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**Original Article**

# Marine heatwaves in the Subarctic and the effect of acute temperature change on the key grazer *Strongylocentrotus droebachiensis* (Echinoidea, Echinodermata)

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## Abstract

Subarctic fjord systems are facing a continuous temperature increase as well as more frequent and more intense marine heatwaves (MHWs). MHWs are periods of exceptionally high temperatures above the long-term average. In the Porsangerfjord (Northern Norway), the average water temperature ranges from 2.5°C in March to 10°C in August. MHWs frequently exceed the summer maximum by up to 6°C with so far unknown ecological effects. The green sea urchin, *Strongylocentrotus droebachiensis*, is a key grazer on habitat-forming kelp in Subarctic fjord systems. At high abundances, sea urchins transform productive kelp beds through pronounced grazing into depleted sea urchin barrens. In a laboratory experiment, we investigated the influence of acute temperature change on the grazing activity and the metabolic performance of the green sea urchin. Grazing rates increased continuously from 2 to 10°C but decreased again at 14°C. At 22°C, rapid decay of sea urchins were associated with changes of the metabolic energy state from aerobiosis to anaerobiosis. We propose two scenarios: Moderate warming might lead to the proliferation of the sea urchin population and increased grazing pressure on kelp forests, while extreme warming, as predicted by the end of the century, as well as the occurrence of extreme MHWs, may severely impair the sea urchin population and, in turn, might favour the proliferation of adaptable kelp species.

*Keywords:* sea urchin; kelp; grazing; thermal stress physiology; marine heatwaves; sea urchin barrens; NMR-based metabolomics

## Introduction

Anthropogenic greenhouse gas emissions, primarily due to extensive consumption of fossil energy sources, caused a significant increase in the global temperature. Comparing preindustrial conditions with today's temperatures (2011–2020), average surface temperatures over land increased by 1.59°C and average sea surface temperature (SST) by 0.88°C (IPCC 2023). A further rise in temperature is inevitable and will entail a higher occurrence of weather extremes such as marine heatwaves (MHWs) (Munasinghe et al. 2012, Goss et al. 2020, IPCC 2023).

MHWs are SST anomalies where the temperature exceeds a certain threshold of the locally expected temperature for more than five consecutive days (Hobday et al. 2018). The intensity of MHWs can be assigned to four categories from moderate to extreme, depending on how far the threshold is exceeded (Hobday et al. 2016). Frequencies and intensities of MHWs have increased significantly over the last century, resulting in a doubling of MHW days in the last three decades (Frölicher et al. 2018, Oliver et al. 2018, Dayan et al. 2023). It is proposed that this trend will continue in the following decades (Frölicher et al. 2018, Darmaraki et al. 2019, Oliver et al. 2019). Some of the recognized effects associated with extreme and long-lasting MHWs in temperate and tropical waters are extensive coral bleaching, seabird mass mortality, and lasting reductions of commercial fish stocks (Le Nohaïc et al. 2017, Jones et al. 2018, Suryan et al. 2021).

Arctic and Subarctic regions are characterized by low temperature and pronounced seasonality, especially in light intensity and primary production. As the fastest warming regions due to a phenomenon called Arctic amplification, they are particularly affected by the upcoming increase in temperature and more frequent and intense summer MHWs (Huang et al. 2021, Rantanen et al. 2022). When marine species experience warming as an adverse change of their environment, they may either adapt to these new conditions or avoid them by migrating to colder places. If neither is successful, these species will eventually become extinct, being the 'losers' of global change (Fulton 2011). Mobile species can react to increasing temperatures by shifting their range to higher latitudes or deeper waters (Caputi et al. 2010, Nicolas et al. 2011, Hiddink et al. 2015). Polar and subpolar species are more constrained in extending their range to colder environments than species from temperate waters because they already approach their upper geographical limits. At the same time, their lower-latitudinal range shifts polewards, decreasing their overall distributional range (Parmesan and Yohe 2003, Morley et al. 2019). Therefore, polar and subpolar species and ecosystems are especially vulnerable to global warming and MHW, emphasizing the importance of physiological adaptations to the changing environment (Barbeaux et al. 2020, Beaudreau et al. 2024, Guibourd de Luzinais et al. 2024 ).

Sea urchins play a vital role as primary consumers in Subarctic and Arctic fjord ecosystems (Blicher et al. 2009). As keystone species, they have a high impact on their environment through their grazing activity on kelp (Bulleri et al. 1999). Kelp, in turn, are habitat-structuring brown macroalgae that provide a multitude of ecosystem services such as food source and food web structure, maintenance of high biodiversity, carbon sequestration, and coastal protection (Christie et al. 2009, Teagle et al. 2017, Vilas et al. 2020). The interactive relationship between kelp and sea urchin is a well-known feedback loop where the presence or absence of sea urchins has a modulating effect on the benthic habitat. High sea urchin densities, due to high recruitment success, migration from deeper areas, or the lack of predators and disease outbreaks can lead to the formation of grazing aggregations or fronts (Scheibling et al. 1999, Fagerli et al. 2013). Increased grazing pressure on kelp beds provokes a shift from a productive kelp forest to only rocky sea floor. It shows little to no macroalgae growth and forms an alternative stable state of the system (Mann 1982). These so-called sea urchin barrens are characterized by low primary production, a less complex food web structure, and a loss in biodiversity (Ling 2008, Bianchelli et al. 2016). Sea urchin barrens were observed globally in various rocky shore ecosystems (Filbee-Dexter and Scheibling 2014 and references therein, Rogers-Bennett and Catton 2019). Along the Norwegian coast, sea urchin barrens appeared in large numbers in the 1970s. Since then, kelp forests have recovered partly, especially along the southwest coast of Norway (Christie et al. 2019). This recovery might be attributed to an increased abundance of sea urchin predators like the edible crab, as well as the decrease of cod populations, which, in turn, feed on larger decapods (Fagerli et al. 2014, Christie et al. 2019). However, this ecological link is not soundly proven and might only partly explain kelp recovery (Christie et al. 2019). Moreover, temperature has been discussed as an important direct or indirect factor for the establishment and persistence of kelp forests or sea urchin barrens. The temperature-dependent grazing by *Mesocentrotus nudus* delayed the formation of kelp forests after the winter temperatures exceeded 5.5°C. This led to the conclusion that low grazing pressure during the beginning of the year favours the establishment of dense kelp forests (Yatsuya and Matsumoto 2023). Conversely, settlement success and postsettlement survival increases with high temperatures. This was reported for *Diadema* aff. *antillarum* during above-average warm years, maintaining the barren state of rocky shore habitats (Hérnandez et al. 2010). It has been proposed that MHWs can trigger the change from productive kelp forest communities to robust sea urchin barrens, as seen after an ocean warming event at the shore of California (Rogers-Bennett and Catton 2019).

The effects of increasing temperatures, especially of extreme temperature events and their ecological implications, are still understudied in species with a polar and boreal distribution. The green sea urchin *Strongylocentrotus droebachiensis* is a common polar-boreal echinoderm with a broad distribution, ranging from Cape Cod, USA (41° N) in the Northwest Atlantic and Southern Scandinavia (57° N) in the Northeast Atlantic to the high Arctic (Scheibling and Hatcher 2007). As an important grazer on macroalgae, the green sea urchin has the potential to affect kelp communities and may cause fundamental ecosystem shifts (Norderhaug and Christie 2009, Filbee-Dexter and Scheibling 2014). However, the grazing behaviour and the physiology over a wide thermal range have not been studied in echinoderms from the Subarctic and Arctic. This is a major knowledge gap in predicting the future dynamics of Arctic kelp forests, and thus Arctic ecosystems.

In the present study, we first analyzed the climatic development of the Porsangerfjord and changes in MHW occurrence and intensity over the last 41 years (1982–2022). Abrupt temperature changes during MHWs are a challenge to marine organisms. Therefore, we explored the effect of fast temperature change on the grazing activity and metabolic physiology of adult green sea urchin *S. droebachiensis* by studying the metabolic profiles by $^{1}$H-NMR (nuclear magnetic resonance) spectroscopy. The results are discussed in view of the ongoing Arctic warming and potential future MHW events, as well as increasing local sea urchin populations and the resulting consequences for the kelp ecosystem and its functions.

