

Linking individual physiological indicators to the productivity of fish populations: A case study of Atlantic herring

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ARTICLE INFO

Keywords:

Clupea harengus
Fish larvae
Cardiac performance
Thermal threshold
Recruitment
Fisheries management

ABSTRACT

Physiological measures can help to identify environmental thresholds that constrain organismal-level performance. Relating these thresholds, in a cause-and-effect manner, to long-term changes in the vital rates (e.g. growth, survival, reproduction) of wild populations has the potential to generate robust science advice needed to support conservation efforts. Here we investigate the hypothesis that the decreasing annual productivity (i.e. larval and juvenile abundances) of Western Baltic Spring-Spawning (WBSS) herring over the last decade is linked to warmer springs exceeding the physiological optimum of early life stages. First, we used laboratory experiments to identify the optimal and arrhythmia-inducing temperatures for cardiac function in herring larvae (approx. 16 °C and 21 °C, respectively), which were not significantly influenced by rearing temperature (7, 11 or 15 °C). These laboratory results matched well the decreased growth rates determined in the wild for larvae at temperatures beyond 17 °C. Second, we calculated a thermal threshold index based on the number of days above the optimal 16 °C threshold during the herring spawning time (March-June), which significantly increased from 1992 to 2017 for a major spawning ground of WBSS herring. Over the same time period, the thermal threshold index was significantly correlated to decreased annual productivity of WBSS herring. This finding suggests that warming is at least partially responsible for the steady decline in annual productivity of this population over the past decade. This study adds to the growing body of evidence that physiological measurements can be used as indicators of population resilience, and that the knowledge gained from laboratory experiments can be translated into advice for effective single-species (and eventually ecosystem-based) conservation and management.

1. Introduction

Ecological indicators can help to identify key aspects or processes of ecosystems and how these processes change over time to support sustainable management actions (Niemi and McDonald, 2004). Typically, these indicators are proxies for the condition of the environment, serving as early-warning signals for changes in ecological resources (e.g. biodiversity, population size). The emergence of conservation physiology as a discipline underscores the potential power of physiological knowledge and tools in supporting the sustainable management of biological resources (Cooke et al., 2013). Physiological indicators can reveal cause-and-effect relationships that can advance understanding of observed changes in the wild and, thus, improve resource management

and conservation efforts (Cooke and O'Connor, 2010; Horodysky et al., 2015). For example, stress hormones have been related to population growth in vulnerable terrestrial ungulates (Lea et al., 2018), respiratory physiology has been linked to the success of invasive marine fish (Marras et al., 2015), and shellfish growth rate has been proposed as an indicator of the carrying capacity and status of coastal marine habitats (Filgueira et al., 2014). The physiological tool box includes measurements made at different levels of biological organization, from genes, tissues or whole-organisms, which can be used as indicators for different management applications (Cooke et al., 2014; Madliger et al., 2018). The cause-and-effect knowledge gained from these physiology indicators can be integrated into numerical models that explore organismal-level performance in future (projected) climate scenarios and

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<https://doi.org/10.1016/j.ecolind.2020.106146>

Received 16 August 2019; Received in revised form 23 January 2020; Accepted 26 January 2020

Available online 26 February 2020

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support management decisions (Koenigstein et al., 2016; Pérez-Ruzafa et al., 2018).

Climate variability and change are challenging the life of ectothermic organisms (such as fish) in many marine systems, and warming is one of the most important physical changes which has been correlated to shifts in abundance, distribution and phenology (Doney et al., 2012; Poloczanska et al., 2013, 2016). Therefore, detailed knowledge on optimal and tolerable temperatures limiting organismal performance can be extremely relevant when assessing environmental impacts on commercial species and developing indicators of ecosystem health for sensitive species (Komoroske et al., 2014; Rodríguez-Fuentes et al., 2017). Growth experiments conducted at different temperatures are a straight forward and traditional method of estimating optimal and tolerable temperatures, but these can be time-consuming if one examines several body sizes/stages and temperatures. A quicker alternative used extensively in recent years is to measure oxygen consumption at different levels of activity to estimate aerobic scope. Aerobic scope is an integrative estimate of an organisms' capacity to supply oxygen to all physiological functions (e.g. growth, locomotion) above maintenance levels (Fry, 1947; Claireaux and Lefrançois, 2007). Above the optimal temperature for aerobic scope, maximum metabolic rate fails to keep pace with standard metabolic rate as temperature increases, limiting the energy available for other functions beyond maintenance. Therefore this optimal temperature is generally within the range of those maximizing other fitness-related processes such as growth and locomotion (Brett, 1971; Claireaux and Lefrançois, 2007; Farrell et al., 2009; but see Clark et al., 2013; Farrell, 2016; Lefevre, 2016). Recent studies suggest that the temperature at which the maximum heart rate occurs coincides with that at which aerobic scope is greatest and, thus, the former has been proposed as an alternative, easier-to-use proxy for the latter (Casselmann et al., 2012; Ferreira et al., 2014).

The range in tolerable temperatures often depends on the life stage and is generally narrower early in life (i.e. embryos, larvae) and during reproduction (Pörtner and Farrell, 2008; Pörtner and Peck, 2010). Laboratory measurements of thermal physiology can help identify the life stages most sensitive to predicted future warming. In fish, for example, the upper thermal limit of larvae of Arctic cod (*Boreogadus saida*) is 3 °C colder than in adults, suggesting that the survival during the larval stage will define the lower latitudinal limit of the distribution of that species (Drost et al., 2015). For delta smelt (*Hypomesus transpacificus*) inhabiting estuaries, juveniles seem to be the stage most sensitive to warming because they often experience temperatures close to their critical (tolerance) limit (Komoroske et al., 2014). These thermal thresholds can be combined later with data from wild populations (e.g. survival, growth) to gain a comprehensive understanding of the impact of environmental stressors to organismal performance (Farrell et al., 2008; Martins et al., 2011; Keefer et al., 2018). Such an approach, however, has been rarely applied to long-term field data to explore population dynamics (e.g. Bartolini et al., 2013).

