using 72 as a conversion factor (Pusceddu et al., 2000), and their sum was reported as the potential C degradation rate (g C g⁻¹ h⁻¹). The turnovers (per day) of the whole protein and carbohydrate pools were calculated as the ratios of the hourly C degradation rates (once multiplied by 24) and the whole protein and carbohydrate C contents in the sediment (Pusceddu et al., 2014). Although these calculations represent only a rough estimate of the potential (maximum) rates of sedimentary C (as not including degradation rates of other macromolecules like lipids), they are regarded as reliable proxies of ecosystem functioning (Pusceddu et al., 2014).

4.2.4 Statistical Analyses

To test the null hypothesis by which there were no differences in organic matter quantity, biochemical composition (in terms of protein, carbohydrate, lipid, and phytopigment contents), degradation rates, and turnover time among treatments (different temperature anomalies), permutational analyses of variance (PERMANOVA) (Anderson and Braak, 2003) were carried out in the univariate context with one fixed factor with four levels: 21°C Before, 21°C After, +4°C, +8°C. The analyses were carried out on Euclidean distance-based resemblance matrices obtained from normalized data, using 999 random permutations of the appropriate units. When PERMANOVA tests revealed significant differences among levels, pairwise tests were also carried out. As PERMANOVA assumes independence and homogeneity of dispersions a PERMDISP test was performed (Anderson et al., 2008; Anderson, 2017), revealing the lack of any pattern in dispersion for all of the investigated variables (Tables S4.1-S4.2).

Multivariate differences in organic matter biochemical composition (in terms of protein, carbohydrate, lipid and phytopigment contents) were visualized with a biplot after a canonical analysis of the principal coordinates (CAP). CAP allows the identification of an axis through the multivariate cloud of points that optimally separates the groups established a priori. Hierarchical cluster analysis was run using group-average linking and the SIMPROF permutation test option (default settings of 999 permutations and significance level threshold at 0.05) to identify significantly different groups of sediments with different biochemical composition at different temperatures. The result of the hierarchical cluster analysis was then over-imposed to the biplot obtained from the CAP results and a SIMPER test was carried out to ascertain the average squared distance among identified clusters and the percentage contribution of each of the biochemical variables to those distances. PERMANOVA, PERMDISP, CAP, Hierarchical Cluster analysis and SIMPER tests were carried out through the software PRIMER 6+ (Anderson, 2017).

4.3. Results

Simulated MHWs significantly affected the quantity and the biochemical composition of sedimentary organic matter (Table 4.1, Table 4.2).

Table 4.1. Results of the PERMANOVA tests addressing differences in sedimentary organic matter contents and biochemical composition among treatments (21°C Before, 21°C After, +4°C and +8°C of thermal anomalies). Df = degrees of freedom; MS = mean square; Pseudo-F = F statistic; P(MC) = P-value obtained after Monte Carlo simulations and 999 permutations. Significant differences are in bold.

Variables	Df	MS	Pseudo-F	P(MC)
Protein	3	2.91	5.59	0.020
Carbohydrate	3	2.09	4.94	0.040
Lipid	3	0.88	2.23	0.180
Chlorophyll-a	3	3.36	23.61	0.001
Phaeopigment	3	0.72	1.11	0.385
Total phytopigment	3	2.54	14.41	0.001
Biopolymeric C	3	3.56	11.81	0.003
Autotrophic fraction of biopolymeric C	3	1.25	3.19	0.091
OM biochemical composition	3	9.95	4.67	0.003

The sedimentary contents of all biochemical compounds, but lipids, did not vary significantly (Table S4.3) because of sediment manipulation at 21°C (i.e., before-after acclimation at 21°C) (Figure 4. 3). The comparison of organic matter contents in sediments acclimated at 21°C and those acclimated at all other temperatures revealed a general significant decrease of values for all

variables (Table S4.3), with exceptions for proteins and lipids that did not vary significantly at both +4° and +8° (Figure 4.3 a,c) and phaeopigments that did not vary at +8 °C. More in details, carbohydrate, chlorophyll-a, and total phytopigment contents in sediments exposed to the highest thermal anomaly (+8°C) were characterized by values significantly lower (by ca. 24, 50, and 37 %, respectively) than those at all other treatments, decreasing from 0.40 ± 0.06 , 0.31 ± 0.05 , 0.44 ± 0.05 to 0.30 ± 0.02 , 0.16 ± 0.01 , 0.27 ± 0.03 mgC g⁻¹, respectively (Figure 4.3b, e-g). The biopolymeric C contents exhibited the same significant decrease (by ca. 18% on average, range 15-21%) at all thermal anomalies, varying from 0.91 ± 0.06 at 21°C to 0.72 ± 0.09 (at +8 °C) mgC g⁻¹ (Figure 4.3d). The algal fraction of biopolymeric C in all heated sediments was consistently lower than that in sediments at 21°C after acclimation (Table S4.3), with values at +4 °C and +8°C temperature anomaly (37 and 38% of BPC, respectively) significantly lower (by 23 and 21%, respectively) than those at 21 °C (48% of BPC) (Figure 4.3h).

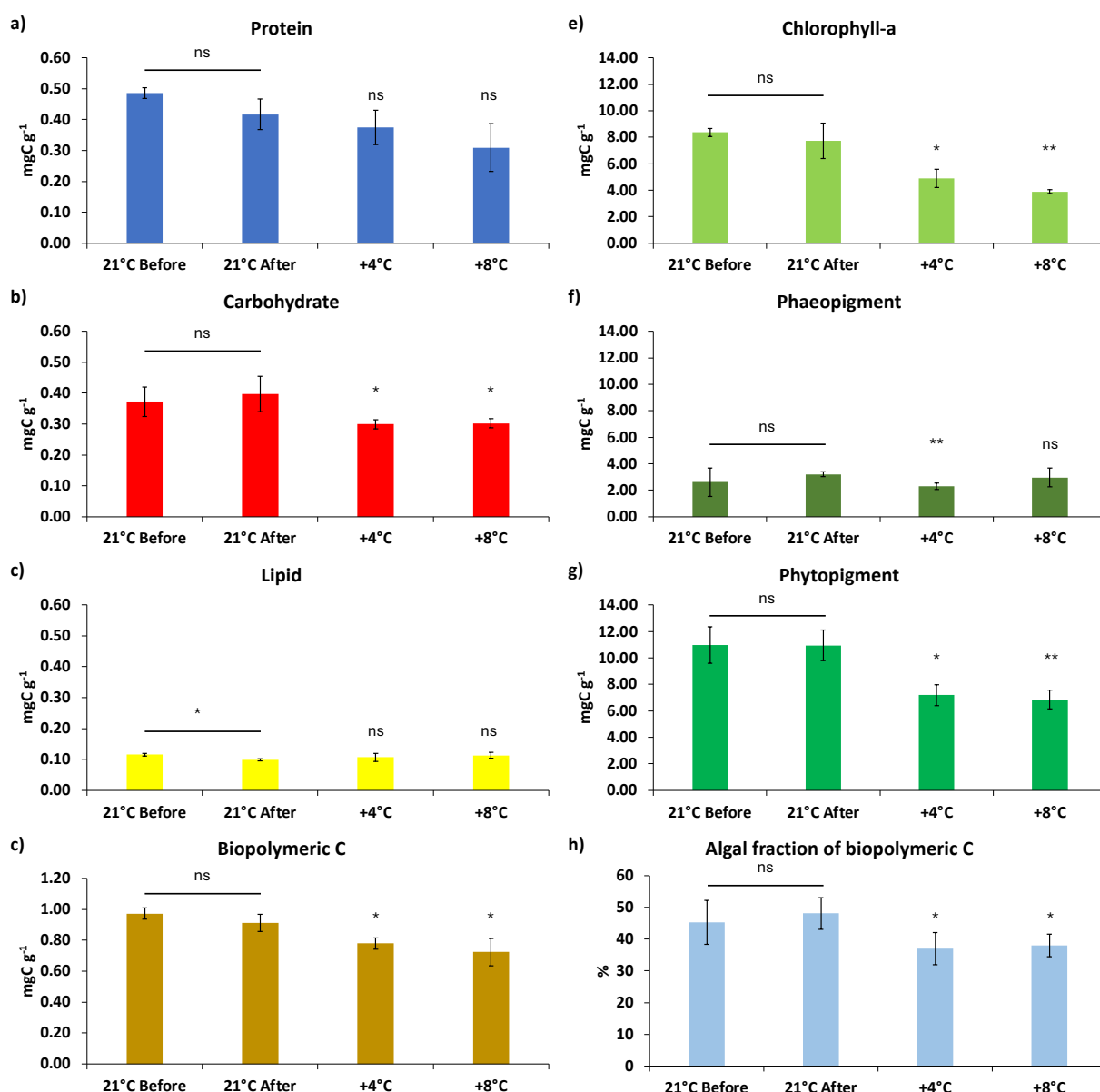


Figure 4.3. Organic matter contents in sediments experiencing heatwaves with different temperature anomalies (+4°C, +8°C): (a) protein, (b) carbohydrate, (c) lipid, (d) biopolymeric C, (e) chlorophyll-a, (f) phaeopigment, (g) total phytopigment, and (h) algal fraction of biopolymeric C. Error bars are standard deviation (n = 3). Asterisks indicate the p-values of pairwise tests between values at 21°C after the experiment and all other temperatures, as reported in Table S3. * = $p < 0.05$; ** = $p < 0.01$; ns = not significant.

The results of the PERMANOVA test revealed also that the biochemical composition of sedimentary organic matter varied significantly among sediments acclimated at different temperatures (Table 4.1) and that sediments before and after acclimation at 21 °C and sediments at +4 and +8 °C showed similar compositions (Table S4.4). The biplot drawn after the CAP analysis (Figure 4.4) with the over-imposed cluster dendrogram (Figure S4.3) segregates two clusters based on biochemical composition of sedimentary OM: sediments at 21°C (either before or after acclimation), vs. sediments at +4 and +8°C. An additional PERMANOVA test revealed significant differences in the

composition of OM among the two identified clusters (Table S4.5a). The SIMPER test revealed that pairs of clusters differed one each other, with chlorophyll-a, lipids, and carbohydrates best explaining differences between the two clusters (Table S4.5b).

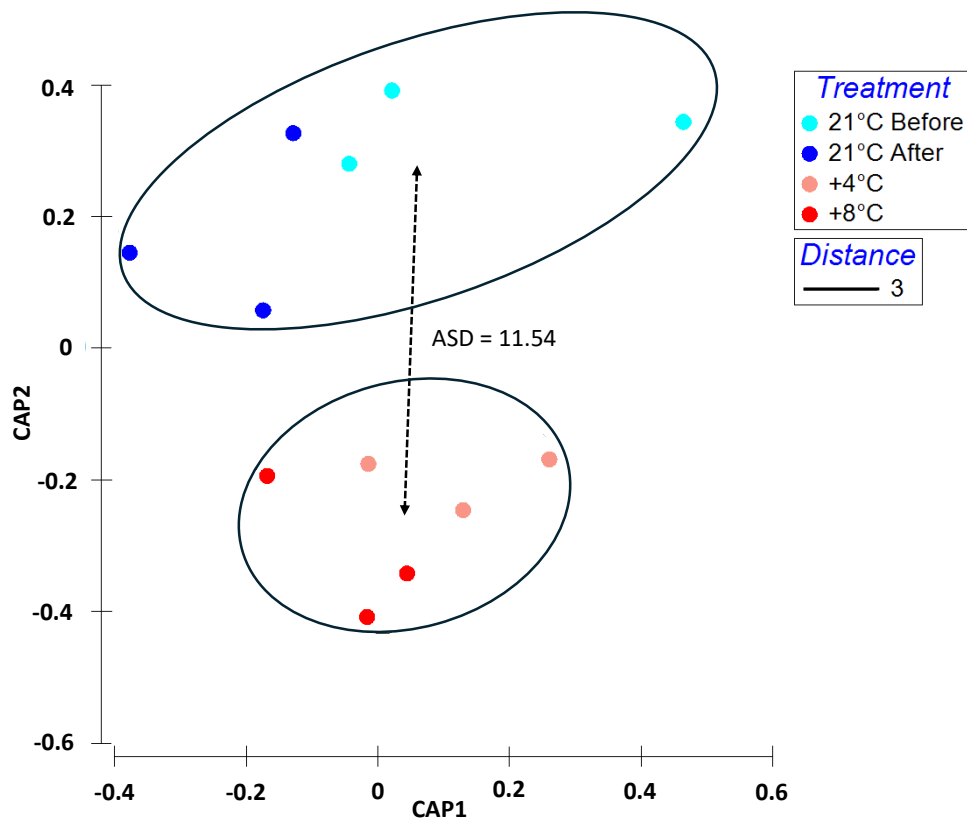


Figure 4.4. Biplot obtained after CAP illustrating OM biochemical composition-based segregation of sediments experiencing heatwaves with different temperature anomalies (+4°C and +8°C), with over imposed the values of average square distance (ASD) between pairs of the three clusters of sediments identified *a posteriori* after the cluster analysis, followed by a dedicated SIMPER test.

Aminopeptidase, β -glucosidase, and C degradation rates, along with protein and C turnover times differed significantly among treatments, whereas carbohydrate turnover time did not (Table 4.2).

Table 4.2. Results of the PERMANOVA tests addressing differences in extracellular enzymatic activities, C degradation rates and turnover time among treatments (21°C Before, 21°C After, +4°C and +8°C). Df = degrees of freedom; MS = mean square; Pseudo-F = F statistic; P(MC) = P-value obtained after Monte Carlo simulations and 999 permutations. Significant differences are in bold.

Variables	Df	MS	Pseudo-F	P(MC)
Aminopeptidase	3	3.78	59.28	0.001
β-glucosidase	3	3.48	11.23	0.005
C degradation rate	3	3.81	64.34	0.001
Protein turnover time (d)	3	2.10	4.93	0.035
Carbohydrate turnover time (d)	3	2.29	3.30	0.090
C turnover time (d)	3	3.44	12.89	0.001

More in details, the results of the pairwise tests (Table S4.6) revealed a significant effect of manipulation at 21°C (i.e., before vs. after acclimation at 21°C), characterized by a significant decrease of aminopeptidase activity and C degradation rates (by ca. 50% both), accompanied by a significant increase of the protein (by ca. 79%) and C turnover times (by >90%), and no changes in β-glucosidase and carbohydrate turnover time (Figure 4.5a-f). Considering changes occurred due to different treatments (when compared to values measured at 21°C), the tests revealed a significantly positive effect of warming on aminopeptidase activity (by ca. 34%) and C degradation rates (by ca. 30%) and a significantly negative effect on β-glucosidase (by ca. 43%), only at +4°C (Figure 4.5a-c). At +8 °C, activities of the extracellular enzymes and the estimated rates of C degradation did not differ significantly from those at 21°C after acclimation.

Protein and carbohydrate turnover times did not vary in response to warming (i.e., when compared to values at 21°C after acclimation), whereas C turnover times at +4°C and +8°C were significantly lower than those at 21°C after acclimation (Figure 4.5f).

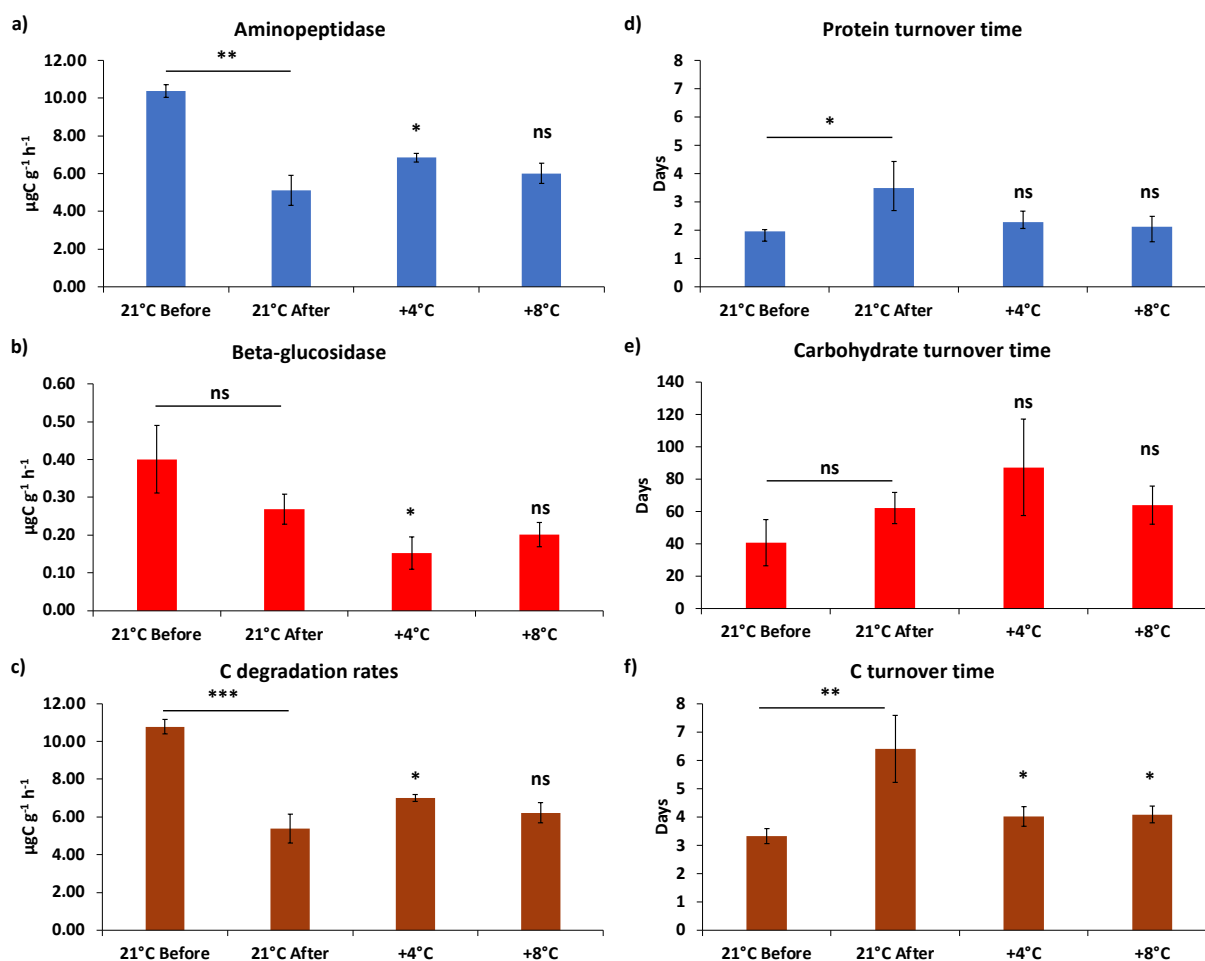


Figure 4.5. Aminopeptidase (a) and β -glucosidase (b) activities, C degradation rates (c), protein (d), carbohydrate (e) and biopolymeric C (f) turnover time in sediments experiencing heatwaves with different temperature anomalies (+4° and +8°). Error bars are standard deviation ($n = 3$). Asterisks indicate the p-values of pairwise tests between values at 21°C after the experiment and all other temperatures, as reported in Table S4: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$; ns = not significant.

4.4. Discussion

Overall, the results of our study show that MHWs of different magnitude (+4 and +8 °C) led to significant effects on both the quantity, biochemical composition and nutritional quality of sedimentary organic matter. More specifically, we found that sedimentary contents of carbohydrates, chlorophyll-a, phaeopigments and total phytopygments and biopolymeric C decreased significantly under the influence of thermal anomalies already at +4°C and even accentuated at the highest thermal anomaly (+8°C).

The observed overall decrease in biopolymeric carbon sedimentary contents could be due to a combination of interacting (possibly synergistic) factors: i) selective decay of labile molecules exposed to warmer conditions, ii) increased consumption of organic substrates due to the increase

of heterotrophic consumption stimulated by warmer temperature, iii) increased degradation due to the stimulation of extracellular enzymatic activities. As far as the labile fraction of biopolymeric C is concerned, we notice that MHWs determined a clear decrease in phytopigment contents. This result is consistent with the results of a manipulative experiment carried out in a coastal marine embayment, during which the long-term (3-11 weeks) exposure of sediments to warmer waters (+5° C) produced by discharge waters coming from a power plant caused a decrease in phytopigment contents (>60%) and of the algal fraction of biopolymeric C (>50%) (Soru et al., 2022). Since phytopigments represent the most labile and fresh component of sedimentary organic C in aquatic sediments (Dell'Anno et al., 2002; Pusceddu et al., 2003; Pusceddu et al., 2010) their contribution to biopolymeric C is proportional to the bio-digestible (labile) fraction of biopolymeric C (Pusceddu et al., 2009). Therefore, the results of our experiments, carried out using an oligotrophic sediment (BPC<1.0; Algal fraction >45%, sensu Pusceddu et al., 2009), indicate that also short-term (5 days) thermal anomalies simulating MHWs can provoke not only a drop in the overall amount of food available for benthic consumers, but also an impoverishment of sedimentary nutritional quality. As also previously hypothesized, the negative response of phytopigments to the occurrence of MHWs could be attributed to a decrease of microphytobenthos production, possibly due to a severe cellular stress and mortality induced by an increased temperature (Soru et al., 2022; Courboulès et al., 2022). Our results, however, are in contrast with those provided by Sarà et al. (2021) who, investigating the combined effects of heatwaves and hypoxia in the sediments of a coastal pond, observed an increase in chlorophyll-a concentrations. Nonetheless, while in our experiment oxygen availability in the benthocosm was artificially maintained, Sarà et al. (2021) included hypoxia as a main factor controlling the trophic conditions of the pond and, indeed, attributed the increase in chlorophyll-a concentrations (and therefore in the overall food availability for the benthos) to the mass mortality of consumers, more than to the heatwave itself. The discrepancy between our results and those obtained in a shallow pond Sarà et al. (2021) are therefore the result of a different experimental architecture. Nonetheless, we cannot exclude that during our experiment changes in oxygen concentration in the sediment could have occurred, even if oxygen levels in the water did not vary (see also below).

The decrease in the food availability of sedimentary organic matter following the MHWs simulated in benthocosm (in terms of decreased phytopigment contents and algal contribution to biopolymeric C) is, however, partly counterbalanced by an increase in the protein to phytopigment ratio. Proteins, in fact, are rich in N which is the most limiting factor for heterotrophic nutrition and,

therefore, are considered a highly bioavailable component of sedimentary organic matter (Dell'Anno et al., 2002; Pusceddu et al., 2009; Ennas et al., 2023). The increased protein to phytopigment ratio suggests, thus, that the reduction of the autotrophic component (phytopigment) occurred in favor of the heterotrophic (nitrogen-rich) one. Such a result suggests that, even at the lowest temperature anomaly (+4° C), the decay of organic loads, irrespectively of their differential lability, could have been caused by an increase in the heterotrophic nutrition, ultimately leading to a consumption-mediated decrease of microphytobenthic biomass and an increase in the heterotrophic bacteria-dominated one. Overall, the results of our experiment, combined with the other few available, on this topic pinpoint that sea warming and, more specifically, MHWs can impair not only the epibenthic flora (e.g., Stipcich et al., 2022a-b; Stipcich et al., 2023) and fauna (Garrabou et al., 2022) but they could also severely affect endobenthic organisms, either directly (by effects mediated by water warming) or indirectly (by effects mediated by changes in the nutritional quality of the sedimentary organic loads caused by the thermal anomalies). However, since we did not measure any proxy of benthic biomass, we can consider this as a mere hypothesis needing further confirmation. Nonetheless, whatever the mechanism behind such sort of nutritional 'oligotrophication' of lagoon sediments caused by MHWs, the results of our experiment suggest that MHWs could severely (and indirectly) influence the ecological performance of benthic fauna by altering the nutritional quality of the available food, with possibly increasing severity of the consequences with increasing thermal anomalies.

The projected warming (up to further +3°C) of the global oceans will affect also the Mediterranean Sea, where temperatures are likely to continue to increase more than the global average (Ali et al., 2022). Moreover, the intensity, frequency and duration of (marine) heatwaves are expected to further increase as well (Benedetti Cecchi, 2021). In such a scenario, our results anticipate that the expectable decrease of lagoon sediments organic loads (especially of their labile component) caused by warmer conditions and consistent with an expected decrease of net primary productivity (Richon et al., 2019), will likely force the lagoon benthos to be facing progressively more oligotrophic conditions. As previously postulated (Soru et al., 2022), this, according to the optimal foraging theory (Stephens and Krebs, 1986), could progressively favor highly thermal-tolerant species with a preference for nutritionally poor but abundant food over limitedly thermal tolerant species with a preference for nutritionally rich but quantitatively limited food sources.

Sedimentary organic matter quantity, biochemical composition, and nutritional quality, and the food accessibility for benthic consumers, are contingent upon the rates at which complex

organic molecules undergo microbial-mediated processes that enhance their susceptibility to consumers' assimilation (Benner and Amon, 2015). In this context, the degradation of sedimentary organic matter, which, especially in coastal wetlands and lagoons, is generally dominated by large and relatively refractory polymeric molecules (Pusceddu et al., 1999; Pusceddu et al., 2003; Pusceddu et al., 2007), must undergo extracellular enzymatic hydrolysis to become nutritionally available for higher trophic levels (Manini et al., 2003). Since the efficiency in transferring energy towards higher trophic levels is deeply constrained by the relative susceptibility of organic matter to heterotrophic consumption (Pusceddu and Danovaro, 2009), carbon degradation rates mediated by extracellular enzymatic activities have often been used as a proxy for benthic ecosystem functioning (Pusceddu et al., 2014; Franzo et al., 2019; Palmas et al., 2019; Soru et al., 2022).

In this study, we report that thermal anomalies (up to +8°C) induced by simulated heatwaves can influence also extracellular enzymatic activities. The initial acclimation process at 21°C (before the exposure to the different temperature anomalies) caused a significantly negative shift of both protease and glucosidase activities, possibly because of processes acting at the microscale. Moreover, significant changes in both activities with respect to reference conditions at 21°C after acclimation) were observed only at +4°C, with protein and carbohydrate degradation rates being stimulated and inhibited, respectively. The different response of protease and glucosidase activities at 25°C is difficult to explain and/or interpret, unless we hypothesize that 25°C is a sort of threshold favoring the shift of bacterial communities with different affinity for protein-rich and carbohydrate-rich substrates. As explained above for the warming-caused changes in organic matter biochemical composition, as we did not consider in our study the characteristics of the heterotrophic microbial community, despite the warming at 25°C resulted cumulatively in a threshold stimulation of C degradation, we must acknowledge that such hypothesis remains unexplored and that other explicative factors could be invoked. Whatever the reason behind the inverse response of protease and glucosidase activity to a moderate heatwave (+4°C), the ultimate result of warming consists overall in an acceleration of organic C degradation, witnessed by the increased turnover of organic C that persisted also under the heatwave characterized by a +8°C temperature anomaly. Such a result is consistent with observations carried out under natural seasonal warming conditions in which higher remineralization rates can be observed in summer (Brin et al., 2015; Middelburg et al., 1996; Tabuchi et al., 2010; Xue et al., 2015) but are opposite to what observed in the field in coastal marine sediments under a simulated marine heatwave (Soru et al., 2022). Again, such an apparent idiosyncratic response of C degradation rates to different warming and heatwaves is difficult to

explain. Also in this case, however, the different approaches of the two studies, of which one (our) carried out on lagoon sediments in benthocosm and the other one (Soru et al., 2022) carried out in the field on marine coastal sediments, can be invoked as a potential confounding factor.

4.5. Weaknesses and strengths of our study

The temperature anomalies simulated in our experiment differed to a certain extent from those typically experienced in the field under natural summer conditions. Therefore, we pinpoint that our findings should be interpreted with caution and cannot be generalized beyond the conclusion that heatwaves may affect lagoons sediment biogeochemistry and benthic ecosystem functioning.

Our experimental set-up did not explicitly account for the impact of water warming on sediment temperatures, which could, in turn, influence benthic responses. In this regard, recent findings by Tassone and Pace (2024) provide a valuable reference highlighting that sediment heatwaves (SHWs) frequently propagate from marine heatwaves (MHWs) in shallow water systems. Their study showed that sediment temperatures in the upper 5 cm often rise in phase with water temperatures (Figure 7 in Tassone and Pace, 2024), with SHWs co-occurring with MHWs 79–81% of the time. Although that study was conducted in an environmental setting (marine seagrass sediments at 5 cm depth) totally different from the one (lagoon sandy sediments and 2.5 cm thick sediment layer) used in our experiment, the findings by Tassone and Pace (2024) allow us to consider the MHWs generated in our experiment to have similarly affected the sediments as well (as also confirmed by the additional data provided in Figure S4.1).

Another possible bias affecting the comparability of our results with the real world consists in the light intensity to which the sediments were exposed during the experiments. Although at the time of sampling we did not measure light intensity that was reaching the sediments in the field (plausibly attenuated because of not fully transparent waters), our experiment was carried out indoor, so that a certain (though unmeasured) light attenuation occurred anyway. Beside this, however, we recall here that all experimental sediments were exposed to the same light conditions, so that changes we observed in our experiment could be conceivably associated with the sole effect of warming. This, however, does not allow us to generalize our results in absolute quantitative terms, especially for the responses of primary production related variables (phytopigments and algal fraction of biopolymeric C).

Although we did not measure oxygen levels within the sediment, the relatively short lasting of the experiment, the sediment sandy texture, the pre-mixing and sieving of the sediments used to

prepare the mesocosms plausibly minimized the risk of the establishment of hypoxic or anoxic conditions in the benthocosms. We acknowledge that the maintenance of water oxygenation during the entire experiment represented another forced condition possibility affecting or, at least, limiting the extent of our results to the real world. Indeed, coastal shallow lagoons can experience, especially during summer, diffused deoxygenation of the top layers of the sediment, which can have complex effects on organic matter diagenesis (Middelburg and Levin, 2009), possibly interacting with the effects of warming per se. In this regard, we recall here that a previous study carried out in a shallow pond in the Mediterranean Sea (Sarà et al., 2021), in which warming, and deoxygenation co-occurred, revealed patterns in sedimentary chlorophyll-a and biopolymeric C contents opposite to the ones we observed in our experiment, in which we tested the sole effect of MHWs. Nonetheless, as discussed above for the light conditions, since the experiment included either control or heated sediments exposed to the same experimental conditions, our results, if not quantitatively, provide sufficiently robust evidence that MHWs alone can alter biogeochemistry of lagoon sediments.

Therefore, we pinpoint the need of future experiments that should consider sediment heat dynamics and the crossing effects of a possible deoxygenation concurrent with heatwaves, altogether possibly impacting lagoon sediment biogeochemistry in variable ways.

Future investigations should include also sediments with different sedimentological properties (i.e., sand vs. mud sediments) exposed to different degree to warming-related deoxygenation and obtained from a broader range of lagoons with varying organic matter quantities and biochemical compositions.

4.6. Conclusions

We showed that warming and, more specifically, the occurrence of heatwaves can alter the biogeochemistry of lagoon sediments, most likely leading to a general decrease of food availability for the benthos, that, in the short-term (i.e., at least during the heatwave lifespan) could be due to the concurring increase in bacterial-mediated extracellular enzymes activity, an increased organic matter consumption, and a decreased production of more labile substrates (like phytopigments). Although the results of our experiment corroborated only partially the results gathered in the field at sea (Soru et al., 2022; Sarà et al., 2021), we stress here that, besides the potential cross effects of deoxygenation, excluded in our experiment, our results could have been biased also by the lack of direct measurements of abundance, biomass and functional diversity of benthic microbes.

Coastal environments are reputed to be major sinks for organic C (Deb and Mandal, 2021). Among these, coastal lagoons are typically considered to behave like organic detritus sinks (Pusceddu et al. 2003). Therefore, since temperature affects the rates of any (bio)chemical reaction (including primary production and C cycling), the results of our experiment provided evidence that MHWs can cause a profound alteration of biogeochemistry of lagoon sediments, possibly affecting their ability to store blue Carbon and increasing their contribution to CO₂ emissions in the atmosphere.

Transitional aquatic environments in the Mediterranean region are particularly vulnerable to climate change due to their typically shallow depths, limited capacity for water stratification, and reduced ability to buffer the effects of increasing air temperatures (de Vicente, 2021; Vidussi et al., 2011). Because of these environmental vulnerabilities and since lagoons' ability to store organic carbon and, therefore, partially buffer atmospheric CO₂ increase are both lowered by MHWs, we can anticipate that further global warming and increased frequency, intensity and duration of marine heatwaves will severely impair the ability of coastal lagoons to provide these two essential ecosystem services. At the same time, we foster the need of further studies to identify changes in the relationships between microbial biodiversity, oxygen concentrations and functioning of coastal lagoon sediments as affected by global warming and MHWs, and their potential consequences of on lagoons' ability to store blue carbon.

4.7. Acknowledgements

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4.9. Supplementary material

Table S4.1. Results of PERMDISP tests for homogeneity dispersions in sedimentary organic matter quantity and biochemical composition (21°C Before, 21°C After, +4°C, and +8°C of thermal anomaly). Df=degree of freedom; Perm-Disp-F = F statistic; P(perm) = P-value obtained by permutations.

Variables	Df	PermDisp-F	P(perm)
Protein	3	0.94	0.580
Carbohydrate	3	1.77	0.422
Lipid	3	2.59	0.228
Chlorophyll-a	3	2.17	0.566
Phaeopigment	3	1.52	0.685
Total phytopigment	3	0.29	0.893
Biopolymeric C	3	0.91	0.629
Autotrophic fraction of biopolymeric C	3	0.70	0.741
Biochemical composition	3	0.58	0.745

Table S4.2. Results of PERMDISP tests for homogeneity of treatment dispersions in extracellular enzymatic activities, C degradation rates and turnover time (21°C Before, 21°C After, +4°C and +8°C of thermal anomaly). Df = degree of freedom; Perm-Disp-F = F statistic; P(perm) = P-value obtained by permutations.

Variables	Df	PermDisp-F	P(perm)
Aminopeptidase	3	1.03	0.651
β-glucosidase	3	0.84	0.736
C degradation rate	3	1.24	0.567
Protein turnover time (d)	3	2.62	0.299
Carbohydrate turnover time (d)	3	1.84	0.437
C turnover time (d)	3	5.73	0.081

Table S4.3. Results of the pair wise comparisons testing for differences among treatments in sedimentary organic matter quantity and biochemical composition (21°C Before, 21°C After, +4°C, and +8°C of thermal anomalies). t = statistic t; p(MC) = probability level after Monte Carlo simulations. Significant differences are in bold.

Variable	Contrast	t	P(MC)
Protein	21°C Before vs. 21°C After	2.30	0.083
	21°C After vs. +4°C	0.98	0.391
	21°C After vs. +8°C	2.02	0.130
Carbohydrate	21°C Before vs. 21°C After	0.60	0.577
	21°C After vs. +4°C	2.87	0.043
	21°C After vs. +8°C	2.79	0.046
Lipid	21°C Before vs. 21°C After	5.01	0.008
	21°C After vs. +4°C	0.99	0.358
	21°C After vs. +8°C	2.45	0.066
Chlorophyll-a	21°C Before vs. 21°C After	0.79	0.494
	21°C After vs. +4°C	3.27	0.034
	21°C After vs. +8°C	4.95	0.013
Phaeopigment	21°C Before vs. 21°C After	0.95	0.393
	21°C After vs. +4°C	4.88	0.012
	21°C After vs. +8°C	0.58	0.601
Total phytopigment	21°C Before vs. 21°C After	0.02	0.988
	21°C After vs. +4°C	4.67	0.012
	21°C After vs. +8°C	5.54	0.005
Algal fraction of biopolymeric C	21°C Before vs. 21°C After	1.57	0.211
	21°C After vs. +4°C	3.44	0.039
	21°C After vs. +8°C	1.02	0.033
Biopolymeric C	21°C Before vs. 21°C After	0.57	0.599
	21°C After vs. +4°C	2.73	0.049
	21°C After vs. +8°C	0.30	0.049
OM biochemical composition	21°C Before vs. 21°C After	1.46	0.171
	21°C After vs. +4°C	2.32	0.019
	21°C After vs. +8°C	2.56	0.023

Table S4.4. Results of the comparisons of sedimentary biochemical composition between pairs of treatment. P(MC) = P-value obtained after Monte Carlo simulations and 999 permutations. Significant differences are in bold.

Contrast	t	P(MC)
21°C Before vs 21°C After	1.4596	0.171
21°C Before vs +4°C	2.2309	0.024
21°C Before vs +8°C	2.7031	0.015
21°C After vs +4°C	2.3189	0.019
21°C After vs +8°C	2.5615	0.023
+4°C vs +8°C	1.1689	0.314

Table S4.5. Results the SIMPER test identifying the average squared distance (ASD) among clusters (**Figure S2**) and the percentage of significant differences among clusters explained by the different organic molecules (a) and the PERMANOVA test showing significant differences between the two clusters (b). Df = degrees of freedom; MS = mean square; Pseudo-F = F statistic; P(permutation) = P-value obtained by permutations; P(MC) = P-value obtained after Monte Carlo simulations and 999 permutations. Significant differences are in bold.

(a) SIMPER

Contrast	ASD	Variable	Contribution %	Cumulative %
21°C vs. +4-8°C	11.54	Chlorophyll-a	30.0	30.0
		Protein	27.7	57.8
		Carbohydrate	22.6	80.3
		Phaeopigment	11.2	91.5

(b) PERMANOVA

Source	Df	MS	Pseudo-F	P(MC)
Groups	1	22.335	9.094	0.002
Residual	10	2.456		

Table S4.6. Results of the pair wise comparisons testing for differences in extracellular enzymatic activities, C degradation rates and turnover time among treatments (21°C Before, 21°C After, +4°C and +8°C of thermal anomalies). t = statistic t; p(MC) = probability level after Monte Carlo simulations. Significant differences are in bold.

Variables	Contrast	t	P(MC)
Aminopeptidase	21°C Before vs. 21°C After	10.63	0.003
	21°C After vs. +4°C	3.65	0.023
	21°C After vs. +8°C	1.63	0.181
β-glucosidase	21°C Before vs. 21°C After	2.33	0.089
	21°C After vs. +4°C	3.45	0.023
	21°C After vs. +8°C	2.31	0.078
C degradation rate	21°C Before vs. 21°C After	10.81	0.001
	21°C After vs. +4°C	3.56	0.026
	21°C After vs. +8°C	1.53	0.200
Potential protein turnover time (d)	21°C Before vs. 21°C After	2.80	0.055
	21°C After vs. +4°C	2.03	0.113
	21°C After vs. +8°C	2.33	0.078
Potential carbohydrate turnover time (d)	21°C Before vs. 21°C After	2.16	0.094
	21°C After vs. +4°C	1.39	0.234
	21°C After vs. +8°C	0.21	0.848
C turnover time (d)	21°C Before vs. 21°C After	4.40	0.010
	21°C After vs. +4°C	3.36	0.039
	21°C After vs. +8°C	3.29	0.027

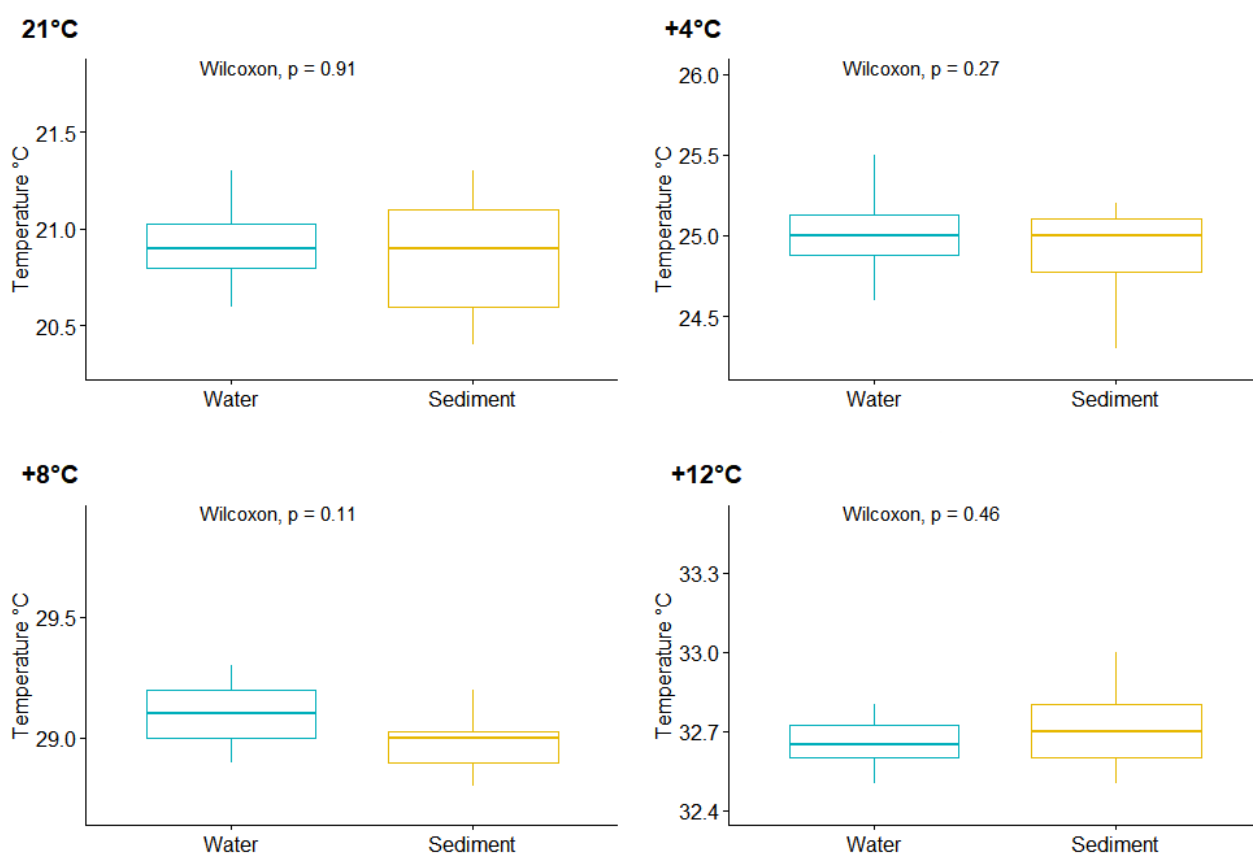


Figure S4.1. Box and whisker plots illustrating the temperature variation across treatments in water bath and sediment in the benthocosms, recorded twice a day over 5 days. The lower side of the box indicates the 25th percentile, the horizontal line is the median, and the upper size is the 75th percentile. The whiskers show the range of temperatures. Results of the statistical comparisons (Wilcoxon-Mann-Whitney tests) between water and sediment are displayed above each boxplot.

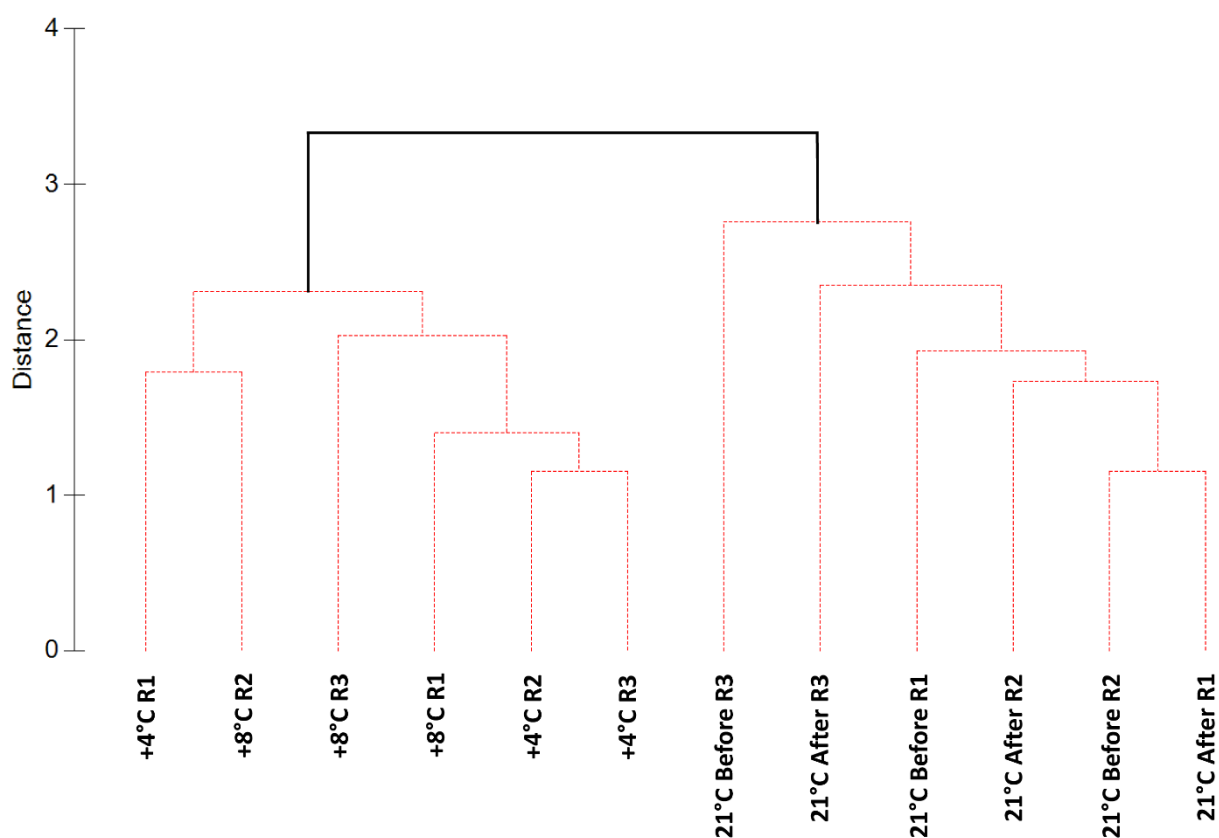


Figure S4.2. Dendrogram obtained from the hierarchical cluster analysis based on Euclidean distances among sediments with different biochemical composition at the different experimental temperatures. hierarchical agglomerative cluster analysis with group-average distances. Solid horizontal black lines indicate significant differences among groups based on SIMPROF permutation tests, while horizontal dashed red lines indicate non-significant differences.

Chapter 5: Impacts of simulated Marine Heat Waves on the benthic metabolism of coastal lagoons: a Baltic and a Mediterranean study cases

5.1 Introduction

Marine heatwaves (MHWs) are defined as periods of five or more days during which sea surface temperature (SSTs) is warmer than the 90th percentile for the location and period of the year, based on a 30-year fixed historical climatological baseline (Hobday et al., 2016). These events occur globally and are projected to intensify in frequency, duration, and severity with increasing global warming (Oliver et al., 2018; Darmaraki et al., 2019; IPCC, 2023). Semi-enclosed basins like the Baltic (Meier et al., 2021; Dabulevičienė & Servaite, 2024) and the Mediterranean Seas (Pastor & Khodayar, 2023; Darmaraki et al., 2024) are particularly vulnerable due to their morphological characteristics, including low water turnover and relatively shallow depths. These features make them prone to the consequences of more frequent and intense MHWs. These seas, thus, can serve as ideal natural laboratories for the full scope of investigating MHW resulting impacts (Lejeusne et al., 2010; Reusch et al., 2018). The coastal ecosystems, including coastal lagoons, will face even greater challenges due to their semi-enclosed nature and shallow waters, often experiencing more severe manifestations of MHWs (Cook et al., 2022).

Coastal lagoons, which are shallow water bodies, show heightened sensitivity to environmental changes (de Vicente, 2021; Ferrarin et al., 2024). These delicate ecosystems serve as “sentinels” for monitoring the impacts of climate change (Eisenreich, 2005; Perez-Ruzafa et al., 2011; Brito et al., 2012; Newton et al., 2018). MHWs in coastal lagoons have been extensively documented through observations and simulations, revealing impacts across multiple ecological levels, including failed recruitment and mass mortality of commercial bivalves like oysters, mussels and clams (Pernet et al., 2010; Ponti et al., 2017; Bertolini and Paster, 2021; Correia-Martins et al., 2022; Bertolini et al., 2023). Studies have also observed changes in benthic macroalgal communities, which may lead to reduced habitat complexity and affect ecosystem stability (Derolez et al., 2020; Bilajac et al., 2024).

While the benthic compartment plays a fundamental role in coastal lagoons functioning and serves as a reliable indicator of environmental changes (Bruto et al., 2009; Pusceddu et al., 2009; Kennish & Paerl, 2010; Arévalo et al., 2013), the effects of MHWs on the sedimentary biogeochemistry of coastal lagoons remain understudied yet (Lopes et al., 2021). In particular, the

sedimentary organic matter pools and their turnover warrant further investigation, given their potential as sources of regenerated nutrients for the overlying waters (Bukaveckas et al., 2023; Pusceddu et al., 2003).

MHWs may impact biogeochemical processes through multiple mechanisms. As temperature rises, bottom-dwelling organisms increase their sediment-mixing activities, enhancing bioturbation that allows deeper oxygen penetration into the seafloor and, thus, accelerating organic matter decomposition (Kauppi et al., 2023). Prolonged MHWs can also alter the benthic food-web, affecting organic matter quantity, composition, and nutritional quality (Soru et al., 2022; Göbeler et al., 2025). The increased microbial activity, stimulated by higher temperatures, enhances degradation of organic matter and the subsequent nutrient release into the bottom water, which, by cascade, affects positively phytoplankton biomass, metabolism, composition and growth (Pulina et al., 2020; Souliè et al., 2022; Wang et al., 2023; Souliè et al., 2023; Göbeler et al., 2025). These cascading effects can ultimately trigger eutrophication and disrupt the lagoon carbon balance and greenhouse gases dynamics (Newton, et al., 2018; Seidel et al., 2021; Burkholz, et al., 2020; Bonaglia et al., 2025).

Moreover, recent studies, demonstrated decreased organic carbon quantity and nutritional quality of sedimentary organic matter following MHWs simulated in mesocosm (Palmas et al., 2025). Such an “oligotrophication” effect may impair food resources for the benthos, negatively feedbacking species vulnerability to thermal anomalies (Correia-Martins et al., 2022; Palmas et al., 2025). At the same time, elevated summer temperatures may induce a shift from eutrophic to oligotrophic conditions at the basin scale, potentially enhancing resilience to anoxic crises (Derolez et al., 2020).

Assessing the vulnerability to climate change of coastal lagoons ecosystem functioning and the potential trade-offs between ecosystem changes and societal needs are essential to guide the development of effective mitigation and adaptation strategies to protect them from climate change associated risks (Parete et al., 2024).

Among the possible useful indicators for describing benthic biogeochemical processes, quantity and biochemical composition of organic matter allow defining the trophic status and the environmental quality of the coastal lagoon ecosystems (Dell’Anno et al., 2002; Pusceddu and Danovaro, 2009; Pusceddu et al., 2011; Pusceddu et al., 2009; Arevalo et al., 2013). In particular, biopolymeric C (BPC), expressed as the sum of protein, carbohydrate and lipid contents converted in C equivalents (Fabriano et al., 1995), is a reliable proxy of the overall food quantity (Pusceddu et

al., 2009), while phytopigments, as the sum of chlorophyll-a and phaeopigments, are a proxy of either the organic matter produced by the photosynthesis (Dell'Anno et al., 2002) or, being the most enzymatically digestible fraction of organic matter, its food quality (Pusceddu et al., 2003).

The protein to BPC, the protein to carbohydrate ratio, and the contribution of phytopigments to biopolymeric C (i.e., autotrophic fraction of BPC; Pusceddu et al., 2010) are then proxies of the nutritional value of sedimentary organic matter (Pusceddu et al., 2003; Pusceddu et al., 2009), as proteins are N-richer compounds are degraded faster than carbohydrates and phytopigments are the most labile component of organic matter (Pusceddu et al., 2000; Dell'Anno et al., 2002; Pusceddu et al., 2003; 2009; 2011). The biopolymeric C content of the sediment and the algal fraction of sediment organic matter are inversely related and can be used to rank the benthic trophic state: high values of the former and lower of the latter are typically associated to eutrophic environments, while the opposite applies to the oligotrophic ones (Pusceddu et al., 2009; Pusceddu et al., 2011).