## Material and methods

### Field investigations

#### Study area

The Porsangerfjord is one of the largest and northernmost fjords in Norway. East of the North Cape, it extends ~120 km in north-northeast direction (70–71 latitude, 25–26 longitude, Fig. 1) and opens into the Barents Sea. The fjord is 15–20 km wide and has a maximum depth of 230 m (Mankettikkara 2013). A sill is located ~30 km from the head of the fjord at a depth of 60 m, separating the inner part from the middle part of the fjord (Stramska et al. 2016). The outer part of the fjord extends north of the island Tamsøya. It is characterized by a relatively free exchange of water masses with the Norwegian Coastal Current (NCC) (Eilertsen and Skarðhamar 2006, Stramska et al. 2016). During the winter, surface and deep-water masses are well mixed in the fjord (Mankettikkara 2013). Increased freshwater river runoffs during summer lead to a stratification of the water body and a gradient of low salinity at the head of the fjord to nearly open ocean conditions at the mouth of the fjord (Stramska et al. 2018). Despite the high latitude, only the inner part of the fjord freezes in winter (Petrich et al. 2017).

The flora and fauna of the Porsangerfjord are characterized by a rich community of macroalgae and associated herbivores. The kelp species *Laminaria digitata* and *Saccharina latissima* dominate the intertidal and the shallow subtidal areas of the fjord (Sivertsen and Björge 2015). In the sublittoral, the sea urchin *Strongylocentrotus droebachiensis* is a common grazer on kelp and has in some places created long-lasting barren grounds (Sivertsen and Björge 2015, Strand et al. 2020). In contrast to other areas along the Norwegian coast, little to no kelp recovery has occurred during the last years in the Porsanger region (Christie et al. 2019).

#### Sea urchin abundance

The sea urchin density and population structure were recorded in the Holmfjord bay (70.367 latitude, 25.466 longitude, red dot in Fig. 1a) close to the coastline within the middle

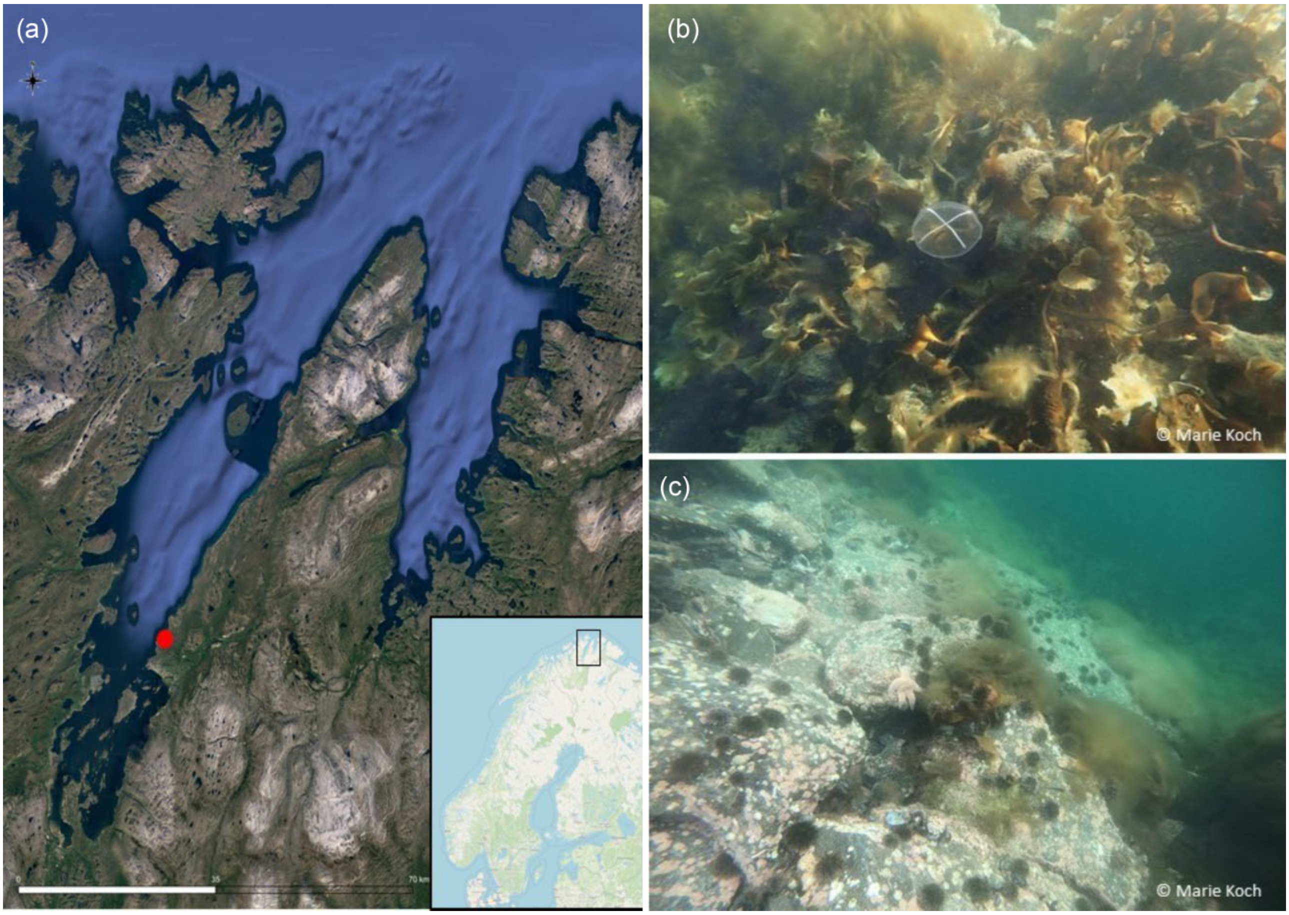

**Figure 1.** (a) Bathymetric map of the Porsangerfjord in Northern Norway. The sampling site at Holmfjord is marked by the red dot. The map was created with QGIS 3.34.3. At the sampling site, two distinct habitats are located: (b) a rich kelp forest, including macroalgae species such as *Saccharina latissima* and (c) a sea urchin barren, which is deprived of algae and dominated by rocky ground.

part of the Porsangerfjord. All sea urchins were collected from randomly selected areas of exactly 1 $m^2$ in the barren and the neighbouring kelp forest ($n = 6$ each) in July 2022 and August 2023. Species, species morphotype, wet mass, and test diameter of each individual were recorded (data: Koch et al. 2024, https://doi.pangaea.de/10.1594/PANGAEA.964580).

### Sea surface temperature data

SST data near the sampling location in the Porsangerfjord (70.375 latitude, 25.375 longitude) were taken as a subset from the NOAA dataset ncdcOisst21Agg_LonPM180 (daily optimum interpolation sea surface temperature, accessed 14 October 2023) (Huang et al. 2020). These data originate from infrared satellite data, which are bias-corrected using *in situ* data (Reynolds et al. 2007, Banzon et al. 2016 ). Daily temperature data were extracted for a period of 41 years prior to the current study (1 January 1982 to 31 December 2022) to describe the recent climatic trends. The mean monthly temperature, including the standard deviation, was calculated over the whole study period. The annual mean and maximum temperatures as well as annual temperature sums were calculated over the whole timespan. Besides the occurrence of MHWs, the rate at which temperatures can change from day to day is an important factor for the interpretation of potential thermal stress in organisms. Therefore, the daily temperature change ($\Delta t$) was calculated over the study period as well.

Additionally, the seawater temperature was recorded manually at 1 m depth directly at the sampling site in the Porsangerfjord with a HQ40D Digital Multimeter (Hach Lange GmbH, Düsseldorf, Germany) over the full course of the temperature experiment (5 July–6 August 2022).

### MHW events

A climate baseline (climatology) for this 41-year period was established with the heatwaveR package (version 0.4.6) in R (version 4.3.1) (Schlegel and Smit 2018) and used for the identification and categorization of sea surface temperature anomalies (SSTA) and, particularly, MHWs. The threshold that defined MHW was based on the 90th percentile of the historical SST distribution. The category of the MHW was defined by exceeding multitudes of this threshold (above threshold = moderate, above 2× threshold = strong, above 3× threshold = severe, and above 4× threshold = extreme).

## Laboratory investigations

### Temperature ramp experiment

A laboratory experiment with discrete temperature increments was run in July 2022 at the Holmfjord Marine Station.

Green morphotypes of the sea urchin *Strongylocentrotus droebachiensis* (33.8 ± 8.7 g) were sampled in July 2022 in low tide at a depth of ca. 1 m depth from the sea urchin barren off the marine station. The animals were brought directly to the laboratories of the marine station and placed into their assigned experiment setups (see also the next section and 'Grazing rates and tissue sampling' section).