The Baltic Sea, one of the largest brackish waterbodies in the world, has been markedly impacted by anthropogenic activities (HELCOM, 2018; Reusch et al., 2018). One iconic species in this ecosystem is Atlantic herring (*Clupea harengus*) (Möllmann et al., 2005 and references herein). Herring plays a key ecological role, acting as a link between zooplankton and piscivorous fish, and has supported important fisheries for millennia. There are several herring populations in the Baltic Sea, each displaying different spawning seasons linked to local environmental conditions (e.g. light, temperature) (Hufnagl and Peck, 2011). Among these populations, the Western Baltic Spring Spawning (WBSS) herring is arguably one of the best studied. The annual productivity of WBSS herring has declined since the beginning of the 2000s and has remained at a relatively low level since 2004 (ICES, 2018). Annual productivity is used in this context as an equivalent of recruitment, the number of young fish entering the population every year. This decrease in productivity seems unrelated to the spawning stock

biomass which has been consistently low since the mid-1990s. This has led to the most recent expert reports advising zero catch for 2019 and 2020 (ICES, 2018, 2019). The ultimate causes behind this low productivity are complex and not yet understood (e.g. Kotterba et al., 2014; Polte et al., 2014; Paulsen et al., 2014a; Dodson et al., 2018). Survival during the first month(s) of life, before larvae reach a body length of 20 mm, seems to be key (Oeberst et al., 2009b; Polte et al., 2014). In this sense, increased temperature during the larval phase has been related to lower larval growth and/or survival in this and other Baltic populations (Fey, 2001; Arula et al., 2015; Dodson et al., 2018). Given this anecdotal evidence, it is surprising that no estimates are available for optimal temperatures (and thermal windows in general) for larvae of this species which would allow an assessment of the impact of recent, anomalously warm temperatures on organismal-level performance. Given the commercial and ecological importance of this species, there is an urgent need to disentangle the cause(s) behind these productivity changes in order to properly understand the drivers of population dynamics and, thus, improve stock assessment and management.

The present study introduces the idea of using estimates of optimal temperature and upper thermal limits of cardiac performance obtained in the laboratory to generate thresholds that can be used as indicators to explore long-term trends of fish growth and survival in the wild. Using WBSS herring as a case study, we hypothesized that recent warming has exceeded the physiological optimum for larvae, leading to decreased larval survival and, thus, lower annual productivity of the population via direct or indirect effects. In order to test this hypothesis, we first estimated the optimal temperature and other thermal endpoints (e.g. temperatures at which arrhythmias were induced) related to the cardiac function in herring larvae reared at 7, 11 and 15 °C. Measuring aerobic scope in marine fish larvae is challenging and only rarely done (Killen et al., 2007; Peck and Moyano, 2016), therefore, cardiac performance was chosen as an alternative method (Drost et al., 2015). Next, we compiled laboratory and field estimates of the range of temperatures supporting growth of Baltic herring larvae. Next, we determined whether daily sea surface temperatures had increased in the major nursery area for this population (Polte et al., 2017; Moll et al., 2019). Finally, we assessed relationships between the thermal conditions and i) the abundance of late-stage larvae caught in the main nursery area by the end of the season, ii) the abundance of 1 year-old juveniles from the following year, and iii) a general productivity index for this population (recruitment estimate from the International Council for the Exploration of the Sea - ICES - Herring Assessment Working Group for the Area South of 62°N (ICES, 2018)).

2. Material and methods

2.1. Ethics

All experiments were done under the German law on experimental animals, and were approved by the ethical committee of the Department for Food Safety and Veterinary Matters from the Hamburg Authority for Health and Consumer Protection (Application Nr. 95/11). Adult fish were obtained from a commercial fisherman.

2.2. Larval rearing

Adult WBSS herring were collected in the Kiel Fjord (54.36 °N, 10.13°E) and transported on ice to the Elbe Aquarium (University of Hamburg) in April 2013. Several males (16) and females (16) were strip spawned in order to avoid parental effects on the offspring. Mean (\pm SD) body length and wet weight of males and females was 26.1 (1.6) cm and 149.8 (25.6) g, and 26.1 (1.5) cm and 148.1 (21.4) g, respectively. Eggs were extruded onto plastic plates and incubated for 10 min with activated milt at 8.5 °C and a salinity of 18.5. Afterwards, the plates were transferred to 90-l tanks loaded with filtered water

(0.5 μm , Reiser Filtertechnik GmbH, Seligenstadt am Main), with a daily exchange rate of 50%. Fertilization success after 24 h was $\sim 55\%$. Embryo rearing conditions were (mean (\pm range)) 10.2 (0.3) $^{\circ}\text{C}$, a salinity of 16.9 (0.1), and a 14L:10D light regime. Embryos hatched 12 days after fertilization, and hatching was synchronized using constant light for the preceding 48 h.

After hatching, approximately 2500 yolk sac larvae were transferred to the experimental tanks (dark green, 90 L, 50% water exchange d^{-1}). Over the next 10 days, the water temperature in tanks was slowly adjusted (0.5 $^{\circ}\text{C d}^{-1}$) to one of three thermal treatments (7, 11, 15 $^{\circ}\text{C}$, 2 replicates each). These temperatures were chosen to span a wide thermal range experienced by the larvae in the wild which, at the same time, allowed the larvae to be successfully reared in the laboratory and avoided increased thermal stress observed $> 17^{\circ}\text{C}$ (Borchardt, 2010; MAP, own observations). Mean (\pm range) temperatures after 12 days post-hatch (dph) were 7.8(0.3), 7.2(0.4), 11.0(0.6), 11.0(0.4), 15.0(0.3) and 15.0(0.3) $^{\circ}\text{C}$ in tanks 7A, 7B, 11A, 11B, 15A and 15B, respectively. Salinity was 16.5 (range 1.0) and the light regime was set to 14L : 10D. Larvae were reared in the presence of algae (*Rhodomonas baltica*, 10,000 cells ml^{-1}) and dinoflagellates (*Oxyrrhis marina*, 1000 cells ml^{-1}). Natural prey (nauplii from the calanoid copepod *Acartia tonsa*) was introduced in the tanks at 2 dph, and later copepod stages (copepodites and adults) were added at 9 and 12 dph, respectively. Small amounts of brine shrimp (*Artemia salina*) nauplii were supplemented after 16 dph. Further details are described in Moyano et al. (2016).

