Eelgrass-associated fishes show large interspecific differences in thermal acclimation to marine heatwaves

Elena Tamarit[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, Medicinaregatan 7B, 41262 Gothenburg, Sweden
[2] Department of Marine Sciences, University of Gothenburg, Medicinaregatan 7B, 41262 Gothenburg, Sweden
[3] Department of Biological and Environmental Sciences, University of Gothenburg, Medicinaregatan 7B, 41262 Gothenburg, Sweden
[4] The Maritime Museum & Aquarium, Karl-Johansgatan 1-3, 41459 Gothenburg, Sweden
[5] Department of Aquatic Resources, Swedish University of Agricultural Sciences, Turistgatan 5, 453 30 Lysekil, Sweden
[6] School of Natural Sciences, Technology and Environmental Studies, Södertörn University, S-141 89 Huddinge, Sweden
* Corresponding author: elena.tamarit@gu.se

Abstract

Global warming is increasingly exposing shallow coastal habitats to thermal extremes, with important consequences for the fish species they support. Eelgrass (*Zostera marina*), the most widespread seagrass in the Northern Hemisphere, provides nursery habitats and foraging opportunities for a high diversity of temperate fishes. However, light limitation is compressing eelgrass depth distribution to shallower waters, increasing exposure of these habitats and their associated fish assemblages to thermal stress during intensifying marine heatwaves. Persistence in warming eelgrass habitats may therefore depend on species-specific differences in thermal tolerance and the capacity for rapid thermal acclimation among fishes. However, interspecific variation in acclimation capacity within shared habitats remains poorly understood. To address this gap, we experimentally exposed twelve wild-caught eelgrass-associated fish species to ambient (19 ºC) and heated (23 ºC) temperatures, representative of current summer conditions of the Swedish west coast (Skagerrak, North Sea). We quantified critical thermal maxima (CT_{max}) as a proxy for upper thermal tolerance and assessed species' short-term acclimation capacity following five days of exposure to a simulated marine heatwave in the laboratory. Most species increased

CT_{max}, but both baseline thermal tolerance and acclimation capacity varied markedly among taxa. Juvenile Atlantic cod, whiting and plaice showed the lowest thermal tolerance and weakest acclimation responses, suggesting limited capacity to physiologically buffer acute warming and a greater reliance on behavioural avoidance. In contrast, sedentary species such as gobies and pipefishes exhibited high thermal tolerance with moderate plasticity, while 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 acclimation capacity among eelgrass-associated fishes. This indicates that ongoing warming and marine heatwaves are likely to reshape eelgrass fish assemblages with implications for coastal food-web structure and functioning.

Keywords

Global warming, marine heatwaves, critical thermal maximum, thermal acclimation, seagrass ecosystems, thermal extremes

Introduction

Coastal vegetated habitats, such as seagrass meadows, rank among the most productive ecosystems on Earth, providing essential nursery grounds, foraging habitats and refuge for juvenile fishes while supporting global biodiversity (Beck et al., 2001; Heck Hay et al., 2003; Lefcheck et al., 2019; McDevitt-Irwin et al., 2016; Orth et al., 2006). However, anthropogenic climate change is increasingly exposing shallow coastal habitats to warming and extreme thermal events that threaten ecological functions (Oliver et al., 2018; D. A. Smale et al., 2019). Marine heatwaves are discrete periods (≥ 5 days) of anomalously high seawater temperature relative to a local historical baseline (Hobday et al., 2016; Smith et al., 2023), that have increased in frequency, intensity and duration over recent decades, posing a pervasive threat to marine biodiversity globally (Calvin et al., 2023; Cheng et al., 2025; Wernberg et al., 2025).

The North Sea is among the fastest-warming regions worldwide, recently experiencing record-breaking sea surface temperatures associated with the longest and most intense heatwave reaching +4ºC (Mohamed et al., 2025). Such events cause widespread impacts on foundation species, including seagrasses, kelp and corals, as well as on fauna with strong habitat specificity, including fish, crustaceans and birds (Brijs et al., 2025; Garrabou et al., 2009; Olsen et al., 2022; Smith et al., 2024; Strydom et al., 2020). Marine heatwaves shape population persistence of species occupying the warm edges of their thermal distributions (Sunday et al., 2019). Understanding species' capacity for physiological acclimation is therefore essential for predicting vulnerability to marine heatwaves and anticipating potential shifts in species distributions and community composition under ongoing climate change (Gómez-Gras et al., 2025).

Fishes can buffer short-term warming through behavioural thermoregulation, such as relocating to cooler waters, or via acclimation, a reversible form of phenotypic plasticity within individuals that can partially offset thermal impacts on metabolism and performance (Brett, 1952; Jr, 2009; Seebacher et al., 2015). Broadly, phenotypic plasticity is the capacity of organisms to alter aspects of their phenotype in response to environmental variation (Morash, 2024). However, when warming exceeds upper thermal limits and outpace their acclimation capacity, individuals lose motor control and can 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}), defined as the temperature-inducing loss of equilibrium (Becker & Genoway, 1979). Despite limited mechanistic insights, CT_{max} remains widely used to assess acute thermal tolerance and acclimation capacity across fishes under climate change scenarios (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). Derived metrics such as acclimation response ratio (ARR) and thermal tolerance gain (TTgain) further quantify the magnitude of thermal acclimation following exposure to elevated temperatures (L.Claussen, 1977; Morley et al., 2019).

Predicting which species are vulnerable to thermal extremes and how fish assemblages will change under climate warming is challenging because thermal tolerance and acclimation capacity vary widely among species (Burton & Einum, 2025; Jutfelt et al., 2024). While acclimation capacity has been examined in subtropical, temperate and Antarctic fishes (Bilyk & DeVries, 2011; De Bonville et al., 2025; Drost et al., 2016; Mottola et al., 2022; Peck et al., 2014), few studies have compared multiple species co-occurring within the same habitat, and to our knowledge, none have focused on seagrass-associated fish assemblages.

Eelgrass (*Zostera marina*) is the most widespread seagrass in the Northern Hemisphere, occurring in Pacific and Atlantic oceans from temperate to Arctic environments (Short, 2003; Yu et al., 2023). Eelgrass meadows host highly diverse fish assemblages including shallow-water generalists (e.g., wrasses, gobies, sticklebacks), stationary specialists (e.g., pipefishes and some gobies), and juvenile migrants such as gadids (codfishes) and flatfishes (Perry et al., 2018; Pihl & Wennhage, 2002). However, eelgrass depth distribution has steeply declined in Europe due to eutrophication and habitat destruction, with complex recovery trajectories and an increasingly constrained distribution to the first meters of the shoreline (Boström et al., 2014; de los Santos et al., 2019; Krause-Jensen et al., 2021; Lefcheck et al., 2017). Eelgrass habitats are also becoming shallower due to deterioration of water quality, which further exposes them to thermal extremes that threaten the provision of their ecosystem services (Krause-Jensen et al., 2021; Nguyen et al., 2021; Saha et al., 2020). Moreover, while eelgrass meadows exhibit strong temperature microclimates driven by depth, hydrodynamics and exposure (Hattich et al., 2025), there is a lack of long-term, high-resolution temperature records from eelgrass meadows (Nordlund et al., 2024). Recent syntheses highlight that the ecological impacts of marine heatwaves depend strongly on local environmental conditions and fine-scale habitat heterogeneity, which can amplify or buffer thermal exposure relative to regional averages (Starko et al., 2024). Consequently, the responses of eelgrass fish assemblages to marine heatwaves remain poorly understood (Robinson et al., 2022; Thalmann et al., 2024).

Here, we experimentally quantified CT_{max} and short-term acclimation capacity in 12 fish species associated with eelgrass habitats on the Swedish Skagerrak coast. Wild-caught individuals were exposed to ecologically relevant ambient (19ºC) and elevated (23ºC) temperatures for five days, followed by measuring CT_{max} through the behavioural response temperature at loss of equilibrium. We then quantified acclimation capacity for all species and further examined relationships between CT_{max} and species' thermal distribution ranges. We also evaluated local thermal regimes using in situ logger records and historical temperature data to detect marine heatwaves. We predicted that generalist species with warmer thermal niches would exhibit higher CT_{max} and greater acclimation capacity, whereas migratory species with narrower or cold ranges would show lower tolerance and limited plasticity, indicating potential vulnerability to future marine heatwaves occurring in eelgrass habitats.

Materials and methods

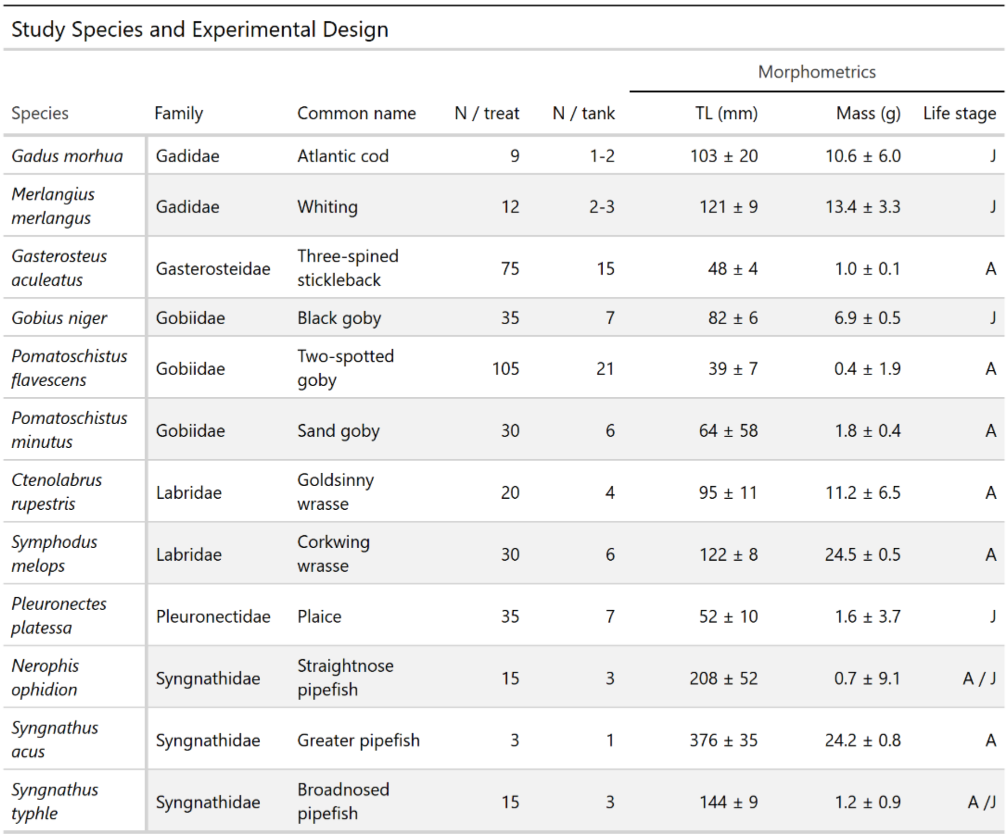
Animal research permit

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 (Sert et al., 2020).

