Global Change Biology Communications

WILEY

Global Change Biology Communications
BIOLOGY FOR A RAPIDLY CHANGING WORLD

RESEARCH ARTICLE OPEN ACCESS

Fishes in Eelgrass Meadows Show Large Interspecific Differences in Thermal Acclimation to Marine Heatwaves

Elena Tamarit-Castro[1] | Felix Steinbrecher[2] | Leon Pfeufer[3] | Emily R. Lechner[3] | Hannah Sauer[2] | Leon Green[3,4] | Diana Perry[5] | Hans W. Linderholm[1] | Martin Gullström[6] | Fredrik Jutfelt[3]

[1]Department of Earth Sciences, University of Gothenburg, Gothenburg, Sweden | [2]Department of Marine Sciences, University of Gothenburg, Gothenburg, Sweden | [3]Department of Biological and Environmental Sciences, University of Gothenburg, Gothenburg, Sweden | [4]The Maritime Museum & Aquarium, Gothenburg, Sweden | [5]Department of Aquatic Resources, Swedish University of Agricultural Sciences, Lysekil, Sweden | [6]School of Natural Sciences, Technology and Environmental Studies, Södertörn University, Huddinge, Sweden

Correspondence: Elena Tamarit-Castro (elena.tamarit@gu.se)

Received: 19 January 2026 | **Revised:** 26 April 2026 | **Accepted:** 19 May 2026

Keywords: critical thermal maximum | global warming | marine heatwaves | seagrass ecosystems | thermal acclimation | thermal extremes

ABSTRACT

Global warming is increasingly exposing shallow coastal habitats to extreme temperatures, with important consequences for associated fish communities. Eelgrass (*Zostera marina*), the most widespread seagrass in northern temperate regions, forms extensive meadows that provide nursery habitats, foraging opportunities, and refuge for a high diversity of coastal fishes. During intensifying marine heatwaves, these species are increasingly exposed to acute thermal stress. Upper thermal tolerance and short-term acclimation capacity may determine which species persist or decline in warming eelgrass ecosystems, yet interspecific differences remain poorly understood. To address this gap, we experimentally exposed 12 wild-caught fish species inhabiting eelgrass habitats in summer to two temperatures, Ambient (19°C) and Heatwave (23°C), representing current conditions on the Swedish Skagerrak coast (North Sea). We quantified critical thermal maxima (CT_{max}) as a proxy for acute upper thermal tolerance and assessed species' short-term acclimation capacity following 5 days of exposure to a simulated marine heatwave. Most species increased their thermal tolerance, but both baseline thermal tolerance and acclimation response ratio (ARR) varied markedly among taxa. Juvenile Atlantic cod, whiting, and European plaice showed the lowest thermal tolerance and weakest ARR, suggesting limited capacity to rapidly buffer acute warming at the tested temperatures and a greater reliance on behavioral avoidance. In contrast, sedentary species such as gobies and pipefishes exhibited high thermal tolerance with moderate plasticity, whereas wrasses showed moderate tolerance but the strongest short-term acclimation capacity. Temperature records from regional eelgrass meadows revealed summer conditions approaching or exceeding the upper thermal limits of several species examined. Together, these results demonstrate pronounced interspecific variation in thermal tolerance and short-term acclimation capacity among fishes occupying eelgrass habitats. This suggests that species-specific physiological limits and plasticity are likely to influence responses to marine heatwaves and reshape eelgrass fish assemblages under climate change.

1 | Introduction

Seagrass meadows rank among the most productive ecosystems on Earth, providing essential nursery habitats for juvenile fishes and supporting coastal biodiversity (Beck et al. 2001; Heck Hay et al. 2003; Lefcheck et al. 2019; McDevitt-Irwin et al. 2016; Orth et al. 2006) Yet, anthropogenic climate change is exposing these habitats and their fish assemblages to warming and extreme thermal events that threaten ecological functioning (Oliver et al. 2018; Smale et al. 2019). Marine heatwaves, discrete periods (≥ 5 days) of anomalously high seawater temperature (Hobday et al. 2016; Smith et al. 2023),

have increased in frequency, intensity and duration, posing a pervasive threat to marine biodiversity worldwide (Calvin et al. 2023; Cheng et al. 2025; Wernberg et al. 2025). These extreme events can cause widespread impacts on seagrasses and associated fauna, particularly species with strong habitat specificity (Brijs et al. 2025; Garrabou et al. 2009; Gómez-Gras et al. 2025; Olsen et al. 2022; Smith et al. 2024; Strydom et al. 2020).

The North Sea is among the fastest-warming marine regions, experiencing record-breaking sea surface temperatures with anomalies reaching +4°C (Mohamed et al. 2025). Many species in this region live near the edge of their thermal tolerance, making them particularly sensitive to further warming (Smale et al. 2019). Species' responses to warming are shaped by their upper thermal limits and their capacity for rapid acclimation (Gunderson and Stillman 2015; Seebacher et al. 2015). Thermal tolerance constrains species' geographic distributions and large-scale biogeographic patterns, thereby influencing community composition (Sunday et al. 2012). Extreme events such as marine heatwaves can shape population persistence, particularly for species occupying the warm edges of their distributions (Sunday et al. 2019). When environmental temperatures outpace acclimation, individuals can lose motor control and no longer escape heat (Fry 1947; Jutfelt et al. 2024; McKenzie et al. 2021).

This threshold is commonly quantified as the critical thermal maximum (CT_{max}), a widely used measure of acute thermal tolerance and acclimation capacity in fishes (De Bonville et al. 2025; Desforges et al. 2023; Lefevre et al. 2021; Madeira et al. 2012; Messmer et al. 2017; Moyano et al. 2017; Raby et al. 2025; Vinagre et al. 2016). Metrics such as acclimation response ratio (ARR) and thermal tolerance gain (TT_{gain}) further quantify the rate and magnitude of thermal acclimation following exposure to elevated temperatures (Claussen 1977; Morley et al. 2019). Through short-term acclimation, phenotypic plasticity can shift thermal limits and partially buffer individuals against warming (Brett 1952; Seebacher et al. 2015). However, species and lifestages differ in both the rate and capacity for acclimation, complicating predictions of vulnerability and community reorganization under climate change (Burton and Einum 2025; Gómez-Gras et al. 2025; Jutfelt et al. 2024). Understanding these interspecific differences is therefore critical for predicting ecological responses to intensifying marine heatwaves.

In addition to physiological plasticity, many fishes can buffer short-term warming through behavioral thermoregulation, such as relocating to cooler waters (Brett 1952; Huey et al. 2012). However, the ability to avoid thermal stress depends on species mobility, life-history strategy, and habitat association (Seebacher et al. 2015; Sunday et al. 2019). Migratory or mobile species may escape unfavorable conditions, whereas resident or habitat-specialist species may be constrained to local environments and rely more on physiological acclimation.

Shallow coastal habitats often experience high thermal variability, meaning that thermal exposure can differ from, and often exceed, modeled regional climate trends (Helmuth et al. 2016). Eelgrass (*Zostera marina*), the most widespread seagrass in northern temperate regions, exemplifies such habitats (Short 2003; Yu et al. 2023). It forms extensive subtidal meadows that support diverse fish assemblages, including shallow-water generalists (e.g., wrasses, gobies, sticklebacks), sedentary specialists (e.g., pipefishes and some gobies), and juvenile migrants such as gadids (codfishes) and flatfishes that use eelgrass as nursery habitat (Perry et al. 2018; Pihl and Wennhage 2002). Temperature regimes within eelgrass meadows are shaped by depth, hydrodynamics, and exposure, creating local microclimates that can amplify thermal variability (Hattich et al. 2025). However, long-term, high resolution temperature records from these habitats remain limited (Bertelli et al. 2021; Plaisted et al. 2022), while evidence suggests that the ecological impacts of marine heatwaves depend strongly on local conditions and fine-scale habitat heterogeneity (Starko et al. 2024). This is because marine organisms respond to fine-scale variability rather than to environmental averages (Helmuth et al. 2014). As a result, the consequences of marine heatwaves on seagrass fish assemblages and their responses remain poorly understood (Robinson et al. 2022; Thalmann et al. 2024).

Furthermore, despite the extensive literature on fish thermal tolerance and acclimation, most studies have focused on single species or a limited number of subtropical, temperate, and Antarctic species (Bilyk and DeVries 2011; De Bonville et al. 2025; Drost et al. 2016; Mottola et al. 2022; Peck et al. 2014). Few studies have compared the capacity for rapid acclimation across multiple species co-occurring within the same habitat, where individuals experience similar environmental conditions. To our knowledge, no study has examined short-term acclimation capacity across fishes associated with seagrass habitats, limiting our understanding of which species have a greater ability to cope with rapid warming in these ecosystems.

Here, we experimentally quantified CT_{max} and short-term acclimation capacity in 12 fish species associated with eelgrass habitats on the Swedish Skagerrak coast. We exposed wild-caught individuals to ecologically relevant ambient (19°C) and heatwave (23°C) temperatures for 5 days, after which we measured CT_{max} as the temperature at loss of equilibrium. We then quantified their short-term acclimation capacity and further examined relationships with species' thermal distribution ranges. We also evaluated local thermal regimes using in situ logger records and historical temperature data to detect marine heatwaves and warming trends. We predicted that generalist species with warmer thermal niches would exhibit higher CT_{max} and greater acclimation capacity, whereas migratory species with narrower or colder ranges would show lower tolerance and limited plasticity, indicating potential vulnerability to future marine heatwaves in eelgrass habitats.

2 | Materials and Methods

2.1 | Animal Research Permit

The Swedish Board of Agriculture's ethical committee and the University of Gothenburg approved this experiment (Ethics Permit Dnr 5.2.18-01447/2022). It followed the regulations set by the Animal Welfare Body at the University of Gothenburg and the ARRIVE guidelines (Animal Research: Reporting of In Vivo Experiments; du Sert et al. 2020).

2.2 | Study Area and Fish Husbandry

The study was conducted between 15 July and 23 September 2024, at the Kristineberg Marine Research Station, in the Gullmar Fjord on the Swedish Skagerrak coast (58.24983° N, 11.44587° E; Figure S1). The fjord is connected to the North Sea and supports productive eelgrass meadows in shallow, semi-sheltered areas.

Wild fish from 12 common temperate species occupying eelgrass meadows were collected within 2 km of Kristineberg at depths of 1–4 m. These species represented six major families found in Nordic eelgrass meadows (Gadidae, Pleuronectidae, Labridae, Gasterosteidae, Gobiidae, and Syngnathidae; Table 1) and included shallow-water generalists, sedentary habitat specialists, and juvenile migratory species. Sample sizes varied among species due to natural differences in abundance and catchability of wild-caught individuals but accounted for using mixed-effects models. All fish were sampled from this geographic location, representing co-occurring populations exposed to a shared local thermal environment. Mean seawater temperature during the collection period was 18.9°C ± 1.2°C (mean ± SD; Figure S1). Fish were captured using beach seines, baited traps, fyke nets, and hand nets while snorkeling and immediately transported to the research station.

Before the experiment, all fish were housed in a holding tank (1350 L, 275 × 79 × 62 cm [$L \times W \times H$]) supplied with flow-through filtered fjord seawater pumped from 7 m depth and acclimated to captivity for 1 week under ambient fjord temperatures (18.6°C ± 1.5°C, mean ± SD) and a 12:12 h light:dark photoperiod. They were fed once daily to satiation with thawed northern shrimp (*Pandalus borealis*) and brine shrimp (*Artemia* sp.), and tanks were cleaned daily to maintain water quality.

