Submitted version

Seasonal warming and marine heatwaves shape thermal acclimation and growth of juvenile European plaice in a coastal nursery habitat

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Total word count

8093

Lay Summary

Shallow coastal nurseries are important habitats for juvenile fishes, but these waters are warming with climate change. We found that juvenile plaice adjust their heat tolerance to seasonal warming, but this flexibility is limited during marine heatwaves and their growth decreases under extreme summer temperatures.

Abstract

Global climate change is driving ocean warming and exposing shallow coastal nursery habitats to increasingly frequent marine heatwaves. The European plaice (*Pleuronectes platessa*) is a flatfish that settles in shallow (<1.5m) sandy bays of the Northeast Atlantic in spring and remains until late summer migration, experiencing peak seasonal temperatures during a critical period for juvenile growth. We combined satellite-derived sea surface temperatures (SSTs), high-resolution *in situ* water temperatures, seasonal field sampling, and laboratory experiments to examine how seasonal warming and marine heatwaves influence thermal acclimation and growth of 0-group plaice between May and September 2025, in a nursery bay on the Swedish Skagerrak coast. Regional SST increased by 0.45°C decade^{-1} between 1982 and 2025, coinciding with increases in marine heatwave frequency, duration and intensity. We identified three marine heatwaves occurring near the nursery site during 2025, but *in situ* temperature records revealed longer lasting and more intense thermal extremes than regional SSTs. Wild plaice showed capacity to acclimate to seasonal temperatures, with Critical Thermal Maximum (CT_{max}) closely tracking seasonal warming. Also, plaice exposed to a simulated heatwave rapidly induced the expression of heat shock proteins. In contrast, plaice's upper thermal tolerance did not increase during a natural marine heatwave, indicating limited acclimation capacity. When exposed to chronic warming, growth was maintained at 19-21°C, but declined at 24°C, a temperature repeatedly recorded within the nursery bay during summer. Together, these results show that newly settled plaice possess substantial physiological plasticity to buffer seasonal warming during the first growth season and to respond to acute heat stress with rapid molecular responses. However, this plasticity was insufficient to maintain length growth under prolonged warming. As marine heatwaves intensify in the North Sea, increasingly stressful temperatures may constrain juvenile fish growth and the quality of shallow coastal nursery habitats may decline.

Keywords

Climate warming; marine heatwaves; thermal acclimation, Critical Thermal Maximum, European plaice, growth,

1 | Introduction

Global climate change is raising ocean temperatures and exposing marine organisms to increasingly frequent and intense marine heatwaves (Frölicher *et al.*, 2018; Oliver *et al.*, 2018; Calvin *et al.*, 2023). Marine heatwaves cause acute temperature stress, and species and populations with narrow distributions, limited mobility and proximity to their warm distribution limits are most vulnerable (Wernberg *et al.*, 2025). Shallow coastal ecosystems are particularly vulnerable to extreme heat because water temperatures can fluctuate rapidly over hours to days due to depth, tides or wave (Smale and Wernberg, 2009; Helmuth *et al.*, 2010, 2014). Shallow-water habitats provide essential nursery grounds for many fish species, supporting juvenile growth, predator avoidance and ultimately recruitment into adult populations (Beck *et al.*, 2001; Levin *et al.*, 2001; Dahlgren *et al.*, 2006). Ecological processes acting during juvenile stages can create a bottleneck for survival and subsequent recruitment (Sogard, 1997). Climate warming is expected to reduce the quality of shallow

coastal nursery habitats for juvenile fishes and change their functioning (McLean *et al.*, 2019), making it increasingly important to understand whether juvenile fishes can maintain growth and survival under warming.

Satellite-derived sea surface temperatures (SSTs) have transformed our understanding of large-scale ocean warming and are widely used to estimate warming trends and marine heatwaves globally (Reynolds *et al.*, 2007). However, SSTs represent only the upper skin layer of the ocean and often underestimate the fine-scale variability and extremes occurring near the shore (Smale and Wernberg, 2009). Consequently, reliance on SSTs often overlooks environmental variability at the scales relevant to physiological stress for individual organisms (Helmuth *et al.*, 2010).

For ectotherms, water temperature governs metabolism, growth and survival (Fry, 1947). Individual fishes respond to warming through behavioural thermoregulation and reversible physiological acclimation (Gunderson and Stillman, 2015; Seebacher *et al.*, 2015; Sunday *et al.*, 2019). Acclimation enables them to buffer thermal stress (Brett, 1952; Schulte, 2024) and is often quantified as changes in Critical Thermal Maximum (CT_{max}), which is the temperature at which locomotor function is lost (Becker and Genoway, 1979; Lee and Rinne, 1980). CT_{max} is a plastic trait that typically increases following warm acclimation (Fangue *et al.*, 2014; Sunday *et al.*, 2019; Stewart *et al.*, 2023; De Bonville *et al.*, 2025; Metz *et al.*, 2025). However, acclimation may become constrained as temperatures approach species-specific thermal ceilings (Sandblom *et al.*, 2016; Morley *et al.*, 2019; Ern *et al.*, 2023; Jutfelt *et al.*, 2024). Consequently, thermal tolerance gains may not be sufficient to fully offset the physiological impacts of warming on organismal performance (Clark *et al.*, 2013; Gräns *et al.*, 2014; Strowbridge *et al.*, 2025).

A key performance trait in juvenile fishes is growth, because it strongly influences predator avoidance, overwinter survival and recruitment (Able *et al.*, 1999; Beck *et al.*, 2001). Short-term warming initially stimulates growth rates by accelerating metabolic processes (Brett, 1979). At supra-optimal temperatures, however, increased maintenance costs, cellular stress responses and changes in food intake can reduce the energy available for growth (Jutfelt *et al.*, 2021; Morgan *et al.*, 2022). Understanding climate vulnerability in fishes therefore requires integrating measures of thermal tolerance with measures of performance under ecologically relevant temperatures (Speers-Roesch and Norin, 2016; Lefevre *et al.*, 2021).

The North Sea is among the fastest warming marine regions globally and has recently experienced record-breaking temperatures (Mohamed *et al.*, 2025). Concurrently, many coastal fish species have shifted towards deeper and more northern habitats (Dulvy *et al.*, 2008). The Wadden Sea, in the southern North Sea, has historically been the largest juvenile flatfish nursery in the region (Zijlstra *et al.*, 1982), where several species settle into intertidal and subtidal areas in spring, and remain there throughout summer until migration to deeper waters (Rijnsdorp *et al.*, 1985). Newly settled flatfish exhibit strong site fidelity within shallow nursery grounds (Pihl *et al.*, 2000; Burrows *et al.*, 2004), and therefore must cope with local environmental conditions. Climate warming has drawn interest in how the quality of these nursery habitats is changing, with several studies linking declines in abundances of European plaice (*Pleuronectes platessa*), flounder (*Platichthys flesus*) and dab (*Limanda limanda*) to an increasing frequency in temperatures unfavourable for growth (Teal *et al.*, 2008; Freitas *et al.*, 2016; Van Der Veer *et al.*, 2022). Also, evidence has shown changes in

phenology and habitat use in response to warming, with earlier seasonal settlement, reductions in time spent in the shallows, and distribution shifts to deeper and more northern waters (van Keeken *et al.*, 2007; Petitgas *et al.*, 2013; van der Veer *et al.*, 2015).

To date, relatively little is known about the physiological mechanisms that coastal fishes use to cope with warming within their nursery habitats. Previous studies on flatfishes have examined dynamic energy budgets (Freitas *et al.*, 2010), while recent experiments suggest limited capacity for rapid acclimation to simulated marine heatwaves (De Bonville *et al.*, 2025; Tamarit-Castro *et al.*, 2026). Yet, it remains unclear how upper thermal tolerance of flatfishes changes throughout the nursery season, how juveniles cope with heat stress, and whether plasticity is sufficient to maintain growth under current extreme summer temperatures. Resolving these responses is important for predicting how climate warming may alter the functional quality of nursery habitats and their contribution to fish populations.

We addressed these questions using European plaice as model species. Plaice is widely distributed across the Northeast Atlantic and supports commercially important fisheries. Population processes are sensitive to climate variability, with spawning phenology and year-class strength negatively correlated with temperature (Van Der Veer and Bergmann, 1986; Rijnsdorp, 1989; Linderholm *et al.*, 2014). Larvae drift to the shallows across Europe and typically settle between March and mid-May (Zijlstra *et al.*, 1982), and juveniles are exposed to seasonal temperatures during their first growth season. Juvenile growth is considered optimal at around 19°C, decreasing at higher temperatures (Freitas *et al.*, 2010; Van Der Veer *et al.*, 2022), making plaice a useful model for examining thermal acclimation and growth under ecologically relevant warming.

