# Effects of marine heatwaves on European perch (*Perca fluviatilis*)

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# Abstract

Marine heatwaves (MHWs) are increasing globally in both frequency and intensity. Despite the potential effects on ecological and economic values, little is known about MHW's effect on fish body growth. This is especially the case for shallow coastal areas, including those in the Baltic Sea. Body growth in fish is known to be affected by gradually increasing temperature and consistently higher temperatures, with small and young individuals often growing faster but reaching a smaller asymptotic size in warmer waters. In this study, I investigated if MHWs affects (i) fish body growth, and (ii) if such effects vary with size and age, and (iii) if size at catch was also affected similarly. This was done using two measurements of MHWs: years with one or more MHW occurring and the yearly total cumulative intensity of MHWs. Using these two measurements I also investigated if MHWs had increased or decreased since the year 2000 in my coastal study sites. I used monitoring data, which included temperature and catch data of European Perch (*Perca fluviatilis*) from sites along the shallow waters of the Swedish east coast. My results indicated that MHWs occurred in all sites. However, I found no increase or decrease in any of my MHW measurements since the 2000s. With some differences depending on the specific measure of MHWs used, MHWs had an overall positive effect on body growth that varied with age and size. Similarly, MHWs had a positive effect on size at catch. Interestingly, during years with one or more MHW the positive effect on growth decreased with age and size. This is in line with how many fish, including perch, respond to gradually warming temperatures. Whether the effects of MHWs will continue to be positive for perch body growth in the future remains unknown as the frequency and intensity of MHWs are expected to increase. The findings in this study highlight the presence of MHWs in shallow coastal waters and its potential to body growth of Baltic Sea fish.



*Keywords: Baltic Sea, Shallow coasts, European Perch, Perca fluviatilis, Marine heatwaves, Body growth*

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# Abbreviations

| Abbreviation | Description |
|---|---|
| $I_{cum}$ | Cumulative intensity |
| MHW | Marine heatwave |
| R2c | Conditional $R^2$-Value |
| R2m | Marginal $R^2$-Value |
| SLU | Swedish University of Agricultural Sciences |
| $totI_{cum}$ | Total cumulative intensity |

# 1. Introduction

Global climate change is an undeniable fact, with widespread effects on marine ecosystems (IPCC19). Among associated long-term trends, rising ocean temperatures are a significant driver affecting marine organisms (Poloczanska et al., 2019, Gulev., et al 2021, IPCC 2019). Sea surface temperatures increase particularly rapidly in northern Europe, where the Baltic Sea is one of the fastest-warming seas in the world (Belkin et al., 2009, Dutheil et al., 2023). Apart from a gradual increase in mean water temperature, climate change also gives rise to a change in the magnitude of extreme weather events, such as floods, tropical storms, droughts and marine heatwaves (MHWs) (IPCC 2023). MHWs have increased in both frequency and duration over the last decades, and these trends are expected to continue due to global warming (Oliver et al., 2018, IPCC 2019). MHWs are commonly defined as a period of consecutive days when the water temperature reaches abnormal temperatures higher than a seasonally varying mean (Hobday et al., 2016).

MHWs are known to cause a wide range of long and short-term deleterious consequences on marine ecosystems (Smith et al., 2023), in turn affecting fisheries due to e.g. range shifts in targeted fish species and stocks (Mills et al., 2013, Cheung & Frölicher 2020). Some well-known MHW events have led to consequences of this sort, as observed in the northwest Atlantic in 2012 (Mills et al., 2013), northeast Pacific in 2014 (also referred to as the blob, Bond et al., 2015) and in the waters around tropical Australia in 2016 (Benthuysen et al., 2018). Although most studies on MHWs have focused on the larger ocean basins, there have been some studies regarding MHWs occurring in coastal areas and inland seas (Marin et al., 2021, Mohamed et al., 2022). This also includes the Baltic Sea, and the few very recent studies use in situ data from very few locations or satellite data (Bashiri et al., 2024, Dabulevičienė & Servaitė 2024, Safonova et al., 2024). Despite their likely importance, however, there are still a limited number of studies addressing the consequences of MHWs on coastal ecosystems in general and, to my knowledge, none concerning coastal fish in the Baltic Sea.

## 1.1 Fish population, community and individual responses to warming and heatwaves

Marine fish and their environment are in many ways affected by the gradual increase in ocean temperature. For example, in the Baltic Sea, an increase in hypoxia events as a result of a combination of higher temperatures and eutrophication has led to some areas becoming temporarily uninhabitable for fish

(Carstensen et al., 2014, Carstensen and Conley 2019). Some other observed consequences for marine organisms include; changes in the timing of seasonal events, geographical range shifts, population declines and shifts toward smaller body size (Cooley et al., 2022, Baudron et al., 2014). Furthermore, studies on coastal European perch (*Perca fluviatilis*, hereafter perch), populations in the Baltic Sea have found that warming can lead to shifts in heat tolerance (Sandblom et al. 2016), in body growth (Huss et al., 2019) and cause earlier maturation independent of warming-induced changes in growth (Niu et al., 2023).

Some studies regarding MHWs have, similar to studies on responses to gradual warming, observed consequences in, for example, fish biomass (Lacheheb et al., 2024) and range shifts (Wernberg et al., 2013). A study including over 230 different fish species commercially fished in the New Zealand Exclusive economic zone found an increase in yield at moderate MHWs but a substantial reduction in yield at high intensity MHWs (Lacheheb et al., 2024). Cheung & Frölicher (2020) used model simulations of fish stocks in the northeast Pacific Ocean and predicted that MHWs can come to cause a decrease in fish stock biomass and range shifts. In contrast, in a large-scale study, Fredson et al (2023) found that fluctuations in fish biomass linked to MHWs did not exceed normal fluctuations and they found no consistent connection between MHWs and fish relocation patterns. Still, traits such as mobility behaviour have been suggested to cause range shifts during MHWs (Harvey et al., 2022, Jacox et al., 2020) and compositional changes in fish communities during and after MHWs have been observed (Wernberg et al., 2013).

Some insights are also available regarding responses of fish individuals and populations to MHWs. A recent study showed that lakes with already high average temperatures had a disproportionately high die off of fish during periods of extreme temperatures (Till et al., 2019). A study on the demersal and temperate fish species Sparus aurata, exposed to different simulated coastal and estuarine summer temperature conditions, suggests that responses to MHWs may differ depending on life stage (Madeira et al., 2020). They found that larval stages of fish seem to be most affected by MHWs as it lacks ability to acclimate while the juvenile stage is suggested to withstand the effects the best, as a result of high phenotypic plasticity. The adult stage displayed lower plasticity and was hence affected to a larger extent compared to juvenile fish. Another example reports earlier hatching of pacific cod larvae during and in-between MHWs (Almeida et al., 2024, Miller et al., 2024). The extent to which those results can be generalized to other fish species is, however, unknown.

Many studies have focused on changes in fish body growth during gradual warming but similar studies regarding MHWs are largely lacking. For fish and other ectotherms, it is commonly expected that they follow the so-called temperature size rule (TSR), referring to the observation that ectotherms in warming temperatures have a faster growth and earlier maturation time but reaches a smaller maximum body size (Atkinson 1994). However, the mechanism behind this observation remains disputed, including those related to effects on body-mass scaling due to oxygen limitation (Pauly 2021, Wootton et al., 2022) Different fish species varies in their minimum, optimum and maximum temperature for body growth (Lindmark et al., 2022). The optimum temperature can decrease with size as a result of a faster increase in maintenance costs relative to gains from faster consumption rates (Lindmark et al., 2022). Life outside this range can cause metabolic stress, increased oxygen demands and an overall decrease in health (Islam et al., 2020, Helcom 2024). Furthermore, temperatures much higher than those preferred not also means higher energy demand but may also include consequential responses such as lower swimming speed, all of which can impact interactions with predators and prey, and thus survival and body growth (Crawford et al., 2024, Lindmark et al., 2018, Queiros et al., 2024). Temperature does not only affect growth directly, but indirectly through changes in biotic factors such as food availability and species composition and interactions (Gårdmark and Huss 2020). Most of what is known about temperature and its effect on fish individuals, their physiology and whole populations are, however, based on small-scale experimental studies or studies comparing individuals and populations across natural thermal gradients and/or in response to gradually increasing temperature. A major knowledge gap, especially concerning the Baltic Sea, is if and how MHWs affect fish body growth under otherwise naturally occurring conditions.