Once per week, twenty larvae were sampled from each tank and body length was measured. These larvae were not previously used for cardiac measurements. The body length was measured from the tip of the snout to the end of the notochord for preflexion larvae and to the end of the posterior margin of the hypural plate for postflexion larvae. Larvae were collected from the tanks, anesthetized (metomidate hydrochloride, 10 mg l^{-1} , Aquacalm, Syndell Laboratories, Canada), digitally photographed under a stereomicroscope (Leica MZ 16, Wetzlar, Germany), shock frozen, and stored at -80°C . Morphometric features were measured using ImageJ (Rasband, 2014).

2.3. Cardiac measurements

Measurements of larval heart rate were made using the protocol in Casselman et al. (2012) adapted to eurythermal fish larvae. In the Casselman method, fish heart rate is recorded under a stereomicroscope while fish are exposed to incremental increases in temperature (e.g. 1 $^{\circ}\text{C}$ increments at a rate of 10 $^{\circ}\text{C h}^{-1}$). This protocol was adapted for use on herring larvae as follows. First, larvae were starved for 3–6 h instead of 24 h, as 3 h is the expected gut evacuation rate for herring larvae (Pedersen, 1984). Second, a ramping temperature protocol was not used because herring have a wide thermal tolerance and individuals would have needed to be anesthetized for an excessive amount of time (> 12 h). Instead, small groups of larvae were exposed to an acute temperature change (between 7 and 27 $^{\circ}\text{C}$, in 2 $^{\circ}\text{C}$ steps) for 10 min. The highest test temperature (27 $^{\circ}\text{C}$) was chosen based on published values of critical thermal maxima for herring larvae (Moyano et al., 2017). Afterwards, they were lightly anesthetized (metomidate hydrochloride, 10 mg L^{-1} , Aquacalm, Syndell Laboratories) and placed in a petri dish at the exposure temperature ($\pm 0.1^{\circ}\text{C}$ via an aluminum-water jacket, 2.5 $\text{mg metomidate L}^{-1}$) (Fig. S1) and a 1.5-min video of the heart was recorded (stereo-microscope (LEICA M165 C microscope and Leica DFC425 Kit camera). Afterwards, each larva was photographed, euthanized by an anesthetic overdose and stored at -80°C . Body length was measured as for the growth samples. Two measurement trials were performed at each temperature treatment (trial 1 had 6, and trial 2 had 12 to 15 larvae at each test temperature), in order to have a wide range of larval sizes. Larvae were randomly but evenly selected from both replicate tanks.

Preliminary trials suggested no effect of anesthetic concentration and type (metomidate, 2.5, 5 or 10 mg l^{-1} , or MS222, 20 or 50 mg l^{-1})

on larval heart rate of other species (e.g., European seabass, *Dicentrarchus labrax*; and European eel, *Anguilla anguilla*, M. Moyano unpub. data; rainbow trout, *Oncorhynchus mykiss*, Mirkovic and Rombough, 1998). To determine heart rate, the time needed to reach 20 beats was measured at three sequences (beginning, middle, end) of the video. From these measures, the mean heart rate (beats min^{-1}) was calculated for each larva.

2.4. Compilation of thermal sensitivity of larval growth

Growth data from published studies on wild-caught and laboratory-reared Atlantic herring larvae were compiled and analyzed to search for trends in thermal sensitivity. In more detail, a literature search was conducted in the topic section of Clarivate Analytics' Web of Science™ core collection, using the search term “(Atlantic herring OR herring OR *Clupea harengus*) AND (temp*) AND (grow* OR size* OR length*) AND (larv* OR early life OR embryo)” (1 June 2016, $n = 372$). Studies that provided field and/or laboratory growth rates of larval herring with precise temperature measurements were added to the compilation. Given the high variability in herring populations (e.g. salinity, photoperiod), results were restricted to WBSS and other Baltic populations (Central Baltic Sea and Gulf of Riga).

2.5. Thermal environment and long-term herring productivity

Sea surface temperatures (SST) in the Greifswald Bay was inferred from satellite data of the NOAA daily Optimum Interpolation Sea Surface Temperature (OISST, <http://neo.sci.gsfc.nasa.gov/>, available at <https://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.highres.html>) with a spatial resolution of $0.25 \times 0.25^{\circ}$ and a daily temporal resolution from 1992 to 2017 (from March to June, the time herring larvae are found in the Bay). These satellite-derived temperatures matched well with in-situ surface temperatures measured weekly during larval surveys (Seabird v19 CTD-probe). Therefore, daily satellite SST data were used for all analyses.

Herring productivity was assessed using three different metrics. First, abundance of larvae > 20 mm (i.e. recruits) in Greifswald Bay. This Bay is surveyed weekly (35 stations) from mid-April to late June (1992–2006) and late March to late June (2007–2017), and herring larvae were collected using a Bongo net (for further details see Polte et al., 2017). Larval abundance > 20 mm (individuals m^{-3}) in this study was calculated as the cumulative sum of the weekly mean of all 35 stations. Second, 1 year-old juvenile abundance (individuals m^{-3}) was estimated from data from the German autumn acoustic survey (GERAS), a survey that covers the western Baltic Sea from the transitional waters of the North Sea to the central Baltic basin of the Arkona Sea. The survey uses acoustic data validated with pelagic trawls (for further information, see Schaber and Gröhsler, 2017) and fish were aged using the winter rings in their otoliths. Third, the ICES recruitment estimate for WBSS (subdivisions 20–24, Skagerrak, Kattegat, and western Baltic) calculated by the ICES Herring Assessment Working Group for the Area South of 62°N was used (ICES 2018). That index takes into consideration several fishery-independent estimators (larvae from the Greifswald Bay, the N20 larval index, Oeberst et al., 2009a, 2009b; the abundance of 1–4 year-old fish from the GERAS; the abundance of 3–6 year-old fish from the Herring Acoustic Summer Survey; abundance data from the International and Baltic Bottom Trawl Surveys) as well as fishery abundance data.

2.6. Statistical analysis

Growth (in body length) in the rearing tanks was estimated by linear regression (body length against age in days post-hatch). Regression equations are reported in Moyano et al. (2016).