Aerated 2-l square, wide-mouth PVC containers (aquaria) were set up in a modified commercial freezer (118 × 92 × 74 cm, 280 l volume, Privileg PFH 606, Stuttgart, Germany). The freezer was equipped with a heating pad (AccuLux, 45 × 65 cm, 40 W, Murrhardt, Germany) and a digital temperature controller (Inkbird, model ITC-380, Shenzhen, China), which maintained a constant temperature of ±0.5°C. The temperature was regularly monitored, and the incubator was continuously illuminated (900 lm, MaxLED 250, Paulmann Licht GmbH, Springe-Völksen, Germany) to simulate polar day in July.

The experiment was conducted in two separate runs to cover the whole thermal range of the sea urchins of 2–22°C. Each run started at the ambient water temperature in the fjord of 14°C. In the first run (warming treatment), the temperature was stepwise increased (14, 18, and 22°C). The second run was a cooling treatment with decreased temperatures (14, 10, 6, and 2°C).

The feeding rates of the sea urchins under ambient conditions were monitored in order to check for changes in feeding behaviour over time. The monitoring was conducted *in situ* in the fjord due to spatial constraints at the field station. Therefore, sea urchins ($n = 6$) were individually maintained in closed 2-l square, wide-mouth PVC containers, which were placed into a plastic pallet cage and submerged at the jetty of the station. The containers were perforated to ensure a steady exchange of fresh fjord water. The sea urchins were fed daily *ad libitum* with fresh *Saccharina latissima* phylloids, and grazing rates were recorded daily over the course of two weeks alongside the temperature ramp experiment (see also the 'Grazing rates and tissue sampling' section).

## Grazing rates and tissue sampling

Immediately after collection, sea urchins designated to the temperature experiment ($n = 21$ per run of the temperature ramp experiment) were placed individually in aquaria and randomly assigned to the final sampling temperatures. The experiment started with an acclimatization time of 3 days at the seawater temperature of the fjord (14°C). The temperature was then either lowered or increased by 4°C over 12 h, followed by an incubation time of 3 days at the new temperature. Sea urchins were fed every 24 h with ∼10 g of fresh *Saccharina latissima* phylloids. The algae pieces were blotted dry and weighted before and after feeding to the sea urchins to obtain grazing rates that were normalized for sea urchin wet mass and time [mg algae fresh mass (AFM) per gram sea urchin fresh mass (SFM) and day: $\mathrm{mg\,g^{-1}\,d^{-1}}$]. Every 24 h, the experimental sea urchin stock was checked for well-being and mortality. Faecal pellets and remaining food were removed, and 50% of the aquarium water was exchanged with fresh fjord water, which was adjusted to the current experimental temperature. After 3 days, tissue samples of the stomach and the intestine were dissected from four randomly assigned individuals ($n = 4$, following the 3R principle: 'replace', 'reduce', and 'refine'). At 22°C the sea urchins showed signs of reduced fitness indicated by shrivelled tube feet, less adhesion power, and a slight purple tint of the water, possibly due to lesions in the ambulacral system (Fig. S2). Therefore, the sampling at this temperature was already conducted at 24 h to ensure that tissue was only collected from live animals. The tissue was flushed with distilled water to remove all food remains within the digestive tract. The samples were then shock frozen in liquid nitrogen, shipped to the Alfred Wegener Institute in Bremerhaven (Germany), and stored at −80°C until further analysis.

## Extraction of metabolites and $^1$H-NMR measurement

For metabolite profiling based on NMR spectroscopy, frozen tissue was pulverized in liquid nitrogen by hand using a mortar and pestle. Approximately 60–80 mg of these samples were transferred into 2-ml Precellys tubes and suspended in 400 µl of methanol and 125 µl Milli-Q water. The tissue samples were homogenized for 20 s at 6000 relative centrifugal force (rcf) and 4°C in a Precellys-24 device (Bertin Technologies, Montigny-Bretonneux, France). A volume of 400 µl of dichloromethane (DCM) and 400 µl of Milli-Q water were added to the tubes. The samples were vortexed for 30 s and left on ice for 15 min. After centrifugation for 10 min at 3000 rcf and 4°C, a typical phase separation appeared. The upper polar phase was transferred into a new reaction tube and dried overnight at room temperature in a vacuum concentrator (Concentrator 5301, Eppendorf, Germany).

The dried metabolites were resuspended 1:2 (w/v) in deuterium oxide ($D_2O$) with 0.75% 3-(trimethylsilyl)propionic-2,2,3,3-$d_4$ acid sodium salt (TSP) (Sigma, 293040) as chemical shape and shift indicator (CSI) and centrifuged after resuspension for 10 min at 15 000 rcf and 4°C. Fifty microlitres of the supernatant was used for untargeted one-dimensional $^1$H-NMR spectroscopy. The sample probe was transferred to a vertical 9.4 T wide-bore NMR spectrometer, Bruker 400 UltraShield NMR (Bruker-BioSpin, GmbH, Germany), using a 1.5 mm triple-tuned $^1$H-$^{13}$C-$^{15}$ N NMR probe. A standard Carr-Purcell-Meiboom-Gill (cpmg) sequence with presaturation was used for all NMR measurements at room temperature, and the number of scans was set to 128. Spectrum acquisition was done with Bruker TopSpin 3.5 software (Bruker-BioSpin GmbH, Germany). Only spectra with a linewidth below 2 Hz were accepted. NMR acquisition parameters are described in detail in Schmidt et al. (2017). For correct peak annotation, the pH of six resuspended metabolite samples was measured using pH indicator paper (Lyphan L670, pH 6.0–8.1) and found to be 6.8. This pH was presumed as the pH of all metabolite samples.

## $^1$H-NMR metabolic profiling

NMR data were imported into a peak annotation software (Chenomx NMR suite 8.4 professional, Chenomx Inc., Canada) and manually line-, phase-, and baseline-corrected. The concentration of metabolites was calculated in relation to the CSI, which was automatically calibrated based on the TSP concentration. Peaks were assigned by chemical shift comparison to metabolites using the Chenomx 400 database as well as custom compound profiles. A set of 31 metabolites was identified from the $^1$H-NMR spectra of stomach and intestine. Concentrations were adjusted according to the dilution factor.

## Statistical analyses

All statistical analyses were conducted in R (version 4.3.1) if not otherwise stated.

Climatic trends were fitted to linear models. A kernel density plot was compiled for visual representation of the temperature distribution.

The mean and standard errors of sea urchin biomass and abundance per square metre were calculated for the kelp forest and the barren. Species distribution between habitats and sampling years (2022 and 2023) was analyzed by the Wilcoxon rank-sum test.

The grazing rates obtained from the temperature ramp experiment were normalized for sea urchin wet mass and time of feeding. Grazing rates at 14°C from both experimental runs were combined. Grazing rates at different temperatures were evaluated with a Kruskal–Wallis rank-sum test.

The metabolic profiles of the stomach and the intestine at different temperatures were analyzed and investigated for changes using the browser-based application MetaboAnalyst 5.0 (Xia and Wishart 2011). In particular, concentrations were mean-centred, $\log_{10}$-transformed, and statistically analyzed by one-way analysis of variance (ANOVA) and Tukey's HSD test. Samples taken at the starting points at 14°C were combined after confirming their statistical equality (ANOVA, $P > .05$).

Data were tested for outliers using the 95th percentile confidence ellipses of the unsupervised principal component analyses (PCA). Divergent metabolic profiles were investigated by supervised partial-least-squares discriminant analyses (PLS-DA), and the reasonableness of this analysis was checked through a permutation test (Fig. S1A–D). The most important metabolites were further identified by their variable importance of projection (VIP) score, considering all compounds with a VIP score above 1 as relevant.

# Results

## Field studies

### Sea surface temperature

The mean monthly SST (derived from satellite data; see the 'Sea urchin abundance' section) at the sampling site in the Porsangerfjord ranged from a minimum of 2.5 ± 1.1°C in March to a maximum of 10.0 ± 1.4°C in August in the period between 1982 and 2022 (Fig. 2a, Table S1). Accordingly, we defined in our study 10°C as the threshold for the maximum average summer temperature.

A statistically significant warming of the fjord of 0.02°C per year from the mean annual of 4.9°C in 1982 to 6.3°C in 2022 was evident (Fig. 2b). The interannual variation of the mean temperature was high. The lowest mean temperature of 4.4°C was measured in 1987 and the highest of 6.1 and 6.2°C in 2005 and 2006, respectively, as well as in the last 3 years of the study period, 2020–2022.

The annual temperature sums correlated closely with the mean temperatures ($r^2 = 0.99$, $P < .001$) and increased by 27.83% within the investigated period.