## 1.2 Aim and hypothesis

The aim of this study is to answer the questions: (1) What is the frequency and intensity of MHWs in shallow Baltic Sea coastal areas? (2) Do MHWs affect fish body growth, and do the extent of the effects vary with age and body size? (3) Do MHWs effect length-at-age-at-catch of fish and do the extent of the effects vary with age? To answer these questions, I used long-term monitoring data of perch, including data on back-calculated growth, and in-situ collected temperature data from different locations along the Swedish Baltic Sea coast. I hypothesise that: (1) MHWs, similar to increased mean temperatures, have an age and size-dependent effect on perch body growth; and (2) that MHWs therefore also have an age-dependent effect on length-at-catch of the fish.

# 2. Method

## 2.1 Study species

Perch is a freshwater species, commonly found in the coastal areas of the Baltic Sea (Helcom 2024). The species commonly matures between ages 2-5 and spawn from April to June After fertilization by multiple males, the eggs hatch after 2-3 weeks (ArtDatabanken 2024). Perch larvae feed on zooplankton and as they grow bigger also includes macroinvertebrates in their diet and finally turn piscivorous (Persson 1988, ArtDatabanken 2024). Perch is included in the regional and national Swedish monitoring programs for coastal fish (Havs- och Vatten myndigheten 2020) and is therefore a well surveyed species subject to comprehensive data collection along the Swedish Baltic Sea coast. Perch in the Baltic Sea is also relatively well studied regarding the effect of warming, with especially juveniles growing faster under warming (Huss et al., 2019). Still, also adult perch may exhibit slight positive growth responses (Lindmark et al., 2023). This does to some degree contradict the TSR, which predicts that size at age decreases with warmer temperatures. However, in line with the TSR, earlier maturation (Niu J et al., 2023) and increased mortality of large perch has been observed (Lindmark et al., 2023).

## 2.2 Fish sampling and data selection

I retrieved previously collected individual-level perch data from the SLU database for coastal fish (KUL 2024). This included age and size at catch data of female perch from 8 sites along the Swedish Baltic Sea coast: Råneå, Kinnbäcksfjärden, Holmön, Norrbyn, Långvindsfjärden, Forsmark, Kvädöfjärden and Torhamn (Figure 1). Back-calculated age and size data of female perch (see explanation below) were retrieved from 4 of the 8 sites; Holmön, Forsmark, Kvädöfjärden and Torhamn (Figure 1). In an attempt to compile as much data as possible, three different methods (gillnets) were deemed similar enough to be used: Nordic coastal survey nets (K064), Coastal survey nets (K009) and Sets of nets (K053).


Figure 1 Map of selected monitoring sites along the Swedish coast of the Baltic Sea, Modified from Havs och Vatten myndigheten 2024.

The Nordic coastal survey nets are deep bottom gill nets. They are 1.8m deep 45m long and consist of 9 sections with different mesh sizes (10, 12, 15, 19, 24, 30, 38, 48, 60mm) (Helcom 2015). An area is divided into four ranges of depth (0-3m, 3-6m, 6-10m, 10-20m), stations are then randomly selected within each depth. Nets are placed at 45 stations in total, to counts as a completed survey. "Sets of nets" are also 1.8m dept bottom set gill nets but are 60m long. They are composed of four nets with mesh sizes 17, 21.5, 25 and 30mm. The coastal survey nets are deep bottom nets with a depth of 3m and are 25m long. These nets consist of 5 sections with mesh sizes 17, 22, 25, 33 and 50mm. For both Sets of nets and coastal survey nets an area is divided into sections with similar environmental disturbances and characteristics such as depth. Within these sections, stations with nets are placed. The number of sections and stations can vary between sites. The surveys are done in mid July to mid/end of August, and usually during a 2-week period (Helcom 2015).

At all sites, I only selected individuals collected during July and August to get as comparable data set as possible. As small individuals are not representatively caught in the gill nets used (Östman et al., 2023), I excluded young-of-the-year perch. Slightly different methods of gillnet fishing have been applied over the years, as the monitoring program has evolved (Table 1)

*Table 1. Sites and monitoring data including Age and Size at Catch and * Back calculated Size at Age*

| Study sites | Years with catch data | Gear | Gear code | Years with temperature data |
|---|---|---|---|---|
| Kinnbäcksfjärden | 2007-2021 | Nordic coastal survey nets | K064 | 2005-2023 |
| Långvindsfjärden | 2004-2021 | Nordic coastal survey nets | K064 | 2004-2023 |
| Norrbyn | 2004-2021 | Nordic coastal survey nets | K064 | 2004-2023 |
| Råneå | 2007-2023 | Nordic coastal survey nets | K064 | 1991-2023 |
| Torhamn<br>* | 2006-2022<br>2007-2023 | Nordic coastal survey nets | K064 | 2006-2022 |
| Kvädöfjärden<br>* | 2002-2019<br>*2003 - 2019 | Sets of nets (17 21,5 25 30 mm) | K053 | 1993-2023 |
| Kvädöfjärden<br>* | *2019-2023 | Nordic coastal survey nets | K064 | |
| Forsmark<br>* | *2002-2021 sporadically | Coastal survey nets (17 22 25 33 50 mm) | K009 | 1989-2023 |
| Forsmark<br>* | *2002-2023 | Nordic coastal survey nets | K064 | |
| Holmön<br>* | 2002-2023<br>*2003-2023 | Nordic coastal survey nets | K064 | 1990-2023 |

## 2.3 Temperature and Marine heatwaves

Water temperatures at 0.5-1.5 meter depth were collected with temperature loggers throughout the main growth season of perch in the same monitoring areas as described above for survey fishing. As part of the monitoring temperature loggers (model TG-4100) are placed in the water at the beginning of the ice-free period and retrieved before ice is covering the bays. Temperature data from all sites were included in the analyses using the condition that the data included must have measurements for the period June 1 to September 30. Only these months were used in the heatwave analyses estimates.

To identify marine heatwaves per site and year I used the R package heatwavesR (Schlegel et al., 2018). This package calculates MHWs based on the definition by Hobday et al (2016), which classifies MHWs as an occurrence when the daily temperature is warmer than the seasonally varying threshold for five or more days in a row. A daily climatological mean value is calculated for each day from a 30-year baseline which is then smoothed in a two-step process: First using a 5-day double-sided moving average (11 days in width) and then a 15-day double-sided moving average (31 days in width). This creates the final seasonally varying mean. The threshold is calculated as the 90th percentile above the daily climatological mean and smoothed in the same manner. As I did not have access to 30-year long time-series in some locations, I instead defined the baseline as the years I had available for temperature (table 1). I tested for two measures of MHWs: the occurrence of one or more MHW (i.e. yes or no) per year (from here on defined as simply occurrence) and the total cumulative intensity for all MHWs/year ($totI_{cum}$). $I_{cum}$ for each MHW is calculated as the integral of the temperature deviation above a set threshold over time. Thus, both the temperature deviation and the duration of a heatwave is considered. $I_{cum}$ was then added together for each year creating $totI_{cum}$.