Moreover, the potential carbon degradation rates (mediated by extracellular enzymatic activities) and turnover time, as well as sediment-water fluxes of nutrients (NH_4) and gases (O_2) are valuable bio-indicators of ecosystem functioning, as altogether provide insights on organic matter decomposition and remineralization, and on total benthic respiration, respectively (Pusceddu et al., 2009; Renzi et al., 2019).

In this study, I assessed the impacts of marine heatwaves on an array of proxies of organic matter quantity, nutritional quality and degradation rate along with nutrient fluxes and benthic respiration in the sediments of two coastal lagoons facing two semi-enclosed seas, the Baltic and the Mediterranean seas, namely the Curonian Lagoon (Lithuania) and the Santa Gilla lagoon (Italy) and treated them as separate study cases.

To do this, manipulative experiments were carried out in the laboratory with intact sediments cores exposed to simulated 5-days lasting marine heatwaves of different intensity (+2 °C vs. +6 °C anomaly compared to in situ water temperature), chosen as representative of future climatic scenarios and recurrently tested in other experimental studies (Jakimavičius et al., 2018; Ferrarin et al., 2024). Considering the differences in organic matter loads among sediments with different textures (Martinez-Garcia et al., 2015; Bonaglia et al., 2025), experiments were carried out on muddy vs. sandy sediments from both lagoons.

The starting null hypothesis beyond is that the quantity and biochemical composition of sedimentary organic matter, organic C degradation rate and turnover, nutrient and gas fluxes do not vary after marine heatwaves of varying temperature anomalies in sediments with different grain size.

5.2 Materials and Methods

5.2.1 Study areas

To test the hypothesis, we selected two lagoons (Curonian and Santa Gilla) located at different latitude and under distinct climatic conditions.

The Curonian Lagoon (SE Baltic Sea; Figure 5.1) is a typically boreal coastal water body with distinctive characteristics. The lagoon, with an area of 1584 km², is shallow (average depth ~4 m) and is connected to the sea through a narrow strait (Zilius et al., 2012). The lagoon experiences significant seasonal temperature variations, with water temperatures ranging from 1°C (in winter) and 25–29°C (in summer) (Bartoli et al., 2021). The lagoon is mostly freshwater (0.1–2.5 PSU) due to strong riverine inflow from the Nemunas River. However, periodic seawater intrusions from the Baltic Sea can temporarily increase salinity up to 8 PSU in the northern area, typically during late summer and early fall months (Pilkaitytė & Razinkovas, 2007; Jurgelenaite & Sarauskiene, 2007). The lagoon is ranked as hypertrophic, experiencing frequent blooms of diatoms and cyanobacteria (Zilius et al. 2021), which result in the accumulation of organic-rich sediments.

The Santa Gilla Lagoon (W Mediterranean Sea; Figure 5.1) is a shallow system (average depth 1 m), located in SE Sardinia, with an area of 13 km², with annual water temperatures ranging from 11°C to 29°C (Cabiddu et al., 2014). Salinity ranges from 15 to 34 PSU, strongly depending on water exchanges with the sea, through a large southern channel and regulated freshwater inputs from the Flumini Mannu and Cixerri rivers in the north (Cabiddu et al., 2014). Due to the high nutrient loads caused by industrial, agricultural, and domestic effluents, the Santa Gilla has been ranked as eutrophicated (Frontalini et al., 2009).

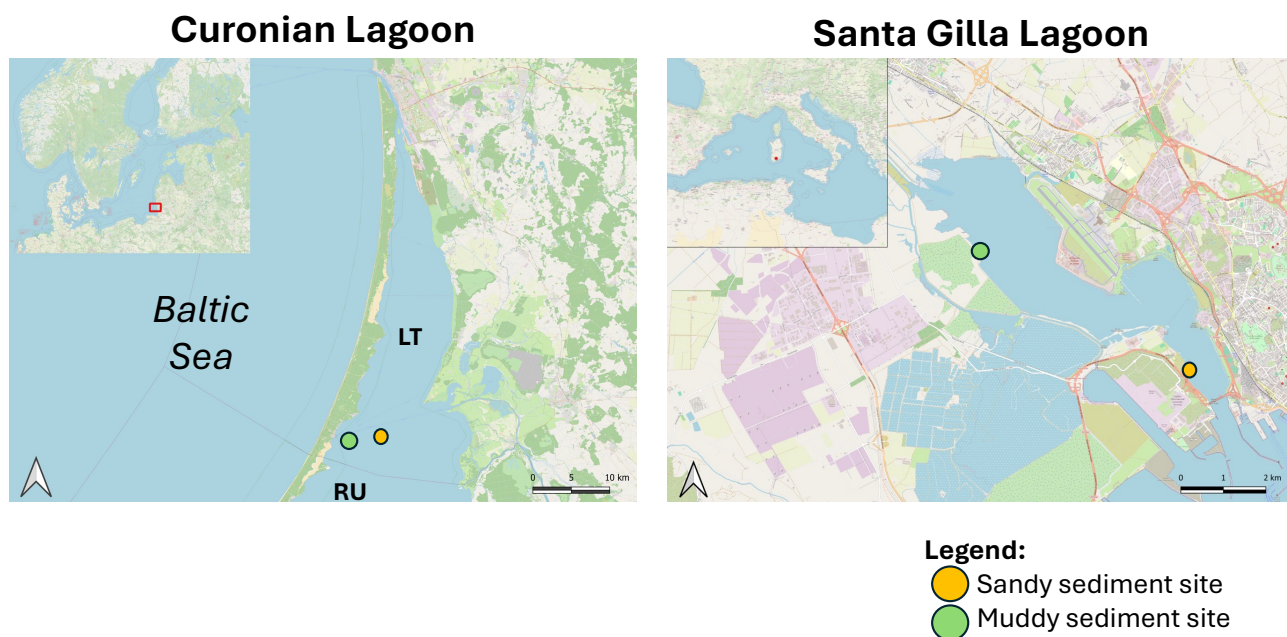


Figure 5.1 Study and sampling areas for Baltic (Curonian lagoon) and Mediterranean (Santa Gilla) lagoons

5.2.2 Sediment sampling

Sediments for the experiments were collected during summer in both the Curonian (July) and Santa Gilla (August) lagoon. In each lagoon, two sites were selected to represent different sediment texture and organic matter loading (muddy vs. sandy; Bartoli et al., 2021). At each site of both lagoons, 12 sediment cores (8 cm diameter, 30 cm length) were collected manually and transported to the laboratory, maintaining the in-situ temperature (22°C for Curonian Lagoon and 25°C for Santa Gilla Lagoon). Additionally, 200 L of lagoon water were collected from each site to maintain experimental activities.

5.2.3 Experimental setup and incubations

Following the same procedure of previous experiments (Palmas et al., 2025), two marine heat waves of different intensities were simulated in mesocosms using temperature regulation systems at the Ecology Lab of the Marine Research Institute, Klaipeda University, and at the Gilla Lab, Department of Life and Environmental Sciences, University of Cagliari.

All cores were acclimatized in tanks (n=3) for 1 day at their respective in-situ temperature (22°C for the Curonian Lagoon and 25°C for Santa Gilla Lagoon) (Figure 5.2). Each tank was equipped with a central magnetic stirrer and air pumps with tubes and porous stones to maintain oxygen levels in the water. Each core was measured for water column height (from the top of the core to the sediment level). Water circulation within each core was ensured with a dedicated stirrer.

After acclimatization, a subset of 6 cores (3 per sediment type: muddy and sandy) was sampled to determine quantity and composition of sedimentary organic matter (procedural control, P-CTRL). The remaining 18 cores were distributed among three tanks, with 3 cores of each sediment type in each tank (n=6 per tank) (Figure 5.2).

In two tanks, temperature was gradually increased through a heating system to simulate the two marine heat waves (+2°C and +6°C), reaching target temperatures in 1.5 (+2°C) and 4 (+6°C) days, corresponding to 24 and 28°C for the Curonian Lagoon sediments, respectively, and 27 and 31°C for the Santa Gilla Lagoon sediments, respectively. Once the target temperatures were reached, cores were exposed to the heat waves for 5 days (minimum duration for marine heat waves; Hobday et al., 2016) (Figure 5.2). The third tank was maintained at the original sampling temperature throughout the experiment (CTRL).

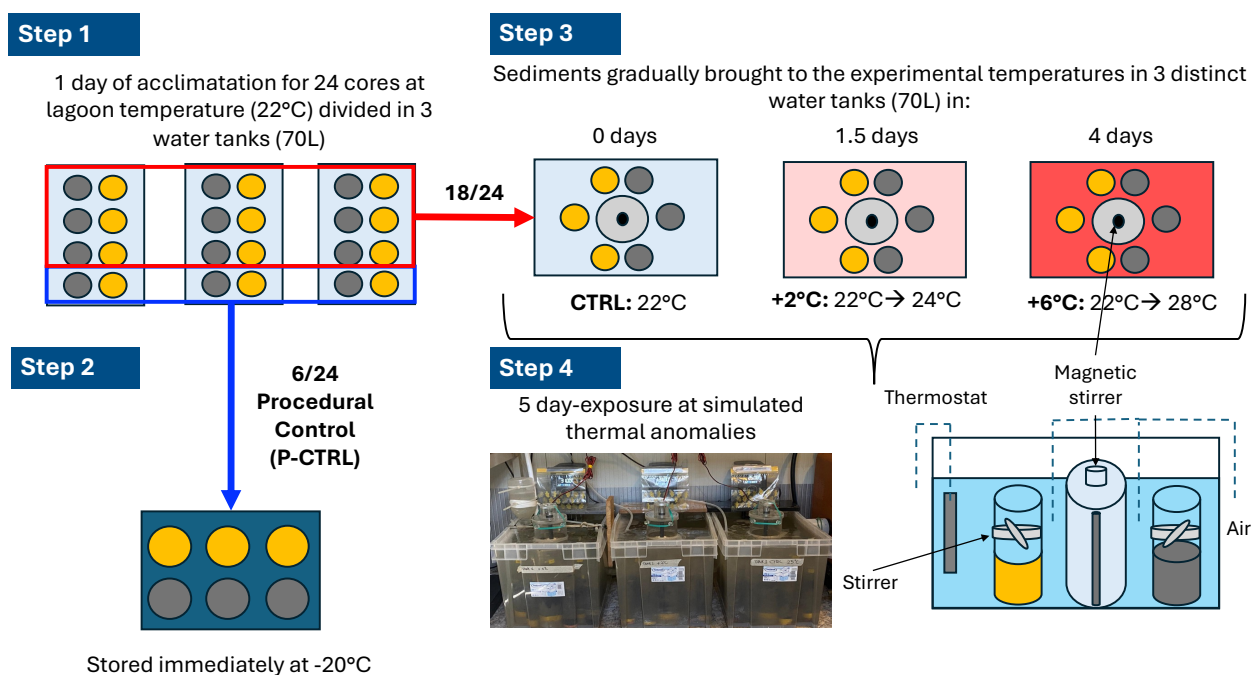


Figure 5.2 Experimental set up of the experiments on Baltic and Mediterranean lagoons.

During the experiment, fluxes of O₂ (both lagoons) and NH₄⁺ (only Curonian lagoon) were measured daily, following standard protocols for incubation (Dalsgaard et al., 2000). Before incubation (t₀), dissolved O₂ was measured using an optical sensor in all cores; water samples for ammonium (NH₄⁺) analysis were collected through 50 mL plastic syringes, filtered using What-man GF/F filters to fill 15 mL falcon tubes. Incubations started after sealing the cores with gas-tight rubber lids and incubation time was set to maintain O₂ concentration at the end within 20–30 % of the initial levels; time of incubation varied, depending on the initial temperature (and the lagoon),

from 4 h (CTRL treatment, Curonian lagoon) to 1 h (+6°C, Santa Gilla lagoon). The same sampling procedures were repeated at the end (tf) of the incubation and samples for NH₄⁺ analysis stored at -20°C. At the end of the experiment, the top 2 cm of each sediment was sliced and stored in Petri dishes or Ziploc bags at -20°C until the analyses. Dissolved ammonium (NH₄⁺) was analyzed following well described protocols in Dalsgaard et al. (2000).

Oxygen (O₂) and ammonium (NH₄⁺) fluxes were calculated as follows:

$$Flux(x) = \frac{(C_f - C_i) \times V}{A \times t} \times 10000$$

where:

Flux(x) = flux of the specific solute (x) targeted, expressed in $\mu\text{mol m}^{-2} \text{h}^{-1}$

C_f and C_i ($\mu\text{mol l}^{-1}$) = final and initial concentrations of the solute x, respectively

V = water column volume (L), measured before the incubations

A = sediment surface in the core (cm²)

t = incubation time (h).

Negative fluxes indicate fluxes from the water column to the sediment, while positive ones from the sediments to the water column.

5.2.4 Quantity, quality and degradation rates of sedimentary organic matter

Quantity, biochemical composition, and degradation rate of sedimentary organic matter was determined following the protocols detailed in Danovaro (2010).

Protein, carbohydrate, and lipid concentrations were determined spectrophotometrically (Danovaro, 2010). Total protein concentrations were measured following the protocol in Lowry et al. (1951), as modified by Hartree (1972) and Rice (1982), based on the reaction of proteins with cupric tartrate and the Folin–Ciocalteu reagent in an alkaline environment. Total carbohydrate concentrations were determined according to Dubois et al. (1956), optimized for sediments with minor modifications by Gerchacov and Hatcher (1972). Total lipid concentrations were determined according to Bligh and Dyer (1959) and Marsh and Weinstein (1966), slightly modified for sediment analysis. In this method, lipids are extracted in chloroform: methanol (1:1), evaporated in a dry hot bath at 100 °C, and carbonized with sulfuric acid. Protein, carbohydrate, and lipid concentrations were converted into carbon equivalents using conversion factors of 0.49, 0.40, and 0.75 mg C mg⁻¹, derived from the carbon content of the standard solutions of bovine serum albumin (BSA), D (+) glucose, and tripalmitin, respectively and their sum was expressed as biopolymeric carbon (BPC) (Fabiano et al., 1995; Pusceddu et al., 2000).

Chlorophyll-a and phaeopigments were extracted from sediment after staying overnight at 4 °C in the dark with 5 mL of 90 % acetone. Extracts were analyzed at 430 nm excitation and 665 nm emission wavelengths to estimate chlorophyll-a (Chla), and, after acidification with 200 µL 0.1N HCl, phaeopigment concentrations. Total phytopigment (sum of chlorophyll-a and phaeopigment) were converted into C equivalents using a 40 mgC mg⁻¹ as a conversion factor and used to estimate the fraction of organic material of autotrophic origin (Pusceddu et al., 2010).

Potential carbon degradation rates were estimated from aminopeptidase and β-glucosidase activities, determined by the cleavage of fluorogenic substrates (L-leucine-4-methylcoumarinyl-7-amide and 4-methylumbelliferone-D-glucopyranoside, respectively) at saturating concentrations (Bianchelli et al., 2020). Prefiltered (0.2 µm) and autoclaved seawater containing the specific substrate up to the final volume of 5 mL were added to 2.5 mL aliquots of the sediment (Danovaro, 2010). The sample incubations were performed in the dark at the in-situ temperature for 1 h, centrifuged (3000 rpm, 5 min) and supernatants were analyzed fluorometrically (at 380 nm excitation and 440 nm emission for aminopeptidase and at 365 nm excitation and 455 nm emission for β-glucosidase) (Bianchelli et al., 2020). Then, data were normalized to sediment dry weight (60 °C, 24 h) and reported as nanomoles of substrate released per g of sediment dry weight h⁻¹. Once protease and glucosidase activities were converted into C equivalents using 72 as a conversion factor (Pusceddu et al., 2000), their sum was reported as the potential C degradation rate (µgC g⁻¹ h⁻¹). The turnovers (per day) of the whole protein and carbohydrate pools were calculated as the ratios of the hourly C degradation rates (multiplied by 24) and the whole protein and carbohydrate C contents in the sediment (Pusceddu et al., 2014).

5.2.5 Statistical analyses

The results of the experiments carried out on sediments of the two lagoons were investigated separately. Moreover, separate analytical pathways were carried out for fluxes and organic matter characteristics.

To test the null hypothesis that oxygen and ammonium fluxes do not vary during marine heatwaves characterized by different temperature anomalies (+2°C vs +6°C) and in sediments with different texture (muddy vs sandy), an analysis of variance (ANOVA) was used to examine differences between 3 factors: sediment (2 levels), treatment (3 levels) and day of the experiment (5 levels). Before the statistical test, conditions of data normality through Shapiro-Wilk test, and homogeneity of variance evaluated using Levene's test were verified. Since ammonium (NH₄⁺) fluxes in Santa Gilla lagoon didn't respect these conditions, Kruskal-wallis-test was applied. When

interactions were significant, pairwise comparisons were carried out applying the `emmeans_test()` (emmeans package, Lenth et al., 2023) function and Tukey's corrections. The analyses were run via the R software v. 4.4.1 (R Core Team, 2022).

To test the null hypothesis by which organic matter (OM) quantity, composition, nutritional quality and degradation rates do not vary after marine heatwaves characterized by different temperature anomalies (+2°C vs +6°C) and in sediments with different texture (muddy vs sandy), permutational analyses of variance (PERMANOVA) were used (Anderson and Braak, 2003). PERMANOVA tests were carried out in both univariate (proteins, carbohydrates, lipids, biopolymeric C, total phytopigments, algal fraction of BPC, proteins to carbohydrates ratio, C Degradation rate and C turnover time) and multivariate (OM biochemical composition of organic matter in terms of protein, carbohydrate, lipid) context. The statistical design was based on two fixed orthogonal factors and their interactions: sediment (2 levels), treatment (4 levels). The analyses were carried out on Euclidean distance-based resemblance matrices obtained from normalized data, using 999 random permutations. When PERMANOVA tests revealed a significant effect of interactions pairwise tests were also carried out. Multivariate differences in the OM biochemical composition were visualized using a biplot after a canonical analysis of the principal coordinates (CAP), allowing the identification of patterns that most effectively separates pre-established groups. PERMANOVA and CAP tests were performed through the software PRIMER 6+ (Anderson, 2017).

5.3 Results

5.3.1 The Baltic study case: the Curonian Lagoon

5.3.1.1 O₂ and NH₄⁺ fluxes

For Baltic lagoon, oxygen (O₂) flux and ammonium (NH₄⁺) flux values are reported in Table S5.1.

The results of three-way ANOVA results confirmed statistically significant separate effects of factors sediment and treatment and of the interaction sediment × treatment on both O₂ and NH₄⁺ fluxes (Table 5.1). Factor time and interaction sediment × time were significant for the NH₄⁺ flux, but not for the O₂ one (Table 5.1).

Table 5.1. Results of Three-way ANOVA testing for differences in O₂ NH₄⁺ flux across sediment types (muddy vs sediment), treatment (n=3 levels; control, +2°C, +6°C) and time (n=5 levels; 5 consecutive days). Df = degrees of freedom; MS = mean square; Pseudo-F = F statistic; P value = probability after Monte Carlo simulations. *** = p < 0.001; ** = p < 0.01; * = p < 0.05.

Variable	Source	Df	MS	F	P value
Oxygen Flux	Sediment (S)	1	3342175	25.583	***
	Treatment (Tr)	2	2634789	20.168	***
	Time (Ti)	4	62276	0.477	ns
	S×Tr	2	881123	6.745	***
	S×Ti	4	50537	0.387	ns
	Tr×Ti	8	27114	0.208	ns
	S×Tr×Ti	8	20168	0.154	ns
	Residuals	60	130643		
Ammonium flux	Sediment (S)	1	1534785	121.443	***
	Treatment (Tr)	2	47281	3.741	*
	Time (Ti)	4	34067	2.696	*
	S×Tr	2	91473	7.238	**
	S×Ti	4	74788	5.918	***
	Tr×Ti	8	5026	0.398	ns
	S×Tr×Ti	8	3865	0.306	ns
	Residuals	60	12638		

Oxygen (O₂) fluxes differed between muddy and sandy at +2°C treatment (Table S5.2). In muddy sediments (Figure 5.3), significantly more negative (bottomward) O₂ fluxes were observed at +2°C and +6°C ($-2089.62 \pm 29.41 \mu\text{mol m}^{-2} \text{h}^{-1}$ and $-2250.00 \pm 77.00 \mu\text{mol m}^{-2} \text{h}^{-1}$, respectively), when compared with CTRL sediments ($-1971.31 \pm 83.87 \mu\text{mol m}^{-2} \text{h}^{-1}$) (Table S5.2). In sandy sediments, O₂ fluxes were more negative in sediments exposed at +6°C ($-1707.88 \pm 35.86 \mu\text{mol m}^{-2} \text{h}^{-1}$) than in the CTRL sediments and in those exposed to +2°C ($-1390.32 \pm 47.53 \mu\text{mol m}^{-2} \text{h}^{-1}$ and $-1409.12 \pm 58.1 \mu\text{mol m}^{-2} \text{h}^{-1}$, respectively) (Table S5.2).

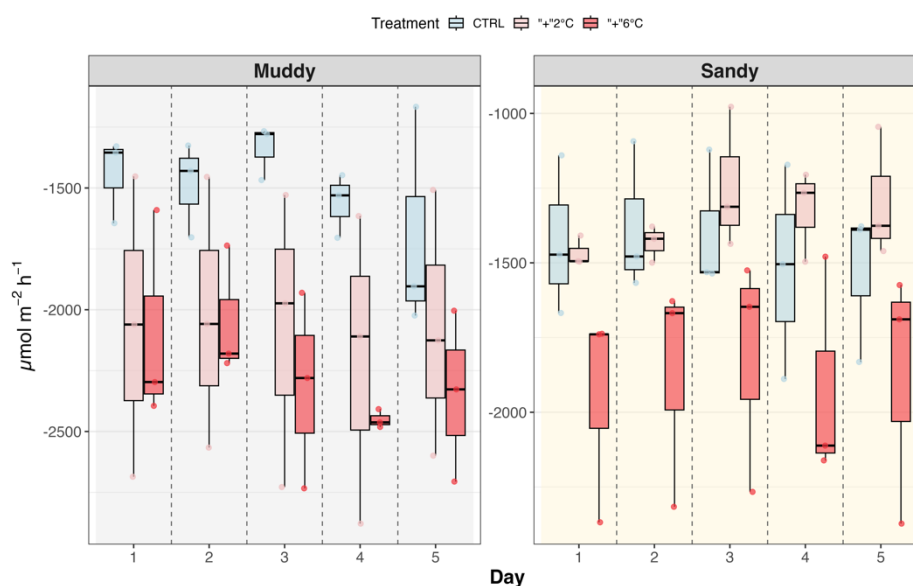


Figure 5.3. O₂ flux in muddy and sandy sediments of the Curonian lagoon during the experiment. Lowercase letters refer to the results of post-hoc comparisons. Boxplots show median (horizontal line), interquartile range (box), and whiskers extending up to $1.5 \times \text{IQR}$ from the box limits. Points beyond this range (if any) are considered outliers.

Ammonium (NH₄⁺) positive fluxes (waterward) were significantly higher in muddy sediments than in the sandy ones in all treatments (Figure 5.4, Table S5.3 and Table S5.4). In muddy sediments (Figure 5.4), ammonium (NH₄⁺) flux to the water column (positive values) was significantly higher at +2°C ($494.03 \pm 38.95 \mu\text{mol m}^{-2} \text{h}^{-1}$) than in CTRL sediments and those exposed at +6°C ($368.97 \pm 59.94 \mu\text{mol m}^{-2} \text{h}^{-1}$ and $382.07 \pm 47.47 \mu\text{mol m}^{-2} \text{h}^{-1}$, respectively) (Table S5.3 and Table S5.4). In sandy sediments, the highest ammonium (NH₄⁺) flux was observed at +6°C ($231.12 \pm 24.33 \mu\text{mol m}^{-2} \text{h}^{-1}$), followed by that in sediments exposed at +2°C and in CTRL sediments ($122.20 \pm 20.58 \mu\text{mol m}^{-2} \text{h}^{-1}$ and $108.25 \pm 7.89 \mu\text{mol m}^{-2} \text{h}^{-1}$, respectively) (Figure 5.4, Table S5.3 and Table S5.4). In muddy sediments, the fluxes at day 5 of the experiment were significantly lower than those measured in all other days, approaching the values observed at the sandy sediment (Figure 5.4, Table S5.3 and Table S5.4).

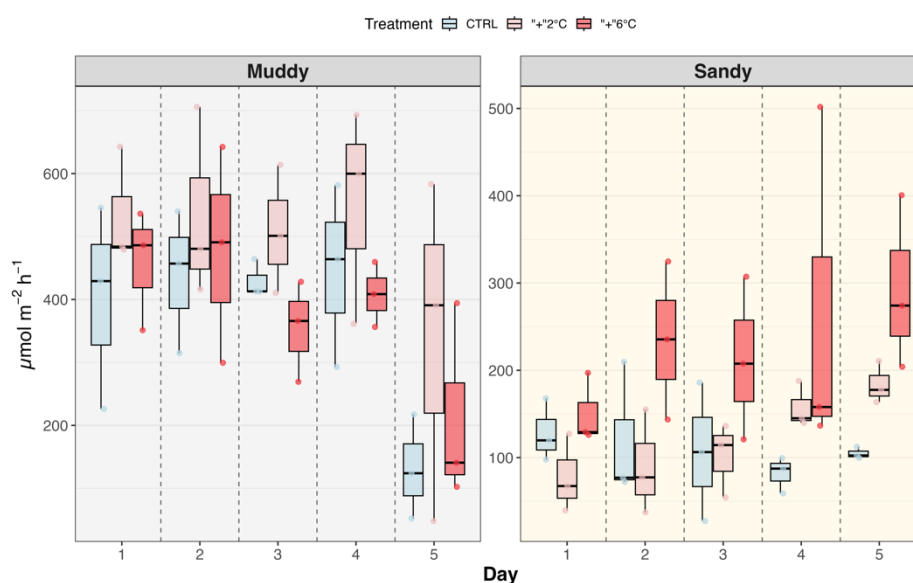


Figure 5.4. NH_4^+ flux in muddy and sandy sediments of the Curonian lagoon during the experiment. Lowercase letters refer to the results of post-hoc comparisons. Boxplots show median (horizontal line), interquartile range (box), and whiskers extending up to $1.5 \times \text{IQR}$ from the box limits. Points beyond this range (if any) are considered outliers.

5.3.1.2 Quantity, nutritional quality and degradation rates of sedimentary organic matter

Protein, carbohydrate, lipid, biopolymeric carbon, total phytopigment sedimentary contents, values of the algal fraction of BPC and of the protein to carbohydrate ratio, C degradation rates and turnover time in muddy and sandy sediments of the Curonian lagoon are reported in Table S5.5

The results of two-way PERMANOVA highlight statistically significant effects of the factor sediment for all the analyzed variables, but algal fraction of BPC (Table 5.2). The factor treatment exerted significant effects on protein, carbohydrate and biopolymeric carbon contents and the OM biochemical composition (Table 5.2). The interaction treatment $\times$ sediment was significant for protein, carbohydrate and BPC contents and values of the protein to carbohydrate ratio (Table 5.2).

Variations of all variables, but algal fraction of BPC and protein to carbohydrate ratios, were mostly explained by differences between sediment types. Variations in algal fraction of BPC were not influenced at all by sediment type nor treatment, whereas values of the protein to carbohydrate ratio were mostly influenced by the interaction treatment $\times$ sediment (Table 5.2).

Considering the large number of different variables considered, patterns of differences are described below separately, in terms of organic matter contents and nutritional quality, organic matter biochemical composition, C degradation rates and turnover time.

Table 5.2. Results of PERMANOVA testing for differences in sediment and treatment in protein, carbohydrate, lipid, biopolymeric C (BPC), and total phytopigment (CPE) contents, algal fraction of BPC (CCPE:BPC), protein to carbohydrate ratio (PRT:CHO) and OM biochemical composition (protein, carbohydrate, lipid C), C degradation rate and turnover time in the sediments of the Curonian lagoon. Df = degrees of freedom; MS = mean square; Pseudo-F = F statistic; P (MC) = probability after Monte Carlo simulations. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$. %EV = percentage of explained variance.

	Source	Df	MS	F	P(MC)	Explained variance (%)
Proteins	Sediment (S)	1	21.885	905.76	***	96.2
	Treatment (Tr)	3	0.122	5.032	**	0.9
	S×Tr	3	0.121	5.018	*	1.7
	Residuals	16	0.024			1.3
	Total	23				
Carbohydrates	Sediment (S)	1	20.760	747.29	***	91.4
	Treatment (Tr)	3	0.299	10.77	***	2.4
	S×Tr	3	0.300	10.78	**	4.8
	Residuals	16	0.0278			1.5
	Total	23				
Lipids	Sediment (S)	1	22.535	828.61	***	99.1
	Treatment (Tr)	3	0.004	0.15	ns	0.0
	S×Tr	3	0.006	0.21	ns	0.0
	Residuals	16	0.027			0.8
	Total	23				
BPC	Sediment (S)	1	22.479	6305.60	***	97.9
	Treatment (Tr)	3	0.081	22.64	***	0.7
	S×Tr	3	0.074	20.74	***	1.2
	Residuals	16	0.004			0.2
	Total	23				
CPE	Sediment (S)	1	20.220	135.44	***	94.0
	Treatment (Tr)	3	0.065	0.43	ns	0.0
	S×Tr	3	0.066	0.44	ns	0.0
	Residuals	16	0.149			6.0
	Total	23				
CCPE:BPC	Sediment (S)	1	0.764	0.70	ns	0.0
	Treatment (Tr)	3	0.964	0.89	ns	0.0
	S×Tr	3	0.650	0.60	ns	0.0
	Residuals	16	1.087			100.0
	Total	23				
PRT:CHO	Sediment (S)	1	7.238	23.25	***	31.8
	Treatment (Tr)	3	0.705	2.26	ns	3.6
	S×Tr	3	2.888	9.28	**	47.4
	Residuals	16	0.311			17.2
	Total	23				
OM Biochemical Composition	Sediment (S)	1	65.180	823.62	***	95.6
	Treatment (Tr)	3	0.425	5.37	***	1.0
	S×Tr	3	0.427	5.39	***	2.0
	Residuals	16	0.079			1.4
	Total	23				
C Degradation Rate	Sediment (S)	1	22.490	1477.20	***	98.4
	Treatment (Tr)	3	0.040	2.65	ns	0.2
	S×Tr	3	0.049	3.18	*	0.6
	Residuals	16	0.244			0.8
	Total	23				
C Turnover Time	Sediment (S)	1	19.079	45.24	***	84
	Treatment (Tr)	3	0.510	2.40	***	4.2
	S×Tr	3	0.595	2.92	***	9.8
	Residuals	16	0.038			2.0
	Total	23				

Organic matter contents and nutritional quality

Protein contents were significantly higher in muddy than in sandy sediment in all treatments ($9.94 \pm 0.38 \text{ mgC g}^{-1}$ vs $0.48 \pm 0.01 \text{ mgC g}^{-1}$; average of all the treatment) (Table S5.6 and S5.7). In muddy sediments, protein contents in sediments exposed at $+6^\circ\text{C}$ ($8.14 \pm 0.36 \text{ mgC g}^{-1}$), were significantly lower than those in sediments exposed at $+2^\circ\text{C}$ ($11.39 \pm 0.92 \text{ mgC g}^{-1}$) and the P-CRTL ones ($10.47 \pm 0.60 \text{ mgC g}^{-1}$) (Figure 5.5A). In sandy sediments, protein contents in sediments exposed at both $+2^\circ\text{C}$ and $+6^\circ\text{C}$ ($0.34 \pm 0.04 \text{ mgC g}^{-1}$ and $0.34 \pm 0.03 \text{ mgC g}^{-1}$, respectively) were significantly lower than those in CTRL sediments ($0.50 \pm 0.03 \text{ mgC g}^{-1}$) (Figure 5.5A).

Carbohydrate contents were significantly higher in muddy than in sandy sediments in all treatments ($9.11 \pm 1.06 \text{ mgC g}^{-1}$ vs $0.25 \pm 0.03 \text{ mgC g}^{-1}$; average of all treatments) (Table S5.6 and S5.7). In muddy sediments, carbohydrate contents in sediments at $+2^\circ\text{C}$ and $+6^\circ\text{C}$ ($8.67 \pm 0.34 \text{ mgC g}^{-1}$ at and to $6.28 \pm 1.11 \text{ mgC g}^{-1}$, respectively) were significantly lower than those in CTRL sediments ($10.94 \pm 0.26 \text{ mgC g}^{-1}$). In sandy sediments, carbohydrate contents in sediments exposed at $+6^\circ\text{C}$ ($0.26 \pm 0.01 \text{ mgC g}^{-1}$) were significantly higher than those in CTRL sediments ($0.20 \pm 0.01 \text{ mgC g}^{-1}$), but similar to those in P-CRTL sediments ($0.31 \pm 0.05 \text{ mgC g}^{-1}$) and in those exposed at $+2^\circ\text{C}$ ($0.21 \pm 0.02 \text{ mgC g}^{-1}$) (Figure 5.5B).

Lipid contents were significantly higher in muddy than sandy sediments in all treatments ($6.39 \pm 0.09 \text{ mgC g}^{-1}$ vs $0.07 \pm 0.01 \text{ mgC g}^{-1}$; average of all the treatment) (Table S5.6 and S5.7). In both muddy and sandy sediments, lipids contents did not vary among treatments (Figure 5.5C).

BPC contents were significantly higher in muddy than in sandy sediment in all treatments ($25.35 \pm 1.44 \text{ mgC g}^{-1}$ vs $0.73 \pm 0.06 \text{ mgC g}^{-1}$; average of all the treatment) (Table S5.6 and S5.7). In muddy sediments, BPC contents in sediments exposed at $+6^\circ\text{C}$ ($21.05 \pm 0.77 \text{ mgC g}^{-1}$) were significantly lower than those in CTRL sediments ($26.58 \pm 0.27 \text{ mgC g}^{-1}$) and sediments exposed at $+2^\circ\text{C}$ ($26.50 \pm 0.67 \text{ mgC g}^{-1}$) (Figure 5.5D). In sandy sediments, BPC contents slightly decreased, though not significantly, at both 2°C and $+6^\circ\text{C}$ compared to the CTRL sediments (Figure 5.5D).

CPE contents were significantly higher in muddy than sandy sediments all treatments ($135.43 \pm 7.45 \text{ mgC g}^{-1}$ vs $0.41 \pm 0.04 \text{ mgC g}^{-1}$; average of all the treatment) (Figure 5.5E, Table S5.6 and S5.7).

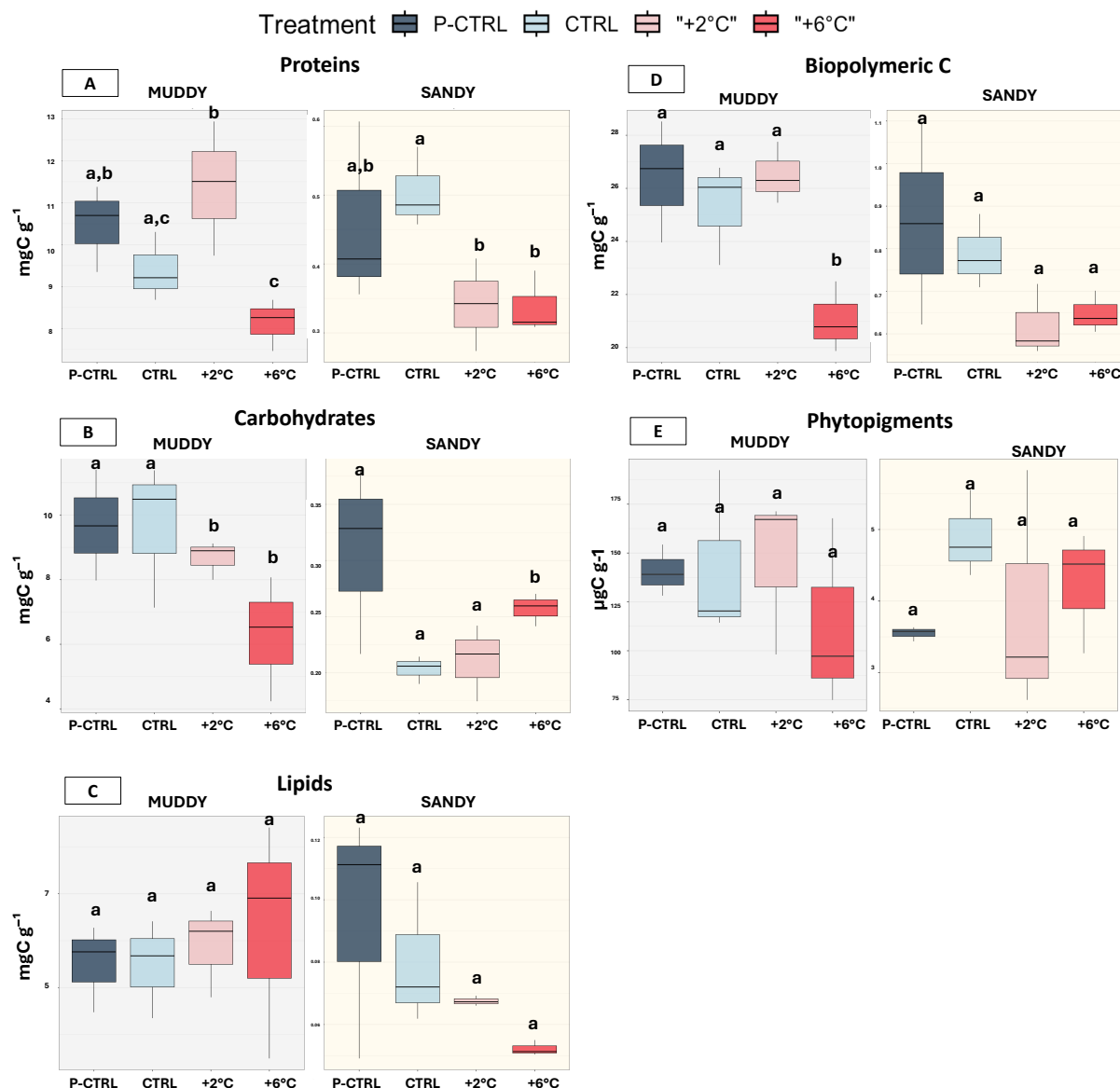


Figure 5.5. Differences in protein, carbohydrate, lipid, biopolymeric C and total phytopigment contents in muddy and sandy sediments of the Curonian lagoon in the four experimental levels of treatment. Boxplots show median (horizontal line), interquartile range (box), and whiskers extending up to $1.5 \times \text{IQR}$ from the box limits. Points beyond this range (if any) are considered outliers. Lowercase letters indicate the results of the post-hoc tests.

In both muddy and sandy sediments, the algal fraction of biopolymeric C (CCPE:BPC) (Figure 5.6A) showed a large intra-treatment variability but no statistical differences among treatments (Figure 5.6A).

Values of the protein to carbohydrate ratio (PRT:CHO) were significantly higher in sandy than in muddy sediments in all treatments ($0.94 \pm 0.11 \text{ mgC g}^{-1}$ vs $1.41 \pm 0.21 \text{ mgC g}^{-1}$; average of all the treatment) (Table S5.6 and S5.7). In muddy sediments, values of the PRT:CHO ratio didn't differ among treatments, while in sandy sediment they significantly decreased at both +2°C (1.34 ± 0.13) and at +6°C (1.07 ± 0.08), when compared to the experimental CTRL (2.02 ± 0.17) (Figure 5.6B).

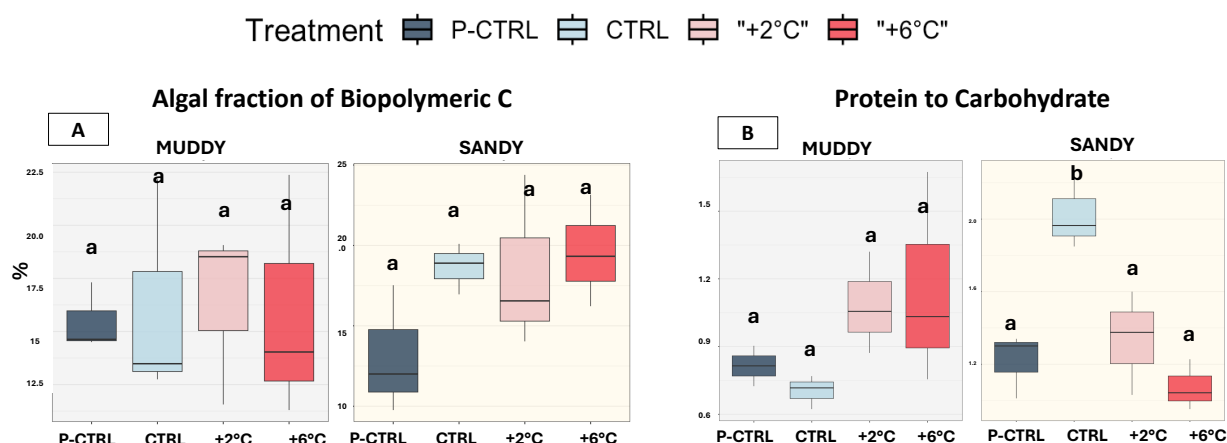


Figure 5.6. Changes in algal fraction of BPC (CCPE:BPC) and Proteins to Carbohydrates (CHO) in different treatments and sediment texture in the Baltic lagoon. Boxplots show median (horizontal line), interquartile range (box), and whiskers extending up to $1.5 \times \text{IQR}$ from the box limits. Points beyond this range (if any) are considered outliers. Lowercase letters indicate the results of the post-hoc tests.

OM biochemical composition

The biochemical composition of organic matter was significantly different between muddy and sandy sediments in all treatments except at +2°C (Table S5.6 and S5.7). In muddy sediments, the post-hoc tests (Table S5.6 and Table S5.7) revealed that the biochemical composition of organic matter at +6°C was statistically different from that in all other treatments, mostly due to lower protein and carbohydrate contents (Figure 5.7A). In sandy sediments, the biochemical composition of organic matter differed from that in CTRL sediments at both +2°C and +6°C, due to protein contents lower than those in the P-CTRL and CTRL sediments (Figure 5.7B).

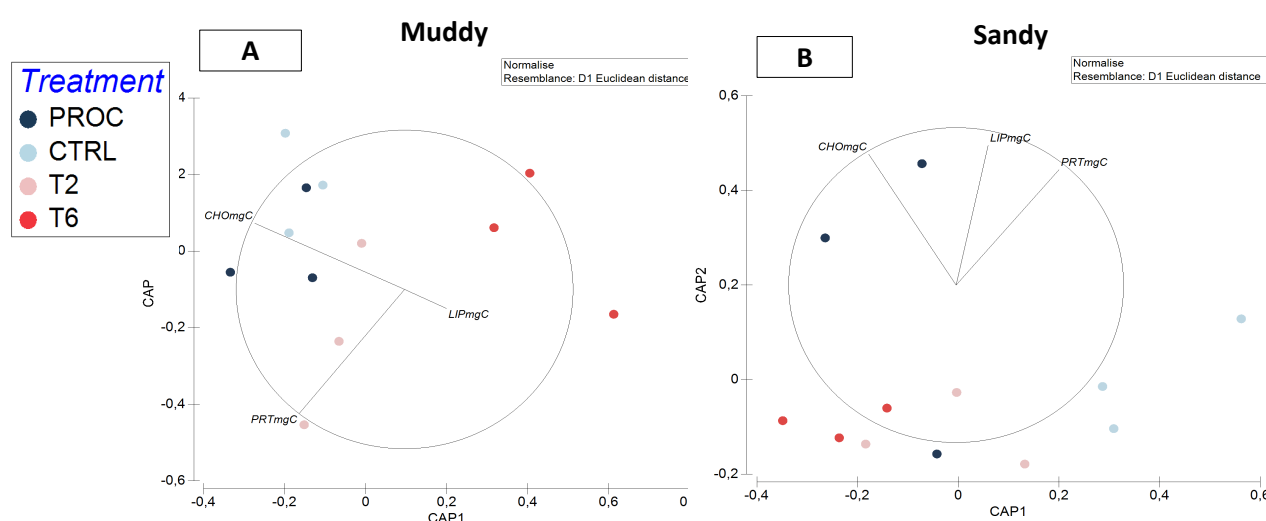


Figure 5.7 Biplot obtained after the CAP analysis showing differences in the biochemical composition of sedimentary organic matter (cPRT, cCHO, cLIP) among treatments in muddy (A) and sandy (B) sediments of the Curonian Lagoon. Vectors are proportional to the percentage of variance explained by the the different biochemical components. cPRT = protein; cCHO = carbohydrate; cLIP = lipid; CPE = total phytopigments.

C degradation rates and turnover time

C degradation rates were significantly higher in muddy than in sandy sediment in all treatments ($14.55 \pm 0.57 \mu\text{gC g}^{-1} \text{ h}^{-1}$ vs $1.23 \pm 0.16 \mu\text{gC g}^{-1} \text{ h}^{-1}$, average of all treatments) (Table S5.6 and S5.7). In muddy sediments, C degradation rates significantly increased at $+2^\circ\text{C}$ ($16.14 \pm 0.74 \mu\text{gC g}^{-1} \text{ h}^{-1}$) compared to the control and at $+6^\circ\text{C}$ ($14.13 \pm 0.94 \mu\text{gC g}^{-1} \text{ h}^{-1}$ and $14.26 \pm 0.51 \mu\text{gC g}^{-1} \text{ h}^{-1}$, respectively). In sandy sediment, they significantly decreased in all experimental treatments compared to the P-CTRL sediments ($1.60 \pm 0.20 \mu\text{gC g}^{-1} \text{ h}^{-1}$) (Figure 5.8A).

C turnover time was significantly longer in muddy sediment than sandy sediment in all the treatments (54.64 ± 1.84 days vs 22.97 ± 1.84 days, average of all the treatment) (Table S5.6 and S5.7). In muddy sediment, C turnover time significantly decreased in $+2^\circ\text{C}$ and $+6^\circ\text{C}$ treatment (51.87 ± 0.93 days and 41.48 ± 0.81 days, respectively) compared to CTRL and P-CTRL sediments (62.18 ± 2.14 days and 63.03 ± 1.58 days, respectively) (Figure 5.8B).

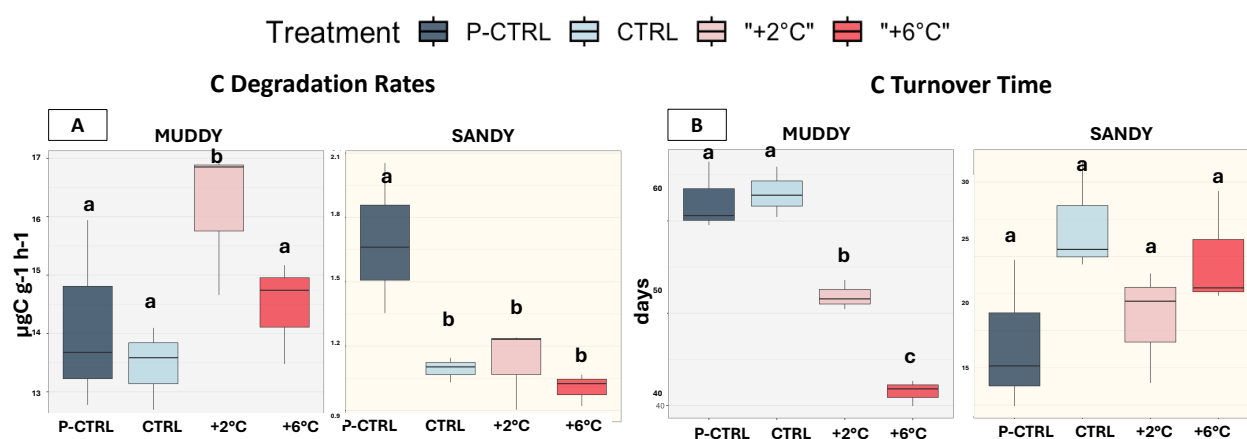


Figure 5.8. Changes in C degradation rates (A) and turnover time (B) in muddy and sandy sediments of the Curonian lagoon exposed at the different treatments [procedural control (P-CTRL), control (CTRL) $+2^\circ\text{C}$, $+6^\circ\text{C}$]. Boxplots show median (horizontal line), interquartile range (box), and whiskers extending up to $1.5 \times \text{IQR}$ (interquartile) from the box limits. Points beyond the range (if any) are considered outliers. Lowercase letters indicate the results of the post-hoc tests.

5.3.2 The Mediterranean study case: the Santa Gilla Lagoon

5.3.2.1 Oxygen (O_2) and (NH_4^+) fluxes

O_2 flux and NH_4^+ fluxes in the sediments of the Santa Gilla lagoon are reported in Table S5.8.

The results of three-way ANOVA testing for differences in O_2 flux in the sediments of the Santa Gilla lagoon highlight statistically significant effects of all the factors. The Treatment $\times$ Time and Sediment $\times$ Treatment $\times$ Time interactions are also significant (Table 5.3).

Table 5.3. Results of three-way ANOVA testing for differences in O₂ and NH₄⁺ fluxes across sediments, treatments and time in the Santa Gilla lagoon. Df = degrees of freedom; MS = mean square; Pseudo-F = F statistic; P value = probability after Monte Carlo simulations. *** = p < 0.001; ** = p < 0.01; * = p < 0.05.

Variable	Source	Df	MS	F	P value
O ₂ Flux	Sediment (S)	1	3.92E+07	138.43	***
	Treatment (Tr)	2	2.11E+07	74.51	***
	Time (Ti)	4	1.53E+06	5.41	***
	S×Tr	2	6.79E+05	2.40	ns
	S×Ti	4	3.42E+05	1.21	ns
	Tr×Ti	8	8.30E+05	2.93	**
	S×Tr ×Ti	8	6.61E+05	2.33	*
	Residuals	60	2.83E+05		

In both muddy and sandy sediments, oxygen fluxes were significantly more negative at +2°C (-5230.65 ± 555.45 μmol m⁻² h⁻¹, and -4191.68 ± 135.04 μmol m⁻² h⁻¹, respectively) than in CTRL sediments only at day 1 (-3837.50 ± 267.44 μmol m⁻² h⁻¹ and -2947.73 ± 83.01 μmol m⁻² h⁻¹, respectively) (Figure 5.9; Table S5.9 and S5.10). The O₂ fluxes at +6°C were more negative from those of both CTRL sediments and sediments exposed at +2°C during the entire experiment, except day 2 (Figure 5.9; Table S5.9 and S5.10). In sandy sediments, O₂ fluxes at +6°C were significantly more negative than the CTRL till day 3, and higher than the +2°C treatment on days 2 and 4 (Figure 5.9; Table S5.9 and S5.10).