Regarding the cardiac measurements, first, the potential effect of body length on heart rate and cardiac dysfunction at each thermal

treatment was inspected visually. Measurements were available for larvae from 7 to 20 mm, but the effect could not be statistically tested because the dataset was too small at both ends of the size range. The dataset was reduced by using a more narrow range in body sizes offering at least 5 (generally 15–20) larvae at each test temperature for each thermal treatment. Afterwards, the transition temperatures of heart rate were calculated. Several thermal points were estimated: T_{MAX} (temperature where the highest mean heart rate value was observed), T_{AR} (temperature where arrhythmia was first observed), and T_{AB} (calculated as the first Arrhenius breakpoint temperature using temperatures up to maximum temperature), following Casselman et al. (2012) and Ferreira et al. (2014). Note that we could not measure heart rate over a wide thermal range in the same individual (as in Drost et al., 2015), but worked with different groups of larvae exposed acutely to the new temperatures, which could slightly influence the Arrhenius breakpoint temperature estimation (see recommendations in Casselman et al., 2012; Ferreira et al., 2014). The Arrhenius breakpoint temperature was calculated from mean heart rate values at each temperature with the “segmented” R package (Muggeo, 2008). The Q_{10} below and above this T_{AB} was also estimated. A Q_{10} value of 2–3 is considered normal when examining the effect of temperature on metabolic and cardiac rates in fish (Fry, 1947; Eliason and Anttila, 2017). Above T_{AB} a reduction in Q_{10} (close to 1) is expected due to the failure of the heart to keep up with the thermal increase, as has been reported on other fish species. The equivalent Q_{10} below and above the T_{AB} was calculated using the following formula, where f_{H1} and f_{H2} were the estimated heart rates from the breakpoint analysis at two different temperatures (T_1 and T_2 , respectively):

$$Q_{10} = \left(\frac{f_{H2}}{f_{H1}} \right)^{\left(\frac{10}{T_2 - T_1} \right)}$$

Regarding the thermal environment experienced by herring larvae in Greifswald Bay, the day of the year at which temperatures were $> T_{AB}$ for at least 8 consecutive days was calculated. No significant differences in the timing of this day were found when different numbers of consecutive days were tested (5–8). Then, the number of days $> T_{AB}$ during this March–June period was calculated and referred to as a “thermal threshold index”. This thermal threshold index was then compared to the three herring productivity measures described in Section 2.5. All correlations (with confidence intervals) were done using a median-based Theil–Sen regression (Theil, 1950; Sen, 1968) using the “mblm” package, since it is less susceptible to outliers and allows more accurate estimations of linear trends in heteroskedastic data in comparison with ordinary least squares regression. A nonparametric Wilcoxon signed rank sum test was used by Median-based model to obtain significance and MAD (mean absolute deviation) instead of standard error of estimates.

All data analyses were done with R (R Core Team, version 3.2.3, 2015).

3. Results

Mean larval growth rate in body length was 0.22 mm d^{-1} at 7°C , 0.25 mm d^{-1} at 11°C , and 0.34 mm d^{-1} at 15°C .

A small effect of larval size on heart rate was observed (Fig. S2). At 7°C , small ($< 16 \text{ mm}$) and larger ($18 - 20 \text{ mm}$) larvae first displayed arrhythmia at 25°C and 19°C , respectively. In order to avoid any potential size-effects, a narrower range in body lengths (4 mm from 13 – 17 mm length, $n = 355$) was selected for further analysis of heart rate. Heart rate increased with temperature up to T_{MAX} , and this T_{MAX} increased (from 19.0 to 23.0°C) with increasing rearing temperature (Fig. 1, Table 1). Regardless of rearing temperature, however, T_{AR} was between 19.0 and 21.0°C and arrhythmia was noted in $\geq 35\%$ of the larvae at 25.0°C .

The T_{AB} ranged between 15.7 and 16.5°C for larvae from the three

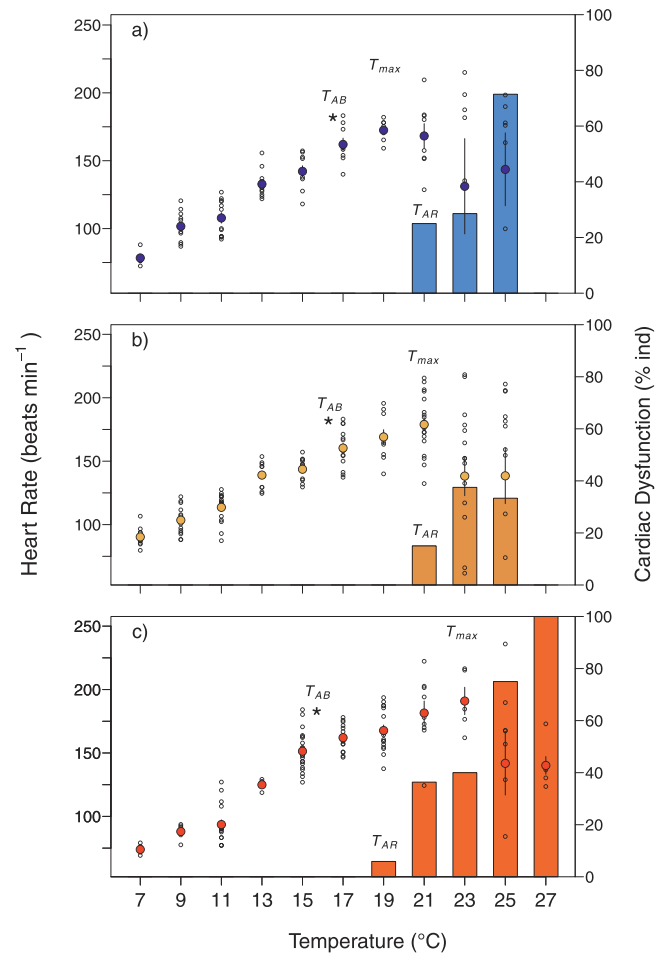


Fig. 1. Heart rate (beats min^{-1}) of Atlantic herring larvae (13–17 mm) after acute exposure to temperatures ranging from 7 to 27°C . Rearing temperatures were a) 7°C , b) 11°C and c) 15°C . Mean (\pm SE) values are shown (filled circles), as well as individual measurements used for the mean calculation (open circles). Bars represent the percentage (%) of larvae presenting cardiac dysfunction, which includes arrhythmia as well as the absence of a heartbeat. Abbreviations: T_{AB} , first Arrhenius breakpoint point (see Fig. S3); T_{MAX} , temperature at which heart rate reaches its maximum value; T_{AR} , temperature at which arrhythmia starts.