## 2.4 Length-at-age and length-specific body growth

The individual-level perch data that is collected as part of the coastal monitoring includes many different measured parameters. For this project the ones used are age at catch, length at catch, and back calculated length at age. Current age and back calculated length at age was derived from the annual rings on the operculum bones (gill covers). Perch and many other fish do not grow during winter and zones are formed due to the annual termination of growth. It is therefore possible to determine the age of the fish based on these annual rings (Thoresson 1996). The back calculated size at age is based on an assumed relationship between the spacing between the annuli rings on the operculum bones and fish length (Thoresson 1996).

I filtered the data to only include age classes with at least five individuals per year to reduce the influence of outliers. As a result, only perch aged 1-6 years at catch were used since older age classes in most cases had too few individuals. When calculating growth all individuals were assigned a size of 5mm at age 0, representing the average size of perch at hatching (Huss et al., 2007).

I calculated yearly absolute growth (in mm) at age and relative size-specific growth (in %) at age as:

$$Growth\ in\ mm = l_{(i+1)} - l_i$$

$$Growth\ in\ \% = \frac{l_{(i+1)} - l_i}{l_i} \times 100$$

*l* is the length of a perch at a specific back calculated year *i*, also known as the year of growth.

## 2.5 Statistical analyses

To test for the effects of MHWs on perch body growth and length-at-age I fitted linear mixed models using the function lmer (package lme4, Bates et al. 2015) as:

Growth ~ MHW * Age + Mean temperature + 1|Location + 1|ID
Growth ~ MHW * Length + Mean temperature + 1|Location + 1|ID
Length-at-age-at-catch ~ MHW * Age + Mean temperature + 1|Location

Both absolute growth and relative growth was transformed with the natural logarithm to improve model fit. Additionally, relative growth was evaluated separately for two age groups (age 0 and age 1-6) for the same reason. The effects of MHWs were tested with MHWs treated both as a fixed variable (occurrence Yes/No) and as a continuous variable ($totI_{cum}$). I also tested if the effect of MHWs (as occurrence or $totI_{cum}$) remained or changed when taking mean growth season water temperature into account by adding the latter as a fixed effect. Location and fish ID were added as random variables to all analysis regarding growth. The only exceptions not including ID were in tests which only include age zero, as the variance in start length was zero in these cases (i.e. they were all assigned the same size at hatching). As measured of model fits, Conditional $R^2$-values ($R^2c$) and Marginal $R^2$-values ($R^2m$) were calculated and can be found in in all tables. I calculated Variance Inflation Factors to test for multicollinearity between explanatory variables for all models with more than one fixed effect (which was not the case). All different model versions (including or excluding average temperature) were compared with Anova, to test if the added covariates improved the fit or not. Best fitted models (based on likelihood ratio tests) where those were all fixed effects available were included but the results (and their significance) did not differ between model versions. I only report on the simplest models (e.g. excluding mean temperature) in the main results section, while the alternative model set-ups can be found in the Supplement. I also tested for correlations between cumulative intensity and year as well as between occurrence of MHWs and year, using Spearman's rank correlation coefficients (Zar 2005). As the available temperature data from different locations differed in timespan, I restricted the first year of MHWs to the year 2000 to make the data more comparable.

# 3. Result

## 3.1 Frequency and occurrence

MHWs were identified in all study sites, but with different timing and intensity. This means that the occurrence of one or more MHWs a certain year can vary between sites, also over relatively short distances (Figure 2). There was no significant correlation between $totI_{cum}$ and year (p-value = 0.0914) or occurrence of one or more MHWs and year (p-value = 0.1246) (Suppl. Table S2). Although there was variation in years with occurring MHWs between sites, some sites also shared years with occurring MHWs (figure 2, Suppl. Table S1). For example, all sites with available temperature data in 2018 also exhibited MHWs 2018.

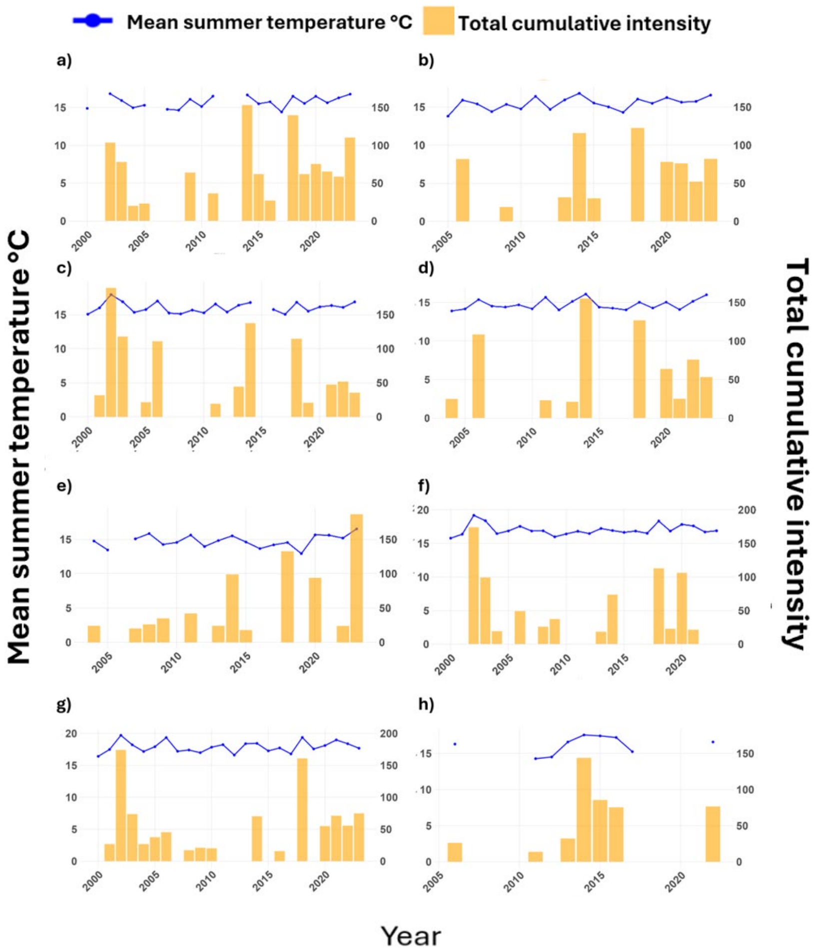


Figure 2 Plots of mean summer water temperature (blue) and total cumulative intensity of MHWs (orange) over years in all sites. From north to south, (a) Råneå (b) Kinnbäcksfjärden (c) Holmön, (d) Norrbyn, (e) Långvindsfjärden (f) Forsmark, (g) Kvädöfjärden, (h) Torhamn

## 3.2 Effects of MHWs on perch body growth

There was small but positive effect of MHWs on both absolute and relative body growth of perch (table 2, figure 3). The positive effect of MHWs on absolute growth decreased with age but not size. The positive effect on relative growth decreased with both age and size (table 2, figure 3, Suppl. Table S6). This was true also when including mean temperature (Suppl. Table S5-7).