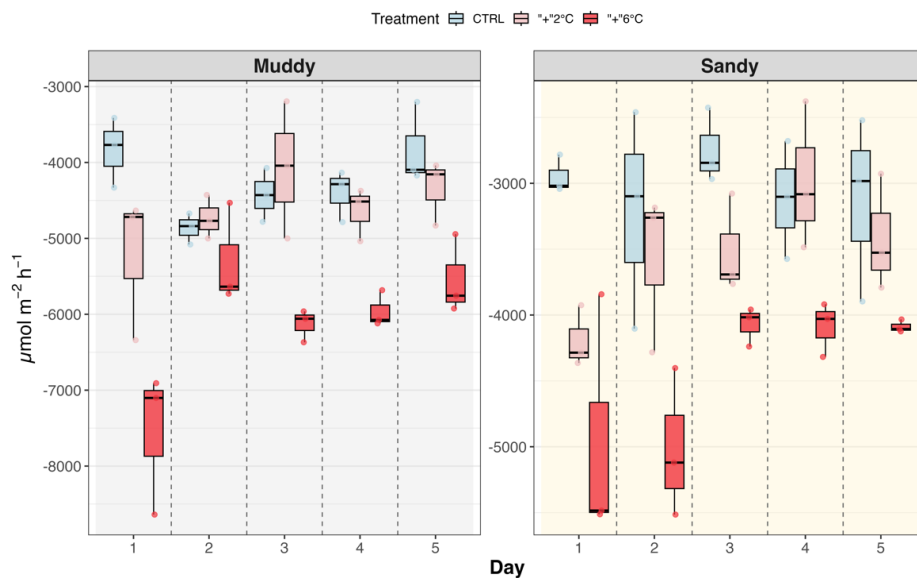


Figure 5.9. O₂ flux for each sediment bottom, each treatment and each day during the experiment for Mediterranean Lagoon. Boxplots show median (horizontal line), interquartile range (box), and whiskers extending up to 1.5 × IQR (interquartile) from the box limits. Points beyond this range (if any) are considered outliers. Lowercase letters indicate the results of the post-hoc tests.

The Kruskal-Wallis test performed on NH₄⁺ fluxes in the Santa Gilla lagoon sediments didn't show any significant variation for the three separate factors (Figure 5.10, Table 5.4).

Table 5.4. Results of Kruskal-wallis testing for differences in sediment, treatment and day in ammonium (NH₄⁺) flux). Df = degrees of freedom P value = probability *** = p < 0.001; ** = p < 0.01; * = p < 0.05.

Variable	Source	chi-squared	Df	P value
NH ₄ ⁺ Flux	Site	3.400	1	ns
	Treatment	1.133	2	ns
	Day	3.002	4	ns

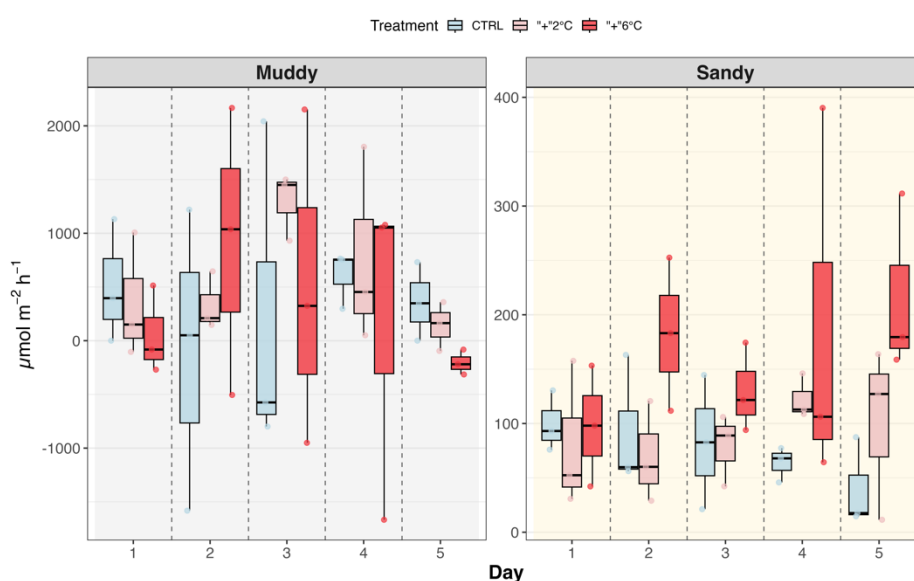


Figure 5.10. NH₄⁺ fluxes in muddy and sandy sediments of the Santa Gilla lagoon in each treatment and day during the experiment. BI Boxplots show median (horizontal line), interquartile range (box), and whiskers extending up to 1.5 × IQR from the box limits. Points beyond this range (if any) are considered outliers.

5.3.2.2 Quantity, quality and degradation rates of sedimentary organic matter

For Santa Gilla lagoon, proteins, carbohydrates, lipids, biopolymeric carbon, total phytopigments sedimentary contents, values of the algal fraction of BPC and of the protein to carbohydrate ratio, C degradation rates and turnover time are reported in Table S5.11.

The results of the two-way PERMANOVA tests highlight statistical significance of the factor treatment for all variables, except carbohydrates and total phytopigments contents, whereas the factor sediment and the interaction treatment × sediment exerted significant effects on all variables, but the algal fraction of BPC and the values of the protein to carbohydrate ratio (Table 5.5). Variations in proteins, lipids, biopolymeric carbon contents, OM biochemical composition and C turnover time are sediment dependent. Variations in CHO and CPE contents, and C degradation

rate are influenced by the sediment $\times$ treatment interactions, whereas the algal fraction of BPC and values of the PRT:CHO ratio by the residuals (Table 5.5).

Table 5.5. Results of PERMANOVA testing for differences in contents of protein, carbohydrates, lipids, biopolymeric C (BPC), total phytopigment (CPE), algal fraction of BPC (CCPE:BPC), protein to carbohydrate ratio (PRT:CHO) and OM biochemical composition (cPRT, cCHO, cLIP), C degradation rate and turnover time across sediment types and treatments in the sediments of the Santa Gilla lagoon. Df = degrees of freedom; MS = mean square; Pseudo-F = F statistic; P (MC) = probability after Monte Carlo simulations. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$. %EV = percentage of explained variance.

	Source	Df	MS	F	P(MC)	EV (%)
Proteins	Sediment	1	6.967	18.10	**	40.7
	Treatment	3	2.940	7.64	**	31.6
	Treatment $\times$ Sediment	3	0.350	0.91	ns	0
	Residuals	16	0.385			27.7
	Total	23				
Carbohydrates	Sediment	1	4.697	14.63	***	18.7
	Treatment	3	0.235	0.73	ns	0
	Treatment $\times$ Sediment	3	4.154	12.94	***	65.6
	Residuals	16	0.321			15.7
	Total	23				
Lipids	Sediment	1	16.737	349.61	***	75.1
	Treatment	3	1.048	21.88	***	9
	Treatment $\times$ Sediment	3	0.785	16.39	***	13.3
	Residuals	16	0.048			2.6
	Total	23				
BPC	Sediment	1	12.693	75.10	***	61
	Treatment	3	1.573	9.31	**	13.7
	Treatment $\times$ Sediment	3	0.962	5.69	*	15.4
	Residuals	16	0.170			9.9
	Total	23				
CPE	Sediment	1	8.848	27.54	***	38.8
	Treatment	3	0.259	0.81	ns	0
	Treatment $\times$ Sediment	3	2.745	8.54	**	44.2
	Residuals	16	0.321			17
	Total	23				
CCPE:BPC	Sediment	1	0.036	0.06	ns	0
	Treatment	3	2.057	3.18	*	17.7
	Treatment $\times$ Sediment	3	2.144	3.31	ns	37.5
	Residuals	16	0.648			44.8
	Total	23				
PRT:CHO	Sediment	1	0.536	0.77	ns	0
	Treatment	3	2.623	3.76	*	27.8
	Treatment $\times$ Sediment	3	1.144	1.64	ns	12.9
	Residuals	16	0.698			59.3
	Total	23				
OM Biochemical Composition	Sediment	1	28.403	37.67	***	44.8
	Treatment	3	4.222	5.60	**	11.2
	Treatment $\times$ Sediment	3	5.289	7.01	***	29.4
	Residuals	16	0.754			14.6
	Total	23				
C Degradation Rate	Sediment	1	5.795	32.75	***	23.4
	Treatment	3	0.926	5.23	*	6.2
	Treatment $\times$ Sediment	3	3.865	21.84	***	61.5
	Residuals	16	0.177			8.9
	Total	23				
C Turnover Time	Sediment	1	8.356	57.65	***	38.6
	Treatment	3	2.114	14.58	***	18.5
	Treatment $\times$ Sediment	3	1.995	13.76	***	34.8
	Residuals	16	0.145			8.1
	Total	23				

Organic matter contents and nutritional quality

Protein contents were significantly higher in muddy than in sandy sediments in all treatments but at +2°C ($1.39 \pm 0.24 \text{ mgC g}^{-1}$ vs $0.73 \pm 0.16 \text{ mgC g}^{-1}$) (Table S5.12 and Table S5.13). In the muddy sediments of the Santa Gilla lagoon, protein contents were highest in CTRL sediments ($1.28 \pm 0.14 \text{ mgC g}^{-1}$) and at +6°C ($1.83 \pm 0.31 \text{ mgC g}^{-1}$), compared to those in the P-CTRL sediments ($0.77 \pm 0.10 \text{ mgC g}^{-1}$) (Figure 5.11A, Table S5.12 and Table S5.13). Likewise, in sandy sediments, protein contents at +6°C ($1.23 \pm 0.25 \text{ mgC g}^{-1}$) were significantly higher than those in CTRL sediments and those exposed at +2°C ($0.49 \pm 0.09 \text{ mgC g}^{-1}$ and $0.73 \pm 0.16 \text{ mgC g}^{-1}$, respectively) (Figure 5.11A, Table S5.12 and Table S5.13).

Carbohydrate contents were significantly higher in muddy than in sandy sediments at CTRL ($1.08 \pm 0.01 \text{ mgC g}^{-1}$ vs $0.2 \pm 0.02 \text{ mgC g}^{-1}$) and +6°C ($1.06 \pm 0.08 \text{ mgC g}^{-1}$ vs $0.53 \pm 0.05 \text{ mgC g}^{-1}$) (Table S5.12 and S5.13). In muddy sediments, carbohydrate contents were statistically higher in CTRL compared to procedural CTRL ($1.08 \pm 0.01 \text{ mgC g}^{-1}$ vs $0.65 \pm 0.1 \text{ mgC g}^{-1}$). They significantly decreased at +2°C compared to CTRL and +6°C (+2°C: $0.75 \pm 0.14 \text{ mgC g}^{-1}$; +6 °C: $1.06 \pm 0.08 \text{ mgC g}^{-1}$). In muddy sediment, they drop in all the treatment compared to P-CTRL ($0.99 \pm 0.10 \text{ mgC g}^{-1}$) (Figure 5.11B; Table S5.12 and Table S5.13)

Lipid contents were significantly higher in muddy than in sandy sediments in all treatments ($0.53 \pm 0.07 \text{ mgC g}^{-1}$ vs $0.18 \pm 0.04 \text{ mgC g}^{-1}$, average of all the treatments) (Table S5.12 and S5.13). Opposite patterns between muddy and sandy sites were observed for LIP contents. Notably, lipid contents were significantly lower at +2°C ($0.32 \pm 0.04 \text{ mgC g}^{-1}$), than in all other treatments (Figure 11C, Table S5.12 and S5.13). In sandy sediment, they were higher at CTRL level compared to P-CTRL ($0.08 \pm 0.00 \text{ mgC g}^{-1}$ vs $0.2 \pm 0.02 \text{ mgC g}^{-1}$). They increased at +6°C treatment compared to all the other treatments ($0.29 \pm 0.02 \text{ mgC g}^{-1}$) (Figure 5.11C; Table S5.12 and Table S5.13).

BPC contents were significantly higher in muddy than sandy in sediments in all treatments but the procedural control (P-CTRL: $2.03 \pm 0.18 \text{ mgC g}^{-1}$ vs $1.63 \pm 0.12 \text{ mgC g}^{-1}$) (Figure 5.11D; Table S5.12 and S5.13). At +6°C, BPC contents significantly increased both in muddy ($3.47 \pm 0.28 \text{ mgC g}^{-1}$) and sandy ($2.04 \pm 0.26 \text{ mgC g}^{-1}$) sediments, when compared to the procedural CTRL sediments ($2.03 \pm 0.18 \text{ mgC g}^{-1}$ and $1.63 \pm 0.12 \text{ mgC g}^{-1}$) and the CTRL ones ($3.00 \pm 0.12 \text{ mgC g}^{-1}$ and $1.13 \pm 0.17 \text{ mgC g}^{-1}$) (Figure 5.11D, Table S5.12 and S5.13).

Total phytopigment contents were significantly lower in muddy than in sandy sediments in all treatments, but the procedural CTRL ($8.34 \pm 0.41 \text{ } \mu\text{gC g}^{-1}$ vs $9.56 \pm 2.38 \text{ } \mu\text{gC g}^{-1}$) (Figure 5.11E, Table S5.12 and S5.13). In muddy sediments, CPE contents in CTRL and +6°C ($15.2 \pm 1.59 \text{ } \mu\text{gC g}^{-1}$ and 14.24

$\pm 1.99 \mu\text{gC g}^{-1}$, respectively) were significantly higher than in P-CTRL ($8.34 \pm 0.41 \mu\text{gC g}^{-1}$) (Figure 5.11E, Table S5.12 and S5.13). In sandy sediments, the highest CPE contents occur at $+2^\circ\text{C}$ ($9.97 \pm 0.41 \mu\text{gC g}^{-1}$), followed by those at $+6^\circ\text{C}$ when compared to CTRL sediments ($6.87 \pm 0.5 \mu\text{gC g}^{-1}$ and $3.27 \pm 0.14 \mu\text{gC g}^{-1}$, respectively) (Figure 5.11E, Table S5.12 and S5.13).

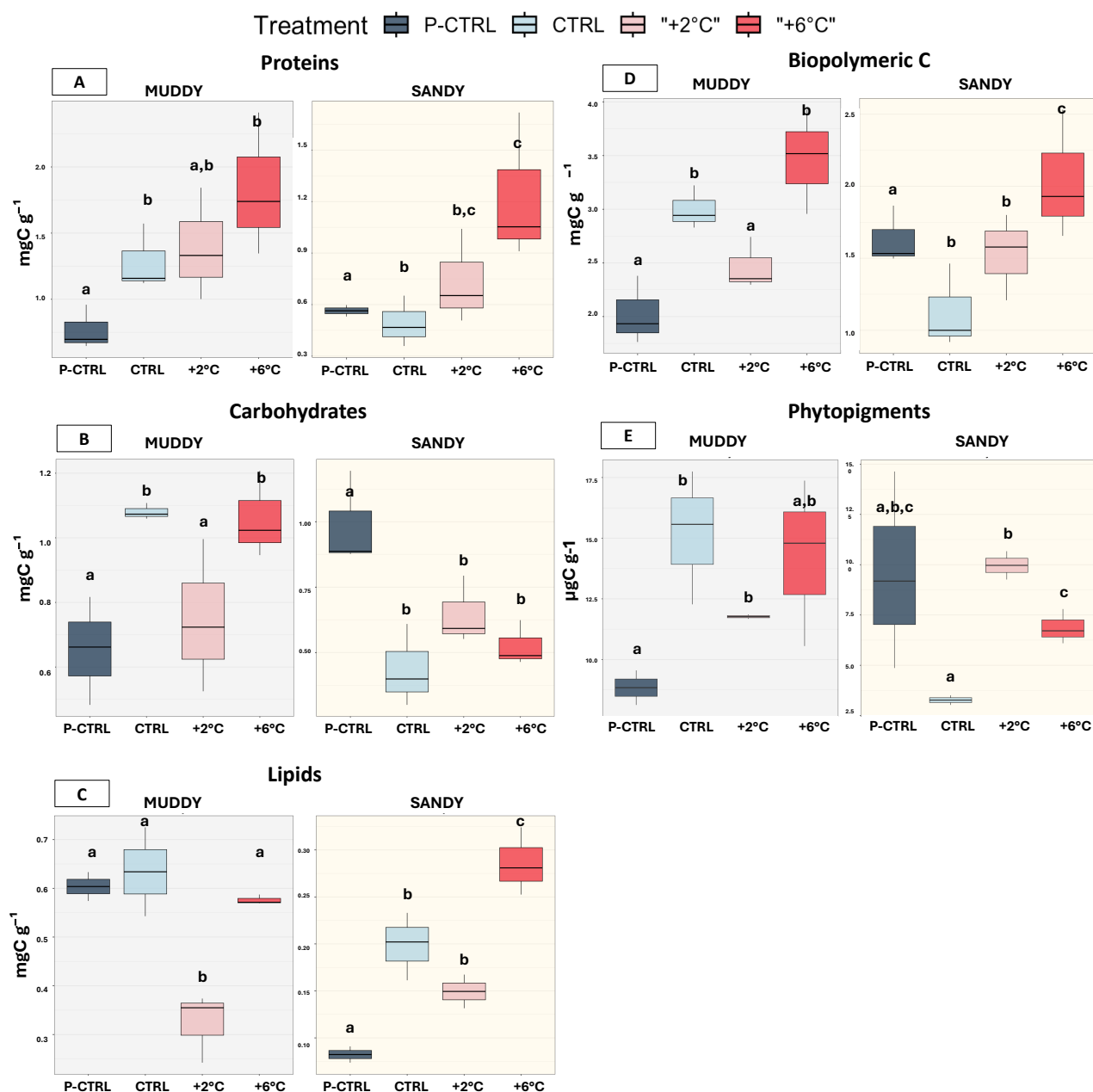


Figure 5.11. Protein, carbohydrate, lipid, biopolymeric C and total phytopigment contents in muddy and sandy sediments of the Santa Gilla lagoon exposed to the different treatments. Boxplots show median (horizontal line), interquartile range (box), and whiskers extending up to $1.5 \times \text{IQR}$ from the box limits. Points beyond this range (if any) are considered outliers. Lowercase letters indicate the results of the post-hoc tests.

Regardless of the sediment type, the algal fraction of BPC was significantly higher (17.28 ± 1.79 %) in sediments exposed at $+2^{\circ}\text{C}$, than in the CTRL sediment and those exposed at $+6^{\circ}\text{C}$ (12.19 ± 1.75 % and 11.47 ± 1.76 %, respectively) (Figure 5.12 A; S5.12 and S5.13).

Evenly, no statistical differences in values of the proteins to carbohydrates ratio between sediment types were observed in the sediments of the Santa Gilla lagoon. Values differed between P-CTRL and CTRL sediments (0.88 ± 0.14 and 1.18 ± 0.14 , respectively); values in sediments at $+6^{\circ}$ (2.08 ± 0.33) were significantly higher than in those exposed at $+2^{\circ}\text{C}$ (1.62 ± 0.41 ,) (Figure 5.12 B; Table S5.12 and S5.13).

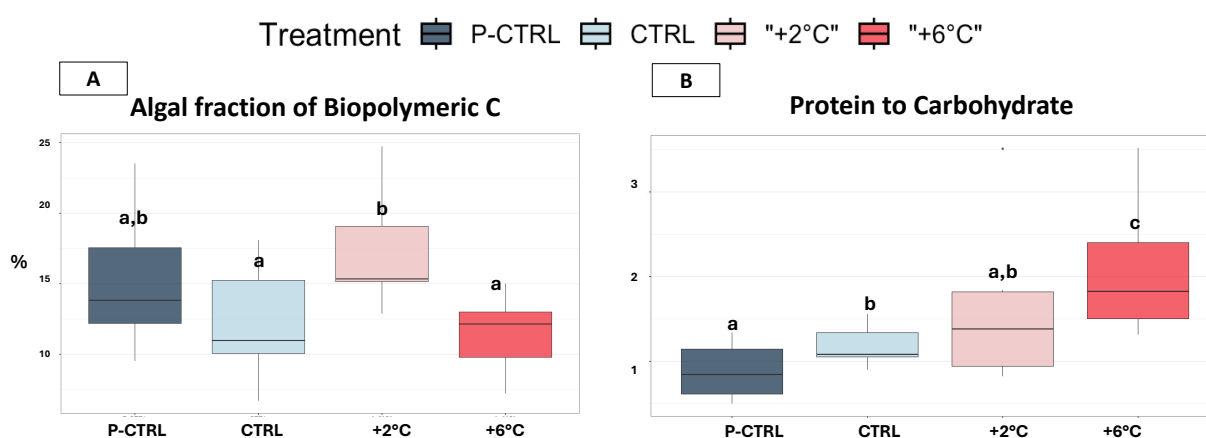


Figure 5.12 Changes in algal fraction of BPC (CCPE:BPC) and Proteins to Carbohydrates (CHO) in treatment in the Mediterranean lagoon. Boxplots show median (horizontal line), interquartile range (box), and whiskers extending up to $1.5 \times \text{IQR}$ from the box limits. Points beyond this range (if any) are considered outliers. Lowercase letters indicate the results of the post-hoc tests.

OM biochemical composition

Muddy and sandy CTRL sediments exhibited a significantly different OM biochemical composition (Table S5.12 and S5.13). In muddy sediments, OM composition of sediments exposed at $+2^{\circ}\text{C}$ was statistically different from that in all the other treatments, due to the lower contents of all OM components (Figure 5.13A; Table S5.12 and S5.13). In sandy sediments, the OM composition of sediments exposed at $+6^{\circ}\text{C}$ was statistically different from that in all other treatments, due to contents of all OM components higher than those in the procedural CTRL and CTRL sediments (Figure 5.13B; Table S5.12 and S5.13).

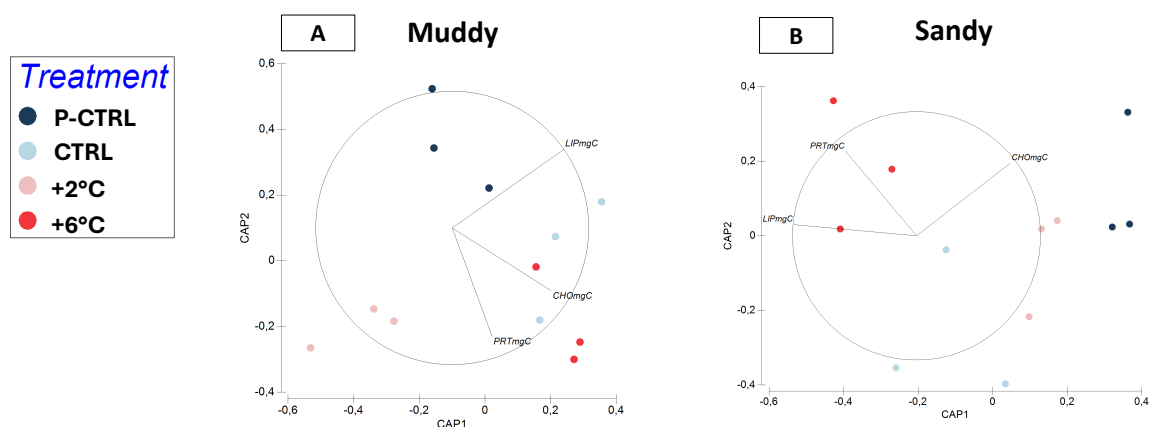


Figure 5.13 Biplot obtained after the CAP analysis showing differences in the biochemical composition (protein, carbohydrate and lipid) of sedimentary organic matter among treatments in muddy (A) and sandy (B) sediments of the Santa Gilla Lagoon. Vectors are proportional to the percentage of variation explained by the different biochemical components. PRTmgC = protein C; CHOMgC = carbohydrate C; LIPmgC = lipid C.

C degradation rates and turnover time

C degradation rates were significantly lower in muddy than in sandy sediments both at +2°C ($2.45 \pm 0.46 \mu\text{gC g}^{-1} \text{h}^{-1}$ vs $13.4 \pm 0.46 \mu\text{gC g}^{-1} \text{h}^{-1}$) and +6°C ($2.49 \pm 0.02 \mu\text{gC g}^{-1} \text{h}^{-1}$ vs $7.1 \pm 1.45 \mu\text{gC g}^{-1} \text{h}^{-1}$). (Figure 5.14A, Table S5.12 and S5.13). In muddy sediments, C degradation rates at +2°C ($2.45 \pm 0.46 \mu\text{gC g}^{-1} \text{h}^{-1}$) and at +6°C ($2.49 \pm 0.02 \mu\text{gC g}^{-1} \text{h}^{-1}$) were significantly lower than those in CTRL sediments ($8.34 \pm 1.59 \mu\text{gC g}^{-1} \text{h}^{-1}$). In sandy sediments, C degradation rates were highest at +2°C ($13.4 \pm 0.46 \mu\text{gC g}^{-1} \text{h}^{-1}$) when compared with those in CTRL sediments ($7.45 \pm 0.32 \mu\text{gC g}^{-1} \text{h}^{-1}$) and those at +6°C ($2.49 \pm 0.02 \mu\text{gC g}^{-1} \text{h}^{-1}$) (Figure 5.14A, Table S5.12 and S5.13).

Overall, C turnover time was significantly longer in muddy than in sandy sediments in all treatments, but the procedural CTRL (3.6 ± 1.2 days vs 4.4 ± 0.2 days) (Figure 5.14 B; Table S5.12 and S5.13). In muddy sediments, C turnover time at +2°C treatment and at +6°C treatment (18.05 ± 3.97 and 22.09 ± 2.32 days respectively) was significantly higher than that in the CTRL sediments (6.36 ± 0.67 days) (Figure 15.4 B; Table S5.12 and S5.13). In sandy sediments, C turnover time in CTRL sediments and those exposed at +2°C (2.3 ± 0.2 and 1.9 ± 0.2 days respectively), were lower than those in P-CTRL sediments (4.4 ± 0.2 days) (Figure 5.14B; Table S5.12 and S5.13). C turnover time in sediments exposed at +6°C (4.9 ± 0.3 days) was significantly higher than that in CTRL sediments (2.3 ± 0.2 days) and that in sediments exposed at +2°C (Figure 5.14 B; Table S5.12 and S5.13).

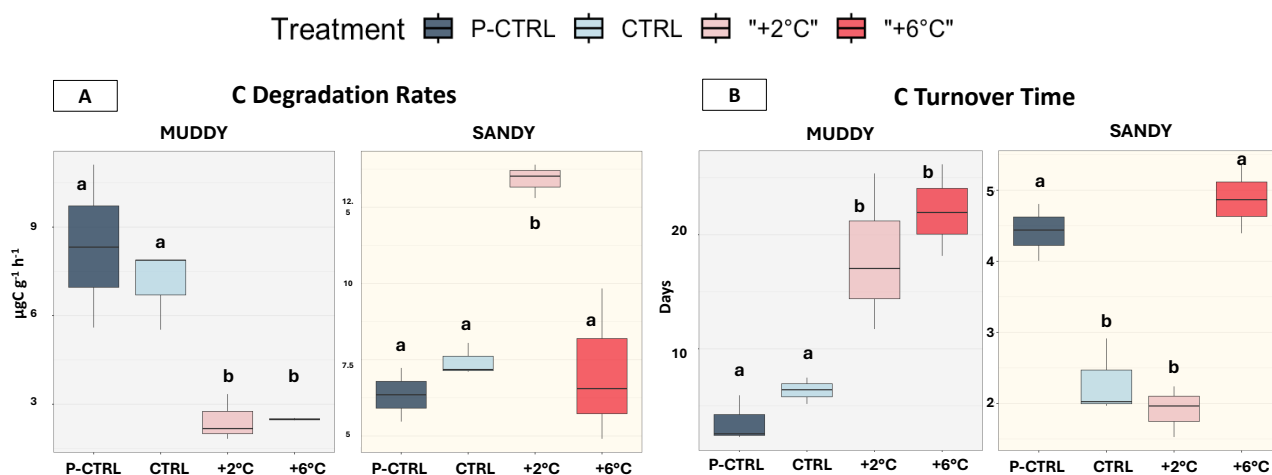


Figure 5.14. Changes in C degradation rate (A) and C turnover time (B) in different treatments and sediment texture in the Santa Gilla lagoon. Boxplots show median (horizontal line), interquartile range (box), and whiskers extending up to $1.5 \times \text{IQR}$ from the box limits. Points beyond this range (if any) are considered outliers. Lowercase letters indicate the results of the post-hoc tests.

5.4 Discussion

Overall, the (null) hypothesis by which the quantity and biochemical composition of organic matter, organic C degradation rate and turnover, and oxygen and ammonium fluxes in muddy and sandy sediments of two lagoons characterized by different climatic regimes are not affected by marine heatwaves of different temperature anomalies was rejected.

Some previous studies focusing on MHWs impact of ecosystem functionality focused on the response of benthic metabolism in terms of either nutrient fluxes (Kauppi and Villnäs, 2022, Kauppi et al., 2023; Göbeler et al., 2025) or changes in organic matter pools (Soru et al., 2022; Palmas et al., 2025). None of those studies focused at the same time on both proxies, but one (Sara et al. (2021)). Therefore, to the best of my knowledge my study is the first ever assessing the response of lagoons benthic metabolism to MHWs considering sediment texture and climatic regime (i.e. latitude) as concurring covariates. Due to the presence of important differences in their environmental characteristics (e.g. salinity, depth, surface etc.), the two case studies provided evidence of distinct responses of Baltic (Curonian) and Mediterranean (Santa Gilla) lagoons sediments to thermal stress.

5.4.1 The Baltic case: Curonian Lagoon

5.4.1.1 Benthic metabolism responses

Due to its unique geographical and climatological features, the semi-enclosed and brackish Baltic Sea (strongly influenced by both Arctic and subtropical air masses) is particularly vulnerable to climate change impacts (Bierstedt et al., 2015; Dailidienė et al., 2023).

As far as MHWs are concerned, recent studies have shown that Baltic Sea temperatures frequently exceeded the 90th percentile by up to 2 °C and can occasionally rise by 5–6 °C, thus matching the thermal anomalies tested in my experiment (Dabulevičienė and Servaitė, 2024). The Curonian Lagoon, indeed, has already experienced anomalous summertime warming events, often coupled with so-called “tropical nights,” with documented detrimental effects on both ecosystem functioning and human well-being (Dailidienė et al., 2023).

As previously observed by Politi et al. (2022), sedimentary properties, such as organic matter content and grain size, can strongly influence benthic fluxes, particularly during summer when macrofaunal community structures are less complex. Accordingly, in the Curonian Lagoon sediments, I observed distinct responses to thermal anomalies depending on sediment texture and the pronounced differences in organic matter content between muddy and sandy bottoms.

Since oxygen consumption is considered a proxy for overall benthic metabolic activity (Sarà et al., 2013; Kauppi et al., 2023), the higher oxygen influx into the sediment (more negative O₂ fluxes) observed at both +2 °C and +6 °C anomaly in both types of sediment suggests intensified metabolic activity of benthic communities with increasing temperature. Consistently, higher oxygen consumption was accompanied by enhanced ammonium release (more positive fluxes) at the +2 °C anomaly in muddy sediments and at +6 °C in the sandy ones. Temperature-sediment type combinations in which benthic respiration and ammonium waterward flux increased reflect either a physical-chemical response (as increased gases diffusion rates are expected due to rising temperature) or enhanced benthic metabolic activities, possibly accompanied by accelerated organic matter degradation (Kauppi and Villnäs, 2023; Farrell et al., 2024). Accordingly, the results of the experiment carried out with sediment from the Curonian lagoon reveal that warming can lead to an acceleration of organic C degradation at both +2 °C and +6°C when compared to the control sediments, as evidenced by increased enzyme-mediated C degradation rates (though not significant at +2°C) coupled with significantly shorter C turnover time. These findings are consistent with those provided by Palmas et al. (2025), who observed similar enzyme-mediated C degradation acceleration in lagoon sediments exposed at +4 °C and +8 °C anomalies. These results indicate that sediments of a typical high-latitude lagoon (like the Curonian lagoon), yearly experiencing relatively low mean temperatures, respond to marine heatwaves with increased benthic ecosystem functioning, by accelerating the liberation of otherwise stored blue C from the lagoon. Nonetheless, as outlined above, such a response is not consistent between sediment types. My results, indeed, reveal that O₂ and NH₄⁺ fluxes show unexpectedly decoupled patterns depending on sediment type and temperature of exposure.

The lack of matching patterns of benthic respiration and ammonium fluxes at +2°C in sandy sediments, suggests that such a temperature anomaly could have not been as high as needed to stimulate significant changes in benthic metabolism, like the one, instead, observed at the same temperature anomaly in muddy sediments. This discrepancy could be the result of a benthic biomass in muddy sediments much higher than that in sandy sediments. At the same time, this result can also suggest that benthic communities in sandy sediments exposed to milder heatwaves still have margins of adaptation to a sudden heating. In muddy sediments increased benthic respiration rates at +6°C were not accompanied by an expected concurrent increase in waterward ammonium fluxes, that remained stable when compared to the control. This unexpected result is difficult to explain, as, generally, muddy sediments show increasing ammonium release rates with

increasing temperature (Kauppi & Vilnas, 2022). A possible explanation for such a lack of increased ammonium release from muddy sediments exposed at the strongest heatwave stems from the levels of thermal stress that, mostly affecting the macroscopic components of the benthic community, could have reduced bioturbation a factor positively influencing release rates. A decreased bioturbation, due to the thermal stress, could have ultimately make gases diffusion less effective. Nonetheless, such hypothesis cannot be corroborated and must be considered with caution, as I did not measure benthic biomass nor assessed bioturbation rates, and, therefore, it claims for further investigations.

5.4.1.2 Benthic trophic status changes

After five days of exposure to the MHWs, the overall quantity (in terms of biopolymeric C) and biochemical composition of organic matter in muddy sediments of the Curonian lagoon did not change significantly at +2 °C, while varied significantly at +6°C. This result suggests that the milder temperature anomaly (+2°C), while having some effects on benthic functions (oxygen consumption, gas exchanges and C degradation) was likely not strong enough to strongly modify organic loads and their composition. This can only be explained by biological mechanisms that, while maintaining organic C loads, stimulate the benthic metabolism. One possible explanation for the invariant quantity and composition of organic matter in muddy sediments exposed at +2°C is the stimulation of the microbial loop (Pusceddu & Danovaro, 2009), with differential effects on the different components of biopolymeric C. Noticeably such hypothesis is corroborated by the increase in protein contents of muddy sediments exposed at +2°C, suggesting an increase of the labile fraction of organic matter associated with microbes, typically having a higher protein to carbohydrate ratio. This result has been observed also by Soru et al. (2022) who reported a similar increase in protein contents of marine coastal sediments exposed to in situ simulated MHWs of comparable intensity though longer duration (three weeks). On the other hand, the concurrent decrease of carbohydrate contents in muddy sediments exposed at both +2°C and +6°C suggests that this pool of biopolymers underwent a relatively fast degradation at both temperature anomalies, as also reported previously (Palmas et al. 2025), but did not enter the microbial loop, possibly due to the lower nutritional quality of individual molecules composing the pool.

Differently from muddy sediments, biopolymeric C contents in sandy sediments of the Curonian lagoon were significantly lower than those in the control ones both at +2°C and +6°C anomaly, indicating that, concurrently with the increased C degradation rates, the organic C pool in sandy sediments were subjected more to consumption than to reprocessing through the microbial

loop, as instead hypothesized for muddy sediments at +2°C. This interpretation is corroborated by the inverse patterns of protein and carbohydrate pools, with lower values of the former and higher values of the latter, values of the protein to carbohydrate ratio and of the algal fraction of BPC consistently lower in heated sediments than in the control ones. The values of the protein to carbohydrate ratio and of the algal fraction of BPC have been consistently used in the literature as a proxy for the nutritional quality of sedimentary organic matter (Pusceddu et al., 2000; 2010) and my results pinpoint that the nutritional quality of organic pools in sandy sediments of the Curonian lagoon could drop significantly in response to marine heatwaves. This result corroborates the hypothesis that sandy sediments of high-latitude lagoons exposed to marine heatwaves could liberate stored blue C stocks, making amounts of food for the benthos quantitatively poorer and of lower nutritional quality, ultimately leading to a general oligotrophication of the system.

5.4.2 The Mediterranean lagoon study case: Santa Gilla lagoon

The Mediterranean Sea is experiencing increasing air and sea temperatures, as well as increasing frequency, duration, and intensity of marine heatwaves, forecasting stronger and more intense response to increasing greenhouse gas forcing (Pastor and Khodayar, 2023; Darmaraki et al., 2019). Due to their transitional nature and specific characteristics (shallow depth, weak hydrodynamics, and strong salinity gradients), coastal lagoons of the Mediterranean Sea may experience even more exacerbated events (Lloret et al., 2008). For instance, in the Mediterranean Sea marine heatwaves with thermal anomalies similar to those simulated in my thesis, have been observed in several lagoons (Bertolini and Pastres, 2021; Ferrarin et al., 2024), and found to be associated with the occurrence of lethal and sub-lethal effects on bivalves, changes in nutrient loads and exacerbated competitive behaviors (Bertolini and Pastres, 2021; Correia-Martins et al., 2022).

5.4.2.1 Benthic metabolism responses

In the Santa Gilla lagoon, benthic respiration (negative oxygen flux) increased at both thermal anomalies in both sediment types, but with patterns of differences varying in time. With a thermal anomaly of +2 °C, oxygen consumption increased in both experimental types compared to the control only on the first day of the experiment, then remained relatively stable in the following ones. This result suggests that, after an initial increase in metabolic requirements, benthic communities showed some physiological adaptation to a moderate thermal stress, as also observed in previous studies (Kordas et al., 2022). Despite the oxygen consumption response was similar in the two types of sediments, when looking at the responses of C degradation rates and turnover some differences between muddy and sandy sediments emerge. In muddy sediments, C

degradation rate at +2°C is almost completely inhibited, resulting in a consequent much longer turnover time. This result would indicate that even a relatively small thermal anomaly processes related to organic matter degradation are impaired. In contrast, in sandy sediments, degradation activities at +2°C appear to be stimulated with turnover times remaining relatively constant when compared to the control. These results pinpoint that organic matter degradation processes in low latitude lagoon sediments are particularly vulnerable to even small temperature anomalies. This result is also in agreement with those reported by Palmas et al., 2025.

Both muddy and sandy sediments exposed to the +6°C anomaly were characterized by respiration rates consistently higher than those observed in sediments exposed to +2°C. This result would suggest that the metabolic response of sediments is tightly related with the amplitude of the thermal anomaly, that was somehow expected and similar to what observed in the sediments of the Curonian lagoon (see above) and previous studies (Göbeler et al., 2025). Nonetheless, respiration rates increased significantly only in the very few days of exposure, then stabilizing till the end of the experiment. This result, on the one hand corroborates the hypothesis by which benthic communities can adapt to thermal stress, but also that the time needed of adapt increases with the increase in the amplitude of the anomaly. In fact, while at +2°C respiration rates moved back to the initial values (suggesting a complete metabolic adaptation), at +6°C they stabilized but remained consistently higher than those in the control. This latter result suggests that the adaptation mechanisms of the benthos exposed to the strongest heatwave, can adapt somehow but are not able to counteract entirely the negative effects of warming. The missed full adaptation of benthic metabolism, especially in muddy sediments characterized by far larger organic loads, to the strongest thermal stress is also corroborated by almost invariant ammonium fluxes, that suggests a possibly impaired functionality of the microbial food webs. Accordingly, organic C degradation rates were apparently inhibited at +6°C in both muddy and sandy sediments with consequent increased C turnover times. This result suggests that, differently from what observed in the Curonian lagoon, in which organic C appeared stimulated at least at +6°C, the thermal stress caused by the more intense heatwave on the sediments of the Santa Gilla lagoon can have far more severe consequences on benthic ecosystem functioning, possibly leading to its full impairment. This result, comparatively, suggests that the sediment biogeochemistry of naturally warmer lagoons like the Santa Gilla one is more prone to a full functional impairment in the occurrence of severe marine heatwaves. This is somehow conceivable as we can hypothesize that even in the occurrence of severe (+6°C) heatwaves, temperature in northern lagoons remains below the threshold of

metabolic impairment, whereas in southern (naturally warmer) lagoons the same anomaly rises the temperature over critical thresholds of ecosystem functioning.

5.4.2.2 Benthic trophic status changes

Previous studies reported that marine coastal sediments exposed to anomalously high temperatures for at least 5 days show a generally decreased availability of food resources for the benthos (Palmas et al., 2025). Accordingly, in muddy sediments of the Santa Gilla lagoon, depletions of carbohydrate and lipid contents and thus of biopolymeric C contents (when compared to the control) were observed at the end of the experiment at +2°C, in combination with reduced organic C degradation rates. Such a result might appear counterintuitive, as a decrease of the microbial activity should have led to an accumulation of organic loads. Unfortunately, I adopted a before-after approach that does not allow me providing any robust mechanistic explanation for such a mismatch. However, considering that the effects of MHWs are the result of a combination of intensity (amplitude of the temperature anomaly) and duration of exposure, I may hypothesize that, at the milder temperature anomaly, the benthic food web in muddy sediments was somehow able to cope (adapt) with the MHWs but not for its entire duration. Such hypothesis is corroborated by the results in muddy sediments exposed at +6°C, in which biopolymeric C accumulated and C degradation rates concurrently dropped: the exposure to a more severe temperature anomaly likely concurred to impair benthic microbial activities well before than those in sediments exposed to the milder (+2°C) MHW. On the one hand, the concurrent decrease of sedimentary organic loads (benthic oligotrophication) and impairment of the benthic microbial food web observed at +2°C could alter nutrient cycling, thus leading to benthic communities' adaptation mechanisms and promoting communities more able to use low-quantity organic C sources (Soru et al. 2022). On the other hand, the accumulation of organic C in the sediments (benthic eutrophication) and the impairment of the microbial food web at +6°C could result in disrupted ecological conditions (Magri et al., 2024) and especially of the microbial degradation activities (Bresciani et al., 2012), with potentially severe consequences in the whole system productivity and biodiversity (Bukaveckas et., 2023). The two differential changes of the benthic trophic status of muddy sediments exposed to the MHWs are somehow supported by changes in the nutritional quality of sedimentary organic matter, in terms of the protein to carbohydrate ratio and the algal fraction of BPC. The hypothesized oligotrophication of muddy sediments exposed to the milder MHW is, in fact, accompanied also by an increase in both the protein to carbohydrate ratio and the algal fraction of BPC, altogether suggesting the presence of fresher organic matter of autotrophic origin (typical of oligotrophic

conditions; Pusceddu et al., 2011). On the other hand, the apparent eutrophication of muddy sediments exposed to the most severe temperature anomaly (+6°C) is accompanied by an increased protein to carbohydrate ratio but a diminished algal fraction of BPC, suggesting a possible impairment of the autotrophic component while the whole organic C pool accumulates (typical of meso-eutrophic conditions; Pusceddu et al., 2011).

The responses of the benthic trophic status (in terms of quantity and nutritional quality) of sandy sediments to MHWs, mirrored those in muddy sediments only at the most severe temperature anomalies (+6°C), with a general eutrophication effect, characterized by increased biopolymeric C contents, higher protein to carbohydrates ratios (due to an accumulation of also labile compounds like proteins) and a lower algal fraction of the BPC (reflecting a possible suffering condition for the autotrophic component). In sandy sediments, the response of the benthic trophic status to the milder (+2°C) temperature anomaly is characterized by an increase in biopolymeric C contents, no significant changes in values of the protein to carbohydrate ratio and an increase in the algal fraction of BPC. This result suggests that the mild MHW, differently from what observed in muddy sediments at the same anomaly, might have had a positive effect on the benthic trophic status, favoring an accumulation of the most labile fraction of organic matter associated with phytopigments, though not influencing the overall biochemical composition of the organic loads. This result may be related to the higher oxygen availability in sandy sediments, due to their greater porosity and permeability, which supports more efficient microbial and autotrophic activity.

Noticeably, phytopigment contents were detected in sandy sediments exposed at both temperature anomalies. Similar positive short-term responses (<3 weeks) of phytopigments to MHWs have been reported in other shallow water ecosystems (Soru et al., 2022) and may reflect not necessarily only a possible stimulation of microphytobenthos activity but also an enhanced sedimentation of heat-impaired phytoplankton (Soulie et al., 2022). In addition, when associated with higher lipid contents, as at the +6°C anomaly, the increase in phytopigments may also represent a stress response of microphytobenthos to elevated temperature (Finkel et al., 2010; Correia-Martins et al., 2022; Soru et al., 2022). The accumulation of undegraded organic material due to longer turnover time under high temperatures (>25 °C), coupled with inefficient aerobic degradation, may enhance sulfate-reducing bacterial activity, promoting the development of anoxic conditions, promoting the occurrence of dystrophic crises (Seidel et al., 2022; Lenzi and Cianchi, 2022). Overall, my results allow me concluding that in sandy sediments mild heatwaves (+2 °C) can transiently enhance primary production and improve organic matter nutritional quality,

while more intense temperature anomalies (+6 °C) may lead to the accumulation of organic C, reduced microbial efficiency, and increased risk of oxygen depletion triggering dystrophic crisis.

5.5 Conclusions

The Mediterranean (Santa Gilla) and Baltic (Curonian) lagoons differ one each other in several initial characteristics such temperature, salinity, nutrient cycling (Inacio et al., 2018; Carstensen, 2020; Soria et al., 2022). Despite these differences, the results obtained in my study allow me addressing several commonalities:

- The benthic metabolism of both lagoons, whichever the direction and intensity of change, responds to MHWs, even under moderate anomalies (+2 °C);
- Sediment texture (muddy vs. sandy) appears to influence whether sedimentary organic loads increase or decrease in response to MHWs, though with patterns depending on the system analyzed;
- The intensity of the heatwave, together with the sediment texture, affects differentially the nutritional quality of sedimentary organic matter.

Overall, the responses of lagoon sediments biogeochemistry to marine heatwaves can be summarized in terms of changes in the trophic status and microbial food webs functioning in the sediments (in terms of C degradation rates). Such changes, however, differ between high- and low-latitude lagoons.

In the Curonian Lagoon (Baltic Sea), benthic metabolism in muddy sediments appeared more resilient to mild warming (+2 °C), showing increased benthic respiration, ammonium release, and C turnover without significant alterations in nutrient cycling or in the quantity and quality of organic matter. Conversely, sandy sediments were more sensitive to MHWs, exhibiting changes in OM biochemical composition, a depletion in OM quality, and enhanced ammonium release under both mild (+2 °C) and severe (+6 °C) heatwaves.

In the Santa Gilla lagoon (Mediterranean Sea), muddy sediments showed that even a mild thermal anomaly (+2 °C) temporarily affected OM quantity and quality, resulting in slower microbial degradation but stimulated microbial loop and potential cascading effects on higher trophic levels. In contrast, sandy sediments experienced a transient enhancement in primary production and OM nutritional quality under mild heatwaves (+2 °C), while more intense events (+6 °C) reduced microbial efficiency and the retention of labile organic matter.

These results, finally, pinpoint that benthic metabolism and trophic status of high-latitude lagoons show an overall functional impairment especially at +6°C, whereas those of low-latitude lagoons are prone to severe ecological disruptions also at mild MHWs.

My results draw attention to the need to pay particular attention to measures to mitigate the effects of heat waves and the consequent necessary adjustments to management practices, especially in low-latitude lagoons.

5.6 Acknowledgements

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5.7 References

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5.8 Supplementary materials

Table S5.1. Average (avg) Oxygen (O₂) and ammonium (NH₄⁺) fluxes during the experiment carried out with muddy and sandy sediments from the Curonian lagoon in all treatments (CTRL, +2°C, +6°C). Standard errors (SE; n=3) are also reported.

Sediment	Treatment	Day	O ₂ Flux (μmol m ⁻² h ⁻¹)		NH ₄ (μmol m ⁻² h ⁻¹)	
		Avg	SE	Avg	SE	SE
Muddy	CTRL	1.00	-1763.68	276.99	400.31	161.73
		2.00	-1813.36	259.37	437.26	114.09
		3.00	-2219.55	105.20	429.96	29.69
		4.00	-2075.40	291.62	446.12	145.09
		5.00	-1984.57	439.52	131.20	82.82
		Average	-1971.31	83.87	368.97	59.94
	+2 °C	1	-2066.29	356.03	535.33	93.03
		2.00	-2026.27	321.34	534.18	152.18
		3.00	-2076.85	350.02	508.54	101.90
		4.00	-2201.11	367.45	551.46	171.06
		5.00	-2077.56	315.97	340.67	271.12
		Average	-2089.62	29.41	494.03	38.95
	+6 °C	1	-2094.05	253.33	457.86	95.71
		2.00	-2045.19	154.83	477.53	171.88
		3.00	-2314.67	232.47	354.38	80.05
		4.00	-2450.59	21.95	408.13	51.66
		5.00	-2345.50	202.78	212.44	158.59
		Average	-2250.00	77.40	382.07	47.47
Sandy	CTRL	1.00	-1426.83	153.97	128.39	35.83
		2.00	-1379.64	145.48	119.63	78.06
		3.00	-1395.98	137.48	106.49	79.34
		4.00	-1521.56	207.13	81.90	20.83
		5.00	-1227.59	155.91	104.84	6.72
		Average	-1390.32	47.53	108.25	7.89
	+2 °C	1	-1466.33	28.82	78.04	44.81
		2.00	-1432.48	35.46	89.91	59.93
		3.00	-1242.21	136.99	101.62	42.45
		4.00	-1322.34	88.69	157.57	26.35
		5.00	-1582.25	350.73	183.87	24.18
		Average	-1409.12	58.81	122.20	20.58
	+6 °C	1	-1784.33	324.85	150.72	40.13
		2.00	-1751.63	304.81	234.59	90.55
		3.00	-1738.12	282.42	211.92	93.28
		4.00	-1579.13	283.02	265.42	204.98
		5.00	-1686.21	351.13	292.92	99.59
		Average	-1707.88	35.86	231.12	24.33

Table S5.2. Results of the post hoc tests with Tukey's correction for the interaction Sediment $\times$ Treatment for O₂ flux in the sediments of the Curonian lagoon. T = statistic t; P value = probability. *** = p < 0.001; ** = p < 0.01; * = p < 0.05; ns = not significant.

	Contrast	t	p value
CTRL	Muddy vs Sandy	-0.406	ns
+2°C	Muddy vs Sandy	-5.593	***
+6°C	Muddy vs Sandy	-2.761	ns
Muddy	CTRL vs +2°C	-4.429	***
	CTRL vs +6°C	-5.645	***
	+2°C vs +6°C	1.215	ns
Sandy	CTRL vs +2°C	0.757	ns
	CTRL vs +6°C	-3.29	*
	+2°C vs +6°C	4.047	**

Table S5.3. Results of the post hoc tests with Tukey's correction for the interaction Sediment $\times$ Treatment for NH₄⁺ flux in the sediments of the Curonian lagoon. T = statistic t; P() = probability level. *** = p < 0.001; ** = p < 0.01; * = p < 0.05; ns = not significant.

	Contrast	t	p value
CTRL	Muddy vs Sandy	6.351	***
+2°C	Muddy vs Sandy	9.058	***
+6°C	Muddy vs Sandy	3.678	**
Muddy	CTRL vs "+2°C"	3.047	*
	CTRL vs "+6°C"	0.319	ns
	" +2°C" vs "+6°C"	2.728	ns
Sandy	CTRL vs "+2°C"	0.34	ns
	CTRL vs "+6°C"	2.993	*
	" +2°C" vs "+6°C"	-2.653	ns

Table S5.4. Results of the post hoc tests with Tukey's correction for the interaction Sediment×Treatment×time for NH_4^+ flux in the sediments of the Curonian lagoon. T = statistic t; P() = probability level. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; ns = not significant.