The maximum temperatures of each year increased significantly from 10.2°C in 1982 to 13.2°C in 2000 (Fig. 2c). The variability of the maximum temperature ($\Delta T_{\max} = |T_{\max\,2} – T_{\max\,1}|$,°C) between subsequent years was 0.75 ± 0.52°C (highest $\Delta T_{\max} = 1.73$°C). After 2000, the interannual variability increased significantly (2.05 ± 1.51°C, highest $\Delta T_{\max} = 5.13$°C, Welch two-sample *t*-test $P < .001$), and the maximum temperatures showed a slightly negative trend. The maximum annual temperatures ranged from 9.6°C in 2012 to 16.4°C in 2014. The high variation occurred simultaneously with higher peak temperatures and stronger heatwaves.

The density plot of the daily temperatures showed a shift towards warmer temperatures in the second half of the investigated time span, as well as an increase in extreme warm and cold temperatures (Fig. 2d). The examination of daily temperature changes revealed similar results for cooling and warming: The highest daily cooling was $-2.7$°C $\mathrm{d}^{-1}$, and the highest daily warming was 2.7°C $\mathrm{d}^{-1}$.

The manually measured mean temperature at the sampling site (1 m depth) was 14.0 ± 0.85°C during the field study. The satellite-derived mean SST temperature during this time was 13.9 ± 0.7°C. We concluded that the NOAA dataset adequately represents the actual temperature at the sampling site.

### Marine heatwaves

During the four decades (1982–2022), 83 MHW events were registered at the sample site, ranging from moderate to extreme (Table S2). The highest temperature (16.4°C) was recorded during a severe MHW in August 2014. Furthermore, a 67-day-long and moderate to severe MHW occurred between July and August 2022 during the sea urchin sampling campaign for the current study (Fig. 3).

While the frequency of MHWs did not change considerably over time, the number of MHW days as well as the intensity of MHW increased (Fig. 4), with a significant increase in strong MHW days after the year 2000 (Wilcoxon sum-rank test, $P < .05$).

### Sea urchin population

The abundance of sea urchins in the Holmfjord bay in summer 2022 was 146 ± 22 Ind $\mathrm{m}^{-2}$ in the barren and 19.8 ± 3.8 Ind $\mathrm{m}^{-2}$ in the kelp (Table 1). The green sea urchin *Strongylocentrotus droebachiensis* was the dominant species, occurring in two different colour morphs, green and purple spines, and accounting for 87.7% of individuals in the barren. The second most common species was *Strongylocentrotus pallidus*. The distribution of species in the kelp forest was similar, with *S. droebachiensis* accounting for 78.3% of total sea urchin abundance. Even though the red sea urchin *Echinus esculentus* was observed at the barren and the kelp forest, no individuals were present in the randomly selected sampling squares deployed in our study. The same survey was repeated in August 2023. The abundance of *S. droebachiensis* increased by up to 182% in the kelp forest, and the biomass increased by 214% compared to the survey in 2022 (Table 1).

## Laboratory results

### Temperature-dependent grazing and thermal limit

Since *Strongylocentrotus droebachiensis* was the most abundant and therefore most influential grazer in the Porsangerfjord, a temperature exposure experiment was conducted with this species. The initial grazing rates at 14°C of both runs were not statistically different (*t*-test, $P = .23$). Therefore, both runs of the experiment were combined in the following analysis. The grazing rates of the caged sea urchins in the fjord, which were incubated concurrently to the temperature exposure experiment, stayed consistent and did not

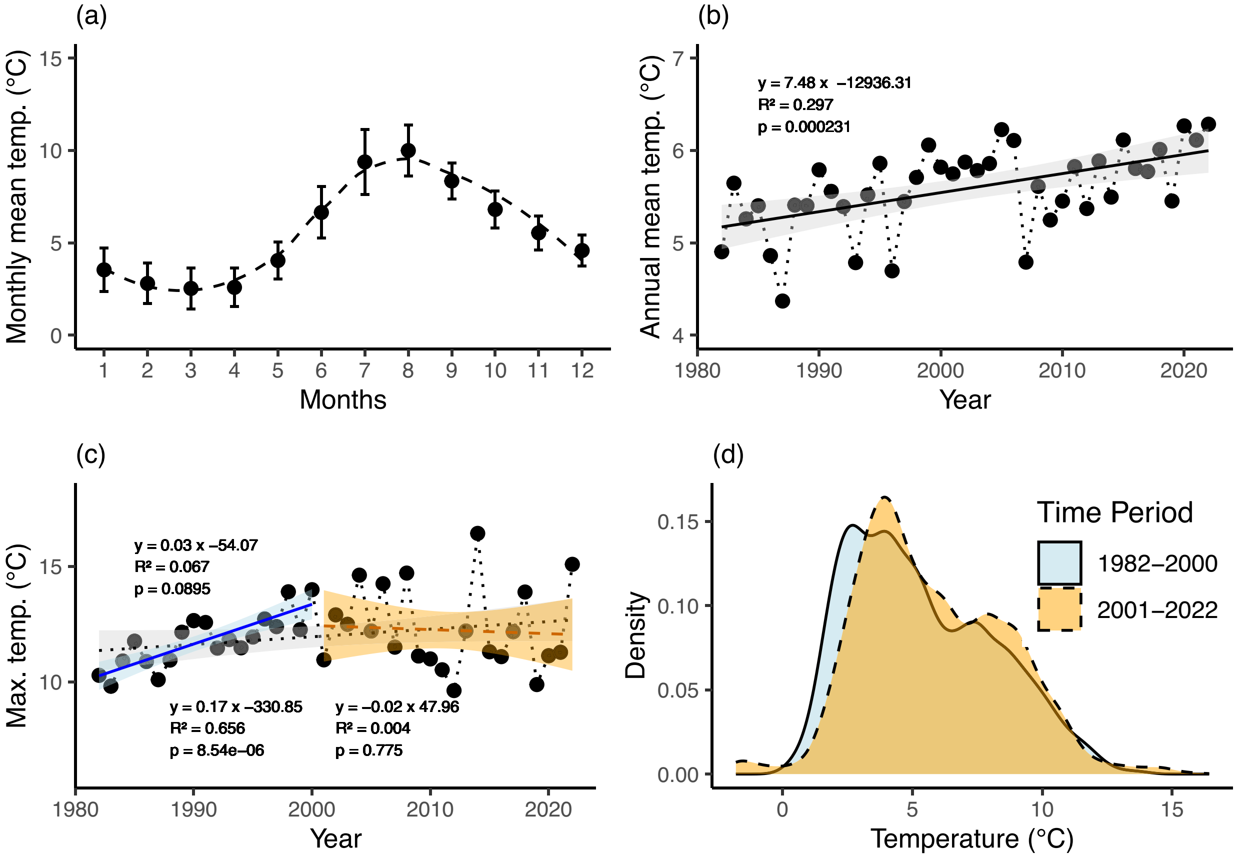

**Figure 2.** (a) The average monthly SST at the Porsangerfjord varied between 2.5°C in March and 10°C in August (1982–2022). (b) Annual mean temperatures at the sampling site between 1982 and 2022. (c) The annual maximum temperatures at the sampling site increased in the first half of the study period. After the year 2000, mainly the interannual variability increased. (d) The daily temperature distribution has shifted towards warmer and more extreme temperatures after the year 2000.

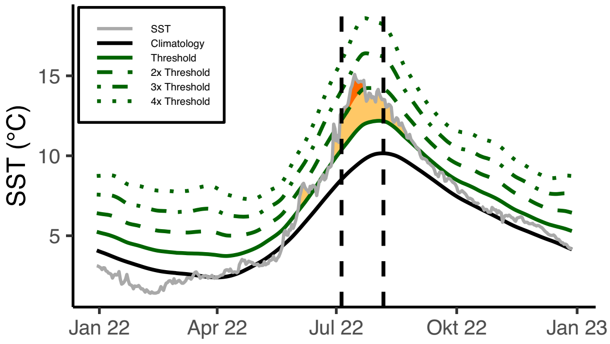

**Figure 3.** The sea surface temperature (SST, grey solid line) at the sampling site in the Porsangerfjord between January 2022 and January 2023. In the year 2022, two MHWs occurred, one in June and one in July/August, exceeding the threshold (multitudes of the threshold are marked through various line types; colours indicate intensity of the MHW: yellow, between threshold and 2x threshold line = moderate; orange, between 2x and 3x threshold line = strong). The later MHW coincided with the sampling period of this study, which is indicated by the dashed vertical lines.