Table 1

Estimated thermal points and transition temperatures of Atlantic herring larvae heart rate reared at 7°C , 11°C and 15°C . Abbreviations: T_{AR} , temperature when cardiac arrhythmia is induced; T_{MAX} , temperature at which highest mean heart rate was observed; T_{AB} , first Arrhenius breakpoint temperature; Q_{10} equivalent slope, slopes at temperatures less than or greater than T_{AB} .

	7°C	11°C	15°C
Rearing T ($^\circ\text{C} \pm$ range)	7.5 ± 0.4	11.0 ± 0.6	15.0 ± 0.3
Size range (mm)	13–17	13–17	13–17
T_{AR} ($^\circ\text{C}$)	21.0	21.0	19.0
T_{MAX} ($^\circ\text{C}$)	19.0	21.0	23.0
T_{AB} (\pm SE) ($^\circ\text{C}$)	16.5 ± 1.0	16.3 ± 1.0	15.7 ± 0.7
Breakpoint heart rate (beats min^{-1})	160.3	155.8	157.8
Q_{10} equivalent slope (low/high)	2.0/1.3	1.8/1.3	2.6/1.3

rearing temperatures (Table 1). It is worth noting that the standard errors of the T_{AB} were relatively high ($\pm 1.0^\circ\text{C}$) (Fig. S3). The heart rate at T_{AB} was between 155 and $160 \text{ beats min}^{-1}$. Q_{10} equivalent slopes for temperatures below T_{AB} were between 1.8 and 2.6 , but steeply decreased to 1.3 after T_{AB} (Table 1).

Growth rates of WBSS larvae (Fig. 2, Table S1, $n = 155$ rates) were

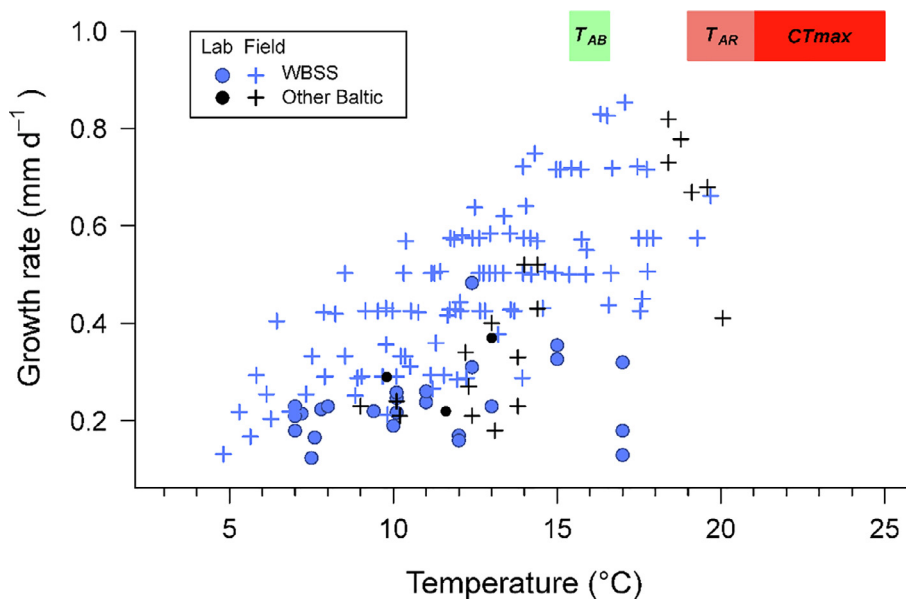


Fig. 2. Compilation of published larval growth rates of Western Baltic Spring Spawning (WBSS) herring and other Baltic stocks (Central Baltic Sea and Gulf of Riga) under controlled laboratory conditions (circles) and in the field (crosses). See Table S1 for a list of the datasets used in this figure. Color boxes on top of the figure show the optimal temperature for cardiac function (first Arrhenius break point temperature, T_{AB}) and the arrhythmia inducing temperature (T_{AR}) estimated in this study, as well as the critical thermal maximum (CT_{max}) estimated in Moyano et al. (2017).

positive from 7 to 17 °C in laboratory studies ($n = 30$), with the highest rates ($> 0.3 \text{ mm d}^{-1}$) between 13 and 17 °C. Unfortunately, no published study has reared herring in the laboratory at $> 17 \text{ °C}$. Growth rates of wild WBSS herring larvae, estimated from length frequencies in cohort analysis ($n = 122$) or otolith microstructure ($n = 3$), were highest ($> 0.7 \text{ mm d}^{-1}$) between 14 and 18 °C. Growth rates of wild larvae from other Baltic herring populations (i.e. Gulf of Riga) declined ($< 0.7 \text{ mm d}^{-1}$) at 19 °C (Fig. 2).

From 1992 to 2017, herring larvae in Greifswald Bay first experienced 8 consecutive days with temperatures beyond T_{AB} (16 °C) earliest in June (calendar day 155) and latest in mid-July (calendar day 200) (Fig. 3). The day of the year (calendar day) when warming beyond 16 °C occurred for 8 consecutive days significantly decreased (was earlier) over the past 25 years (Theil-Sen regression, $p < 0.001$). The interannual variability of the onset of this warming period has decreased since 2005. The thermal threshold index (number of days beyond T_{AB} between March and June) has, thus, significantly increased in the last decades (Fig. 3b) (Theil-Sen regression, $p < 0.001$). Since 2011 there has been a series of consecutive, warmer years when the thermal threshold index was exceeded for > 12 days before the end of June.

The thermal threshold index was significantly correlated with the abundance of larvae $> 20 \text{ mm}$ in the Greifswald Bay, the 1 year-old juveniles in the Western Baltic basin (GERAS), and the ICES recruitment estimate (Fig. 4, Table 2). In years with an increased number of warm days, all three of these metrics of herring productivity were low.