*Table 2 Mixed models on the effects of occurrence of MHWs and age on a) Absolute growth b) Relative growth age 1-6 and c) Relative growth age 0*

a)

Formula: Absolute_growth ~ MHW * age + (1 | location) + (1 | fish_id)

| Explanatory Variables | Estimate | SE | CI Low | CI High | t | p |
|---|---|---|---|---|---|---|
| (Intercept) | 4.207 | 0.034 | 4.132 | 4.282 | 123.03 | <0.001 *** |
| MHWYes | 0.113 | 0.003 | 0.106 | 0.119 | 32.92 | <0.001 *** |
| age | -0.172 | 0.002 | -0.175 | -0.169 | -117.41 | <0.001 *** |
| MHWYes:age | -0.018 | 0.002 | -0.021 | -0.014 | -9.51 | <0.001 *** |

Note: R2m = 0.43 R2c = 0.49

b)

Formula: Relative_growth ~ MHW * age + (1 | location) + (1 | fish_id)

| Explanatory Variables | Estimate | SE | CI Low | CI High | t | p |
|---|---|---|---|---|---|---|
| (Intercept) | 4.582 | 0.040 | 4.495 | 4.670 | 114.917 | <0.001 *** |
| MHWYes | 0.142 | 0.007 | 0.127 | 0.157 | 18.965 | <0.001 *** |
| age | -0.444 | 0.003 | -0.449 | -0.439 | -175.665 | <0.001 *** |
| MHWYes:age | -0.033 | 0.003 | -0.039 | -0.026 | -9.881 | <0.001 *** |

Note: R2m = 0.67, R2c = 0.69

c)

Formula: Relative_growth ~ MHW + (1 | location)

| Explanatory Variables | Estimate | SE | CI Low | CI High | t | p |
|---|---|---|---|---|---|---|
| (Intercept) | 7.271 | 0.050 | 7.161 | 7.380 | 145.770 | < 0.001 *** |
| MHWYes | 0.058 | 0.003 | 0.052 | 0.063 | 20.790 | < 0.001 *** |

Note: R2m = 0.017, R2c = 0.256

a) b)

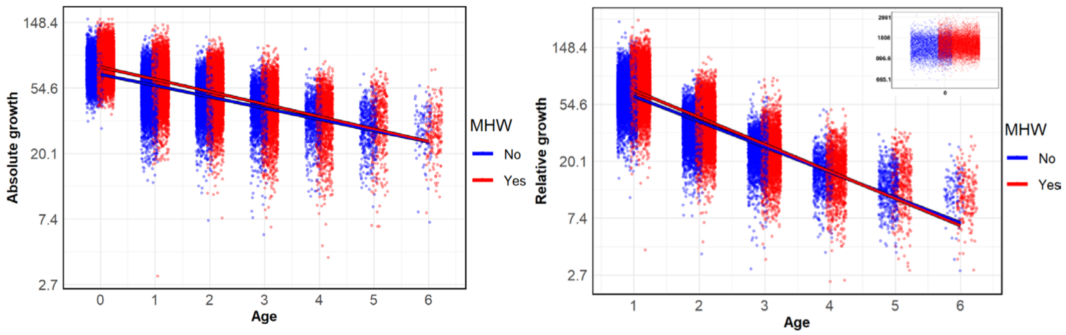


Figure 3 Relationships between absolute (in mm) (a) and relative (in %) (b) body growth of perch and age. Regression lines are predicted values based on the model presented in table 2. All values are colour coded by presence (red) or absence (blue) of MHW. The Y axis scales are converted from log values. Plot b also include a subplot with data for age zero perch.

## 3.3 Effects of total cumulative intensity of MHWs on perch body growth

The effect of tot$I_{cum}$ on absolute growth varied with size and age and the effect on relative growth with age (table 3 and Suppl. Table S9). Concerning absolute growth, there was a minor but statistically significant effect of tot$I_{cum}$ that increased with age and size (figure 3). However, the effect changed sign when mean temperature was included as a fixed effect, making the direction hard to disentangle (Supplement table S8-9). There was a positive effect of tot$I_{cum}$ on relative growth that increased with age (figure 4). The individual effect on relative growth was also small but remained significant and positive also when including mean temperature as a fixed effect (Suppl. Table S10-12).

*Table 3 Mixed models on the effects of total cumulative intensity ($totI_{cum}$) and age on a) Absolute growth b) Relative growth age 1-6 and c) Relative growth age 0*

a)

Formula: Absolute_growth ~ $totI_{cum}$ * age + (1 | location) + (1 | fish_id)

| Explanatory Variables | Estimate | SE | CI Low | CI High | t | p |
|---|---|---|---|---|---|---|
| (Intercept) | 4.28 | 0.03 | 4.21 | 4.35 | 137.69 | <0.001 *** |
| $totI_{cum}$ | 0.0006 | 0.00004 | 0.0005 | 0.0006 | 15.58 | <0.001 *** |
| age | -0.23 | 0.002 | -0.23 | -0.22 | -125.55 | <0.001 *** |
| $totI_{cum}$ :age | 0.0006 | 0.00002 | 0.0006 | 0.0007 | 29.03 | <0.001 *** |
| Note: R2c= 0.54, R2m = 0.47 | | | | | | |

b)

Formula: Relative_growth ~ $totI_{cum}$ * age + (1 | location) + (1 | fish_id)

Age 1-6

| Explanatory Variables | Estimate | SE | CI Low | CI High | t | p |
|---|---|---|---|---|---|---|
| Intercept | 4.63 | 0.046 | 4.53 | 4.73 | 101.46 | <0.001 *** |
| $totI_{cum}$ | 0.0015 | 0.00009 | 0.0013 | 0.0017 | 15.92 | <0.001 *** |
| Age | -0.501 | 0.0035 | -0.508 | -0.494 | -141.96 | <0.001 *** |
| $totI_{cum}$ :Age | 0.0005 | 0.00004 | 0.00037 | 0.0005 | 10.93 | <0.001 *** |
| Note: R2m: 0.698 R2c: 0.731 | | | | | | |

c)

Formula: Relative_growth ~ $totI_{cum}$ + (1 | location)

| Explanatory Variables | Estimate | SE | CI Low | CI High | t | p |
|---|---|---|---|---|---|---|
| (Intercept) | 7.30 | 0.045 | 7.2 | 7.4 | 162.1 | <0.001 *** |
| $totI_{cum}$ | 0.0005 | 0.00003 | 0.0004 | 0.0005 | 16.2 | <0.001 *** |
| Note: R2m = 0.02 R2c = 0.22 | | | | | | |

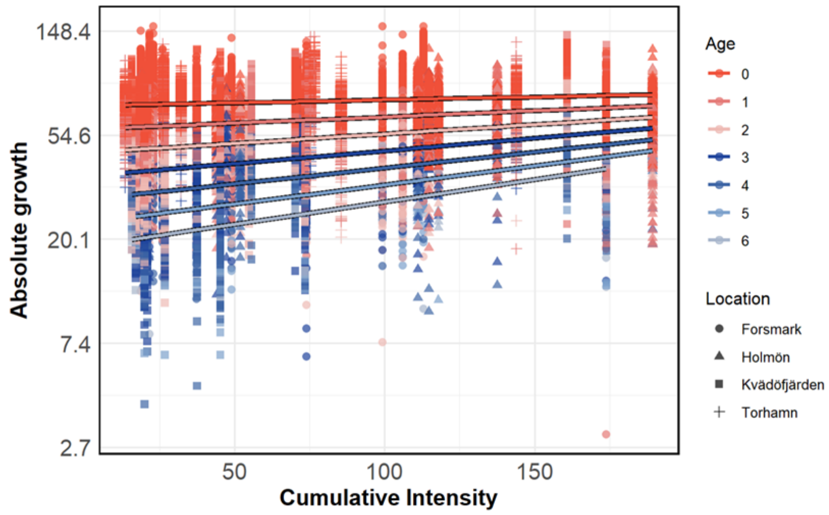


Figure 4 Perch absolute body growth (in mm) per age as a function of the tot$I_{cum}$ of MHWs. The linear regression lines are based on predicted values from the mixed effect model in table 3. Values are colour coded by age. The Y axis scales are converted from log values.

a) b)

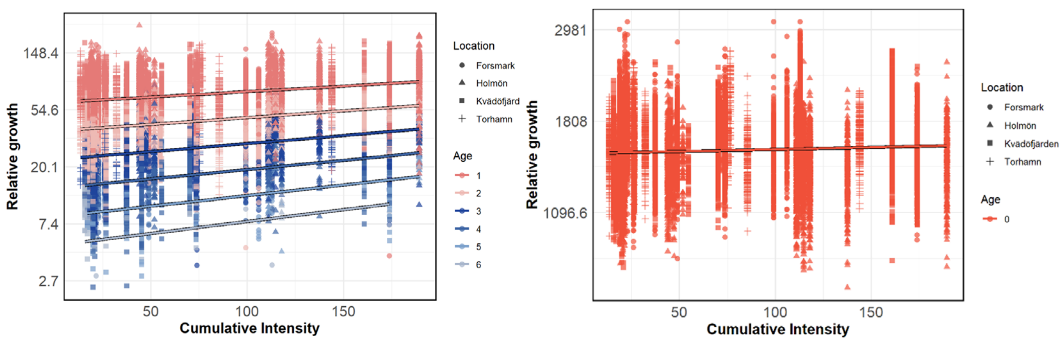


Figure 5 Perch relative body growth (in %) as a function of tot$I_{cum}$ of MHWs for age group 1-6 (a) and 0 (b). Regression lines are based on predicted values from the mixed effect model in table 3. Values are colour coded by age. The Y axis scales are converted from log values.