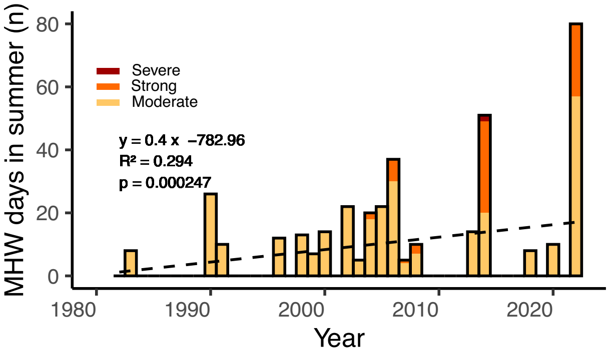

**Figure 4.** MHWs in the Porsangerfjord during the summer of the last four decades. The number of MHW days is depicted. Colours indicate the category of the MHW. A positive trend in MHW days is apparent, with an increase of nearly half a day per year. Especially the number of strong MHW days increased over this time.

change significantly over the course of 2 weeks (linear regression, *P*-value = .44). The grazing rates of the sea urchins in the temperature exposure experiment increased steadily from 2 to 10°C with a maximum at 10°C (26.9 ± 11.9 $\mathrm{mg\,g^{-1}\,d^{-1}}$) (Fig. 5). At higher temperatures, grazing decreased until it almost completely ceased at 22°C. At 22°C, sea urchins showed signs of severely reduced fitness and were, therefore, sampled at 24 h instead of after 3 days. After 36 h, all remaining sea urchins died. No mortality occurred at lower temperatures nor in the caged sea urchins in the fjord.

**Table 1.** Sea urchin densities and abundances at the Holmfjord bay in 2022 and 2023

| | 2022 | | 2023 | | Increase (%) | |
|---|---|---|---|---|---|---|
| | Kelp | Barren | Kelp | Barren | Kelp | Barren |
| Abundance | Ind $m^{-2}$ | Ind $m^{-2}$ | Ind $m^{-2}$ | Ind $m^{-2}$ | | |
| Total | 19.8 ± 9.2 | 146 ± 21.9 | 29.7 ± 23.8 | 184.5 ± 79.3 | 150 | 126 |
| *S. droebachiensis* | 15.5 ± 2.4 | 128 ± 49.8 | 28.2 ± 7.3 | 164 ± 30.4 | 182 | 128 |
| *S. pallidus* | 6.5 ± 1.3 | 18.7 ± 3.5 | 7.4 ± 2.7 | 21 ± 5.7 | 114 | 112 |
| Biomass | g $m^{-2}$ | g $m^{-2}$ | g $m^{-2}$ | g $m^{-2}$ | | |
| Total | 676 ± 324 | 1163 ± 270 | 1130 ± 860 | 1526 ± 745 | 167 | 131 |
| *S. droebachiensis* | 535 ± 99 | 1092 ± 120 | 1143 ± 287 | 1435 ± 305 | 214 | 131 |
| *S. pallidus* | 210 ± 50 | 70.5 ± 24 | 213 ± 64 | 91 ± 31 | 101 | 129 |

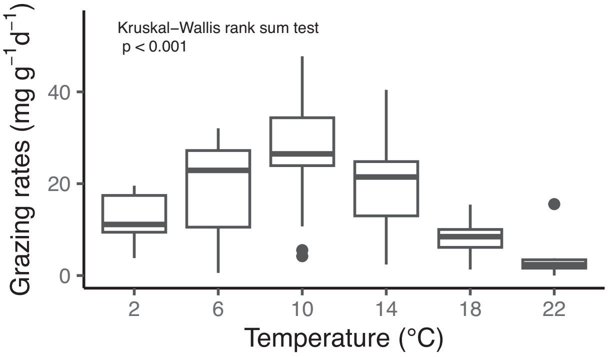

**Figure 5.** Thermal profile of the grazing rates of *Strongylocentrotus droebachiensis* under experimental conditions. Grazing increased up to 10°C, but decreased again at higher temperatures (Kruskal–Wallis rank-sum test, $P < .001$). At 22°C, marginal feeding was only observed during the first 24 h. No feeding was recorded thereafter. All sea urchins died after 36 h [$n = 9$ (2°C), 13 (6°C), 17 (10°C), 42 (14°C), 17 (18°C), 8 (22°C)].

### Metabolic profiles

In total, 31 metabolites were identified by their chemical shift in the $^1$H-NMR spectra of *Strongylocentrotus droebachiensis* stomach and intestine (Fig. S3 and Table S3). Since there was no significant difference in the metabolic profiles at 14°C of both experimental runs (*t*-tests for each metabolite, $P > .05$), the data of both runs were combined to obtain a consistent thermal profile from 2 to 22°C. Stomach and intestine tissue were analyzed separately.

The main metabolites were free amino acids and osmolytes. Of the main amino acids, glycine, alanine, taurine, and glutamine were the most abundant, while homarine dominated among the osmolytes. The adenylates AMP, ADP, and ATP were combined since their unambiguous distinction in the NMR spectra was not possible.

PCAs of metabolomes at all test temperatures for both tissues showed no outliers. The ANOVA revealed two significant changes in metabolite concentration in the stomach and nine in the intestine (Table S4A and B).

The supervised PLS-DA revealed a shift of the metabolome along the temperature gradient and a visible separation from the metabolic profile at 22°C in both tissues (Fig. 6a and c). In the stomach, the datapoints are clustered closely together at 2, 6, and 10°C, indicating high similarity. This is further supported by the overlap of the 95% confidence ellipse of the profiles. A progressive separation of the metabolic profiles appeared at higher temperatures. Finally, a clear distinction was evident at 22°C in both tissues. The shift is mostly driven by changes of amino acid concentrations and metabolites associated with the energy metabolism. Among the most important features (VIP score > 1) defining the metabolome shift in both tissues were glucose and lactate as well as several amino acids (Fig. 6b and d).

The glucose concentration in the stomach and in the intestine followed closely the thermal profile of the feeding rate. The concentrations increased continuously to a maximum at 10°C but decreased at higher temperature rapidly and reached lowest values at 22°C (Fig. 7). At each temperature, the glucose levels were higher in the stomach than in the intestine. A similar progression was observed for aspartate in the stomach.

Lactate, succinate, and acetate increased in both tissues at 22°C (Figs 8 and 9). Amino acids (tyrosine, valine, tryptophan, isoleucine, lysine, and phenylalanine) increased up to 14°C, decreased at 18°C, and showed maxima at 22°C (data not shown).

Furthermore, *N*,*N*-dimethylglycine decreased continuously at temperatures above 10°C, and ethylmalonate increased in the intestine drastically at 22°C.

## Discussion

### Sea surface temperature

The warming of the Subarctic Porsangerfjord during the last four decades is evident in the significant increase in the mean annual surface water temperatures. This trend is confirmed by Cieszyńska and Stramska (2018), who reported a climate change-related warming trend in air temperature of the Porsanger region over a 30-year time interval (1986–2015). Since 2000, the inflow of warm Atlantic waters into the European Arctic has increased, resulting in a warming of the Southern Barents Sea. The warming is accompanied by the establishment of boreal species and the decline in the abundance of endemic Arctic species (Ingvaldsen et al. 2021, Wang et al. 2023). In addition to this intensified 'Atlantification' of the Arctic, the Arctic amplification increased around 1999, resulting in a nearly four times faster warming rate of the Arctic and Subarctic compared to the global average (Chylek et al. 2022, Rantanen et al. 2022). However, according to Davy and Griewank (2023), Arctic amplification peaked in the early 2000s, suggesting no further acceleration of the Arctic warming compared to the global average. Besides the continuously increasing average temperatures, our data show a discontinuous trend in the seasonal maximum temperatures of the Porsangerfjord. While the maximum temperatures continuously increased during the first half of the investigated period (1982–2000), a slight negative trend was apparent after