4. Discussion

The present study reveals the potential benefit of combining short-term laboratory experiments on cardiac performance and long-term field data to help provide a mechanistic understanding of changes in the productivity of an iconic marine fish. Here, we show that, over a > 20 -year period, the number of days beyond the optimal temperature for larval cardiac performance during spring (April – June) is correlated with annual productivity (the number of young fish entering the population) in a temperate stock of Atlantic herring. This study also highlights the usefulness of the optimal temperature of cardiac performance as an indicator to support fisheries management decisions. Such ecologically-relevant, physiological indicators are powerful tools to support modelling efforts in wild fish populations (Horodysky et al., 2015). In particular, such models can be used to anticipate ecosystem-wide effects of climate-driven processes, such as phenological changes,

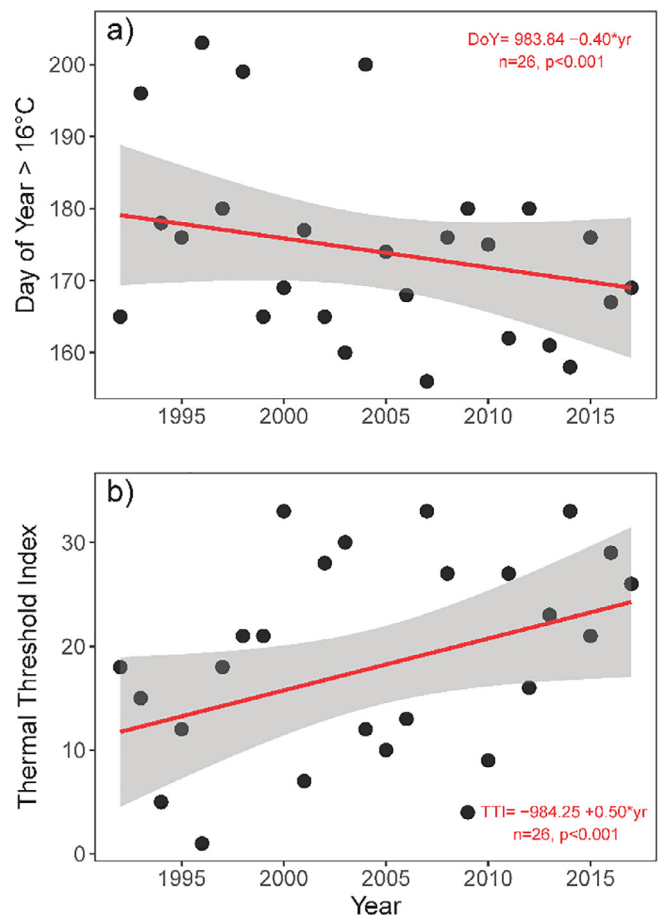


Fig. 3. Sea surface temperature in the Greifswald Bay in the 1992–2017 period. a) Day of the year (DoY) at which temperatures $> 16 \text{ °C}$ were first reached for 8 consecutive days. Theil-Sen regression lines ($\pm 95\%$ CI) and equations are included in the graphs. Abbreviations: thermal threshold index, TTI (number of days $> 16 \text{ °C}$ between March and June).

cold snaps and heatwaves, at the population level relevant for the assessment of ecosystem status (Figueira et al., 2014; Horodysky et al., 2015; Pérez-Ruzafa et al., 2018).

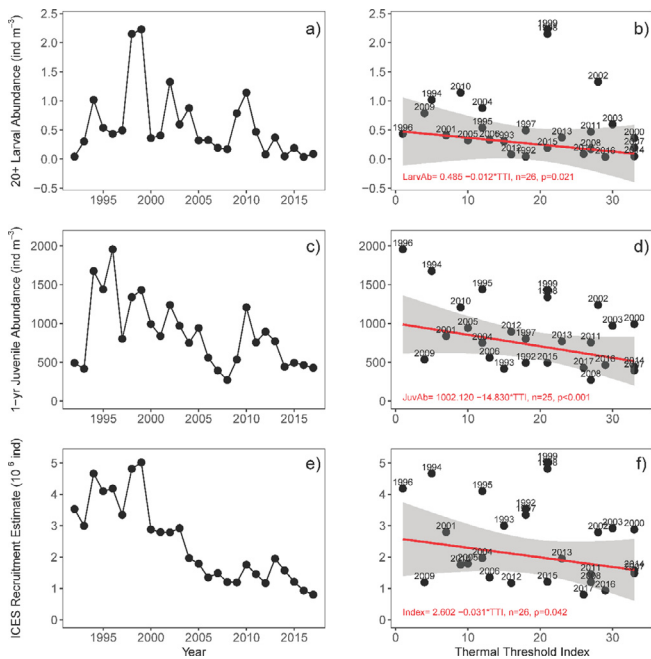


Fig. 4. Annual productivity of Western Baltic Spring-Spawning herring in the 1992–2017 period. Time series and relationship with thermal threshold index of a-b) 20 + mm larval abundance (individuals m^{-3}) in the Greifswald Bay, c-d) 1 year-old juvenile abundance (individuals m^{-3}) in the western Baltic, and e-f) recruitment estimate from the International Council of the Exploration of the Sea (ICES) (10^6 individuals). The thermal threshold index is calculated as the number of days beyond 16 °C (optimal temperature of cardiac performance estimated in the laboratory). Theil-Sen regressions lines (\pm 95% CI) and equations are included in the graphs (further details in Table 2). Abbreviations: ind, individuals; yr, year; LarvAb, 20 + mm larval abundance; TTI, thermal threshold index; JuvAb, 1-yr juvenile abundance; Index, ICES recruitment index.

Table 2

Details from the Theil-Sen regressions relating the thermal threshold index (number of days > 16 °C) in the Greifswald Bay spawning ground and the different annual productivity metrics (20 + larval abundance, 1 year-old juvenile abundance, and ICES recruitment estimate). Abbreviation: ICES, International Council for the Exploration of the Sea; MAD, median absolute deviation; V value, statistic from Wilcoxon test.