Study area and fish husbandry

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

Wild fish belonging to twelve different common temperate fish species associated with eelgrass were collected within two kilometres from Kristineberg at one to four meters depth. Species represented six families (Gadidae, Pleuronectidae, Labridae, Gasterosteidae, Gobiidae and Syngnathidae; Table 1) and included shallow water generalists, sedentary habitat specialists and juvenile migratory species. Fish were captured using beach seines, baited traps, fyke nets and hand nets while snorkelling, and immediately transported to the research station.



Study Species and Experimental Design

Species	Family	Common name	N / treat	N / tank	Morphometrics 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	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

TABLE 1. Metadata for study species and experimental design. N/treat = number of individuals per treatment; N/tank = number of fish per tank; TL (mm) = total length in millimeter, mean ± S.D.; Mass (g) = mass in grams, mean ± S.D. For life stage J = Juvenile; A = Adult.

At the lab, fish were housed in a holding tank (1350 L, 275 × 79 × 62 cm, [L × W × H]) supplied with flow-through filtered seawater pumped from seven meters depth and acclimated to captivity for one week under ambient fjord temperatures (18.6 ± 1.5ºC, mean ± S.D.) and a 12:12 hour 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.

Experimental design

Separate experiments were conducted for each species, exposing the fish to two temperature treatments for five days to trigger a short-term acclimation response. Each experiment consisted of five replicated tanks with seawater at 19ºC ("Ambient") and five at 23ºC ("Heated"). These temperatures reflected ecologically realistic summer conditions on the Swedish Skagerrak coast based on high resolution *in situ* temperature records at one meter depth at Kristineberg (https://www.weather.loven.gu.se/kristineberg/en/)."Ambient" approximated the mean daily maximum sea temperature from 1st of June to 30th of September for 2020-2023 (18.6 ± 1.9ºC, mean ± S.D.), while "Heated" simulated a +4ºC marine heatwave anomaly.

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 (18.8ºC ± 0.3 and 22.8 ± 0.2, mean ± S.D.; Thermometer Testo-112, Testo, Lenzkirch, Germany). Fish were randomly assigned to treatments, and tank size was adjusted according to species: small glass tanks (45 L): 35 x 37x 35 cm [L × W × H]; big glass tanks (80 L): 38 x 60 x 35 cm. Tanks were dispersed throughout the room to minimize location effects, and contained 2cm of sand substrate and plastic seaweed, mussel shells, and PVC pipes for shelter. The feeding regime and photoperiod matched the holding period.

Testing of acute warming tolerance (CT_{max}) on fish

After the five-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 hours 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 fish (Beitinger et al., 2000; Morgan et al., 2018). LOE was a behavioural response defined as the fish's inability to maintain an upright position for three seconds.

Trials were conducted in a custom arena filled with water from the corresponding experimental tank. The CT_{max} arena was a plastic box (34 x 25 x 17 cm; ~14 liters) 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 x 30 x 25 cm; ~23 liters) 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 three and 20 depending on species (Table S1).

To start the test, all fish from one tank were placed into the arena and allowed to habituate for ten minutes at the experimental temperature. Thereafter, the trial was started by plugging the heater and the water temperature gradually increased at a rate of 0.3ºC min^{-1} (thermal ramping curves and rates shown in Fig. 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 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 labelled jar with water at the original experiment temperature for recovery. After monitoring survival for 30 minutes, fish were lightly anaesthetized (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.

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.

Comparing upper thermal tolerance across species

We analysed CT_{max} using a linear mixed-effects model with species, treatment group (Ambient vs. Heated), and their interaction as fixed effects, and CT_{max} trial as a random intercept: 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 x group interaction). Fish from the same tank were tested together within a CT_{max} trial and therefore, the trial represented the experimental unit. Due to complete mortality of *Gadus morhua* in the Heated 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 x group combination and pairwise comparisons were obtained with *emmeans*.

Comparing acclimation capacity across species

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

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

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

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

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

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

$ARR_{individual} = (CT_{max,Heated, individual} − mean\ CT_{max, Ambient, Species}) / 4$

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.

Exploring upper thermal tolerance across fish families

To explore broad taxonomic patterns in upper thermal tolerance, we conducted an additional family-level analysis using species as the unit of replication. Species-level CT_{max} (estimated marginal means from the mixed-effects model) for Ambient and Heated treatments were separately analysed as a function of family using a linear model (lm(emmean ~ family)), followed by Tukey-adjusted pairwise comparisons. Given the number of species per family was limited (1-3), this analysis was considered exploratory.

Eelgrass summer temperatures and fish distribution ranges

To investigate how current thermal regimes of eelgrass habitats compare to fish thermal distribution ranges, we first selected a reference eelgrass meadow with *in situ* sea temperature data available publicly. The meadow was located outside the Tjärnö Marine Laboratory, 72 km northwest from Kristineberg (58.87877 N, 11.13467 E), and hosted 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)). For 1st of June to 30th of September (2020-2023), negative values were filtered and data were aggregated to daily maximum temperature. Then for each day of year, we calculated a multi-year mean and the minimum and maximum of daily maxima. We also identified the warmest period in the season and computed the multi-year mean, minimum and maximum, to obtain the warmest temperature range of the reference eelgrass meadow. Then for each fish species, we obtained the thermal limits (preferred and absolute) from AquaMaps’ defined native range 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). Finally, the relationship between species' maximum range temperature and their mean CT_{max} (after acclimation to 19ºC) was explored using Pearson's correlation and simple linear regression.

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 1m depth in 5-min intervals available for 1996-2024, except 1997 and 2001-2006. Data from the 1st of June to the 30th of 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.

Since a 30-year climatology baseline is required for standard marine heatwave detection (Smith et al., 2025), we used satellite-derived daily mean SST from the NOAA Optimum Interpolation Sea Surface Temperature version 2.1 (NOAA OISST; (Huang et al., 2024; Reynolds et al., 2007)), with 0.25º (27 km) resolution, extending back to 1982, and extracted for the grid cell nearest Kristineberg (58.125ºN, 11.375ºE). For the 1st of January 1982 to the 31st of December 2024 temporal trends modelled with linear regression. Marine heatwave frequency and cumulative intensity (ºC and days) for each year were estimated using the *heatwaveR* package (W. Schlegel & J. Smit, 2018), following the definition from Hobday et al. (2016), with a 30-year climatology baseline record (1982-2011). Marine heatwave frequency was modelled 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 (ºC·days) (Oliver et al., 2018) was modelled 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, we compared *in situ* daily SST means from Kristineberg and satellite SSTs 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).

Results

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 significant species x 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.

Acclimation to 19ºC (Ambient)

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

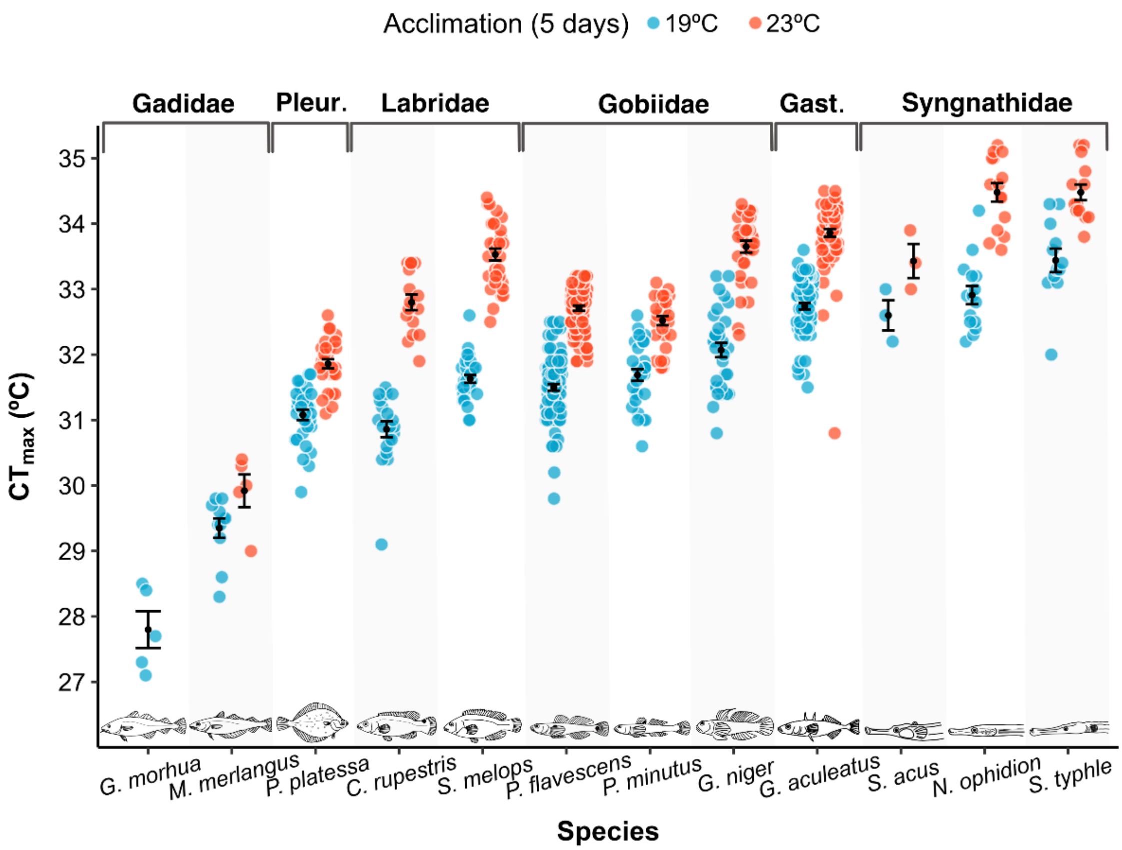


FIGURE 1. Upper thermal tolerance (CT_{max}) of twelve eelgrass-associated fish species following five days of acclimation to 19ºC (Ambient; blue) or 23ºC (Heated; orange). Coloured points represent individual CT_{max} measurements and are jittered horizontally for clarity. Black points and error bars indicate species means ± S.E. Y-axis values show temperature in ºC; 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, Pleur. = *Pleuronectidae*; Gast. = *Gasterosteidae*.