2.3 | Experimental Design

Separate experiments were conducted for each species, exposing fish to two temperature treatments for 5 days to trigger a short-term acclimation response. Each experiment consisted of five replicated tanks with seawater at 19°C ("Ambient") and five at 23°C ("Heatwave"). These temperatures reflect ecologically realistic summer conditions on the Swedish Skagerrak coast based on high resolution in situ temperature records at 1 m depth at Kristineberg (https://www.weather.loven.gu.se/kristineberg/en/).

The Ambient treatment was based on the mean daily maximum sea temperature from 1 June to 30 September for 2020–2023 (18.6°C ± 1.9°C, mean ± SD), whereas the "Heatwave" treatment simulated a +4°C warming scenario based on recently reported temperature anomalies in the North Sea (Mohamed et al. 2025).

Experiments were conducted in a temperature-controlled room with centralized air and sea water heating. Tanks received flow-through seawater adjusted to target temperatures, which were monitored daily (18.8°C ± 0.3°C and 22.8°C ± 0.2°C, mean ± S.D.; Thermometer Testo-112, Testo,

TABLE 1 | Metadata for study species and experimental design.

Study species and experimental design							
					Morphometrics		
Species	**Family**	**Common name**	***N*/treat**	***N*/tank**	**TL (mm)**	**Mass (g)**	**Life stage**
Gadus morhua	Gadidae	Atlantic cod	9	1–2	103 ± 20	10.6 ± 6.0	J
Merlangius merlangus	Gadidae	Whiting	12	2–3	121 ± 9	13.4 ± 3.3	J
Gasterosteus aculeatus	Gasterosteidae	Three-spined stickleback	75	15	48 ± 4	1.0 ± 0.1	A
Gobius niger	Gobiidae	Black goby	35	7	82 ± 6	6.9 ± 0.5	J
Pomatoschistus flavescens	Gobiidae	Two-spotted goby	105	21	39 ± 7	0.4 ± 1.9	A
Pomatoschistus minutus	Gobiidae	Sand goby	30	6	64 ± 58	1.8 ± 0.4	A
Ctenolabrus rupestris	Labridae	Goldsinny wrasse	20	4	95 ± 11	11.2 ± 6.5	A
Symphodus melops	Labridae	Corkwing wrasse	30	6	122 ± 8	24.5 ± 0.5	A
Pleuronectes platessa	Pleuronectidae	European plaice	35	7	52 ± 10	1.6 ± 3.7	J
Nerophis ophidion	Syngnathidae	Straightnose pipefish	15	3	208 ± 52	0.7 ± 9.1	A/J
Syngnathus acus	Syngnathidae	Greater pipefish	3	1	376 ± 35	24.2 ± 0.8	A
Syngnathus typhle	Syngnathidae	Broadnosed pipefish	15	3	144 ± 9	1.2 ± 0.9	A/J

Note: For life stage—A, adult; J, juvenile.
Abbreviations: Mass (g), mass in grams, mean ± SD; *N*/tank, number of fish per tank; *N*/treat, number of individuals per treatment; TL (mm), total length in millimeter, mean ± SD.

Lenzkirch, Germany). Fish were randomly assigned to treatments, and tank size was adjusted according to species: small glass tanks (45 L): 35 × 37 × 35 cm ($L \times W \times H$); big glass tanks (80 L): 38 × 60 × 35 cm. Tanks were dispersed throughout the room to minimize location effects and contained 2 cm of sand substrate and plastic seaweed, mussel shells, and PVC pipes for shelter. The feeding regime and photoperiod matched the holding period.

2.4 | Testing of Acute Warming Tolerance (CT_{max}) on Fish

After the 5-day exposure, one CT_{max} trial was conducted per experimental tank (five per treatment), testing all fish from a tank simultaneously. Fish were fasted 24 h before trials (Raby et al. 2025). CT_{max} was measured using a standardized test with temperature at loss of equilibrium (LOE) as the response variable for each individual fish (Beitinger et al. 2000; Morgan et al. 2018). LOE was a behavioral response defined as the fish's inability to maintain an upright position for 3 s.

Trials were conducted in a custom arena filled with water from the corresponding experimental tank. The CT_{max} arena was a plastic box (34 × 25 × 17 cm; ~14 L) divided into one small (a third of the box size) and one big compartment (two thirds) by a mesh. The smaller compartment contained the heating elements (a coil heater and a heating chamber), a submersible water pump for mixing and an air stone for aeration, while the larger compartment housed the fish. A 300 W coil heater was placed inside a custom-made cylindrical steel heating chamber, which was connected to the water pump (Eheim compactON 1000 aquarium pump) for even heat distribution. The water pump was set to a minimum level, so fish did not have to swim actively. A larger box (41 × 30 × 25 cm; ~23 L) and a 500 W heater (Aqua Medic TH-500) were used for species with body sizes over 100 mm. The number of fish per trial ranged between 3 and 20 depending on species size and availability (Table S1).

To start the test, all fish from one tank were placed into the arena and allowed to habituate for 10 min at the experimental temperature. Thereafter, the trial was started by plugging in the heater and the water temperature gradually increased at a rate of 0.3°C min^{-1} (thermal ramping curves and rates shown in Figure S2 and Table S2). To avoid observer bias, one person observed the fish and identified LOE blinded from the thermometer (Holman et al. 2015), while another person recorded the time, temperature, and ramping rate (Testo-112 Digital Thermometer, Lenzkirch, Germany) (Raby et al. 2025). The CT_{max} arena was drained and refilled between trials. Pilot trials were run to define species' LOE and were performed by the same observer for all trials of a given species.

At LOE, the CT_{max} was recorded, and each fish was immediately transferred to a labeled jar with water at the original experiment temperature for recovery. After monitoring survival for 30 min, fish were lightly anesthetized (using 0.25 g/L Tricaine mesylate, MS222) to measure total length (mm), mass (g), and, when possible, life stage, and sex. The order of CT_{max} trials was randomized across treatments and performed during daytime.

2.5 | Data Analysis

All data analyses were conducted in R (v 4.4.2, R Core Team 2024). Linear mixed-effect models were fitted using the *lme4* package (Bates et al. 2015). The packages *dplyr* and *ggplot2* (Wickham 2016) were used for data wrangling and visualization, and *emmeans* was used to obtain estimated marginal means and pairwise contrasts.

2.5.1 | Upper Thermal Tolerance Across Species

CT_{max} was analyzed using a linear mixed-effects model with species, treatment group (Ambient vs. Heatwave), and their interaction as fixed effects, and CT_{max} trial as a random effect: lmer(ctmax ~ species × group + (1|trial)).

This model tested: (i) differences in Ambient CT_{max} among species (species effect), (ii) the overall effect of acclimation to elevated temperature (group effect), and (iii) species-specific differences in acclimation capacity (species × group interaction). Fish from the same tank were tested together within a CT_{max} trial for consistent thermal exposure within trials. Trial identity was included as a random effect to account for potential nonindependence among individuals. Due to complete mortality of *Gadus morhua* during exposure to the Heatwave treatment, CT_{max} was only measured for Ambient conditions for this species, and it was excluded from within-species acclimation contrasts. Estimated marginal means for each species × group combination and pairwise comparisons were obtained with *emmeans*.

2.5.2 | Upper Thermal Tolerance Across Fish Families and Habitat Preference Guilds

To explore broad taxonomic patterns in upper thermal tolerance, we conducted additional analyses using species as the unit of replication. First, species-level CT_{max} (estimated marginal means from the mixed-effects model) for Ambient and Heatwave treatments were analyzed as a function of family (taxonomic level) using a linear model (lm(emmean ~ family)), followed by Tukey-adjusted pairwise comparisons.

We also analyzed CT_{max} across functional guilds, grouping species based on habitat preference into juvenile migrants (JM), stationary specialists (SS), and shallow-water generalists (Perry et al. 2018). Given the limited number of species per category (1–3), these analyses were considered exploratory.

2.5.3 | Acclimation Responses Across Species

Acclimation capacity was quantified using thermal tolerance gain (TTgain), defined as the increase in thermal tolerance following acclimation (Fangue et al. 2014). For each species:

$$TTgain_{species} = \text{mean } CT_{max,Heatwave} - \text{mean } CT_{max,Ambient}$$

To compare short-term acclimation capacity among species, we calculated the acclimation response ratio (ARR), which expresses the change in CT_{max} per °C of change in acclimation temperature (Morley et al. 2019). For each species:

$$ARR_{species} = \left(\text{mean } CT_{max,Heatwave} - \text{mean } CT_{max,Ambient}\right) / 4$$

where mean $CT_{max,\ Heatwave}$ and mean $CT_{max,\ Ambient}$ are the estimated marginal means for each species and treatment obtained from the mixed-effects model and 4°C is the difference between treatments (23°C–19°C).

To visualise within-species variation in acclimation responses, we also calculated an individual-level ARR for fish exposed to the Heatwave treatment as follows:

$$ARR_{individual} = \left(CT_{max,Heatwave,individual} - \text{mean } CT_{max,Ambient,Species}\right) / 4$$

where "mean $CT_{max,\ Ambient,\ Species}$" is the species' ambient CT_{max} baseline estimated as the marginal mean from the mixed-effects model. Negative ARR values were set to zero as they indicate no measurable acclimation capacity.

2.5.4 | Eelgrass Summer Temperatures and Fish Distribution Ranges

To provide biogeographic context for the experimental results, thermal regimes of eelgrass habitats were compared with species-specific thermal distribution ranges and illustrated in Figure 3B. A reference eelgrass meadow with publicly available in situ sea temperature time-series data was selected for illustrating fine-scale habitat variability. It was located outside the Tjärnö Marine Laboratory, 72 km northwest from Kristineberg (58.87877 N, 11.13467 E), with a logger at 1.5 m depth, recording temperature in 5-min intervals (https://snd.se/en/catalogue/dataset/2024-45; Jahnke et al. 2024). This site is shallower and more sheltered than Kristineberg (1–4 m depth) and therefore experiences higher temperatures than the fish collection site.

For 1 June to 30 September (2020–2023), negative values were filtered and data were aggregated to daily maximum temperature. For each day of the year, multiyear means and the minimum and maximum of daily maxima were calculated. The warmest period in the season was identified, and corresponding multiyear mean, minimum, and maximum of daily maxima were used to define the thermal range of the reference eelgrass meadow. For each fish species, thermal limits (preferred and absolute) were obtained from AquaMaps' defined native ranges and environmental envelopes via FishBase. AquaMaps derive species-specific temperature envelopes from occurrence records (GBIF, OBIS) and expert-defined distributional ranges (https://www.aquamaps.org/; Kaschner et al. 2019).

2.5.5 | Upper Thermal Tolerance and Thermal Ranges

The relationship between species' maximum range temperature and their mean CT_{max} (after acclimation to 19°C) was explored using Pearson's correlation and simple linear regression.

2.5.6 | Thermal Variability, Warming Trends, and Marine Heatwaves

To investigate longer trends in local summer temperatures, we used in situ measurements of sea temperature from the Kristineberg weather station (https://www.weather.loven.gu.se/kristineberg/en/), at 1 m depth in 5-min intervals available for 1996–2024, except 1997 and 2001–2006. Data from the 1 June to the 30 September (referred to as "summer") were aggregated to daily maxima and used to calculate decadal averages. Trends in annual summer maxima were calculated with linear regression.