	Contrast	t	p value
Day 1		6.519	***
Day 2		6.32	***
Day 3	Muddy vs	5.49	***
Day 4	Sandy	5.666	***
Day 5		0.646	ns
Muddy	Day1 vs Day2	-0.349	ns
	Day1 vs Day3	0.633	ns
	Day1 vs Day4	-0.077	ns
	Day1 vs Day5	4.461	**
	Day2 vs Day3	0.982	ns
	Day2 vs Day4	0.272	ns
	Day2 vs Day5	4.81	***
	Day3 vs Day4	-0.71	ns
	Day3 vs Day5	3.828	*
	Day4 vs Day5	4.538	*
Sandy	Day1 vs Day2	-0.547	ns
	Day1 vs Day3	-0.396	ns
	Day1 vs Day4	-0.929	ns
	Day1 vs Day5	-1.412	ns
	Day2 vs Day3	0.151	ns
	Day2 vs Day4	-0.382	ns
	Day2 vs Day5	-0.865	ns
	Day3 vs Day4	-0.534	ns
	Day3 vs Day5	-1.016	ns
	Day4 vs Day5	-0.483	ns

Table S5.5. Average (avg) sedimentary contents of proteins (cPRT), carbohydrates (cCHO), lipids (cLIP), biopolymeric C (BPC) and total phytopigments (CPE), algal fraction of BPC (CCPE:BPC), protein to carbohydrate ratio (PRT:CHO), C degradation rate and C turnover time in muddy and sandy sediments of the Curonian lagoons in all experimental levels. Average and standard errors (SE; n=3) are reported.

Sediment	Treatment	cPRT (mgC g ⁻¹)		cCHO (mgC g ⁻¹)		cLIP (mgC g ⁻¹)		BPC (mgC g ⁻¹)		CPE (µgC g ⁻¹)	
		avg	ES	avg	ES	avg	ES	avg	ES	avg	ES
Muddy	PROC CTRL	10.47	0.60	10.53	0.50	6.25	0.27	27.26	0.63	140.53	7.58
	CTRL	9.40	0.48	10.94	0.26	6.24	0.30	26.58	0.27	142.36	25.08
	+2 °C	11.39	0.92	8.67	0.34	6.44	0.28	26.50	0.67	145.54	23.75
	+6 °C	8.14	0.36	6.28	1.11	6.64	0.73	21.05	0.77	113.28	28.01
Sandy	PROC CTRL	0.46	0.08	0.31	0.05	0.10	0.02	0.86	0.14	3.55	0.06
	CTRL	0.50	0.03	0.20	0.01	0.08	0.01	0.79	0.05	4.89	0.35
	+2 °C	0.34	0.04	0.21	0.02	0.07	0.00	0.62	0.05	3.89	0.99
	+6 °C	0.34	0.03	0.26	0.01	0.05	0.00	0.65	0.03	4.23	0.49

Sediment	Treatment	PRT:CHO		CCPE:BPC (%)		C degradation rates (µgC g ⁻¹ h ⁻¹)		C turnover time (Days)	
		avg	ES	avg	ES	avg	ES	avg	ES
Muddy	PROC CTRL	0.81	0.05	15.48	0.92	14.13	0.94	62.18	2.14
	CTRL	0.70	0.04	16.13	3.03	13.46	0.41	63.03	1.58
	+2 °C	1.08	0.13	16.38	2.42	16.14	0.74	51.87	0.93
	+6 °C	1.15	0.27	15.90	3.33	14.46	0.51	41.48	0.81
Sandy	PROC CTRL	1.22	0.10	13.10	2.31	1.69	0.20	19.11	2.94
	CTRL	2.02	0.17	18.65	0.91	1.09	0.11	27.10	2.21
	+2 °C	1.34	0.13	18.32	3.12	1.12	0.74	20.77	0.93
	+6 °C	1.07	0.08	19.57	2.00	1.00	0.04	24.88	2.26

Table S5.6. Results of the post-hoc tests revealing differences in contents of proteins (cPRT), carbohydrates (cCHO), biopolymeric C (BPC), and protein to carbohydrate ratio (PRT:CHO), C degradation rate and turnover time between muddy and sandy sediments of the Curonian lagoon in each treatment level. T = statistic t; P(MC) = probability level after Monte Carlo simulation. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; ns = not significant.

Variable	Treatment	Contrasts	t	P(MC)
Proteins	PROC CTRL	Muddy vs Sandy	16.667	***
	CTRL		18.628	***
	+2°C		11.940	**
	+6°C		21.775	***
Carbohydrates	PROC CTRL	Muddy vs Sandy	20.292	***
	CTRL		41.563	***
	+2°C		24.664	***
	+6°C		54.023	**
Biopolymeric C	PROC CTRL	Muddy vs Sandy	40.810	****
	CTRL		93.421	****
	+2°C		38.521	****
	+6°C		26.523	***
PRT:CHO	PROC CTRL	Muddy vs Sandy	3.489	*
	CTRL		10.205	**
	+2°C		1.201	ns
	+6°C		2.802	ns
OM Composition	PROC CTRL	Muddy vs Sandy	13.084	***
	CTRL		10.560	**
	+2°C		16.023	***
	+6°C		8.464	**
C degradation rate	PROC CTRL	Muddy vs Sandy	13.084	***
	CTRL		10.560	**
	+2°C		16.023	***
	+6°C		8.464	**
C turnover time	PROC CTRL	Muddy vs Sandy	11.861	***
	CTRL		13.451	**
	+2°C		12.968	***
	+6°C		6.906	**

Table S5.7. Results of the post-hoc tests revealing differences in contents of proteins (cPRT), carbohydrates (cCHO), biopolymeric C (BPC), and protein to carbohydrate ratio (PRT:CHO) , C degradation rate and C turnover time among treatments in muddy and sandy sediments of the Curonian lagoon. T = statistic t; P(MC) = probability level after Monte Carlo simulation. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; ns = not significant.

Variable	Sediment	Contrast	t	P(MC)
Proteins	Muddy	PROC CTRL vs CTRL	1.408	ns
		PROC CTRL vs +2°C	0.836	ns
		PROC CTRL vs +6°C	3.364	*
		CTRL vs +2°C	1.917	ns
		CTRL vs +6°C	2.123	ns
		+2°C vs +6°C	3.286	*
	Sandy	PROC CTRL vs CTRL	0.571	ns
		PROC CTRL vs +2°C	1.345	ns
		PROC CTRL vs +6°C	1.466	ns
		CTRL vs +2°C	3.172	*
		CTRL vs +6°C	3.888	*
		+2°C vs +6°C	0.070	ns
Carbohydrates	Muddy	PROC CTRL vs CTRL	0.714	ns
		PROC CTRL vs +2°C	3.069	*
		PROC CTRL vs +6°C	3.482	*
		CTRL vs +2°C	5.285	**
		CTRL vs +6°C	4.071	*
		+2°C vs +6°C	2.051	ns
	Sandy	PROC CTRL vs CTRL	2.153	ns
		PROC CTRL vs +2°C	1.869	ns
		PROC CTRL vs +6°C	1.051	ns
		CTRL vs +2°C	0.368	ns
		CTRL vs +6°C	4.867	*
		+2°C vs +6°C	2.152	ns
Biopolymeric C	Muddy	PROC CTRL vs CTRL	0.99	ns
		PROC CTRL vs +2°C	0.823	ns
		PROC CTRL vs +6°C	6.241	**
		CTRL vs +2°C	0.103	ns
		CTRL vs +6°C	6.780	**
		+2°C vs +6°C	5.347	**
	Sandy	PROC CTRL vs CTRL	0.493	ns
		PROC CTRL vs +2°C	1.641	ns
		PROC CTRL vs +6°C	1.511	ns
		CTRL vs +2°C	2.387	ns
		CTRL vs +6°C	2.429	ns
		+2°C vs +6°C	0.484	ns
PRT:CHO	Muddy	PROC CTRL vs CTRL	1.658	ns

	Sandy	PROC CTRL vs +2°C	1.918	ns
		PROC CTRL vs +6°C	1.227	ns
		CTRL vs +2°C	2.772	ns
		CTRL vs +6°C	1.637	ns
		+2°C vs +°6C	0.236	ns
		PROC CTRL vs CTRL	5.038	**
		PROC CTRL vs +2°C	0.604	ns
		PROC CTRL vs +6°C	1.091	ns
		CTRL vs +2°C	3.348	*
		CTRL vs +6°C	6.483	**
OM biochemical Composition	Muddy	+2°C vs +°6C	1.419	ns
		PROC CTRL vs CTRL	1.011	ns
		PROC CTRL vs +2°C	1.547	ns
		PROC CTRL vs +6°C	2.699	*
		CTRL vs +2°C	2.392	*
		CTRL vs +6°C	2.817	*
	Sandy	+2°C vs +°6C	2.095	*
		PROC CTRL vs CTRL	1.147	ns
		PROC CTRL vs +2°C	1.481	ns
		PROC CTRL vs +6°C	1.426	ns
		CTRL vs +2°C	2.771	*
C Degradation rate	Muddy	CTRL vs +6°C	3.706	*
		+2°C vs +°6C	1.025	ns
		PROC CTRL vs CTRL	0.321	ns
		PROC CTRL vs +2°C	4.427	ns
		PROC CTRL vs +6°C	9.065	ns
		CTRL vs +2°C	6.097	*
	Sandy	CTRL vs +6°C	1.216	ns
		+2°C vs +°6C	8.464	ns
		PROC CTRL vs CTRL	2.194	*
		PROC CTRL vs +2°C	0.453	ns
		PROC CTRL vs +6°C	1.556	*
C turnover time	Muddy	CTRL vs +2°C	2.049	ns
		CTRL vs +6°C	0.711	ns
		+2°C vs +°6C	1.296	ns
		PROC CTRL vs CTRL	0.32068	ns
		PROC CTRL vs +2°C	4.427	*
		PROC CTRL vs +6°C	9.065	**
	Sandy	CTRL vs +2°C	6.097	**
		CTRL vs +6°C	1.216	***
		+2°C vs +°6C	8.464	*
		PROC CTRL vs CTRL	2.194	ns
		PROC CTRL vs +2°C	0.453	ns

PROC CTRL vs +6°C	1.556	ns
CTRL vs +2°C	2.049	ns
CTRL vs +6°C	0.711	ns
+2°C vs +°6C	1.296	ns

Table S5.8. Oxygen (O₂) and ammonium (NH₄⁺) fluxes in the sediment of the Santa Gilla lagoon during the experiments in all treatments and day. Average and standard errors (SE; n=3) are reported.

Sediment	Treatment	Day	O ₂ flux μmol m ⁻² h ⁻¹		NH ₄ ⁺ μmol m ⁻² h ⁻¹	
			avg	SE	avg	SE
Muddy	CTRL	1.00	-3837.50	267.44	763.80	212.32
		2.00	-4863.38	118.57	-103.99	812.60
		3.00	-4427.73	204.67	222.91	911.89
		4.00	-4401.93	196.80	604.92	153.96
		5.00	-3823.12	311.35	539.67	110.56
		Average	-4270.73	197.63	405.46	154.77
	+2°C	1.00	-5230.65	555.45	351.00	336.12
		2.00	-4732.62	166.35	334.26	156.79
		3.00	-4078.97	521.86	1293.70	182.00
		4.00	-4641.89	201.86	769.66	530.59
		5.00	-4342.38	246.67	142.55	131.64
		Average	-4605.30	194.26	578.23	206.10
	+6°C	1.00	-7549.66	547.65	53.98	236.16
		2.00	-5298.94	384.66	899.66	774.41
		3.00	-6165.40	122.73	508.62	900.53
		4.00	-5958.62	138.75	154.86	910.97
		5.00	-5541.14	302.52	-205.49	67.21
		Average	-6102.75	392.41	282.33	192.18
Sandy	CTRL	1.00	-2947.73	83.01	99.86	16.09
		2.00	-3220.71	478.48	93.05	35.05
		3.00	-2745.94	163.95	82.83	35.63
		4.00	-3118.43	258.51	63.70	9.35
		5.00	-3133.71	404.27	39.90	23.79
		Average	-3033.30	84.37	75.87	10.87
	+2°C	1.00	-4191.68	135.04	80.26	39.19
		2.00	-3576.22	354.09	69.93	26.91
		3.00	-3511.26	217.67	79.04	19.06
		4.00	-2982.08	323.87	122.56	11.83
		5.00	-3415.29	255.64	100.79	45.91
		Average	-3535.30	194.11	90.51	9.47
	+6°C	1.00	-4946.31	552.19	97.80	32.07
		2.00	-5012.44	325.65	182.46	40.66
		3.00	-4071.51	85.48	130.01	23.58
		4.00	-4088.74	119.05	186.96	102.37
		5.00	-4087.84	27.73	216.58	47.86
		Average	-4441.37	219.91	162.76	21.40

Table S5.9. Results of the post hoc tests with Tukey's correction for the interaction Treatment $\times$ Time for O₂ flux in the sediments of the Santa Gilla lagoon. T = statistic t; P = probability level. *** = p < 0.001; ** = p < 0.01; * = p < 0.05; ns = not significant.

Day	Contrast	t	p value
Day 1	CTRL vs "+2°C"	-4.290	***
Day 2		-0.366	ns
Day 3		-0.678	ns
Day 4		-0.169	ns
Day 5		-1.303	ns
Day 1	CTRL vs "+6°C"	-9.289	***
Day 2		-3.623	**
Day 3		-4.925	***
Day 4		-4.111	***
Day 5		-4.347	***
Day 1	"+2°C" vs "+6°C"	5.000	***
Day 2		3.257	**
Day 3		4.248	***
Day 4		3.942	***
Day 5		3.044	*

Table S5.10. Results of the post hoc tests with Tukey's correction for the interaction Sediment × Treatment × Time for O₂ flux in the sediments of the Santa Gilla lagoon. T = statistic t; P = probability level. *** = p < 0.001; ** = p < 0.01; * = p < 0.05; ns = not significant.

		Contrast	t.ratio	p.value
Muddy	Day 1	CTRL vs "+2°C"	-3.2048935	**
	Day 2	CTRL vs "+2°C"	0.30080143	ns
	Day 3	CTRL vs "+2°C"	0.80232844	ns
	Day 4	CTRL vs "+2°C"	-0.5520046	ns
	Day 5	CTRL vs "+2°C"	-1.1945511	ns
	Day 1	CTRL vs "+6°C"	-8.539675	***
	Day 2	CTRL vs "+6°C"	-1.0019823	ns
	Day 3	CTRL vs "+6°C"	-3.9157163	***
	Day 4	CTRL vs "+6°C"	-3.5810969	**
	Day 5	CTRL vs "+6°C"	-3.9522471	***
	Day 1	" +2°C" vs "+6°C"	5.33478147	***
	Day 2	" +2°C" vs "+6°C"	1.30278377	ns
	Day 3	" +2°C" vs "+6°C"	4.7180447	***
	Day 4	" +2°C" vs "+6°C"	3.02909232	*
	Day 5	" +2°C" vs "+6°C"	2.75769605	*
Sandy	Day 1	CTRL vs "+2°C"	-2.8616415	*
	Day 2	CTRL vs "+2°C"	-0.8178199	ns
	Day 3	CTRL vs "+2°C"	-1.7605798	ns
	Day 4	CTRL vs "+2°C"	0.31366603	ns
	Day 5	CTRL vs "+2°C"	-0.6477677	ns
	Day 1	CTRL vs "+6°C"	-4.5976371	***
	Day 2	CTRL vs "+6°C"	-4.1217908	***
	Day 3	CTRL vs "+6°C"	-3.0494163	*
	Day 4	CTRL vs "+6°C"	-2.2321519	ns
	Day 5	CTRL vs "+6°C"	-2.1949376	ns
	Day 1	" +2°C" vs "+6°C"	1.73599564	ns
	Day 2	" +2°C" vs "+6°C"	3.30397089	**
	Day 3	" +2°C" vs "+6°C"	1.28883649	ns
	Day 4	" +2°C" vs "+6°C"	2.54581795	*
	Day 5	" +2°C" vs "+6°C"	1.54716993	ns

Table S5.11. Contents of proteins (cPRT), carbohydrates (cCHO), lipids (cLIP), biopolymeric C (BPC) and total phytopigments (CPE), algal fraction of BPC (CCPE:BPC) and protein to carbohydrate ratio (PRT:CHO), C degradation rate and turnover time in Santa Gilla lagoon sediments with different texture exposed to the different treatments. Average and standard errors (SE; n=3) are reported for each level

Sediment	Treatment	cPRT (mgC g ⁻¹)		cCHO (mgC g ⁻¹)		cLIP (mgC g ⁻¹)		BPC (mgC g ⁻¹)		CPE (µgC g ⁻¹)	
		avg	ES	avg	ES	avg	ES	avg	ES	avg	ES
Muddy	PROC CTRL	0.77	0.1	0.65	0.1	0.6	0.02	2.03	0.18	8.84	0.41
	CTRL	1.28	0.14	1.08	0.01	0.63	0.05	3	0.12	15.2	1.59
	+2 °C	1.39	0.24	0.75	0.14	0.32	0.04	2.46	0.14	11.77	0.05
	+6 °C	1.83	0.31	1.06	0.08	0.58	0.01	3.47	0.28	14.24	1.99
Sandy	PROC CTRL	0.56	0.02	0.99	0.1	0.08	0.00	1.63	0.12	9.56	2.83
	CTRL	0.49	0.09	0.44	0.09	0.2	0.02	1.13	0.17	3.27	0.14
	+2 °C	0.73	0.16	0.65	0.07	0.15	0.01	1.53	0.17	9.97	0.41
	+6 °C	1.23	0.25	0.53	0.05	0.29	0.02	2.04	0.26	6.87	0.5

Sediment	Treatment	PRT:CHO		CCPE:BPC (%)		C degradation rates (µgC g ⁻¹ h ⁻¹)		C turnover time (Days)	
		avg	ES	avg	ES	avg	ES	avg	ES
Muddy	PROC CTRL	13.23	0.92	1.19	0.08	8.34	1.59	3.59	1.17
	CTRL	15.34	2.01	1.19	0.12	7.1	0.79	6.36	0.67
	+2 °C	14.41	0.77	2.12	0.74	2.45	0.46	18.05	3.97
	+6 °C	12.43	1.79	1.77	0.39	2.49	0.02	22.09	2.32
Sandy	PROC CTRL	17.15	4.09	0.58	0.04	6.35	0.51	4.42	0.23
	CTRL	9.04	1.18	1.18	0.3	7.45	0.32	2.3	0.21
	+2 °C	20.15	2.69	1.17	0.74	13.4	0.46	1.91	3.97
	+6 °C	10.51	1.64	2.39	0.57	7.1	1.45	4.88	0.28

Table S5.12. Results of the post-hoc tests ascertain difference in contents of proteins (cPRT), carbohydrates (cCHO), lipids (cLIP), biopolymeric C (BPC) and total phytopigments (CPE), OM composition, C degradation rate and C turnover time between typologies of the sediments from the Santa Gilla lagoon in all treatments. T = statistic t; P(MC) = probability level after Monte Carlo simulation. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; ns = not significant.

		Contrasts	t	P(MC)
PRT	P-CTRL	Muddy vs Sandy	4.877	**
	CTRL		6.476	**
	+2°C		1.866	ns
	+6°C		3.185	**
CHO	P-CTRL	Muddy vs Sandy	2.339	ns
	CTRL		6.978	**
	+2°C		0.657	ns
	+6°C		5.800	**
LIP	P-CTRL	Muddy vs Sandy	29.28	***
	CTRL		7.6923	**
	+2°C		4.1129	*
	+6°C		13.471	***
BPC	P-CTRL	Muddy vs Sandy	1.804	ns
	CTRL		9.086	**
	+2°C		4.208	**
	+6°C		3.741	*
CPE	P-CTRL	Muddy vs Sandy	0.253	ns
	CTRL		7.465	**
	+2°C		4.392	**
	+6°C		3.598	*
OM Composition	P-CTRL	Muddy vs Sandy	4.877	**
	CTRL		6.476	**
	+2°C		1.866	ns
	+6°C		3.185	*
C degradation rate	P-CTRL	Muddy vs Sandy	1.192	ns
	CTRL		0.414	ns
	+2°C		19.591	***
	+6°C		3.181	*
C turnover time	P-CTRL	Muddy vs Sandy	0.695	ns
	CTRL		5.529	**
	+2°C		4.062	*
	+6°C		7.377	**

Table S5.13. Results of the post-hoc tests ascertaining difference in contents of proteins (cPRT), carbohydrates (cCHO), lipids (cLIP), biopolymeric C (BPC) and total phytopigments (CPE), OM composition, algal fraction of BPC (CCPE:BPC) and protein to carbohydrate ratio (PRT:CHO), C degradation rate and C turnover time between sediment typologies from the Santa Gilla lagoon in all treatments. T = statistic t; P(MC) = probability level after Monte Carlo simulation. *** = p < 0.001; ** = p < 0.01; * = p < 0.05; ns = not significant.

		Contrasts	t	P(MC)
PRT	Muddy	P-CTRL vs CTRL	2.973	*
		P-CTRL vs +2°C	2.373	ns
		P-CTRL vs +6°C	3.270	*
		CTRL vs +2°C	0.380	ns
		CTRL vs +6°C	1.600	ns
		+2°C vs +6°C	1.113	ns
	Sandy	P-CTRL vs CTRL	0.813	ns
		P-CTRL vs +2°C	1.059	ns
		P-CTRL vs +6°C	2.657	*
		CTRL vs +2°C	1.333	ns
		CTRL vs +6°C	2.791	*
		+2°C vs +6°C	1.670	ns
CHO	Muddy	P-CTRL vs CTRL	0.113	*
		P-CTRL vs +2°C	0.608	ns
		P-CTRL vs +6°C	0.113	*
		CTRL vs +2°C	0.105	ns
		CTRL vs +6°C	0.811	ns
		+2°C vs +6°C	0.202	ns
	Sandy	P-CTRL vs CTRL	0.471	ns
		P-CTRL vs +2°C	0.350	ns
		P-CTRL vs +6°C	0.051	ns
		CTRL vs +2°C	0.248	ns
		CTRL vs +6°C	0.056	ns
		+2°C vs +6°C	0.169	ns
LIP	Muddy	P-CTRL vs CTRL	0.547	ns
		P-CTRL vs +2°C	6.294	**
		P-CTRL vs +6°C	1.537	ns
		CTRL vs +2°C	4.648	**
		CTRL vs +6°C	1.095	ns
		+2°C vs +6°C	6.086	**
	Sandy	P-CTRL vs CTRL	5.455	**
		P-CTRL vs +2°C	5.852	**
		P-CTRL vs +6°C	9.520	***
		CTRL vs +2°C	2.128	ns
		CTRL vs +6°C	2.961	*
		+2°C vs +6°C	5.874	**
BPC	Muddy	P-CTRL vs CTRL	4.468	**
		P-CTRL vs +2°C	1.899	ns
		P-CTRL vs +6°C	4.293	*
		CTRL vs +2°C	2.931	*
		CTRL vs +6°C	1.541	ns
		+2°C vs +6°C	3.195	*
	Sandy	P-CTRL vs CTRL	2.451	ns
		P-CTRL vs +2°C	0.495	ns
		P-CTRL vs +6°C	1.432	ns
		CTRL vs +2°C	1.660	ns
		CTRL vs +6°C	2.947	*
		+2°C vs +6°C	1.639	ns
CPE	Muddy	P-CTRL vs CTRL	3.868	*
		P-CTRL vs +2°C	7.062	**
		P-CTRL vs +6°C	2.661	ns
		CTRL vs +2°C	2.155	ns
		CTRL vs +6°C	0.376	ns

	Sandy	+2°C vs +°6C	1.244	ns
		P-CTRL vs CTRL	2.224	ns
		P-CTRL vs +2°C	0.142	ns
		P-CTRL vs +6°C	0.938	ns
		CTRL vs +2°C	15.611	***
		CTRL vs +6°C	6.983	**
		+2°C vs +°6C	4.831	**
CCPE:BPC		P-CTRL vs CTRL	1.249	ns
		P-CTRL vs +2°C	0.831	ns
		P-CTRL vs +6°C	1.537	ns
		CTRL vs +2°C	2.797	*
		CTRL vs +6°C	0.432	ns
		+2°C vs +°6C	3.145	**
PRT:CHO		P-CTRL vs CTRL	1.249	ns
		P-CTRL vs +2°C	0.831	ns
		P-CTRL vs +6°C	1.537	ns
		CTRL vs +2°C	2.797	*
		CTRL vs +6°C	0.432	ns
		+2°C vs +°6C	3.145	**
C degradation rates	Muddy	P-CTRL vs CTRL	0.702	ns
		P-CTRL vs +2°C	3.557	*
		P-CTRL vs +6°C	3.675	*
		CTRL vs +2°C	5.108	*
		CTRL vs +6°C	5.856	**
		+2°C vs +°6C	0.092	ns
	Sandy	P-CTRL vs CTRL	1.849	ns
		P-CTRL vs +2°C	11.744	**
		P-CTRL vs +6°C	0.487	ns
		CTRL vs +2°C	13.499	***
		CTRL vs +6°C	0.234	ns
		+2°C vs +°6C	4.250	*
C turnover time	Muddy	P-CTRL vs CTRL	2.051	ns
		P-CTRL vs +2°C	3.495	*
		P-CTRL vs +6°C	7.124	**
		CTRL vs +2°C	2.907	*
		CTRL vs +6°C	6.528	**
		+2°C vs +°6C	0.879	ns
	Sandy	P-CTRL vs CTRL	5.508	**
		P-CTRL vs +2°C	8.075	**
		P-CTRL vs +6°C	1.261	ns
		CTRL vs +2°C	1.056	ns
		CTRL vs +6°C	6.195	**
		+2°C vs +°6C	8.507	***

Chapter 6: Effects of seasonality and episodic dystrophy on sedimentary organic loads and meiobenthic communities in a Sardinian lagoon (S'Ena Arrubia)

6.1 Introduction

Coastal lagoons are semi-enclosed, shallow aquatic transitional ecosystems, separated from the sea by physical barriers such as sandbanks, shingle, or rocks, and connected to it through one or more inlets (Pérez-Ruzafa et al., 2011; Cataudella et al., 2015; Newton et al., 2018). Covering 13% of the world's coastline (Barnes, 1980), the Mediterranean Sea alone contains over 400 lagoons (~6,400 km²) (Cataudella et al., 2015), with Sardinia hosting the largest number and highest surface of lagoons of the entire Italian coastline (Abbiati et al., 2010).

These transitional ecosystems are highly productive and biodiverse and provide essential ecosystem services (flood control, nutrient and sediment retention, water purification, biodiversity conservation, and local climate regulation). At the same time, these services allow sustaining fundamental human activities such as fisheries, aquaculture, tourism, and recreation (Danovaro and Pusceddu, 2007; Newton et al., 2018; Cataudella et al., 2015; Amaral et al., 2023). Nonetheless, many of these activities, like agriculture, aquaculture, and tourism, if not kept within boundaries of sustainability, make coastal lagoons furtherly vulnerable also to other anthropogenic pressures, like industrial discharges, that jointly contribute to nutrient enrichment and environmental degradation (Newton et al., 2014, 2018; Cloern et al., 2016; Newton et al., 2020).

Coastal lagoons are naturally exposed to strong environmental gradients that render them physically unstable and prone to episodic meteorological events, like floods (León et al., 2017; Machado Toffolo et al., 2022). Nutrient overloads from human activities, combined with those caused by these phenomena, can impair ecological processes, sometimes triggering eutrophication and dystrophic crises, the latter being triggered also by elevated summer temperatures associated with heatwaves (Ennas et al., 2025; Zaldívar et al., 2003; Derolez et al., 2020; Fernández-Alías et al., 2022). Future climate change scenarios, with more frequent and intense heatwaves, are expected to exacerbate these events (Lloret and Marín, 2009). The derived disruptions will likely compromise lagoons functioning and reduce their capacity to sequester nutrients and carbon, ultimately affecting their role in climate mitigation (Hopkinson et al., 2012).

Nutrient pollution causing eutrophication stimulates excessive primary production of phytoplankton and macroalgae. This, along with limited water exchange with the sea, can lead to

temporary oxygen depletion and accumulation of toxic compounds, ultimately causing mass mortality of aquatic organisms and biodiversity loss (Cloern, 2001; Pannard et al., 2024). Unfortunately, assessing the response of coastal lagoons to these episodic dystrophic events isn't possible with single indicators, since they rarely capture the complexity of these dynamics (McQuatters-Gollop et al., 2009). Traditionally, parameters such as inorganic phosphorus and chlorophyll-a concentrations in water, and water turbidity have been used alone or jointly in algorithms (Vollenweider et al., 1998), but these, especially in shallow, dynamic systems, may not fully reflect primary production patterns nor organic C degradation processes priming dystrophy, which are initiated typically on the bottoms (Dell'Anno et al., 2002; Pusceddu et al., 2009).

Trophic conditions of coastal lagoon sediments, besides being influenced by hydrodynamics and sedimentological patterns, are influenced also by many concurrent biological mechanisms that include organic C in situ production, heterotrophic consumption and microbe-mediated degradation. Trophic status of sediments is generally more conservative than that of the water column, and this holds particularly true in shallow water ecosystems, like coastal lagoons. Indeed, the faster hydrological and biological dynamics in the water column make descriptors of waters' trophic state far more variable (thus than those in the sediment (Dell'Anno et al., 2002). Most investigations on sediment trophic status in coastal lagoons have been carried out considering total organic C (TOC) contents, which, however, do not distinguish between refractory and labile fractions (Pusceddu et al., 2009). In this regard, the trophic status of coastal lagoons, has been increasingly assessed in terms of contents, biochemical composition and nutritional quality of their organic deposits (Manini et al., 1999; Pusceddu et al., 2011). More in details, the biopolymeric fraction of organic C (as the sum of protein, carbohydrate and lipid C equivalents, hereafter BPC) has been increasingly used for this purpose, as it combines quantitative and qualitative information (Fabiano et al., 1995; Pusceddu et al., 2009).

In addition to BPC, the proportion of algal-derived material (the ratio of phytopigment converted in carbon equivalents to BPC) has been also recurrently used as a companion descriptor of benthic trophic web, as algal-derived material is tightly associated with the most labile fraction of sedimentary organic C (Pusceddu et al., 2003). These proxies are inversely related: eutrophic sediments exhibit high BPC and low algal contributions to BPC, whereas oligotrophic sediments display the opposite pattern (Pusceddu et al., 2009). Other indicators like the protein-to-BPC and protein-to-carbohydrate ratios provide insights into the freshness and nutritional quality of sedimentary organic matter, with higher values of both indicating more recently produced, and

more labile material, due to the more reactive nature of proteins over carbohydrates (Pusceddu et al., 2000; Dell'Anno et al., 2002; Pusceddu et al., 2009). These sedimentary proxies, alone or combined, have been repeatedly applied across a variety of aquatic environments, including deep-sea ecosystems (Pusceddu et al., 2010), highlighting their robustness in evaluating trophic status over time and across most aquatic environments.

Changes in sediments trophic status can conceivably have cascading effects on benthic communities. Meiofauna — small organisms ranging from 30 to 500 μm — are the most abundant benthic metazoans (Giere et al., 2009) and play key roles in organic C remineralization and energy transfer to higher trophic levels (Schratzberger and Ingels, 2018). They mainly feed on microalgae, prokaryotes, or detritus and serve as essential components of marine food webs (Bianchelli et al., 2016).

Meiofaunal communities respond rapidly to changes in abiotic factors, including temperature, hydrodynamics, oxygen, and food availability (Coull, 1999; Ingels et al., 2011; Pusceddu et al., 2014), as well as biotic factors (Danovaro et al., 2007; Nascimento et al., 2011). They are also sensitive to environmental disturbances such as pollution, eutrophication, and climate change (Pusceddu et al., 2007; Zeppilli et al., 2015; Bianchelli et al., 2016b). Their short generation times and limited larval dispersal enhance this sensitivity, making meiofauna reliable bioindicators for coastal lagoon ecological health (Danovaro et al., 2004; Pusceddu et al., 2007; Carugati et al., 2018; Semprucci et al., 2019b).

With these premises in mind, this chapter aims to investigate spatial and temporal changes in organic matter quantity, composition, nutritional quality and degradation and meiofauna in the S'Ena Arrubia Lagoon, located on the central-western coast of Sardinia, Italy (Western Mediterranean). Moreover, this study aims to assess the present ecological condition of the S'Ena Arrubia Lagoon and explore its potential susceptibility to future climate-driven stressors by interpreting current ecological patterns in light of processes influenced by climate change. In this sense, I specifically tested the null hypothesis that sedimentary organic matter features and meiofaunal communities do not vary across seasons and along a confinement gradient. Additionally, I also assessed the biogeochemical characteristics, meiofaunal abundance, and taxonomic richness of lagoon sediments during and immediately after a major dystrophic crisis that occurred in May 2024.

6.2 Material and Methods

6.2.1 Study area

The study was carried out in the S'Ena Arrubia (OR) lagoon, a brackish (salinity levels ranging from 0.9 to 39.5) and shallow coastal wetland (average depth of 0.4 m), located in the Gulf of Oristano (Central-Western coast of Sardinia, Italy) (Figure 6.1) (Frongia et al., 2023). The lagoon spans in a small area of 120 hectares (Frongia et al., 2023) and is the residual wetland left from the drying up of a larger original lagoon of over 3000 hectares (Trebini et al., 2005).

It is connected to the sea by means of a single artificial channel built in the 1970s and widened in 2000 (35 m width, 0.7-2.0 m depth) (Frongia et al., 2023). Freshwater inputs come from the lagoon by three main channels: Rio Sant'Anna (also called 'Diversivo'), Canale delle Acque Basse (also called 'Idrovora') and Canale delle Acque Medie (Trebini et al., 2005). The surrounding area is primarily characterized by farming and intensive agricultural activities, receiving inputs rich in nitrogen and phosphorus. Consequently, the lagoon is characterized by high levels of primary production and is ranked as eutrophic (Frongia et al., 2023). Due to its ecological value and richness in biodiversity, S'Ena Arrubia lagoon is, also, designated under the Ramsar Convention (1971) and classified as SCIs (Site of Community Importance) under the Habitats Directive (92/43/EEC), SPAs (Special Protection Area) under the Birds Directive 2009/147/EC, and recognized as an important permanent oasis for wildlife protection and conservation (Sardinia regional law LR 31/1998) (Fois et al., 2021)".

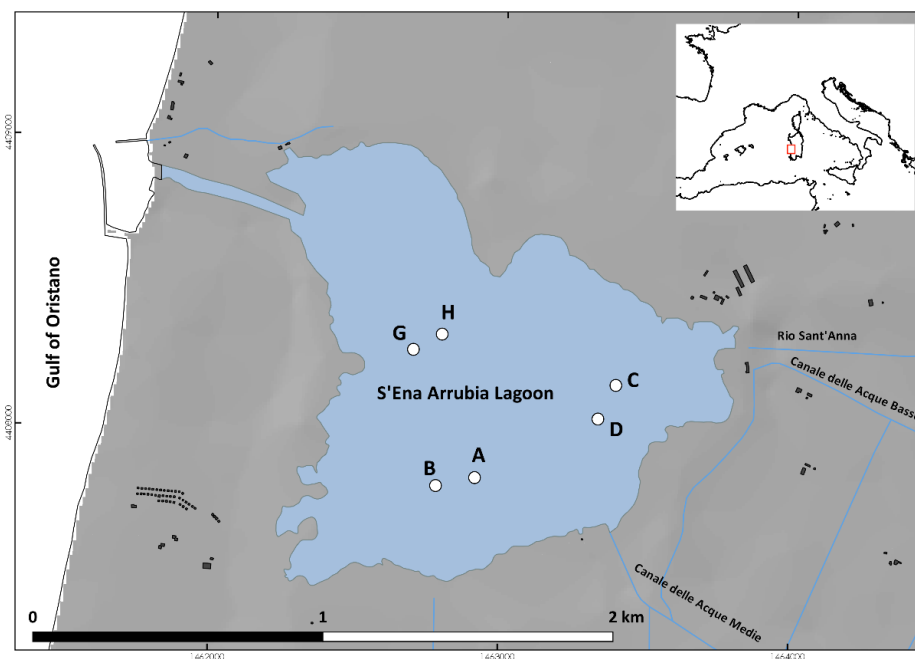


Figure 6.1. Study area and sediment sampling location. Coordinate reference system (EPSG: 3003).

6.2.2 Environmental variables

At each station and sampling date, water salinity, temperature (°C) and dissolved oxygen concentration ($\text{mgO}_2 \text{ L}^{-1}$) were recorded using a multi-parameter probe (In-Situ Inc. Smart Troll MP).

For sediment grain size analyses, aliquots of sediment were treated with 10% hydrogen peroxide in a large beaker for 24–48h, then wet-sieved using a 0.063 mm diameter mesh sieve and oven-dried at 100 °C until constant weight. Further mechanical sorting of the dried samples was performed using a nest of graded sieves (mesh sizes in mm: 4, 2, 1, 0.5, 0.125, and 0.063) and the weight of each fraction was recorded. The fine-grained fraction was estimated by difference. Sediment grain sizes were then grouped into three categories and expressed as percentage of the initial total dry weight (Gravel > 2 mm; 2 > Sand > 0.063 mm; Mud < 0.063 mm).

6.2.3 Sediment sampling

Sediment sampling was carried out four times a year, approximately every 3 months, from October 2023 to July 2024. An additional sampling campaign was conducted on May 27, 2024, following the dystrophic crisis that occurred during the third week of May. Six stations were selected along a putative gradient of confinement. More in details, stations G and H were in front of the lagoon mouth (outer sector), A and B in the southern and sheltered part of the lagoon (central sector) and C and D in front of the main freshwater inputs (inner sector). Within each station, 3 independent replicates of the topmost 1 cm of sediment samples per station were collected using plexiglass cores for the sedimentary OM quantity, biochemical composition, and degradation rates and the abundance and diversity of meiofauna. The sediment samples were kept at *in situ* temperature till brought to the laboratory and then immediately stored in Petri dishes at -20 °C until the analysis.

6.2.4 OM quantity, biochemical composition, nutritional quality and degradation rates

The first layer (0–1 cm) of each sediment core was analyzed to determine the quantity, biochemical composition, and degradation rates of sedimentary organic matter, following the protocols detailed in Danovaro (2010). Protein, carbohydrate, and lipid concentrations were determined spectrophotometrically (Danovaro, 2010). Total protein content was measured according to Lowry et al. (1951), as modified by Hartree (1972) and Rice (1982), based on the reaction of proteins with cupric tartrate and the Folin–Ciocalteu reagent in alkaline environment. Total carbohydrate content was determined according to Dubois et al. (1956), optimized for sediments by Gerchacov

and Hatcher (1972) with minor modifications; this method relies on the reaction of saccharides with phenol in the presence of concentrated sulfuric acid. Total lipid concentrations were determined according to Bligh and Dyer (1959) and Marsh and Weinstein (1966), slightly modified for sediment analysis. In this method, lipids are extracted in chloroform: methanol (1:1), evaporated in a dry hot bath at 100 °C, and carbonized with sulfuric acid. Protein, carbohydrate and lipid concentrations were normalized to sediment dry weight (24 h at 60°C; mg g⁻¹) and then, converted into carbon equivalents using conversion factors of 0.49, 0.40, and 0.75 mg C mg⁻¹ derived from the carbon content of bovine serum albumin (BSA), D (+) glucose, and tripalmitin, respectively, used as standards. Their sum was expressed as biopolymeric carbon (BPC) (Fabiano et al., 1995).

Chlorophyll-a and phaeopigment contents were determined fluorometrically (Danovaro, 2010). Briefly, pigments were extracted from 1 g sediment aliquots with 5 mL of 90 % acetone (overnight at 4°C in the dark). Extracts were analyzed at 430 nm excitation and 665 nm emission wavelengths to estimate chlorophyll-a (Chl-a), and, after acidification with 200µL 0.1N HCl, phaeopigment concentrations. Total phytopigments (as sum of chlorophyll-a and phaeopigment) were converted into C equivalents using a 40 mgC mg⁻¹ as a conversion factor and used to estimate the amount of organic material of autotrophic origin (Pusceddu et al., 2010).

Potential carbon degradation rates were estimated from aminopeptidase and β-glucosidase activities, measured by the cleavage of fluorogenic substrates (L-leucine-4-methylcoumarinyl-7-amide and 4 methylumbelliferone-D-glucopyranoside, respectively) at saturating concentrations (Bianchelli et al., 2020). Prefiltered (0.2 µm) and autoclaved seawater containing the specific substrate up to the final volume of 5 mL were added to 2.5 mL aliquots of the sediment (Danovaro, 2010). The sample incubations were performed in the dark at the in-situ temperature for 1 h, centrifuged (3000 rpm, 5 min) and supernatants were analyzed fluorometrically (at 380 nm excitation and 440 nm emission for aminopeptidase and at 365 nm excitation and 455 nm emission for β-glucosidase) (Bianchelli et al., 2020). Activities were normalized to sediment dry weight (60 °C, 24 h) and expressed as nanomoles of substrate released per g of sediment dry weight per hour. Protease and glucosidase activities were converted into C equivalents using 72 as a conversion factor (Pusceddu et al., 2000), and their sum reported as the potential C degradation rate (g C g⁻¹ h⁻¹). The daily turnover rates of the whole protein and carbohydrate pools were calculated as the ratios of the hourly C degradation rates (once multiplied by 24) and the whole protein and carbohydrate C contents in the sediment (Pusceddu et al., 2014).

6.2.5 Abundance, diversity and taxonomical composition of meiofaunal communities

For the quantification of the abundance and taxa richness of meiofauna, the first layer (0–1 cm) of each sediment core was sieved through 500- μm and 30- μm meshes (Danovaro et al., 2010). The fraction collected with on the finest mesh was re-suspended and centrifuged three times with Ludox HS40 (diluted with water to a final density of 1.18 g cm⁻³), according to Danovaro (2010). After centrifugation, the supernatant was passed again through a 30- μm mesh net, washed with tap water and the material retained on the net stored in 50 mL Falcon tubes, fixed with ethanol (70%) and stained with Rose Bengal (0.5 g L⁻¹) (Danovaro et al., 2010). Despite 4% buffered formalin is still considered the best fixative for morphological identification of meiofaunal communities, ethanol-based fixatives are considered as safer alternatives for morphological and molecular analysis (Garraffoni et al., 2017; Rahman et al., 2022). All animals were counted and identified at the highest taxonomic level under a stereomicroscope (x40 magnification). The abundance of individuals from each core was expressed as number of individuals in 10 cm² $\pm$ standard error (SE; n=3). Alpha richness was expressed as richness of meiofaunal higher taxa.

6.2.6 Statistical analyses

A priori non-metric multidimensional scaling (nMDS), based on Euclidean distance matrices of normalized data, was used to ordinate either sediments grain size (muddy, sand and gravel fractions) or water environmental variables (salinity, temperature and dissolved oxygen). Prior to analysis, the environmental variables were tested for collinearity (Draftsman plot and Spearman correlation matrix). Sand and Gravel fractions were thus omitted from the analysis because tightly correlated with mud % ($\rho > 0.90$). For a more general characterization of spatial-temporal variation in environmental variables, the results of a hierarchical cluster analysis, based on the Euclidean matrix, were overlaid on nMDS graph.

To test the null hypothesis by which organic matter (OM) quantity, biochemical composition and nutritional quality, extracellular enzymatic activities, abundance, taxa richness and composition of meiofaunal communities do not vary across seasons and along the salinity–trophic gradient, permutational analyses of variance (PERMANOVA) were used (Anderson and Braak, 2003). PERMANOVA tests were carried out in both univariate (BPC, CPE, CCPE:BPC, PRT:CHO, C degradation rate and C turnover time; Nematoda, Copepoda, Ostracoda, Other taxa and total abundance, taxonomical richness) and multivariate (OM biochemical composition; meiofauna community

composition) contexts. Statistical routines were conducted using a design based on two fixed orthogonal factors: Period (P; 5 levels) and Station (S; 6 levels). The analyses on organic matter variables were carried out on Euclidean distance-based resemblance matrices of normalized data, whereas those in meiofauna were carried out on Bray–Curtis similarity matrixes of $\log(x+1)$ transformed abundance data, using 999 random permutations. Prior to PERMANOVA, a PERMDISP test was also performed to test if group dispersions differ, helping separate real compositional differences from differences in spread. (Anderson et al., 2008; Anderson, 2017). In case PERMANOVA tests revealed significant differences among levels, pairwise tests were also carried out. Multivariate differences in the biochemical composition of organic matter were visualized using a biplot after a canonical analysis of the principal coordinates (CAP). CAP enables the identification of patterns that most effectively separates pre-established groups.

A Similarity percentage (SIMPER) analysis was carried out to assess the percentage dissimilarity in the meiofaunal taxonomic composition among periods and stations.

To investigate the relationships between meiofaunal community structure and environmental variables (including OM), I applied distance-based linear models (DistLM). The response matrix consisted of meiofaunal abundances ($\log(x+1)$ transformed), with Bray–Curtis similarity as resemblance measure. Predictor variables included the environmental parameters and organic matter contents (BPC and CPE), previously screened to avoid collinearity. Model selection was carried out using the forward procedure, with 9999 permutations to assess the significance of marginal and conditional tests. The fitted models were visualized by distance-based redundancy analysis (dbRDA) ordinations.

PERMANOVA, PERMDISP, CAP, SIMPER and DistLM tests were carried out using the dedicated routines included in the software PRIMER 6+ (Anderson, 2017).

6.3 Results

6.3.1 Environmental variables

Environmental variables in the lagoon varied significantly either among stations or sampling periods (Figure 6.2 and Table S6.1).

Mean salinity (across all stations) was highest in May (33.78 ± 2.30) and lowest in October (24.56 ± 1.58) (Figure 6.2a). In all seasons, highest salinity occurred generally in the outer lagoon

sector (stations G-H) (31.66 ± 4.38 and 32.52 ± 3.93 , respectively), followed by stations A (28.31 ± 3.22), B (28.08 ± 3.00) and D (28.24 ± 4.399). Station C, nearby the main freshwater input in the lagoon (inner sector), showed the lowest mean value (27.62 ± 4.25).

In all periods, water temperature did not show significant differences among stations but was highest in July (26.59 ± 0.49 °C; average of all stations) and lowest in January (14.83 ± 0.22 °C) (Figure 6.2b).

In all periods but in May, O₂ concentrations showed very limited spatial variability (Figure 6.2c). In May, O₂ concentration in the inner sector (C-D), nearby the freshwater input, approached anoxic conditions (0.05 and 0.14 mgO₂ L⁻¹, respectively). In May, O₂ concentrations were low also in all other stations, with highest values in stations G and H, facing the opening to the sea, (3.35 and 3.02 mgO₂ L⁻¹, respectively). Lowest dissolved O₂ concentrations occurred in May (1.71 ± 1.40 mgO₂ L⁻¹ on average) and showed a clear raising pattern from October (4.41 ± 0.49 mgO₂ L⁻¹ on average) to April (9.82 ± 1.98 mgO₂ L⁻¹ on average). Low values of oxygen concentrations were also measured in July with average of 5.46 ± 0.81 mgO₂ L⁻¹.

Sediments were largely dominated by the sand fraction in most stations and sampling periods (Figure 6.3 and Table S6.1), with the highest contribution measured in the outer sector (stations G and H), near the lagoon opening to the sea ($96 \pm 1.95\%$ and $96 \pm 1.14\%$, respectively). Mud content was higher at the inner stations C and D ($29 \pm 12\%$ and $20 \pm 3\%$). The mud content increased in January at station C, rising from 10% to 43%, and then gradually decreased in subsequent months (Table S6.1).

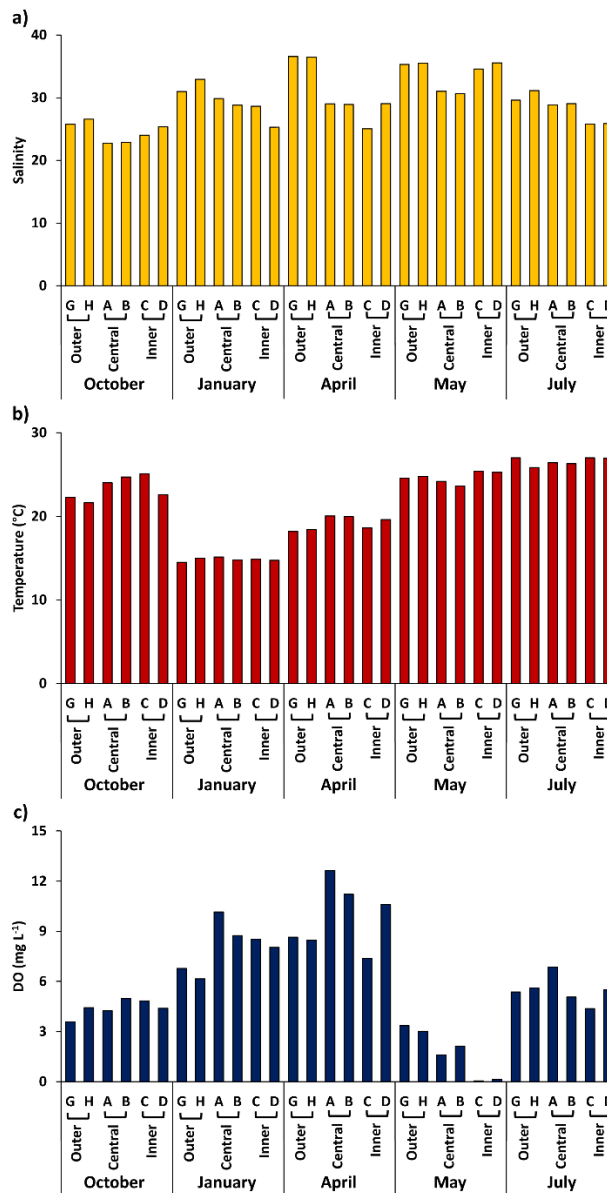


Figure 6.2. Seasonal and spatial variability of near-bottom water salinity, temperature and dissolved oxygen concentrations in the S'Ena Arrubia Lagoon.

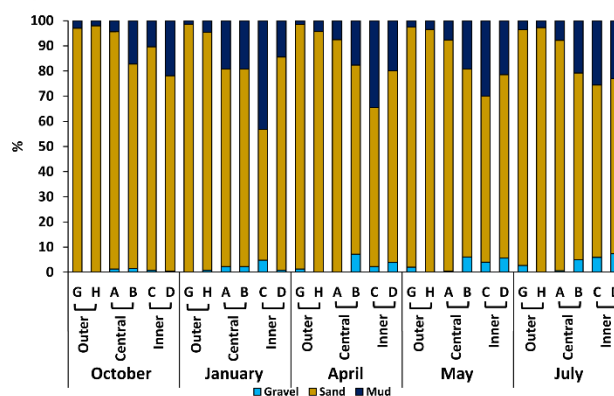


Figure 6.3. Seasonal and spatial variation of sediment granulometry in the S'Ena Arrubia Lagoon.

The nonmetric Multi-Dimensional Scaling MDS (nMDS) ordination revealed a clear segregation of environmental conditions in January and April from those of all other sampling periods (Figure 6.4), mostly led by temperature (lowest) and dissolved oxygen concentrations (highest). Noticeably, conditions in May segregate well apart from those in all other sampling periods, particularly because of lowest dissolved oxygen concentrations.