Acclimation to 23ºC (Heated)

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

Family-level patterns

An exploratory family-level analysis indicated differences in CT_{max} under both Ambient (linear model, F = 15.11, $p < 0.01$; Table S5) and Heated conditions (linear model, F = 8.80, $p < 0.05$; Table S6). Gadidae showed substantially lower CT_{max} (28.6 ± 0.4ºC, mean ± S.E.) than all other families, whereas Gasterosteidae and Syngnathidae were the most heat tolerant (≈33ºC). Pleuronectidae, Labridae and Gobiidae showed intermediate mean CT_{max} levels, with comparatively small and non-significant differences among these families.

Acclimation capacity

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). TTgain varied nearly threefold among species, ranging from 0.62ºC to 1.94ºC (Table S8). The largest gains were observed in *C. rupestris* (1.94ºC), *S. melops* (1.89ºC), *N. ophidion* (1.58ºC), and *G. niger* (1.58ºC), whereas juvenile gadids and plaice exhibited comparatively weak responses. No TTgain could be estimated for *G. morhua* due to complete mortality in the heated treatment.

Acclimation response ratio (ARR)

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

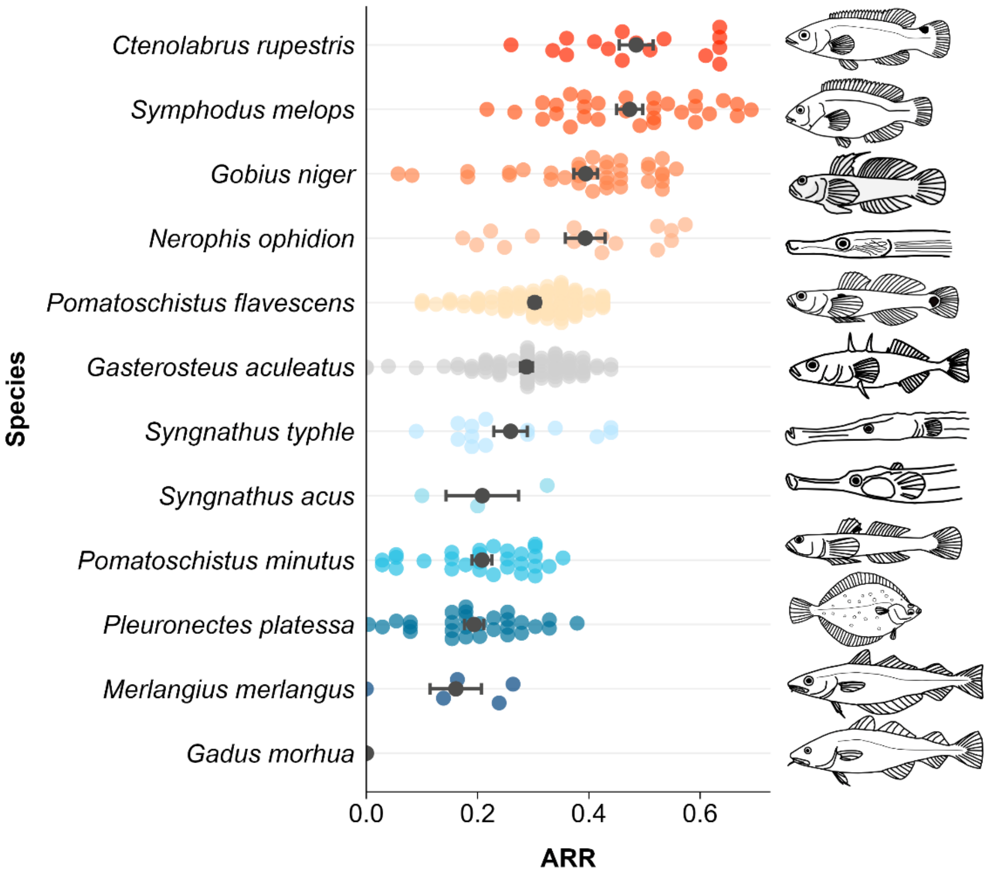


FIGURE 2. Acclimation response ratio (ARR) following five days of exposure to 23ºC for twelve eelgrass-associated fish species. Coloured points represent individual-level ARR values calculated for fish exposed to 23ºC. Black points and error bars show species-level ARR mean ± S.E. An ARR of 1.0 represents a complete thermal compensation. *Gadus morhua* did not survive the heated treatment and is therefore shown without ARR values.

Eelgrass summer temperatures and fish distribution ranges

Temperature records from the reference eelgrass meadow revealed that the warmest seawater conditions occurred from the 15th of June to the 1st of September, when daily maximum temperatures averaged 20.5ºC, ranged between 19.0 and 22.3ºC, and frequently approached or exceeded 23ºC (Fig. 3A). Over the full summer period (1st of June to the 30th of September), daily maximum temperatures followed a clear seasonal pattern, averaging 19.3ºC and ranging from 15.1 to 22.3ºC (Fig. 3A).

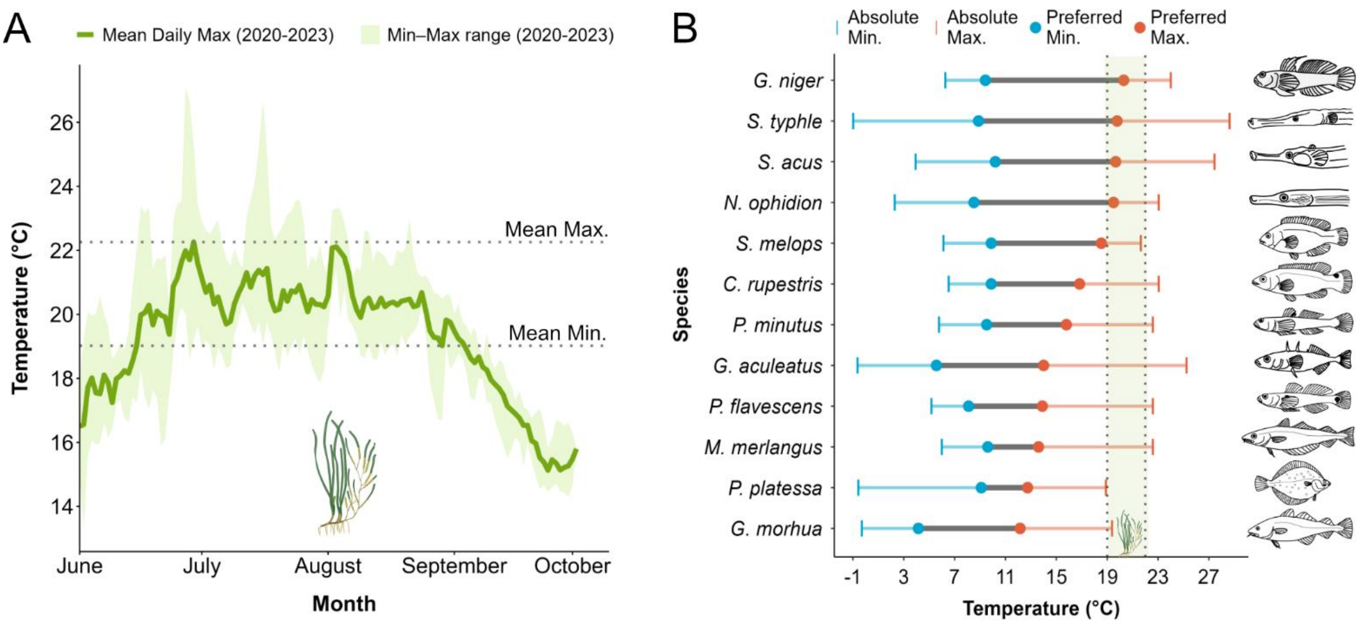


FIGURE 3. Summer sea temperatures in a temperate eelgrass (*Zostera marina*) meadow and fish species thermal distribution ranges. A) Daily maximum seawater temperature in an eelgrass meadow at 1.5 m depth during the summer (the 1st of June to the 30th of September, 2020-2023). Green line: mean daily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

Thermal niches varied substantially among species (Fig. 3B). Most occupied broad thermal ranges spanning approximately 5-23ºC, while some taxa, including the three-spined stickleback and broadnosed pipefish, exhibited wider distributions extending to 25-28ºC. In contrast, cod and plaice were restricted to cooler thermal environments, with upper distribution limits around 19ºC (Fig. 3B).

For several species, preferred temperature maxima were below present summer temperatures measured in eelgrass habitats. Juvenile cod, whiting, plaice, two-spotted goby, three-spined stickleback, sand goby, and goldsinny wrasse, showed preferred temperatures in the range of ≈ 12–18ºC, 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 (≈19-21ºC), with some species occupying waters exceeding 24ºC (Fig. 3B).

Upper thermal tolerance and thermal ranges

Mean CT_{max} increased with the absolute maximum temperatures experienced across species' geographic distributions ($R^2 = 0.489$, $p < 0.05$; Fig. 4). Hence, species from warmer environments exhibited higher upper thermal limits, with CT_{max} broadly tracking the upper bounds of their thermal ranges.