## 3.4 Effects of occurrence and total cumulative intensity on length at age at catch

Occurrence of MHWs had a small positive effect on length at age at catch (table 4, figure 6). The interaction between length and occurrence of MHWs is negative and significant, meaning that the positive effect of MHWs becomes smaller with age. There was no effect of tot$I_{cum}$ on length at age at catch, irrespective of age (table 4, figure 5). However, when including mean temperature as an explanatory variable, $totI_{cum}$ had a positive effect on length at age at catch (Suppl. Table S14).

*Table 4 Mixed models on the effects of a) occurrence of MHWs and age on length and b ) total cumulative intensity ($totI_{cum}$) and age on length.*

a)

Formula: length ~ MHW * age + (1 | location)

| Explanatory Variables | Estimate | SE | CI Low | CI High | t | p |
|---|---|---|---|---|---|---|
| (Intercept) | 91.810 | 8.257 | 74.668 | 108.950 | 11.119 | < 0.001 *** |
| MHWYes | 7.204 | 0.697 | 5.839 | 8.570 | 10.338 | < 0.001 *** |
| age | 36.636 | 0.175 | 36.293 | 36.978 | 209.909 | < 0.001 *** |
| MHWYes:age | -1.672 | 0.221 | -2.104 | -1.240 | -7.584 | < 0.001 *** |
| Note: R2m = 0.656, R2c = 0.797 | | | | | | |

b)

Formula: length ~ $totI_{cum}$ * age + (1 | location)

| Explanatory Variables | Estimate | SE | CI Low | CI High | t | p |
|---|---|---|---|---|---|---|
| (Intercept) | 98.77 | 8.31 | 81.52 | 116.02 | 11.88 | <0.001 *** |
| $totI_{cum}$ | 0.0028 | 0.0089 | -0.0146 | 0.0202 | 0.31 | 0.755 |
| age | 34.87 | 0.24 | 34.40 | 35.33 | 145.82 | <0.001 *** |
| $totI_{cum}$:age | 0.0017 | 0.0028 | -0.0038 | 0.0072 | 0.59 | 0.553 |
| Notes: R2m = 0.646 R2c = 0.789 | | | | | | |

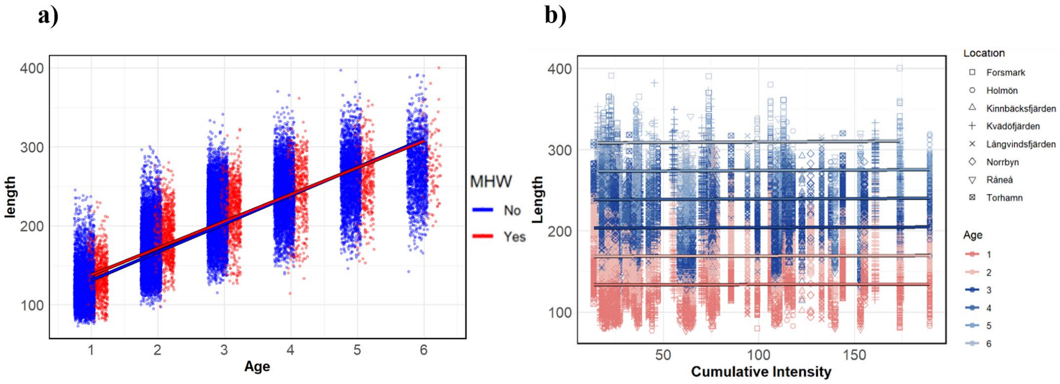


Figure 6 Perch length at catch as a function of (a) age for years without (blue) and with (red) MHWs and (b) the $totI_{cum}$ of MHWs for different age groups. Regression lines are predicted values based on the models presented in table 4.

# 4. Discussion

Range shifts, decreased population biomasses and earlier hatching are some of the observed and predicted consequences of marine heatwaves (MHWs) (Mills et al., 2013, Cheung & Frölicher 2020, Almeida et al., 2024). This escalates the need for understanding not only the prevalence of MHWs but also their effects. Still, little is known about the impacts that MHWs might have on organisms, including fish body growth. Using monitoring data from the Swedish east coast, I attempted to partly fill this knowledge gap by investigating the occurrence and intensity of MHWs and how MHWs might impact perch body growth and size. I found that MHWs occurred in all study sites since the year 2000. However, neither occurrence of MHWs or the total cumulative intensity ($totI_{cum}$) had increased or decreased significantly. There was some difference in the results of effects on growth and size depending on which measurement of MHWs was used and if growth was calculated as absolute (in mm) or relative (in %). Still, as hypothesized, occurrence of MHWs had an overall small positive effect on size at catch that declined with age. Similarly, occurrence of MHWs also had a small positive effect on perch body growth that declined with both age and size.

Body growth of ectotherms generally increases with temperature (Atkinson 1994, Ohlberger 2013) Studies of body growth and climate warming often concern gradual increases in temperature (Baudron et al. 2014) or use gradients to infer how warming may come to impact body growth (Van Dorst et al. 2019). MHWs, on the other hand, are bursts of high temperatures over five or more days and studies regarding their effect on fish growth are still very few. Interestingly, despite this difference, the positive effect on relative and absolute growth by MHWs found in my study are in line with studies concerning longer periods of warming (e.g. comparing my results to the study by Huss et al., 2019). As hypothesized, I found an age dependant effect of MHWs on both absolute and relative growth, and in addition a size dependant effect on relative growth. Some of my study's findings are in line with those of previous studies where the positive effect of warming on growth decreases with age or size (Ohlberger 2013, ). In my study the positive effect on absolute growth by occurrence of MHWs decreased with age and on relative growth the effect decreased with both age and size (table 2, figure 3). Unexpectedly, however, and in contrast to previous studies on gradual warming, I instead found that the positive effect of $totI_{cum}$ on relative growth increased with age (table 3, figure 4). This means that older perch were the ones most positively affected by summers with high $totI_{cum}$ (i.e. summers with long and/or temperature extreme MHWs). To compare these differences was beyond the scope of my study, but I suggest that this finding should be further explored.

The positive effect of occurrence and intensity of MHWs on relative body growth is of great interest. To further investigate these results specifically for perch, understanding their response to temperature is of importance. Optimum growth temperatures are commonly calculated given that there are no other limitations such as food and are known to vary with perch body size (Huss et al., 2019). These temperatures are estimated to be around 27-30°C for the smallest perch and decline down to 20-21°C for perch around 300mm (Huss et al., 2019). In my study there were only some perch above 300mm and the biggest was 358 mm. The mean summer water temperature in my data (figure 2) thus never reaches above the suggested optimum for most perch, during years with recorded MHWs or otherwise. This is also reflected by an increase in the relative growth for all ages at high cumulative intensity (figure 5). It is thus possible that MHWs might not reach high enough temperatures to be sub-optimal for perch (although I do not know if prey resources are affected) or perhaps the length of the MHWs is too short to have a negative impact on body growth. However, since the frequency and intensity of marine heatwaves are expected to increase (Oliver et al 2018) this might change, especially in combination with an increase in mean temperatures (IPCC 2019). We could possibly see a future were MHWs are longer, and high enough in temperature to negatively affect body growth of larger perch individuals, linked to that increased costs for maintenance may not be compensated for by increased consumption rates (Gårdmark and Huss 2020).