	Estimate	MAD	V value	Pr(> V)
20 + mm larval abundance ~ Thermal threshold index				
Intercept	0.4855	0.1832	351	< 0.0001
Days > 16 °C	-0.0118	0.0138	84	0.0208
1 year-old juvenile abundance ~ Thermal threshold index				
Intercept	1002.1196	435.7136	351	< 0.0001
Days > 16 °C	-14.8299	14.8365	44	0.0004
ICES recruitment estimate ~ Thermal threshold index				
Intercept	2.6022	1.4153	351	< 0.0001
Days > 16 °C	-0.0306	0.0529	95	0.0421

4.1. Thermal sensitivity of herring larvae

The optimal temperature for cardiac performance of herring larvae ranged between 15.7 and 16.5 °C, and was not influenced by rearing temperature (7, 11, or 15 °C). It is worth noting that the standard error of those means were up to \pm 1.0 °C, due to the coarse resolution of the temperatures used in this study (i.e. 2 °C stepwise increases). Below this optimum temperature, Q_{10} values for changes in cardiac performance with temperatures were close to 2.0, which is a common value for Q_{10} of heart rate in larval fish studies (e.g. Barrionuevo and Burggren, 1999; Perrichon et al., 2017). Above the optimum, heart rate failed to

continue the temperature-related increase, leading to Q_{10} values of 1.3 for all thermal treatments. To the best knowledge, no estimates of optimal temperature for cardiac performance or metabolism exist for herring larvae to compare with the present dataset. The only dataset on metabolic rates available covering a wide range of temperatures is limited to 7–15 °C (Moyano et al., 2018).

At temperatures above 19 °C, herring larvae started to exhibit evidence of cardiac distress. Arrhythmia was generally induced at 21 °C, and cardiac dysfunction was present in \geq 35% of the herring larvae at temperatures \geq 25 °C. These temperatures agree well with the upper thermal limits (mean critical thermal maximum, when 50% of the tested larvae lost their equilibrium) estimated in WBSS herring larvae (21–25 °C), as has been described for other species (Eliason and Anttila, 2017). Also, these values compare well with the temperature (22.5 °C) causing 50% mortality in young herring larvae after 24 h (Blaxter, 1960; Yin and Blaxter, 1987). Comparing these “critical” and “lethal” temperatures is challenging because of the time-dependency of the response (Lutterschmidt and Hutchison, 1997b; Peck et al., 2009; Terblanche et al., 2011). For example, a difference of up to 8 °C was observed in upper lethal temperature of herring larvae between a 0.5- or 24-h exposure to temperatures > 18 °C (Moyano et al., 2017 and references therein).

Upper thermal limits of several Atlantic herring populations seem to be similar, despite the contrasting environmental settings (i.e. spawning season, salinity) experienced by the larvae. For example, temperatures at which hatching success is highest (7–13, Danielssen and Iversen, 1974; Peck et al., 2012) and the upper thermal tolerance of larvae (~21–22 °C, Blaxter, 1960) are similar for Baltic and North Sea herring. These results suggest that thermal tolerance in the early stages of herring is hardwired, conferring these organisms little potential for adaptation beyond these limits. This lack of phenotypic plasticity in herring larvae has been reported in other traits such as salinity tolerance across herring populations inhabiting a significant salinity gradient (6 to 33, Illing et al., 2016b). However, the adaptation potential of thermal limits in fish seems to be highly species-specific. For example, phenotypic plasticity has not been observed in the upper tolerance of Pacific salmon (*Oncorhynchus tshawytscha*) and European perch (*Perca fluviatilis*) (Muñoz et al., 2014; Sandblom et al., 2016), but it has been observed to some degree in Atlantic salmon (*Salmo salar*) (Anttila et al., 2014). It is important to note the potential impact of methodology when addressing phenotypic plasticity in thermal tolerance, as aspects such as warming rate can lead to variability in the mean and variance of the estimate (Chown et al., 2009). Generating standard protocols valid across life-stages and taxa is, thus, essential to generate reliable predictions of the population responses to current and projected environmental scenarios and further develop mitigation measures that ensure future viability of fish populations.

4.2. Linking cardiac function to annual herring productivity in the field

Our laboratory estimates of thermal optima and upper limits of the cardiac function in Baltic herring larvae agreed well with temperatures (7–17 °C) supporting growth in wild and laboratory-reared larvae. In the laboratory, larvae grew fastest at 13 °C. Although there have been few attempts to grow herring larvae in the laboratory above 15 °C, larvae reared at 17 °C grew slower and were very sensitive to stress (M.A. Peck, unpublished obs.), suggesting suboptimal thermal conditions for growth. Growth rates of WBSS wild larvae decreased from 17.5 °C in the Greifswald Bay (Oeberst et al., 2009a) and 18 °C in the Vistula Lagoon (Fey, 2001). Similarly, growth rates also decreased at temperatures > 18 °C in autumn-spawned wild larvae in the Gulf of Riga (Arula et al., 2015, 2016). These growth rates in wild larvae were faster than those from laboratory-reared larvae, which is a well-known issue likely due to a variety of factors (e.g. artificial tank environments and density-dependence limiting growth in the laboratory, size-based mortality over-estimating growth in the field) (Takasuka et al., 2003;

Huebert and Peck, 2014). Moreover, growth rates of wild larvae are impacted by other factors besides temperature (e.g. prey abundance and quality, salinity). Temperature alone, however, explained > 50% of the variability in growth rates of wild WBSS larvae, and this prediction was not significantly improved by adding other variables (Oeberst et al., 2009a).