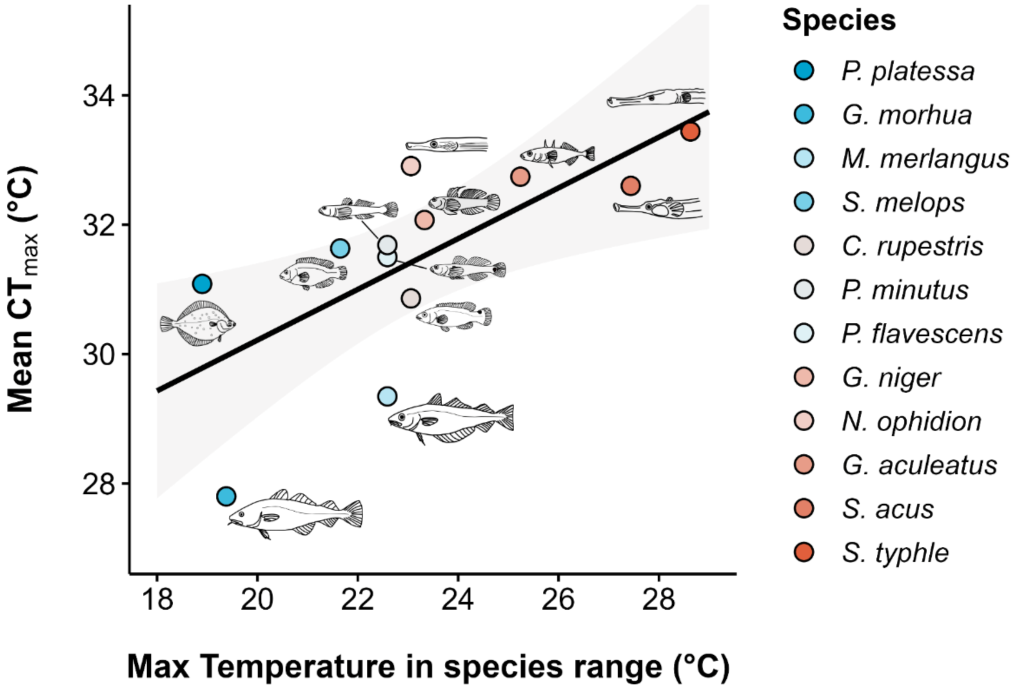


FIGURE 4. Relationship between species' mean CT_{max} (at 19ºC) and maximum temperatures of its predicted distribution range (AquaMaps, Froese et al., 2019)**.** Each point represents the mean Critical Thermal maximum (CT_{max}) for a species under ambient conditions, with colors distinguishing species. The black line shows the fitted linear regression (± 95% confidence interval in gray), indicating a positive association between CT_{max} and range maximum temperature.

Thermal variability, warming trends and marine heatwaves

Long-term *in situ* measurements at Kristineberg indicated substantial warming of summer seawater temperatures between 1996 and 2024, with annual daily maximum temperatures increasing by 2.6ºC, equivalent to 0.92ºC per decade (0.092ºC yr^{-1}; 95% CI: 0.014–0.170ºC yr^{-1}; $R^2 = 0.23$, $p < 0.05$; Fig. 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 20ºC and occasionally surpassing 23ºC.

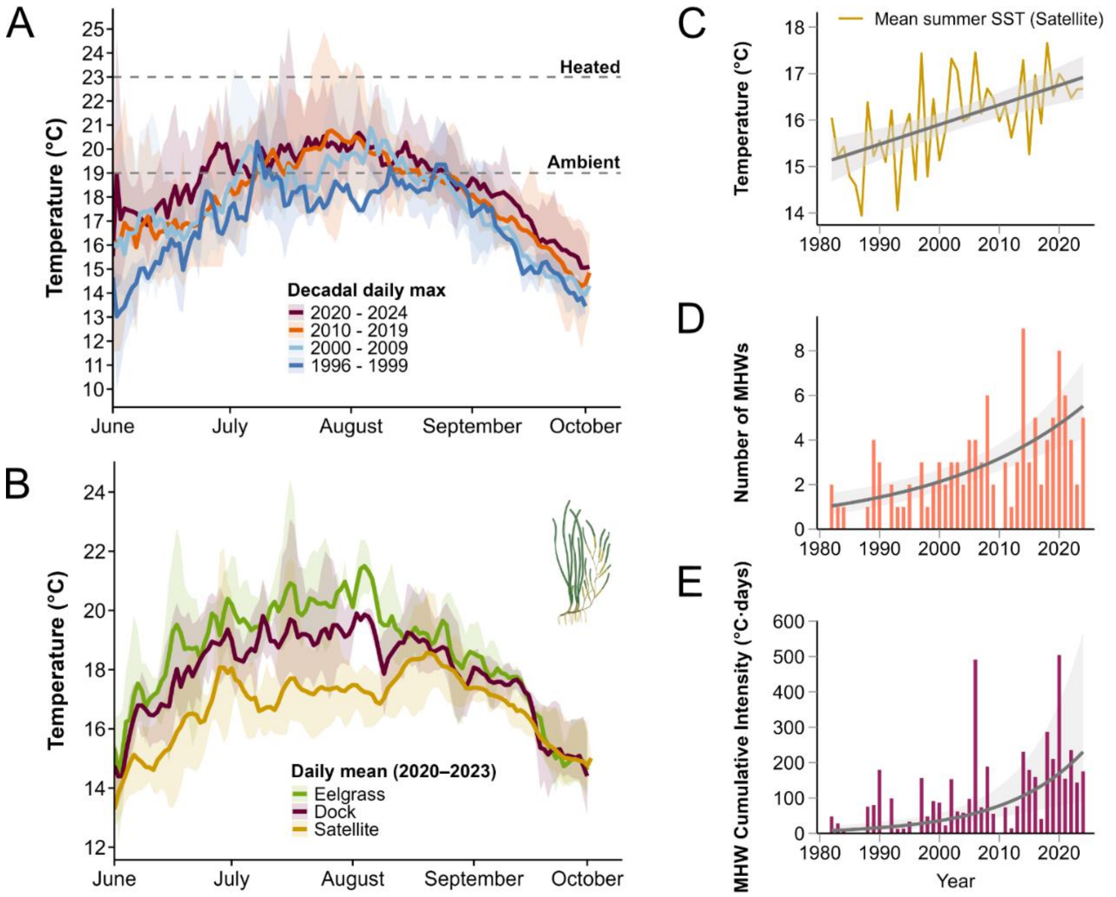


FIGURE 5. Long-term summer sea surface temperature (SST) and marine heatwaves at Kristineberg (1982 - 2024). **A)** Daily maximum SST at 1m depth (1st of June to 30th of September), grouped by decade: 1996 - 1999 (dark blue), 2000 - 2009 (light blue), 2010 - 2019 (orange), and 2020 - 2024 (purple-red). 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 “Heated”). **B)** Daily mean SST (2020-2023) measured *in situ* within an eelgrass meadow at 1.5m depth (Tjärnö; green), at the dock at 1m 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 with linear trend and 95% CI; warming rate = 0.42ºC·decade^{-1} (95% CI 0.29-0.56). **D)** Annual frequency of marine heatwaves (MHWs) with fitted temporal trend and 95% CI; change = 49%·decade^{-1} (95% CI 28-73); **E)**

Annual cumulative MHW intensity with fitted temporal trend and 95% CI; change = 116%·decade^{-1} (95% CI 49-212).

Daily mean eelgrass temperatures were consistently higher than those measured at the dock or estimated from satellite data during summer (2020-2023; Fig. 5B). Eelgrass temperatures exceeded dock measurements by an average of 0.67ºC, and satellite-derived SST by 1.76ºC, 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: -1.09ºC, RMSE = 1.45ºC; eelgrass: -1.76ºC, RMSE = 2.25ºC), 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 4ºC and reached a maximum of 5.82ºC, 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 1982-2024. Mean summer SST increased by 0.42ºC per decade (95% CI 0.29-0.56; $p < 0.001$; Fig 5C). Marine heatwave frequency increased by 49% per decade (95% CI 28-73; $p < 0.001$; Fig. 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; $p < 0.001$; Fig. 5E), equivalent to 48.6ºC·days per decade (95% CI 26.6–70.7; $p < 0.001$; Fig. 5E), indicating a marked rise in total thermal exposure associated with marine heatwaves.

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 long-term habitat warming and regional trends in marine heatwaves. We reveal pronounced interspecific variation in upper thermal tolerance (CT_{max}) and rapid acclimation capacity. Although most species increased their CT_{max} following short-term warming, the magnitude of acclimation differed markedly among species. Cold-water juvenile migrants using eelgrass and nearby sandy habitats as nurseries (e.g., Atlantic cod, whiting, and plaice) exhibited weak acclimation capacity and high mortality, whereas warm-tolerant generalists and stationary species (e.g. three-spined stickleback, black goby, goldsinny wrasse and corkwing wrasse) showed higher tolerance and greater plasticity. Importantly, these physiological differences occur in shallow eelgrass-associated fish communities that already experience temperatures near or exceeding the upper thermal limits of several associated species. Together, our results indicate that ongoing warming and intensifying marine heatwaves are likely to restructure eelgrass fish assemblages through differential physiological vulnerability.

Warming eelgrass habitats

During summer (2020-2023) daily mean and maximum temperatures in the reference eelgrass meadow (1.5m depth) frequently reached 22-23ºC, approaching or exceeding the preferred thermal ranges of several associated fishes. Eelgrass temperatures were consistently warmer than those recorded at the research station dock and were underestimated from satellite-derived SST by approximately 1–3ºC on average and up to 4–5ºC during thermal extremes. This pattern is consistent with previous work showing that satellite SST products capture broad temporal variability reasonably well, but systematically underestimate thermal extremes in shallow, vegetated habitats with restricted water exchange (Pearce et al., 2006; Phinn et al., 2018; D. Smale & Wernberg, 2009). Sheltered eelgrass meadows also experience greater thermal variability and more frequent extremes than wave-exposed habitats (Hattich et al., 2025). Such variability can have disproportionate effects on organismal performance compared to changes in mean temperature (Vasseur et al., 2014), particularly when extremes push individuals to their physiological limits. Microhabitat differences therefore modulate the temperatures organisms experience, creating opportunities for behavioural thermoregulation and refugia from extremes (Sunday et al., 2019). Broadly, the ecological impacts of marine heatwaves depend strongly on local environmental conditions and fine-scale habitat heterogeneity, which can amplify or buffer thermal exposure relative to regional averages (Starko et al., 2024).

Furthermore, our findings show that shallow eelgrass habitats warm faster than the regional warming trends. Although global oceans have warmed by ~0.13ºC per decade since 1982 (Calvin et al., 2023; Von Schuckmann et al., 2024), the North Sea has warmed nearly four times faster, at ~0.38ºC per decade (Mohamed et al., 2025). We detected a comparable warming rate on the Swedish west coast (~0.42ºC per decade) together with an increase in marine heatwave frequency. However, the cumulative intensity change was 48.6ºC·days per decade, which is about ten times stronger than in the full basin at 4.23ºC·days per decade (Mohamed et al., 2025). Therefore, our findings suggest that shallow eelgrass meadows may already be experiencing more severe and biologically relevant heatwaves than what is inferred from regional satellite time series, and future summer temperatures are likely to outpace the acclimation capacity of less plastic species.