Here, we combined seasonal field observations with laboratory experiments to quantify physiological plasticity in juvenile European plaice during their first summer after settlement. We recorded *in situ* seawater temperatures, seasonal growth and acute thermal tolerance (CT_{max}) in wild juveniles and experimentally tested how simulated marine heatwaves and chronic warming will influence thermal tolerance, growth and HSP70 expression. We hypothesized that (1) juvenile plaice will seasonally acclimate to warming through increases in acute thermal tolerance; (2) acute heat stress will rapidly induce HSP70 expression; and (3) physiological acclimation will be insufficient to maintain growth under chronic warming.

2 | Materials and methods

2.1. | Ethical declaration

All procedures were approved by the Swedish Board of Agriculture's Ethical Committee and the University of Gothenburg (Permit Dnr 5.8.18-07281/2025) and complied with the regulations of the University of Gothenburg Animal Welfare Body and the ARRIVE guidelines (Sert *et al.*, 2020).

2.2. | Study species and site

This study was conducted between May and October 2025 at the Kristineberg Marine Research Station, on the Swedish Skagerrak coast (58.248047° N, 11.446605°E, Fig. 1).

The adjacent semi-sheltered bay was selected as study site because it functions as a nursery habitat for European plaice, where larvae originating from spawning grounds in the North Sea and Kattegat settle during spring and remain until late-summer (Modin and Pihl, 1996).

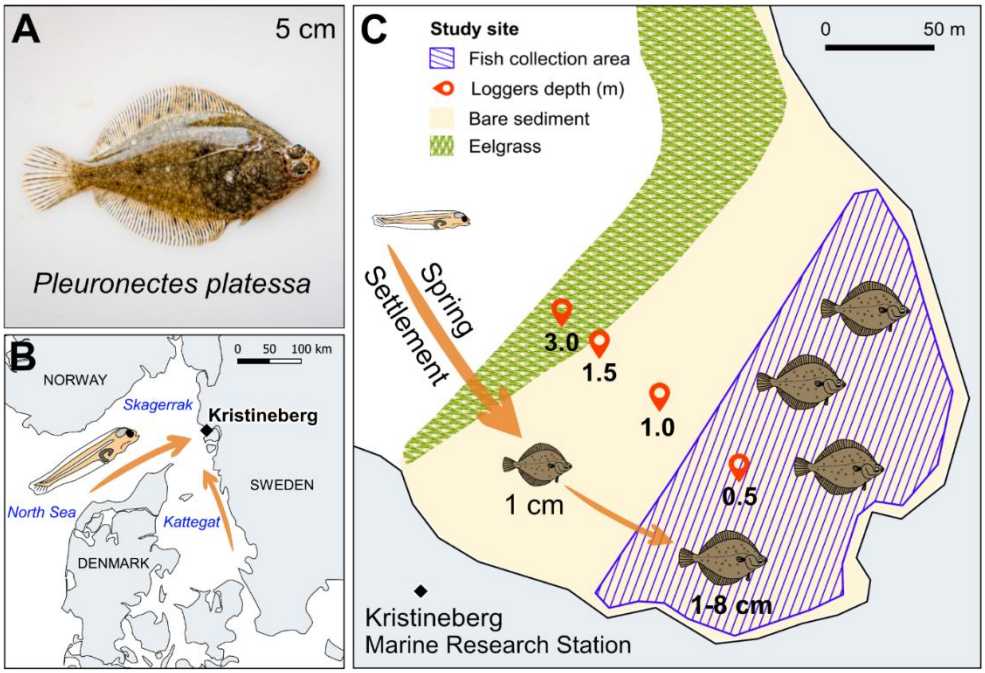

FIGURE. 1. Study species and study site. A) Juvenile European plaice, *Pleuronectes platessa*; B) Location map of the study site on the Swedish Skagerrak coast; C) Map of the study site with bottom type (bare sediment or eelgrass), depth positions of temperature loggers and fish collection area.

The bay has a tidal amplitude of approximately 20 cm. Sandy-silt sediments extend from the shoreline to 1.5 m depth before transitioning into a 30 m wide eelgrass (*Zostera marina*) meadow between 1.5 and 4 m depth, beyond which the seabed slopes rapidly to 15 m. Juvenile plaice were collected at ~0.5 m depth using a small beach seine. Fish were identified morphologically following (Haynes *et al.*, 2008), and species was confirmed genetically by sequencing fin clips from 20 randomly selected individuals.

2.3. | In situ temperatures and regional warming trends

Temperature loggers (HOBO Pendant UA-002-64; Onset, USA) were deployed at 0.5 m (bare sand), 1.0 m (bare sand), 1.5 m (sand - eelgrass boundary), and 3.0 m (eelgrass), where they recorded water temperature every 10 min throughout the study. Hourly temperature-change rates were calculated from consecutive logger measurements separated by 1 h (including six 10-min recording intervals) between 1 May and 30 September 2025. All warming, cooling and stable periods were retained in the analysis, after which mean and maximum positive warming rates were summarized to characterize natural warming events.

Regional warming trends and historical marine heatwaves were quantified from daily NOAA Optimum Interpolation Sea Surface Temperature (OISST v2.1) satellite data (1982-2025) extracted for the grid cell nearest the study site (0.25° spatial resolution, ~ 27 km pixel size).

Temporal trends in mean seasonal SST (1 March – 30 September) were analysed using linear regression. Marine heatwaves were identified using the *heatwaveR* package following (Hobday *et al.*, 2016) and defined as periods when the SST exceeded the seasonally varying 90th percentile climatological threshold for at least five consecutive days. The climatology baseline was calculated from 1982 to 2011. Long-term trends in annual marine heatwave frequency were analysed using Poisson generalized linear models. Annual marine heatwave duration was analysed using quasi-Poisson generalized linear models, where annual cumulative intensity was analysed using gamma generalized models with a log link, while trends in annual maximum cumulative intensity (°C·days) were analysed using generalized linear models.

To compare regional SST with temperatures recorded in situ within the nursery bay, daily mean satellite SSTs were compared with daily mean logger temperatures between 15 May and 1 October 2025. Agreement between datasets was assessed using Pearson correlation, linear regression, mean bias (logger temperature − SST) and root mean square error (RMSE).

2.4. | Seasonal field observations

2.4.1. | Seasonal upper thermal tolerance and growth in the nursery bay

From 14 May to 1 October 2025, 40 juvenile plaice were captured monthly from the study bay, immediately transported to the laboratory and tested for CT_{max} within three hours. For each month's sample, four replicated CT_{max} trials were conducted with 10 fish per trial, at a ramping rate of 0.3°C per minute (Morgan *et al.*, 2018; Raby *et al.*, 2025) (Fig.S1-S2). The test arena was a plastic container (34 x 25 x 17 cm: 14 liters) equipped with a custom-made cylindrical steel-chamber containing coil heater (300 W) and an aquarium water pump (Eheim compact ON 1000) for heat distribution, and an air stone for oxygenation. A mesh divider separated the fish from the instruments. First, fish were introduced into the arena and allowed to habituate for ten minutes at the temperature of collection. Then, heaters were switched on to create a warming rate of 0.3°C per minute, which was monitored by one observer using a Testo 112 Digital Thermometer (±0.1 °C accuracy). A second, blind observer, exclusively monitored fish behaviour. CT_{max} was defined as the temperature at which an individual fish lost equilibrium for more than three seconds. Fish were then immediately transferred to aerated seawater for recovery and measured for total length (mm) and wet mass (g).

To examine seasonal variation in thermal tolerance, CT_{max} means and 95% confidence intervals were calculated for each monthly sample. Relationships between CT_{max}, sample date and water temperature were analysed using linear mixed-effects models fitted with the package *lme4*. Trial identity was included as a random intercept to account for non-independence among individuals tested during the same CT_{max} trial. Seasonal water temperature change was represented by the daily mean temperature at 1 m depth for the fish collection date. Model significance was assessed using the package *lmerTest*, and marginal and conditional R^2 values were calculated with the package *performance*.

To estimate early-season growth of the population at the study site, mean body length was calculated for fish sampled in May, June and July, which were considered a single cohort based on their narrow size distribution (Geffen *et al.*, 2011). Daily growth rate was estimated

as the change in mean body length between sampling dates divided by the number of days between samples. Growth rates were not estimated for late summer because increased size variation suggested the arrival of a second cohort.

2.4.2. | Responses during a natural marine heatwave

Following the July sampling, a natural marine heatwave developed in the region of the study bay. Additional fish were collected on 22 July (~23°C, N = 40) and 28 July (~21°C, N=40) to determine whether CT_{max} had changed during the heatwave (Fig. S1). To investigate molecular responses to natural heat stress, an additional 20 fish were collected on 22 July for HSP70 mRNA analyses in liver tissue. Fish were euthanised in 0.250 g/L of Tricain mesylate (MS-222) and measured for total length (mm) and wet mass (g). Livers (0.0068 ± 0.0029g, mean ± SD) were dissected, weighed to the nearest 0.0001 g (Metler Toledo Excellence Plus XP205 DeltaRange Scale), frozen in liquid nitrogen and stored at -80°C until further analysis. Gene expression of heat shock proteins (HSP70) was measured with quantitative PCR (see methods in 2.5.1).