A 30-year climatology baseline is required for standard marine heatwave detection (Smith et al. 2025). Satellite-derived daily mean sea surface temperature (SST) was therefore obtained from the NOAA Optimum Interpolation Sea Surface Temperature version 2.1 (NOAA OISST; Huang et al. 2024; Reynolds et al. 2007), which has a spatial resolution of 0.25° (27 km) and extends back to 1982. Data were extracted for the grid cell nearest Kristineberg (58.125° N, 11.375° E). For 1 January 1982 to 31 December 2024, temporal trends were modeled with linear regression. Marine heatwave frequency and cumulative intensity (°C and days) for each year were estimated using the *heatwaveR* package (Schlegel and Smit 2018), following the definition from Hobday et al. (2016), with a 30-year climatology baseline record (1982–2011). Marine heatwave frequency was modeled using a Poisson Generalized Linear Model (GLM) with robust (HC1) confidence intervals. Marine heatwave annual cumulative intensity (the sum of daily sea temperature anomalies across heatwave days within a year (°C·days); Oliver et al. 2018) was modeled using a Gamma GLM with a log link and robust confidence intervals, with a log-transformed linear model and Newey-West correction when it did not converge. All trends were expressed per decade.

Finally, to assess if the long-term data sets were representative of eelgrass habitats, in situ daily SST means from Kristineberg and satellite SSTs were compared to in situ daily means from the reference eelgrass meadow in Tjärnö (described above) for the summers 2020–2023. Agreement among datasets was evaluated using Pearson correlations, mean bias, and root-mean-square error (RMSE).

3 | Results

3.1 | Upper Thermal Tolerance (CT_{max}) Across Species and Families

A linear mixed-effects model revealed strong effects of species ($F = 123.23$, $p < 0.001$) and temperature treatment ($F = 540.91$, $p < 0.001$) on CT_{max}, as well as a significant species × treatment interaction ($F = 10.96$, $p < 0.001$), indicating pronounced interspecific differences in upper thermal tolerance and species-specific responses to short-term warming. Subsequent analyses using estimated marginal means are presented below.

3.1.1 | Acclimation to 19°C

Under acclimation to 19°C, CT_{max} differed significantly among species ($F = 94.3$, $p < 0.001$; Figure 1; Table S4). Estimated marginal mean CT_{max} ranged from 27.8 in *Gadus morhua* to 33.4°C in *Syngnathus typhle*. Juvenile gadids (Gadidae) exhibited

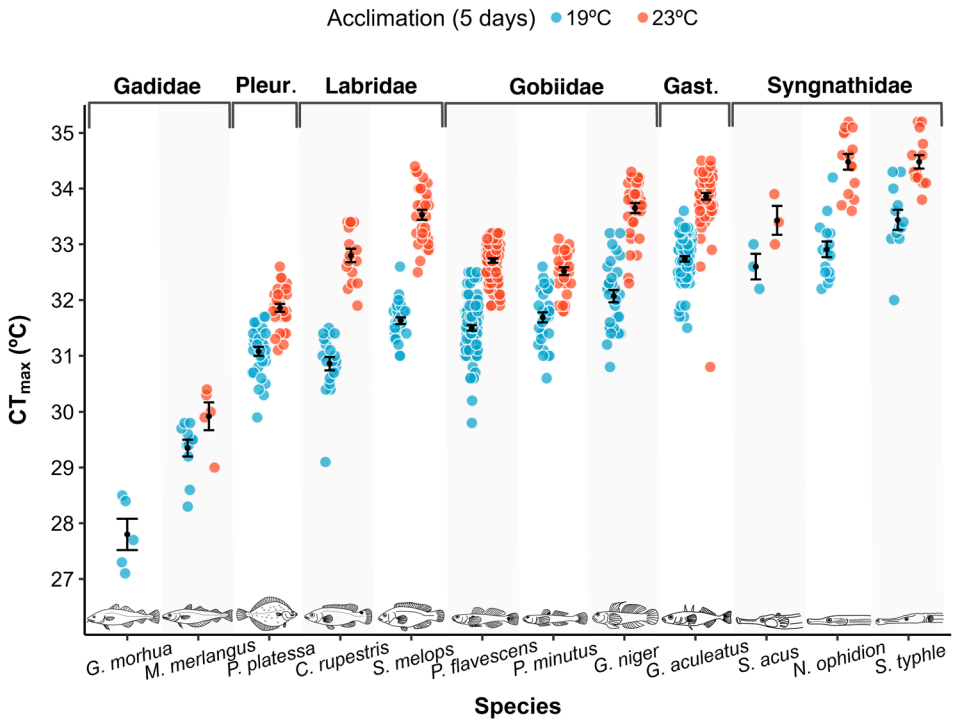

FIGURE 1 | Upper thermal tolerance (CT_{max}) of 12 eelgrass-associated fish species following 5 days of acclimation to 19°C (Ambient; blue) or 23°C (Heatwave; orange). Colored points represent individual CT_{max} measurements and are jittered horizontally for clarity. Black points and error bars indicate species means ± SE. *Y*-axis values show temperature in °C; *X*-axis values are shortened species names (left to right): *Gadus morhua; Merlangius merlangus; Pleuronectes platessa; Ctenolabrus rupestris; Symphodus melops; Pomatoschistus flavescens; Pomatoschistus minutus; Gobius niger; Gasterosteus aculeatus; Syngnathus acus; Nerophis ophidion; Syngnathus typhle*. Among families, Gast. = Gasterosteidae; Pleur. = Pleuronectidae.

the lowest thermal tolerance, followed by juvenile plaice and wrasses, whereas gobies, sticklebacks, and pipefishes showed higher CT_{max} values, with pipefishes (Syngnathidae) representing the most heat-tolerant family.

3.1.2 | Acclimation to 23°C

Under acclimation to 23°C, CT_{max} also differed significantly among species ($F = 71.51$, $p < 0.001$; Figure 1; Table S3). All juvenile *G. morhua* and 58.3% of the juvenile whiting (*M. merlangus*) died during the exposure period prior to CT_{max} testing (Table S4). Among surviving fish, whiting exhibited the lowest CT_{max} (29.9°C), whereas pipefishes reached values up to 34.5°C. The relative ranking of species under 23°C broadly mirrored that observed at 19°C, although the gobies *P. flavescens* and *P. minutus* displayed slightly lower CT_{max} than the wrasses *C. rupestris* and *S. melops*.

3.1.3 | Family-Level and Habitat-Preference Guilds

An exploratory family-level analysis indicated differences in CT_{max} under both Ambient (linear model, $F = 15.11$, $p < 0.01$; Table S5) and Heatwave conditions (linear model, $F = 8.80$, $p < 0.05$; Table S6). Gadidae showed substantially lower CT_{max} (28.6°C ± 0.4°C, mean ± SE) than all other families, whereas Gasterosteidae and Syngnathidae were the most heat tolerant (≈33°C). Pleuronectidae, Labridae, and Gobiidae showed intermediate mean CT_{max} levels, with comparatively small and nonsignificant differences among these families. These patterns were also reflected when species were grouped by habitat preference, with CT_{max} differing significantly among guilds at Ambient ($F_{2,8} = 9.63$, $p = 0.007$) and Heatwave ($F_{2,8} = 12.35$, $p = 0.004$) conditions. Juvenile migrants (including cod, whiting and plaice) showed lower CT_{max} than stationary specialists (pipefishes), while shallow-water generalists (gobies, sticklebacks and wrasses) showed intermediate values.

3.2 | Acclimation Responses Across Species

3.2.1 | Thermal Tolerance Gain (TT_{gain})

Species-specific contrasts revealed significant increases in CT_{max} following the short-term warming for all species with measurements in both treatments (all $p < 0.02$; Table S7). TT_{gain} varied nearly threefold among species, ranging from 0.62°C to 1.94°C (Table S8). The largest gains were observed in *C. rupestris* (1.94°C), *S. melops* (1.89°C), *N. ophidion* (1.58°C), and *G. niger* (1.58°C), whereas juvenile gadids and plaice exhibited comparatively weak responses. No TT_{gain} could be estimated for *G. morhua* due to complete mortality in the Heatwave treatment.

3.2.2 | Acclimation Response Ratio (ARR)

Full thermal acclimation (ARR = 1), equivalent to a 4°C increase in CT_{max}, was not observed in any species after 5 days at 23°C. Species-level ARR values derived from estimated marginal means ranged from 0.13 to 0.48, showing partial but variable short-term acclimation capacity among species (Figure 2;

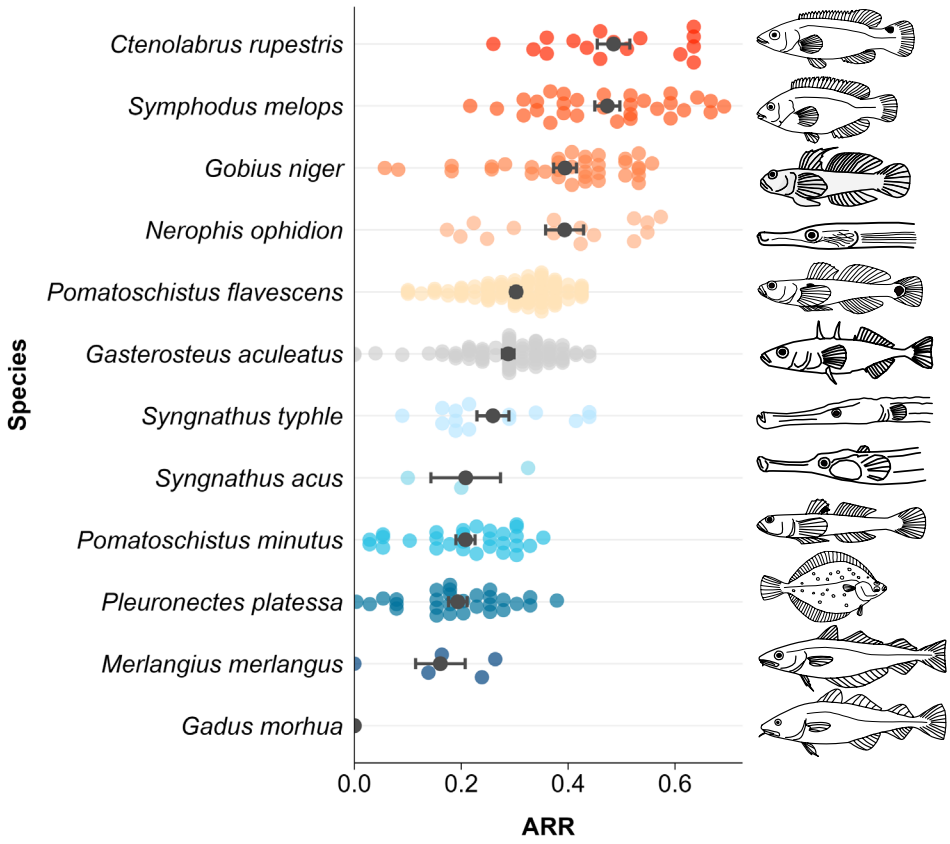

FIGURE 2 | Acclimation response ratio (ARR) following 5 days of exposure to 23°C for 12 eelgrass-associated fish species. Colored points represent individual-level ARR values calculated for fish exposed to 23°C. Black points and error bars show species-level ARR mean ± SE. An ARR of 1.0 represents a complete thermal compensation. *Gadus morhua* did not survive the Heatwave treatment and ARR can therefore not be concluded for this species.