Species-specific vulnerability to marine heatwaves

Species living close to their upper thermal limits showed the weakest acclimation capacity and the highest vulnerability to the simulated heatwave. Juvenile Atlantic cod suffered complete mortality at 23ºC, while juvenile whiting showed high mortality and negligible acclimation despite higher survival. These results indicate that gadids occupying warm nursery habitats have little scope for thermal acclimation under acute warming (Ern et al., 2023; Jutfelt et al., 2024). Cod and whiting are cold-temperate demersal fishes whose juveniles rely on shallow coastal nursery habitats, including eelgrass meadows (Heck Hay et al., 2003). Juvenile cod prefers temperatures below 16ºC and actively avoids warmer conditions by diurnal vertical migration, and migrating between eelgrass meadows (Bjornsson, 2001; Claireaux et al., 1995; Freitas et al., 2016; Staveley et al., 2017). Growth also declines sharply above 16ºC (Rogers et al., 2011). Juvenile whiting similarly prefers temperatures around 15ºC, despite occupying a warmer distribution than cod (Asciutto et al., 2024; Calì et al., 2023). Our sea temperature analysis shows that eelgrass habitats routinely exceed these preferred temperatures during summer (Hattich et al., 2025), suggesting that juvenile gadids with strong behavioural thermoregulation are already excluded from these shallow habitats during warm periods. With continued warming, such exclusion is likely to intensify, compromising the ability of young gadids to access nursery habitats that provide shelter and foraging opportunities, likely with negative consequences for population persistence (Freitas et al., 2016).

Another juvenile migrant, plaice, showed higher thermal tolerance than gadids but low 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 reliance on behavioural thermoregulation, such as habitat shifting or substrate burial (Ziegler & Frisk, 2019). While the juvenile migrants studied showed low acclimation capacity, the shallow-water habitat generalists proved more tolerant to thermal stress. Gobies and sticklebacks displayed comparatively high thermal tolerance and moderate acclimation capacity, consistent with their broad habitat use. These generalist species are among the most abundant fishes in eelgrass habitats and play key roles as mesopredators and prey for fishes at higher trophic levels (Perry et al., 2018; Staveley et al., 2017). The black goby was both the most heat-tolerant and most plastic goby, with CT_{max} and ARR exceeding most other species, in line with previous estimates (Cowan et al., 2023).

Sticklebacks exhibited high thermal tolerance and a moderate acclimation capacity, consistent with previous work (Cowan et al., 2023; De Bonville et al., 2025; Mottola et al., 2022). Their ability to tolerate temperatures up to 25ºC, combined with rapid generation time and increasing abundance under warming and eutrophication, suggests they may increase in dominance in warming eelgrass habitats (Olin et al., 2022). While sticklebacks are highly robust species, the wrasses outperformed them in terms of acclimation capacity.

Wrasses exhibited the strongest short-term acclimation capacity of all species tested, despite intermediate CT_{max} values under ambient conditions. Their high ARR values matched earlier work on goldsinny wrasse (De Bonville et al., 2025) and suggests substantial phenotypic plasticity, consistent with their broad thermal niches and generalist habitat use across rocky reefs and seagrass meadows. Previous studies have documented high aerobic performance and plasticity in wrasses at temperatures exceeding those currently experienced in northern regions (Palma et al., 2025; Yuen et al., 2019), supporting the idea that these species are better equipped to tolerate future warming than others. However, wrasses have also shown significant physiological stress and mortality with exposure to multiple ocean stressors (Perry, Tamarit, Morgenroth, et al., 2024). The high acclimation capacity exhibited by wrasses is well suited to their habitat generalist strategy as they move regularly between different environmental conditions.

In contrast, stationary species may be less able to avoid longer-term temperature extremes. For example, the stationary pipefishes tested in our study displayed the highest thermal tolerance among all taxa but showed moderate acclimation capacity. As they are strongly associated with eelgrass meadows, pipefishes may benefit from high thermal tolerance in warming habitats, although limited plasticity could constrain their ability to cope with extreme temperatures. The three tested pipefishes all had preferred thermal maxima well above the simulated heatwave (Fig. 3B). Among pipefishes, the straightnose pipefish showed relatively high ARR, suggesting it might be better equipped to withstand increasingly frequent marine heatwaves in their northern distribution ranges (Monteiro et al., 2023).

A partial explanation for the observed interspecific differences in CT_{max} and ARR is the declining gain in thermal tolerance as species approach their upper thermal limits (Brett, 1952; Doudoroff, 1942; Fangue et al., 2014; Sandblom et al., 2016). Theoretically, cold-water species living above their optimal temperature have limited scope for further warm acclimation, whereas warm-tolerant species living below their optimum retain greater capacity for plasticity (Ern et al., 2023). This likely explains the weak acclimation observed in gadids and flatfishes, but it does not fully account for all patterns observed in the current study. Notably, pipefishes exhibited high CT_{max} but modest acclimation capacity, whereas wrasses showed strong plasticity despite intermediate tolerance. These differences likely reflect evolutionary and phylogenetic constraints of the tested groups (Comte & Olden, 2017). In our study, we measured CT_{max} using a standardized rapid ramping protocol to facilitate interspecific comparison, but such approaches may overestimate tolerance relative to natural warming rates and should be interpreted as comparative indices rather than direct predictors of survival under heatwaves (Ern et al., 2023; Jutfelt et al., 2019; Lefevre et al., 2021). Also, we designed the five-day exposure to reflect the minimum duration of a marine heatwave, but longer-term acclimation, long-term heat injury, developmental plasticity, or transgenerational effects could further modify responses. Population-level variation and local adaptation may also contribute to interspecific differences, as phenotypic and genotypic divergence has been documented in gobies, wrasses, and sympatric cod ecotypes 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).

Community and ecosystem implications

Differential thermal tolerance and acclimation capacity among eelgrass-associated fishes are likely to have cascading consequences for assemblage structure and ecosystem functioning. Such cascading effects are increasingly recognized as a hallmark of marine heatwave impacts in coastal ecosystems (Wernberg et al., 2025). Seagrass ecosystems experiencing warming have already shown increased dominance of warm-water species and declines of cold-water species, accompanied by poleward or depth distribution shifts in coastal regions globally (Burrows et al., 2019; Cheung et al., 2013; Fodrie et al., 2010). Such temperature-driven changes in community composition can modify predator–prey interactions and grazing pressure, triggering cascading effects through food webs and altering ecosystem functioning (Baden et al., 2012; Casini et al., 2009; Frank et al., 2005; Olin et al., 2022). Experimental and field studies have shown that increased abundance of mesopredatory fishes, such as gobies and sticklebacks, can intensify predation on invertebrate grazers, thereby promoting filamentous algal growth and reducing eelgrass resilience (Moksnes et al., 2008; Östman et al., 2016). If warming disproportionately excludes cold-affinity predators while favouring thermally tolerant mesopredators, temperature may act as an additional driver amplifying predator-release cascades in seagrass ecosystems, with implications for the long-term stability of coastal seascapes.

To conclude, our study demonstrates that eelgrass-associated fishes differ markedly in both upper thermal tolerance and short-term acclimation capacity, with important consequences for species persistence in warming eelgrass habitats. By analysing fine-scale temperature data, we show that eelgrass meadows off the Swedish West coast already experience larger extremes than reported regional warming trends estimated with satellite products, and that approach the thermal distribution ranges of several associated fishes. As a result, juveniles of cold-affinity demersal species that rely on behavioural thermoregulation are likely to become increasingly excluded from this important nursery habitat during warm periods. In contrast, mesopredatory fishes with generalist life histories and moderate-to-high thermal tolerance or acclimation capacity may persist or increase in dominance as marine heatwaves intensify. Together, our findings highlight how species-specific physiological constraints combined with habitat specific warming can shape future eelgrass fish assemblages.

Acknowledgements

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. E.T. was supported by the Center for Sea and Society, the Department of Earth Sciences at the University of Gothenburg and Wåhlströms Stiftelse.

CRediT

Conceptualization: ET, FJ; Methodology: ET, FS, FJ; Investigation: ET, FS, LP, ERL, HS; Validation: LG, DP, HL, MG, FJ; Visualization: ET; Data Curation: ET; Formal Analysis: ET; Resources: LG, HL, DP, MG, FJ; Project Administration: ET; Software: ET; Writing – original draft: ET; Supervision: DP, HL, MG, FJ; Writing-review & editing: ET, FS, LP, ERM, HS, LG, DP, HL, MG, FJ.

Supporting information

Table S1. Metadata for CT_{max} trials.

Figure S1. Thermal ramping curves of CT_{max} trials for each species.

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} (Heated).

Table S7. CT_{max} statistical contrasts.

Table S8. Thermal tolerance gain (TTgain) and acclimation response ratio (ARR) by species.

References

Asciutto, E., Maioli, F., Manfredi, C., Anibaldi, A., Cimini, J., Isailović, I., Marčeta, B., & Casini, M. (2024). Spatio-temporal patterns of whiting (Merlangius merlangus) in the Adriatic Sea under environmental forcing. *PLOS ONE*, *19*(3), e0289999. https://doi.org/10.1371/journal.pone.0289999

Baden, S., Emanuelsson, A., Pihl, L., Svensson, C., & Åberg, P. (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., Mächler, M., Bolker, B., & Walker, S. (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., Heck, K. L., Able, K. W., Childers, D. L., Eggleston, D. B., Gillanders, B. M., Halpern, B., Hays, C. G., Hoshino, K., Minello, T. J., Orth, R. J., Sheridan, P. F., & Weinstein, M. P. (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*(8), 633–641. https://doi.org/10.1641/0006-3568(2001)051[0633:TICAMO]2.0.CO;2

Becker, C. D., & Genoway, R. G. (1979). Evaluation of the critical thermal maximum for determining thermal tolerance of freshwater fish. *Environmental Biology of Fishes*, *4*(3), 245–256. https://doi.org/10.1007/BF00005481

Beitinger, T. L., Bennett, W. A., & McCauley, R. W. (2000). Temperature Tolerances of North American Freshwater Fishes Exposed to Dynamic Changes in Temperature. *Environmental Biology of Fishes*, *58*(3), 237–275. https://doi.org/10.1023/A:1007676325825

Bilyk, K. T., & DeVries, A. L. (2011). Heat tolerance and its plasticity in Antarctic fishes. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *158*(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*(1), 29–38. https://doi.org/10.1006/jmsc.2000.0986

Boström, C., Baden, S., Bockelmann, A., Dromph, K., Fredriksen, S., Gustafsson, C., Krause-Jensen, D., Möller, T., Nielsen, S. L., Olesen, B., Olsen, J., Pihl, L., & Rinde, E. (2014). Distribution, structure and function of Nordic eelgrass *(Zostera marina)* ecosystems: Implications for coastal management and conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *24*(3), 410–434. https://doi.org/10.1002/aqc.2424