2.5. | Laboratory experiments

2.5.1. | Acute warming: HSP70 expression during a simulated marine heatwave

To investigate molecular responses to acute warming, a five-day heatwave was simulated in the laboratory. Juvenile plaice (N=100) were collected on 28 July 2025 (ambient temperature ~21°C) and distributed in 10 tanks (10 fish/tank), in a temperature-controlled room and flow through seawater pumped from the Gullmar fjord. Fish were first acclimated at 19°C for seven days. Then, to induce a heat shock, five tanks were exposed to a warming rate of 2.2°C per hour, corresponding to the maximum rate recorded by field loggers, until reaching 24°C (Fig. S3). The remaining five tanks stayed at 19°C throughout the experiment. Fish were sampled before warming (0 h) and after 3 h, 24 h, 72 h, and 120 h (two fish per tank at each time point). Individuals were euthanised, measured for total length and wet mass, and liver tissue (0.0068 ± 0.0029, mean ± SD) was dissected and stored following 2.4.2.

Total RNA was extracted from frozen liver tissue using the RNeasy Plus Mini Kit (Qiagen) with on-column genomic DNA removal. RNA concentration and purity were assessed using a NanoDrop 2000 spectrophotometer (Thermo Fisher Scientific), and RNA integrity was verified in a random subset of 16 samples using the RNA ScreenTape Assay (Agilent). cDNA was synthesized from 1 µg of total RNA using the iScript™ cDNA Synthesis Kit (Bio-Rad) and diluted 1:20 prior to qPCR. Amplification reactions were performed in 10 µL volumes containing 4 µL diluted cDNA and SsoAdvanced™ Universal SYBR® Green Supermix (Bio-Rad). Samples were analyzed in technical triplicates, with each target gene run across four qPCR plates. Each plate included no-template controls, no-reverse transcriptase controls, and a pooled inter-run calibrator. qPCR was performed on a CFX Duet Real-Time PCR Detection System (Bio-Rad). Primer sequences and amplification conditions are provided in Table S2.

Statistical analyses were performed on ΔCq values, calculated as $\Delta Cq = Cq_{HSP} - Cq_{reference}$. Effects of warming on ΔCq were analysed using a linear-mixed effects model with treatment, sampling time (0, 3, 24, 72 and 120 h), and their interaction as fixed effects, and tank identity as a random intercept. Fixed effects were evaluated using Type III tests with Satterthwaite's

approximation for denominator degrees of freedom. Treatment differences within sampling times were evaluated using estimated marginal means with Holm-adjusted *p*-values. For visualisation, HSP70 expression is presented as relative expression ($2^{-\Delta Cq}$ × 1000) and displayed in logarithmic scale.

2.5.2. | Chronic warming: upper thermal tolerance and growth

To examine the effects of chronic warming on upper thermal tolerance and growth, juvenile plaice (N = 105) were exposed to three ecologically relevant temperatures (19°C, 21.5°C and 24°C) in a separate laboratory experiment. Fish were sedated in 0.1 gL^{-1} MS-222 and individually tagged with visible implant elastomer tags (NorthWest Marine Technology, Inc.), measured for total length and wet mass, and randomly assigned to 15 flow-through glass tanks (38 x 35 x 35 cm; volume: 47 L). Each temperature treatment was replicated in five tanks, with seven fish per tank. Following three days of recovery at 19°C, water temperature was gradually increased at 0.33°C/hour until the target temperatures were reached. A 1-cm layer of washed sand collected from the study bay was added to each tank for enrichment. Temperature loggers (HOBO MX2201) recorded water temperature continuously in two tanks per treatment (Mean ± SD: 18.90 ± 0.22°C; 21.50 ± 0.25°C; 23.90 ± 0.31°C, Figure S4). At the start, fish measured 47 mm (46-48 mm; mean total length ± 95% CI), and 0.97 g (0.89-1.04 g; mean wet mass ± 95% CI). Initial body size did not differ among temperature treatments (one-way ANOVA; length [$F_{2,102}$ = 0.45, p = 0.636]; mass [$F_{2,102}$ = 1.01, p = 0.369]).

Fish were maintained for 34 days under experimental conditions and fed to satiation twice daily with 3.3 g thawed *Mysis* shrimp and *Artemia* tank. Uneaten food was removed daily, and water temperature and dissolved oxygen were monitored daily too. Room air temperature was maintained at 20°C, under a 16 h light : 8h dark photoperiod. Tanks were partially covered with opaque plastic lids to reduce direct light exposure and disturbance. Overall mortality during the experiment was 3.8% (one fish at 24°C and three at 21.5°C).

At the end of the exposure period, fish were tested for CT_{max} and later measured for final total length and wet mass, following the methods in section 2.4.1. One CT_{max} trial was conducted per experimental tank, testing all fish from a given tank together (Figure S5). CT_{max} was analysed using a linear-mixed effects model with acclimation temperature as a fixed effect and tank identity as a random intercept (lmer (ctmax ~ treat + (1 | tank)). The overall effect of acclimation temperature was evaluated using Kenward-Roger degrees of freedom and Tukey-adjusted estimated marginal means were used for pairwise treatment comparisons.

Individual length and mass growths rate were calculated as the difference between final and initial measurements divided by the duration of the experiment (38 days including tagging). Effects of acclimation temperature on growth were tested using linear mixed effects models of final body size, accounting for initial body size as a covariate: (lmer (final length ~ temperature treatment + initial length + (1 | tank) and lmer (final mass ~ temperature treatment + initial mass + (1 | tank)). Overall treatment effects were evaluated using Kenward–Roger degrees of freedom, and Tukey-adjusted estimated marginal means were used for pairwise treatment comparisons.

2.6. | Statistical analysis

All analyses were conducted in RStudio, with R version 4.4.2. (R Core Team, 2024). Statistical significance was evaluated at α = 0.05. Data are presented as mean ± 95% confidence intervals unless otherwise stated. Details for analyses are in their corresponding methods sections.

3. | Results

3.1. Regional ocean warming and marine heatwaves

From 1 March to 30 September (the flatfish nursery period), the mean seasonal sea surface temperature (SST; 1982 - 2025) increased by 0.45°C decade $^{-1}$ (linear regression: β = 0.045°C year^{-1}, R^2 = 0.5, p < 0.001; Fig. 2A). Regional marine heatwaves also became more frequent (Poisson regression, β = 0.035 ± 0.009 SE, p < 0.001; Fig. 2B; Table S3-4), with the mean events per year increasing from 0.6 yr^{-1} to 3.0 events yr^{-1}. Mean total MHW days per year also increased (quasi-Poisson regression: β = 0.040 ± 0.011 SE, p < 0.001; Fig. 2C), rising from a mean of 7.6 to 48.1 days yr^{-1}, while the mean annual cumulative intensity increased from 20.9 to 126.0 °C days (Gamma regression: β = 0.023 ± 0.011 SE, p = 0.001; Fig. 2D). The most intense marine heatwaves for that period occurred in 2018, reaching 287°C days .