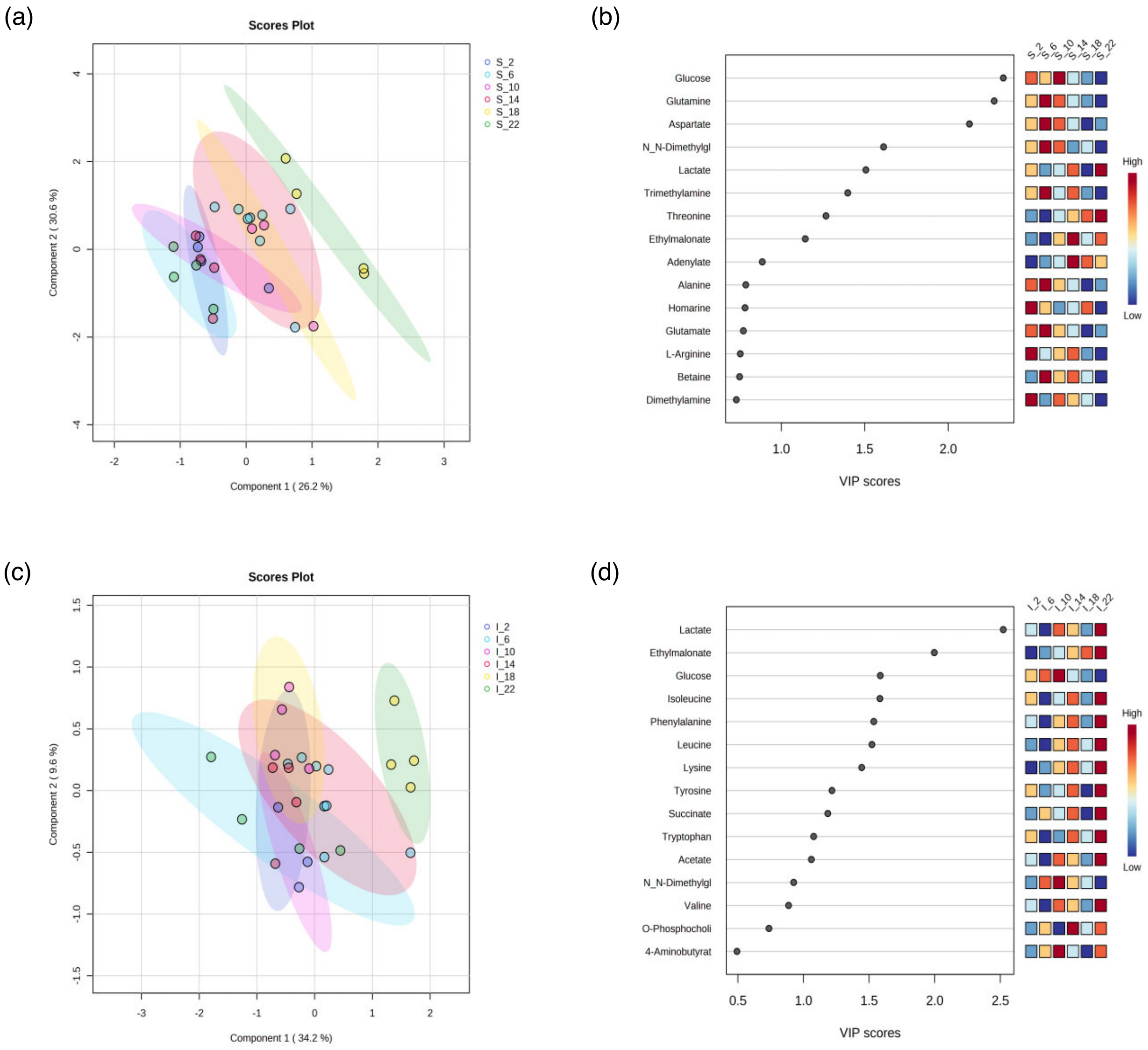

**Figure 6.** PLS-DA plots of the metabolome at different temperatures in (a) the stomach and (c) the intestine. (b) and (d) Metabolites with the highest weight listed in order of their VIP scores for both tissues. Legends indicate type of tissue (S = stomach, I = intestine) and incubation temperature (2–22). Changes in metabolite concentrations are indicated in the heatmaps next to the respective VIP scores.

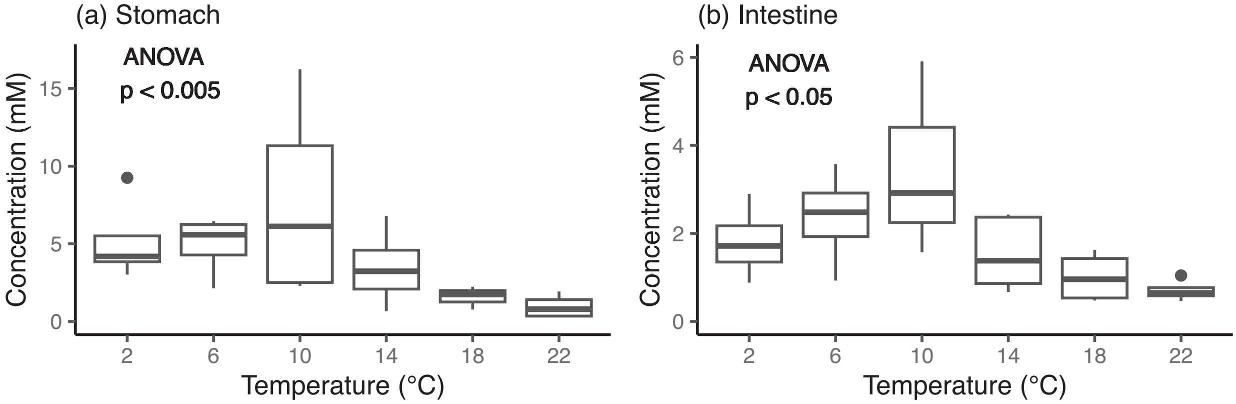

**Figure 7.** Glucose levels in (a) stomach and (b) intestine of *Strongylocentrotus droebachiensis* at 2–22°C. One-way ANOVA, $n = 4$.

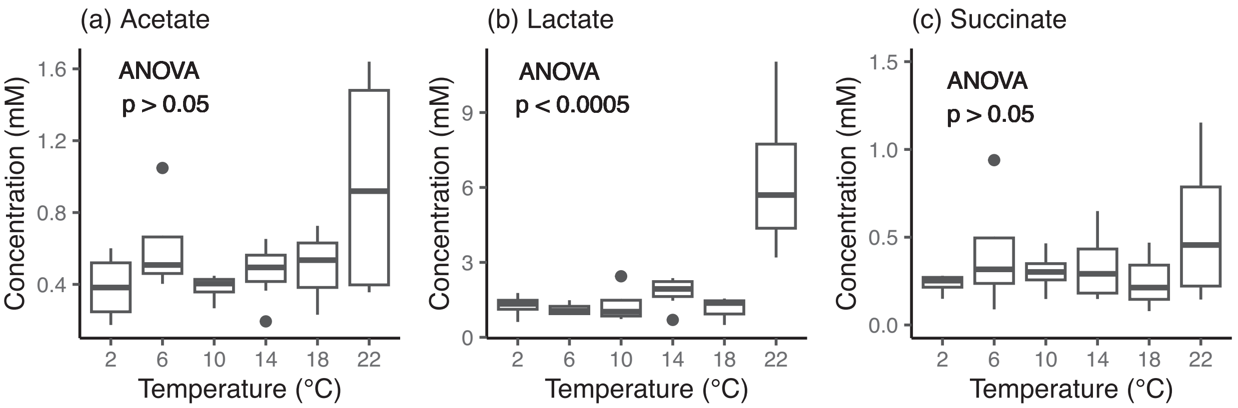

**Figure 8.** Concentration of the anaerobic markers acetate, lactate, and succinate in the stomach of *Strongylocentrotus droebachiensis* at 2–22°C. One-way ANOVA, $n = 4$.

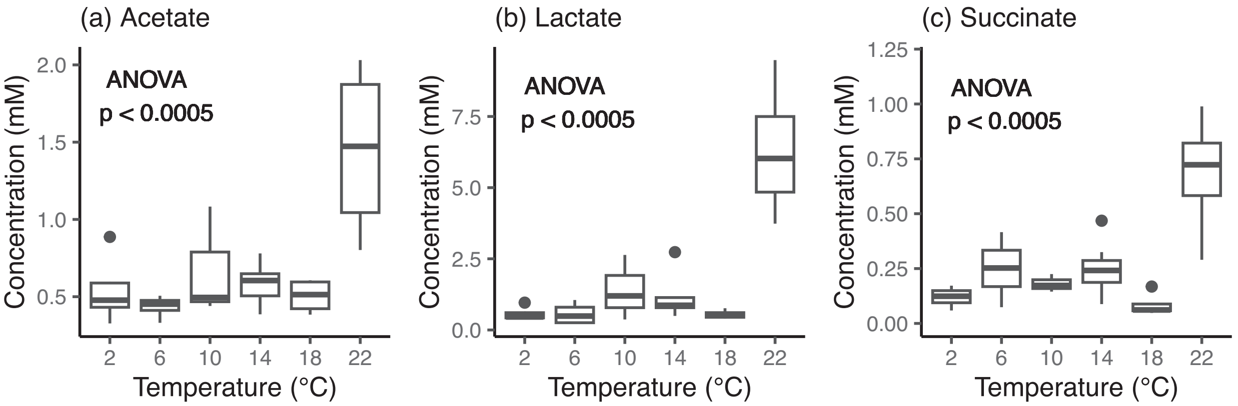

**Figure 9.** Concentration of the anaerobic markers acetate, lactate, and succinate in the intestine of *Strongylocentrotus droebachiensis* at 2–22°C. One-way ANOVA, $n = 4$.

the year 2000. Concurrently, the interannual variability of the maximum temperature as well as the number and intensity of MHW days increased after 2000. These results indicate a recent intensification of extreme weather events. This coincides with forecasts where new temperature records and an increase in MHW days are projected along with future Arctic warming (Thornton et al. 2014, Carvalho et al. 2021). Therefore, marine Arctic species face a continuously warming environment and the challenge of more dynamic and uncertain conditions.