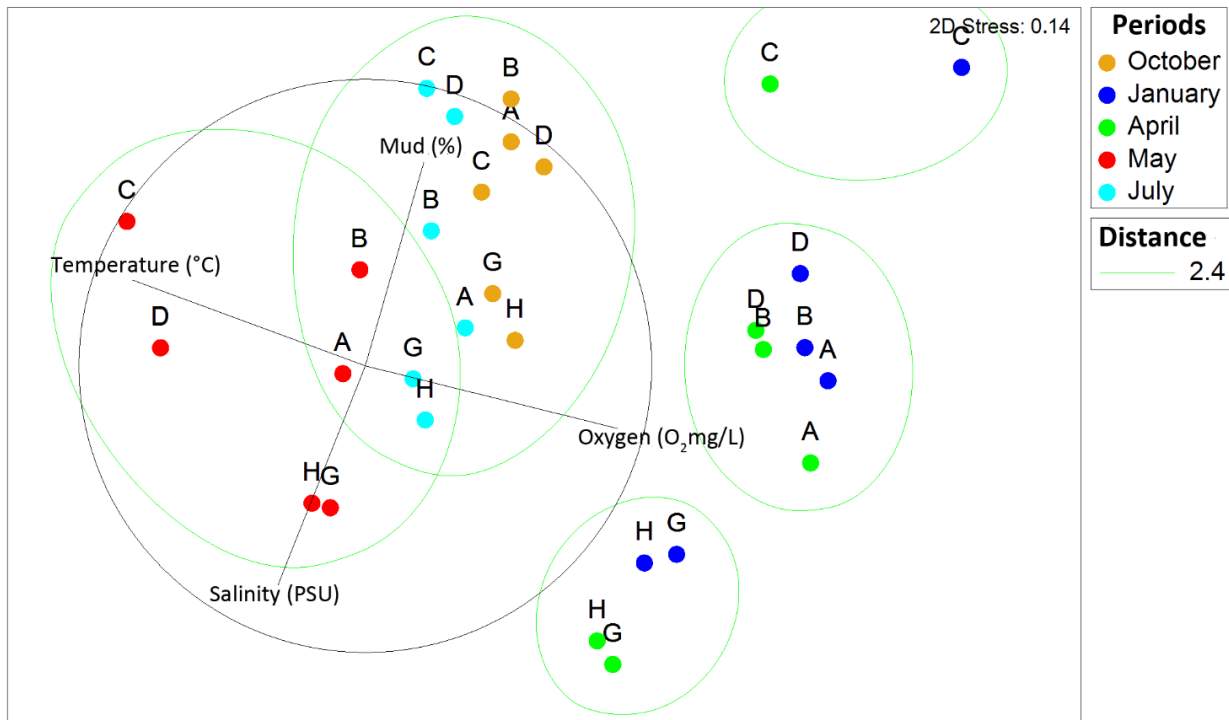


Figure 6.4. Nonmetric multidimensional scaling (nMDS) ordination of the sampling stations based on temperature, salinity and dissolved oxygen in the water and mud fraction of the sediment.

6.3.2 OM quantity and biochemical composition

Biopolymeric carbon (BPC) and total phytopigments (CPE) sedimentary contents, values of the algal fraction of BPC (CCPE:BPC) and for the protein to carbohydrate ratio (PRT:CHO) are reported in Table S6.2. The results of two-way PERMANOVA analysis confirmed statistically significant effects of both factors (period and station) and their interaction (period × station) for all variables (Table 6.1). Variations of BPC and CPE contents and OM biochemical composition were mostly explained by spatial differences. Variations in CCPE:BPC and PRT:CHO were mostly influenced by the interaction of space and time (Table 6.1).

Table 6.1 Results of PERMANOVA testing for spatial and temporal differences in biopolymeric C (BPC), total phytopigment (CPE), algal fraction of BPC (CCPE:BPC), protein to carbohydrate ratio (PRT:CHO) and OM biochemical composition (cPRT, cCHO, cLIP and CPE). Df = degrees of freedom; MS = mean square; Pseudo-F = F statistic; P (MC) = probability after Monte Carlo simulations. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$. %EV = percentage of explained variance.

Variable	Source	Df	MS	F	P(MC)	%EV
BPC	Period (P)	4	2.693	75.46	***	12.1
	Station (S)	5	12.740	356.99	***	69.1
	P × S	20	0.619	17.36	*	15.9
	Residual	60	0.036			2.9
	Total	89				
CPE	Period (P)	4	5.499	69.89	***	23.9
	Station (S)	5	7.519	95.55	***	39.3
	P × S	20	1.234	15.68	***	30.5
	Residual	60	0.079			6.2
	Total	89				
CCPE:BPC	Period (P)	4	3.856	25.28	***	15.4
	Station (S)	5	2.036	13.35	***	9.4
	P × S	20	2.712	17.79	***	63.8
	Residual	60	0.152			11.4
	Total	89				
PRT:CHO	Period (P)	4	1.519	5.09	**	5.1
	Station (S)	5	0.760	2.55	*	2.3
	P × S	20	3.061	10.26	***	69.9
	Residual	60	0.298			22.6
	Total	89				
OM biochemical composition	Period (P)	4	17.593	74.01	***	19.3
	Station (S)	5	37.341	157.08	***	49.4
	P × S	20	4.233	17.81	***	26.6
	Residual	60	0.238			4.7
	Total	89				

BPC and CPE sedimentary contents displayed significant spatial and temporal variability (Figure 6.5, Table S6.2, Figure S6.1-S6.2).

In October, BPC and CPE contents were lowest in station H ($2.09 \pm 0.18 \text{ mgC g}^{-1}$ and $18.16 \pm 2.41 \text{ } \mu\text{gC g}^{-1}$, respectively). Higher BPC contents were observed in station C ($5.69 \pm 0.44 \text{ mgC g}^{-1}$) whereas highest CPE contents occurred in station D ($50.03 \pm 6.26 \text{ } \mu\text{gC g}^{-1}$).

In January, both BPC and CPE contents showed a large spatial heterogeneity, with the lowest concentrations persisting in station H (BPC: $0.26 \pm 0 \text{ mgC g}^{-1}$; CPE: $3.33 \pm 0.12 \text{ } \mu\text{gC g}^{-1}$), and the highest in station C for BPC ($4.87 \pm 0.13 \text{ mgC g}^{-1}$) and in station D for CPE ($34.32 \pm 2.52 \text{ } \mu\text{gC g}^{-1}$).

In April, BPC contents showed persistent spatial heterogeneity with a pattern of variation like the one observed in January. Indeed, the highest values occurred again in station C for both BPC ($4.55 \pm 0.29 \text{ mgC g}^{-1}$) and CPE ($52.04 \pm 6.03 \text{ } \mu\text{gC g}^{-1}$) and the lowest in stations G ($0.67 \pm 0.06 \text{ mgC g}^{-1}$).

g^{-1} and $6.96 \pm 0.77 \mu\text{gC g}^{-1}$, respectively) and H ($1.00 \pm 0.14 \text{ mgC g}^{-1}$ and $9.72 \pm 0.04 \mu\text{gC g}^{-1}$, respectively).

In May, concomitantly with the dystrophic crisis, BPC contents in station C reached the highest values ever ($6.13 \pm 0.03 \text{ mgC g}^{-1}$) and CPE contents ($17.29 \pm 0.16 \mu\text{gC g}^{-1}$) were significantly lower than those measured in April. BPC contents in stations D and B ($3.48 \pm 0.25 \text{ mgC g}^{-1}$ and $4.51 \pm 0.23 \text{ mgC g}^{-1}$, respectively) were second only to those in station C, whereas values in stations G ($1.15 \pm 0.12 \text{ mgC g}^{-1}$), H ($1.01 \pm 0.10 \text{ mgC g}^{-1}$) and A ($1.05 \pm 0.05 \text{ mgC g}^{-1}$) did not vary when compared with those in April and were again the lowest ones. When compared with values in April, CPE sedimentary contents in May decreased significantly in all stations, with the lowest values measured in station H ($2.28 \pm 0.09 \mu\text{gC g}^{-1}$) and highest in station G ($22.79 \pm 3.86 \mu\text{gC g}^{-1}$) and B ($18.71 \pm 7.84 \mu\text{gC g}^{-1}$).

In July BPC contents in station C ($6.29 \pm 0.45 \text{ mgC g}^{-1}$) remained as high as those measured in May. Second to values in station C, BPC contents in station D ($5.34 \pm 0.27 \text{ mgC g}^{-1}$) increased when compared to those measured in May. BPC contents in stations G, H and A remained relatively similar to those in May, resulting again the lowest among all stations (1.56 ± 0.12 , 2.10 ± 0.17 and $0.65 \pm 0.04 \text{ mgC g}^{-1}$, respectively). Values in station B ($1.15 \pm 0.04 \text{ mgC g}^{-1}$) were also low and showed a clear drop when compared to those in May. CPE contents were lowest in stations G ($8.63 \pm 0.41 \mu\text{gC g}^{-1}$) and B ($2.56 \pm 0.14 \mu\text{gC g}^{-1}$) and dropped significantly when compared with values measured in May. In all other stations CPE content remained similar to those in May or slightly increased.

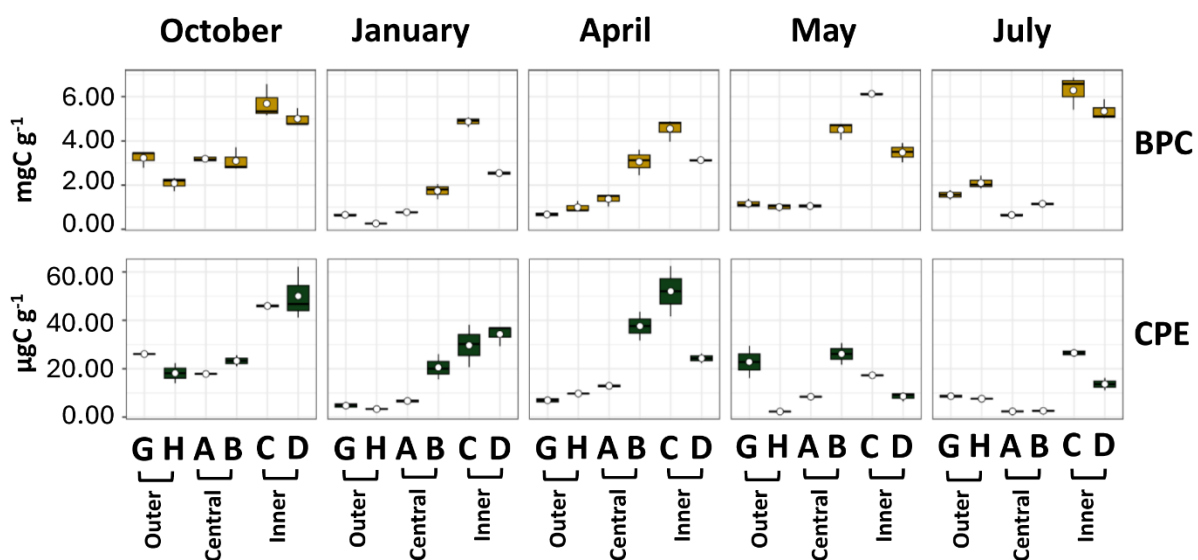


Figure 6.5 Spatial-temporal changes in biopolymeric C (BPC) and total phytopigment (CPE) contents in surface sediments of the lagoon. The median is indicated with a black line and the mean value with the white dot symbol. Boxplots show interquartile ranges (IQR), and whiskers extending to $1.5 \times \text{IQR}$; outliers are values beyond the whiskers.

PERMDISP tests revealed differences in data dispersion. Specifically, significant heterogeneity was detected for the factor "Period" across all variables except PRT:CHO ratio and OM biochemical composition. Likewise, significant heterogeneity was noted for the factor "Station" for all variables but PRT:CHO and BPC (Table 6.2).

Table 6.2 Results of PERMDISP testing for spatial (Station) and temporal (Period) dispersion of biopolymeric C (BPC), total phytopigment (CPE), algal fraction of BPC (CCPE:BPC), protein to carbohydrate ratio (PRT:CHO) and OM biochemical composition (cPRT, cCHO, cLIP and CPE). Df = degrees of freedom; Pseudo-F = F statistic; P (perm) = probability after permutations. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; ns = not significant.

Variable	Source	Df	PermDisp-F	P(perm)
Biopolymeric C (BPC)	Period (P)	4	3.969	*
	Station (S)	5	1.532	ns
	P ∩ S	29	4.105	**
Total phytopigment (CPE)	Period (P)	4	4.367	*
	Station (S)	5	5.192	**
	P ∩ S	29	3.217	ns
CCPE:BPC	Period (P)	4	10.596	***
	Station (S)	5	3.349	*
	P ∩ S	29	5.329	**
PRT:CHO	Period (P)	4	1.899	ns
	Station (S)	5	0.720	ns
	P ∩ S	29	2.626	ns
OM Biochemical Composition	Period (P)	4	0.942	ns
	Station (S)	5	20.224	***
	P ∩ S	29	7.021	**

Results of the pairwise tests investigating differences in the biochemical composition of sedimentary OM among periods for each station and differences among stations in each period are illustrated in Figures S6.1-S6.2. The biplots obtained after the CAP analysis to illustrate such differences revealed that in October the OM biochemical composition was rather homogenous among stations, whereas in January and April stations facing the opening to the sea (outer sector, stations G-H) and one of the most central and sheltered stations (A) segregated well apart from the others, mostly due to the lowest concentrations of all biochemical compounds (Figure 6.6). In January stations C and D (inner sector), though located in the same putative conditions (i.e. close to the main freshwater tributary) were well different one each other, due to higher carbohydrate contents in station C and higher phytopigment contents in station D. In April, station B segregated well apart from the others, due to higher lipid contents. In May (dystrophic crisis) and, though at a lesser extent, in July, station C segregated from all the others, due to an accumulation of all biochemical compounds. The biplot obtained after the CAP analysis shows also differences among

sampling periods in each station, with the biochemical composition of OM in May generally far different from that in all other periods, mostly because of higher OM contents (Figure 6.6).

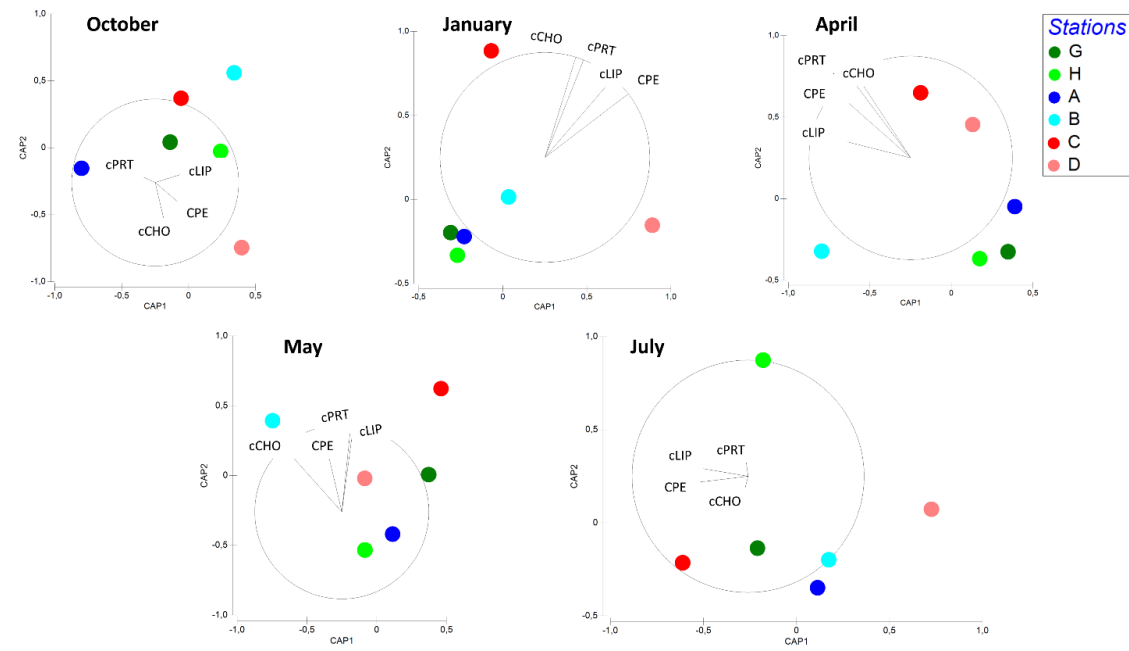


Figure 6.6. Biplot obtained after the CAP analysis showing differences in the biochemical composition of sedimentary organic matter among stations in each sampling period. Vectors are proportional to the percentage of differences explained by the different biochemical components. cPRT = protein; cCHO = carbohydrate; cLIP = lipid; CPE = total phytopygments.

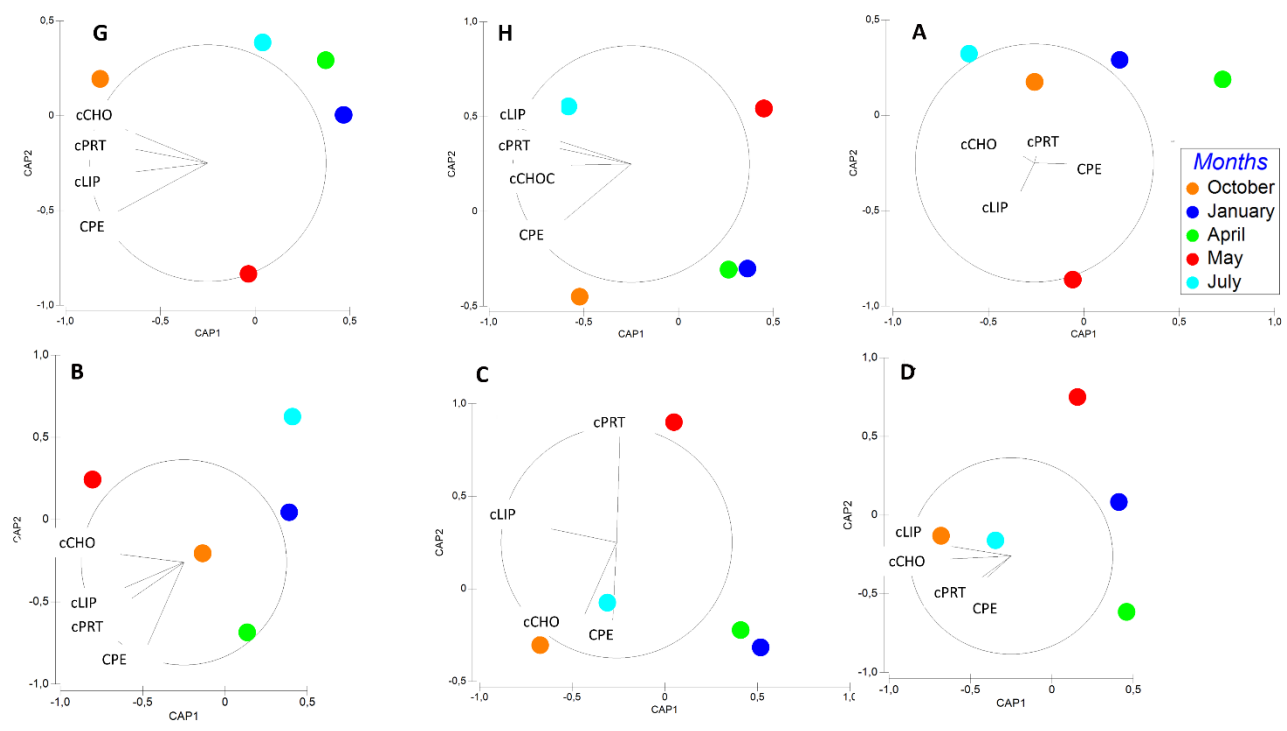


Figure 6.7. Biplot obtained after the CAP analysis showing differences in the biochemical composition of sedimentary organic matter among periods in each station. Vectors are proportional to the percentage of

differences explained by the different biochemical components. cPRT = protein; cCHO = carbohydrate; cLIP = lipid; CPE = total phytopigments.

6.3.2.1.OM nutritional quality

The algal fraction of biopolymeric C and the values of the protein to carbohydrate ratio (PRT:CHO) showed significant spatial-temporal variability (Figure 6.8, Table S6.2, Figure S6.1-S6.2).

Overall, values of the algal fraction of BPC were relatively homogeneous among stations from October to April, when spatial differences were very narrow (on average $28 \pm 1\%$). In May, values of the ratio increased to the highest values ever in station G ($79 \pm 11\%$), but dropped in all other stations, when compared to values in April. Values in July, when compared to those in May, dropped in station G, A and B and remained almost constant in all other stations.

In October values of the PRT:CHO ratio were lowest in stations C and D (inner sector) nearby the freshwater input (1.7 ± 0.3 and 1.0 ± 0.1 , respectively), whereas in January the values increased in stations G (+42%) and A (+60%) but decreased in station H (-40%), where values (38 ± 2 on average) were highest than those in stations G, C and A (27 ± 2 on average). In January, values of the PRT:CHO ratio were highest in stations G (5.1 ± 1) and A (3.4 ± 0.4) and, when compared with values in October, they increased in stations G, D and A and decreased in all others. In April, values of the PRT:CHO ratio dropped in station G (1.7 ± 0.4) and increased in almost all other stations (but station A, in which values slightly decreased). In May, values of the ratio showed a remarkable spatial heterogeneity, with highest values in station C (4.6 ± 0.1) and, when compared to those in April, increased values in stations G and C and decreased values in stations D, A, and B. In July, the ratio was rather homogeneous and relatively low (<2) in all stations, but station H (4.4 ± 1.2).

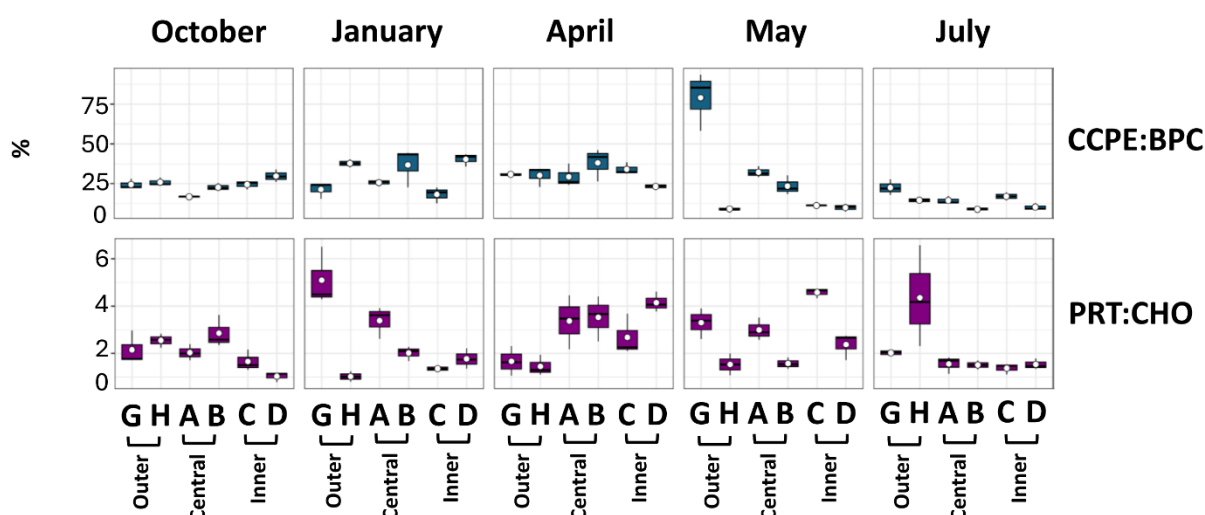


Figure 6.8. Spatial-temporal changes in the algal fraction of BPC (CCPE:BPC) and protein to carbohydrate ratio values (PRT:CHO) in surface sediments of the S'Ena Arrubia Lagoon. The median is indicated with a black line and the mean value with the white dot symbol. Boxplots show interquartile ranges (IQR), and whiskers extending to $1.5 \times \text{IQR}$; outliers are values beyond the whiskers.

6.3.2.2 C degradation rates and turnover time

Spatial-temporal variations in C degradation rates and turnover time are reported in Table S6.2 and illustrated in Figure 6.9, with results of the post-hoc tests reported in Figures S6.1-S6.2.

In October, C degradation rates in stations G ($8.45 \pm 0.35 \mu\text{gC g}^{-1} \text{h}^{-1}$), H ($8.16 \pm 0.19 \mu\text{gC g}^{-1} \text{h}^{-1}$), C ($8.51 \pm 0.19 \mu\text{gC g}^{-1} \text{h}^{-1}$) and D ($9.9 \pm 0.19 \mu\text{gC g}^{-1} \text{h}^{-1}$) were the highest ever measured during the entire study and significantly higher than those in station A ($4.47 \pm 0.15 \mu\text{gC g}^{-1} \text{h}^{-1}$) and B ($3.67 \pm 0.06 \mu\text{gC g}^{-1} \text{h}^{-1}$). C degradation rates dropped to the lowest values ever in January ($2.10 \pm 0.26 \mu\text{gC g}^{-1} \text{h}^{-1}$). C degradation rates increased again in April, when values in stations C ($8.36 \pm 0.34 \mu\text{gC g}^{-1} \text{h}^{-1}$) and D ($5.40 \pm 0.29 \mu\text{gC g}^{-1} \text{h}^{-1}$) were highest than those in all other stations ($2.77 \pm 0.30 \mu\text{gC g}^{-1} \text{h}^{-1}$). With the exception for station C (decreased to $6.14 \pm 0.39 \mu\text{gC g}^{-1} \text{h}^{-1}$) and station A (invariant, $1.31 \pm 0.17 \mu\text{gC g}^{-1} \text{h}^{-1}$), C degradation rates stabilized in all other stations (on average $3.72 \pm 0.15 \mu\text{gC g}^{-1} \text{h}^{-1}$). In July, C degradation rates increased in stations H and D (on average $6.36 \pm 0.74 \mu\text{gC g}^{-1} \text{h}^{-1}$), slightly decreased in station B and remained constant in stations G and A. Overall, in July C highest C degradation rates were in stations H, C and D.

In October, C turnover time was relatively similar among stations (on average 20 ± 2 d). In January the C turnover time remained relatively constant in stations G, H, A and B (19 ± 2 d on average), whilst almost doubled, when compared to values in October, in stations C and D (on 57 ± 3 d on average). In April C turnover time showed a marked hump-shaped gradient, with highest

values in the most sheltered area (stations A and B; 38 ± 3 d, on average) and dropped values in stations C (22 ± 1 d), D (23 ± 1 d) and G (6 ± 0.3 d) and relatively invariant ones in station H (16 ± 1 d). In May C turnover time was highest in stations A, B, C and D (38 ± 3 d) and lowest in stations G and H (10 ± 1); when compared to values in April, C turnover time increased in stations C and D remained nearly constant in stations A and B.

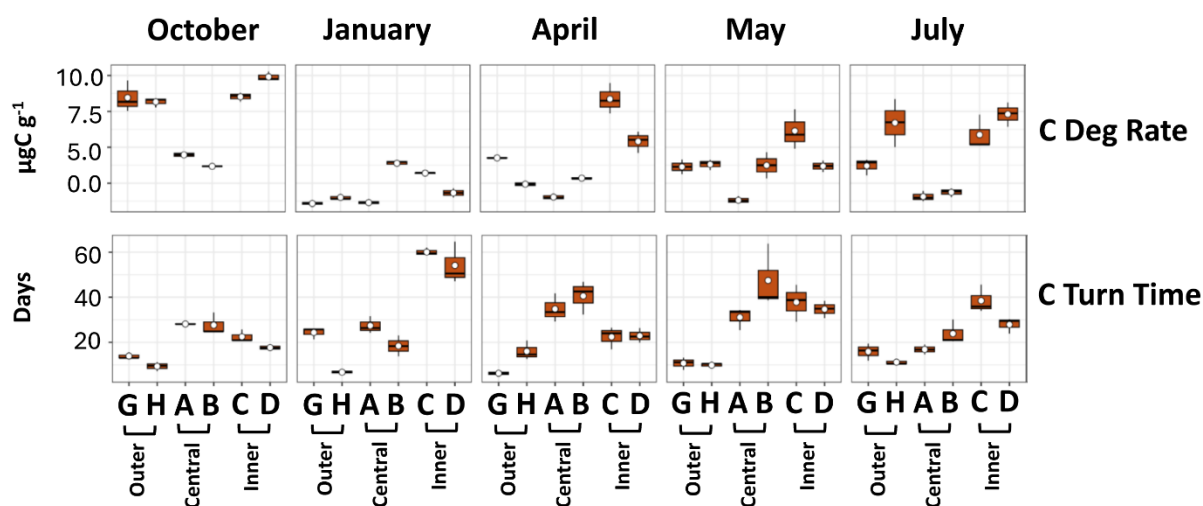


Figure 6.9. Spatial-temporal changes in C degradation rates (C Deg) and turnover time (C turn) in surface sediments of the S'Ena Arrubia lagoon. The median is indicated with a black line and the mean value with the white dot symbol. Boxplots show interquartile ranges (IQR), and whiskers extending to $1.5 \times$ IQR; outliers are values beyond the whiskers.

6.3.3. Abundance, community composition and taxa richness of meiofauna

Abundance and taxa richness of meiofauna are reported in Table S6.3.

The results of the two-way PERMANOVA analysis showed statistically significant effects of both period and station, as well as their interaction (period $\times$ station), for most of the variables considered. The exceptions were the abundance of ostracods, the abundance of other taxa, and the taxonomical richness, for which the interaction of factors was not significant; furthermore, for the abundance of other taxa, the station factor did not show significant effects (Table 6.3).

Variations in abundance of Copepoda, taxonomical composition and n° di taxa were mostly explained by temporal differences, whereas those in abundance of Nematoda, Ostracoda and other taxa were mostly related to residuals. Variations in total abundance were equally influenced by spatial differences and residuals (Table 6.3).

Table 6.3. Results of PERMANOVA testing for spatial and temporal differences in total abundance, Nematoda abundance, Copepoda abundance, other taxa abundance, taxonomical richness and taxonomical composition. Df = degrees of freedom; MS = mean square; Pseudo-F = F statistic; P (MC) = probability after Monte Carlo simulations. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$. %EV = percentage of explained variance.

Variable	Source	Df	MS	F	P(MC)	%EV
Total	Period (P)	4	678.2	18.75	**	27.1
	Station (S)	5	580.0	16.02	**	27.5
	P $\times$ S	20	106.8	2.95	**	17.9
	Residual	60	36.3			27.5
	Total	89	678.3	18.75		27.1
Nematoda	Period (P)	4	794.7	14.53	***	23.0
	Station (S)	5	777.5	14.22	***	27.0
	P $\times$ S	20	158.7	2.90	**	19.4
	Residual	60	54.7			30.6
	Total	89				
Copepoda	Period (P)	4	10816.0	51.34	***	57.9
	Station (S)	5	1236.0	5.87	***	6.7
	P $\times$ S	20	659.0	3.13	***	14.7
	Residual	60	210.7			20.7
	Total	89				
Other taxa	Period (P)	4	3679.1	18.48	***	43.0
	Station (S)	5	345.0	1.73	ns	2.2
	P $\times$ S	20	341.6	1.72	ns	10.6
	Residual	60	199.1			44.3
	Total	89				
Taxa richness	Period (P)	4	2520.2	27.10	***	58.2
	Station (S)	5	277.1	2.98	**	5.3
	P $\times$ S	20	67.4	0.73	ns	0
	Residual	60	93.0			33.8
	Total	89				
Community composition	Period (P)	4	5015.7	21.47	***	38.1
	Station (S)	5	1796.3	7.69	***	14.9
	P $\times$ S	20	514.7	2.20	***	13.4
	Residual	60	234.0			33.5
	Total	89				

PERMDISP tests revealed further differences in data dispersion. Specifically, significant heterogeneity was detected for the factor "Period" across all variables except abundance of Copepoda and other taxa, and taxonomical richness. Likewise, significant heterogeneity was noted for the factor "Station" for all variables but other taxa abundance and number of taxa. (Table 6.4).

Table 6.4 Results of PERMDISP testing for spatial (Station) and temporal (Period) dispersion of total abundance, Nematoda abundance, Copepoda abundance, other taxa abundance, taxonomical richness and taxonomical composition. Df = degrees of freedom; Pseudo-F = F statistic; P (perm) = probability after permutations. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; ns = not significant.

Variable	Source	Df	PermDisp-F	P(perm)
Total Abundance	Period (P)	4	14.05	***
	Station (S)	5	6.87	**
	P $\times$ S	29	4.56	*
Nematoda	Period (P)	4	13.97	***
	Station (S)	5	8.45	***
	P $\times$ S	29	4.34	*
Copepoda	Period (P)	4	2.75	ns
	Station (S)	5	5.88	**
	P $\times$ S	29	3.92	***
Ostracoda	Period (P)	4	4.21	*
	Station (S)	5	4.88	**
	P $\times$ S	29	3.92	**
Other taxa	Period (P)	4	1.83	Ns
	Station (S)	5	0.10	Ns
	P $\times$ S	29	3.99	**
Taxa Richness	Period (P)	4	1.10	Ns
	Station (S)	5	1.84	Ns
	P $\times$ S	29	4.20	*
Community composition	Period (P)	4	3.17	*
	Station (S)	5	4.04	**
	P $\times$ S	29	4.04	**

Abundance of meiofaunal taxa

As outlined by the results of the PERMANOVA tests (Table 6.3), total abundance and abundance of the main meiofaunal taxa showed significant temporal and spatial patterns (Figure 6.10; Figure S6.3 and S6.4).

In October, total meiofaunal abundance was highest in station G (307 ± 9 ind. 10cm^{-2}) and H (369 ± 5 ind. 10cm^{-2}), and lowest in stations C (99 ± 37 ind. 10cm^{-2}) and D (67 ± 21 ind. 10cm^{-2}). Nematoda followed the same patterns with peaks in G (272 ± 3 ind. 10cm^{-2}) and H (359 ± 48 ind. 10cm^{-2}) and the lowest in stations C (90 ± 36 ind. 10cm^{-2}) and D (60 ± 21 ind. 10cm^{-2}). Copepods were scarce (4 ± 3 ind. 10cm^{-2} , mean of the season) and absent in station D. Ostracoda peaked in station G (29 ± 13 ind. 10cm^{-2}) and were minimal in station A (1 ± 0.3 ind. 10cm^{-2}). Other taxa occurred at very low densities (3 ± 1 ind. 10cm^{-2} ; mean of the season).

In January, both total and Nematoda abundance reached their seasonal maxima (480 ± 97 ind. 10cm^{-2} and 395 ± 93 ind. 10cm^{-2} , respectively), with station G showing the most pronounced

increase (661 ± 0 ind. 10 cm^{-2} total, 584 ± 61 ind. 10 cm^{-2} Nematoda). Copepoda abundance rose significantly at stations G (71 ± 28 ind. 10 cm^{-2}), H (106 ± 31 ind. 10 cm^{-2}), A (132 ± 3 ind. 10 cm^{-2}), and D (58 ± 27 ind. 10 cm^{-2}). These increases made the differences between stations insignificant, except for station A and C (10 ± 7 ind. 10 cm^{-2} , lowest value). Ostracod abundance did not vary among stations, but there was a significant increase at stations H and A compared to the previous month. Other taxa abundance was generally slightly higher (5 ± 2 ind. 10 cm^{-2}).

In April, total and Nematoda densities declined significantly at station B (132 ± 26 and 118 ± 20 ind. 10 cm^{-2}), contrasting with higher values at G (480 ± 97 and 306 ± 35 ind. 10 cm^{-2}) and C (370 ± 35 and 307 ± 37 ind. 10 cm^{-2}). Copepoda abundance dropped sharply in B (2 ± 1 ind. 10 cm^{-2}) compared to A (84 ± 62 ind. 10 cm^{-2}) and H (31 ± 5 ind. 10 cm^{-2}), whereas Ostracoda and other taxa reached their monthly maxima (12 ± 7 and 7 ± 2 ind. 10 cm^{-2} , respectively).

During the dystrophic crisis in May, total and Nematoda abundance dropped to the lowest values of all seasons (136 ± 36 ind. 10 cm^{-2} and 129 ± 35 ind. 10 cm^{-2} , respectively). Stations G and H maintained relatively higher densities in total (G: 314 ± 38 ind. 10 cm^{-2} ; H: 280 ± 72 ind. 10 cm^{-2}) and Nematoda abundances (G: 302 ± 37 ind. 10 cm^{-2} ; H: 269 ± 71 ind. 10 cm^{-2}). In contrast, the most pronounced declines were experienced in station B (39 ± 9 ind. 10 cm^{-2} and 29 ± 6 ind. 10 cm^{-2} , respectively) and C (9 ± 1 ind. 10 cm^{-2} and 5 ± 3 ind. 10 cm^{-2}); the latter differed from all the stations except for D. Copepoda disappeared from all stations except H (4.67 ± 2.03 ind. 10 cm^{-2}). Ostracoda peaked in B (10 ± 3 ind. 10 cm^{-2}) and were absent in A, although B, G, and H experienced a significant drop compared to April. Other taxa were nearly absent across all stations.

In July, total abundance recovered, increasing in stations B and C. Despite this, station C and D still registered the lowest values in total (86.00 ± 23.00 ind. 10 cm^{-2} and 78.00 ± 27.30 ind. 10 cm^{-2} , respectively) and Nematoda (41.33 ± 14.31 ind. 10 cm^{-2} and 58.00 ± 16.82 ind. 10 cm^{-2} , respectively) abundances, differing from stations G (for Nematoda) and H (for both). Copepoda abundance increased, peaking in stations A (91.67 ± 31.93 ind. 10 cm^{-2}) and B (62.67 ± 21.26 ind. 10 cm^{-2}), while in station D it remained low (14.00 ± 11.14 ind. 10 cm^{-2}). Ostracoda were almost absent in station H, differing from all the stations but B and C, and other taxa showed a slight seasonal increase (3 ± 2 ind. 10 cm^{-2}).

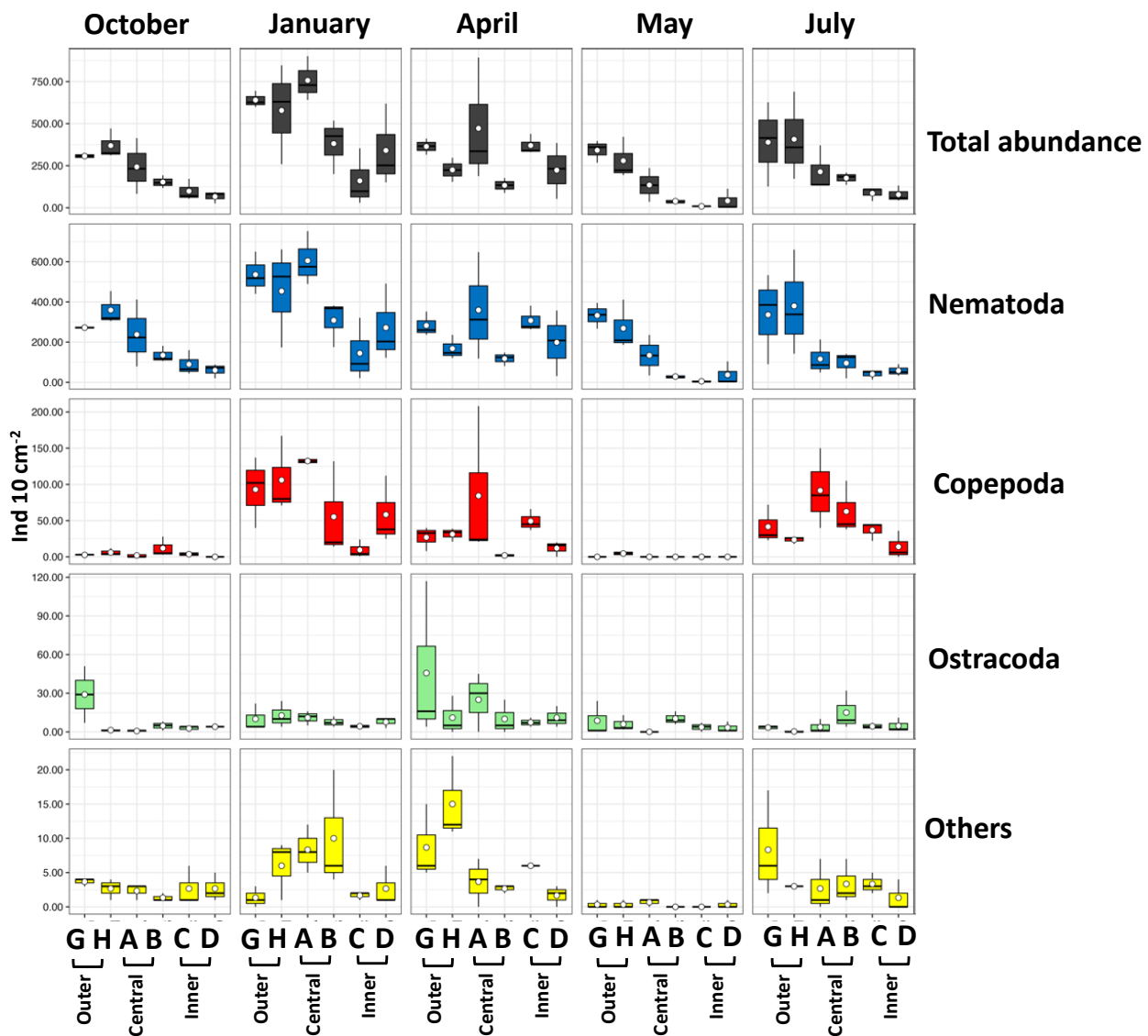


Figure 6.10. Boxplot of the abundance of main meiofaunal taxa (Nematoda, Copepoda, Ostracoda, Others) and total abundance, expressed as n° of individuals in an area of 10 cm², in surface sediments, at each station (G, H, C, D, A and B) in each period (October, January, April, May and July). The median is indicated with a black line and the mean value with the white dot symbol. Boxplots show interquartile ranges (IQR), and whiskers extending to 1.5 × IQR; outliers are values beyond the whiskers.

Taxonomical richness and composition

Taxa richness and composition of the meiofaunal community of S'Ena Arrubia varied significantly in time and space (Figures 6.11-6.12; Table S6.3-S6.4; Figure S6.3-S6.4). Taxa richness displayed temporal changes larger than the spatial one, with the highest values in January (5 ± 1), April (4 ± 1) and July (4 ± 1 taxa), and the lowest in October (4 ± 0) and especially May (2 ± 0). During the dystrophic crisis in May, taxa richness dropped in station (2 ± 0), resulting significantly lower than that at station H (3 ± 0). Station D also displayed reduced richness, being significantly poorer than stations H and B in October and poorer than station G in April.

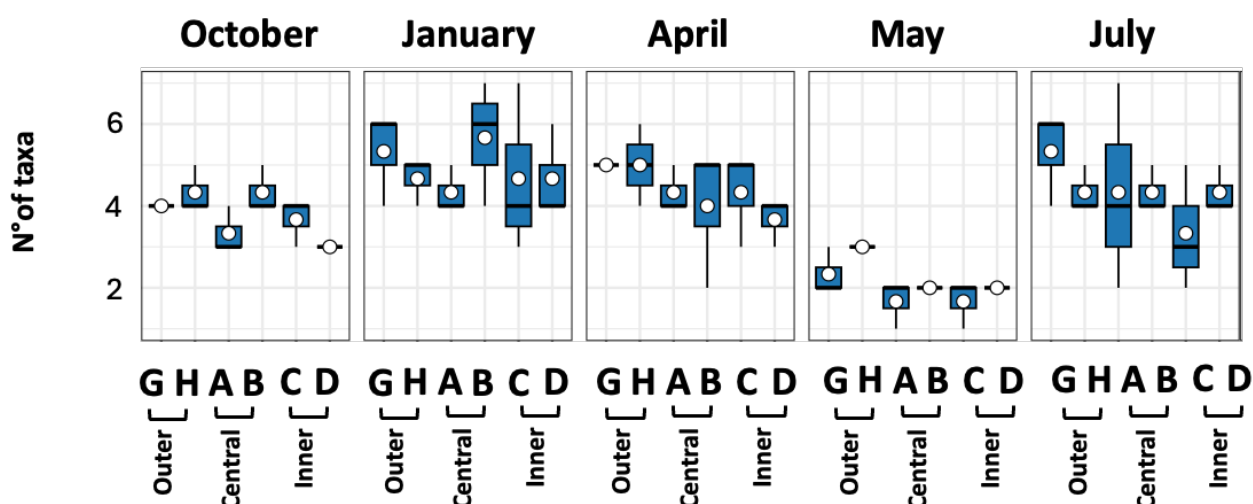


Figure 6.11. Boxplot of meiofaunal taxa richness in surface sediments, at each station (G, H, C, D, A and B) in each period (October, January, April, May and July). The median is indicated with a black line and the mean value with the white dot symbol. Boxplots show interquartile ranges (IQR), and whiskers extending to $1.5 \times \text{IQR}$; outliers are values beyond the whiskers.

These patterns reflected significant shifts also in community composition. Nematoda dominated throughout the study, contributing between 68.6 % and 92.2 % of the total community (average between stations per month). The second most abundant taxon alternated between Copepoda and Ostracoda: Copepoda contributed more in January (14.0 %), April (10.3 %) and July (25.8 %), while Ostracoda prevailed in October (3.64 %) and May (13.84 %). All other taxa contributed never more than 2%, with slight fluctuations across periods and stations. Overall, stations G, H and C showed the highest temporal and spatial variability in taxonomic composition.

In October, pairwise tests indicated that stations G and D differed from most stations except C. Abundance-based SIMPER analysis showed that dissimilarities between G and A–B were mainly driven by higher contributions of Ostracoda and Turbellaria with Copepoda being more represented in station B (Table S6.5). Presence/absence-based SIMPER analysis highlighted the near absence of Turbellaria in stations A and B, the absence of Copepoda in station A, and the exclusive presence of Gasteropoda in station B (Table S6). Station G also differed from H (due to higher contributions of Ostracoda and Copepoda and absence of Amphipoda (Table S6.5-S6.6). Station D differed from A and B due to lower contribution of Nematoda and exclusive presence of Turbellaria (Table S6.5-S6.6). Ostracoda contributed also to differences between station D and station A. Copepoda were absent in station B (Table S6.5-S6.6).

In January, station C differed from all stations except H and D. Differences with A and B were driven by lower contribution of Copepoda and Nematoda and absence of Polychaeta, absence of Rotifera, and presence of Turbellaria (Table S5-S6). In April, station B differed from H and C for lower contribution of Copepoda and higher contribution of Ostracoda. Additional differences were related to the absence of Isopoda, absence of Rotifera, and presence of Chironomid larvae and Polychaeta (Table S6.5-S6.6).

During the dystrophic crisis in May, the meiofauna community composition changed sharply. Pairwise tests showed significant differences among stations G, H, A and C, explained by a strong reduction in Nematoda contribution and the disappearance of several taxa (Copepoda, Isopoda, Polychaeta) compared to April (SIMPER presence/absence) (Table S6.6). Station G showed higher contribution of Nematoda and Ostracoda than B and C and absence of Turbellaria (Table S6.5-S6.6). Station H differed from A due to higher contribution of Nematoda and presence of Ostracoda, and from A and B due to the presence of Copepoda (Table S6.5-S6.6). Station A differed from B and C due to higher contribution of Nematoda, absence of Ostracoda (~63 % and 50 % of dissimilarity, respectively), and presence of Gasteropoda (Table S6.5-S6.6).

In July, no significant differences between stations were detected, although all communities showed recovery after the dystrophic event. The reappearance of Copepoda strongly explained the variation in G, A, and C, while Turbellaria contributed in G and A. Ostracoda almost disappeared from G and H. Other taxa, such as Chironomid larvae, reappeared in all stations (Table S6.5-S6.6).

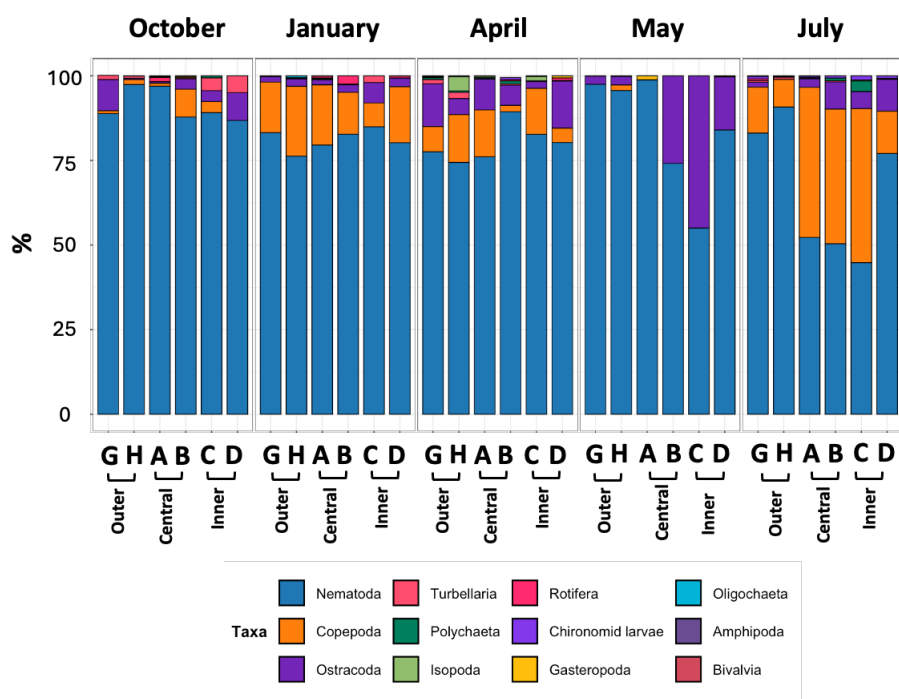


Figure 6.12. Taxonomical composition of meiofaunal communities in S'Ena Arrubia lagoon at each station (G, H, C, D, A and B) in each period (October, January, April, May and July).

6.3.3.4 Environmental drivers of meiofaunal communities' composition

The DistLM analysis applied on taxonomical composition of all Periods and stations indicated that dissolved oxygen (CRDO) was the main driver of community composition, explaining the largest proportion of variation (21.05 %). This variable contributes with percentage of mud, water temperature, phytopigments (CPE), salinity and biopolymeric C (BPC) in explaining just 37.6% of the total variation (Table 6.5).

Table 6.5. DistLM results on environmental predictors of meiofaunal taxonomical composition

Variables	Pseudo-F	P	%EV	% Cumulative EV
Dissolved O₂(C RDO)	23.46	***	21.1	21.1
Mud %	10.57	***	8.6	29.6
Water Temperature	2.85	**	2.3	31.9
Phytopigments (CPE)	2.78	*	2.2	34.0
Salinity	2.04	*	1.6	35.6
Biopolymeric C	2.67	*	2.0	37.6

The dbRDA ordination showed that meiofaunal communities sampled in January and April were associated with higher dissolved oxygen concentration, while with intermediate in July, and lower in October and May (Figure 6.13). Communities from the inner stations (C and D) were also related with higher percentage of mud and organic matter contents (Figure 6.13). Within this context, the

group of inner stations during the dystrophic event was clearly separated from the others, probably due to the association with the combination of CRDO and mud percentage (Figure 6.13).

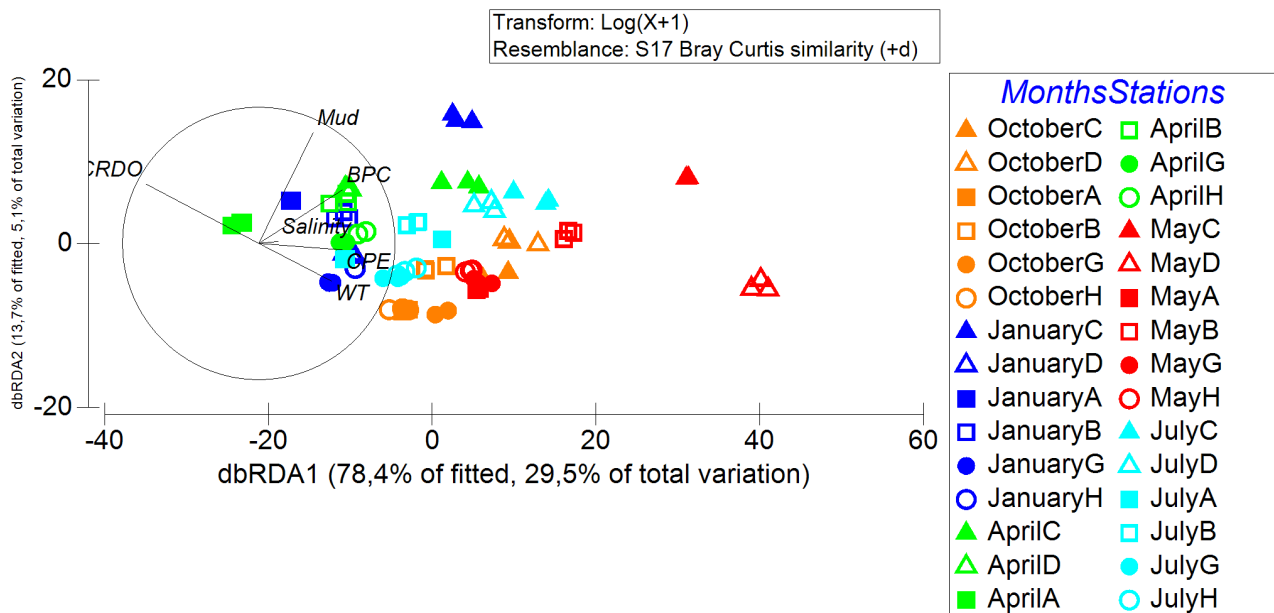


Figure 6.13. Distance-based redundancy analysis (dbRDA) ordination plot showing the relationships between meiofaunal community composition and environmental variables across sampling periods and stations. Vectors indicate the strength and direction of the correlations with explanatory variables (salinity, temperature, oxygen, sediment grain size, and organic matter fractions). The position of samples in the ordination space reflects similarities in community composition, with closer points representing more similar communities.