Brett, J. R. (1952). Temperature Tolerance in Young Pacific Salmon, Genus Oncorhynchus. *Journal of the Fisheries Research Board of Canada*, *9*(6), 265–323. https://doi.org/10.1139/f52-016

Brijs, J., Tran, L. L., Moore, C., Souza, T., Schakmann, M., Grellman, K., & Johansen, J. L. (2025). Outlasting the Heat: Collapse of Herbivorous Fish Control of Invasive Algae During Marine Heatwaves. *Global Change Biology*, *31*(8), e70438. https://doi.org/10.1111/gcb.70438

Burrows, M. T., Bates, A. E., Costello, M. J., Edwards, M., Edgar, G. J., Fox, C. J., Halpern, B. S., Hiddink, J. G., Pinsky, M. L., Batt, R. D., García Molinos, J., Payne, B. L., Schoeman, D. S., Stuart-Smith, R. D., & Poloczanska, E. S. (2019). Ocean community warming responses explained by thermal affinities and temperature gradients. *Nature Climate Change*, *9*(12), 959–963. https://doi.org/10.1038/s41558-019-0631-5

Burton, T., & Einum, S. (2025). High Capacity for Physiological Plasticity Occurs at a Slow Rate in Ectotherms. *Ecology Letters*, *28*(1), e70046. https://doi.org/10.1111/ele.70046

Calì, F., Stranci, F., La Mesa, M., Mazzoldi, C., Arneri, E., & Santojanni, A. (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*(7), 341. https://doi.org/10.3390/fishes8070341

Calvin, K., Dasgupta, D., Krinner, G., Mukherji, A., Thorne, P. W., Trisos, C., Romero, J., Aldunce, P., Barrett, K., Blanco, G., Cheung, W. W. L., Connors, S., Denton, F., Diongue-Niang, A., Dodman, D., Garschagen, M., Geden, O., Hayward, B., Jones, C., … Péan, C. (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 [Core Writing Team, H. Lee and J. Romero (eds.)]. IPCC, Geneva, Switzerland.* (First). Intergovernmental Panel on Climate Change (IPCC). https://doi.org/10.59327/IPCC/AR6-9789291691647

Casini, M., Hjelm, J., Molinero, J.-C., Lövgren, J., Cardinale, M., Bartolino, V., Belgrano, A., & Kornilovs, G. (2009). Trophic cascades promote threshold-like shifts in pelagic marine ecosystems. *Proceedings of the National Academy of Sciences*, *106*(1), 197–202. https://doi.org/10.1073/pnas.0806649105

Cheng, L., Abraham, J., Trenberth, K. E., Reagan, J., Zhang, H.-M., Storto, A., Von Schuckmann, K., Pan, Y., Zhu, Y., Mann, M. E., Zhu, J., Wang, F., Yu, F., Locarnini, R., Fasullo, J., Huang, B., Graham, G., Yin, X., Gouretski, V., … Gues, F. (2025). Record High Temperatures in the Ocean in 2024. *Advances in Atmospheric Sciences*, *42*(6), 1092–1109. https://doi.org/10.1007/s00376-025-4541-3

Cheung, W. W. L., Watson, R., & Pauly, D. (2013). Signature of ocean warming in global fisheries catch. *Nature*, *497*(7449), Article 7449. https://doi.org/10.1038/nature12156

Claireaux, G., Webber, D. M., Kerr, S. R., & Boutilier, R. G. (1995). Physiology and Behaviour of Free-Swimming Atlantic COD (Gadus Morhua) Facing Fluctuating Temperature Conditions. *Journal of Experimental Biology*, *198*(1), 49–60. https://doi.org/10.1242/jeb.198.1.49

Comte, L., & Olden, J. D. (2017). Evolutionary and environmental determinants of freshwater fish thermal tolerance and plasticity. *Global Change Biology*, *23*(2), 728–736. https://doi.org/10.1111/gcb.13427

Cowan, Z.-L., Andreassen, A. H., De Bonville, J., Green, L., Binning, S. A., Silva-Garay, L., Jutfelt, F., & Sundin, J. (2023). A novel method for measuring acute thermal tolerance in fish embryos. *Conservation Physiology*, *11*(1), coad061. https://doi.org/10.1093/conphys/coad061

De Bonville, J., Andreassen, A. H., Cowan, Z.-L., Silva-Garay, L., Leeuwis, R. H. J., Åsheim, E. R., Speers-Roesch, B., Raby, G. D., Binning, S. A., & Jutfelt, F. (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

de los Santos, C. B., Krause-Jensen, D., Alcoverro, T., Marbà, N., Duarte, C. M., van Katwijk, M. M., Pérez, M., Romero, J., Sánchez-Lizaso, J. L., Roca, G., Jankowska, E., Pérez-Lloréns, J. L., Fournier, J., Montefalcone, M., Pergent, G., Ruiz, J. M., Cabaço, S., Cook, K., Wilkes, R. J., … Santos, R. (2019). Recent trend reversal for declining European seagrass meadows. *Nature Communications*, *10*(1), 3356. https://doi.org/10.1038/s41467-019-11340-4

Desforges, J. E., Birnie-Gauvin, K., Jutfelt, F., Gilmour, K. M., Eliason, E. J., Dressler, T. L., McKenzie, D. J., Bates, A. E., Lawrence, M. J., Fangue, N., & Cooke, S. J. (2023). The ecological relevance of critical thermal maxima methodology for fishes. *Journal of Fish Biology*, *102*(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). *The Biological Bulletin*, *83*(2), 219–244. https://doi.org/10.2307/1538144

Drost, H. E., Lo, M., Carmack, E. C., & Farrell, A. P. (2016). Acclimation potential of Arctic cod (Boreogadus saida) from the rapidly warming Arctic Ocean. *Journal of Experimental Biology*, *219*(19), 3114–3125. https://doi.org/10.1242/jeb.140194

Ern, R., Andreassen, A. H., & Jutfelt, F. (2023). Physiological Mechanisms of Acute Upper Thermal Tolerance in Fish. *Physiology*, *38*(3), 141–158. https://doi.org/10.1152/physiol.00027.2022

Fangue, N. A., Wunderly, M. A., Dabruzzi, T. F., & Bennett, W. A. (2014). Asymmetric Thermal Acclimation Responses Allow Sheepshead Minnow Cyprinodon variegatus to Cope with Rapidly Changing Temperatures. *Physiological and Biochemical Zoology*, *87*(6), 805–816. https://doi.org/10.1086/678965

Faust, E., Jansson, E., André, C., Halvorsen, K. T., Dahle, G., Knutsen, H., Quintela, M., & Glover, K. A. (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*(6), 1572–1587. https://doi.org/10.1111/eva.13220

Fodrie, F. J., HECK Jr, K. L., Powers, S. P., Graham, W. M., & Robinson, K. L. (2010). Climate-related, decadal-scale assemblage changes of seagrass-associated fishes in the northern Gulf of Mexico. *Global Change Biology*, *16*(1), 48–59. https://doi.org/10.1111/j.1365-2486.2009.01889.x

Frank, K. T., Petrie, B., Choi, J. S., & Leggett, W. C. (2005). Trophic Cascades in a Formerly Cod-Dominated Ecosystem. *Science*, *308*(5728), 1621–1623. https://doi.org/10.1126/science.1113075

Freitas, C., Olsen, E. M., Knutsen, H., Albretsen, J., & Moland, E. (2016). Temperature-associated habitat selection in a cold-water marine fish. *Journal of Animal Ecology*, *85*(3), 628–637. https://doi.org/10.1111/1365-2656.12458

Garrabou, J., Coma, R., Bensoussan, N., Bally, M., Chevaldonné, P., Cigliano, M., Diaz, D., Harmelin, J. G., Gambi, M. C., Kersting, D. K., Ledoux, J. B., Lejeusne, C., Linares, C., Marschal, C., Pérez, T., Ribes, M., Romano, J. C., Serrano, E., Teixido, N., … Cerrano, C. (2009). Mass mortality in Northwestern Mediterranean rocky benthic communities: Effects of the 2003 heat wave. *Global Change Biology*, *15*(5), 1090–1103. https://doi.org/10.1111/j.1365-2486.2008.01823.x

Gómez-Gras, D., Linares, C., & Capdevila, P. (2025). Novel contributions to marine heatwave ecology: Identifying and addressing knowledge gaps in ecological impacts. *Journal of Animal Ecology*, *94*(8), 1481–1491. https://doi.org/10.1111/1365-2656.70084

Green, L., Faust, E., Hinchcliffe, J., Brijs, J., Holmes, A., Englund Örn, F., Svensson, O., Roques, J. A. C., Leder, E. H., Sandblom, E., & Kvarnemo, C. (2023). Invader at the edge—Genomic origins and physiological differences of round gobies across a steep urban salinity gradient. *Evolutionary Applications*, *16*(2), 321–337. https://doi.org/10.1111/eva.13437

Hattich, G. S. I., Jahnke, M., Enge, S., Niemi, N., Bernal-Gómez, M., De Wit, P., Havenhand, J. N., & Pansch, C. (2025). Small-scale thermal habitat variability may not determine seagrass resilience to climate change. *Limnology and Oceanography*, *n/a*(n/a). https://doi.org/10.1002/lno.70049

Heck Hay, K., Hays, G., & Orth, R. (2003). Critical evaluation of the nursery role hypothesis for seagrass meadows. *Marine Ecology Progress Series*, *253*, 123–136. https://doi.org/10.3354/meps253123

Henriksson, S., Pereyra, R. T., Sodeland, M., Ortega-Martinez, O., Knutsen, H., Wennhage, H., & André, C. (2023). Mixed origin of juvenile Atlantic cod (*Gadus morhua*) along the Swedish west coast. *ICES Journal of Marine Science*, *80*(1), 145–157. https://doi.org/10.1093/icesjms/fsac220

Hobday, A. J., Alexander, L. V., Perkins, S. E., Smale, D. A., Straub, S. C., Oliver, E. C. J., Benthuysen, J. A., Burrows, M. T., Donat, M. G., Feng, M., Holbrook, N. J., Moore, P. J., Scannell, H. A., Sen Gupta, A., & Wernberg, T. (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., Head, M. L., Lanfear, R., & Jennions, M. D. (2015). Evidence of Experimental Bias in the Life Sciences: Why We Need Blind Data Recording. *PLOS Biology*, *13*(7), e1002190. https://doi.org/10.1371/journal.pbio.1002190

Huang, B., Yin, X., Carton, J. A., Chen, L., Graham, G., Hogan, P., Smith, T., & Zhang, H.-M. (2024). Record High Sea Surface Temperatures in 2023. *Geophysical Research Letters*, *51*(14), e2024GL108369. https://doi.org/10.1029/2024GL108369

Jr, M. J. A. (2009). *Thermal Adaptation: A Theoretical and Empirical Synthesis*. Oxford University Press.