## Fitness and mortality

The upper thermal limit of *Strongylocentrotus droebachiensis* from the Porsangerfjord was reached at 22°C, where full mortality occurred at 36 h of exposure. Similar temperature limits concerning the activity and survival of the green sea urchin were found in previous studies investigating the effect of temperature on *S. droebachiensis* (Percy 1973, Pearce et al. 2005, Richard et al. 2012). After a few hours of exposure at 22°C, the sea urchins in our experiment already showed clear signs of stress like flattened spines, shortened and shrivelled tube feet, and low adhesion power to the walls of the aquaria. Similar signs of advancing morbidity were observed by Percy (1973) and Lauzon-Guay and Scheibling (2007) at elevated temperatures. We also observed a purple colouration of the aquarium water, which we interpreted as signs of lesions of the ambulacral system and leaking of ambulacral fluid into the water. Similarly, Roberts-Regan et al. (1988) reported the occurrence of purplish wound secretion on sea urchins after bacterial infections. However, injuries due to elevated temperature have not been described in the literature. The ambulacral system has vital functions for echinoderms: It provides mobility, adhesion to rocky surfaces, and is the main respiratory organ (Steen 1965). Gas exchange takes place at the tube feet, where oxygen is transported to the sea urchin organs. The ambulacral fluid has the same oxygen capacity as the surrounding seawater due to the absence of respiratory pigments (Steen 1965), making sea urchins susceptible to oxygen deficiency. We hypothesize that the abrupt onset of mortality could be induced by respiratory failure as a consequence of deleterious effects of temperature stress on the ambulacral system. However, this assumption needs experimental support. The impact of temperature on the functionality of the ambulacral system has to be addressed in future studies.

## Grazing

Kelp is the foundation of the subtidal ecosystem in the Subarctic Porsangerfjord and provides a multitude of ecosystem functions. As the principal herbivores, sea urchins' grazing activity has been investigated with regard to temperature. Generally, grazing rates are positively correlated with temperature as shown for *Mesocentrotus nudus* and *Strongylocentrotus* species (McBridge et al. 1997, Siikavuopio et al. 2006, Yatsuya and Matsumoto 2023). Only one study on *S. droebachiensis* reported decreasing feeding rates with increasing temperatures (Wheeler 2017). Starting at 13°C, the authors exposed the sea urchins to fast increasing temperatures, but neglected the lower thermal range of *S. droebachiensis*. Our study, in contrast, addressed the temperature dependency of the grazing rates over the entire thermal range of *S. droebachiensis* from 2 to 22°C and identified highest grazing activity at 10°C. On average, medium-sized sea urchins consumed at 10°C ~844 mg of kelp per day. Considering the annual temperature range in the Porsangerfjord from 2.5 to 10°C, grazing activity of the sea urchin population would continuously increase with temperature, reaching its maximum in late summer. Only warmer temperatures above the average summer maximum of 10°C would entail lower grazing rates. This happens during the increasingly frequent MHW in summer.

The grazing rates were closely correlated with the glucose content of the digestive organs, which indicates the uptake and utilization of carbohydrates from the food. The offered kelp, *Saccharina latissima* (common name 'sugar kelp'), is rich in carbohydrates, particularly glucose, mannitol, and uronic acids (Lamb et al. 2018, Sharma et al. 2018, 2019). The glucose is liberated during the digestion of algal storage products and structure compounds such as laminarin and cellulose (Watanabe and Tokuda 2010, Becker et al. 2017). *S. droebachiensis* possesses efficient digestive enzymes, which are capable of hydrolyzing these algal storage products (Obrietan et al. 1991, Koch personal observation) to fuel metabolic demands. The glucose levels decreased at incubation temperatures above 10°C concomitantly with the feeding rates, which may entail a deficiency of external energy supply.

## Metabolic profiles

The metabolic energy demand of *Strongylocentrotus droebachiensis* from the Porsangerfjord is uncertain. Previous studies showed increasing oxygen consumption with temperature (Percy 1972, Schuster et al. 2022). The metabolic response to temperature can vary between populations, which are adapted to the local temperature range (Sokolova and Pörtner 2003, Sanford and Kelly 2011). In a study by Percy (1972), *S. droebachiensis* experienced temperatures between 0 and 15°C in Newfoundland and, thus, could have been adapted to slightly higher temperatures during summer than the Porsanger population. The study showed a reduced rate of respiration increase at temperatures above 10°C, and even decreasing rates in small, winter-acclimated individuals, indicating respiratory disturbances when approaching the upper thermal tolerance range (Pörtner 2001). Therefore, it is possible that declining respiration rates might occur already at lower temperature in the Porsanger population, although data on the respiration and metabolic rates of this Subarctic population are needed to draw final conclusions.

The metabolic profiles of *S. droebachiensis* changed with temperature in both tissues, but most pronounced in the stomach. The glycogenic amino acids glutamine, glutamate, and aspartate drive the metabolic shift in the stomach by decreasing in concentration at temperatures above 6°C, but most pronounced above 10°C. Decreasing levels are associated with the depletion of the citric acid cycle intermediate oxaloacetate, suggesting an early onset of a perturbation of the aerobic energy metabolism and the activation of gluconeogenetic pathways (Shao et al. 2015, Yang et al. 2020). The metabolic performance of ectothermic invertebrates is a result of the relationship between oxygen uptake capacity and the consumed energy. At higher temperatures, and therefore higher metabolic rates, energetic needs of the viable limit are determined by the oxygen uptake capacity of an organism (oxygen-capacity-limited thermal tolerance) (Pörtner 2002). To counteract the energetic imbalance, alternative ATP-producing pathways become active, resulting finally in a shift from 'normal' aerobic metabolism to anaerobiosis when $Tc_{\max}$, the maximum critical temperature, is reached (Pörtner and Farrell 2008). Concentrations of the typical anaerobic markers, lactate, succinate, and acetate rose rapidly in tissues of sea urchins exposed to 22°C. The accumulation of lactate indicates the anaerobic fermentation of pyruvate, which produces less ATP (Klutymans and Zandee 1983, Sokolova et al. 2012). Succinate accumulation is a marker for anaerobic ATP production in the mitochondria and can be facilitated through the conversion of aspartate, which decreased at higher temperatures in the stomach (Sokolova and Pörtner 2001, 2003, Sokolova et al. 2012). Furthermore, the levels of acetate rose rapidly as well, suggesting that pyruvate or aspartate is metabolized anaerobically into acetate for ATP production (Klutymans and Zandee 1983).

We expected a slow rise in anaerobic metabolites, indicating an ongoing supply of the energy budget by anaerobic pathways, the closer the experimental temperature would approach the thermal limit of the sea urchin. Corresponding results were found in the European flat oyster *Ostrea edulis*, where anaerobic metabolites increased 10°C below the lethal temperature (Eymann et al. 2020) and in the gastropod *Cellana toreuma*, where the expression of genes, encoding enzymes involved in anaerobic metabolism, was partly upregulated at increased temperatures several degrees below the Arrhenius break temperature of cardiac function (Han et al. 2017). The only indication for such metabolic shift was apparent through changes in some amino acid levels in the stomach. We conclude from our observations that at temperatures above 10°C a 'critical threshold' was exceeded, resulting in reduced performance of *S. droebachiensis*. However, the very abrupt onset of anaerobiosis is probably not only due to a mismatch between oxygen supply and demand but also due to respiratory failure probably due to a compromised ambulacral system, resulting in impaired oxygen supply.

## Ecological implications

Global environmental warming, which is most pronounced in the Arctic and Subarctic, will pose new challenges to ecological interactions between key species. Thereby, two principal aspects have to be considered: (i) the continuous year-round warming and (ii) the occurrence of summer heatwaves with exceptionally high temperatures.