A recent study on MHWs using both in-situ and satellite data in the Lithuanian Baltic Sea coastal waters found an increase in the intensity of MHWs, but in that case only when intensity was calculated as the average maximum temperature during an MHW (i.e. a different measure than used in my study, Dabulevičienė & Servaitė 2024). Another study, that used a combination of in situ data as well as modelled data, found an increase in the occurrence of MHWs in bottom waters of relatively shallow coastal areas of the Baltic Sea (Safonova et al., 2024). Worth mentioning, however, is that these studies had few locations with in-situ temperature data and instead mainly relied on modelling or satellite data to expand their study area. Furthermore, they used slightly different methods when calculating MHWs, although both were based on the same definition. In my study, multiple MHWs were found to have occurred since the year 2000 in the shallow waters along the Swedish Baltic Sea coastline that constitute national monitoring sites for coastal fish (Figure 2). These MHWs where based on the common definition where MHWs occur if temperature exceeds the 90th percentile of the seasonally varying threshold for five consecutive days or more. I found no significant increase or decrease in the occurrence or $totI_{cum}$ of MHWs over time (Suppl. Table S2). However, I observed a notable variation in the timing and $totI_{cum}$ of MHWs between locations. Still, there are also some years where MHWs coincide between all locations (figure 2). All locations had MHWs occurring in 2014 and 2018, except Torhamn for 2018 (Suppl. Table S1). The non-existing trends in my study might indicate that site-specific differences may mitigate or amplify broader trends in MHW intensity or reflect that the timespan in my study is too short for an increase in the intensity of MHWs to be detected. I did not look at the number of MHWs occurring during one year and instead only if one or more occurred (and the total intensity). A next step could be to rather look at number of MHWs per year and their individual intensity to further understand possible patterns and consequences.

Fisheries are already impacted by MHWs due to range shifts (Cavole et al., 2016) but they could be even further affected if the size of the fish in their catches decreases. Apart from growth I also looked at size-at-age in the annual catches in the coastal monitoring program as a way of understanding if MHWs effect on growth in turn might impact size at catch. The positive effect on growth found in my study can explain the findings concerning size at catch only to some degree. Similarly to body growth, the occurrence of MHWs had a positive effect on size at catch in that same year, but only for young perch. This might be because in this scenario I only looked at how size was affected by heatwaves occurring the same year as catch. While this is relevant for the youngest perch, the growth of older fish was most likely also affected by previous MHWs. It is thus likely that MHWs occurring earlier and throughout life affect the size of older perch at catch more. It is important to mention that the size distribution in costal perch can also be affected by mortality. A study on perch have found that the mortality increases in higher temperatures. However, despite leading to a lower mean age this does not necessarily decrease mean body size (Lindmark et al., 2023). The latter was suggested to be due to a temperature-induced increase in growth that potentially outpaced the increase in mortality. If MHWs directly or indirectly affect mortality in perch should be further studied as it, combined with body growth responses, can contribute to our understanding of how size distributions change with MHWs.

In my study, I investigated if and how coastal perch body growth is affected by MHWs in the Baltic Sea. It may serve as a baseline for future research to build upon when studying MHWs and their effect on perch as well as other fish species. It could for example be of interest to look at the cumulative occurrence of MHWs during the life history of perch and how that might impact size at older age. There is also a need for studies looking more into the mechanisms of these responses and if and how they may differ from the effects of gradual warming. Since temperature can affect growth not only directly through physiological responses but also indirectly through species interactions (Gårdmark and Huss 2020) it might be of interest to understand how MHWs impact surrounding prey species as well. Furthermore, while mean summer water temperature never exceeded the suggested optimum growth temperature for perch, it is possible that temperatures during MHWs could have exceeded this optimum. I therefore suggest a more detailed investigation of temperature fluctuations during MHWs for a deeper understanding. I acknowledge that my study has some limitations that may impact the results. My sample size is large, which generally is good, but which also increases the chance of significant p-values despite weak effects. I also did not look at the effects of individual MHWs in this study. I argue that when studying the effects on growth, it is likely the cumulated effect of all MHWs during a growth season that matters. However, I suggest investigating the use of the heatwaveR package and the definition used therein and if there are better ways of defining MHWs in a study like this.

## 4.1 Conclusion

The results of this study highlights the potential for MHWs to affect fish in shallow coastal waters, adding to previous knowledge concerning MHWs in offshore areas and the effect of gradually increasing temperatures. Even though I mostly found positive effects on growth in this study, mean water temperatures as well as the occurrence and intensity of MHWs are expected to increase. This could possibly push temperatures high enough to negatively affect body growth of larger individuals. My novel results indicate that MHWs has a positive effect on perch body growth, but if this is still the case in an even warmer Baltic Sea remains to be seen.

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# Popular science summary

Global warming occurs both on land and in water and just like heatwaves occur on land they also occur in our oceans. In that case, they are called Marine heatwaves or in short MHWs. Increasing temperature has led to an increase in the occurrence and intensity of MHWs globally. Understanding how fish are affected by MHWs is of grave importance as they hold great value both to the ecosystems and to the economy.

Fish body growth is known to be affected by gradually increasing temperature. Young fish generally grow faster with increasing temperatures but reach a smaller size and mature earlier. Fish also has optimum growth temperatures, which usually are higher for small fish and lower for large fish. But what about MHWs, which are shorter periods with temperatures much higher than normal? Is fish body growth affected by MHWs as well?

To answer this question, I used monitoring data from different sites along the Swedish shallow coast of the Baltic Sea. This data included temperature and catch data of European perch (Perca fluviatilis). I used this information to understand if perch body growth was affected by MHWs depending on their age and size. I also looked at how size at catch was affected by MHWs depending on age. Lastly, I looked at if the years with MHWs and their intensity increased or decreased since the year 2000.

I found no evidence of an increase or decrease in the occurrence of MHWs or their intensity over time since the year 2000 in any of my study sites. However, all sites had years with occurring MHWs, but with the timing and intensity varying from site to site. Generally, perch had a larger size at catch and grew more during years with MHWs. My study also suggests that this positive effect was less strong in older and larger perch. This is similar to how fish such as perch respond to consistently higher temperatures. Whether MHWs' positive effect on perch growth and size will still be true in the future is unknown. If the intensity and frequency of MHWs continue to increase it might cause an unfavourable environment for at least larger perch. Studying the effects of MHWs on perch and other fish further is needed. By building an understanding of their effects we might be able to successfully manage and mitigate possible consequences in the future.