6.4 Discussion

As transitional ecosystems, coastal lagoons are typically characterized by strong environmental gradients that make them physically unstable and subject to unpredictable fluctuations of most environmental variables (Whitfield et al., 2012). Accordingly, the results of my thesis revealed strong spatial and temporal fluctuations in sedimentary biogeochemistry and meiofaunal communities of the S'Ena Arrubia Lagoon.

6.4.1 Spatial-temporal variability of sedimentary biogeochemistry

My results are consistent with previous studies carried out in the same lagoon, which also reported marked variability of biogeochemical features of the lagoon sediments, despite its relatively small extent surface area (120 ha) (Giampaolletti et al., 2025; Pagani et al., 2025). Both my thesis and previous papers observe the largest spatial-temporal variation of biopolymeric C (BPC) and total phyt pigment (CPE) contents at both stations facing the sea (G-H) as well as at the two stations facing the main freshwater input (C-D). More specifically, I observed that, during almost the entire study period (with exception of values in July), the two stations closest to the lagoon's opening to the sea (G-H) showed the lowest BPC and CPE contents across all investigated periods.

The low BPC content observed in those stations contrasts with findings from previous studies in S'Ena Arrubia lagoon, where generally higher BPC concentrations were measured in the lagoon sector closest to the sea (Giampaoletti et al., 2025). Such a discrepancy may stem from differences in the exact position of sampling stations between the two studies, as those from the literature were closer to the sea than those in my thesis, but were also close to an oyster farm, a potential additional source of organic matter inputs during the previous study (Frongia et al., 2023; Giampaoletti et al., 2025; Pagani et al., 2025).

The peculiar distribution of OM contents in the S'Ena Arrubia lagoon can be also related to the influence of the continuous seawater influx, which exacerbates water exchanges and, by a merely dilution process, promotes a more oligotrophic state in this sector of the lagoon (Padedda et al., 2019). In general, BPC and CPE contents in the sediments of the most sheltered sector of the lagoon (stations A and B) show intermediate values when compared to the outer (G-H) and inner (C-D) sectors. This result is consistent with the co-occurrence of relatively low hydrodynamics ($<3 \text{ cm s}^{-1}$, Pagani et al., 2025) and the diminished inputs of allochthonous organic material from either the sea and the freshwater sources. This pattern is not observed in July, when stations A and B showed the lowest OM contents. This counterintuitive result suggests that the effects of the decreased seawater and freshwater allochthonous OM inputs in summer pervaded more importantly the most sheltered sector of the lagoon. Moreover, stations A and B differed one each other in both temporal and spatial variability: station B generally exhibited higher values and greater fluctuations in several biochemical features, especially BPC and CPE contents. Although the reason for these differences remains unclear, I hypothesized that higher OM values at station B may be related to the presence of bird nesting and resting areas nearby, which can act as localized sources of organic enrichment (Ligeza and Smal, 2003; Fois et al., 2021).

Noticeably, in July stations directly receiving the freshwater inputs (C-D) showed the highest biopolymeric C and phytopigment contents ever, also likely as a delayed effect of OM accumulation in the sediments due to the dystrophic crisis occurred in May. I also notice that BPC and CPE sedimentary contents showed temporal variations during my study far different from those reported by Giampaoletti et al. (2025). Such further mismatch, on the one hand, finds foundation in the difference in sampling timing adopted in the two studies, but also pinpoints that the sedimentary biogeochemistry of coastal lagoons exhibits significant interannual variability, which poses challenges for implementing management strategies that could be consistently repeated year

after year. This result highlights also the need for continuous and temporally consistent lagoons' monitoring activities.

Overall, the values of the PRT:CHO ratio in the lagoon sediments (on average 2.4 ± 0.2) never decreased below 1, which is the threshold above which OM is considered relatively fresher (Pusceddu et al., 1999), indicating a relatively rapid turnover of OM in the sediments. Nonetheless, the values of the PRT:CHO ratio in the S'Ena Arrubia showed remarkable spatial variations at each sampling date indicating that, despite the OM loads in the sediments were relatively fresh across the entire lagoon, their origin was most likely highly variable. Indeed, the values of the PRT:CHO ratio and the protein contribution to BPC are also largely influenced by the OM origin (Manini et al., 2003): for instance, OM matter associated with remains of terrestrial origin is typically characterized by very low PRT:CHO values (well < 1), whereas OM associated with recently deposited plankton debris has much higher values (well > 1) (Pusceddu et al., 1999; Dell'Anno et al., 2002). Accordingly, besides values in April and May, values of the PRT:CHO ratio were typically lower in the inner sector of the lagoon (1.5 ± 0.1), influenced by OM loads transported by the freshwater coming from inland (and thus relatively richer in terrestrial OM), when compared with those measured in the central (2.2 ± 0.2) and outer (3.0 ± 0.4) sectors.

The algal fraction of biopolymeric C was far less spatially variable than the values of the PRT:CHO ratio, though exhibited a general decrease in summer (July), indicating a depletion of the OM loads nutritional quality in the sediments. The only exception to this emerges for the value of the algal contribution to BPC in May at station G, where the sediments were characterized by an overwhelming accumulation of macroalgal debris (possibly due to tidal movements), that possibly inflated randomly the value.

Changes in the quantity and quality of organic loads also influenced the potential carbon degradation rates and turnover time in the S'Ena Arrubia Lagoon. Overall, C degradation rates were generally higher in both the outer and inner sectors of the lagoon, likely reflecting the activation of distinct biogeochemical processes. OM reactivity is known to be closely linked to water residence time and nutrient availability (Evans et al., 2017; Kothawala et al., 2021). In the outer area, the highly dynamic conditions near the sea outlet likely enhanced microbial respiration and associated degradation processes, also favored by the activity of benthic organisms such as meiofauna, which play a key role in sedimentary remineralization (Schratzberger and Ingels, 2018). Conversely, in the more confined inner stations, high terrestrial organic inputs from river discharge and fluctuating environmental conditions may have stimulated heterotrophic bacterial degradation (Jilbert et al.,

2021). These processes were particularly pronounced at station C during the dystrophic event, which exhibited the highest degradation rates. The peaks recorded in October and July may reflect enhanced microbial activity driven by elevated temperatures during these periods, whereas the lower values observed in January are consistent with reduced organic matter inputs and more stable conditions (Maliverno and Martinez, 2015; Bouvet et al., 2024; Palmas et al., 2025).

Nevertheless, C turnover times showed an opposite pattern, being shorter in the outer stations and longer in the central and inner lagoon, particularly during the dystrophic crisis. This apparent decoupling between degradation dynamics and turnover time in the inner sector is likely associated with the more refractory nature of the organic matter and the lower consumption rates by benthic organisms. This is exacerbated under oxygen depletion conditions (Jensen et al., 2017).

6.4.2 Spatial-temporal variability of meiofauna

To our knowledge, this study is among the very few focused on meiobenthic communities in Sardinian lagoon environments (Semprucci et al., 2019a; Magni et al., 2022) and the first ever conducted in the S'Ena Arrubia lagoon, thus addressing an already noticed knowledge gap (Pagani et al., 2025). The supposed peculiar importance of meiofauna in the S'Ena Arrubia lagoon also arises because previous studies assigned the low density of macrofauna as a minor factor influencing benthic processes in the S'Ena Arrubia lagoon (Pagani et al., 2015). In this context, micro-bioturbation by meiofauna could potentially contribute to sustain sediment reworking, benthic respiration, and nutrient mobilization (Bonaglia et al., 2014; Bonaglia and Nascimento, 2023; Maciute et al., 2023; Pagani et al., 2025).

Meiofaunal communities varied seasonally in response to the lagoonal environmental gradient. Outer stations near the lagoon mouth (G, H) supported higher meiofaunal densities and taxa richness, while inner stations (C, D), located in front of the main inlets, consistently showed lower values. This pattern has been most likely shaped by the abiotic variables that have had the greatest influence on the community over time and space. Among the predictors already known to affect meiofauna (temperature, biopolymeric carbon, phytopigments, and salinity), oxygen concentration—followed by the proportion of fine sediments—emerged as the main driver of meiofaunal distribution in S'Ena Arrubia. These results are consistent with previous findings in other lagoon ecosystems (Tagliapietra et al., 2012; Semprucci et al., 2019a; Magni et al., 2022; Santos et al., 2024).

The observed trends in meiofauna distribution and temporal variations were inversely related to organic matter content. This result contrasts with some studies (Semprucci et al., 2010; Bianchelli et al., 2020) but is consistent with most findings in other Mediterranean lagoons, including Sardinian ones (Pusceddu et al., 2007; Jouili et al., 2017; Semprucci et al., 2019; Magni et al., 2022). Outer areas experience greater water renewal due to seawater exchange, which regulates oxygen concentration, sedimentary organic matter, and the removal of catabolites (Tagliapietra et al., 2012). Balanced organic matter inputs, typical of oligo- to mesotrophic environments, sustain higher meiofaunal density and diversity by providing food resources (Neira et al., 2001). Under moderate OM enrichment not yet associated with oxygen depletion, meiofauna contribute significantly to remineralization processes (Nascimento et al., 2012). Altogether these “requisites” characterized stations G, H, and occasionally station A, particularly between January and April, when higher oxygen concentrations were associated with higher meiofaunal densities and taxa richness (Figures 6.4, 6.12). On the other hand, according to the confinement model (Guelorget & Perthuisot, 1983, 1989) and the habitat saprobity gradient (Tagliapietra et al., 2012; Foti et al., 2014), more reducing conditions develop in inner sectors, where organic matter decomposition is enhanced. Under eutrophic conditions, microbial degradation of excessive organic matter leads to oxygen depletion and the production of toxic metabolites (e.g., ammonia, sulfide). These conditions impair the survival of sensitive taxa, ultimately reducing richness, abundance, and biomass (Pusceddu et al., 2007; Tagliapietra et al., 2012). Consistently, inner stations (C, D) exhibited the lowest abundance and taxonomic richness. Station C experienced a drastic decline during the dystrophic crisis, coinciding with the highest organic matter content and the lowest oxygen concentration. A similar, though less pronounced, pattern occurred also at station B, likely linked to organic enrichment from nearby bird seasonal nesting areas.

Variations in community composition possibly provide further elements to clarify these dynamics. Overall, Nematoda were always and everywhere the dominant taxon, as typically observed in lagoon ecosystems worldwide. Their densities are usually high in disturbed environments, such as those receiving large inputs of runoff and pollutants (Ferraz et al., 2022), as in the S'Ena Arrubia lagoon. At the same time, Nematode can enhance nitrogen removal by stimulating nitrification and denitrification, thereby partly mitigating eutrophication (Bonaglia et al., 2014; Bianchelli et al., 2018). Copepod and ostracod distribution patterns and temporal succession in the S'Ena Arrubia lagoon appeared shaped by their ecology. In fact, these organisms usually stay at the sediment-water interface where the oxygen concentration is higher (Maciute et al., 2023).

Consequently, copepods abundance declined significant in October and disappeared under near-anoxic conditions ($<2 \text{ mg L}^{-1}$) recorded during the dystrophic event in May, particularly in the inner stations, confirming their general sensitivity to oxygen limitation (Grego et al., 2013). Their recovery in July likely reflects rapid life cycles, adaptability to shifts in food webs, tolerance to fluctuating conditions, or recolonization by more tolerant species (Grego et al., 2013; Kawano et al., 2021).

In contrast, the dominance of ostracods in October and May was unexpected given their reported sensitivity to perturbations. However, some ostracod species can exhibit adaptive responses to natural and anthropogenic stressors such as organic enrichment and trace element contamination (Semprucci et al., 2019a). The merely sporadic occurrence of rare taxa (e.g., Turbellaria, Polychaeta, Rotifera, Chironomid larvae) highlighted both stress responses and recovery phases. Opportunistic taxa such as Chironomidae larvae were also detected after the dystrophic event in July, consistent with their tolerance of hypoxia and high organic matter (Jones et al., 2008), but also with more elevated freshwater inputs. Altogether, these shifts in meiofaunal community composition suggest a turnover from sensitive, functionally important taxa to stress-tolerant opportunists, with likely delayed implications for lagoon ecosystem functioning under disturbance (Grassi et al., 2023). Spatial contrasts were also evident, with outer stations (G, H) showing higher variability and resilience, while inner stations (C, D) remained consistently impoverished.

6.4.3. The effects of the dystrophic event on sediment biogeochemistry and meiofauna

Dystrophic crises are rather recurrent in Mediterranean coastal lagoons (Specchiulli et al., 2018; Fernández-Alías et al., 2022; Lenzi and Cianchi, 2022; Pagani et al., 2025). Also the S'Ena Arrubia Lagoon has historically suffered repeated dystrophic crises (1989, 1995, 1988 and 1999) often associated with massive mortality events (Trebini et al., 2005). To prevent further events, a widening of the outlet channel was carried out in the early 2000s to improve tidal flushing, lower trophic status, and improve hydrodynamics (Trebini et al., 2005). Nonetheless, freshwater discharges, particularly from the Canale delle Acque Basse, has continued to release organic wastes maintaining a high risk of eutrophication and dystrophic crises (Pagani et al., 2025), especially in association with temperature rise and the occurrence of heatwaves.

In May 2024, the S'Ena Arrubia Lagoon experienced another dystrophic crisis that triggered huge algal biomass accumulation and fish mass mortality (Figure 6.14-15).



Figure 6.14. Accumulation of dead *Gracilaria* sp and the brown-green water color in S'Ena Arrubia Lagoon following the dystrophic crisis in May 2024.



Figure 6.15. Dead fish in the S'Ena Arrubia Lagoon following the dystrophic crisis in May 2024.

High loads of organic matter, combined with elevated water temperatures (exceeding 25 °C) and limited hydrodynamics ($< 3\text{--}4 \text{ cm s}^{-1}$) are recognized as the main drivers of most dystrophic crises and their consequences in coastal lagoons (Lenzi and Cianchi, 2022). These conditions, indeed, occurred altogether in the S'Ena Arrubia Lagoon in May 2024.

By combining data of OM contents and nutritional quality (in terms of algal fraction of BPC), I estimated the overall spatial and temporal variations of the lagoon sediments trophic status, based on proxies modified from Pusceddu et al. (2011) and summarized in Table 6.6 and Figure 6.16.

Table 6.6 Thresholds of trophic status identified by Pusceddu et al. (2011) and converted into scores, then used to define the status according to Figure 3.

Trophic status	Biopolymeric C content		Algal fraction of BPC	
	(mgC g ⁻¹)	Score	(%)	Score
Oligotrophic	< 1.0	1	< 25	1
Mesotrophic	1.0-3.0	2	12-25	2
Eutrophic	> 3.0	3	< 12	3

		Algal fraction (score)		
		1	2	3
BPC content (score)	1	Oligotrophic	Mesotrophic	Eutrophic
	2	Mesotrophic	Eutrophic	Hypereutrophic
	3	Eutrophic	Hypereutrophic	Dystrophic

Figure 6.16. Classification of the benthic trophic status of shallow water environments. Definition is based on the sum of the scores reported in Table 6.6.

On average, based on ranks and definitions reported above, the S'Ena Arrubia Lagoon 's sediments can be ranked as eutrophic (median score = 4), confirming previous observations (Giampaoletti et al, 2025; Pagani et al, 2025). Despite this, the trophic status of the sediments varied considerably among sectors of the lagoon and among sampling periods (Figure 6.17). Mesotrophic conditions occurred only in January and April, indicating the period of OM accumulation starving, whereas hypereutrophic conditions appeared in May in the inner sector (concomitantly with the dystrophic crisis) and persisted in July pervading also the central sector. These results, besides providing evidence of the large spatial and temporal variability of the lagoon trophic status clearly pinpoint that concomitantly with the occurrence of the dystrophic crisis (in May) and immediately

after (in July) the lagoon sediments experienced a shift towards hypereutrophic conditions, that are, at the same time a prerequisite (May) and the consequence (July) of detrimental environmental effects of the dystrophic crisis.

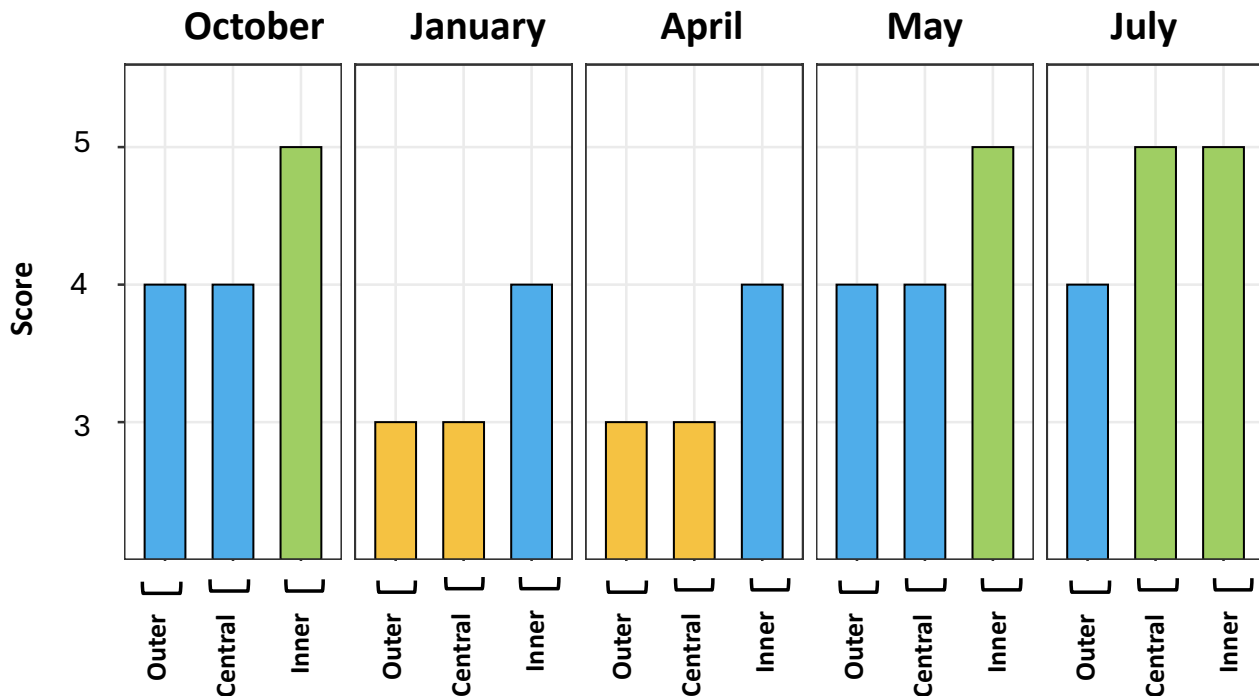


Figure 6.17. Temporal variations in the trophic status of the sediments across the three sectors of the S'Ena Arrubia Lagoon.

To measure the impact of the trophic shifts on each lagoonal sector, I also used taxa richness as a proxy of environmental quality as designed by Danovaro et al., 2004 and applied in Pusceddu et al., 2007 and Bianchelli et al., 2016. The ranges are specified in Table 6.7.

Table 6.7. Classification of environmental quality of sediments based on biodiversity (as the number of meiofaunal taxa identified by Danovaro et al., 2004).

Number of taxa	Environmental quality
<=4 taxa	Poor
From 4 to 7 taxa	Moderate
From 8 to 11 taxa	Sufficient
From 12 to 16 taxa	Good
>=16 taxa	Excellent

Considering this ranking, the S'Ena Arrubia lagoon can be considered as moderately impacted, a typical condition of eutrophic lagoons. Worst conditions were observed during the dystrophic event when all the lagoon sectors can be considered as highly impacted (Figure 6.18). Additionally, the inner sector was considered as highly impacted in almost all the sampling period beside January,

while the central sector showed a poor environmental quality both in October and May (Figure 6.18).

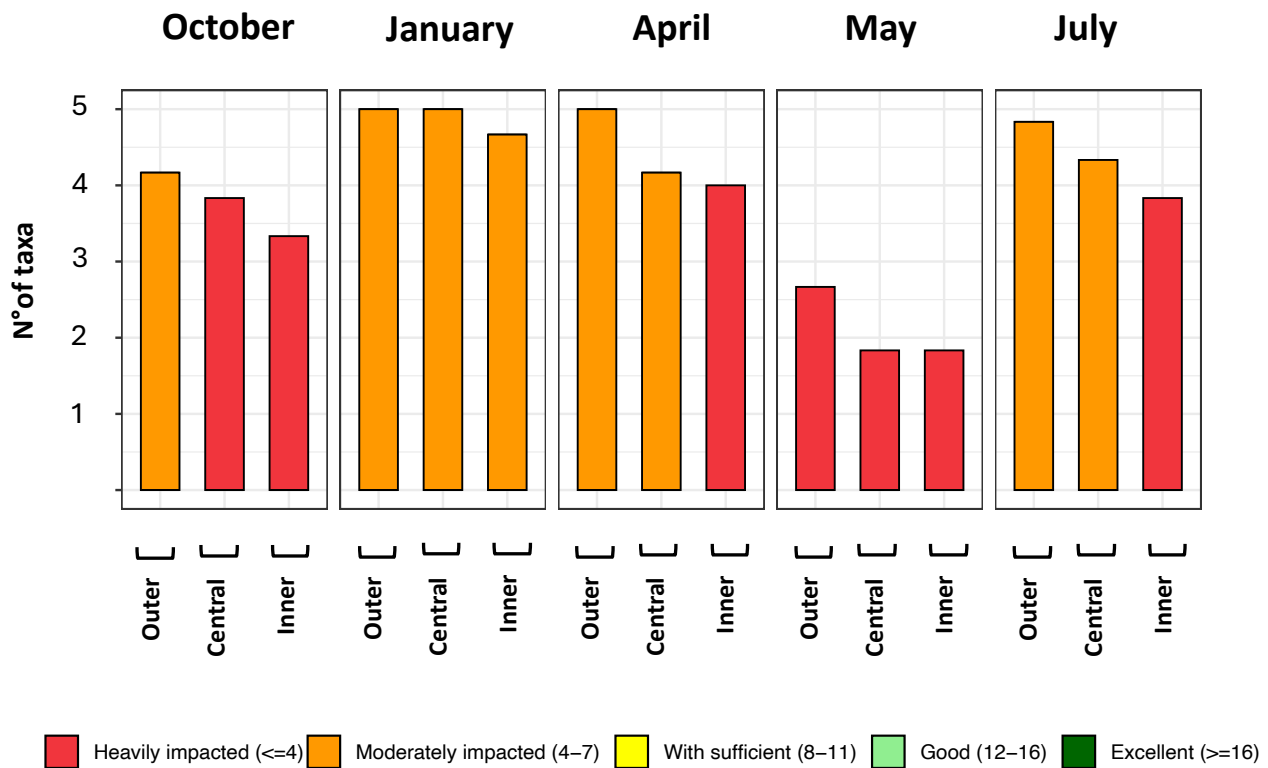


Figure 6.18. Temporal variations in the environmental quality of the sediments across the three sectors of the S'Ena Arrubia Lagoon.

6.5 Conclusions

The results of this chapter allow me to reject the null hypothesis that the OM quantity, quality and OM biochemical composition and abundance, taxonomical richness and composition of meiofaunal communities do not vary along the confinement gradient in different periods of the year and across the dystrophic crisis occurred in May 2024.

Overall, my results revealed marked and significant spatial and temporal variabilities in the biogeochemical features of the sediments, with clear seasonal patterns especially evident at stations facing the sea and those facing the main freshwater tributary. The benthic trophic status of the lagoon, generally eutrophic, turned to hypereutrophic during and immediately after the dystrophic event, with the most severe biogeochemical effects observed in both the inner and central sectors of the lagoon, most likely due to the sewage and agricultural runoff from the surrounding hydrological catchment.

The observed changes in the benthic trophic status of the lagoon following the dystrophic crisis could have had important impacts on the benthic fauna. Ecosystem resistance to stressors such as nutrient enrichment and eutrophication relies on homeostatic regulation mechanisms, that channel primary production outputs towards the benthos (Lacoste et al., 2023). In coastal lagoons, indeed, excess nutrients sustain large biomasses of primary producers, filter-feeders and detritivores, many of which of commercial interest (Fernández-Alías et al., 2022). In contrast, resilience, the capacity to return to a pre-disturbance state, depends on species turnover, resilience and adaptation of key communities (Basset et al., 2013). These processes are generally much faster in the water column than in the sediments (Dell'Anno et al., 2002), so that the results of this chapter pinpoint that the benthic compartment of the S'Ena Arrubia Lagoon will most likely experience longer-lasting consequences due to the dystrophic crisis and the associated hyper-eutrophication than the planktonic counterpart (Basset et al., 2013; Cladas et al., 2016).

Meiofauna is considered an important mediator of sediment biogeochemical cycles and benthic ecosystem processes, especially in anthropogenic disturbed environments (Bonaglia and Nascimento, 2023). According to the "saprobity" concept, ecosystem state reflects the balance between organic matter input, decomposition and the removal of its catabolites (Tagliapietra et al., 2012). Further organic enrichment, like the one observed during the dystrophic crisis in May 2024, impacted S'Ena Arrubia Lagoon functioning, reducing community abundance and taxa richness, directly impacted by anoxia and associated toxic byproducts (Renzi et al., 2019). Such reductions would mine the lagoon stability by disrupting nutrient cycling and weakening its filtering capacity, further exacerbating hyper-eutrophication and potentially leading to persistent anoxic conditions (Grego et al., 2009; Lloret and Marín, 2009). Altered community structure will also have cascade effects on higher trophic levels, locking the system into a persistent and worsened state of ecological degradation (Levin et al., 2009; Villnas et al., 2014).

Although nutrient pollution triggered the dystrophy event in S'Ena Arrubia, other environmental factors, including climate change, will soon act as exacerbating catalysts of the lagoons degradation. As previously mentioned, warming and extreme weather events, like flash floodings and marine heatwaves, can stimulate the release of nutrients, accelerate bacterial decomposition of organic matter and the proliferation of algae (Phlips et al., 2015; Lenzi and Cianchi, 2022). Altogether, these processes contribute to hypoxia and/or anoxia, increased releases of toxic gases and a shift in dominance from macrophytes to phytoplankton-dominated systems. This would further destabilize the lagoon homeostasis and threaten biodiversity as a whole. In addition, altered meteorological

and hydrodynamic conditions can trigger these events, as has been observed in other lagoons (Vignes et al, 2010; Lenzi and Cianchi, 2022). Such positive feedback process could compromise the blue C sink role of lagoons in mitigating climate change: higher organic loads and increased microbe-mediated reactivity would increase the release of toxic and greenhouse gases such as methane (Middelburg and Levin, 2009; Bonaglia et al., 2025).

Co-stressors such as harmful algal blooms (HABs) may further exacerbate consequences of (hyper)eutrophication. HABs are favored by nutrient enrichment and warming (Padedda et al., 2017; Griffith et al., 2019). When combined with high OM loads, blooms exacerbated hypoxia and acidification through oxygen depletion and CO₂ release (Griffith et al., 2019). Moreover, some HABs produced potent biotoxins, threatening marine organisms across multiple trophic levels (Griffith et al., 2019). In Sardinian lagoons, blooms of dinoflagellates species belonging to the *Alexandrium* genus, were documented between 2002 to 2012, and again in 2018 (Lorenzoni et al., 2013). Since these species produce saxitoxins responsible for paralytic shellfish poisoning PSP harvesting and marketing of bivalve mollusks can be temporarily banned (Van Egmond, 2004; Camacho et al., 2007; Lorenzoni et al., 2013), with conceivable impacts on the local fisheries. With climate change expected to further increase eutrophication, maintaining and improving lagoons' water quality is therefore crucial to mitigate HAB risks.

Given the ecological and socio-economic importance of coastal lagoons, avoiding or reducing dystrophic crises is therefore a management priority. Tested mitigation strategies in non-tidal systems include: (i) reducing nutrient inputs or diverting tributaries carrying wastewater and agricultural runoff, (ii) harvesting macroalgal biomass or enhancing filter-feeders and grazers, and (iii) resuspending soft sediments to oxygenate the anoxic upper-layers. Additional measures, such as dredging submerged channels, have been proposed and positively tested in S'Ena Arrubia Lagoon to improve water circulation (Trebini et al., 2005; Lenzi, 2021).

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6.8 Supplementary Materials

Table S6.1. Salinity, temperature (°C), oxygen (mgO₂ L⁻¹) and sediment granulometry expressed as percentages of gravel, sand and mud. For each period are reported mean ± sd.

Period	Stations	Salinity	Temperature (°C)	Oxygen (mgO ₂ /L)	Gravel (%)	Sand (%)	Mud (%)
October	G	25.78	22.28	3.59	0	97	3
	H	26.57	21.62	4.42	0	98	2
	C	24.02	25.11	4.83	1	89	10
	D	25.35	22.61	4.39	0	78	22
	A	22.76	24.02	4.24	1	94	4
	B	22.89	24.72	4.97	2	81	17
	Total	24.56 ± 1.58	23.39 ± 1.42	4.41 ± 0.49	1 ± 0.64	90 ± 8.47	10 ± 8.23
January	G	31.01	14.49	6.77	0	99	1
	H	32.93	14.99	6.16	1	95	5
	C	28.65	14.85	8.52	5	52	43
	D	25.30	14.74	8.03	1	85	14
	A	29.86	15.13	10.15	2	79	19
	B	28.81	14.80	8.74	2	79	19
	Total	29.43 ± 2.57	14.83 ± 0.22	8.06 ± 1.44	2 ± 1.69	81 ± 16.52	17 ± 14.86
April	G	36.57	18.20	8.64	1	97	1
	H	36.47	18.42	8.46	0	96	4
	C	25.06	18.60	7.37	2	63	34
	D	29.07	19.61	10.60	4	76	20
	A	29.05	20.05	12.63	0	92	8
	B	28.93	19.95	11.21	7	75	18
	Total	30.86 ± 4.65	19.14 ± 0.83	9.82 ± 1.98	2 ± 2.71	83 ± 13.75	14 ± 12.33
May	G	35.33	24.57	3.35	2	95	3
	H	35.50	24.78	3.02	0	96	4
	C	34.58	25.40	0.05	4	66	30
	D	35.58	25.26	0.14	6	73	21
	A	31.04	24.19	1.60	0	92	8
	B	30.68	23.64	2.12	6	75	19
	Total	33.78 ± 2.30	24.64 ± 0.66	1.71 ± 1.40	3 ± 2.62	83 ± 13.26	14 ± 11.15
July	G	29.62	27.01	5.36	3	94	4
	H	31.15	25.84	5.60	0	97	3
	C	25.81	27.02	4.37	6	69	26
	D	25.89	26.98	5.49	7	70	23
	A	28.83	26.41	6.85	1	92	8
	B	29.07	26.29	5.06	5	74	21
	Total	28.39 ± 2.13	26.59 ± 0.49	5.46 ± 0.81	4 ± 2.96	83 ± 13.07	14 ± 10.34

Table S6.2. Sedimentary contents of proteins (cPRT), carbohydrates (cCHO), lipids (cLIP), biopolymeric C (BPC) and total phytopigments (CPE), algal fraction of BPC (CCPE:BPC) and protein to carbohydrate ratio (PRT:CHO) in the sediments of the S'Ena Arrubia lagoon in each period and station. Average and standard errors (SE; n=3) are reported for each station.

Period	Stations	cPRT mgC g ⁻¹		cCHO mgC g ⁻¹		cLIP mgC g ⁻¹		BPC mgC g ⁻¹		CPE (PHYTO tot) µg g ⁻¹		CCPE:BPC %		PRT:CHO		C Degradation rates µgC g ⁻¹ h ⁻¹		C Turnover Time days	
		Avg	Se	Avg	Se	Avg	Se	Avg	Se	Avg	Se	Avg	Se	Avg	Se	Avg	Se	Avg	Se
October	G	1.90	0.23	0.91	0.09	0.42	0.01	3.23	0.22	26.07	0.08	24.48	1.80	2.15	0.41	8.45	0.63	13.91	0.84
	H	1.31	0.17	0.51	0.03	0.26	0.02	2.09	0.18	18.16	2.41	25.92	1.45	2.55	0.17	8.16	0.19	9.35	1.17
	C	2.83	0.24	1.78	0.26	1.08	0.03	5.69	0.44	45.97	0.45	24.49	1.62	1.66	0.26	4.47	0.11	28.15	0.09
	D	2.11	0.17	2.08	0.12	0.81	0.11	5.01	0.24	50.03	6.26	29.79	2.32	1.03	0.12	3.67	0.02	27.65	2.81
	A	2.01	0.01	1.01	0.09	0.17	0.02	3.19	0.09	17.85	0.12	16.81	0.38	2.03	0.20	8.51	0.18	22.49	1.63
	B	1.79	0.17	0.65	0.10	0.66	0.06	3.10	0.31	23.23	1.30	22.74	1.38	2.86	0.39	9.90	0.19	17.65	0.73
January	G	0.52	0.03	0.11	0.02	0.03	0.00	0.66	0.04	4.72	0.79	21.43	2.95	5.10	0.71	1.08	0.06	24.36	1.32
	H	0.12	0.01	0.12	0.01	0.02	0.00	0.26	0.00	3.33	0.12	37.80	1.46	1.02	0.13	1.51	0.09	6.72	0.39
	C	2.65	0.01	1.97	0.11	0.26	0.03	4.87	0.13	29.66	5.04	18.24	2.95	1.36	0.07	1.14	0.06	27.42	1.92
	D	1.47	0.12	0.85	0.05	0.22	0.01	2.54	0.05	34.32	2.52	40.40	2.31	1.77	0.25	3.89	0.10	18.39	2.31
	A	0.57	0.02	0.17	0.01	0.03	0.00	0.78	0.02	6.67	0.41	25.68	1.16	3.39	0.39	3.20	0.03	60.11	0.84
	B	1.14	0.17	0.56	0.04	0.03	0.00	1.74	0.20	20.53	3.04	36.78	7.02	2.02	0.18	1.82	0.16	54.13	4.65
April	G	0.39	0.04	0.25	0.05	0.03	0.00	0.67	0.06	6.96	0.77	30.88	0.55	1.66	0.37	4.26	0.02	6.24	0.60
	H	0.54	0.08	0.39	0.08	0.07	0.01	1.00	0.14	9.72	0.04	30.24	3.63	1.45	0.25	2.43	0.11	16.01	2.46
	C	3.16	0.07	1.26	0.22	0.13	0.01	4.55	0.29	52.04	6.03	34.09	2.18	2.68	0.50	1.53	0.13	34.82	3.68
	D	2.36	0.02	0.57	0.03	0.20	0.01	3.13	0.03	24.30	1.15	23.27	0.95	4.15	0.25	2.85	0.05	40.57	4.32
	A	0.99	0.17	0.30	0.02	0.07	0.01	1.37	0.17	12.91	0.42	29.31	4.22	3.37	0.66	8.36	0.61	22.46	2.88
	B	2.17	0.34	0.61	0.00	0.27	0.01	3.06	0.34	37.61	3.43	38.09	5.99	3.53	0.55	5.40	0.43	22.92	1.91
May	G	0.71	0.11	0.21	0.01	0.23	0.02	1.15	0.12	22.79	3.86	79.02	10.62	3.30	0.37	3.64	0.29	10.72	1.60
	H	0.53	0.05	0.37	0.07	0.10	0.02	1.01	0.10	2.28	0.09	9.18	0.65	1.53	0.27	3.81	0.21	9.84	0.67
	C	4.42	0.05	0.97	0.02	0.74	0.01	6.13	0.03	17.29	0.16	11.28	0.07	4.58	0.12	1.31	0.15	31.11	2.84
	D	2.14	0.23	0.91	0.05	0.43	0.06	3.48	0.25	8.59	1.11	9.95	1.38	2.37	0.33	3.74	0.53	47.50	8.16
	A	0.72	0.06	0.24	0.00	0.09	0.01	1.05	0.05	8.42	0.10	32.20	2.02	3.00	0.28	6.14	0.80	37.80	4.75
	B	2.47	0.08	1.60	0.17	0.43	0.02	4.51	0.23	18.71	7.84	23.51	3.51	1.57	0.14	3.68	0.23	34.72	2.23
July	G	0.92	0.08	0.46	0.04	0.18	0.02	1.56	0.12	8.63	0.41	22.55	2.86	2.02	0.08	3.70	0.34	15.89	2.21
	H	1.41	0.20	0.36	0.08	0.33	0.00	2.10	0.17	7.58	0.12	14.61	1.03	4.36	1.23	6.70	0.97	11.20	0.73
	C	3.07	0.19	2.28	0.30	0.94	0.00	6.29	0.45	26.52	0.87	17.06	1.45	1.37	0.13	1.56	0.21	16.83	1.27
	D	2.94	0.25	1.91	0.01	0.49	0.03	5.34	0.27	13.63	1.47	10.27	1.31	1.54	0.13	1.87	0.17	23.89	3.11
	A	0.38	0.04	0.24	0.01	0.03	0.00	0.65	0.04	2.34	0.16	14.49	1.45	1.55	0.21	5.87	0.70	38.49	3.61
	B	0.63	0.04	0.42	0.00	0.11	0.01	1.15	0.04	2.56	0.14	8.93	0.69	1.51	0.11	7.30	0.49	27.89	1.99

Table S6.3 Abundances of each meiofaunal taxon identified, total abundance, and number of taxa in the sediments of the S'Ena Arrubia lagoon during each period and at each station. By "Others" we mean the sum of abundances of the minor taxa (all except Nematoda, Copepoda, and Ostracoda). Abundances are expressed as ind. 10 cm⁻². Mean values and standard errors (SE; n = 3) are reported for each station.

Period	Stations	Nematoda		Copepoda		Polichaeta		Bivalvia		Ostracoda		Turbellaria		Oligochaeta		Amphipoda		Isopoda		Gasteropoda		Rotifera		Chironomidae larvae		Others (tot)		Total		N° TAXA		
		Avg	Se	Avg	Se	Avg	Se	Avg	Se	Avg	Se	Avg	Se	Avg	Se	Avg	Se	Avg	Se	Avg	Se	Avg	Se	Avg	Se	Avg	Se	Avg	Se	Avg	Se	
October	G	272.00	2.89	2.50	0.29	0.00	0.00	0.00	0.00	29.00	12.70	3.50	0.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.50	0.29	307.00	9.24	4.00	0.00		
	H	359.33	47.51	6.00	3.06	0.00	0.00	0.00	0.00	1.33	0.33	2.33	0.67	0.00	0.00	0.33	0.33	0.00	0.00	0.00	0.00	0.00	0.00	2.67	0.88	369.33	50.97	4.33	0.33			
	A	238.00	96.42	2.00	2.00	0.00	0.00	0.00	0.00	0.67	0.33	0.00	0.00	0.67	0.33	0.00	0.00	0.58	0.67	0.67	1.00	1.00	0.00	0.00	2.33	0.67	243.00	95.71	3.33	0.33		
	B	134.67	23.38	12.00	8.02	0.00	0.00	0.00	0.00	4.67	2.03	0.33	0.33	0.33	0.33	0.00	0.00	0.58	0.67	0.33	0.00	0.00	0.00	0.00	1.33	0.33	152.67	22.06	4.33	0.33		
	C	89.67	35.69	3.67	2.03	0.33	0.33	0.00	0.00	2.67	1.33	2.33	1.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.67	1.67	98.67	36.96	3.67	0.33		
	D	60.00	20.53	0.00	0.00	0.00	0.00	0.00	0.00	4.00	0.00	2.67	1.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.67	1.20	66.67	20.63	3.00	0.00		
Total		192.28	37.73	4.36	2.57	0.06	0.06	0.00	0.00	7.06	2.79	1.86	0.64	0.17	0.11	0.06	0.06	0.00	0.19	0.22	0.17	0.17	0.17	0.00	0.00	2.53	0.84	206.22	39.26	3.78	0.22	
January	G	584.00	61.29	71.00	28.36	1.50	0.58	0.00	0.00	4.00	6.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	2.00	0.00	661.00	0.00	6.00	0.00		
	H	453.67	145.16	106.00	30.61	0.33	0.33	0.00	0.00	12.67	5.93	1.00	0.58	4.00	2.08	0.00	0.00	0.67	3.61	0.00	0.00	0.00	0.00	0.00	6.00	2.52	578.33	171.41	5.00	0.33		
	A	605.33	77.42	132.33	2.60	2.00	0.58	0.00	0.00	11.00	3.21	0.33	0.33	0.00	0.00	0.33	0.33	1.33	0.00	0.33	0.33	4.00	2.00	0.00	8.33	2.03	757.00	76.35	4.33	0.33		
	B	308.33	66.79	55.33	38.37	0.67	0.33	0.00	0.00	7.67	2.33	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	9.00	4.51	0.00	10.00	5.03	381.33	94.48	5.67	0.88		
	C	144.67	90.52	9.67	7.22	0.00	0.00	0.00	0.00	4.33	0.88	1.67	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.67	0.33	160.33	98.31	4.67	1.20		
	D	272.00	111.97	58.33	27.09	0.33	0.33	0.00	0.00	7.67	2.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.33	2.00	1.00	0.00	0.00	2.67	1.67	340.67	142.19	4.67	0.67		
Total		394.67	92.19	72.11	22.38	0.81	0.36	0.00	0.00	7.89	3.45	0.50	0.21	0.67	0.35	0.06	0.06	0.39	0.60	0.11	0.11	2.58	1.25	0.00	0.00	5.11	1.93	479.78	97.12	5.06	0.57	
April	G	306.00	35.35	36.50	9.71	3.00	1.15	0.00	0.00	10.00	3.46	6.50	3.18	0.00	0.33	1.00	0.67	0.00	0.58	0.00	1.00	0.00	0.00	0.00	10.50	3.18	363.00	44.38	5.00	0.00		
	H	167.67	34.92	31.33	5.36	1.33	1.33	0.00	0.00	11.00	8.62	4.00	1.53	0.33	0.33	0.00	0.00	9.33	0.58	0.00	0.00	0.00	0.00	0.00	15.00	3.51	225.00	41.28	5.00	0.58		
	A	359.33	154.82	84.33	61.84	1.33	0.88	0.00	0.00	25.00	13.23	0.33	0.33	0.00	0.00	0.00	0.00	1.33	0.00	0.33	0.33	0.33	0.33	0.00	3.67	2.03	472.33	214.63	4.33	0.33		
	B	117.67	19.60	2.00	1.15	1.00	0.58	0.00	0.00	10.00	7.64	0.67	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.33	0.67	0.33	2.67	0.33	132.33	25.69	4.00	1.00	
	C	307.33	37.02	49.33	8.65	0.67	0.33	0.00	0.00	7.33	2.03	0.00	0.00	0.00	0.00	0.00	0.00	4.67	0.00	0.00	0.00	0.67	0.33	0.00	0.00	6.00	0.00	370.00	34.60	4.33	0.67	
	D	198.67	94.22	12.00	6.11	0.00	0.00	0.00	0.00	11.00	4.73	0.00	0.00	0.00	0.00	0.00	0.00	0.67	0.00	0.33	0.33	0.67	0.33	0.00	0.00	1.67	0.88	223.33	95.94	3.67	0.33	
Total		242.78	62.66	35.92	15.47	1.22	0.71	0.00	0.00	12.39	6.62	1.92	0.95	0.06	0.11	0.17	0.11	2.67	0.19	0.11	0.28	0.33	0.22	0.11	0.06	6.58	1.66	297.67	76.09	4.39	0.49	
May	G	301.50	36.99	0.00	0.00	0.00	0.00	0.00	0.00	12.50	7.67	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.33	314.00	38.35	2.33	0.33
	H	268.67	71.48	4.67	2.03	0.00	0.00	0.00	0.00	6.00	3.51	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.33	0.00	0.00	0.00	0.00	0.33	0.33	279.67	71.66	3.00	0.00		
	A	134.33	58.32	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.67	0.33	0.00	0.00	0.00	0.00	0.67	0.33	135.00	58.03	1.67	0.33		
	B	28.67	5.70	0.00	0.00	0.00	0.00	0.00	0.00	10.33	2.96	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	39.00	8.50	2.00	0.00	
	C	5.00	2.52	0.00	0.00	0.00	0.00	0.00	0.00	3.67	2.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	8.67	0.88	1.67	0.33	
	D	37.33	33.33	0.00	0.00	0.00	0.00	0.00	0.00	3.33	2.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.33	0.00	0.00	0.00	0.00	0.00	0.33	0.33	41.00	36.00	2.00	0.00	
Total		129.25	34.72	0.78	0.34	0.00	0.00	0.00	0.00	5.97	3.08	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.22	0.17	0.00	0.00	0.00	0.00	0.00	0.22	0.22	136.22	35.57	2.11	0.17	
July	G	237.50	130.21	26.50	15.30	0.00	0.00	0.00	0.00	2.50	1.20	1.00	1.45	1.00	0.67	0.00	0.00	0.00	1.15	0.00	0.00	1.00	0.67	4.33	3.38	4.00	4.48	270.50	145.19	5.33	0.67	
	H	380.00	151.00	23.67	2.85	0.33	0.33	0.33	0.33	0.33	0.33	1.33	0.67	0.00	0.00	0.00	0.00	0.00	0.33	0.33	0.00	0.00	0.67	0.67	3.00	0.00	407.00	151.45	4.33	0.33		
	A	116.00	49.66	91.67	31.93	1.00	1.00	0.00	0.00	3.67	3.18	0.33	0.33	0.00	0.00	0.00	0.00	0.00	0.33	0.33	0.00	0.00	1.00	0.58	2.67	2.19	214.00	78.50	4.33	1.45		
	B	95.33	37.95	62.67	21.26	1.67	1.67	0.00	0.00	15.00	8.62	0.67	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.58	3.33	1.86	176.33	21.42	4.33	0.33		
	C	41.33	14.31	37.00	7.51	1.67	0.67	0.00	0.00	4.33	1.45	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	1.33	0.88	3.33	0.88	86.00	23.00	3.33	0.88		
	D	58.00	16.82	14.00	11.14	0.33	0.33	0.00	0.00	4.67	3.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	1.00	1.33	1.33	78.00	27.30	4.33	0.33		
Total		154.69	66.66	42.58	15.00	0.83	0.67	0.06	0.06	5.08	2.99	0.56	0.52	0.17	0.11	0.00	0.00	0.06	0.19	0.11	0.11	0.17	0.11	1.56	1.18	2.94	1.79	205.31	74.48	4.33	0.67	

Table S6.4. Contribution of each taxon (%) at the total community composition during each period and at each station

		Nematoda	Copepoda	Polychaeta	Bivalvia	Ostracoda	Turbellaria	Oligochaeta	Amphipoda	Isopoda	Gastropoda	Rotifera	Chironomidae larvae	Others (tot)	Total
October	G	88.60	0.81	0.00	0.00	9.45	1.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100.00
	H	97.29	1.62	0.00	0.00	0.36	0.63	0.00	0.09	0.00	0.00	0.00	0.00	0.00	100.00
	A	97.94	0.82	0.00	0.00	0.27	0.00	0.27	0.00	0.00	0.27	0.41	0.00	0.27	100.00
	B	88.21	7.86	0.00	0.00	3.06	0.22	0.22	0.00	0.00	0.44	0.00	0.00	0.44	100.00
	C	90.88	3.72	0.34	0.00	2.70	2.36	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100.00
	D	90.00	0.00	0.00	0.00	6.00	4.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100.00
	Total	92.15	2.47	0.06	0.00	3.64	1.39	0.08	0.02	0.00	0.12	0.07	0.00	0.12	100.00
January	G	88.35	10.74	0.23	0.00	0.61	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00	100.00
	H	78.44	18.33	0.06	0.00	2.19	0.17	0.69	0.00	0.12	0.00	0.00	0.00	0.00	100.00
	A	79.96	17.48	0.26	0.00	1.45	0.04	0.00	0.04	0.18	0.04	0.53	0.00	0.04	100.00
	B	80.86	14.51	0.17	0.00	2.01	0.00	0.00	0.00	0.09	0.00	2.36	0.00	0.00	100.00
	C	90.23	6.03	0.00	0.00	2.70	1.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100.00
	D	79.84	17.12	0.10	0.00	2.25	0.00	0.00	0.00	0.00	0.10	0.59	0.00	0.10	100.00
	Total	82.95	14.04	0.14	0.00	1.87	0.21	0.12	0.01	0.06	0.02	0.59	0.00	0.02	100.00
April	G	84.30	10.06	0.83	0.00	2.75	1.79	0.00	0.28	0.00	0.00	0.00	0.00	0.00	100.00
	H	74.52	13.93	0.59	0.00	4.89	1.78	0.15	0.00	4.15	0.00	0.00	0.00	0.00	100.00
	A	76.08	17.85	0.28	0.00	5.29	0.07	0.00	0.00	0.28	0.07	0.07	0.00	0.07	100.00
	B	88.92	1.51	0.76	0.00	7.56	0.50	0.00	0.00	0.00	0.00	0.25	0.50	0.00	100.00
	C	83.06	13.33	0.18	0.00	1.98	0.00	0.00	0.00	1.26	0.00	0.18	0.00	0.00	100.00
	D	88.96	5.37	0.00	0.00	4.93	0.00	0.00	0.00	0.30	0.15	0.30	0.00	0.15	100.00
	Total	82.64	10.34	0.44	0.00	4.57	0.69	0.02	0.05	1.00	0.04	0.13	0.08	0.04	100.00
May	G	96.02	0.00	0.00	0.00	3.98	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100.00
	H	96.07	1.67	0.00	0.00	2.15	0.00	0.00	0.00	0.00	0.12	0.00	0.00	0.12	100.00
	A	99.51	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.49	0.00	0.00	0.49	100.00
	B	73.50	0.00	0.00	0.00	26.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100.00
	C	57.69	0.00	0.00	0.00	42.31	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100.00
	D	91.06	0.00	0.00	0.00	8.13	0.00	0.00	0.00	0.00	0.81	0.00	0.00	0.81	100.00
	Total	85.64	0.28	0.00	0.00	13.84	0.00	0.00	0.00	0.00	0.24	0.00	0.00	0.24	100.00
July	G	87.80	9.80	0.00	0.00	0.92	0.37	0.37	0.00	0.00	0.00	0.37	1.60	0.00	100.00
	H	93.37	5.81	0.08	0.08	0.08	0.33	0.00	0.00	0.00	0.08	0.00	0.16	0.08	100.00
	A	54.21	42.83	0.47	0.00	1.71	0.16	0.00	0.00	0.00	0.16	0.00	0.47	0.16	100.00
	B	54.06	35.54	0.95	0.00	8.51	0.38	0.00	0.00	0.00	0.00	0.00	0.57	0.00	100.00
	C	48.06	43.02	1.94	0.00	5.04	0.00	0.00	0.00	0.39	0.00	0.00	1.55	0.00	100.00
	D	74.36	17.95	0.43	0.00	5.98	0.00	0.00	0.00	0.00	0.00	0.00	1.28	0.00	100.00
	Total	64.81	29.03	0.77	0.02	4.26	0.17	0.00	0.00	0.08	0.05	0.00	0.81	0.05	100.00

Table S6.5. Output of SIMPER analysis (cut of 90%), on the log transformed data of taxonomical composition testing for % dissimilarity among systems in each season and between seasons in each system.