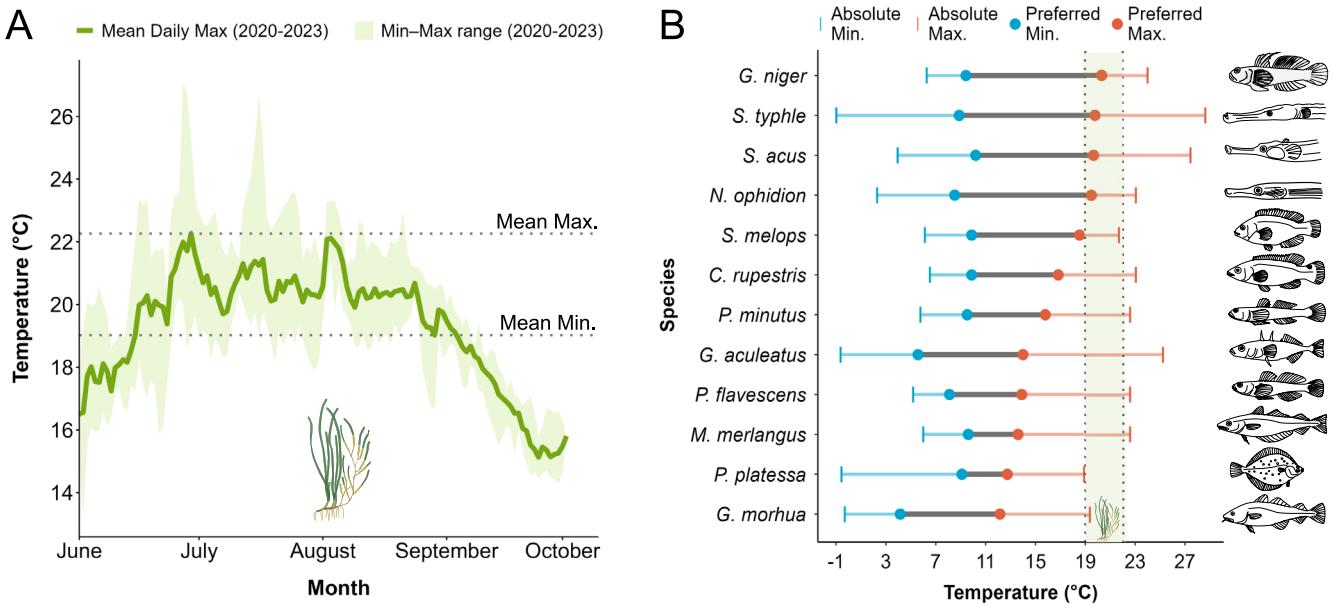

FIGURE 3 | Summer sea temperatures in a temperate eelgrass (*Zostera marina*) meadow and fish species thermal distribution ranges. (A) Daily maximum seawater temperature in an eelgrass meadow at 1.5 m depth during the summer (the 1st of June to the 30th of September, 2020–2023). Green line: mean daily maximum across the four years; Shaded green ribbon: range between minimum and maximum daily maxima across years; Gray dotted horizontal lines: minimum and maximum of the daily mean during the warmest period (the 15th of June to the 1st of September). (B) Thermal distribution ranges of the species ordered by maximum preferred temperatures. Red and blue dots indicate preferred maximum and minimum temperatures, respectively, while the gray segment indicates preferred temperature ranges. Red and blue ticks indicate absolute maximum and minimum temperatures, respectively. Vertical gray dotted lines at 19°C and 22°C highlight the current temperatures in eelgrass relating to panel A.

Table S8). Species exhibiting the highest ARR were primarily wrasses and sedentary taxa, whereas juvenile gadids and flatfish had the lowest values. Individual-level ARR values showed substantial within-species variation (Figure 2). Most individuals displayed positive acclimation responses, although some exhibited ARR values near zero, indicating no measurable increase in CT_{max}. No ARR could be reported for *G. morhua*.

3.3 | Eelgrass Summer Temperatures and Fish Distribution Ranges

Temperature records from the reference eelgrass meadow at Tjärnö revealed that the warmest seawater conditions occurred from 15 June to 1 September, when daily maximum temperatures averaged 20.5°C, ranged between 19.0°C and 22.3°C, and frequently approached or exceeded 23°C (Figure 3A). Over the full summer period (1 June to 30 September), daily maximum temperatures followed a clear seasonal pattern, averaging 19.3°C and ranging from 15.1°C to 22.3°C (Figure 3A), showing that this shallower eelgrass meadow reached extremes close to the treatments tested in the laboratory.

The species tested had substantially different thermal niches (Figure 3B). Most occupied broad thermal ranges spanning approximately 5°C–23°C, while some taxa, including the three-spined stickleback and broadnosed pipefish, exhibited wider ranges extending to 25°C–28°C. In contrast, cod and plaice were restricted to cooler thermal environments, with their thermal envelopes having upper distribution limits around 19°C (Figure 3B).

For several species, preferred temperature maxima were below present summer temperatures measured in the reference eelgrass habitat. Juvenile cod, whiting, plaice, two-spotted goby, three-spined stickleback, sand goby, and goldsinny wrasse, showed preferred temperatures in the range of ≈12°C–18°C, despite absolute maxima indicating persistence at higher temperatures. In contrast, corkwing wrasse, pipefishes, and black goby exhibited preferred temperatures within or above the summer range of regional eelgrass (≈19°C–21°C), with some species occupying waters exceeding 24°C (Figure 3B).

3.4 | Upper Thermal Tolerance and Thermal Ranges

Mean CT_{max} increased with the absolute maximum temperatures experienced across species' geographic distributions ($R^2 = 0.489$, $p < 0.05$; Figure 4), indicating a moderate positive relationship in which species from warmer environments exhibited higher upper thermal limits.

3.5 | Thermal Variability, Warming Trends, and Marine Heatwaves

Long-term in situ measurements at Kristineberg (the fish collection site) indicated substantial warming of summer seawater temperatures between 1996 and 2024, with annual daily maximum temperatures increasing by 2.6°C, equivalent to 0.92°C per decade (0.092°C year^{-1}; 95% CI: 0.014°C–0.170°C year^{-1}; $R^2 = 0.23$, $p < 0.05$;

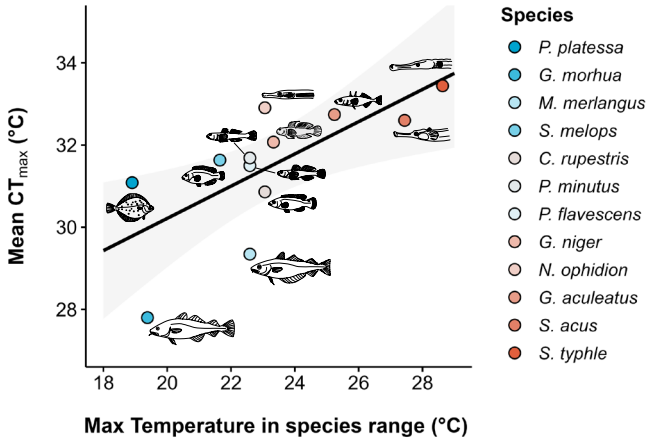

FIGURE 4 | Relationship between species' mean CT_{max} (at 19°C) and maximum temperatures of its predicted environmental envelope (AquaMaps; Kaschner et al. 2019). Each point represents the mean critical thermal maximum (CT_{max}) for a species under ambient conditions, with colors distinguishing species. The black line shows the fitted linear regression (±95% confidence interval in gray), indicating a positive association between CT_{max} and range maximum temperature.

Figure 5A). Seasonal patterns showed progressive warming from early June to late July or early August, followed by cooling through September. Decadal comparisons revealed that the most recent period (2020–2024) experienced the highest daily maxima, frequently exceeding 20°C and occasionally surpassing 23°C.

Daily mean eelgrass temperatures were consistently higher than those measured at the dock or estimated from satellite data during summer (2020–2023; Figure 5B). Eelgrass temperatures exceeded Kristineberg's measurements by an average of 0.67°C, and satellite-derived SST by 1.76°C, with both offsets being statistically significant (one-sample *t*-tests on paired daily differences: $p < 0.001$ in both cases). Satellite SST showed a systematic cool bias relative to both in situ measurements (dock: −1.09°C, RMSE = 1.45°C; eelgrass: −1.76°C, RMSE = 2.25°C), although temporal variability was captured reasonably well (Pearson $r = 0.86$ for satellite vs. dock; $r = 0.75$ for satellite vs. eelgrass). Differences between eelgrass and satellite temperatures frequently exceeded 4°C and reached a maximum of 5.82°C, indicating that satellite SST substantially underestimates thermal extremes in shallow eelgrass meadows.

Satellite-derived SST further revealed a significant long-term warming in the summers and increasing marine heatwaves at Kristineberg between 1982 and 2024. Mean summer SST increased by 0.42°C per decade (95% CI 0.29–0.56; $p < 0.001$; Figure 5C). Marine heatwave frequency increased by 49% per decade (95% CI 28–73; $p < 0.001$; Figure 5D), corresponding to an additional 1.02 events per decade (95% CI 0.65–1.39; $p < 0.001$). Annual cumulative marine heatwave intensity increased by 116% per decade (95% CI 49–212; $p < 0.001$; Figure 5E), equivalent to 48.6°C·days per decade (95% CI 26.6–70.7; $p < 0.001$; Figure 5E), indicating a marked rise in total thermal exposure associated with marine heatwaves. Peak marine heatwave intensity reached up to 6.8°C above the seasonal climatology (1982–2011), demonstrating that thermal anomalies exceeding +4°C already occur in the study region. Maximum absolute temperatures in the long-term satellite record gridded at

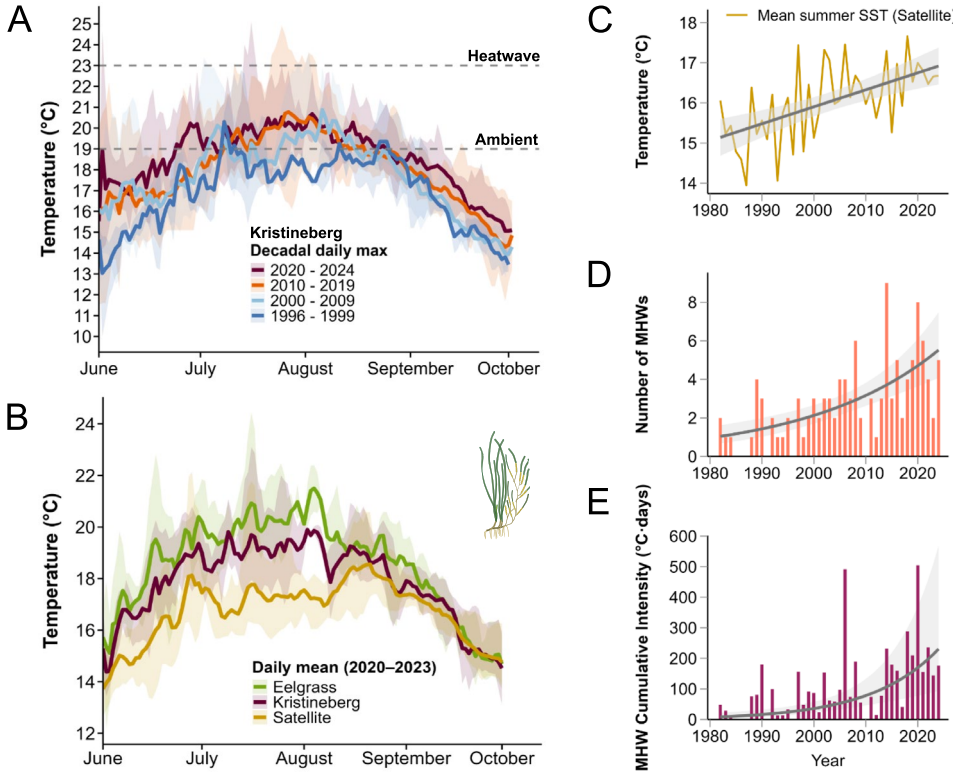

FIGURE 5 | Long-term summer sea surface temperature (SST) and marine heatwaves at Kristineberg (1982–2024). (A) Daily maximum SST at 1 m depth at Kristineberg (1 June to 30 September), grouped by decade: 1996–1999 (dark blue), 2000–2009 (light blue), 2010–2019 (orange), and 2020–2024 (purple-red). Thin lines represent individual years; thick lines represent decadal means, and shaded ribbons show the interannual minimum–maximum range. Dashed horizontal lines indicate experimental temperature treatments ("Ambient" and "Heatwave"). (B) Daily mean SST (2020–2023) measured in situ within an eelgrass meadow at 1.5 m depth (Tjärnö; green), at the dock at 1 m depth at Kristineberg (purple-red), and from satellite SST (yellow). Shaded ribbons indicate the interannual minimum-maximum range. (C) Mean summer SST by year derived from satellite data, with linear trend and 95% CI; warming rate = 0.42°C·per decade (95% CI 0.29–0.56). (D) Annual frequency of marine heatwaves (MHWs) with fitted temporal trend and 95% CI; change = 49%·per decade (95% CI 28–73); (E) Annual cumulative MHW intensity with fitted temporal trend and 95% CI; change = 116%·per decade (95% CI 49–212).