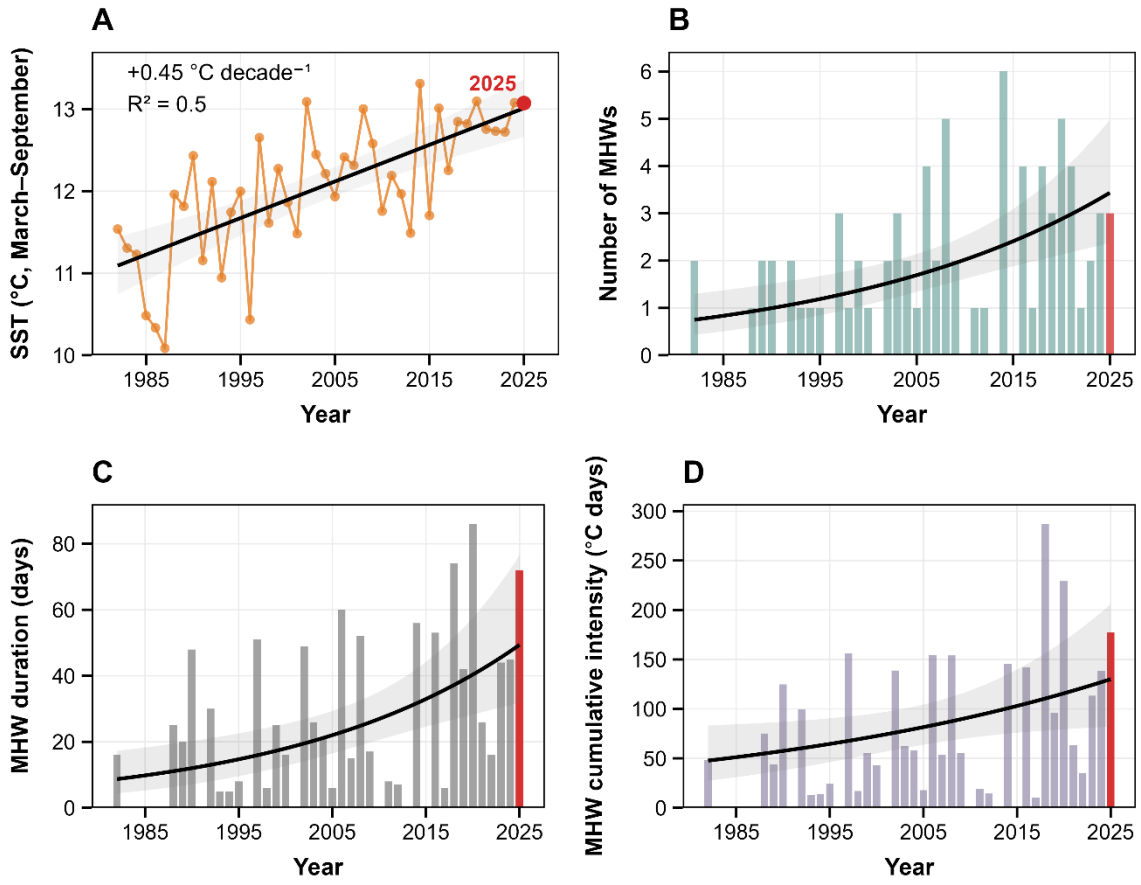

FIGURE 2. Long-term warming trends and marine heatwaves on the Swedish Skagerrak coast for the period 1 March - 30 September, for 1982-2025. (**A**) Mean seasonal sea surface temperature (SST) derived

from NOAAOISST v2.1 satellite data, with the fitted linear regression in black. (**B**) Marine heatwave (MHW) frequency, expressed as the number of events per year, following Hobday et al. (2016), with the fitted Poisson regression. (**C**) Total MHW duration (days) per year for the study period, with the fitted quasi-Poisson regression. (**D**) Cumulative MHW intensity (°C days) per year, with the fitted Gamma regression. The year 2025 is highlighted in red in all panels.

3.2. Regional marine heatwaves in 2025

Three marine heatwaves were identified in 2025 near the study site during spring, summer and late summer, coinciding with the growth season of newly-settled plaice (Fig. 3).

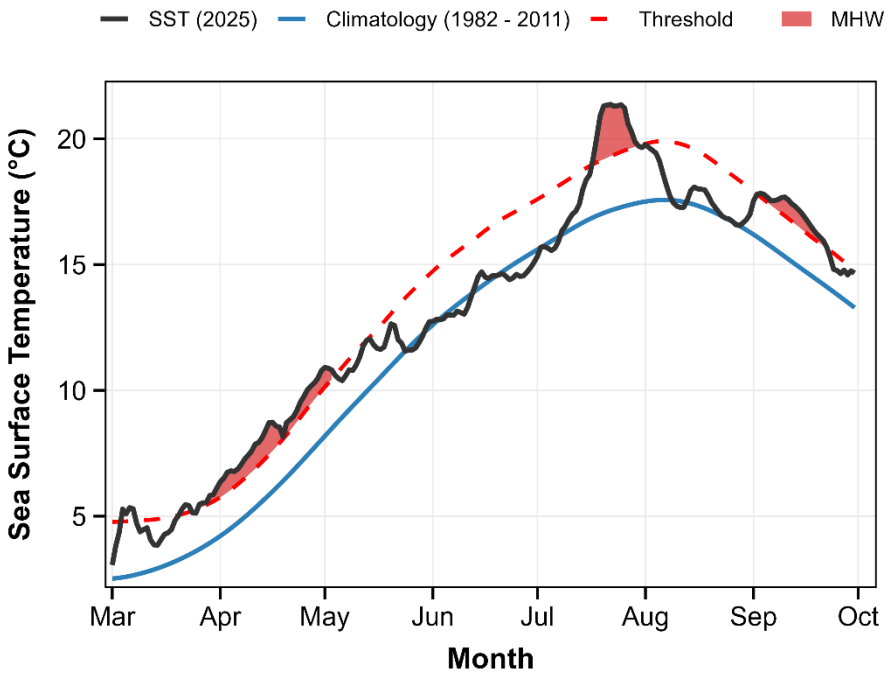

FIGURE 3. Marine heatwaves identified in 2025 near the study site, a shallow coastal nursery habitat on the Swedish Skagerrak coast. Marine heatwaves (MHW, red shade) were identified within the nearest grid cell to the study site (within 27km) following Hobday et al. (2016), using data from NOAA OISST v2.1 satellite-derived sea surface temperature (SST) relative to a climatological mean (1982-2011) and marine heatwave threshold.

The most intense heatwave was detected in July, lasting 13 days, with a peak SST of 21.4°C and a maximum intensity of 4.3°C above the climatological threshold. The other two heatwaves spanned 39 days in March-May, and 20 days during September, with maximum intensities of 2.4°C and 2.9°C, respectively (Table S5). The heatwaves coincided with

3.3. | Thermal acclimation to seasonal temperatures and marine heatwaves in a shallow nursery habitat

The acute upper thermal tolerance (CT_{max}) of plaice closely tracked the seasonal change in water temperatures in the nursery habitat (Fig. 4). Mean CT_{max} increased from 27.9°C (95% CI: 27.6-28.3°C) in May to a peak of 31.6°C (31.4-31.8°C) during late July, gaining 3.7°C in thermal tolerance, and later decreased until 29.1°C (28.8 – 29.4°C) at the end of September (Table S6).

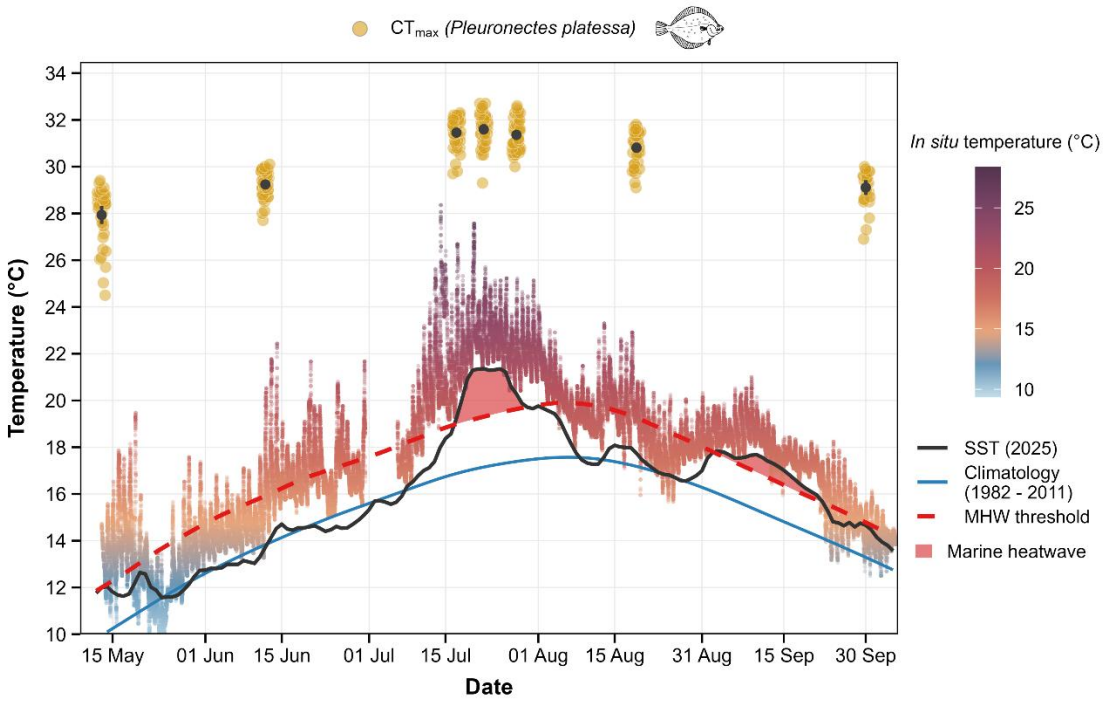

FIGURE 4. Seasonal variation in acute upper thermal tolerance of wild juvenile European plaice (*Pleuronectes platessa*) in relation to satellite-derived sea surface temperature (SST) and *in situ* water temperature in a shallow nursery habitat on the Swedish west coast. Gold points show individual critical thermal maximum (CT_{max}) measurements of (N = 27-40) fish tested within three hours of collection; black points and error bars show mean ± 95% for each sampling event. The colour gradient shows pooled individual in situ temperature measurements recorded every 10 minutes at 0.5, 1 and 1.5 m depth. The black line shows satellite-derived SST for 2025, the blue line the 1982-2011 climatological mean, and red dashed line the 90th percentile marine heatwave (MHW) threshold, following Hobday et al., 2016. Red shading indicates identified MHWs based on satellite data on the nearest grid cell to the study site (within 27km, dataset from NOAAOISST v.2.1.).