Current CMIP6 (Coupled Model Intercomparison Project Phase6) results predict an ocean surface temperature increase of ~4°C by the year 2050 and 7°C by the year 2100 in the European Arctic and Subarctic, considering the SSP585 scenario (Drinkwater et al. 2021). In the first half of this century, the year-round warming of the fjord could lead to an intensification of the overall grazing pressure by sea urchins on kelps. The stabilization of already existing barrens as well as the transition of more kelp forests into sea urchin barrens seems likely in the near future. Whether a shift from kelp forest to barren is accomplished also depends on the sea urchin density. Scheibling et al. (1999) found that *Strongylocentrotus droebachiensis* formed aggressive grazing fronts at densities above 2 kg biomass (fresh weight) per square metre. Even though our data on the sea urchin population are limited to 2 years, we saw an increase in sea urchin density and biomass from 2022 to 2023 by up to 150% in the kelp and 167% in the barren. The required sea urchin densities for forming aggressive grazing fronts were partly reached in the existing barren in 2023, making the further propagation and intensification of the barren state likely. This concludes a rise of daily algae mass consumption by sea urchins from ∼14 and 24 $\mathrm{g\,m^{-2}}$ (2022) to ∼30 and 40 $\mathrm{g\,m^{-2}}$ (2023) in the kelp forest and barren, respectively, at the expected temperature of 10°C in August.

Increased sea urchin densities originate from low predation pressure as well as high recruitment success. *S. droebachiensis* usually spawns between mid-February and mid-April. Embryonic development is positively correlated with temperature but requires temperatures <10°C (Stephens 1972). Settlement and recruitment usually take place between late May and July (Lambert and Harris 2005), and declining recruitment success has been linked to warming temperatures at the southern distribution limits of the species (Fagerli et al. 2013, Harris and Gibson 2023 ). Adult *S. droebachiensis* from the Porsangerfjord showed the highest grazing rates at 10°C, which coincides with the maximum average summer temperature. This temperature also marks a physiological tipping point beyond which sea urchins might progressively run into metabolic energy deficiency due to decreased grazing activity but proposed increased metabolic rate (Schuster et al. 2022). Further increase in temperature in a more distant future could reduce grazing and recruitment success and therefore could facilitate kelp proliferation.

Nevertheless, kelps are as well affected by increasing temperatures and MHWs. While generally higher growth rates are expected with increasing temperature (Filbee-Dexter et al. 2019), several common species show impaired fitness at higher temperatures that can already appear in the Porsangerfjord during summer (Simonson et al. 2015). The impact of increasing temperature on *Saccharina latissima*, a widely distributed kelp species with a temperate to Arctic distribution range and one of the most common kelp species in the Porsangerfjord (Sivertsen and Björge 2015), has been the goal of many studies. Long-term exposure to elevated but not lethal temperatures affects a multitude of physiological parameters like growth rate and photosynthetic pathways (Andersen 2013, Diehl et al. 2024, and references within). The more frequent occurrence of MHW in the last decades is associated with the loss of *S. latissima*-dominated kelp forests along both sides of the North Atlantic coast (e.g., southern Norway, Filbee-Dexter et al. 2020). The simultaneous appearance of warm years and MHWs impairs the fitness of *S. latissima* stronger than either event alone (Niedzwiedz et al. 2022). However, Diehl et al. (2021) showed that more northern populations of *S. latissima* were less affected by experimentally elevated summer temperatures of up to 6°C than southern populations, indicating a higher resistance of these populations to MHW events. So far, the biomass of *S. latissima* in the European Arctic has remained stable or even increased, although changes in depth distribution have occurred (Krause-Jensen et al. 2020, Düsedau et al. 2024). Experimental studies on Arctic populations of *S. latissima* confirmed increasing growth rates up to 15°C (Li et al. 2020). A recent review concluded that *S. latissima* might benefit from further warming in Arctic and Subarctic regions (Diehl et al. 2024).

Whether grazing pressure and/or temperature rise lead to a more stable kelp forest or a shift to sea urchin barrens depends on a multitude of factors that are hard to predict. The physiological plasticity of local kelp stock such as *S. latissima* will determine if kelp habitats can prevail or even benefit from changing conditions in the future.

Unfavourable environmental conditions can be evaded by migrating to deeper water, as observed in a shift of distribution of some marine benthic invertebrates towards colder and deeper waters (Hiddink et al. 2015). Habitat compression and evasion to deeper waters was reported for some echinoid species (Sato et al. 2017), but not for Subarctic *S. droebachiensis*. Movement patterns of *S. droebachiensis* do not seem to be impacted by temperature except above 17°C (Dumont et al. 2007, Lauzon-Guay and Scheibling 2007). *S. droebachiensis* has been found as deep as 300 m in some habitats (Scheibling and Hatcher 2007). However, the depths of the Porsangerfjord host a sustaining population of red King crabs (*Paralithodes camtschasticus*), which are opportunistic predators of sea urchins. Fuhrmann et al. (2017) reported that the stomachs of King cabs contain only a few sea urchin remains, pointing towards little overlapping of the habitats of both species. Apparently, a downward migration of sea urchins is prevented by the presence of predators, and, thus, a repopulation of shallow waters from the depth is unlikely as well.

The adaptive potential of species to new conditions depends on their physiological background and the dynamic of change. A slow increase in temperature over a longer period, e.g., 0.2°C per day over 30 days, may pose different challenges to the performance of species than a faster warming rate of 2°C per day over 3 days (Peck et al. 2009). During slow increase, adaptive mechanisms like the utilization of reserves or adaptation to changes in prey/predator interactions play vital roles, while the fast increase of temperature, as during MHW events, is generally only tolerated by species for a limited time. Therefore, the physiological plasticity (Clusella-Trullas et al. 2014) of sea urchins under thermal stress and oxygen limitation determines the species survival.

## Concluding remarks

The sea urchin, *Strongylocentrotus droebachiensis*, successfully occupies its thermal window in the Porsangerfjord, even during the most intense MHW events. Nevertheless, future predictions of warming in the Subarctic indicate a drastic reduction of the thermal safety margin.

In the near future, however, a complete vanishing of the sea urchin population due to MHWs in summer appears unlikely. Instead, the continuous year-round warming might increase grazing pressure by sea urchins, leading to a shift from kelp forest to barren. The complete grazing of underwater forests prohibits the use of this habitat as a nursing ground for coastal fishes, crustaceans, and other animals, ultimately leading to decreasing populations. In areas like the Porsangerfjord, which economically (at least partially) depend on small-scale indigenous fisheries and recreational fishing (Chen and

Chen 2016, Brattland et al. 2019), changes in sea urchin population and grazing pressure might cause economic disadvantages.

In a more distant future (end of the century predictions), the warming of the Porsangerfjord as well as the extent of MHW events could reach a point where the maintenance of the *S. droebachiensis* stock is critical. While a reduction or vanishing of the sea urchin population might, at first, seem positive for kelp restoration and preservation of the associated ecosystem functions, further cascading effects at other trophic levels beyond the kelp-sea urchin relationship are hard to predict. The adaptive potential, flexibility, and resilience of the key players will define the development of Subarctic fjord ecosystems.

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## Author contributions

Marie Koch (Conceptualization, Methodology, Data curation, Formal analysis, Investigation, Validation, Visualization, Writing—original draft), Simon Jungblut (Investigation, Data curation, Writing—review and editing), Sandra Götze (Data curation, Formal analysis, Writing—review and editing), Christian Bock (Resources, Supervision of NMR analysis and processing, Data curation, Writing—review and editing), and Reinhard Saborowski (Conceptualization, Funding acquisition, Resources, Supervision, Validation, Writing—review and editing).

## Supplementary data

Supplementary data is available at *ICES Journal of Marine Science* online.

Detailed information on MHW events, the metabolic compound table as well as ANOVA-results for changes in metabolite concentration in the stomach and intestine are available as supplementary material at ICESJMS online. The supplementary material includes also across-validation statistics of the PLSDA models, a photo of stressed sea urchins at 22°C and an exemplary $^1$H-NMR spectrum.

*Conflict of interest*: The authors declare no conflict of interest.

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## Data availability

The sea urchin population data are publicly available in the PANGAEA database under the digital identifier https://doi.pangaea.de/10.1594/PANGAEA.964580. Metabolite concentration data are listed in the supplementary information (Table S3). Daily SST data between the years 1982 and 2022 were taken from the ncdcOisst21Agg_LonPM180 NOAA dataset (Huang et al. (2020), doi: https://doi.org/10.25921/RE9P-PT57, accessed 14 October 2023) and downloaded from the ERDDAP homepage under https://coastwatch.pfeg.noaa.gov/erddap/index.html.

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