Kristineberg reached 22.4°C, while in situ measurements from the reference eelgrass meadow frequently approached or exceeded 23°C during summer. Together, these observations indicate that the experimental heatwave was consistent with both regional anomalies and locally observed thermal extremes on the Swedish west coast.

4 | Discussion

This study provides the first comparative assessment of upper thermal tolerance and short-term acclimation capacity across multiple eelgrass-associated fish species, linking experimental physiology with regional warming and marine heatwave trends. Following a 5-day simulated heatwave, we found large differences in acute upper thermal tolerance and acclimation response ratio (ARR) across 12 fish species inhabiting summer eelgrass meadows on the Swedish West Coast. Although most species increased their CT_{max}, the magnitude of acclimation differed markedly. Cold-water juvenile migrants (e.g., Atlantic cod, whiting, and plaice) exhibited low acclimation capacity and high mortality during the heatwave, whereas warm-tolerant generalists and more sedentary species (e.g., three-spined stickleback, black goby, goldsinny wrasse, and corkwing wrasse) showed higher tolerance and greater plasticity.

Importantly, regional eelgrass meadows experienced summer temperatures that approach or exceed the preferred thermal ranges of several species studied. Juvenile gadids and flatfishes appear to occupy the warm edge of their thermal distributions when using eelgrass meadows and adjacent sandflats. Given their limited capacity for rapid acclimation, these populations appear most vulnerable to exclusion from these habitats during intensifying heatwaves and may increasingly rely on behavioral habitat shifts to avoid short-term thermal stress. In contrast, wrasses exhibited the strongest acclimation responses, whereas pipefishes showed the highest innate thermal tolerance.

All species showed CT_{max} values that exceeded the maximum temperatures of their modeled ecological thermal ranges (AquaMaps, Fishbase). This distinction was expected, as CT_{max} represents an acute physiological failure threshold, whereas thermal ranges reflect long-term physiological and ecological constraints shaped by performance, behavior and species interactions. In this context, ARR provided a comparative measure of the differences in short-term plasticity among species. As the experimental heatwave lasted 5 days, individuals may not have reached full acclimation, and additional gains in ARR could occur during prolonged heatwaves (De Bonville et al. 2025). Together, these findings suggest that

intensifying marine heatwaves are likely to reshape eelgrass fish assemblages through differential physiological vulnerability in local populations and potential thermal exclusion from certain microhabitats.

4.1 | Warming Eelgrass Habitats

During summer, temperatures at the fish collection site remained below the experimental heatwave but approached the maximum preferred temperatures of the distribution range of several species. Long-term satellite-derived SST (1982–2025) and in situ records at Kristineberg showed increasing warming trends and marine heatwave intensity on the Swedish west coast. We detected a local ocean warming rate of ~0.42°C per decade, comparable to the rate for the North Sea (~0.38°C per decade, Mohamed et al. 2025), which itself is nearly four times higher than the global ocean average (~0.13°C per decade since 1982; Calvin et al. 2023; Von Schuckmann et al. 2024). Marine heatwave frequency and cumulative intensity also increased, with a cumulative intensity change of 48.6°C·days per decade, which is about 10 times stronger than in the full basin at 4.23°C·days per decade (Mohamed et al. 2025). Together, these results indicate substantial warming of nearshore coastal habitats.

Satellite-derived data underestimated nearshore temperatures by approximately 1°C–3°C on average, and up to 4°C–5°C during thermal extremes. This is consistent with previous research showing that satellite products capture broad temporal variability reasonably well, but systematically underestimate thermal extremes in shallow habitats with restricted water exchange (Pearce et al. 2006; Phinn et al. 2018; Smale and Wernberg 2009). In eelgrass meadows, microhabitat conditions such as depth and hydrodynamics shape thermal exposure and can amplify temperature extremes (Hattich et al. 2025; Starko et al. 2024). Such variability can disproportionately affect organismal performance relative to changes in mean temperature (Vasseur et al. 2014), while also providing opportunities for behavioral thermoregulation and refugia (Sunday et al. 2019). Consequently, the ecological impacts of marine heatwaves are likely to depend strongly on fine-scale habitat heterogeneity.

Shallow, sheltered eelgrass meadows often experience higher thermal variability and more frequent extremes than more exposed sites (Hattich et al. 2025). This pattern was evident in our reference eelgrass meadow, where summer temperatures frequently reached 22°C–23°C. As eelgrass meadows are rarely monitored at fine spatial scales, such extremes are likely underestimated in regional datasets. As a result, these important nursery habitats may experience more severe warming and marine heatwaves than suggested by coarse resolution observations.

4.2 | Species-Specific Vulnerability to Marine Heatwaves

Species living close to their upper thermal distribution range limits showed the weakest short-term acclimation capacity and the greatest vulnerability to the simulated heatwave. Juvenile Atlantic cod suffered complete mortality at 23°C, while juvenile whiting showed high mortality and negligible acclimation despite higher survival. These results indicate that these juveniles may already live near their upper thermal limits and have little scope for additional warm acclimation (Ern et al. 2023; Jutfelt et al. 2024). However, while 23°C exceeded survivable conditions in this experiment, this does not imply a lack of acclimation capacity at lower temperatures (Leeuwis et al. 2025; Norin et al. 2019).

Atlantic cod and whiting are cold-temperate demersal fishes whose juveniles (0–2 years) rely on shallow coastal nursery habitats, shelter, and foraging (Heck Hay et al. 2003). Juvenile cod typically prefer temperatures below ~16°C and actively avoid warmer conditions through vertical migration (Bjornsson 2001; Claireaux et al. 1995; Freitas et al. 2016; Staveley et al. 2017), with similar preferences observed in whiting (Asciutto et al. 2024; Calì et al. 2023). Our temperature analysis shows that eelgrass meadows routinely exceed these thresholds during summer, suggesting that juvenile gadids in the region may already avoid shallow eelgrass habitats during warm periods. Continued warming is likely to intensify such habitat exclusion, potentially reducing access to essential nursery areas (Freitas et al. 2016). Given that these species are also commercially important and undergoing distributional shifts (Engelhard et al. 2014; Perry et al. 2005), limited short-term acclimation capacity may further constrain their persistence in warming coastal habitats. Juvenile European plaice showed higher thermal tolerance than juvenile gadids but low short-term acclimation capacity, indicating limited physiological buffering against thermal extremes. This pattern aligns with previous work on juvenile flatfish (De Bonville et al. 2025) and suggests greater reliance on habitat shifting or substrate burial (Ziegler and Frisk 2019).

In contrast, shallow-water habitat generalists such as gobies and sticklebacks displayed comparatively high thermal tolerance and moderate acclimation capacity, consistent with their broader habitat use and previous estimates (Cowan et al. 2023; De Bonville et al. 2025; Mottola et al. 2022). These generalist species are among the most abundant fishes in eelgrass habitats and play key ecological roles as intermediate predators (Perry et al. 2018; Staveley et al. 2017). Three-spined sticklebacks, in particular, have increased in abundance under warming and eutrophication (Olin et al. 2022), while black gobies were the most heat tolerant and plastic gobies, suggesting these two species may benefit from ongoing environmental change.

Wrasses exhibited intermediate upper thermal tolerance, but the strongest short-term acclimation capacity, consistent with previous findings (De Bonville et al. 2025) and their broad thermal niches and habitat flexibility across rocky reefs and seagrass meadows. Previous studies have documented strong plasticity and high performance in wrasses at temperatures exceeding those currently experienced in northern regions (Palma et al. 2025; Yuen et al. 2019), although they may still experience stress under multiple environmental stressors (Perry, Tamarit, Morgenroth, et al. 2024).

Pipefishes showed the highest thermal tolerance but only moderate acclimation capacity. As relatively sedentary habitat specialists (Castejón-Silvo et al. 2021), they may rely more on physiological tolerance than behavioral avoidance. The three

tested species all had preferred thermal maxima well above the simulated heatwave, and they are undergoing a northwards distribution range shift due to climate change (Monteiro et al. 2023). Their high thermal tolerance suggests they may persist in warming eelgrass meadows, although limited plasticity could constrain responses to extreme events.

4.3 | Interpreting CT_{max} and Short-Term Acclimation in an Ecological Context

Interspecific differences in CT_{max} and ARR may partly reflect reduced gains in thermal tolerance as species approach their upper physiological limits (Brett 1952; Doudoroff 1942; Fangue et al. 2014; Sandblom et al. 2016). Across the species studied, cold-affinity species occur near their upper range limits during summer, while warm-tolerant species occupy conditions within their modeled thermal optima. Theoretically, species or populations living above their optimal temperature have limited scope for further acclimation, whereas species living below their optimum retain greater plasticity (Ern et al. 2023). This likely explains the weak acclimation observed in our juvenile gadids and flatfishes, but it does not fully account for all patterns observed in the current study.

CT_{max} represents an acute upper thermal limit under rapid warming and does not directly predict tolerance to marine heatwaves, which involve longer exposure and can induce cumulative or sublethal effects (Ern et al. 2023; Rezende et al. 2014). As the impact of any stress depends both on intensity and duration, it remains unclear if individuals with high tolerance to fast warming are also highly tolerant to slow warming (Åsheim et al. 2020). Slow ramping during high temperatures may decrease the thermal safety margin, potentially due to more accumulation of thermal injury (Åsheim et al. 2020; Ern et al. 2023). While some species increased thermal tolerance after the simulated heatwave, the extent to which repeated heatwaves enhance resilience or lead to cumulative stress remains unresolved. We observed partial retention of elevated thermal tolerance in *Symphodus melops* exposed to a heatwave and then returned to control temperature (Figure S3), losing more than half of the gain in CT_{max}. Such rapid loss of warm acclimation could indicate that "memory" of an earlier heatwave would only marginally benefit tolerance during subsequent heatwaves, unless they were very close in time. Together, these findings highlight that the ecological relevance of CT_{max} and ARR depends on both temporal scale and environmental context.

Mean CT_{max} increased with the maximum temperatures from the species' modeled environmental envelopes (AquaMaps), although this relationship was moderate ($R^2 = 0.49$), indicating substantial unexplained variation. Global analyses show that thermal limits are broadly associated with environmental extremes, but do not fully determine species distributions (Sunday et al. 2019). Finally, as the studied species represented co-occurring populations exposed to a shared local thermal environment, population-level variation and local adaptation may further contribute to interspecific differences, as documented in coastal fish populations in the Skagerrak (Faust et al. 2021; Green et al. 2023; Henriksson et al. 2023; Leder et al. 2021; Perry, Tamarit, Sundell, et al. 2024).