In situ temperatures recorded at 0.5 - 1.5 meters depth showed a daily variability of 5°C and generally exceeded satellite-derived SSTs. During the warmest period (12 July to 4 August), the logger at 0.5 m recorded a maximum daily mean temperature of 24.1°C and an absolute maximum of 28.0°C. The discrepancy was particularly evident during the July marine heatwave: satellite SST exceeded 21°C for seven consecutive days, whereas *in situ* temperatures exceeded 21°C for 15–22 days across depths. Overall, satellite SST closely tracked the seasonal variation in nursery temperatures (R^2 = 0.91, slope = 1.07, Fig. S6) but underestimated *in situ* values by an average of 1.36°C (RMSE = 1.63°C), but daily differences of up to 5.7°C. Positive hourly warming rates at 0.5 m averaged 0.37°C h^{-1} and reached a maximum of 2.15°C h^{-1} (Table. S7).

Importantly, the mean CT_{max} of plaice did not differ across the July marine heatwave (ANOVA, 31.45 – 31.60°C; $F_{2,119}$ = 1.21, p = 0.302; Fig. 4), despite the occurrence of the strongest warming in the nursery habitat. However, when considering the entire season, CT_{max} was positively related to the mean *in situ* water temperature of each fish collection date (Linear mixed-effects model, β = 0.37°C ± 0.03 SE acclimation response per 1°C increase in water temperature, marginal R^2 = 0.71, p < 0.001; Fig. 5).

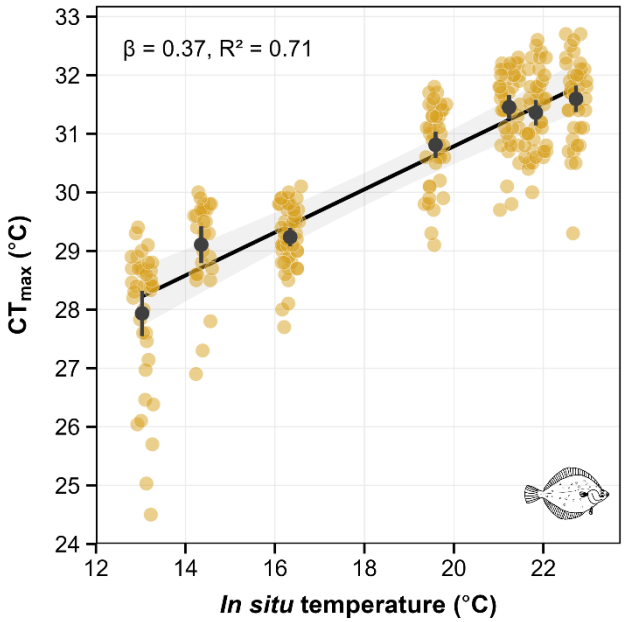

FIGURE 5. Relationship between Critical Thermal Maximum (CT_{max}) and daily mean water temperature on the fish collection date. CT_{max} of wild European plaice (*Pleuronectes platessa*) measured within three hours of collection in a shallow nursery habitat from 1 May to 30 September 2025. Gold points = individual fish measurements (N = 40 per sampling date); Black points and error bars = mean ± 95%. Solid black line = linear relationship, grey shading = 95% CI.

3.4. | Seasonal growth of newly settled European plaice in a shallow nursery habitat

Juvenile plaice sampled in May-July exhibited relatively narrow size distributions (Fig. 6). Mean body length was 23.6 ± 0.5 mm (mean ± SE, *n* = 39) in May, 35.0 ± 0.6 mm (*n* = 48) in June, and 50.1 ± 0.8 mm (*n* = 42) in July (Fig. 6A). Mean body mass also increased substantially, from 0.165 ± 0.010 g in May to 0.440 ± 0.020 g in June and 1.110 ± 0.050 g in July (Fig. 6B).

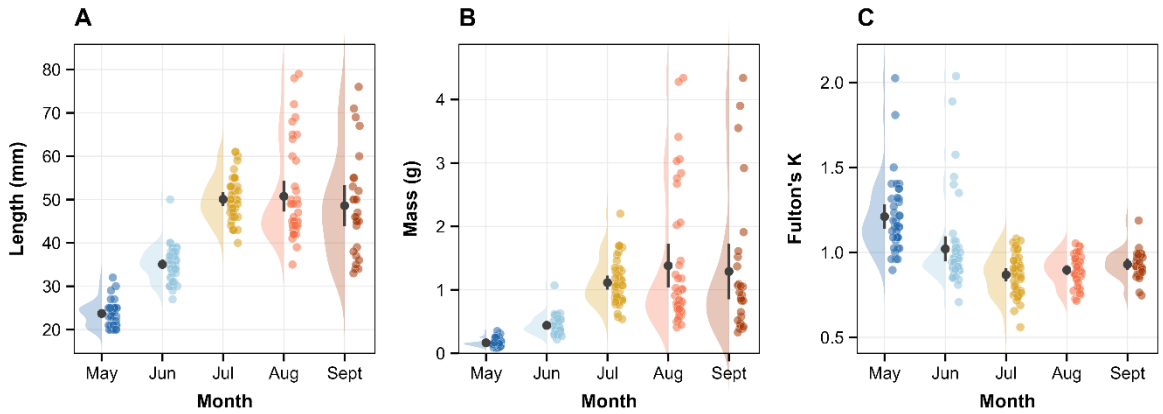

FIGURE 6. Seasonal variation in body size and condition of newly settled European *plaice (Pleuronectes platessa)* from May to September 2025. Seasonal distributions of (A) total length, (B) body mass, and (C) Fulton's condition factor (K). Half violins show density distributions, coloured points represent individual fish, and dark points with error bars indicate mean ± 95% confidence intervals. Colours differentiate sampling events.

However, fish collected in August and October showed greater size heterogeneity, suggesting cohort mixing later in the season. Fulton's condition factor declined markedly from 1.21 (95% CI: 1.14–1.28) in May to 0.87 (95% CI: 0.83–0.91) in July, indicating that increases in body length outpaced increases in body mass during this period (Fig. 6C). Estimated length growth rates were similar during May–June (0.38 mm day^{-1}) and June–July (0.43 mm day^{-1}) (linear model, $F_{1,88} = 2.68$, $P = 0.105$), being overall 0.41 mm day^{-1} (linear model fitted May-July, $R^2 = 0.87$, $P < 0.001$). In contrast, estimated mass growth rates increased significantly between intervals, from 0.009 g day^{-1} in May and June to 0.019 g day^{-1} in June and July ($F_{1,88} = 38.06$, $P < 0.001$).

3.5. Heat shock responses to a simulated marine heatwave

In the laboratory, HSP70 gene expression significantly increased and peaked within 3 hours of a simulated heatwave (warming rate of 2.2°C/hour) (Fig. 7A). Then, the mRNA declined and was similar to control levels at 24 h, 72 h and 120 h. HSP70 mRNA in the controls remained unchanged through time. Therefore, expression of HSP70 changed with treatment, sampling time and their interaction (linear mixed-effects model: treatment: $F_{1,62} = 9.09$, $p = 0.004$; time: $F_{4,62} = 6.14$, $P < 0.001$; treatment × time: $F_{4,62} = 7.58$, $P < 0.001$, Fig. 6A). Also, before the heat shock (t_0), HSP70 mRNA did not differ between treatments ($p = 0.838$). For comparison, HSP70 mRNA was also significantly higher in fish sampled from the nursery bay during the July heatwave than in the laboratory controls (linear model: $F_{1,47} = 8.17$, $p = 0.006$; Fig. 7B), with mean expression approximately 2.1-fold higher in wild fish, although lower than in laboratory controls.