Jutfelt, F., Ern, R., Leeuwis, R. H. J., & Clark, T. D. (2024). Effects of climate warming. In *Encyclopedia of Fish Physiology* (pp. 14–31). Elsevier. https://doi.org/10.1016/B978-0-323-90801-6.00183-X

Jutfelt, F., Roche, D. G., Clark, T. D., Norin, T., Binning, S. A., Speers-Roesch, B., Amcoff, M., Morgan, R., Andreassen, A. H., & Sundin, J. (2019). Brain cooling marginally increases acute upper thermal tolerance in Atlantic cod. *Journal of Experimental Biology*, *222*(19), jeb208249. https://doi.org/10.1242/jeb.208249

Krause-Jensen, D., Duarte, C. M., Sand-Jensen, K., & Carstensen, J. (2021). Century-long records reveal shifting challenges to seagrass recovery. *Global Change Biology*, *27*(3), 563–575. https://doi.org/10.1111/gcb.15440

L.Claussen, D. (1977). Thermal acclimation in ambystomatid salamanders. *Comparative Biochemistry and Physiology Part A: Physiology*, *58*(4), 333–340. https://doi.org/10.1016/0300-9629(77)90150-5

Leder, E. H., André, C., Le Moan, A., Töpel, M., Blomberg, A., Havenhand, J. N., Lindström, K., Volckaert, F. A. M., Kvarnemo, C., Johannesson, K., & Svensson, O. (2021). Post-glacial establishment of locally adapted fish populations over a steep salinity gradient. *Journal of Evolutionary Biology*, *34*(1), 138–156. https://doi.org/10.1111/jeb.13668

Lefcheck, J. S., Hughes, B. B., Johnson, A. J., Pfirrmann, B. W., Rasher, D. B., Smyth, A. R., Williams, B. L., Beck, M. W., & Orth, R. J. (2019). Are coastal habitats important nurseries? A meta-analysis. *Conservation Letters*, *12*(4), e12645. https://doi.org/10.1111/conl.12645

Lefcheck, J. S., Wilcox, D. J., Murphy, R. R., Marion, S. R., & Orth, R. J. (2017). Multiple stressors threaten the imperiled coastal foundation species eelgrass (Zostera marina) in Chesapeake Bay, USA. *Global Change Biology*, *23*(9), 3474–3483. https://doi.org/10.1111/gcb.13623

Lefevre, S., Wang, T., & McKenzie, D. J. (2021). The role of mechanistic physiology in investigating impacts of global warming on fishes. *Journal of Experimental Biology*, *224*(Suppl_1), jeb238840. https://doi.org/10.1242/jeb.238840

Madeira, D., Narciso, L., Cabral, H. N., & Vinagre, C. (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., Iacarella, J. C., & Baum, J. K. (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., Zhang, Y., Eliason, E. J., Schulte, P. M., Claireaux, G., Blasco, F. R., Nati, J. J. H., & Farrell, A. P. (2021). Intraspecific variation in tolerance of warming in fishes. *Journal of Fish Biology*, *98*(6), 1536–1555. https://doi.org/10.1111/jfb.14620

Messmer, V., Pratchett, M. S., Hoey, A. S., Tobin, A. J., Coker, D. J., Cooke, S. J., & Clark, T. D. (2017). Global warming may disproportionately affect larger adults in a predatory coral reef fish. *Global Change Biology*, *23*(6), 2230–2240. https://doi.org/10.1111/gcb.13552

Mohamed, B., Barth, A., Van Der Zande, D., & Alvera-Azcárate, A. (2025). Amplified warming and marine heatwaves in the North Sea under a warming climate and their impacts. *Ocean Science*, *21*(5), 2505–2525. https://doi.org/10.5194/os-21-2505-2025

Moksnes, P.-O., Gullström, M., Tryman, K., & Baden, S. (2008). Trophic cascades in a temperate seagrass community. *Oikos*, *117*(5), 763–777. https://doi.org/10.1111/j.0030-1299.2008.16521.x

Monteiro, N., Pinheiro, S., Magalhães, S., Tarroso, P., & Vincent, A. (2023). Predicting the impacts of climate change on the distribution of European syngnathids over the next century. *Frontiers in Marine Science*, *10*. https://doi.org/10.3389/fmars.2023.1138657

Morash, A. J. (2024). Measures of thermal tolerance. In *Encyclopedia of Fish Physiology* (pp. 32–46). Elsevier. https://doi.org/10.1016/B978-0-323-90801-6.00136-1

Morgan, R., Finnøen, M. H., & Jutfelt, F. (2018). CTmax is repeatable and doesn't reduce growth in zebrafish. *Scientific Reports*, *8*(1), Article 1. https://doi.org/10.1038/s41598-018-25593-4

Morley, S. A., Peck, L. S., Sunday, J. M., Heiser, S., & Bates, A. E. (2019). Physiological acclimation and persistence of ectothermic species under extreme heat events. *Global Ecology and Biogeography*, *28*(7), 1018–1037. https://doi.org/10.1111/geb.12911

Mottola, G., López, M. E., Vasemägi, A., Nikinmaa, M., & Anttila, K. (2022). Are you ready for the heat? Phenotypic plasticity versus adaptation of heat tolerance in three-spined stickleback. *Ecosphere*, *13*(4), e4015. https://doi.org/10.1002/ecs2.4015

Moyano, M., Candebat, C., Ruhbaum, Y., Álvarez-Fernández, S., Claireaux, G., Zambonino-Infante, J.-L., & Peck, M. A. (2017). Effects of warming rate, acclimation temperature and ontogeny on the critical thermal maximum of temperate marine fish larvae. *PLOS ONE*, *12*(7), e0179928. https://doi.org/10.1371/journal.pone.0179928

Nguyen, H. M., Ralph, P. J., Marín-Guirao, L., Pernice, M., & Procaccini, G. (2021). Seagrasses in an era of ocean warming: A review. *Biological Reviews*, *96*(5), 2009–2030. https://doi.org/10.1111/brv.12736

Nordlund, L. M., Unsworth, R. K. F., Wallner-Hahn, S., Ratnarajah, L., Beca-Carretero, P., Boikova, E., Bull, J. C., Chefaoui, R. M., de los Santos, C. B., Gagnon, K., Garmendia, J. M., Gizzi, F., Govers, L. L., Gustafsson, C., Hineva, E., Infantes, E., Canning-Clode, J., Jahnke, M., Kleitou, P., … Wilkes, R. (2024). One hundred priority questions for advancing seagrass conservation in Europe. *PLANTS, PEOPLE, PLANET*, *6*(3), 587–603. https://doi.org/10.1002/ppp3.10486

Olin, A. B., Olsson, J., Eklöf, J. S., Eriksson, B. K., Kaljuste, O., Briekmane, L., & Bergström, U. (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*(5), 1419–1434. https://doi.org/10.1093/icesjms/fsac073

Oliver, E. C. J., Donat, M. G., Burrows, M. T., Moore, P. J., Smale, D. A., Alexander, L. V., Benthuysen, J. A., Feng, M., Sen Gupta, A., Hobday, A. J., Holbrook, N. J., Perkins-Kirkpatrick, S. E., Scannell, H. A., Straub, S. C., & Wernberg, T. (2018). Longer and more frequent marine heatwaves over the past century. *Nature Communications*, *9*(1), 1324. https://doi.org/10.1038/s41467-018-03732-9

Olsen, A. Y., Larson, S., Padilla-Gamiño, J. L., & Klinger, T. (2022). Changes in fish assemblages after marine heatwave events in West Hawaiʻi Island. *Marine Ecology Progress Series*, *698*, 95–109. https://doi.org/10.3354/meps14156

Orth, R. J., Carruthers, T. J. B., Dennison, W. C., Duarte, C. M., Fourqurean, J. W., Heck, K. L., Hughes, A. R., Kendrick, G. A., Kenworthy, W. J., Olyarnik, S., Short, F. T., Waycott, M., & Williams, S. L. (2006). A Global Crisis for Seagrass Ecosystems. *BioScience*, *56*(12), 987–996. https://doi.org/10.1641/0006-3568(2006)56[987:AGCFSE]2.0.CO;2

Östman, Ö., Eklöf, J., Eriksson, B. K., Olsson, J., Moksnes, P.-O., & Bergström, U. (2016). Top-down control as important as nutrient enrichment for eutrophication effects in North Atlantic coastal ecosystems. *Journal of Applied Ecology*, *53*(4), 1138–1147. https://doi.org/10.1111/1365-2664.12654

Palma, P. A., Bekaert, M., Gutierrez, A. P., Abacan, E. J. C., Migaud, H., & Betancor, M. B. (2025). Plasticity of thermal tolerance and associated gill transcriptome in ballan wrasse (Labrus bergylta). *Frontiers in Marine Science*, *11*. https://doi.org/10.3389/fmars.2024.1507994

Pearce, A., Faskel, F., & Hyndes, G. (2006). Nearshore sea temperature variability off Rottnest Island (Western Australia) derived from satellite data. *International Journal of Remote Sensing*, *27*(12), 2503–2518. https://doi.org/10.1080/01431160500472138

Peck, L. S., Morley, S. A., Richard, J., & Clark, M. S. (2014). Acclimation and thermal tolerance in Antarctic marine ectotherms. *Journal of Experimental Biology*, *217*(1), 16–22. https://doi.org/10.1242/jeb.089946

Perry, D., Staveley, T. A. B., & Gullström, M. (2018). Habitat Connectivity of Fish in Temperate Shallow-Water Seascapes. *Frontiers in Marine Science*, *4*, 440. https://doi.org/10.3389/fmars.2017.00440

Perry, D., Tamarit, E., Morgenroth, D., Gräns, A., Sturve, J., Gullström, M., Thor, P., & Wennhage, H. (2024). The heat is on: Sensitivity of goldsinny wrasse to global climate change. *Conservation Physiology*, *12*(1), coae068. https://doi.org/10.1093/conphys/coae068