4.4 | Eelgrass Fish Assemblages Under Warming

Differential thermal tolerance and short-term acclimation capacity among fishes occupying eelgrass meadows suggest that warming will influence species composition and relative abundance within these communities. Species living near the warm edge of their distribution range (e.g., juvenile gadids) may become excluded from eelgrass nurseries during warm periods, whereas thermally tolerant generalist species may be favored. Declines in top predators and increases in mesopredatory fishes have already been documented in the Baltic Sea and on the Swedish West Coast (Baden et al. 2012; Olin et al. 2022). Globally, warming seagrass ecosystems show increasing dominance of warm-affinity species and poleward or depth distribution shifts, as well as ecosystem reorganization (Burrows et al. 2019; Casini et al. 2009; Cheung et al. 2013; Fodrie et al. 2010; Frank et al. 2005; Olin et al. 2022).

To conclude, our study demonstrates that eelgrass-associated fishes differ markedly in upper thermal tolerance and short-term acclimation capacity, while showing that fine-scale habitat variability can expose individuals to higher thermal extremes than predicted by regional datasets. These combined effects are likely to drive shifts in eelgrass fish assemblages by favoring thermally tolerant species and constraining those living near their thermal limits.

Author Contributions

Elena Tamarit-Castro: conceptualization, investigation, funding acquisition, writing – original draft, methodology, validation, visualization, writing – review and editing, formal analysis, resources, project administration, data curation, software. **Felix Steinbrecher:** investigation, methodology, writing – review and editing. **Leon Pfeufer:** investigation, writing – review and editing. **Emily R. Lechner:** investigation, writing – review and editing. **Hannah Sauer:** investigation, writing – review and editing. **Leon Green:** writing – review and editing, validation, resources. **Diana Perry:** writing – review and editing, validation, resources, supervision. **Hans W. Linderholm:** writing – review and editing, validation, funding acquisition, supervision, resources. **Martin Gullström:** writing – review and editing, validation, funding acquisition, supervision, resources. **Fredrik Jutfelt:** writing – review and editing, supervision, resources, methodology, conceptualization, validation.

Acknowledgments

We are grateful to Jelena Lewin for assistance in the laboratory, to Sara Forsberg for help with fieldwork, and to Joachim Sturve for lending tanks. We thank Kristineberg Marine Research Station and its staff for access to excellent infrastructure and work environment. We thank the editor and two anonymous reviewers for their insightful feedback.

Funding

This work was supported by the Center for Sea and Society at the University of Gothenburg, Department of Earth Sciences at the University of Gothenburg, Birgit och Birger Wåhlströms Stiftelse, and Rådman och Fru Ernst Collianders Stiftelse.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and scripts supporting this study are openly available in Zenodo at: 10.5281/zenodo.20356752.

References

Asciutto, E., F. Maioli, C. Manfredi, et al. 2024. "Spatio-Temporal Patterns of Whiting (*Merlangius merlangus*) in the Adriatic Sea Under Environmental Forcing." *PLoS One* 19, no. 3: e0289999. https://doi.org/10.1371/journal.pone.0289999.

Åsheim, E. R., A. H. Andreassen, R. Morgan, and F. Jutfelt. 2020. "Rapid-Warming Tolerance Correlates With Tolerance to Slow Warming but Not Growth at Non-Optimal Temperatures in Zebrafish." *Journal of Experimental Biology* 223, no. 23: jeb229195. https://doi.org/10.1242/jeb.229195.

Baden, S., A. Emanuelsson, L. Pihl, C. Svensson, and P. Åberg. 2012. "Shift in Seagrass Food Web Structure Over Decades Is Linked to Overfishing." *Marine Ecology Progress Series* 451: 61–73. https://doi.org/10.3354/meps09585.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67: 1–48. https://doi.org/10.18637/jss.v067.i01.

Beck, M. W., K. L. Heck, K. W. Able, et al. 2001. "The Identification, Conservation, and Management of Estuarine and Marine Nurseries for Fish and Invertebrates: A Better Understanding of the Habitats That Serve as Nurseries for Marine Species and the Factors That Create Site-Specific Variability in Nursery Quality Will Improve Conservation and Management of These Areas." *Bioscience* 51, no. 8: 633–641. https://doi.org/10.1641/0006-3568(2001)051[0633:TICAMO]2.0.CO;2.

Beitinger, T. L., W. A. Bennett, and R. W. McCauley. 2000. "Temperature Tolerances of North American Freshwater Fishes Exposed to Dynamic Changes in Temperature." *Environmental Biology of Fishes* 58, no. 3: 237–275. https://doi.org/10.1023/A:1007676325825.

Bertelli, C. M., J. C. Bull, L. C. Cullen-Unsworth, and R. K. F. Unsworth. 2021. "Unravelling the Spatial and Temporal Plasticity of Eelgrass Meadows." *Frontiers in Plant Science* 12: 664523. https://doi.org/10.3389/fpls.2021.664523.

Bilyk, K. T., and A. L. DeVries. 2011. "Heat Tolerance and Its Plasticity in Antarctic Fishes." *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* 158, no. 4: 382–390. https://doi.org/10.1016/j.cbpa.2010.12.010.

Bjornsson, B. 2001. "Optimal Temperature for Growth and Feed Conversion of Immature Cod (*Gadus morhua* L.)." *ICES Journal of Marine Science* 58, no. 1: 29–38. https://doi.org/10.1006/jmsc.2000.0986.

Brett, J. R. 1952. "Temperature Tolerance in Young Pacific Salmon, Genus *Oncorhynchus*." *Journal of the Fisheries Research Board of Canada* 9, no. 6: 265–323. https://doi.org/10.1139/f52-016.

Brijs, J., L. L. Tran, C. Moore, et al. 2025. "Outlasting the Heat: Collapse of Herbivorous Fish Control of Invasive Algae During Marine Heatwaves." *Global Change Biology* 31, no. 8: e70438. https://doi.org/10.1111/gcb.70438.

Burrows, M. T., A. E. Bates, M. J. Costello, et al. 2019. "Ocean Community Warming Responses Explained by Thermal Affinities and Temperature Gradients." *Nature Climate Change* 9, no. 12: 959–963. https://doi.org/10.1038/s41558-019-0631-5.

Burton, T., and S. Einum. 2025. "High Capacity for Physiological Plasticity Occurs at a Slow Rate in Ectotherms." *Ecology Letters* 28, no. 1: e70046. https://doi.org/10.1111/ele.70046.

Calì, F., F. Stranci, M. La Mesa, C. Mazzoldi, E. Arneri, and A. Santojanni. 2023. "Whiting (*Merlangius merlangus*) Grows Slower and Smaller in the Adriatic Sea: New Insights From a Comparison of Two Populations With a Time Interval of 30 Years." *Fishes* 8, no. 7: 341. https://doi.org/10.3390/fishes8070341.

Calvin, K., D. Dasgupta, G. Krinner, et al. 2023. *IPCC, 2023: Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*, edited by Core Writing Team, H. Lee, and J. Romero. (First) Intergovernmental Panel on Climate Change (IPCC). https://doi.org/10.59327/IPCC/AR6-9789291691647.

Casini, M., J. Hjelm, J.-C. Molinero, et al. 2009. "Trophic Cascades Promote Threshold-Like Shifts in Pelagic Marine Ecosystems." *Proceedings of the National Academy of Sciences of the United States of America* 106, no. 1: 197–202. https://doi.org/10.1073/pnas.0806649105.

Castejón-Silvo, I., J. Terrados, T. Nguyen, F. Jutfelt, and E. Infantes. 2021. "Increased Energy Expenditure Is an Indirect Effect of Habitat Structural Complexity Loss." *Functional Ecology* 35, no. 10: 2316–2328. https://doi.org/10.1111/1365-2435.13876.

Cheng, L., J. Abraham, K. E. Trenberth, et al. 2025. "Record High Temperatures in the Ocean in 2024." *Advances in Atmospheric Sciences* 42, no. 6: 1092–1109. https://doi.org/10.1007/s00376-025-4541-3.

Cheung, W. W. L., R. Watson, and D. Pauly. 2013. "Signature of Ocean Warming in Global Fisheries Catch." *Nature* 497: 7449. https://doi.org/10.1038/nature12156.

Claireaux, G., D. M. Webber, S. R. Kerr, and R. G. Boutilier. 1995. "Physiology and Behaviour of Free-Swimming Atlantic COD (*Gadus morhua*) Facing Fluctuating Temperature Conditions." *Journal of Experimental Biology* 198, no. 1: 49–60. https://doi.org/10.1242/jeb.198.1.49.

Claussen, D. L. 1977. "Thermal Acclimation in Ambystomatid Salamanders." *Comparative Biochemistry and Physiology Part A: Physiology* 58, no. 4: 333–340. https://doi.org/10.1016/0300-9629(77)90150-5.

Cowan, Z.-L., A. H. Andreassen, J. De Bonville, et al. 2023. "A Novel Method for Measuring Acute Thermal Tolerance in Fish Embryos." *Conservation Physiology* 11, no. 1: coad061. https://doi.org/10.1093/conphys/coad061.

De Bonville, J., A. H. Andreassen, Z.-L. Cowan, et al. 2025. "Dynamics of Thermal Tolerance Plasticity Across Fish Species and Life Stages." *Journal of Thermal Biology* 127: 104024. https://doi.org/10.1016/j.jtherbio.2024.104024.

Desforges, J. E., K. Birnie-Gauvin, F. Jutfelt, et al. 2023. "The Ecological Relevance of Critical Thermal Maxima Methodology for Fishes." *Journal of Fish Biology* 102, no. 5: 1000–1016. https://doi.org/10.1111/jfb.15368.

Doudoroff, P. 1942. "The Resistance and Acclimatization of Marine Fishes to Temperature Changes. I. Experiments With *Girella nigricans* (Ayres)." *Biological Bulletin* 83, no. 2: 219–244. https://doi.org/10.2307/1538144.

Drost, H. E., M. Lo, E. C. Carmack, and A. P. Farrell. 2016. "Acclimation Potential of Arctic Cod (*Boreogadus saida*) From the Rapidly Warming Arctic Ocean." *Journal of Experimental Biology* 219, no. 19: 3114–3125. https://doi.org/10.1242/jeb.140194.

du Sert, N. P., A. Ahluwalia, S. Alam, et al. 2020. "Reporting Animal Research: Explanation and Elaboration for the ARRIVE Guidelines 2.0." *PLoS Biology* 18, no. 7: e3000411. https://doi.org/10.1371/journal.pbio.3000411.

Engelhard, G. H., D. A. Righton, and J. K. Pinnegar. 2014. "Climate Change and Fishing: A Century of Shifting Distribution in North Sea Cod." *Global Change Biology* 20, no. 8: 2473–2483. https://doi.org/10.1111/gcb.12513.

Ern, R., A. H. Andreassen, and F. Jutfelt. 2023. "Physiological Mechanisms of Acute Upper Thermal Tolerance in Fish." *Physiology* 38, no. 3: 141–158. https://doi.org/10.1152/physiol.00027.2022.

Fangue, N. A., M. A. Wunderly, T. F. Dabruzzi, and W. A. Bennett. 2014. "Asymmetric Thermal Acclimation Responses Allow Sheepshead Minnow *Cyprinodon variegatus* to Cope With Rapidly Changing Temperatures." *Physiological and Biochemical Zoology* 87, no. 6: 805–816. https://doi.org/10.1086/678965.

Faust, E., E. Jansson, C. André, et al. 2021. "Not That Clean: Aquaculture-Mediated Translocation of Cleaner Fish Has Led to Hybridization on the Northern Edge of the Species' Range." *Evolutionary Applications* 14, no. 6: 1572–1587. https://doi.org/10.1111/eva.13220.