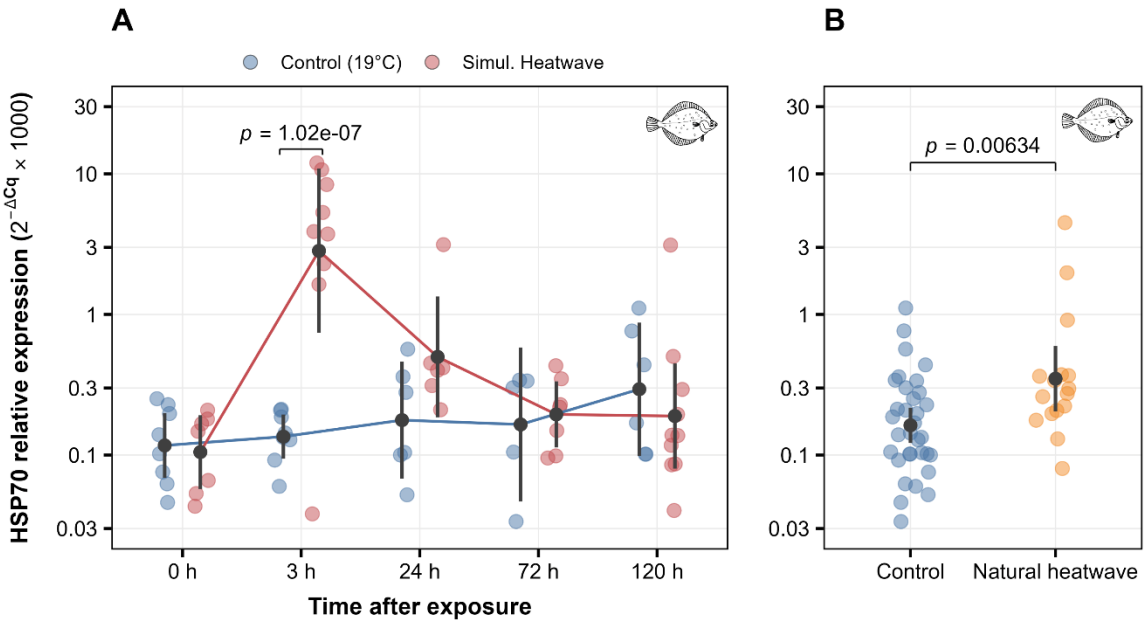

FIGURE 7. Heat-shock protein (HSP70) gene expression in newly settled European plaice following a simulated marine heatwave and a natural marine heatwave exposure. (**A**) Relative HSP70 gene expression after acclimation to control (19°C) or simulated heatwave (24°C), measured immediately before the heat shock (0 h) (an increase of 2.2°C per hour from 19°C until 24°C in the simulated heatwave) and after 3, 24, 72 and 120 h. (**B**) Relative HSP70 expression in fish acclimated to 19°C in the laboratory compared with wild-caught fish sampled during the July 2025 natural marine heatwave (at ~22°C). Coloured points represent individual fish, dark

points and vertical bars show treatment means ± 95% confidence intervals, and lines in panel A connect treatment means through time for visualisation. HSP70 gene expression values are shown on a $\log_{10}$ scale.

3.6. Upper thermal tolerance and growth responses to simulated chronic warming

Under simulated chronic warming, mean CT_{max} increased from 31.1°C in fish acclimated to 19°C to 31.8°C in fish acclimated to 21.5°C (Fig. 8A). At 24°C, mean CT_{max} was 31.9°C, similar to 21.5°C. CT_{max} tended to increase between 19°C and 21.5°C (linear mixed model: $F_{2,11} = 3.75$, $P = 0.057$).

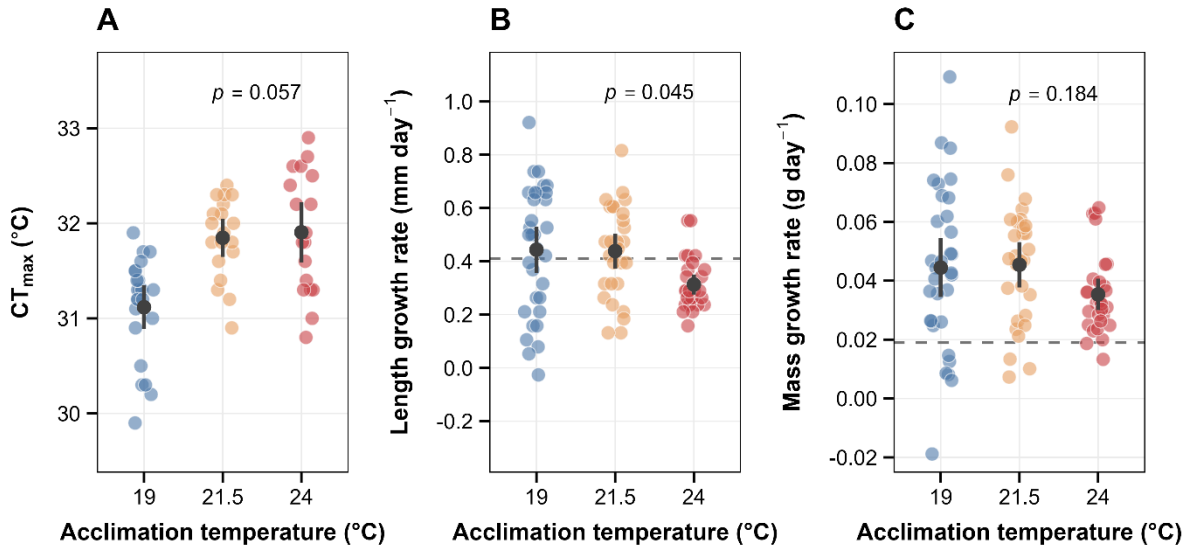

FIGURE 8. Effects of acclimation temperature on upper thermal tolerance and growth of newly settled European plaice (*Pleuronectes platessa*). (A) Critical thermal maximum (CT_{max}), (**B**) length growth rate, and (C) mass growth rate following a 33-day acclimation to 19, 21.5 and 24°C. Coloured points represent individual fish and large black points indicate treatment means ± 95% confidence intervals. Dashed horizontal lines in panels B and C denote mean growth rates measured under ambient field conditions during the same period (May-July 2025).

All fish except one grew during the experiment (Fig. S7). Mean length growth rates were 0.443, 0.438 and 0.313 mm day^{-1} at 19, 21.5 and 24°C, respectively (Fig. 8B). After accounting for initial body length, length growth rates differed among treatments and were lowest at 24°C (ANCOVA, $F_{2,10.60} = 4.23$, p = 0.045). Tukey-adjusted pairwise comparisons were:19 vs 24°C: p = 0.072; 21.5 vs 24°C: p = 0.064. Fishes that were initially smaller grew faster ($F_{1,66.94} = 4.59$, p = 0.036, Fig. S8), and this relationship was similar across all acclimation treatments. Mean mass growth rates were 0.046 and 0.045 at 19, 21.5°C, respectively, and 0.035 g day^{-1} at 24°C, although the effects of the acclimation treatment ($F_{2,10.65} = 1.99$, p = 0.184) and initial body mass ($F_{1,70.36} = 0.84$, p = 0.363) were not statistically significant. For comparison, the estimated length growth rate in the field (dashed line, Fig.8B) from May to July was approximately 0.41 mm day^{-1}, closely matching the laboratory means at 19 and 21.5°C.

Overall, the nursery bay experienced sustained elevated water temperatures from mid-July to mid-August, with temperatures frequently ranging between 21 and 24°C and exceeding 24°C during the July heatwave (Fig. 9). In conjunction with the laboratory growth experiment,

these conditions identified a period of potential limitation to growth in the nursery habitat, when the pooled daily mean temperature across 0.5–1.5 m exceeded 21°C. During this period, mean water temperatures were 22.7°C at 0.5 m, 21.9°C at 1 m and 21.8°C at 1.5 m (Fig.S9).