Perry, D., Tamarit, E., Sundell, E., Axelsson, M., Bergman, S., Gräns, A., Gullström, M., Sturve, J., & Wennhage, H. (2024). Physiological responses of Atlantic cod to climate change indicate that coastal ecotypes may be better adapted to tolerate ocean stressors. *Scientific Reports*, *14*(1), 12896. https://doi.org/10.1038/s41598-024-62700-0

Phinn, S. R., Kovacs, E. M., Roelfsema, C. M., Canto, R. F., Collier, C. J., & McKenzie, L. J. (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*(8), 803–824. https://doi.org/10.1080/17538947.2017.1359343

Pihl, L., & Wennhage, H. (2002). Structure and diversity of fish assemblages on rocky and soft bottom shores on the Swedish west coast. *Journal of Fish Biology*, *61*(sA), 148–166. https://doi.org/10.1111/j.1095-8649.2002.tb01768.x

Raby, G. D., Morgan, R., Andreassen, A. H., Stewart, E. M. C., De Bonville, J., Hoots, E. C., Kuchenmüller, L., Metz, M., Rowsey, L. E., Green, L., Griffin, R. A., Martin, S., Reid, H. B., Ern, R., Åsheim, E. R., Cowan, Z.-L., Leeuwis, R. H. J., Blewett, T. A., Speers-Roesch, B., … Jutfelt, F. (2025). Measuring critical thermal maximum in aquatic ectotherms: A practical guide. *Methods in Ecology and Evolution*, *16*(10), 2208–2228. https://doi.org/10.1111/2041-210X.70103

Reynolds, R. W., Smith, T. M., Liu, C., Chelton, D. B., Casey, K. S., & Schlax, M. G. (2007). Daily High-Resolution-Blended Analyses for Sea Surface Temperature. *Journal of Climate*, *20*(22), 5473–5496. https://doi.org/10.1175/2007JCLI1824.1

Robinson, C. L. K., Yakimishyn, J., & Evans, R. (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*. https://doi.org/10.3389/fmars.2022.980703

Rogers, L. A., Stige, L. C., Olsen, E. M., Knutsen, H., Chan, K.-S., & Stenseth, N. Chr. (2011). Climate and population density drive changes in cod body size throughout a century on the Norwegian coast. *Proceedings of the National Academy of Sciences*, *108*(5), 1961–1966. https://doi.org/10.1073/pnas.1010314108

Saha, M., Barboza, F., Somerfield, P., Al-Janabi, B., Beck, M., Brakel, J., Ito, M., Pansch, C., Nascimento-Schulze, J., Thor, S., Weinberger, F., & Sawall, Y. (2020). Response of foundation macrophytes to near-natural simulated marine heatwaves. *GLOBAL CHANGE BIOLOGY*, *26*(2), 417–430. https://doi.org/10.1111/gcb.14801

Sandblom, E., Clark, T. D., Gräns, A., Ekström, A., Brijs, J., Sundström, L. F., Odelström, A., Adill, A., Aho, T., & Jutfelt, F. (2016). Physiological constraints to climate warming in fish follow principles of plastic floors and concrete ceilings. *Nature Communications*, *7*(1), 11447. https://doi.org/10.1038/ncomms11447

Seebacher, F., White, C. R., & Franklin, C. E. (2015). Physiological plasticity increases resilience of ectothermic animals to climate change. *Nature Climate Change*, *5*(1), 61–66. https://doi.org/10.1038/nclimate2457

Sert, N. P. du, Ahluwalia, A., Alam, S., Avey, M. T., Baker, M., Browne, W. J., Clark, A., Cuthill, I. C., Dirnagl, U., Emerson, M., Garner, P., Holgate, S. T., Howells, D. W., Hurst, V., Karp, N. A., Lazic, S. E., Lidster, K., MacCallum, C. J., Macleod, M., … Würbel, H. (2020). Reporting animal research: Explanation and elaboration for the ARRIVE guidelines 2.0. *PLOS Biology*, *18*(7), e3000411. https://doi.org/10.1371/journal.pbio.3000411

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

Smale, D. A., Wernberg, T., Oliver, E. C. J., Thomsen, M., Harvey, B. P., Straub, S. C., Burrows, M. T., Alexander, L. V., Benthuysen, J. A., Donat, M. G., Feng, M., Hobday, A. J., Holbrook, N. J., Perkins-Kirkpatrick, S. E., Scannell, H. A., Sen Gupta, A., Payne, B. L., & Moore, P. J. (2019). Marine heatwaves threaten global biodiversity and the provision of ecosystem services. *Nature Climate Change*, *9*(4), 306–312. https://doi.org/10.1038/s41558-019-0412-1

Smale, D., & Wernberg, T. (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

Smith, K. E., Aubin, M., Burrows, M. T., Filbee-Dexter, K., Hobday, A. J., Holbrook, N. J., King, N. G., Moore, P. J., Sen Gupta, A., Thomsen, M., Wernberg, T., Wilson, E., & Smale,

D. A. (2024). Global impacts of marine heatwaves on coastal foundation species. *Nature Communications*, *15*(1), 5052. https://doi.org/10.1038/s41467-024-49307-9

Smith, K. E., Burrows, M. T., Hobday, A. J., King, N. G., Moore, P. J., Sen Gupta, A., Thomsen, M. S., Wernberg, T., & Smale, D. A. (2023). Biological Impacts of Marine Heatwaves. *Annual Review of Marine Science*, *15*(1), 119–145. https://doi.org/10.1146/annurev-marine-032122-121437

Smith, K. E., Sen Gupta, A., Amaya, D., Benthuysen, J. A., Burrows, M. T., Capotondi, A., Filbee-Dexter, K., Frölicher, T. L., Hobday, A. J., Holbrook, N. J., Malan, N., Moore, P. J., Oliver, E. C. J., Richaud, B., Salcedo-Castro, J., Smale, D. A., Thomsen, M., & Wernberg, T. (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., van der Mheen, M., Pessarrodona, A., Wood, G. V., Filbee-Dexter, K., Neufeld, C. J., Montie, S., Coleman, M. A., & Wernberg, T. (2024). Impacts of marine heatwaves in coastal ecosystems depend on local environmental conditions. *Global Change Biology*, *30*(8), e17469. https://doi.org/10.1111/gcb.17469

Staveley, T. A. B., Perry, D., Lindborg, R., & Gullström, M. (2017). Seascape structure and complexity influence temperate seagrass fish assemblage composition. *Ecography*, *40*(8), 936–946. https://doi.org/10.1111/ecog.02745

Strydom, S., Murray, K., Wilson, S., Huntley, B., Rule, M., Heithaus, M., Bessey, C., Kendrick, G. A., Burkholder, D., Fraser, M. W., & Zdunic, K. (2020). Too hot to handle: Unprecedented seagrass death driven by marine heatwave in a World Heritage Area. *Global Change Biology*, *26*(6), 3525–3538. https://doi.org/10.1111/gcb.15065

Sunday, J., Bennett, J. M., Calosi, P., Clusella-Trullas, S., Gravel, S., Hargreaves, A. L., Leiva, F. P., Verberk, W. C. E. P., Olalla-Tárraga, M. Á., & Morales-Castilla, I. (2019). Thermal tolerance patterns across latitude and elevation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *374*(1778), 20190036. https://doi.org/10.1098/rstb.2019.0036

Thalmann, H. L., Laurel, B. J., Almeida, L. Z., Osborne, K. E., Marshall, K., & Miller, J. A. (2024). Marine heatwaves alter the nursery function of coastal habitats for juvenile Gulf of Alaska Pacific cod. *Scientific Reports*, *14*(1), 14018. https://doi.org/10.1038/s41598-024-63897-w

Vasseur, D. A., DeLong, J. P., Gilbert, B., Greig, H. S., Harley, C. D. G., McCann, K. S., Savage, V., Tunney, T. D., & O’Connor, M. I. (2014). Increased temperature variation poses a greater risk to species than climate warming. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1779), 20132612. https://doi.org/10.1098/rspb.2013.2612

Vinagre, C., Leal, I., Mendonça, V., Madeira, D., Narciso, L., Diniz, M. S., & Flores, A. A. V. (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., Moreira, L., Cancet, M., Gues, F., Autret, E., Baker, J., Bricaud, C., Bourdalle-Badie, R., Castrillo, L., Cheng, L., Chevallier, F., Ciani, D., De Pascual-Collar, A., De Toma, V., Drevillon, M., Fanelli, C., Garric, G., Gehlen, M., Giesen, R., … Zuo, H. (2024). The state of the global ocean. *State of the Planet*, *4-osr8*, 1–30. https://doi.org/10.5194/sp-4-osr8-1-2024

W. Schlegel, R., & J. Smit, A. (2018). heatwaveR: A central algorithm for the detection of heatwaves and cold-spells. *Journal of Open Source Software*, *3*(27), 821. https://doi.org/10.21105/joss.00821

Wernberg, T., Thomsen, M. S., Burrows, M. T., Filbee-Dexter, K., Hobday, A. J., Holbrook, N. J., Montie, S., Moore, P. J., Oliver, E. C. J., Sen Gupta, A., Smale, D. A., & Smith, K. (2025). Marine heatwaves as hot spots of climate change and impacts on biodiversity and ecosystem services. *Nature Reviews Biodiversity*, *1*(7), 461–479. https://doi.org/10.1038/s44358-025-00058-5

Wickham, H. (2016). Programming with ggplot2. In H. Wickham (Ed.), *Ggplot2: Elegant Graphics for Data Analysis* (pp. 241–253). Springer International Publishing. https://doi.org/10.1007/978-3-319-24277-4_12

Yu, L., Khachaturyan, M., Matschiner, M., Healey, A., Bauer, D., Cameron, B., Cusson, M., Emmett Duffy, J., Joel Fodrie, F., Gill, D., Grimwood, J., Hori, M., Hovel, K., Hughes, A. R., Jahnke, M., Jenkins, J., Keymanesh, K., Kruschel, C., Mamidi, S., … Reusch, T. B. H. (2023). Ocean current patterns drive the worldwide colonization of eelgrass (Zostera marina). *Nature Plants*, *9*(8), 1207–1220. https://doi.org/10.1038/s41477-023-01464-3

Yuen, J. W., Dempster, T., Oppedal, F., & Hvas, M. (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., & Frisk, M. G. (2019). Flatfish utilize sediment blanket to facilitate thermoregulation. *Marine Ecology Progress Series*, *609*, 179–186. https://doi.org/10.3354/meps12817