Fodrie, F. J., K. L. Heck Jr., S. P. Powers, W. M. Graham, and K. L. Robinson. 2010. "Climate-Related, Decadal-Scale Assemblage Changes of Seagrass-Associated Fishes in the Northern Gulf of Mexico." *Global Change Biology* 16, no. 1: 48–59. https://doi.org/10.1111/j.1365-2486.2009.01889.x.

Frank, K. T., B. Petrie, J. S. Choi, and W. C. Leggett. 2005. "Trophic Cascades in a Formerly Cod-Dominated Ecosystem." *Science* 308, no. 5728: 1621–1623. https://doi.org/10.1126/science.1113075.

Freitas, C., E. M. Olsen, H. Knutsen, J. Albretsen, and E. Moland. 2016. "Temperature-Associated Habitat Selection in a Cold-Water Marine Fish." *Journal of Animal Ecology* 85, no. 3: 628–637. https://doi.org/10.1111/1365-2656.12458.

Fry, F. E. J. 1947. "Effects of the Environment on Animal Activity. Publications of the Ontario Fisheries Research Laboratory, No. 68." In *University of Toronto Studies Biological Series, No. 55*. University of Toronto Press.

Garrabou, J., R. Coma, N. Bensoussan, et al. 2009. "Mass Mortality in Northwestern Mediterranean Rocky Benthic Communities: Effects of the 2003 Heat Wave." *Global Change Biology* 15, no. 5: 1090–1103. https://doi.org/10.1111/j.1365-2486.2008.01823.x.

Gómez-Gras, D., C. Linares, and P. Capdevila. 2025. "Novel Contributions to Marine Heatwave Ecology: Identifying and Addressing Knowledge Gaps in Ecological Impacts." *Journal of Animal Ecology* 94, no. 8: 1481–1491. https://doi.org/10.1111/1365-2656.70084.

Green, L., E. Faust, J. Hinchcliffe, et al. 2023. "Invader at the Edge—Genomic Origins and Physiological Differences of Round Gobies Across a Steep Urban Salinity Gradient." *Evolutionary Applications* 16, no. 2: 321–337. https://doi.org/10.1111/eva.13437.

Gunderson, A. R., and J. H. Stillman. 2015. "Plasticity in Thermal Tolerance Has Limited Potential to Buffer Ectotherms From Global Warming." *Proceedings of the Royal Society B: Biological Sciences* 282, no. 1808: 20150401. https://doi.org/10.1098/rspb.2015.0401.

Hattich, G. S. I., M. Jahnke, S. Enge, et al. 2025. "Small-Scale Thermal Habitat Variability May Not Determine Seagrass Resilience to Climate Change." *Limnology and Oceanography* 70: 2039–2052. https://doi.org/10.1002/lno.70049.

Heck Hay, K., G. Hays, and R. Orth. 2003. "Critical Evaluation of the Nursery Role Hypothesis for Seagrass Meadows." *Marine Ecology Progress Series* 253: 123–136. https://doi.org/10.3354/meps253123.

Helmuth, B., F. Choi, A. Matzelle, et al. 2016. "Long-Term, High Frequency In Situ Measurements of Intertidal Mussel Bed Temperatures Using Biomimetic Sensors." *Scientific Data* 3, no. 1: 160087. https://doi.org/10.1038/sdata.2016.87.

Helmuth, B., B. D. Russell, S. D. Connell, et al. 2014. "Beyond Long-Term Averages: Making Biological Sense of a Rapidly Changing World." *Climate Change Responses* 1, no. 1: 6. https://doi.org/10.1186/s40665-014-0006-0.

Henriksson, S., R. T. Pereyra, M. Sodeland, et al. 2023. "Mixed Origin of Juvenile Atlantic Cod (*Gadus morhua*) Along the Swedish West Coast." *ICES Journal of Marine Science* 80, no. 1: 145–157. https://doi.org/10.1093/icesjms/fsac220.

Hobday, A. J., L. V. Alexander, S. E. Perkins, et al. 2016. "A Hierarchical Approach to Defining Marine Heatwaves." *Progress in Oceanography* 141: 227–238. https://doi.org/10.1016/j.pocean.2015.12.014.

Holman, L., M. L. Head, R. Lanfear, and M. D. Jennions. 2015. "Evidence of Experimental Bias in the Life Sciences: Why We Need Blind Data Recording." *PLoS Biology* 13, no. 7: e1002190. https://doi.org/10.1371/journal.pbio.1002190.

Huang, B., X. Yin, J. A. Carton, et al. 2024. "Record High Sea Surface Temperatures in 2023." *Geophysical Research Letters* 51, no. 14: e2024GL108369. https://doi.org/10.1029/2024GL108369.

Huey, R. B., M. R. Kearney, A. Krockenberger, J. A. M. Holtum, M. Jess, and S. E. Williams. 2012. "Predicting Organismal Vulnerability to Climate Warming: Roles of Behaviour, Physiology and Adaptation." *Philosophical Transactions of the Royal Society B: Biological Sciences* 367, no. 1596: 1665–1679. https://doi.org/10.1098/rstb.2012.0005.

Jahnke, M., P. de Wit, and J. Havenhand. 2024. "High Temporal Resolution Environmental Data From Eelgrass Meadow (Version 1)" [Data Set]. University of Gothenburg. https://doi.org/10.5878/kwxf-d021.

Jutfelt, F., R. Ern, R. H. J. Leeuwis, and T. D. Clark. 2024. "Effects of Climate Warming." In *Encyclopedia of Fish Physiology*, 14–31. Elsevier. https://doi.org/10.1016/B978-0-323-90801-6.00183-X.

Kaschner, K., K. Kesner-Reyes, C. Garilao, J. Rius-Barile, T. Rees, and R. Froese. 2019. *AquaMaps: Predicted Range Maps for Aquatic Species*. World Wide Web Electronic Publication. Version 10/2019. https://www.aquamaps.org.

Leder, E. H., C. André, A. Le Moan, et al. 2021. "Post-Glacial Establishment of Locally Adapted Fish Populations Over a Steep Salinity Gradient." *Journal of Evolutionary Biology* 34, no. 1: 138–156. https://doi.org/10.1111/jeb.13668.

Leeuwis, R. H. J., R. Morgan, A. H. Andreassen, et al. 2025. "Putative Neural and Endocrine Control of Thermal Acclimation in Fish." *Conservation Physiology* 13, no. 1: coaf042. https://doi.org/10.1093/conphys/coaf042.

Lefcheck, J. S., B. B. Hughes, A. J. Johnson, et al. 2019. "Are Coastal Habitats Important Nurseries? A Meta-Analysis." *Conservation Letters* 12, no. 4: e12645. https://doi.org/10.1111/conl.12645.

Lefevre, S., T. Wang, and D. J. McKenzie. 2021. "The Role of Mechanistic Physiology in Investigating Impacts of Global Warming on Fishes." *Journal of Experimental Biology* 224, no. S1: jeb238840. https://doi.org/10.1242/jeb.238840.

Madeira, D., L. Narciso, H. N. Cabral, and C. Vinagre. 2012. "Thermal Tolerance and Potential Impacts of Climate Change on Coastal and Estuarine Organisms." *Journal of Sea Research* 70: 32–41. https://doi.org/10.1016/j.seares.2012.03.002.

McDevitt-Irwin, J. M., J. C. Iacarella, and J. K. Baum. 2016. "Reassessing the Nursery Role of Seagrass Habitats From Temperate to Tropical Regions: A Meta-Analysis." *Marine Ecology Progress Series* 557: 133–143. https://doi.org/10.3354/meps11848.

McKenzie, D. J., Y. Zhang, E. J. Eliason, et al. 2021. "Intraspecific Variation in Tolerance of Warming in Fishes." *Journal of Fish Biology* 98, no. 6: 1536–1555. https://doi.org/10.1111/jfb.14620.

Messmer, V., M. S. Pratchett, A. S. Hoey, et al. 2017. "Global Warming May Disproportionately Affect Larger Adults in a Predatory Coral Reef Fish." *Global Change Biology* 23, no. 6: 2230–2240. https://doi.org/10.1111/gcb.13552.

Mohamed, B., A. Barth, D. Van der Zande, and A. Alvera-Azcárate. 2025. "Amplified Warming and Marine Heatwaves in the North Sea Under a Warming Climate and Their Impacts." *Ocean Science* 21, no. 5: 2505–2525. https://doi.org/10.5194/os-21-2505-2025.

Monteiro, N., S. Pinheiro, S. Magalhães, P. Tarroso, and A. Vincent. 2023. "Predicting the Impacts of Climate Change on the Distribution of European Syngnathids Over the Next Century." *Frontiers in Marine Science* 10: 1138657. https://doi.org/10.3389/fmars.2023.1138657.

Morgan, R., M. H. Finnøen, and F. Jutfelt. 2018. "CTmax Is Repeatable and Doesn't Reduce Growth in Zebrafish." *Scientific Reports* 8, no. 1: 1. https://doi.org/10.1038/s41598-018-25593-4.

Morley, S. A., L. S. Peck, J. M. Sunday, S. Heiser, and A. E. Bates. 2019. "Physiological Acclimation and Persistence of Ectothermic Species Under Extreme Heat Events." *Global Ecology and Biogeography* 28, no. 7: 1018–1037. https://doi.org/10.1111/geb.12911.

Mottola, G., M. E. López, A. Vasemägi, M. Nikinmaa, and K. Anttila. 2022. "Are You Ready for the Heat? Phenotypic Plasticity Versus Adaptation of Heat Tolerance in Three-Spined Stickleback." *Ecosphere* 13, no. 4: e4015. https://doi.org/10.1002/ecs2.4015.

Moyano, M., C. Candebat, Y. Ruhbaum, et al. 2017. "Effects of Warming Rate, Acclimation Temperature and Ontogeny on the Critical Thermal Maximum of Temperate Marine Fish Larvae." *PLoS One* 12, no. 7: e0179928. https://doi.org/10.1371/journal.pone.0179928.

Norin, T., P. Canada, J. A. Bailey, and A. K. Gamperl. 2019. "Thermal Biology and Swimming Performance of Atlantic Cod (*Gadus morhua*) and Haddock (*Melanogrammus aeglefinus*)." *PeerJ* 7: e7784. https://doi.org/10.7717/peerj.7784.

Olin, A. B., J. Olsson, J. S. Eklöf, et al. 2022. "Increases of Opportunistic Species in Response to Ecosystem Change: The Case of the Baltic Sea Three-Spined Stickleback." *ICES Journal of Marine Science* 79, no. 5: 1419–1434. https://doi.org/10.1093/icesjms/fsac073.

Oliver, E. C. J., M. G. Donat, M. T. Burrows, et al. 2018. "Longer and More Frequent Marine Heatwaves Over the Past Century." *Nature Communications* 9, no. 1: 1324. https://doi.org/10.1038/s41467-018-03732-9.

Olsen, A. Y., S. Larson, J. L. Padilla-Gamiño, and T. Klinger. 2022. "Changes in Fish Assemblages After Marine Heatwave Events in West Hawai'i Island." *Marine Ecology Progress Series* 698: 95–109. https://doi.org/10.3354/meps14156.

Orth, R. J., T. J. B. Carruthers, W. C. Dennison, et al. 2006. "A Global Crisis for Seagrass Ecosystems." *Bioscience* 56, no. 12: 987–996. https://doi.org/10.1641/0006-3568(2006)56[987:AGCFSE]2.0.CO;2.