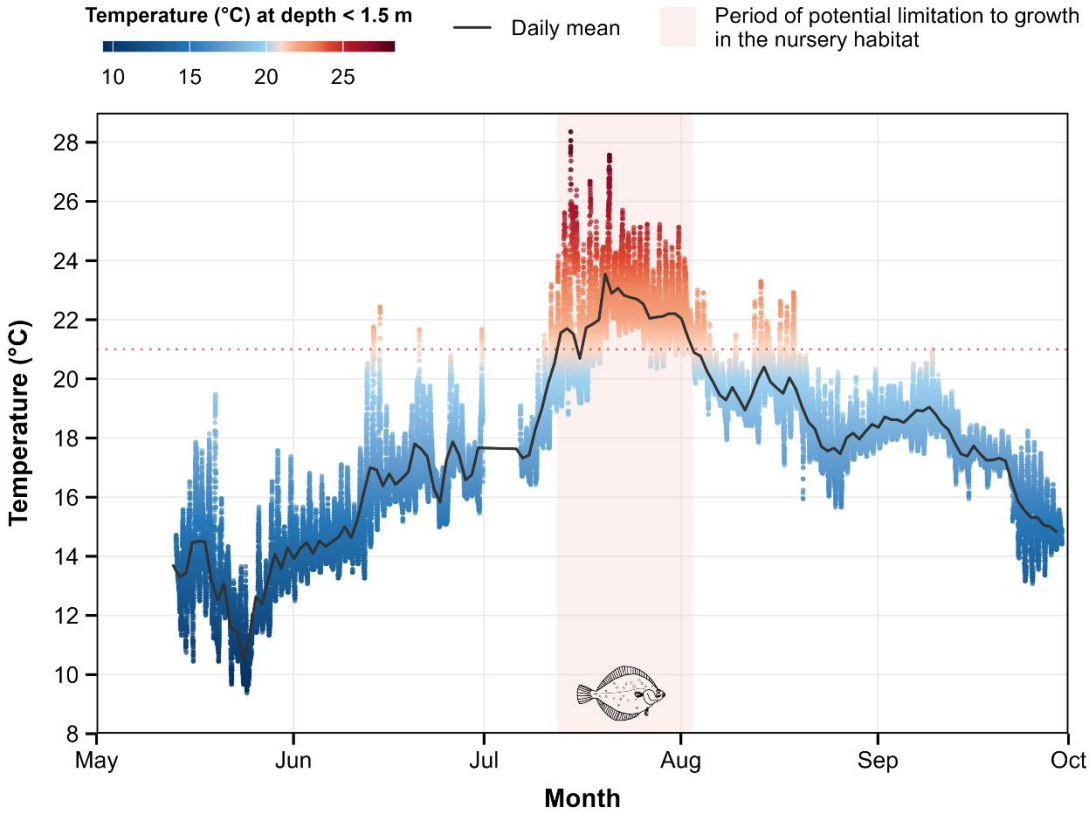

FIGURE 9. Seasonal temperatures and period of potential limitation to growth in a shallow nursery habitat for juvenile European plaice (*Pleuronectes platessa*) on the Swedish Skagerrak coast from 1 May - 30 September 2025. Coloured points represent temperature observations recorded at 10-min intervals by three loggers deployed at 0.5, 1.0 and 1.5 m depth, covering the depth range of the bay. Point colour indicates water temperature, and the dark grey line shows the overall daily mean. The dotted red line indicates 21°C, and red shading denotes the period when daily mean is higher than 21°C, representing a period of potential limitation to growth in the nursery habitat.

Discussion

Main findings

In this study, we show that (i) shallow coastal nursery habitats on the Swedish Skagerrak coast (North Sea) have warmed and currently experience greater thermal variability and extremes than indicated by regional satellite-derived sea surface temperatures, (ii) newly-settled European plaice possess physiological plasticity to acclimate to seasonal temperatures and induce molecular responses to acute thermal stress in both the laboratory and in nature, (iii) newly-settled plaice are exposed to marine heatwaves during the first months after settlement, (iv) acute upper thermal tolerance shows little additional plasticity during marine heatwaves, and (v) length growth declines at extreme summer temperatures that are increasingly common in shallow habitats along the Swedish Skagerrak coast. Together, these findings suggest that juvenile physiological plasticity may buffer seasonal

warming but may be insufficient to maintain optimal growth performance during increasingly warm summer temperatures in the region.

Climate warming is changing the thermal environments in nursery habitats

Climate change is driving unprecedented ocean temperatures across Europe, with severe consequences for marine life (Bergin, Claire *et al.*, 2026). We found a regional warming of ~0.45°C per decade (May-September, 1982-2025), which is comparable to the full North Sea basin (~ 0.38°C per decade, Mohamed *et al.*, 2025), but nearly four times the global average (~0.13°C per decade; Calvin *et al.*, 2023). Marine heatwave frequency, duration and intensity also increased over this period and were consistent with the North Sea trends (Mohamed *et al.*, 2025). However, *in situ* temperatures within the nursery habitat (<1.5 m) were 1-5°C higher than satellite SSTs, indicating that satellite data underestimated local thermal variability and extremes, as reported in other shallow coastal environments (Pearce *et al.*, 2006; Smale and Wernberg, 2009; Phinn *et al.*, 2018). Satellite derived daily mean SST represents temperatures of the first centimeters of the ocean surface over relatively large spatial scales, whereas nearshore temperatures are strongly influenced by local depth and hydrodynamics (Reynolds *et al.*, 2007). The most common statistical method to detect and calculate trends in marine heatwaves requires a 30-year baseline climatology (Hobday *et al.*, 2016), but publicly available long-term data series of *in situ* temperature records are often scarce, meaning that for many regions, satellite data is the only option available. We also statistically identified three marine heatwave events occurring within 27km of the study site (the satellite pixel size). These heatwaves coincided with local plaice settlement (March-April) (Pihl and Rosenberg, 1982), the peak of the summer (July), and the late-summer migration (September). However, *in situ* data revealed that the July heatwave might have lasted one to three weeks longer and been several degrees more intense than shown by daily mean SST. This is important because fine-scale thermal variability can disproportionally affect organismal performance relative to changes in mean temperature alone (Vasseur *et al.*, 2014). Thus, relying solely on large-scale derived SSTs and statistical detections to characterize marine heatwaves may underestimate the magnitude of temperatures experienced by organisms in coastal habitats and their impacts on them (Kearney and Porter, 2009; Villeneuve and White, 2025).

We found no change in acute upper thermal tolerance (measured as CT_{max}) of wild plaice during the July heatwave, when *in situ* water temperatures remained above 21°C for three weeks. Juvenile flatfish exposed to simulated heatwaves have previously shown small increases in CT_{max} when shifted from 19°C to 23°C (De Bonville *et al.*, 2025; Tamarit-Castro *et al.*, 2026). The absence of a further increase in CT_{max} in the July heatwave may align with the hypothesis of ‘plastic floors and concrete ceilings’, where chronically warmed fish face plasticity constraints to further increase their thermal tolerance (Sandblom *et al.*, 2016). Environmental temperatures nevertheless remained below measured CT_{max} values, which could be interpreted as relatively large thermal safety margins. However, thermal safety margins based on CT_{max} can overestimate resilience to prolonged warming by several degrees °C, because thermal damage accumulates as a function of both temperature and exposure duration (Ern *et al.*, 2023; Iacarella *et al.*, 2025; Molina *et al.*, 2025). Therefore, without further information on the effects of long-term exposure to marine heatwaves, the actual safety margins of juvenile plaice remain uncertain.

Physiological plasticity buffers seasonal warming, but has limits

This is the first study to quantify seasonal variation in physiological upper thermal tolerance of wild European plaice throughout their first summer in a shallow nursery habitat. We found that acute upper thermal tolerance (CT_{max}) closely tracked seasonal changes in environmental temperature, increasing by ~3.7°C in thermal tolerance across an approximately 10°C seasonal rise in water temperature. This corresponds to an acclimation response ratio of almost 0.4, consistent with other high latitude fishes (Morley *et al.*, 2019; Tamarit-Castro *et al.*, 2026). Thermal tolerance was also strongly correlated with environmental temperature ($r^2 = 0.7$), supporting broader evidence that upper thermal limits are associated with maximum environmental temperatures across latitudinal ranges (Pinsky *et al.*, 2019; Sunday *et al.*, 2019). Together, these results demonstrate plasticity in upper thermal tolerance during the first months after settlement but also suggest physiological constraints on further increases in CT_{max} as summer temperatures approach their seasonal maximum.

Measuring CT_{max} of wild fish *in situ* is informative because it can capture natural thermal conditions that influence thermal tolerance, including temperature variability across multiple timescales (Leclair *et al.*, 2020), and has been successfully applied in other fishes (Gilbert *et al.*, 2020; Reemeyer and Chapman, 2024; Stewart *et al.*, 2024). However, CT_{max} is a plastic trait strongly influenced by thermal history, and its estimation can also depend on the warming rate used during testing (Fangue *et al.*, 2014; Stewart *et al.*, 2023; De Bonville *et al.*, 2025). We used the standard rate of 0.3°C/min (or 18°C/hour), recommended for small fishes (Becker and Genoway, 1979), to facilitate comparisons with other studies. In our study, this method allowed us to efficiently estimate the acclimation state of fish with very low mortality (Raby *et al.*, 2025). Nevertheless, the warming rate used for tests was substantially faster than the natural warming rates we recorded within the nursery habitat (typically ~0.3-1C°/hour, maximum 2 C°/hour), highlighting the trade-off between experimental standardization and ecological realism (Desforges *et al.*, 2023; Iacarella *et al.*, 2025). Recent research has examined how CT_{max} measured with fast ramping rates predicts tolerance under slower-more realistic rates of warming (Åsheim *et al.*, 2020; Penman *et al.*, 2023). As the physiological mechanisms underlying CT_{max} remain incompletely understood (Ern *et al.*, 2023), we interpret CT_{max} here as a standardized measure of acute upper thermal tolerance, and its change as a measure of physiological plasticity, rather than as the temperature that juvenile plaice can tolerate in nature. Thermal tolerance should be interpreted alongside ecologically relevant measures of organismal performance (Speers-Roesch and Norin, 2016). Our complementary measurements of growth and the heat shock response can reveal earlier signs of thermal stress below acute tolerance limits, providing a wider view on the capacity of juvenile plaice to cope with seasonal warming and marine heatwaves.