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# Supplement

*Table S1 Years with occurring MHWs in study sites*

| Location | Years with occurring MHWs |
|---|---|
| Forsmark | 2002, 2003, 2004, 2006, 2008, 2009, 2013, 2014, 2018, 2019, 2020, 2021 |
| Holmön | 2001, 2002, 2003, 2005, 2006, 2011, 2013, 2014, 2018, 2019, 2021, 2022, 2023 |
| Kinnbäcksfjärden | 2006, 2009, 2013, 2014, 2015, 2018, 2020, 2021, 2022, 2023 |
| Kvädöfjärden | 2001, 2002, 2003, 2004, 2005, 2006, 2008, 2009, 2010, 2014, 2016, 2018, 2020, 2021, 2022, 2023 |
| Långvindsfjärden | 2004, 2007, 2008, 2009, 2011, 2013, 2014, 2015, 2018, 2020, 2022, 2023 |
| Norrbyn | 2004, 2006, 2011, 2013, 2014, 2018, 2020, 2021, 2022, 2023 |
| Råneå | 2002, 2003, 2004, 2005, 2009, 2011, 2014, 2015, 2016, 2018, 2019, 2020, 2021, 2022, 2023 |
| Torhamn | 2006, 2011, 2013, 2014, 2015, 2016, 2022 |

*Table S2 Spearman correlation test between a) $totI_{cum}$ and year b) occurrence of MHW and year*

a)

| $totI_{cum}$ ~ Year | |
|---|---|
| S = 117994 | p-value = 0.0914 |
| sample estimates: rho 0.1741718 | |

b)

| Occurrence of MHWs ~ Year | |
|---|---|
| S = 576707 | p-value = 0.1246 |
| sample estimates: rho 0.1226903 | |

*Table S3 Mixed model on the effects of occurrence of MHWs, mean temperature and age on Absolute growth.*

Formula: Absolute_growth ~ MHW * age + Mean_temp + (1 | location) + (1 | fish_id)

| Explanatory Variables | Estimate | SE | CI Low | CI High | t | p |
|---|---|---|---|---|---|---|
| (Intercept) | 2.727 | 0.070 | 2.577 | 2.877 | 38.739 | <0.001 *** |
| MHWYes | 0.024 | 0.004 | 0.017 | 0.031 | 6.678 | <0.001 *** |
| age | -0.172 | 0.001 | -0.175 | -0.170 | -121.545 | <0.001 *** |
| Mean_temp | 0.091 | 0.002 | 0.088 | 0.094 | 59.722 | <0.001 *** |
| MHWYes:age | -0.012 | 0.002 | -0.015 | -0.008 | -6.635 | <0.001 *** |
| Note: R2m = 0.42, R2c = 0.57 | | | | | | |

*Table S4 Mixed models on the effects of occurrence of MHWs and length on Absolute growth a) simple model b) including mean temperature as a fixed effect*

a)

Formula: Absolute_growth ~ MHW * length + (1 | location) + (1 | fish_id)

| Explanatory Variables | Estimate | SE | CI Low | CI High | t | p |
|---|---|---|---|---|---|---|
| (Intercept) | 4.262 | 0.042 | 4.170 | 4.355 | 101.38 | <0.001 *** |
| MHWYes | 0.103 | 0.004 | 0.095 | 0.110 | 27.607 | <0.001 *** |
| length | -0.003 | 0.00003 | -0.003 | -0.003 | -119.84 | <0.001 *** |
| MHWYes:length | -0.0002 | 0.00003 | -0.0003 | -0.0001 | -6.089 | <0.001 *** |
| Note: R2m = 0.414, R2c = 0.564 | | | | | | |

b)

Formula: Absolute_growth ~ MHW * length + Mean_temp + (1 | location) + (1 | fish_id)

| Explanatory Variables | Estimate | SE | CI Low | CI High | t | p |
|---|---|---|---|---|---|---|
| (Intercept) | 2.879 | 0.073 | 2.723 | 3.035 | 39.477 | <0.001 *** |
| MHWYes | 0.017 | 0.004 | 0.009 | 0.025 | 4.371 | <0.001 *** |
| length | -0.003 | 0.00003 | -0.003 | -0.003 | -124.25 | <0.001 *** |
| Mean_temp | 0.085 | 0.001 | 0.082 | 0.088 | 57.020 | <0.001 *** |
| MHWYes:length | -0.00006 | 0.00003 | -0.0001 | 0.00001 | -1.756 | 0.079 . |
| Note: R2m = 0.408, R2c = 0.626 | | | | | | |

*Table S5 Mixed model on the effects of occurrence of MHWs, mean temperature and age on Relative growth age 1-6.*

Formula: Relative_growth ~ MHW * age + Mean_temp + (1 | location) + (1 | fish_id)

| Explanatory Variables | Estimate | SE | CI Low | CI High | t | p |
|---|---|---|---|---|---|---|
| (Intercept) | 2.198 | 0.109 | 1.965 | 2.429 | 20.182 | <0.001 *** |
| MHWYes | 0.011 | 0.007 | -0.003 | 0.026 | 1.532 | 0.126 |
| age | -0.447 | 0.002 | -0.452 | -0.442 | -185.439 | <0.001 *** |
| Mean_temp | 0.147 | 0.002 | 0.142 | 0.152 | 60.241 | <0.001 *** |
| MHWYes:age | -0.029 | 0.003 | -0.036 | -0.023 | -9.272 | <0.001 *** |
| Note: R2m = 0.64, R2c = 0.75 | | | | | | |

*Table S6 Mixed models on the effects of occurrence of MHWs and length on Relative growth age 1-6 a) simple model b) including mean temperature as a fixed effect*

a)

Formula: Relative_growth ~ MHW * length + (1 | location) + (1 | fish_id)

| Explanatory Variables | Estimate | SE | CI Low | CI High | t | p |
|---|---|---|---|---|---|---|
| (Intercept) | 4.978 | 0.048 | 4.873 | 5.084 | 103.47 | < 0.001 *** |
| MHWYes | 0.177 | 0.008 | 0.161 | 0.193 | 21.24 | < 0.001 *** |
| length | -0.01 | 0.00005 | -0.01 | -0.009 | -214.5 | < 0.001 *** |
| MHWYes:length | -0.0007 | 0.00006 | -0.0008 | -0.0006 | -12.01 | < 0.001 *** |
| Note: R2m = 0.728, R2c = 0.816 | | | | | | |

b)

Formula: Relative_growth ~ MHW * length + Mean_temp + (1 | location) + (1 | fish_id)

| Explanatory Variables | Estimate | SE | CI Low | CI High | t | p |
|---|---|---|---|---|---|---|
| (Intercept) | 3.070 | 0.100 | 2.855 | 3.284 | 30.590 | < 0.001 *** |
| MHWYes | 0.059 | 0.008 | 0.043 | 0.075 | 7.110 | < 0.001 *** |
| length | -0.01 | 0.00004 | -0.010 | -0.010 | -225.46 | < 0.001 *** |
| Mean_temp | 0.118 | 0.002 | 0.113 | 0.122 | 55.696 | < 0.001 *** |
| MHWYes:length | -0.0006 | 0.00006 | -0.001 | -0.0004 | -9.495 | < 0.001 *** |
| Note: R2m = 0.695, R2c = 0.843 | | | | | | |

*Table S7 Mixed model on the effects of occurrence of MHWs, mean temperature and length on Relative growth of age 0*

Formula: Relative_growth ~ MHW + Mean_temp + (1 | location)

| Explanatory Variables | Estimate | SE | CI Low | CI High | t | p |
|---|---|---|---|---|---|---|
| (Intercept) | 6.656 | 0.059 | 6.533 | 6.775 | 113.76 | < 0.001 *** |
| MHWYes | 0.020 | 0.003 | 0.014 | 0.026 | 6.30 | < 0.001 *** |
| Mean_temp | 0.038 | 0.002 | 0.035 | 0.041 | 23.06 | < 0.001 *** |
| Note: R2m = 0.056, R2c = 0.305 | | | | | | |

*Table S8 Mixed models on the effects of totI$_{cum}$, mean temperature and age on Absolute growth*

Formula: Absolute_growth ~ totI$_{cum}$ * age + Mean_temp + (1 | location) + (1 | fish_id)

| Explanatory Variables | Estimate | SE | CI Low | CI High | t | p |
|---|---|---|---|---|---|---|
| (Intercept) | 3.16 | 0.0704 | 3.02 | 3.30 | 44.87 | <0.001 *** |
| totI$_{cum}$ | -0.0004 | 0.00005 | -0.0005 | -0.0003 | -6.81 | <0.001 *** |
| age | -0.2245 | 0.00178 | -0.2281 | -0.2210 | -126.15 | <0.001 *** |
| Mean_temp | 0.0689 | 0.00274 | 0.0635 | 0.0743 | 25.12 | <0.001 *** |
| totI$_{cum}$:age | 0.000607 | 0.00002 | 0.0006 | 0.00065 | 28.72 | <0.001 *** |
| Note: R2m= 0.45 R2c= 0.58 | | | | | | |