Palma, P. A., M. Bekaert, A. P. Gutierrez, E. J. C. Abacan, H. Migaud, and M. B. Betancor. 2025. "Plasticity of Thermal Tolerance and Associated Gill Transcriptome in Ballan Wrasse (*Labrus bergylta*)." *Frontiers in Marine Science* 11: 1507994. https://doi.org/10.3389/fmars.2024.1507994.

Pearce, A., F. Faskel, and G. Hyndes. 2006. "Nearshore Sea Temperature Variability Off Rottnest Island (Western Australia) Derived From Satellite Data." *International Journal of Remote Sensing* 27, no. 12: 2503–2518. https://doi.org/10.1080/01431160500472138.

Peck, L. S., S. A. Morley, J. Richard, and M. S. Clark. 2014. "Acclimation and Thermal Tolerance in Antarctic Marine Ectotherms." *Journal of Experimental Biology* 217, no. 1: 16–22. https://doi.org/10.1242/jeb.089946.

Perry, A. L., P. J. Low, J. R. Ellis, and J. D. Reynolds. 2005. "Climate Change and Distribution Shifts in Marine Fishes." *Science* 308, no. 5730: 1912–1915. https://doi.org/10.1126/science.1111322.

Perry, D., T. A. B. Staveley, L. Hammar, A. Meyers, R. Lindborg, and M. Gullström. 2018. "Temperate Fish Community Variation Over Seasons in Relation to Large-Scale Geographic Seascape Variables." *Canadian Journal of Fisheries and Aquatic Sciences* 75, no. 10: 1723–1732. https://doi.org/10.1139/cjfas-2017-0032.

Perry, D., E. Tamarit, D. Morgenroth, et al. 2024. "The Heat Is on: Sensitivity of Goldsinny Wrasse to Global Climate Change. *Conservation*." *Physiology* 12, no. 1: coae068. https://doi.org/10.1093/conphys/coae068.

Perry, D., E. Tamarit, E. Sundell, et al. 2024. "Physiological Responses of Atlantic Cod to Climate Change Indicate That Coastal Eco types May Be Better Adapted to Tolerate Ocean Stressors." *Scientific Reports* 14, no. 1: 12896. https://doi.org/10.1038/s41598-024-62700-0.

Phinn, S. R., E. M. Kovacs, C. M. Roelfsema, R. F. Canto, C. J. Collier, and L. J. McKenzie. 2018. "Assessing the Potential for Satellite Image Monitoring of Seagrass Thermal Dynamics: For Inter- and Shallow Sub-Tidal Seagrasses in the Inshore Great Barrier Reef World Heritage Area, Australia." *International Journal of Digital Earth* 11, no. 8: 803–824. https://doi.org/10.1080/17538947.2017.1359343.

Pihl, L., and H. Wennhage. 2002. "Structure and Diversity of Fish Assemblages on Rocky and Soft Bottom Shores on the Swedish West Coast." *Journal of Fish Biology* 61, no. sA: 148–166. https://doi.org/10.1111/j.1095-8649.2002.tb01768.x.

Plaisted, H. K., E. C. Shields, A. B. Novak, et al. 2022. "Influence of Rising Water Temperature on the Temperate Seagrass Species Eelgrass (*Zostera marina* L.) in the Northeast USA." *Frontiers in Marine Science* 9: 920699. https://doi.org/10.3389/fmars.2022.920699.

R Core Team. 2024. *R: A Language and Environment for Statistical Computing (Version 4.4.2)*. R Foundation for Statistical Computing. https://www.R-project.org/.

Raby, G. D., R. Morgan, A. H. Andreassen, et al. 2025. "Measuring Critical Thermal Maximum in Aquatic Ectotherms: A Practical Guide." *Methods in Ecology and Evolution* 16, no. 10: 2208–2228. https://doi.org/10.1111/2041-210X.70103.

Reynolds, R. W., T. M. Smith, C. Liu, D. B. Chelton, K. S. Casey, and M. G. Schlax. 2007. "Daily High-Resolution-Blended Analyses for Sea Surface Temperature." *Journal of Climate* 20, no. 22: 5473–5496. https://doi.org/10.1175/2007JCLI1824.1.

Rezende, E. L., L. E. Castañeda, and M. Santos. 2014. "Tolerance Landscapes in Thermal Ecology." *Functional Ecology* 28, no. 4: 799–809. https://doi.org/10.1111/1365-2435.12268.

Robinson, C. L. K., J. Yakimishyn, and R. Evans. 2022. "Minimal Effects of the 2014-16 Marine Heatwave on Fish Assemblages Found in Eelgrass Meadows on the Southwestern Coast of Vancouver Island, British Columbia, Canada." *Frontiers in Marine Science* 9: 980703. https://doi.org/10.3389/fmars.2022.980703.

Sandblom, E., T. D. Clark, A. Gräns, et al. 2016. "Physiological Constraints to Climate Warming in Fish Follow Principles of Plastic Floors and Concrete Ceilings." *Nature Communications* 7, no. 1: 11447. https://doi.org/10.1038/ncomms11447.

Schlegel, R. W., and A. J. Smit. 2018. "heatwaveR: A Central Algorithm for the Detection of Heatwaves and Cold-Spells." *Journal of Open Source Software* 3, no. 27: 821. https://doi.org/10.21105/joss.00821.

Seebacher, F., C. R. White, and C. E. Franklin. 2015. "Physiological Plasticity Increases Resilience of Ectothermic Animals to Climate Change." *Nature Climate Change* 5, no. 1: 61–66. https://doi.org/10.1038/nclimate2457.

Short, F. T. 2003. *World Atlas of Seagrasses*. University of California Press.

Smale, D., and T. Wernberg. 2009. "Satellite-Derived SST Data as a Proxy for Water Temperature in Nearshore Benthic Ecology." *Marine Ecology Progress Series* 387: 27–37. https://doi.org/10.3354/meps08132.

Smale, D. A., T. Wernberg, E. C. J. Oliver, et al. 2019. "Marine Heatwaves Threaten Global Biodiversity and the Provision of Ecosystem Services." *Nature Climate Change* 9, no. 4: 306–312. https://doi.org/10.1038/s41558-019-0412-1.

Smith, K. E., M. Aubin, M. T. Burrows, et al. 2024. "Global Impacts of Marine Heatwaves on Coastal Foundation Species." *Nature Communications* 15, no. 1: 5052. https://doi.org/10.1038/s41467-024-49307-9.

Smith, K. E., M. T. Burrows, A. J. Hobday, et al. 2023. "Biological Impacts of Marine Heatwaves." *Annual Review of Marine Science* 15, no. 1: 119–145. https://doi.org/10.1146/annurev-marine-032122-121437.

Smith, K. E., A. Sen Gupta, D. Amaya, et al. 2025. "Baseline Matters: Challenges and Implications of Different Marine Heatwave Baselines." *Progress in Oceanography* 231: 103404. https://doi.org/10.1016/j.pocean.2024.103404.

Starko, S., M. van der Mheen, A. Pessarrodona, et al. 2024. "Impacts of Marine Heatwaves in Coastal Ecosystems Depend on Local Environmental Conditions." *Global Change Biology* 30, no. 8: e17469. https://doi.org/10.1111/gcb.17469.

Staveley, T. A. B., D. Perry, R. Lindborg, and M. Gullström. 2017. "Seascape Structure and Complexity Influence Temperate Seagrass Fish Assemblage Composition." *Ecography* 40, no. 8: 936–946. https://doi.org/10.1111/ecog.02745.

Strydom, S., K. Murray, S. Wilson, et al. 2020. "Too Hot to Handle: Unprecedented Seagrass Death Driven by Marine Heatwave in a World Heritage Area." *Global Change Biology* 26, no. 6: 3525–3538. https://doi.org/10.1111/gcb.15065.

Sunday, J., J. M. Bennett, P. Calosi, et al. 2019. "Thermal Tolerance Patterns Across Latitude and Elevation." *Philosophical Transactions of the Royal Society B: Biological Sciences* 374, no. 1778: 20190036. https://doi.org/10.1098/rstb.2019.0036.

Sunday, J. M., A. E. Bates, and N. K. Dulvy. 2012. "Thermal Tolerance and the Global Redistribution of Animals." *Nature Climate Change* 2, no. 9: 686–690. https://doi.org/10.1038/nclimate1539.

Thalmann, H. L., B. J. Laurel, L. Z. Almeida, K. E. Osborne, K. Marshall, and J. A. Miller. 2024. "Marine Heatwaves Alter the Nursery Function of Coastal Habitats for Juvenile Gulf of Alaska Pacific Cod." *Scientific Reports* 14, no. 1: 14018. https://doi.org/10.1038/s41598-024-63897-w.

Vasseur, D. A., J. P. DeLong, B. Gilbert, et al. 2014. "Increased Temperature Variation Poses a Greater Risk to Species Than Climate Warming." *Proceedings of the Royal Society B: Biological Sciences* 281, no. 1779: 20132612. https://doi.org/10.1098/rspb.2013.2612.

Vinagre, C., I. Leal, V. Mendonça, et al. 2016. "Vulnerability to Climate Warming and Acclimation Capacity of Tropical and Temperate Coastal Organisms." *Ecological Indicators* 62: 317–327. https://doi.org/10.1016/j.ecolind.2015.11.010.

Von Schuckmann, K., L. Moreira, M. Cancet, et al. 2024. "The State of the Global Ocean." *State of the Planet* 4: 1–30. https://doi.org/10.5194/sp-4-osr8-1-2024.

Wernberg, T., M. S. Thomsen, M. T. Burrows, et al. 2025. "Marine Heatwaves as Hot Spots of Climate Change and Impacts on Biodiversity and Ecosystem Services." *Nature Reviews Biodiversity* 1, no. 7: 461–479. https://doi.org/10.1038/s44358-025-00058-5.

Wickham, H. 2016. "Programming With ggplot2." In *Ggplot2: Elegant Graphics for Data Analysis*, edited by H. Wickham, 241–253. Springer International Publishing. https://doi.org/10.1007/978-3-319-24277-4_12.

Yu, L., M. Khachaturyan, M. Matschiner, et al. 2023. "Ocean Current Patterns Drive the Worldwide Colonization of Eelgrass (*Zostera marina*)." *Nature Plants* 9, no. 8: 1207–1220. https://doi.org/10.1038/s41477-023-01464-3.

Yuen, J. W., T. Dempster, F. Oppedal, and M. Hvas. 2019. "Physiological Performance of Ballan Wrasse (*Labrus bergylta*) at Different Temperatures and Its Implication for Cleaner Fish Usage in Salmon Aquaculture." *Biological Control* 135: 117–123. https://doi.org/10.1016/j.biocontrol.2019.05.007.

Ziegler, C. M., and M. G. Frisk. 2019. "Flatfish Utilize Sediment Blanket to Facilitate Thermoregulation." *Marine Ecology Progress Series* 609: 179–186. https://doi.org/10.3354/meps12817.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Daily seawater temperature at Kristineberg during fish collection period. **Figure S2:** Thermal ramping curves of CT_{max} trials for each species. **Figure S3:** CT_{max} of *Symphodus melops* following acclimation to a simulated heatwave and TT_{gain} retention. **Table S1:** Metadata for CT_{max} trials. **Table S2:** Thermal ramping rates estimated for all CT_{max} trials. **Table S3:** Estimated marginal means of CT_{max} for each species and treatment. **Table S4:** Percentage mortality of each species at the end of experimental exposure. **Table S5:** Family-level differences in CT_{max} (Ambient). **Table S6:** Family-level differences in CT_{max} (Heatwave). **Table S7:** CT_{max} statistical contrasts. **Table S8:** Thermal tolerance gain (TT_{gain}) and acclimation response ratio (ARR) by species.