		Average similarity (%)	Top contributing taxa	Cumulative contribution (%)
October	G vs H	17.4	Ostracoda (62%), Copepoda (15.8%), Turbellaria (9.6%), Nematoda (6.8%)	94.2
	B vs H	23.3	Nematoda (21.7%), Turbellaria (20.2 %), Copepoda (19.9%), Ostracoda (18.4 %), Gasteropoda (10.1%)	90.3
	A vs H	29.4	Copepoda (27%), Turbellaria (22.5), Nematoda (14.5%), Rotifera (9.7%), Oligochaeta (6.9%), Gasteropoda (6.6%)	95.9
	D vs H	31.1	Nematoda (38 %), Copepoda (33.6 %), Ostracoda (15.2%), Turbellaria (9.2%)	95.9
	C vs H	24	Nematoda (36.1%), Copepoda (22.3%), Ostracoda (18.9%), Turbellaria (12.3%), Polichaeta (5,5%)	95
	B vs G	24.6	Ostracoda (30.5%), Turbellaria (24.5%), Copepoda (17.7%), Nematoda (14.1%), Gasteropoda (8.8%)	95.7
	A vs G	37.4	Ostracoda (37%), Turbellaria (21.1%), Copepoda (15.1%), Nematoda (8.9%), Rotifera (6.9%), Oligochaeta (6.3%)	95.3
	D vs G	27.2	Nematoda (34.2%), Ostracoda (30.5%), Copepoda (25.2%), Turbellaria (10%)	100
	C vs G	26	Ostracoda (41.5%), Nematoda (25.3%), Copepoda (15.9%), Turbellaria (12.7%)	95.4
	A vs B	30.1	Copepoda (33.4 %), Ostracoda (21.2%), Nematoda (14.1%), Gasteropoda (9.9%), Rotifera (9.6%), Oligochaeta (7.4%)	95.4
	D vs B	32.6	Copepoda (40.8 %), Nematoda (18.2%), Turbellaria (17.8 %), Ostracoda (10.4%)	95.8
	C vs B	26.1	Copepoda (26.4 %), Ostracoda (20.3%), Turbellaria (18%), Nematoda (15.2%), Gasteropoda (10%)	90
	D vs A	38.7	Nematoda (24.6%), Turbellaria (21.4 %), Ostracoda (20.4%), Copepoda (10.6 %), Rotifera (9.1%), Oligochaeta (8%)	94
	C vs A	36.34	Copepoda (19.5 %), Nematoda (19%), Turbellaria (18.8 %), Ostracoda (15.9%), Rotifera (8.9%), Oligochaeta (7.9%), Gasteropoda (5.9%)	95.9
	C vs D	22.89	Copepoda (36.5 %), Nematoda (23%), Ostracoda (17.8%), Turbellaria (15.9%)	93.1
January	G vs H	16.8	Oligochaeta (24.8%), Ostracoda (15.9%), Turbellaria (12.3%), Copepoda (11.8%), Nematoda (11%), Polichaeta (10.8%), Isopoda (8.9%)	95.4
	B vs H	24.8	Rotifera (28.8%), Copepoda (18.2%), Oligochaeta (16.6%), Ostracoda (9.1%), Nematoda (8.8%), Turbellaria (8.2%), Polichaeta (5.3%)	94.8
	A vs H	21	Rotifera (21.3%), Oligochaeta (17.7%), Polichaeta (12.3%), Isopoda (9,9%), Ostracoda (9.8%), Nematoda (8.3%), Turbellaria (7.5%), Copepoda (6.5%)	93.3
	D vs H	21.8	Oligochaeta (19.7%), Rotifera (15.8%), Copepoda (15%), Nematoda (13.1%), Ostracoda (11.4%), Turbellaria (9.8%), Isopoda (7.1%)	91.9
	C vs H	31.4	Copepoda (37.5%), Nematoda (22.2%), Oligochaeta (15.7%), Ostracoda (10.4%), Turbellaria (5.9%)	91.6
	B vs G	18.3	Rotifera (37.1%), Copepoda (24.2%), Ostracoda (13.1%), Nematoda (12.4%), Polichaeta (8.9%)	95.6
	A vs G	14.5	Rotifera (27.4%), Ostracoda (17.1%), Polichaeta (12.2%), Isopoda (11.8%), Copepoda (11.2%), Turbellaria (5.2%), Amphipoda (5.2%), Gasteropoda (5.1%)	95.1
	D vs G	15	Nematoda (23.1%), Copepoda (21%), Ostracoda (19.1%), Rotifera (18.7%), Polichaeta (13.4%)	94.9
	C vs G	31.1	Copepoda (38.2 %), Nematoda (27.5%), Turbellaria (13.7%), Ostracoda (8.8%), Polichaeta (8.6%)	96.8
	A vs B	17.4	Copepoda (25.5 %), Rotifera (15.8 %), Nematoda (13.5%), Polichaeta (11.2%), Isopoda (11.1%), Ostracoda (10%), Turbellaria (4.3%)	91.5
	D vs B	15.3	Rotifera (27.9%), Copepoda (24.3%), Nematoda (15.1%), Ostracoda (12.8%), Polichaeta (9.4%), Isopoda (5.5%)	95
	C vs B	33	Rotifera (28%), Copepoda (25%), Nematoda (18.7%), Turbellaria (12.7%), Ostracoda (6.8%)	91.2
	D vs A	18.4	Copepoda (19.2 %), Nematoda (18%), Polichaeta (15.4%), Rotifera (12.7 %), Ostracoda (11.3%), Isopoda (9.6%), Gasteropoda (5.4%)	91.6
	C vs A	38.9	Copepoda (30.7 %), Nematoda (19.7%), Rotifera (14.4 %), Polichaeta (10.4%), Ostracoda (7.8%), Turbellaria (7.1%)	90.2
	C vs D	29.3	Copepoda (33.1 %), Nematoda (20.9%), Rotifera (15.3 %), Turbellaria (15.3%), Ostracoda (9.1%)	93.7
April	G vs H	25.8	Isopoda (29.8%), Ostracoda (18.4%), Polichaeta (11.1%), Turbellaria (9.8%), Copepoda (8%), Nematoda (7.4%), Gasteropoda (6.5%)	91.2

	B vs H	40.3	Copepoda (27%), Isopoda (23.5%), Ostracoda (15.7%), Turbellaria (12.2%), Polichaeta (7.7%), Chironomidae larvae (5%)	90.7
	A vs H	27	Ostracoda (24.4%), Isopoda (20.7%), Turbellaria (16.9%), Copepoda (10%), Nematoda (10%), Polichaeta (9.6%)	92
	D vs H	35.6	Isopoda (21.6%), Copepoda (17.7%), Turbellaria (17.1%), Ostracoda (16%), Nematoda (10.8%), Polichaeta (5.7%), Rotifera (5.3%)	94.2
	C vs H	20.3	Turbellaria (25.5%), Ostracoda (22%), Polichaeta (11.5%), Nematoda (11%), Isopoda (9.8 %), Copepoda (8.1%), Rotifera (7.9%)	95.7
	B vs G	34.5	Copepoda (27.5%), Ostracoda (16.5%), Turbellaria (14.1%), Nematoda (11%), Polichaeta(8.87%), Gasteropoda (6.2%), Chironomidae larvae (5.9%), Amphipoda (4.3%)	93.9
	A vs G	26.2	Ostracoda (23.7%), Turbellaria (16%), Copepoda (14.7 %), Polichaeta (10.3%), Isopoda (9,1%), Nematoda (8.1%), Gasteropoda (7.5%), Amphipoda (4.8%)	94
	D vs G	30.2	Copepoda (21.4 %), Turbellaria (18.85), Nematoda (13%), Polichaeta (11.9%), Ostracoda (8.6%), Gasteropoda (7.7%), Rotifera (6.3%), Amphipoda (4.7%)	92.2
	C vs G	24.2	Isopoda (24.9%), Turbellaria (20.1%), Copepoda(11.4%), Polichaeta (10.7%), Ostracoda (7.8%), Gasteropoda (7%), Rotifera (6.7%), Amphipoda (5%)	93.6
	A vs B	37	Copepoda (34.5%), Ostracoda (22.5), Nematoda (11.5%), Isopoda (7.8%), Polichaeta (7%), Chironomidae larvae (5.8%), Turbellaria (5.2%)	94.2
	D vs B	33.5	Copepoda (25.4%), Ostracoda (21%), Nematoda (15.9%), Polichaeta (9.7%), Chironomidae larvae (7.5%), Rotifera(6%), Turbellaria (5.3%)	90.9
	C vs B	36.8	Copepoda (34.9%), Isopoda (20. %), Ostracoda (14.2), Nematoda (11.4%), Chironomidae larvae (5.6%), Polichaeta(5.2%)	91.5
	D vs A	29.5	Copepoda (27.3 %), Ostracoda (25.1%), Nematoda (17.1%), Polichaeta (6.6%), Isopoda (8.4%), Rotifera (5.8%)	78.1
	C vs A	20.5	Ostracoda (31.2%), Isopoda (18.8%), Copepoda (16.4%), Nematoda (10.1%), Polichaeta (9.1%), Rotifera (7%)	92.7
	C vs D	25	Copepoda (33.3%), Isopoda (23.1%), Nematoda (16.6%), Ostracoda (9%), Turbellaria (7.5%), Isopoda(6.3%), Rotifera(5.8%)	94.2
May	G vs H	21.8	Copepoda (43%), Ostracoda (32.5%), Nematoda (11.5%), Gasteropoda (6.5%)	93.5
	B vs H	32.8	Nematoda (45.1%), Copepoda (32%), Ostracoda (18%)	95.2
	A vs H	32.9	Ostracoda (37%), Copepoda (33.3%), Nematoda (1.1%)	91.7
	D vs H	46.9	Nematoda (52.8%), Copepoda (26%), Ostracoda (1.4%)	95.1
	C vs H	56.4	Nematoda (58%), Copepoda (23%), Ostracoda (15.5%)	96.5
	B vs G	31.1	Nematoda (59.7%), Ostracoda (34.6%)	94.3
	A vs G	26.6	Ostracoda (43.3%), Nematoda (35.7%), Gasteropoda (14.1%)	91.5
	D vs G	42.7	Nematoda (72.8%), Ostracoda (22.7%)	95.9
	C vs G	55	Nematoda (72.9%), Ostracoda (34.6%)	94.3
	A vs B	38	Ostracoda (57.1%), Nematoda (31.4%), Gasteropoda (11.5%)	100
	D vs B	34	Nematoda (52.2%), Ostracoda (42.7%)	94.9
	C vs B	33.6	Nematoda (59%), Ostracoda (41%)	100
	D vs A	45.8	Nematoda (62,9%), Ostracoda (26,4%), Gasteropoda (10.7%)	100
	C vs A	58.2	Nematoda (63,7%), Ostracoda (25,9%), Gasteropoda (10.3%)	100
	C vs D	34.6	Nematoda (47,4%), Ostracoda (46,1%)	93.5
July	G vs H	23.9	Ostracoda (19.5%), Chironomidae larvae (17.1%), Nematoda (14.5%), Turbellaria (12%), Copepoda (8%), Rotifera (7.1%), Oligochaeta (6.4%), Gasteropoda (4.1%), Bivalvia (4%)	93.8
	B vs H	29.6	Ostracoda (32%), Nematoda (21.7%), Copepoda (12.7 %), Turbellaria (9.2 %), Polichaeta (9%), Chironomidae larvae (8.5%)	93.1
	A vs H	25.7	Nematoda (23 %), Copepoda (20.8 %), Ostracoda (16.6%), Turbellaria (12%), Chironomidae larvae (9.6%), Polichaeta (8.6%)	90.5
	D vs H	36.6	Nematoda (26.1%), Copepoda (25.4%), Ostracoda (18.3%), Turbellaria (11.1%), Chironomidae larvae (7.9%), Polichaeta (4.2%)	93
	C vs H	32	Nematoda (32.5%), Ostracoda (19.7 %), Turbellaria (11%), Polichaeta (10.7%), Chironomidae larvae (9.3%), Copepoda (6.8%), Gasteropoda (3,5%)	93.5
	B vs G	25.3	Nematoda (22.3%), Ostracoda (17 %), Chironomidae larvae (14.4%), Turbellaria (12.4%), Copepoda (10.4%), Polichaeta (8.3%), Rotifera (6.3%)	91.2
	A vs G	26.3	Nematoda (18.1%), Ostracoda (16.2%), Chironomidae larvae (14.6%), Copepoda (13.7), Turbellaria (12.9), Rotifera (6.4%), Polichaeta (6.2%), Oligochaeta (5.7%)	94.7
	D vs G	35.1	Copepoda (27%), Nematoda (20.8%), Chironomidae larvae (13.8%), Turbellaria(11.8%), Ostracoda (10.7%), Rotifera (5.7%), Oligochaeta (5%)	94.7

	C vs G	28.8	Nematoda (28.8%), Chironomidae larvae (14.2%), Polichaeta (13.8%), Turbellaria(12.8%), Ostracoda (7.8%), Copepoda (7%), Rotifera (6%)	90.4
	A vs B	21.1	Ostracoda (32.8%), Nematoda (18.9%), Polichaeta (13.19%), Copepoda (13 %), Chironomidae larvae (9.9%), Turbellaria (8.2%)	96
	D vs B	30.7	Copepoda (38.7%), Ostracoda (20%), Nematoda (15, 3%), Chironomidae larvae (11%), Polichaeta (9.9%)	94.8
	C vs B	20.8	Nematoda (24.8%), Ostracoda (20,1%), Polichaeta (19.5), Chironomidae larvae (12.3%), Copepoda (12%), Turbellaria (6.9%)	91.5
	D vs A	31.6	Copepoda (44,9%), Ostracoda (18.9%), Nematoda (11.7%), Chironomidae larvae (10.4%), Polichaeta(7.9%)	93.6
	C vs A	23	Ostracoda (22.4%), Nematoda (21%), Copepoda (16.9 %), Polichaeta (16.1 %), Chironomidae larvae (11.5%), Isopoda (4.2%)	92.1
	C vs D	28.1	Copepoda (38,6%), Ostracoda (15.3%), Polichaeta (15%), Nematoda (14%), Chironomidae larvae (13%)	96
	Oct vs Jan	29.5	Copepoda (42.7 %), Turbellaria (20.3%), Ostracoda (17%)	79.9
	Oct vs April	22.4	Copepoda (32.3%), Ostracoda (18.7%), Polichaeta(15.2%), Turbellaria (12.6%)	78.7
	Oct vs May	24.3	Ostracoda (41.1%), Turbellaria (27.6%), Copepoda (27.1%)	95.7
G	Oct vs July	30.9	Copepoda (30.5%), Ostracoda (23.1%), Chironomidae larvae (14.1%), Turbellaria(10.2%)	77.9
	Jan vs Apr	21.7	Turbellaria (22,9%),Copepoda (21.3%), Ostracoda (12.1%), Polichaeta (12%), Nematoda (10.7%), Gasteropoda (8%), Amphipoda(5.7%)	92.3
	Jan vs May	34.7	Copepoda (60.6%), Ostracoda(18.2%), Polichaeta (8.2%), Nematoda(6.7%)	93.7
	Jan vs July	22.9	Chironomidae larvae (17.7%), Copepoda (15%), Turbellaria(14.4%), Ostracoda (13.4%), Nematoda (13%), Polichaeta (9.7%), Rotifera (7.5%)	90.8
	April vs May	31.7	Copepoda (39.6%), Ostracoda(17.7%), Turbellaria (14.7 %), Polichaeta (11.1%), Gastereopoda(6.3%), Amphipoda (4.4%)	93.8
	April vs July	26.2	Chironomidae larvae (15.1%), Ostracoda (13.4%), Turbellaria(13.1%), Polichaeta (12.1%), Copepoda (10.5%), Nematoda (9.8%), Gasteropoda (6.7%), Oligochaeta (6.2%), Rotifera (5.6%)	92.4
	May vs July	39.2	Copepoda (43.8%), Chironomidae larvae (13%), Ostracoda (12.6%), Turbellaria (10%), Nematoda (8.4%), Rotifera (5.2%)	93.1
	Oct vs Jan	30.5	Copepoda (37.5 %), Ostracoda (19.8%), Oligochaeta(15.6%), Turbellaria(8.3 %), Nematoda (7.7%), Isopoda (5.6%)	94.4
	Oct vs April	31.1	Isopoda (29.3%), Copepoda (22.3%), Ostracoda(18.6%), Nematoda (10.5%), Polichaeta (6.5%), Turbellaria (6.5%)	93.7
	Oct vs May	19.6	Turbellaria (31.1%), Ostracoda(23.9%), Copepoda (20.5%), Nematoda (12.4%), Gasteropoda (6.3%)	94.3
H	Oct vs July	21.6	Copepoda (33%), Ostracoda(13.8%), Turbellaria (13%), Nematoda(12.5%), Chironomidae larvae (7.7%), Gasteropoda (5.4%), Bivalvia (5.3%)	90.4
	Jan vs Apr	26.5	Isopoda (22.7%), Ostracoda(17.7%), Copepoda (14.7%), Oligochaeta (14.5%), Nematoda (11.7%), Turbellaria (1.5%)	92.7
	Jan vs May	30.1	Copepoda (41.6%),Oligochaeta (16.3%), Ostracoda (13%), Nematoda (9.1%), Turbellaria (8.2%), Isopoda (5.8%)	94
	Jan vs July	28.6	Ostracoda (28.3 %), Copepoda (18.6%), Oligochaeta (15.9%), Nematoda (9.5%), Turbellaria (7.1%), Isopoda (5.7%), Chironomidae larvae (4.6%), Polichaeta (3.9%)	93.7
	April vs May	35.9	Isopoda(26..2%), Copepoda(20.1%), Turbellaria (17.7%), Ostracoda (16.1%), Nematoda (6.3%), Polichaeta (5.8%)	94.2
	April vs July	28.7	Isopoda(30.3%), Ostracoda (21.4%), Nematoda (10.7%), Turbellaria (10.2%), Polichaeta (7.9%), Chironomidae larvae (4.7%), Copepoda (4.7%)	90
	May vs July	28.3	Copepoda (29.1%), Ostracoda (26.6%), Turbellaria (13.4%), Nematoda (11.4%), Chironomidae larvae (6.1%), Gasteropoda (5.5%)	92
	Oct vs Jan	45.5	Copepoda (37.6%), Ostracoda (16.9%), Nematoda (10%), Rotifera (9.8%), Polichaeta (9.3%), Isopoda (4.7%), Oligochaeta (4%)	92
	Oct vs April	42.4	Copepoda (35.3%), Ostracoda (23.1%), Nematoda (9.6%), Isopoda (7.2%), Polichaeta (6.6%), Rotifera (6.2%), Oligochaeta (5.1%)	92.9
	Oct vs May	28.1	Nematoda (28.9%), Copepoda (16.2%), Gastreropoda (14.6%), Rotifera (14.3%), Ostracoda (13.7%), Oligochaeta (12.4%)	100
A	Oct vs July	43.1	Copepoda (46.7%), Nematoda (12%), Ostracoda (11%), Chironomidae larvae (6.6%), Rotifera (6.1%), Oligochaeta (5.5%), Gasteropoda (5.1%)	92.9
	Jan vs Apr	23.9	Ostracoda (23%), Copepoda (18.6%), Rotifera (17.2%), Nematoda (11.3%), Isopoda (10.3%), Polichaeta (8.5%), Turbellaria (4.2%)	92.8
	Jan vs May	57.6	Copepoda (45.7%), Ostracoda (24.2%), Nematoda (11.7%), Rotifera (11.4%)	92.9

	Jan vs July	28.6	Nematoda(22.7%, Ostracoda (18.6%), Rotifera (17.9%), Polichaeta (10.3%), Copepoda (7.2%), Chironomidae larvae (6.8%), Isopoda (6.5%), Turbellaria (3.7%)	93.5
	April vs May	49.1	Copepoda (41.5%), Ostracoda (23.1%), Nematoda (13.2%), Isopoda (7%), Polichaeta (6.3%)	91.1
	April vs July	28.2	Ostracoda (28.4%), Nematoda (17.7%), Copepoda (16.5%), Isopoda (9.4%), Polichaeta (9.3%), Chironomidae larvae (7.9%), Turbellaria (4.2%)	93.3
	May vs July	47.5	Copepoda (56.8%), Ostracoda (12.7%), Nematoda(11.2%), Chironomidae larvae (6.8%), Gasteropoda (5.3%)	92.7
B	Oct vs Jan	28.5	Rotifera (31.3%), Copepoda (23.1%), Nematoda (11.6%), Ostracoda (10.5%), Gasteropoda (6.8%), Polichaeta (6.5%), Turbellaria (3.5%)	93.3
	Oct vs April	28.8	Copepoda (24.8%), Ostracoda (23.3%), Polichaeta (11.7%), Chironomidae larvae (9%), Gasteropoda (8.6%), Turbellaria (8.1%), Nematoda (5.9%)	91.3
	Oct vs May	35.7	Copepoda (39.7%), Nematoda (28.2%), Ostracoda (15.2%), Gasteropoda (8.3%)	91.5
	Oct vs July	27.5	Copepoda (31.8%), Ostracoda (17.1%), Nematoda (13.2%), Chironomidae larvae (10.6%), Polichaeta (8.9%), Gasteropoda (7.6%), Turbellaria (7.1%)	96.3
	Jan vs Apr	35.2	Copepoda (32.1%), Rotifera (23%), Ostracoda (15.2%), Nematoda (11.3%), Chironomidae larvae (5.9%), Polichaeta (5.6%)	93
	Jan vs May	45.8	Copepoda (38.7%), Nematoda (25.5%), Rotifera (23.2%), Ostracoda (5.4%)	92.8
	Jan vs July	27.4	Rotifera (29.1%), Nematoda (19.4%), Copepoda (15.1%), Ostracoda (10.1%), Polichaeta (9.9%), Chironomidae larvae (8.7%)	92.3
	April vs May	36	Nematoda (126.3%), Ostracoda (24.6%), Copepoda (17.1%), Polichaeta (11.9%), Chironomidae larvae(9.2%), Turbellaria (6.3%)	95.4
	April vs July	34.2	Copepoda (43.8%), Ostracoda (19.3%), Polichaeta (10.8%), Nematoda (10.3%), Turbellaria (6.4%)	90.7
	May vs July	41.1	Copepoda (55.4%), Nematoda (15.1%), Ostracoda (9.5%), Chironomidae larvae (88.7%), Polichaeta (95.7%)	95.7
C	Oct vs Jan	21.7	Copepoda(32.2%), Nematoda (29.2%), Oligochaeta (19.6%), Turbellaria (12.6%)	93.6
	Oct vs April	39.2	Copepoda (30.7%), Isopoda (19.9%), Nematoda (15.8%), Turbellaria (12.2%), Ostracoda(11.7%)	90.3
	Oct vs May	56.9	Nematoda (44.1%), Copepoda (20%), Turbellaria (17.4%), Ostracoda (14.8%)	96.2
	Oct vs July	36.4	Copepoda (35.1%), Turbellaria (15.9%), Nematoda (13.9%), Ostracoda (11.6%), Polichaeta (10.9%), Chironomidae larvae (9.6%)	96.9
	Jan vs Apr	33.2	Copepoda (28%), Isopoda (22.7%), Nematoda (18.4%), Turbellaria (12.5%), Ostracoda (6.4%), Rotifera (6.1%)	94
	Jan vs May	53.1	Nematoda (43.8%), Copepoda (28%), Turbellaria (15.6%), Ostracoda (12.7%)	100
	Jan vs July	32.7	Copepoda (29.4%), Nematoda (20.4%), Polichaeta (15.3%), Turbellaria (15.2%), Chironomidae larvae (10.2%)	90.5
	April vs May	67.4	Nematoda (35.3%), Copepoda (33.7%), Isopoda (15%), Ostracoda (8.2%)	92.1
	April vs July	25.4	Nematoda (34.8%), Isopoda (24.1%), Chironomidae larvae (10.4%), Ostracoda (9.3%), Polichaeta (7.8%), Rotifera (7.3%)	93.6
	May vs July	60.5	Copepoda (44.4%), Nematoda (23.1%), Polichaeta (12.1%), Ostracoda(10.2%), Chironomidae larvae (7.7%)	97.5
D	Oct vs Jan	43.4	Copepoda (45.6%), Nematoda (17.4%), Turbellaria (14.2%), Rotifera (11.4%), Ostracoda (6.9%)	91.8
	Oct vs April	36.6	Copepoda (29.8%), Nematoda (21.6%), Turbellaria (19.4%), Ostracoda (12.2%), Rotifera (7.6%)	90.5
	Oct vs May	40	Nematoda (46.8%), Turbellaria (28.7%), Ostracoda (20.5%)	95.9
	Oct vs July	33.7	Copepoda (34.3%), Turbellaria (24.4%), Ostracoda (16.4%), Nematoda (13.4%), Chironomidae larvae (7.6%)	96.2
	Jan vs Apr	22.2	Copepoda (26.9%), Nematoda (21%), Ostracoda (13.7%), Rotifera (9.8%), Isopoda (6.5%), Gasteropoda (6.2%)	96.1
	Jan vs May	56.8	Copepoda (41.3%), Nematoda (31.9%), Ostracoda (11.7%), Rotifera (10.2%)	95.1
	Jan vs July	31.2	Copepoda (34.5%), Nematoda (22.5%), Rotifera (15.1%), Ostracoda (14.3%), Chironomidae larvae (6.2%)	92.5
	April vs May	50.3	Nematoda (37.8%), Copepoda (26.1%), Ostracoda (20.5%), Rotifera (6.8%)	91%
	April vs July	31.6	Copepoda (29.3%), Nematoda (21.4%), Ostracoda (20.4%), Rotifera (8.3%), Chironomidae larvae (6.8%), Isopoda (5.6%)	91.9
	May vs July	45.4	Nematoda (38.1%), Copepoda (31.8%), Ostracoda (16.6%), Chironomidae larvae (6.8%)	93.3

Table S6.6 Output of SIMPER analysis (cut of 90%), on presence/absense data of taxonomical composition testing for % dissimilarity among systems in each season and between seasons in each system

		Average similarity (%)	Top contributing taxa	Cumulative contribution (%)
October	G vs H	3.7	Amphipoda (100%)	100
	B vs H	22.4	Turbellaria (34%), Gasteropoda (34%), Oligochaeta (16%), Amphipoda (16%)	100
	A vs H	47.4	Turbellaria (27.7%), Copepoda(19.2%), Oligochaeta (18.1%), Rotifera (9.6%), Ostracoda (8.5%), Amphipoda (8.5%)	91.50
	D vs H	17.9	Copepoda (76.7%), Amphipoda (23.3%)	100
	C vs H	16.5	Ostracoda (27.8%), Copepoda (24.4%), Polichaeta(24.4%), Amphipoda (23.5%)	100
	B vs G	19.4	Turbellaria(40.5%), Gasteropoda (40.5%), Oligochaeta (19.1%)	100
	A vs G	45.3	Turbellaria (30.3%), Copepoda (21.1%), Oligochaeta(19.7%), Rotifera (10.5%), Ostracoda (9.2%)	90.8
	D vs G	14.3	Copepoda (100%)	100
	C vs G	13.1	Ostracoda (36.7%), Copepoda (31.8%), Polichaeta (31.8%)	100
	A vs B	37	Copepoda (24.7%), Oligochaeta (19.9%), Gasteropoda (19.9%), Turbellaria (12.4%), Rotidera (12.4%), Ostracoda (10.9)	100
	D vs B	35.7	Copepoda (38.3%), Turbellaria (25%), Gasteropoda (25%), Oligochaeta (11.7%)	100
	C vs B	32.9	Turbellaria (25%), Gasteropoda (25%), Ostracoda (13.9%), Copepoda (12.2%), Polichaeta (12.2%), Oligochaeta (11.7%)	100
	D vs A	46	Turbellaria (34.5%), Oligochaeta (22.4%), Rotifera (12.1%), Copepoda (10.3%), Ostracoda (10.3%), Gasteropoda (10.3%)	100
	C vs A	52.5	Turbellaria (27.5%), Oligochaeta (17.9%), Copepoda (15.7%), Ostracoda (12.3%), Rotifera (9.6%), Polichaeta (8.7%)	91.7
	C vs D	20.6	Copepoda (50%), Ostracoda (26.9%), Polichaeta (23.1%)	100
January	G vs H	30.2	Turbellaria (24.1%), Oligochaeta (22.5%), Isopoda (22.5%), Polichaeta (20.2%), Rotifera (10.9%)	100
	B vs H	33.4	Rotifera (29.6%), Turbellaria (19.5%), Oligochaeta (18.4%), Polichaeta (16.4%), Isopoda (16.1%)	100
	A vs H	35.6	Rotifera (24.4%), Polichaeta (17.4%), Oligochaeta (15.3%), Turbellaria (13.7%), Isopoda (13.2%), Gasteropoda (8.4%)	92.30%
	D vs H	36.8	Rotifera (27.8%), Turbellaria (18.4%), Oligochaeta (17.3%), Isopoda (17.3%), Polichaeta (11.2%)	91.9
	C vs H	20.2	Oligochaeta (33.3%), Isopoda (33.3%), Turbellaria (18.3%), Polichaeta (15%)	100
	B vs G	16.6	Rotifera (48%), Polichaeta (31.7%), Isopoda (20.3%)	100
	A vs G	23.2	Rotifera (29.4%), Polichaeta (15.4%), Isopoda (14.5%), Gasteropoda (14.5%), Turbellaria (13.1%), Amphipoda (13.1%)	100
	D vs G	18.1	Rotifera (45.8%), Polichaeta (35.7%), Gasteropoda (18.5%)	100
	C vs G	24.2	Turbellaria (52.2%), Polichaeta (35.7%), Rotifera (15.3%)	100
	A vs B	15.8	Isopoda (24.8%), Polichaeta (20.5%), Gasteropoda (19.3%), Turbellaria (17.7%), Amphipoda (17.7%)	100
	D vs B	12	Polichaeta (48.4%), Isopoda (26.2%), Gasteropoda (25.4%)	100
	C vs B	32.8	Turbellaria (34.2%), Rotifera (34.2%), Polichaeta(21.5%), Isopoda (10.2%)	100
	D vs A	19.4	Polichaeta (33.4%), Gasteropoda (20.7%), Isopoda (16.3%), Turbellaria (14.9%), Amphipoda (14.9%)	100
	C vs A	35.8	Polichaeta (27.1%), Rotifera (27.1%), Turbellaria (18.6%), Isopoda(9.3%), Gasteropoda (9.3%)	91.5
	C vs D	30	Turbellaria (38.9%), Rotifera (38.9%), Polichaeta (11.1%), Gasteropoda (11.1%)	100
April	G vs H	27.4	Isopoda (33.3%), Polichaeta (18.9%), Oligochaeta (14.8%), Ostracoda (11.4%), Amphipoda (10.8%), Gasteropoda (10.8%)	100
	B vs H	44.8	Isopoda (23.2%), Turbellaria (15.2%), Chironomidae larvae (15.2%), Polichaeta (13%), Ostracoda (10.3%), Copepoda (8%), Oligochaeta (8%)	92.8
	A vs H	31	Turbellaria (23.5%), Polichaeta (17%), Ostracoda (15.9%), Isopoda (14.8%), Oligochaeta (11.4%), Gasteropoda (8.8%)	91.3
	D vs H	43.2	Turbellaria (25.1%), Isopoda (17.6%), Rotifera (15.8%), Ostracoda (8.6%), Oligochaeta (8.6%), Copepoda (8.3%), Gasteropoda (8.3%)	92.2
	C vs H	27.3	Turbellaria (34.5), Rotifera (22.6%), Polichaeta (19.2%), Ostracoda (11.8%), Oligochaeta (11.8%)	100
	B vs G	37.1	Turbellaria (17.8), Chironomidae larvae (17.8), Polichaeta (12.1%), Copepoda (9.3%), Oligochaeta (8.7%), Amphipoda (8.7%), Gasteropoda (8.7%), Ostracoda (8.5%)	91.5
	A vs G	34.7	Turbellaria (20.2%), Isopoda (15.9%), Polichaeta (13.7%), Ostracoda (12.6%), Gasteropoda (11.8%), Oligochaeta (9.1%), Amphipoda(9.1%)	92.4

	D vs G	42	Rotifera (22.9%), Polichaeta (19.2%), Ostracoda (17.9%), Isopoda (17.6349%), Turbellaria (), Gasteropoda ()	93.6
	C vs G	37.1	Turbellaria (24.6%), Isopoda (24.6%), Rotifera (16.1%), Polichaeta (10.9%), Oligochaeta (7.9%), Amphipoda(7.9%)	92.1
	A vs B	41.4	Chiromidae larvae (18.1%), Isopoda (14.9%), Ostracoda (13.6%), Polichaeta (13.4%), Turbellaria (12%), Rotifera (11.1%), Copepoda (9.6%)	92.9
	D vs B	43.5	Polichaeta (18.3%), Chironomidae larvae (18.3%), Rotifera (15.3%), Copepoda (12.5%), Turbellaria (9.7%), Gasteropoda (9.2%), Ostracoda (8.6%)	91.8
	C vs B	38.1	Isopoda (27.3%), Chironomidae larvae (17.9%), Rotifera (15.2%), Polichaeta (12.3%), Copepoda (9.4%), Turbellaria (9.4%)	91.5
	D vs A	37.1	Rotifera (18%), Polichaeta (17.3%), Isopoda (16.3%), Ostracoda (15.3%), Gasteropoda (13.5%), Copepoda (10.7%)	91
	C vs A	25.5	Rotifera (22.9%), Polichaeta (19.2%), Ostracoda (17.9%), Isopoda (17.9%), Turbellaria (11.5%), Gasteropoda (10.6%)	100
	C vs D	26.8	Isopoda (28.3%), Polichaeta (26.4%), Rotifera (18.5%), Copepoda (13.4%), Gasteropoda (8.2%)	91.8
May	G vs H	28.5	Copepoda (62.8%), Turbellaria (18.6%), Gasteropoda (18.6%)	100
	B vs H	24.4	Copepoda (77.3%), Gasteropoda (22.7%)	100
	A vs H	51.9	Copepoda (39.3%), Ostracoda (39.3%), Gasteropoda (21.4%)	100
	D vs H	25.3	Copepoda (70.71%), Gasteropoda (29.3)	100
	C vs H	34.1	Copepoda (59.8%), Ostracoda (22.8%), Gasteropoda (17.4%)	100
	B vs G	6.7	Turbellaria (100%)	100
	A vs G	48.5	Ostracoda (53.1%), Gasteropoda (32.1%), Turbellaria (14.9%)	100
	D vs G	12.6	Turbellaria (50%), Gasteropoda (50%)	100
	C vs G	17.4	Ostracoda (58.5%), Turbellaria (41.5%)	100
	A vs B	44.4	Ostracoda (62.5%), Gasteropoda (37.5%)	100
	D vs B	6.7	Gasteropoda (100%)	100
	C vs B	11.1	Ostracoda (100%)	100
	D vs A	39.6	Ostracoda (65%), Gasteropoda (35%)	100
	C vs A	37	Ostracoda (50%), Gasteropoda (50%)	100
	C vs D	17.4	Ostracoda (58.5%), Gasteropoda (41.5%)	100
July	G vs H	38.7	Ostracoda (18.7%), Chironomidae larvae (14.7%), Turbellaria (12.4%), Rotifera (10.4%), Bivalvia (9.3%), Gasteropoda (9.3%), Polichaeta (8.4%), Oligochaeta (8.4%)	100
	B vs H	34.3	Ostracoda (23.4%), Turbellaria (19.4%), Chironomidae larvae (19.4%), Polichaeta (14.4%), Bivalvia (11.7%), Gasteropoda (11.7%)	100
	A vs H	34.5	Turbellaria(21.5%), Ostracoda (18.5%), Chironomidae larvae (18.5%), Gasteropoda (15%), Polichaeta (14.1%), Bivalvia (12.3%)	100
	D vs H	44.2	Ostracoda (21.1%), Turbellaria (21.1%), Polichaeta (12.3%), Chironomidae larvae(12.3%), Copepoda (12%), Bivalvia (10.6%), Gasteropoda (10.6%)	100
	C vs H	39	Polichaeta (19.1%), Ostracoda (19.1%), Turbellaria (19.1%), Chironomidae larvae (15.2%), Bivalvia (9.6%), Gasteropoda (9.6%)	100
	B vs G	24.2	Turbellaria (23.5%), Chironomidae larvae (19.8%), Rotifera (16.6%), Polichaeta(13.4%), Oligochaeta (13.4%), Isopoda (13.4%)	100
	A vs G	32.2	Turbellaria (21.7%), Chironomidae larvae (19.3%), Ostracoda (14.4%), Rotifera (13.9%), Oligochaeta (10.4%), Isopoda (10.4%), Polichaeta (8.4%)	91.6
	D vs G	33.6	Turbellaria (21.7%), Chironomidae larvae (19.3%), Rotifera (13.9%), Copepoda (13.8%), Oligochaeta (10.8%), Isopoda (10.8%)	90.3
	C vs G	31.4	Polichaeta (31.3%), Turbellaria (19.4%), Chironomidae larvae(14.5%), Isopoda (13.2%), Rotifera (11.9%)	90.3
	A vs B	23.8	Chironomidae larvae (24.7%), Ostracoda (22.2%), Polichaeta(20.4%), Turbellaria (20.4%), Gasteropoda (12.4%)	100
	D vs B	22.8	Chironomidae larvae (35%), Polichaeta (23.9%), Copepoda (23.2%), Turbellaria (17.9%)	100
	C vs B	19	Polichaeta (39.4%), Chironomidae larvae (25.8%), Turbellaria (17.7%), Isopoda (17.1%)	100
	D vs A	31.5	Chironomidae larvae (23.4%), Ostracoda (20.9%), Copepoda (18.6%), Polichaeta (16.4%), Turbellaria (10.4%), Gasteropoda (10.4%)	100
	C vs A	27.7	Polichaeta (30.9%), Chironomidae larvae (19.4%), Ostracoda (17.4%), Isopoda (12.1%), Turbellaria (10.1%), Gasteropoda (10.1%)	100
	C vs D	24.3	Polichaeta (37.1%), Chironomidae larvae (28.1%), Copepoda (19.8%), Isopoda (14.9%)	100
G	Oct vs Jan	24.2	Turbellaria (52.2%), Polichaeta (32.5%), Rotifera (15.3%)	100
	Oct vs April	17	Polichaeta (38.7%), Oligochaeta (19.6%), Amphipoda (19.6%), Gasteropoda (19.6%)	100
	Oct vs May	28.4	Turbellaria (36.8%), Polichaeta (16.7%), Oligochaeta (11.8%), Amphipoda (11.8%),Gasteropoda (11.8%), Rotifera (11%)	100

	Oct vs July	21.7	Chironomidae larvae (30.8%), Turbellaria (19.2%), Rotifera (19.2%), Oligochaeta (15.4%), Isopoda (15.4%)	100
	Jan vs Apr	28.4	Turbellaria (36.8%), Polichaeta (16.7%), Oligochaeta (11.8%), Amphipoda (11.8%), Gasteropoda (11.8%), Rotifera (11%)	100
	Jan vs May	35.4	Copepoda (45.6%), Polichaeta (27.8%), Turbellaria (13.6%), Rotifera (12.9%)	100
	Jan vs July	32	Polichaeta (21.5%), Turbellaria (21%), Chironomidae larvae (21%), Rotifera (15.6%), Oligochaeta (10.5%), Isopoda (10.5%)	100
	April vs May	41.9	Copepoda (30%), Turbellaria (20.8%), Polichaeta (20.5%), Oligochaeta (9.6%), Amphipoda (9.6%)	90.4
	April vs July	31.6	Polichaeta (19.7%), Chironomidae larvae (18.1%), Oligochaeta (12.6%), Turbellaria (10.9%), Rotifera (10.9%), Amphipoda (9.4%), Gasteropoda (9.4%)	91
	May vs July	41.8	Copepoda (31.9%), Chironomidae larvae (19.2%), Turbellaria (17.1%), Rotifera(12.7%), Oligochaeta (9.4%)	90.4
H	Oct vs Jan	22.9	Oligochaeta (33.3%), Isopoda (28.6%), Turbellaria (15.7%), Amphipoda (14.3%), Polichaeta (12.9%)	100
	Oct vs April	24	Isopoda (43.3%), Ostracoda (14.9%), Oligochaeta (14.9%), Polichaeta (13.5%), Amphipoda (13.5%)	100
	Oct vs May	21.2	Turbellaria (62.1%), Amphipoda (19%), Gasteropoda (19%)	100
	Oct vs July	30.4	Ostracoda (26.4%), Bivalvia (13.2%), Gasteropoda (13.2%), Polichaeta (11.8%), Turbellaria (11.8%), Amphipoda (11.8%), Chironomidae larvae (11.8%)	100
	Jan vs Apr	19.2	Oligochaeta (26.8%), Polichaeta (20.7%), Isopoda (18.7%), Ostracoda(17%), Turbellaria (16.8%)	100
	Jan vs May	29.2	Turbellaria (26.7%), Oligochaeta(24.9%), Isopoda (24.9%), Gasteropoda(12.5%), Polichaeta(11.1%)	100
	Jan vs July	39.9	Ostracoda (18.2%), Oligochaeta (16.4%), Isopoda (16.4%), Turbellaria (11.6%), Polichaeta (11%), Bivalvia(9.1%), Gasteropoda(9.1%)	100
	April vs May	38.4	Turbellaria (30.2%), Isopoda (30.2%), Ostracoda(10.5%), Oligochaeta(10.5%), Polichaeta (9.32%)	90.7
	April vs July	37.9	Isopoda (27.5%), Ostracoda (15.3%), Polichaeta (11.7%), Bivalvia (9.5%), Oligochaeta (9.5%), Gasteropoda (9.5%), Turbellaria (8.5%)	100
A	May vs July	36.7	Ostracoda(24.9%), Turbellaria (24.9%), Gasteropoda (15.8%), Bivalvia (12.5%), Polichaeta (11%), Chironomidae larvae (11%)	100
	Oct vs Jan	49.1	Polichaeta (21.2%), Copepoda (14.6%), Oligochaeta (13.9%), Rotifera (13.9%), Gasteropoda (9.4%), Isopoda (7.3%), Ostracoda (6.6%), Turbellaria (6.6%)	93.4
	Oct vs April	52.2	Copepoda (17.5%), Oligochaeta (16.4%), Polichaeta (13.1%), Isopoda (13.1%), Ostracoda (12.6%), Rotifera (10.7%), Gasteropoda (9.9%)	93.1
	Oct vs May	51.9	Ostracoda (27.9%), Oligochaeta (25.4%), Gasteropoda(21.4%), Rotifera(13.9%), Copepoda(11.4%)	100
	Oct vs July	51	Copepoda (19.5%), Oligochaeta (18.2%), Chironomidae larvae (15.4%), Ostracoda (13.6%), Gasteropoda (10.8%), Rotifera (9.7%), Polichaeta (6.4)	93.6
	Jan vs Apr	30.3	Rotifera (22.2%), Isopoda (15.9%), Polichaeta (13.3%), Ostracoda (13.3%), Gasteropoda (13.1%), Turbellaria (12.8%)	90.5
	Jan vs May	69.3	Copepoda (18.2%), Polichaeta (18.2%), Ostracoda (18.2%), Rotifera (18.2%), Gasteropoda (9.9%), Isopoda (6.3%), Turbellaria (5.6%)	94.5
	Jan vs July	41.2	Rotifera (23.6%), Polichaeta (17.6%), Chironomidae larvae (13.9%), Gasteropoda (10.1%), Ostracoda (9.7%), Turbellaria (9.6%), Isopoda (8.1%)	92.6
	April vs May	60.1	Copepoda (29.1%), Gasteropoda (16.2%), Polichaeta (13.7%), Ostracoda (13.7%), Isopoda (13.7%), Turbellaria (7.3%)	93.60
B	April vs July	36.8	Chironimidae larvae(18.6%), Isopoda(17.4%), Polichaeta (16,2%), Ostracoda (15.5%), Turbellaria (12.3%), Gasteropoda (11.8%)	91.8
	May vs July	57	Copepoda (33.4%), Gasteropoda (18.7%), Ostracoda (17.2%), Chironomidae larvae (17.2%), Polichaeta (6.8%)	93.2
	Oct vs Jan	35.1	Rotifera (31%), Gasteropoda (20.2%), Polichaeta(19.4%), Turbellaria(10.7%), Oligochaeta(9.6%)	90.8
	Oct vs April	42.8	Gasteropoda(17.8%), Polichaeta(17.8%), Chironomidae larvae (17.8%), Turbellaria (12.3%), Copepoda (9.4%), Ostracoda (8.4%), Oligochaeta (8.4%)	91.6
	Oct vs May	36.5	Copepoda(50%), Turbellaria (50%)	100
	Oct vs July	27.9	Chironomidae larvae (28.8%), Gasteropoda (27.2%), Turbellaria (18.4%) Polichaeta (12.8%), Oligochaeta (12.8%)	100
	Jan vs Apr	33.6	Rotifera (22.2%), Chironomidae larvae (21.1%), Polichaeta(14.8%), Copepoda(11.1%), Turbellaria(11.1%), Ostracoda(10%)	100
	Jan vs May	42.1	Copepoda (53%), Polichaeta(32.2%), Rotifera (14.9%)	100
	Jan vs July	30.8	Rotifera (35.1%), Chironomidae larvae (24.2%), Polichaeta(19.2%), Turbellaria (10.9%), Isopoda (10.5%)	100

C	April vs May	46	Copepoda (22.4%), Polichaeta(22.4%), Chironomidae larvae (22.4%), Turbellaria (12.1%), Ostracoda (10.3%), Rotifera (10.3 %)	100
	April vs July	27.9	Polichaeta (23.2%), Turbellaria (18.4%), Chironomidae larvae (18.4%), Copepoda(14.4%), Ostracoda (12.8%), Rotifera(12.8%)	100
	May vs July	36.5	Copepoda (43.5%), Chironomidae larvae (30.4%), Polichaeta (13%), Turbellaria (13%)	100
	Oct vs Jan	13.1	Ostracoda (36.4%), Copepoda (31.8%), Polichaeta (31.8%)	100
	Oct vs April	43.5	Turbellaria (25.7%), Isopoda (25.7%), Rotifera (16.8%),Polichaeta (14.3%), Ostracoda (9.2%)	100
	Oct vs May	47	Turbellaria (40.6%), Copepoda (28%), Ostrracoda (18.9%), Polichaeta (12.6%)	100
	Oct vs July	38.3	Turbellaria (30.5%), Polichaeta (20.7%),Chironomidae larvae (19.1%),Ostracoda (11%), Copepoda (9.7%)	91
	Jan vs Apr	35.6	Turbellaria (30.2%), Isopoda (30.2%), Polichaeta (19.8%), Rotifera (19.8%)	100
	Jan vs May	42.2	Copepoda (42.1%), Turbellaria (42.1%), Ostracoda (15.8%)	100
	Jan vs July	32.8	Polichaeta (34.2%), Turbellaria (34.2%), Chironomidae larvae (21.5%), Isopoda (10.2%)	100
	April vs May	52.9	Copepoda (27.3%), Isopoda (27.3%), Polichaeta (17.8%), Rotifera (17.8%)	90
	April vs July	22.8	Isopoda (30%), Rotifera (28.2%), Chironomidae larvae (27.2%), Polichaeta (14.8%)	100
	May vs July	50.1	Copepoda (31.1%), Polichaeta(31.1%), Chironomidae larvae (19.3%), Gasteropoda (9.5%)	91
	Oct vs Jan	47.1	Copepoda (28.1%), Turbellaria (28.1%), Rotifera(28.1%), Polichaeta (7.9%)	90.6
	Oct vs April	42.1	Turbellaria (34.4%), Copepoda (23.1%), Rotifera (21.2%), Gasteropoda(11.3%)	90.1
	Oct vs May	24.4	Turbellaria (77.3%), Gasteropoda (22.7%)	100
	Oct vs July	34.4	Turbellaria (47.6%), Copepoda (28.3%), Polichaeta (12.1%), Chironomidae larvae (12.1%)	100
	Jan vs Apr	20.2	Gasteropoda (24.9%), Rotifera (21.9%), Copepoda (19.3%), Isopoda (17.3%), Polichaeta (16.7%)	100
	Jan vs May	39.2	Copepoda(37.3%), Rotifera (37.3%), Gasteropoda(15..2%), Polichaeta(10.3%)	100
	Jan vs July	30.3	Rotifera (42.9%), Copepoda (16.8%), Polichaeta (16.8%), Gasteropoda (12%), Chironomidae larve (11.5%)	100
D	April vs May	32.2	Copepoda (33.7%), Rotifera (30.6%), Gasteropoda (21.6%), Isopoda (14.2%)	100
	April vs July	31.6	Rotifera (27.7%), Copepoda (21%), Gasteropoda (14.8%), Isopoda (12.9%), Polichaeta (11.8%), Chironomidae larvae (11.8%)	100
	May vs July	25.5	Copepoda(42.7%), Gasteropoda(21.5%), Polichaeta(18%), Chironomidae larvae (18%)	100

		*** = p < 0.001; ** = p < 0.01; * = p < 0.05																							
		October					January					April					May								
BPC		G	H	A	B	C	D	G	H	A	B	C	D	G	H	A	B	C	D	G	H	A	B	C	D
	G							G						G						G					
	H							H						H						H					
	A							A						A						A					
	B							B						B						B					
CPE		G	H	A	B	C	D	G	H	A	B	C	D	G	H	A	B	C	D	G	H	A	B	C	D
	G							G						G						G					
	H							H						H						H					
	A							A						A						A					
	B							B						B						B					
OM Composition		G	H	A	B	C	D	G	H	A	B	C	D	G	H	A	B	C	D	G	H	A	B	C	D
	G							G						G						G					
	H							H						H						H					
	A							A						A						A					
	B							B						B						B					
CCPE:BPC		G	H	A	B	C	D	G	H	A	B	C	D	G	H	A	B	C	D	G	H	A	B	C	D
	G							G						G						G					
	H							H						H						H					
	A							A						A						A					
	B							B						B						B					
PRT:CHO		G	H	A	B	C	D	G	H	A	B	C	D	G	H	A	B	C	D	G	H	A	B	C	D
	G							G						G						G					
	H							H						H						H					
	A							A						A						A					
	B							B						B						B					
C Degradation Rates		G	H	A	B	C	D	G	H	A	B	C	D	G	H	A	B	C	D	G	H	A	B	C	D
	G							G						G						G					
	H							H						H						H					
	A							A						A						A					
	B							B						B						B					
C Turnover Time		G	H	A	B	C	D	G	H	A	B	C	D	G	H	A	B	C	D	G	H	A	B	C	D
	G							G						G						G					
	H							H						H						H					
	A							A						A						A					
	B							B						B						B					

Figure S6.1. Results of post-hoc tests on BPC, CPE, OM composition, CCPE:BPC, PRT:CHO, C degradation and C turnover time identifying differences between stations in each period of S'Ena Arrubia lagoon. T = statistic t; P(MC) = probability level after Monte Carlo simulation. *** = p < 0.001; ** = p < 0.01; * = p < 0.05; ns = not significant. The colors in the tables were assigned to the combinations following the order of the rows. Gray = ns; red= significantly decrease; green=significantly increase.