*Table S9 Mixed models on the effects of totI$_{cum}$ and length on Absolute growth a) simple model b) including mean temperature as a fixed effect*

a)

Formula: Absolute_growth ~ totI$_{cum}$ * length + (1 | location) + (1 | fish_id)

| Explanatory Variables | Estimate | SE | CI Low | CI High | t | p |
|---|---|---|---|---|---|---|
| (Intercept) | 4.326 | 0.0385 | 4.242 | 4.411 | 112.51 | <0.001 *** |
| totI$_{cum}$ | 0.0005048 | 0.00004 | 0.00043 | 0.00058 | 12.73 | <0.001 *** |
| length | -0.003875 | 0.00003 | -0.0039 | -0.0038 | -120.10 | <0.001 *** |
| totI$_{cum}$:length | 0.0000095 | 0.0000004 | 0.00001 | 0.00001 | 23.82 | <0.001 *** |
| R2m: 0.447 R2c: 0.602 | | | | | | |

b)

Formula: Absolute_growth ~ totI$_{cum}$ * length + Mean_temp + (1 | location) + (1 | fish_id)

| Explanatory Variables | Estimate | SE | CI Low | CI High | t | p |
|---|---|---|---|---|---|---|
| (Intercept) | 3.349 | 0.07143 | 3.204 | 3.491 | 46.88 | <0.001 *** |
| totI$_{cum}$ | -0.0003 | 0.00005 | -0.0004 | -0.0002 | -5.43 | <0.001 *** |
| length | -0.0039 | 0.00003 | -0.0039 | -0.0038 | -120.12 | <0.001 *** |
| Mean_temp | 0.06 | 0.0027 | 0.05462 | 0.06521 | 22.209 | <0.001 *** |

| | | | | | | |
|---|---|---|---|---|---|---|
| $totI_{cum}$:length | 0.00001 | 0.0000004 | 0.00001 | 0.00001 | 23.422 | <0.001 *** |
| R2m: 0.429 R2c: 0.625 | | | | | | |

*Table S10 Mixed model on the effects of $totI_{cum}$, mean temperature and age on Relative growth for age 1-6*

Formula: Relative_growth ~ $totI_{cum}$ * age + Mean_temp + (1 | location) + (1 | fish_id)

| Explanatory Variables | Estimate | SE | CL Low | CL High | t | p |
|---|---|---|---|---|---|---|
| Intercept | 2.974 | 0.1137 | 2.751 | 3.197 | 26.153 | <0.001 *** |
| $totI_{cum}$ | 0.000001 | 0.0001 | -0.0002 | 0.0002 | 0.007 | 0.994 |
| age | -0.5068 | 0.0035 | -0.5136 | -0.5 | -144.7 | <0.001 *** |
| Mean_temp | 0.1025 | 0.0047 | 0.0933 | 0.1117 | 21.81 | <0.001 *** |
| $totI_{cum}$:age | 0.0005 | 0.00004 | 0.0004 | 0.0005 | 11.674 | <0.001 *** |
| R2m: 0.666 R2c: 0.745 | | | | | | |

*Table S11 Mixed models on the effects of $totI_{cum}$ and length on Relative growth for age 1-6 a) simple model b) including mean temperature as a fixed effect*

a)

Formula: Relative_growth ~ $totI_{cum}$ * length + (1 | location) + (1 | fish_id)

| Explanatory Variables | Estimate | SE | CI Low | CI High | t | p |
|---|---|---|---|---|---|---|
| (Intercept) | 5.01 | 0.049 | 4.90 | 5.11 | 102.6 | <0.001 *** |
| $totI_{cum}$ | 0.00191 | 0.00011 | 0.00171 | 0.00212 | 18.16 | <0.001 *** |
| length | -0.0105 | 0.000066 | -0.0106 | -0.0103 | -158. | <0.001 *** |
| $totI_{cum}$:length | -0.0000004 | 0.000001 | - 0.000002 | 0.000001 | -0.46 | 0.646 |
| Notes: R2m: 0.741 R2c: 0.837 | | | | | | |

b)

Formula: Relative_growth ~ $totI_{cum}$ * length + Mean_temp + (1 | location) + (1 | fish_id)

| Explanatory Variables | Estimate | SE | CI Low | CI High | t | p |
|---|---|---|---|---|---|---|
| (Intercept) | 3.83 | 0.10 | 3.63 | 4.03 | 38.45 | <0.001 *** |
| $totI_{cum}$ | 0.00085 | 0.00012 | 0.00062 | 0.00109 | 7.10 | <0.001 *** |
| length | -0.0105 | 0.000066 | -0.0107 | -0.0104 | -160.2 | <0.001 *** |
| Mean_temp | 0.07297 | 0.00407 | 0.06488 | 0.08088 | 17.92 | <0.001 *** |
| $totI_{cum}$:length | 0.000000 1 | 0.000001 | -0.000002 | 0.000002 | 0.11 | 0.913 |
| Notes: R2m: 0.719, R2c: 0.842. | | | | | | |

*Table S12 Mixed model on the effects of $totI_{cum}$, mean temperature and age on relative growth for age 0*

Formula: Relative_growth ~ $totI_{cum}$ + Mean_temp + (1 | location)

| Explanatory Variables | Estimate | SE | CI Low | CI High | t | p |
|---|---|---|---|---|---|---|
| (Intercept) | 6.91 | 0.0660 | 6.78 | 7.03 | 104.56 | <0.001 *** |
| $totI_{cum}$ | 0.0001 | 0.00005 | 0.00005 | 0.00024 | 2.98 | 0.00291 ** |
| Mean_temp | 0.0242 | 0.00290 | 0.0185 | 0.0299 | 8.33 | <0.001 *** |
| Note: R2m = 0.03 R2c = 0.24 | | | | | | |

*Table S13 Mixed model on the effects of occurrence of MHWs, mean temperature and age on length.*

Formula: length ~ MHW * age + Mean_temp + (1 | location)

| Explanatory Variables | Estimate | SE | CI Low | CI High | t | p |
|---|---|---|---|---|---|---|
| (Intercept) | 111.651 | 9.174 | 93.027 | 130.334 | 12.170 | < 0.001 *** |
| MHWYes | 8.441 | 0.730 | 7.008 | 9.871 | 11.557 | < 0.001 *** |
| age | 36.624 | 0.175 | 36.282 | 36.966 | 209.924 | < 0.001 *** |
| Mean_temp | -1.287 | 0.229 | -1.734 | -0.838 | -5.629 | < 0.001 *** |
| MHWYes:age | -1.642 | 0.221 | -2.075 | -1.210 | -7.450 | < 0.001 *** |
| Note: R2m = 0.652, R2c = 0.799 | | | | | | |

*Table S14 Mixed model on the effects of $totI_{cum}$, mean temperature and age on length.*

Formula: length ~ $totI_{cum}$ * age + Mean_temp + (1 | location)

| Explanatory Variables | Estimate | SE | CI Low | CI High | t | p |
|---|---|---|---|---|---|---|
| (Intercept) | 165.90 | 10.88 | 144.27 | 187.68 | 15.25 | <0.001 *** |
| $totI_{cum}$ | 0.0524 | 0.0099 | 0.0329 | 0.0719 | 5.28 | <0.001 *** |
| age | 35.06 | 0.24 | 34.59 | 35.52 | 146.39 | <0.001 *** |
| Mean_temp | -4.31 | 0.38 | -5.05 | -3.56 | -11.34 | <0.001 *** |
| $totI_{cum}$:age | 0.0005 | 0.0028 | -0.0050 | 0.0060 | 0.19 | 0.852 |
| Notes: R2m = 0.632, R2c = 0.798 | | | | | | |

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