Acute warming rapidly induced heat shock protein expression

Exposure to a simulated marine heatwave induced a rapid increase in HSP70 mRNA expression within 3 hours, which returned to baseline levels within 24 hours. Wild plaice sampled during the July heatwave also showed elevated HSP70 mRNA, although the response was lower than under laboratory conditions. This difference between laboratory- and field conditions may reflect the slower rate of warming experienced in nature and possible return towards baseline expression levels before sampling. To our knowledge, this is the first study to quantify HSP70 expression in European plaice, although similarly rapid

induction of heat shock proteins have been reported in other flatfish species exposed to acute heat stress (Benítez-Dorta *et al.*, 2017).

HSP70 are highly conserved molecular chaperones that stabilize and refold damaged proteins, thereby helping to maintain cellular function during thermal stress (Basu *et al.*, 2002). Rapid induction of HSP70 has been linked to increased thermal tolerance in numerous fish species (Dietz and Somero, 1992; Lewis *et al.*, 2016; Metzger *et al.*, 2016). The coincidence of elevated HSP70 expression with acute warming therefore is therefore consistent with a role for this molecular response in coping with short-term heat exposure (Ern *et al.*, 2023; Metz *et al.*, 2025).

Natural fish growth in the nursery habitat

Wild juvenile plaice grew at approximately 0.4 mm/day during May-July after settlement. This growth rate falls within the range previously reported for wild juvenile plaice in nursery grounds along the Swedish west coast (Wennhage *et al.*, 2007). Fulton K declined from May to July, indicating a faster growth in length than in mass, coinciding with the period when they must outgrow their invertebrate predators brown shrimp and green crab (Wennhage, 2000). Juvenile growth can vary spatially and interannually due to differences in habitat quality, hydrodynamics and density-dependent processes (Nash *et al.*, 1994; Van Der Veer *et al.*, 2010; Ciotti *et al.*, 2013). However, the relative contributions of food availability, intra- or interspecific competition, and temperature to this variation remain difficult to disentangle in flatfishes (Teal *et al.*, 2008; Freitas *et al.*, 2010). Interestingly, mass growth rates measured in the field closely matched those observed in the laboratory treatments 19-21.5°C, where fish were fed until satiation. This suggests that food availability was unlikely to have limited wild juvenile growth at our study site, also consistent with previous work in the same region (Pihl *et al.*, 2000).

Acclimation did not preserve growth performance in the laboratory

Despite a month of laboratory exposure to elevated temperatures, juvenile plaice exhibited only a modest increase in acute upper thermal tolerance (CT_{max}), with no difference between fish held at 21.5°C and 24°C. These CT_{max} values closely matched those measured in wild fish during July and were consistent with those reported in our previous study (Tamarit-Castro *et al.*, 2026), suggesting once more that upper thermal tolerance approaches a hard physiological ceiling beyond which further acclimation is limited (Sandblom *et al.*, 2016; Morgan *et al.*, 2022). Together with our field observations, these findings indicate that warming beyond 21-24°C provides little further increase in upper thermal tolerance.

In contrast, length growth rates were lower at 24°C than at 19 and 21.5°C, indicating that physiological acclimation was insufficient to preserve performance at the highest temperature. Previous studies in the Wadden Sea have reported a thermal optimum for juvenile plaice growth of 19°C (Freitas *et al.*, 2016; Van Der Veer *et al.*, 2022). Our results indicate that length growth begins to decline between 21 and 24°C in the population studied. However, mass growth did not differ among temperature treatments. Multiple processes can affect growth, and we cannot exclude reduced feeding as a contributing mechanism, as fishes can decrease meal size at supra-optimal temperatures to preserve aerobic scope (Jutfelt *et al.*, 2021). A potential mechanism for reduced length growth in our experiment may be increased energetic costs of maintaining homeostasis at elevated temperatures, in combination with reduced food intake (Jutfelt *et al.*, 2024). Together, our results provide

individual-level patterns that may contribute to the broader reductions in juvenile growth and ecosystem productivity under climate warming (Lindmark *et al.*, 2022).

Ecological implications for nursery habitats under climate change

Our results show that shallow nursery habitats for juvenile plaice along the Swedish Skagerrak coast are undergoing marine heatwaves coinciding with a vulnerable life stage after settlement and substantial regional warming. In the southern North Sea, warming has already reduced the suitability of shallow habitats for flatfish nurseries during summer (Teal *et al.*, 2008; Freitas *et al.*, 2012; Van Der Veer *et al.*, 2022). There, juvenile plaice abundance has concurrently declined in intertidal habitats, accompanied by shifts towards deeper and more northerly areas (van Keeken *et al.*, 2007; Engelhard *et al.*, 2011). Our findings show that the Swedish Skagerrak coast may not necessarily be a refuge from North Sea warming: temperatures associated with reduced length growth are consistently occurring during summer marine heatwaves. Continued ocean warming and intensification of thermal extremes may therefore further narrow the thermal window for optimal juvenile growth in these habitats (Frölicher *et al.*, 2018).

This observed warming of shallow nurseries has potential consequences for survival and recruitment for juvenile plaice. Climate variability has previously been linked to long-term fluctuations in plaice recruitment in the Skagerrak–Kattegat (Linderholm *et al.*, 2014), while juvenile growth is known to vary substantially among nurseries through time (Ciotti *et al.*, 2014). North Sea plaice have strong site fidelity with the bay they settled for months until late summer migration (Wennhage and Gibson, 1998). Although juveniles can move within the same bay (Gibson *et al.*, 1998), access to cooler, deeper habitats can involve ecological trade-offs, including increased exposure to larger predatory fishes and birds (Freitas *et al.*, 2016). Therefore, staying in warm nurseries may prolong the period during which juveniles remain vulnerable to local invertebrate predators, whose responses to warming differ from those of juvenile plaice (Tomás *et al.*, 2026). Such effects could increase size-dependent mortality during a life stage that can strongly influence year-class strength (Wennhage, 2000).

From a conservation perspective, these findings highlight that the value of nursery habitats depend not only on the abundance of juveniles, but on its capacity to support growth, survival and ultimately recruitment to the adult population (Ciotti *et al.*, 2025). While larval supply is the most important determinant of year-class in plaice (Wennhage *et al.*, 2007), a decrease in habitat quality due to warming could increasingly constrain the contribution of shallow nursery grounds to adult stocks for this and other commercial species. Therefore, not only current conditions but also projected warming scenarios should be considered when evaluating conservation priorities for shallow coastal areas.

Although this study focused on European plaice, many temperate coastal fishes depend on shallow coastal habitats during their early life stages (Beck *et al.*, 2001). As marine heatwaves intensify (Oliver *et al.*, 2018), intertidal and shallow subtidal habitats may increasingly become thermal bottlenecks for juvenile fishes. Predicting the resilience of coastal fishes to climate change will therefore require linking thermal tolerance not only to acute survival limits, but also to temperature-dependent performance and to how warming alters the ecological function of essential habitats (Madeira *et al.*, 2012; Lefevre *et al.*, 2021). By integrating laboratory measurements of thermal tolerance, molecular responses and growth with the thermal conditions experienced within a natural nursery habitat, our study

demonstrates how conservation physiology can help identify climate-driven changes in habitat quality for coastal fishes.

Acknowledgements

We warmly thank Mariella Hilk, Lin Kalkowski, Mona Pick, Ella Eklund, Zacharias Zouhair, Emily R. Lechner, Leon Pfeuffer, Hannah Sauer, Andreas Ljung, Banu Sig, and Leon Green for assisting with field and lab work, Britt Wassmur for her help with DNA primers and Marko Wramén for the fish photo in Figure 1. We also thank the staff at Kristineberg Marine Research Station for their valuable support.

Author Contributions

Tamarit-Castro E.: Conceptualization, Funding acquisition, Methodology, Investigation, Data Curation, Formal analysis, Visualization, Project administration; Writing - original draft. **Molinari F.:** Investigation, Writing - Review & Editing. **Burden M.:** Methodology, Investigation, Writing - Review & Editing. **Spiering M.:** Investigation, Writing - Review & Editing. **Steinbrecher F.:** Investigation, Writing - Review & Editing. **Sturve J.:** Resources, Writing - Review & Editing. **Jutfelt F.:** Conceptualization, Resources, Writing - Review & Editing. **Perry D.:** Supervision, Writing - Review & Editing. **Gullström M.:** Funding acquisition, Supervision, Writing - Review & Editing. **Linderholm HW.:** Funding acquisition, Supervision, Writing - Review & Editing.

Conflict of Interest

The authors declare no competing or financial interests that could influence the work reported in this study.

Funding

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

Data availability

The data and R scripts underlying this article will be made available on a public repository upon acceptance of the manuscript for publication.

Supplementary material

Attached

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