	*** = p < 0.001; ** = p < 0.01; * = p < 0.05																			
	G					H					A					B				
	Oct	Jan	Apr	May	Jul	Oct	Jan	Apr	May	Jul	Oct	Jan	Apr	May	Jul	Oct	Jan	Apr	May	Jul
BPC	Oct	***	***	***	***	Oct	***	***	***	***	Oct	***	***	***	***	Oct	***	***	***	***
	Jan	***				Jan	***				Jan	***				Jan	***			
	Apr	***				Apr	***				Apr	***				Apr	***			
	May	***				May	***				May	***				May	***			
	Jul	***				Jul	***				Jul	***				Jul	***			
CPE	Oct	***	***	***	***	Oct	***	***	***	***	Oct	***	***	***	***	Oct	***	***	***	***
	Jan	***				Jan	***				Jan	***				Jan	***			
	Apr	***				Apr	***				Apr	***				Apr	***			
	May	***				May	***				May	***				May	***			
	Jul	***				Jul	***				Jul	***				Jul	***			
OM Composition	Oct	***	***	***	***	Oct	***	***	***	***	Oct	***	***	***	***	Oct	***	***	***	***
	Jan	***				Jan	***				Jan	***				Jan	***			
	Apr	***				Apr	***				Apr	***				Apr	***			
	May	***				May	***				May	***				May	***			
	Jul	***				Jul	***				Jul	***				Jul	***			
CCPE:BPC	Oct	***	***	***	***	Oct	***	***	***	***	Oct	***	***	***	***	Oct	***	***	***	***
	Jan	***				Jan	***				Jan	***				Jan	***			
	Apr	***				Apr	***				Apr	***				Apr	***			
	May	***				May	***				May	***				May	***			
	Jul	***				Jul	***				Jul	***				Jul	***			
PRT:CHO	Oct	***	***	***	***	Oct	***	***	***	***	Oct	***	***	***	***	Oct	***	***	***	***
	Jan	***				Jan	***				Jan	***				Jan	***			
	Apr	***				Apr	***				Apr	***				Apr	***			
	May	***				May	***				May	***				May	***			
	Jul	***				Jul	***				Jul	***				Jul	***			
C Degradation Rates	Oct	***	***	***	***	Oct	***	***	***	***	Oct	***	***	***	***	Oct	***	***	***	***
	Jan	***				Jan	***				Jan	***				Jan	***			
	Apr	***				Apr	***				Apr	***				Apr	***			
	May	***				May	***				May	***				May	***			
	Jul	***				Jul	***				Jul	***				Jul	***			
C Turnover Time	Oct	***	***	***	***	Oct	***	***	***	***	Oct	***	***	***	***	Oct	***	***	***	***
	Jan	***				Jan	***				Jan	***				Jan	***			
	Apr	***				Apr	***				Apr	***				Apr	***			
	May	***				May	***				May	***				May	***			
	Jul	***				Jul	***				Jul	***				Jul	***			

Figure S6.2 Results of post-hoc tests on BPC, CPE, OM composition, CCPE:BPC, PRT:CHO, C degradation and C turnover time identifying differences between period in each station of S'Ena Arrubia lagoon. T = statistic t; P(MC) = probability level after Monte Carlo simulation. *** = p < 0.001; ** = p < 0.01; * = p < 0.05; ns = not significant. The colors in the tables were assigned to the combinations following the order of the rows. Gray = ns; red= significantly decrease; green=significantly increase.

		*** = p < 0.001; ** = p < 0.01; * = p < 0.05										ns										sign >										sign <									
Total Abundance		October					January					April					May					July																			
		G	H	A	B	C	D	G	H	A	B	C	D	G	H	A	B	C	D	G	H	A	B	C	D	G	H	A	B	C	D										
	G				**	*		G						G				*		G				****	*	G				*											
	H				*	*		H						H						H				*****		H				*	*										
	A							A						A						A				**		A															
	B	**	*					B						B	*				*	B	*****					B															
Nematoda		October					January					April					May					July																			
		G	H	A	B	C	D	G	H	A	B	C	D	G	H	A	B	C	D	G	H	A	B	C	D	G	H	A	B	C	D										
	G				*	*		G						G				*		G				*		G				*	*										
	H							H						H						H				**		H				*	*										
	A							A						A						A						A															
	B	**	*					B						B	*			*		B				*	*	B															
Copepoda		October					January					April					May					July																			
		G	H	A	B	C	D	G	H	A	B	C	D	G	H	A	B	C	D	G	H	A	B	C	D	G	H	A	B	C	D										
	G					****		G						G				*		G				*		G				*	*										
	H					**		H						H			*		H						H			*	*	*											
	A							A				*		A			*		A						A			*													
	B						**	B					*	B	*	*	*	*	B						B			*													
Ostracoda		October					January					April					May					July																			
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Figure S6.3. Results of post-hoc tests on total, Nematoda, Copepoda, Ostracoda and other taxa abundance, taxonomical richness and composition identifying differences between stations in each period of S'Ena Arrubia lagoon. T = statistic t; P(MC) = probability level after Monte Carlo simulation. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; ns = not significant. The colors in the tables were assigned to the combinations following the order of the rows. Gray = ns; red= significantly decrease; green=significantly increase.

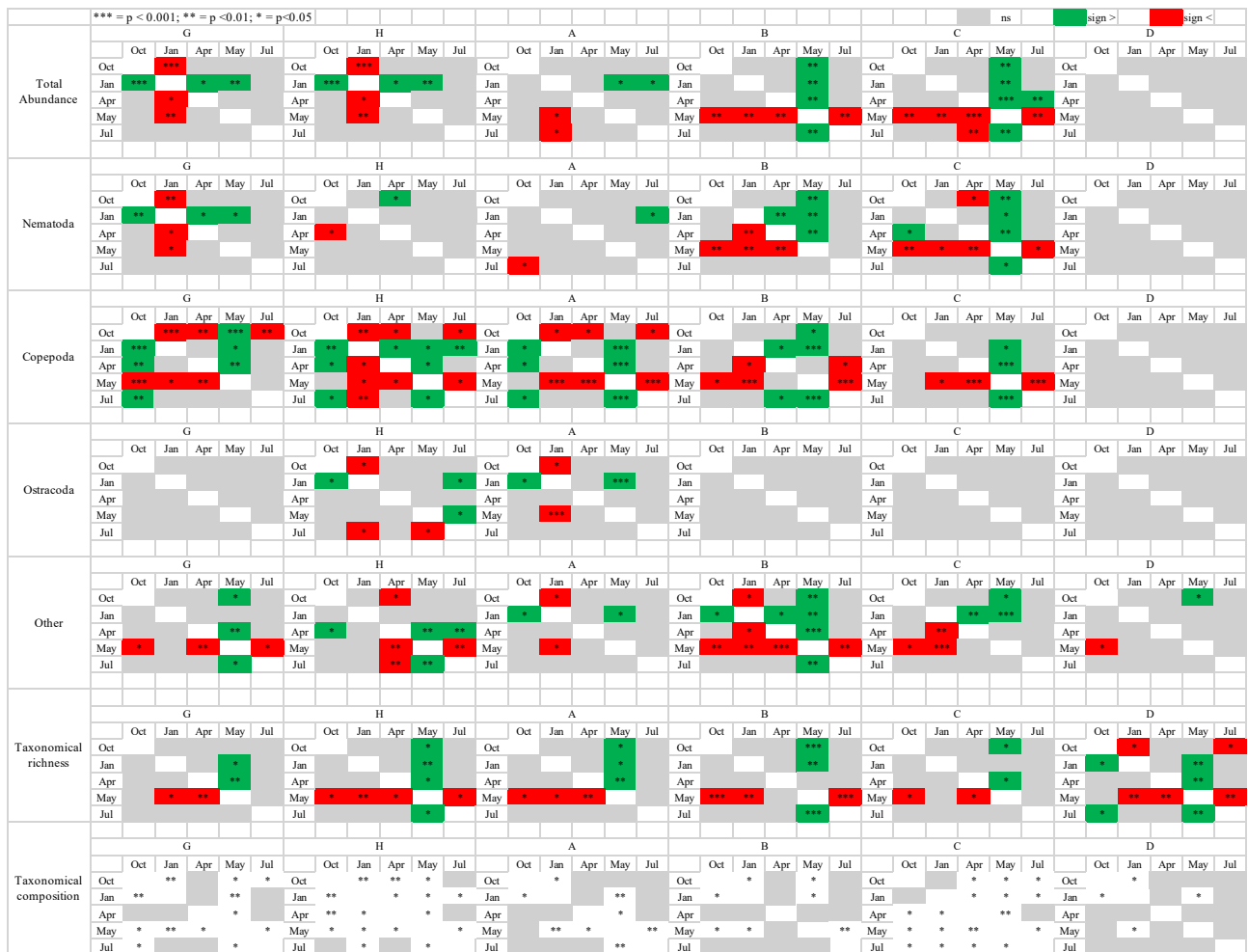


Figure S6.4. Results of post-hoc tests on total, Nematoda, Copepoda, Ostracoda and other taxa abundance, taxonomical richness and composition identifying differences between periods in each station of S'Ena Arrubia lagoon. T = statistic t; P(MC) = probability level after Monte Carlo simulation. *** = p < 0.001; ** = p < 0.01; * = p < 0.05; ns = not significant. The colors in the tables were assigned to the combinations following the order of the rows. Gray = ns; red= significantly decrease; green=significantly increase

Chapter 7. Impact Chains: a new climate change-related risk analysis tool

7.1 Introduction

Climate change (CC) is a global threat with numerous impacts on ecosystems, human health, economies, and societies worldwide (IPCC, 2022). As climate change progresses, understanding how different types of climate hazards affect natural and socio-ecological systems is crucial for identifying risks, assessing vulnerabilities, and designing effective mitigation and adaptation strategies.

Recently, research objectives have shifted from merely studying the physical components of the climate system to analyzing the technological, political, social, and economic dimensions of climate change, to better disentangle the complex and interdisciplinary nature of CC-related problem (Jorgenson et al, 2018; Schipper et al., 2021)

Among the tools developed within the framework of the Intergovernmental Panel on Climate Change (IPCC), Climate Change, the Risk and Vulnerability Assessments (CRVA) provide policymakers with the necessary information for being prepared in facing the consequences of CC. CRVA, indeed, identify the main risk drivers and support interventions and decision-making processes related to Climate Change Adaptation (CCA) and Disaster Risk Reduction (DRR) (Menk et al., 2022; GIZ and EURAC 2017).

In this context, a conceptual framework known as the Climate Impact Chain (IC) has been developed (Schneiderbauer et al. 2013). This tool is used to describe cause-and-effect sequences, serving as an analytical framework to systematically understand and prioritize the factors driving risk and vulnerability within specific systems and to identify the most relevant elements contributing to a specific risk (GIZ and EURAC 2017).

The objective of this chapter is to narratively synthesize the knowledge gained from previous studies, including models for assessing the probability of thermal habitat suitability, mesocosm experiments, and field observations, in order to construct formal logical frameworks of impact chains based on risk identification.

Although traditional risk assessment frameworks typically involve first delineating impact chains through participatory activities with the scientific community and stakeholders, the impact chains designed in this chapter should be considered a preliminary, qualitative exercise aimed at providing greater clarity on more complex ecological processes and, potentially, serving as a basis

for future discussions with stakeholders. Specifically, empirical observations and insights from the literature led to the development of impact chains addressing risks for the target species and coastal lagoons.

7.2 Methodology

I followed the framework currently defined by the IPCC in the AR5 report for constructing climatic impact chains based on the identification of climate risk, which results from the interaction among three components: hazard, exposure and vulnerability (GIZ and EURAC 2017). Each component of the impact chain (vulnerability, exposure, and hazard) is described by elements and/or causal factors (GIZ and EURAC 2017).

Based on my thesis work, the hazards I consider here were

- Sea warming
- Marine heatwaves (MHWs).

The impact chains based on “species” systems were structured separately using a socio-ecological approach, given the primarily commercial interest of some species along the Sardinian coasts and included the same species investigated in Chapter 3: the mussel *Mytilus galloprovincialis*, the sea urchin *Paracentrotus lividus*, the fish *Mullus barbatus*, the sea cucumber *Holothuria tubulosa*.

The impact chains based on the “coastal lagoon” system were structured, under an ecological perspective, based on the results of the chapters 4, 5 and 6, considering the responses and/or system risks related to the expected shift between oligotrophic to and eutrophic conditions because of warmer temperatures.

7.3 Results and Discussion

7.3.1 Impact chain for *Mytilus galloprovincialis* mass mortality risk

As outlined in Chapter 3, the mussel *Mytilus galloprovincialis* may face a reduction in thermal habitat suitability under future warming scenarios, particularly during summer months, with a potential up to 40% decrease in July and August. Given the limited natural mussel beds along the Sardinian coasts and the high economic interest in mussel farming at national and regional levels, a climatic impact chain for the Mediterranean mussel has been developed based on pre-eminently socio-ecological considerations. Based on the thermal habitat suitability maps and the commercial importance of

this species (farmed in coastal marine embayment and lagoon ecosystems like Olbia, Porto Pozzo, Arbatax, Arborea, and Cagliari) as well as considering past adverse climatic events, mass mortality events have been identified as the main risk associated with climate change at the regional level. Other potential risks may include also reduced or absent fertility, increased pathogen infections, and bioaccumulation of heavy metals and other pollutants (including organic compounds). The scheme of the impact chain for *Mytilus galloprovincialis* mass mortality risk due to climate change (in terms of sea warming and marine heatwaves) is illustrated in **Figure 8.1**.

The hypothesized mechanistic explanations for the separate components of risk (hazards, impacts, vulnerability – in terms of both sensitivity and capacity -, and exposure) are delineated below.

As far as the **hazards** are concerned, sea warming and particularly, marine heatwaves caused by climate change may reduce dissolved oxygen in the water (physical impact of the hazard). Consequently, sudden or persistent warming events like marine heatwaves can enhance the duration, frequency, and extent of hypoxia events (Vaquer-Sunyer & Duarte, 2008; Parisi et al., 2021). These anoxic events (like the one that affected the S'Ena Arrubia lagoon; see Chapter 5) can induce a prolonged state of thermal stress in the species (**impact**), causing behavioral changes (e.g., valve gapping-behavior; Comeau et al., 2018), resulting in reduced filtration rates and triggering metabolic responses (production of heat shock proteins) (Anestis et al., 2007 and 2010; Parisi et al., 2021). When water temperature surpasses the threshold at which mussels drastically reduce their filtration rate, due to reduced food acquisition, mortality occurs (risk) (Anestis et al., 2007; Bejaoui-Omri et al., 2014). The **vulnerability** of mussels to the risk “mortality” is modulated by its **sensitivity** to water warming, that relies on the intrinsic thermal tolerance of the species, in turn influencing its capacity to cope with (resist to) these events. Along with sensitivity, the capacity component of vulnerability to the risk of mortality relies on physiological mechanisms allowing to cope and adapt to the hazard (in this case, the thermal stress). Mechanisms such as “hormesis” and “hardening” can induce resistant phenotypes in marine bivalves, improving their aerobic capacity, energy production, and survival thresholds under elevated thermal stress (Georgoulis et al., 2023). These adaptive responses can be applied in aquaculture, by exposing mussels to controlled, short-term heat stress, that could increase their tolerance to future warming events (Georgoulis et al., 2025). Another possible adaptation action consists in the retrieval (or movement in colder waters) of the species before the most critical warming period (July–August), that could reduce the risk of unsustainable losses of reared biomass caused by sudden mass mortality events. According to such

an impact chain, the most exposed sectors (**exposure**) of *Mytilus galloprovincialis* exploitation under future sea warming scenarios will be the aquaculture sector, the fish market and associated selling sectors, seafood consumers and institutions.

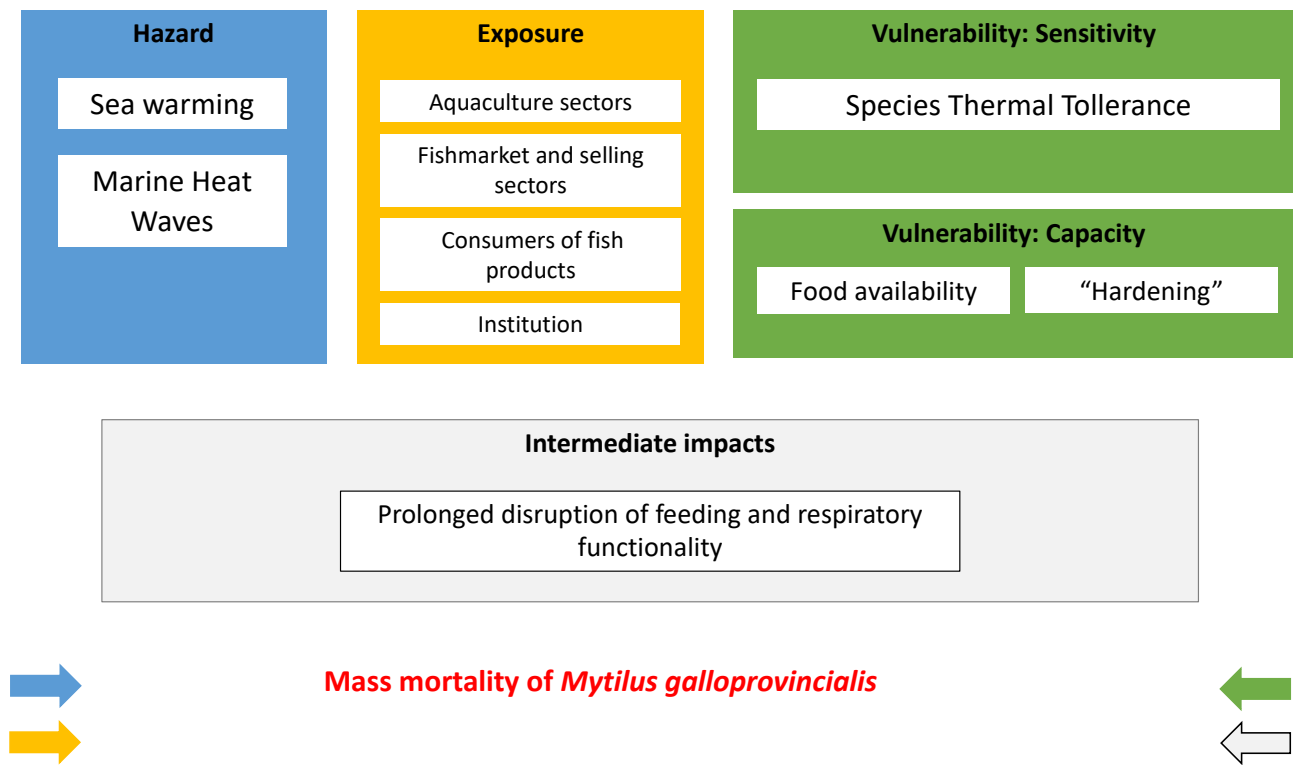


Figure 8.1. Climate Impact Chain for *Mytilus galloprovincialis*

7.3.2 Impact chain for the potential loss of *Paracentrotus lividus* abundance and/or distribution

Based on the results illustrated in Chapter 3, the sea urchin *Paracentrotus lividus* may experience, under the (worst) SSP5-8.5 climate scenario, a strong contraction (up to 80%) of its suitable habitat during the summer months (July–August). *P. lividus* is a key component of the benthic trophic web of Mediterranean rocky reefs (Guidetti et al., 2014) as well as of sensitive-to-warming coastal habitats (e.g., *Posidonia oceanica* meadows and macroalgal communities; Tomas et al., 2005; Cardoso et al., 2020). Moreover, *P. lividus* is also a crucial and economically valuable target of artisanal fishing and seafood processing in Sardinia, particularly in the areas of Stintino, Alghero, Oristano–Cabras, Buggerru, Cagliari, and Olbia (Furesi et al., 2016). Due to intense fishing pressure, harvesting in Sardinian seas has been subject to strict regulations (at times prohibited) and is currently allowed only to professional fishers from November to April, with a minimum harvestable test diameter of 50 mm and a daily catch quota of 1,500–3,000 individuals (Ceccherelli et al., 2022). Although intense

fishing pressure along the Sardinian coasts can be considered one of the main causes of population decline (Ceccherelli et al., 2022), like in other Italian coastal areas (Coppa et al., 2021; Toso et al., 2025), sea warming has been identified as a potential concurrent driver of sea urchins' population impairment at the basin scale (Yeruham et al., 2015; Toso et al., 2025).

Based on the above-declined premises, I built up an impact chain addressing the risk of potential variations in abundance and/or distribution of *P. lividus* due to climate change (in terms of sea warming and marine heatwaves), as these could have cascade effects on the entire ecosystem and the local socio-economic system (Ceccherelli et al., 2022).

The scheme of the impact chain addressing the risk of *P. lividus* population impairment due to climate change manifestations (sea warming and marine heatwaves) is illustrated in **Figure 8.2**.

Sea warming and marine heat waves (**hazards**) may exert detrimental effects on *P. lividus* populations particularly in summer months, when the species is generally protected to allowing its reproduction. The initial response of warming-exposed populations consists in increased feeding rates, arranged to compensate for the higher energy demand and the reduced absorption efficiency at higher temperatures (Yeruham et al., 2019). Persisting warming, and energy allocation mechanisms diverted to survivorship, will negatively affect growth rates and the overall physiological performance, ultimately disrupting the species metabolism, possibly leading to mass mortality events (**risk**; Pagès et al., 2013; 2018; Yeruham et al., 2019). Such responses are tightly linked with the **sensitivity** of the species metabolic traits to water warming. The thermal performance of *P. lividus* in terms of growth rate depends also on the food quantity, composition and nutritional quality, that regulate key life-history processes in echinoderms, including somatic growth and gonad development (Yeruham et al., 2019). In addition, the strong fishing effort on the species may alter population density, even under regimes of structured protection (Ceccherelli et al., 2022). Other possible factors influencing energy allocation shifts in *P. lividus* exposed to sea warming include also the spreading of invasive or toxic allochthonous macroalgae affecting their feeding strategies (due to adaptation to lower quality resources, like the alga *Caulerpa racemosa*; Pusceddu et al., 2021) or increasing their vulnerability (like in the case of the toxic alga *Rugulopteryx okamurae*; Bernal-Ibáñez et al., 2025).

According to such an impact chain, the most exposed sectors (**exposure**) of *Paracentrotus lividus* include the natural distribution area of the species occurrence (see also Chapter 3), the presence/enforcement of Marine Protected Areas, the number and pressure of professional fisheries, consumers behavior, and institutions.

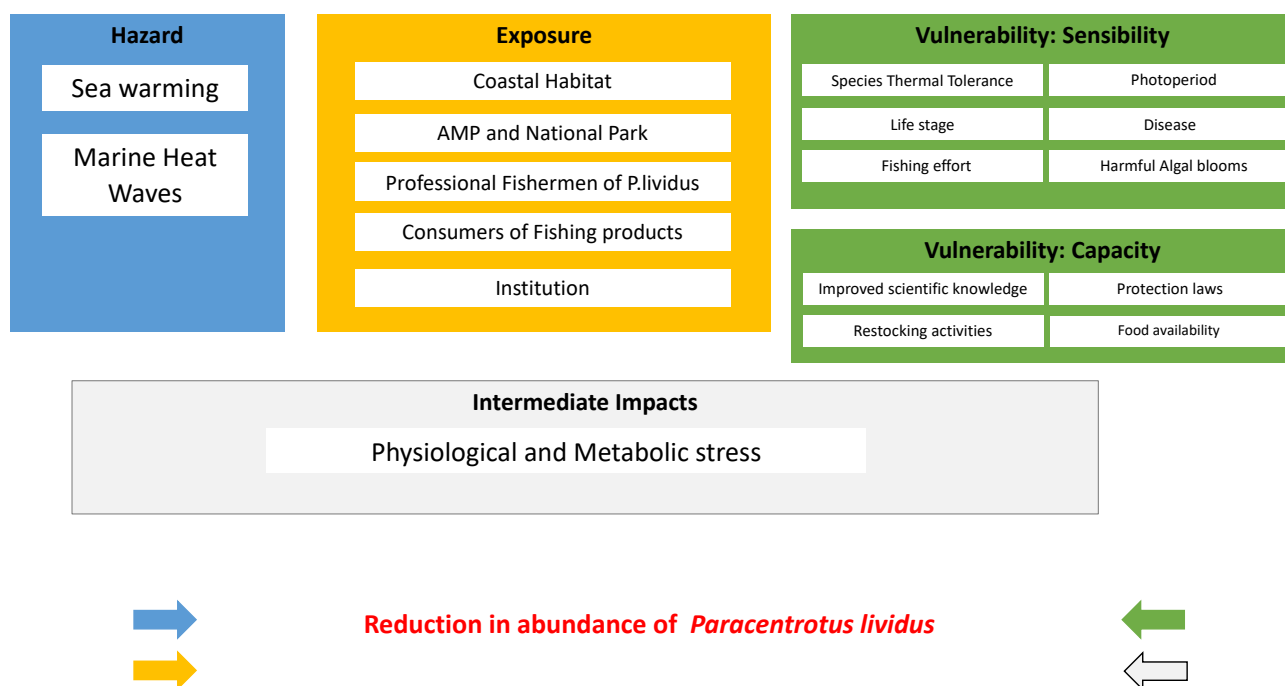


Figure 8.2. Climate Impact Chain for *Paracentrotus lividus*

7.3.3 Impact chain for changes in the reproductive potential and maintenance of *Mullus barbatus*

Based on the literature review and the thermal habitat suitability maps for *Mullus barbatus* reported in Chapter 3, a possible mismatch between the reproductive periods of males and females has been highlighted. Therefore, the risk chosen for building up the impact chain for *Mullus barbatus* refers to the potential changes in reproductive potential resulting from the effects of climate change (in terms of sea warming and heatwaves), with cascading implications for both the natural environment and the fishery production chain.

The importance of *M. barbatus* relates to its commercial values as well as to its documented role as a pollution bioindicator (Cresson, 2015; Geraci et al., 2023).

The scheme of the impact chain addressing the risk of *M. barbatus* reproductive metabolism impairment due to climate change manifestations (sea warming and marine heatwaves) is shown in **Figure 8.3**.

A long-term increase in sea temperature and/or frequency, intensity and duration of marine heatwaves (**hazard**) could affect timing and duration of the optimal period for gamete release of *Mullus barbatus*. Their gonadal development depends in fact upon temperature (**sensitivity**), and their reproductive cycle is aligned with zooplankton peaks in order to guarantee a higher survival of the larvae (Kokokiris et al., 2013): accordingly, their abundance is typically higher in warmer waters

(>16°C) and rich in zooplankton pasture for the juveniles (Maravelias et al., 2007). The potentially different effects of climate change in males and females (see Chapter 3) might lead to misaligned periods of gamete maturity of the two sexes, possibly altering their **capacity** to contribute to the population reproductive fitness. The natural stocks of *Mullus barbatus* occupying coastal and shelf areas (**exposure**) between the 50–200 m depth range, the region most exposed especially to sea warming, claims for prompt adaptations of regional fisheries, seafood consumers behavior and institutions.

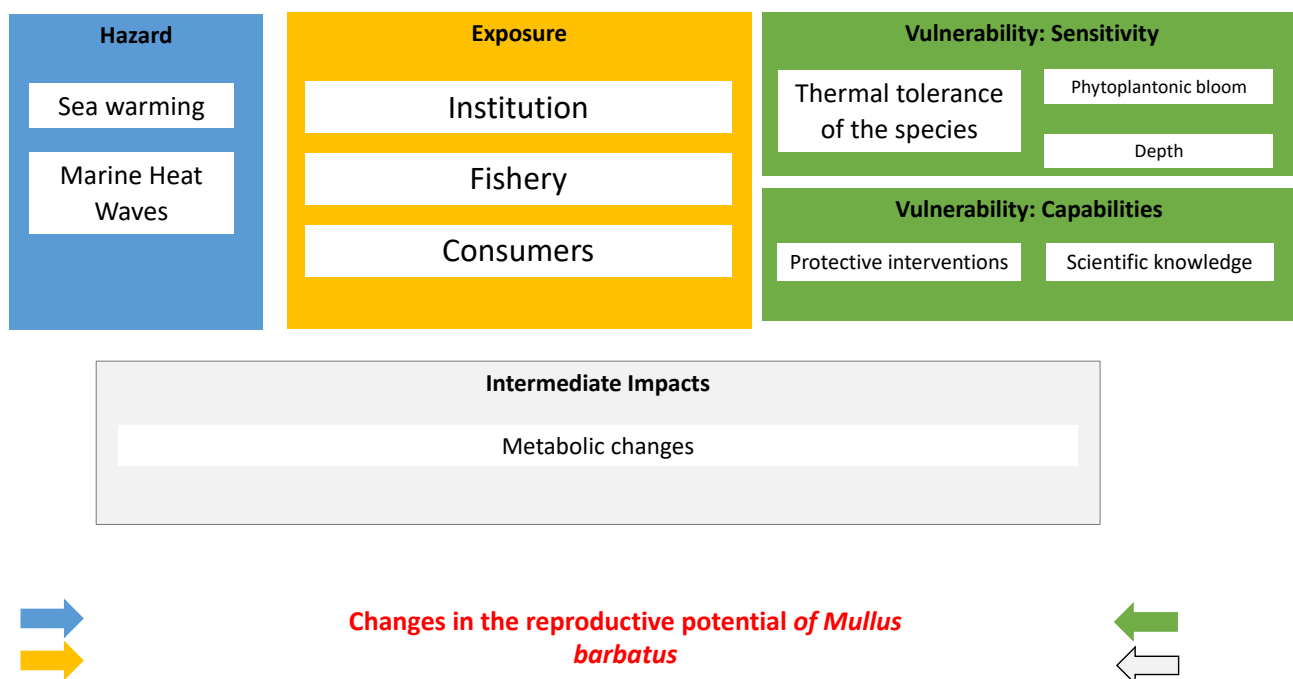


Figure 8.3. Climate Impact Chain for *Mullus barbatus*

7.3.4 Impact chain for changes in the reproductive potential and maintenance of the sea cucumber *Holothuria tubulosa*

The results delineated in Chapter 3 indicate that the thermal habitat suitability of *Holothuria tubulosa* in warmer scenarios may increase (up to +40–60% under the worst SSP5-8.5 projections) in early summer (June), especially in the north-eastern sector of Sardinia. Such an ameliorated thermal suitability, however, is projected to drop considerably (up to –80%) from July to September, along the almost entire coastline of the island. Based on these findings, the risk assessed in the impact chain refers to the potential changes in reproductive potential and maintenance of the species caused by climate change (in terms of sea warming and heatwaves), ultimately leading to the loss of a key natural “bioremediator” and ecosystem functions provider (Pasquini et al., 2022;

Grosso et al., 2023; Pasquini et al., 2023; Abyaba et al., 2025). Alongside with the risks associated with climate change it is worthy of notation (as a possible mitigating action) that after the Autonomous Region of Sardinia designated areas for experimental commercial production of *Holothuria tubulosa* and *H. polii* along the northern, southern, and western coasts of Sardinia, a national law (Ministerial Decree n° 9403901, 30 December 2020) prohibited harvesting of sea cucumbers along the entire national seas.

The scheme of the impact chain assessing the components of risk for the reproduction potential and maintenance of the sea cucumber *Holothuria tubulosa* is illustrated in **Figure 8.4**.

The results of the projected changes in thermal habitat suitability of *H. tubulosa* under future warming scenarios allowed me to identify sea warming and marine heatwaves as major hazards on the reproduction capacity of the scrutinized species especially in summer months, when, after an improvement in autumn, the thermal habitat conditions will degrade considerably especially under the worst scenario (SSP5-8.5). The *pejus* conditions eventually reached in summer could severely alter the metabolism of *H. tubulosa* (**intermediate impact**), affecting its energy budget for maintaining vital functions, including reproduction. Although Increasing temperatures may stimulate gamete release, these, over certain thresholds, can also lead to important shifts in timing (shortening or lengthening) of the optimal reproductive period (Desplatovic et al., 2004; Kazanidis et al., 2010; Pasquini et al., 2022). Nonetheless, it is noticeable that the reproductive cycle of *H. tubulosa* is also influenced by other environmental factors, such as photoperiod, phytoplankton blooms, and lunar cycles, all related to climate change (**sensitivity**; Culha et al., 2017). In warmer scenarios, natural adaptation mechanisms, such as estivation, could allow the sea cucumber to reduce its metabolism and energy consumption in response to environmental stress additive to excessive temperature, allowing them to partially counteract mitigate the physiological impact of the thermal stress (Feidantsis et al., 2021). Noticeably, despite the temporary harvesting prohibition, this species is experimentally cultivated and the interest of marine ecologists on this species ability to potentially be used as a natural bioremediator of benthic eutrophication has recently raised (Pasquini et al., 2022; Pasquini et al., 2023; Ennas et al., 2023; Abyaba et al., 2015). Risks of *H. tubulosa* altered reproduction periods and outcome will affect mostly the aquaculture sector, the seafood market, seafood consumers behavior, institutions, basic and applied research devoted to identifying natural based solutions to counteract coastal eutrophication (Grosso et al., 2023; Ciriminna et al., 2024).

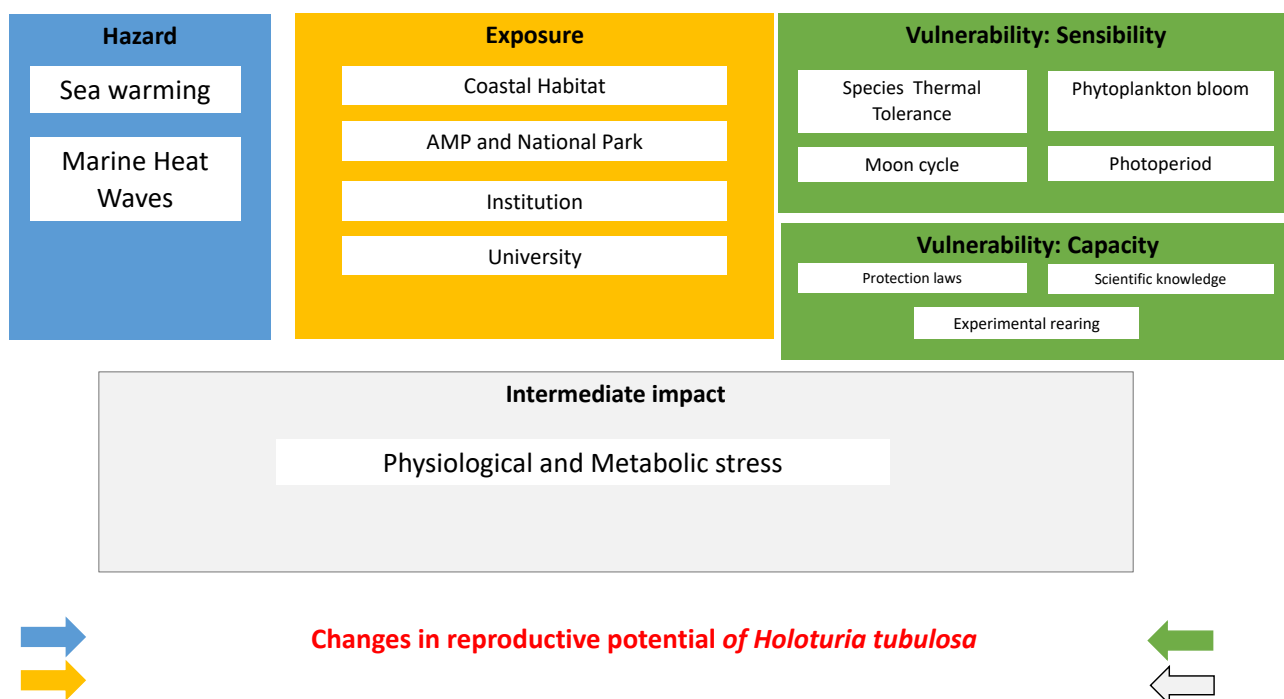


Figure 8.4 Climate Impact Chain for *Holothuria tubulosa*

7.3.5 Impact chain for *Posidonia oceanica* variations in abundance and/or distribution

The thermal habitat suitability models under both tested future scenarios for *Posidonia oceanica* along the Sardinia coasts, delineated in Chapter 3, suggest a minimal contraction (<20%) only during summer. Despite this, the potential risks for this seagrass under climate change **hazards** (sea warming and heatwaves) may arise from local population contractions over time, to the extent that possible local extinctions could occur at Mediterranean basin scale (Garcia et al., 2012; Marbà & Duarte, 1997; Diaz-Almela et al., 2009).

The scheme of the impact chain assessing the components of risk of changes in abundance and/or distribution of *P. oceanica* is illustrated in **Figure 8.5**.

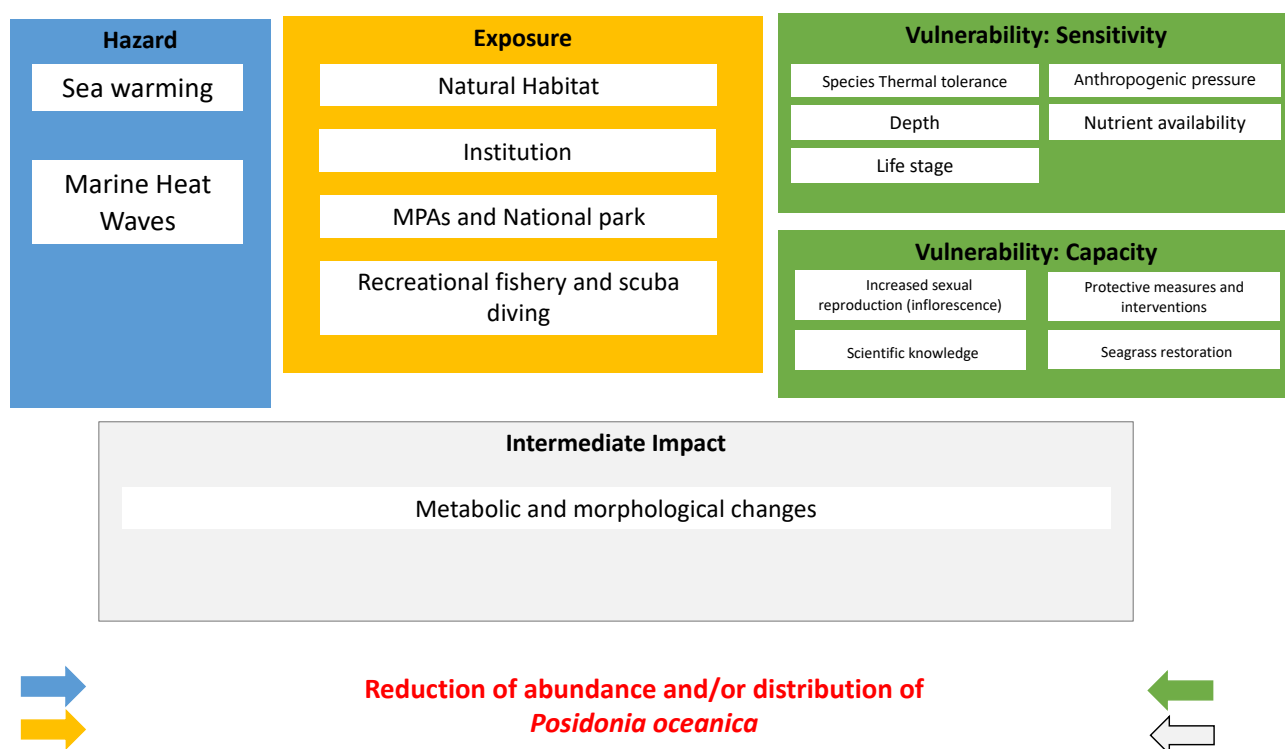


Figure 8.5 Climate Impact Chain for *Posidonia oceanica*

7.3.6 Impact chain for change in coastal lagoons trophic status

Based on the results obtained from mesocosm experiments (Chapters 4 and 5) and from field observations (Chapter 6), even mild intensity heatwaves, though with some exceptions, can alter the quantity and nutritional quality of sedimentary organic matter, that ultimately led to cascading effects on either ecosystem functioning (in terms of C degradation rates) or benthic trophic status. For this reason, to build the impact chain for coastal lagoons I considered the risk of possible alterations of its benthic trophic status. The direction of this change ("oligotrophication" vs. "eutrophication") is determined by synergies between response variables that altogether can be allocated in **sensitivity**: benthic microbial communities, benthic faunal communities, pools and degradation rates of sedimentary organic matter.

The scheme of the impact chain assessing the components of risk of changes in the benthic trophic status of coastal lagoons is illustrated in **Figure 8.6**.

As outlined in the previous chapters, sea warming and marine heatwaves are major hazards for the integrity of biogeochemical cycles in coastal lagoon sediments (Palmas et al., 2025). Considering the whole lagoon ecosystem, its **sensitivity** to the designated risk is determined by an ample set of ecological elements that, at different scales, influence its functioning. As mentioned in

Chapter 6, the trophic status of coastal lagoon sediments reflects a complex balance between organic matter inputs, C accumulation and decomposition, and the removal of catabolites produced by consumption and degradation mechanisms (the “saprobity” concept; Tagliapietra et al., 2012). The relationships between sedimentary features (in terms of sediment grain size), quantity, composition and nutritional quality of sedimentary organic matter pools and the benthic microbial, vegetal and faunal communities, influence the whole energetic balance of the system (Manini et al., 2003; Pusceddu & Danovaro, 2009). For instance, organic matter loads are usually correlated with sediment grain size, with muddy sediments typically richer and sandy sediments usually less nutrient-loaded (Martinez-Garcia et al., 2015). As oxygen consumption is typically higher in organic matter-rich sediments (Pusceddu et al., 2009), oxygen availability in muddy sediments is typically more limiting than in sandy bottoms, thus affecting the differential composition of the benthic communities that inhabit them (Politi et al., 2022). At the same time, contents and nutritional quality of sedimentary organic matter influence metabolism, taxonomic composition, and biodiversity of benthic lagoon communities (Pusceddu et al., 2011). For instance, either meio- or macrofauna are able to modify the chemical and physical characteristics of the sediment, displacing sediment grains during burrow construction and stimulating microbial activity capable of degrading sedimentary organic pools (Schratzberger and Ingels, 2018; Giampaoletti et al., 2025).

Depending on sedimentary organic pools to warming and marine heatwaves, I pinpointed two possible patterns of altered benthic metabolism (intermediate impacts): 1) a general decrease of food availability and nutritional quality for the benthos due to an increase in bacterial-mediated extracellular enzymes activities and a shift of energy transfer towards the microbial loop (Manini et al., 2003) and, following an increase in organic matter consumption rates, shifting to more oligotrophic condition impairing the ability of lagoon sediments to store blue carbon; 2) an increase in organic loads and a slowdown in bacterial degradation efficiency, leading to organic matter accumulation, shifting to a general eutrophication of lagoons bottoms possibly fostering the occurrence of dystrophic crises. Possible capacity actions to counteract mined vulnerability of coastal lagoons benthic trophic status caused by climate change include interventions aimed at reducing inorganic and organic nutrient inputs, privileging filter feeders farming on any other aquaculture practice, avoiding any intensive fishery practice. The most exposed coastal lagoons to the risks of climate change (exposure) include lagoons with restricted water exchange, high anthropogenic pressures, and proximity to agricultural or urban areas, altogether influencing nutrient loading and sediment dynamics.

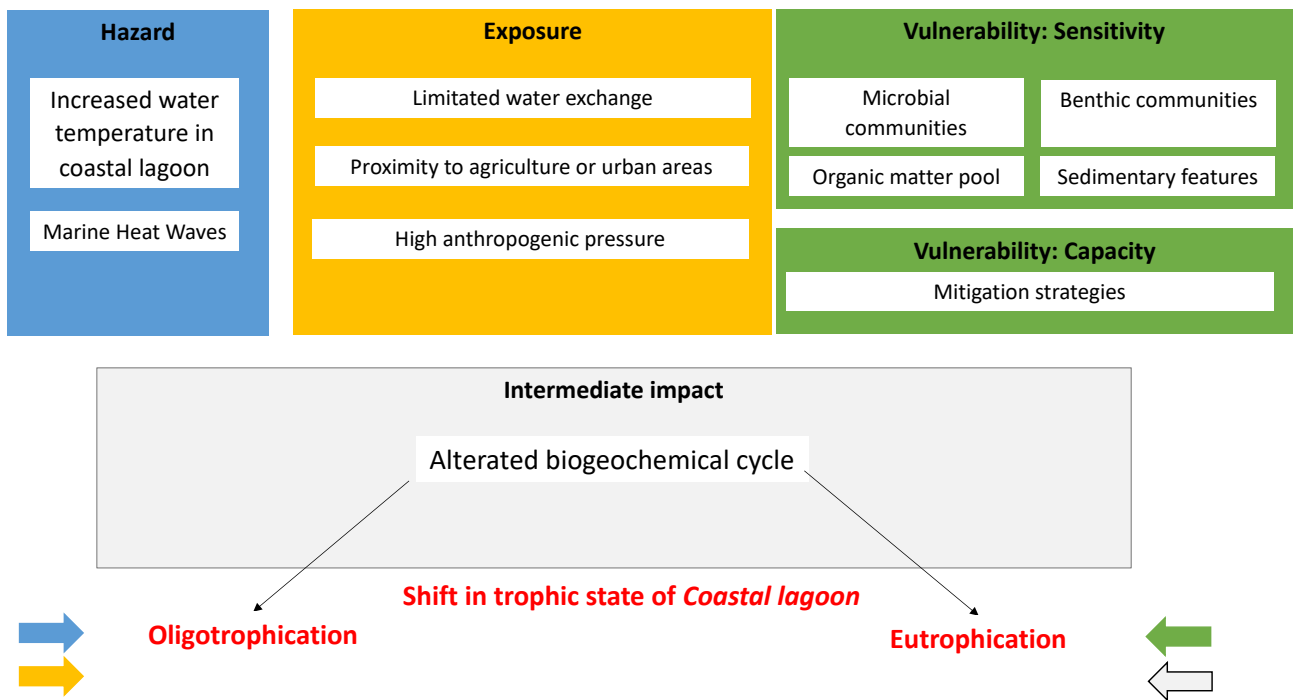


Figure 8.6 Climate Impact Chain for coastal lagoons

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General conclusion

Climate change manifestations like ocean warming and marine heatwaves, are becoming increasingly widespread and impactful phenomena, affecting especially marine coastal ecosystems and lagoons.

These phenomena, acting both synchronously and cumulatively, can alter ecosystem functioning dynamics at multiple biological levels. Variations in the distribution and abundance of key species, in the functional balance within communities, and in the trophic status affect not only the integrity of ecosystems themselves but also their ability to produce the goods and services they provide to the humanity.

Within the 'One Health' perspective, the scientific community is striving to address the climate challenge by increasing knowledge and understanding of the mechanisms through which these phenomena act, with the goal of informing policy makers to let them be capable of putting in place mitigation or adaptation strategies to protect the society.

In this context, my PhD thesis (through the use of an array of different approaches and methodologies, including systematic literature review, modeling approaches, mesocosm experiments, and field investigations) has contributed to expanding current knowledge on the assessment of vulnerability and impacts of climate change manifestations (sea warming and marine heatwaves) across different levels of biological organization, from species to communities and ecosystem functions in marine coastal and lagoon ecosystems.

The cumulative results of my Thesis show that sea warming and marine heatwaves can modify the structure and functionality of coastal and lagoon communities. Sea warming influences the potential distribution of key species of both ecological and economic importance.

The reconstruction, based on literature data, of thermal performance curves derived from metabolic–functional traits of key species provided valuable information on species-specific temperature sensitivity. Then, the integration of these data into a predictive model, informed with climatic projections for Sardinian coasts, allowed the estimation of the potential variations in thermally suitable habitat for these species in the present and future scenarios (2021–2050), thus allowing to envisage the most severe impacts of sea warming and marine heatwaves.

Species such as the mussel *Mytilus galloprovincialis* and the sea urchin *Paracentrotus lividus*, which play crucial ecological roles as a bioremediator and an ecosystem engineer, respectively, may face reductions in suitable habitat for their survival and maintenance. The potential loss of these

species would also have significant economic implications especially in Sardinia, considering the regional importance of mussel aquaculture and the strong fishing pressure on sea urchins.

Habitat-forming and carbon-stocking species such as *Posidonia oceanica* may experience comparatively smaller reductions, offering some optimism for their long-term persistence. Conversely, species such as the holothurian *Holothuria tubulosa* and the fish *Mullus barbatus* may experience reductions in their reproductive potential. Besides the risks for their fishing and the associated market, the anticipations of their spawning periods may no longer coincide with key natural dynamics (e.g., zooplankton blooms facilitating fertilization and recruitment), potentially leading to population declines and cascading effects on nutrient cycling and trophic networks.

The promising results of my thesis allow me to contend that thermal habitat suitability models, initially categorized in the IPCC AR4 framework as tools for merely assessing species vulnerability, can now be reconsidered as valuable tools for quantifying the level of impact to which species are exposed. When integrated with exposure assessments, these models can contribute to comprehensive risk evaluations. The use of high-resolution climate data would enable finer-scale interpretations, improving the identification of priority areas for conservation. Furthermore, the experimental reconstruction of thermal performance curves under controlled conditions would provide a more precise understanding of species' intrinsic vulnerability to temperature variation.

By analyzing the impact of heatwaves on sediment biogeochemistry in coastal lagoons, my thesis also contributed to filling a major knowledge gap concerning these systems, which serve as sentinels of climate change. The results of mesocosm and field experiments highlight the profound alterations marine heatwaves can cause in lagoons' sediment biogeochemistry, characterized by a general decline in both the quantity and nutritional quality of food available for benthic organisms, what I termed a sort of "oligotrophication." These experiment, initially conducted on a homogeneous "ideal" sediment in the field (from the S'Ena Arrubia lagoon, Sardinia, Italy), were subsequently deepened through controlled mesocosm experiments carried out using sediments retrieved from two lagoons characterized by different latitude and temperature regime: a northern lagoon in the Baltic Sea (Curonian lagoon, Estonia) and a southern lagoon in the Mediterranean Sea (the Santa Gilla lagoon, Sardinia, Italy), to explore potential covariates, such as climatology, sediment type and associated organic matter loads, regulating sediment biogeochemistry responses to marine heatwaves.

The results of the benthocosm experiments reveal that both the intensity of the heatwave and sediment grain size distinctly influenced system responses. Three main response patterns were

identified: a potential enhancement of ecosystem functioning during lower-intensity heatwaves (+2 °C), a process of lagoon sediment oligotrophication, or, in some cases, possible eutrophication processes. Overall, marine heatwaves have been identified as important factors causing altered benthic metabolism, ultimately causing shifts in the trophic state of coastal lagoon sediments.

Moreover, the use of incubation techniques for measuring gas (e.g., oxygen) and nutrient (e.g., ammonium) fluxes further enriched my research, helping to assess the indirect response dynamics of benthic communities and associated biogeochemical cycles. On the one hand, mesocosm experiments allowed for a better control of abiotic variability, providing clearer insights into the specific effects of the thermal anomalies; on the other hand, they have not been able to fully capture the complex dynamics occurring in natural environments.

Ultimately, but not less importantly, I directly observed that changes in the trophic state of lagoon sediment biogeochemistry can have severe effects also on benthic communities like meiofauna. Given the crucial role of meiofauna in stimulating microbial degradation of organic matter, CC induced alterations of this important component of the benthos can reduce the filtering capacity of the system, increasing the risk of enhancing eutrophication, potentially co-leading to persistent anoxic conditions in lagoons.

Finally, the studies carried out within my thesis, with a particular focus on the Sardinian coasts, aimed to provide locally relevant knowledge to support the implementation, revision, and validation of strategies adopted by policymakers (such as the Regional Strategy for Climate Change Adaptation; SRACC) for climate change mitigation and adaptation in coastal Sardinian lagoons



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