Temperature has a pervasive effect on the biology of ectothermic organisms, including fish (Fry, 1947), and, therefore, it is difficult to disentangle its direct and indirect effects. WBSS herring spawners enter Greifswald Bay and start spawning when temperatures reach 3–4 °C (Klinkhardt, 1986; Moll, 2018). Optimal temperatures for hatching range between 5 and 17 °C (Peck et al., 2012), which matches the thermal window (9–13 °C) maximizing yolk sack larval abundance in the field (Dodson et al., 2018). Later larvae perform some ontogenetic migrations inside the Bay, moving to the center as early larvae, coming back to the shallow areas (> 20 mm cm) during the postflexion stage until they metamorphose into juveniles and then leave the Bay to offshore areas to recruit by the beginning of the summer (Polte et al., 2017). Considering this life history, a direct, negative impact of temperature could likely occur via cold snaps during the spawning season, where either the spawners or the eggs are affected. Direct effects of warming on late larval physiology may be more unlikely as temperatures rarely reach 21 °C before the beginning of July, and larvae have a strong swimming capacity at those sizes to move out of the Bay to colder waters (Moyano et al., 2016; Polte et al., 2017). However, our results suggest that indirect effects of warming impact larval herring physiology, and thus growth and survival in Greifswald Bay. Temperatures beyond 16 °C can already be suboptimal for larval growth due to decreased cardiac performance and likely reductions in aerobic scope (not measured). Such reduction in aerobic scope would imply that herring larvae will have less energy available not only for somatic growth but also for other key survival processes such as escaping from predators or battling diseases. These physiological impacts translate into observed decreased growth in wild larvae at temperatures > 17.5 °C.

In the Greifswald Bay, the number of days > 16 °C (our Thermal Threshold Index) has significantly increased, especially since 2014. Such warming partially explains the decrease in herring productivity over the last decade as calculated using three different indices: abundance of larval survivors in Greifswald Bay, WBSS 1 year-old juvenile abundance in the whole western Baltic, and the ICES recruitment estimate. All three indices have their strengths and pitfalls. First, the abundance of 20 + mm larvae in Greifswald Bay needs to be carefully interpreted as the sampling device (Bongo net, 60 cm) does not effectively capture relatively large larvae but, rather, provide an approximation of the total number of large larvae in the system. Second, the ICES recruitment estimate is calculated using a wide variety of larval and fishery-data, potentially leading to masking effects in comparison to true abundance data. We consider the abundance of 1 year-old juveniles to be the best proxy of annual productivity in the WBSS population as it is based on a survey of the whole Western Baltic and captures a life stage at which year-class success has been already set. The fact that all three productivity indices were significantly related to our physiologically-based thermal threshold index adds confidence in the robustness of our results and approach.

The annual productivity of marine fishes is the result of a complex interaction of abiotic and biotic factors (Houde, 2008). Our results suggest a significant adverse effect of temperatures > 16 °C on the annual productivity of the WBSS herring population, but there are several additional factors influenced by spring warming that can impact the growth and survival of larval fish such as phenological shifts in spawning times and changes in the magnitude of exposure to predators of herring eggs (Kotterba et al., 2014; Polte et al., 2014; in prep.). Earlier spawning by herring in warm winters/springs could be an adaptive response allowing fish to spawn at the same temperature, but such a phenological shift will be maladaptive if a mismatch occurs with

the timing of the spring bloom of prey, a phenomenon controlled by both temperature and light in temperate regions. Short-term studies highlight the importance of both prey type (high quality copepods vs low quality cirripeds) and abundance to larval growth (Paulsen et al., 2014a,b). Unfortunately, there are no long-term records of the prey field experienced by WBSS herring larvae and the relationship between interannual variation in the timing, abundance and type of prey and water temperature is unknown. Long-term records (1993–2014) relate changes in the physiological status of herring adults and changes in food abundance and size (i.e. plankton mean size) (Karlson et al., 2019), emphasizing the relevance of including plankton size as an ecological indicator in the Baltic Sea (Gorokhova et al., 2016). Therefore, additional information on the spawning timing and potential changes in the age and physiological status of the spawners, as well as on the feeding environment (prey abundance and type) experienced by the larvae will help to further understand the mechanisms behind the dramatic decrease in productivity in this iconic fish species in the western Baltic Sea.

Changes in the population dynamics of terrestrial and marine animals have been related to an earlier onset of the spring worldwide (Schwartz et al., 2006; Rogers and Dougherty, 2019). In the specific case of the Baltic Sea, since 1980 seawater has warmed at a rate of 0.3 to 0.6 °C decade⁻¹ (depending on the region) (Reusch et al., 2018), and the most drastic changes have occurred in the 15–16 °C isotherms (Kahru et al., 2016). According to those authors, the number of days > 16 °C has doubled between 1982 and 2014. Crossing this 16 °C threshold has been related to a variety of ecological changes observed in the SW Baltic Sea, including a shift in the growth peak of cyanobacteria (Hense et al., 2013), and protracted spawning seasons in mollusks (Appelqvist and Havenhand, 2016). Our results on the productivity of herring adds to the growing body of evidence that earlier warming in the spring is leading to changes across species and multiple trophic levels. Further research on the thermal physiology of different, key taxa in the Baltic Sea can provide knowledge and indices useful for the assessing ecosystem-wide responses to early spring warming and yield indicators of ecosystem status.

4.3. Linking short-term physiological measurements to long-term past and future trends in population dynamics

Thermal sensitivity of aerobic scope and/or cardiac function has been successfully used to mechanistically explain the impact of global warming on population dynamics/distribution and to make projections of future scenarios (Bozinovic and Pörtner, 2015; McKenzie et al., 2016). For example, warmer temperatures experienced during river migration in sockeye salmon (*Oncorhynchus nerka*) exceed those of the optimal for aerobic scope and have been linked with high-mortality events in recent years (Farrell et al., 2008; Martins et al., 2011). To the best knowledge, however, relatively few studies have linked thermal tolerance measured in wild or laboratory-reared animals (not derived from distribution maps) to changes in the annual productivity of a species (Teal et al., 2018). For example, a recent study showed that warmer summers are leading to higher offspring abundance (due to a longer spawning season) in a mollusk in the Baltic Sea (Appelqvist and Havenhand, 2016). On the other hand, warmer temperatures have been related to a decreased productivity of another invertebrate, the Mediterranean green crab *Carcinus aestuarii*, due to deleterious effects to the early life stages (Bartolini et al., 2013). Our study provides a new, physiologically-based indicator, the thermal threshold index, of poor year class strength in WBSS herring. Similar metrics, based on the number of days over a specific threshold, have been extensively used in phenology studies, especially in invertebrates, but these have been rarely combined mechanistically with optimal thermal ranges estimated in the laboratory (Bartolini et al., 2013). This present study emphasizes the importance of: i) estimating key aspects of thermal sensitivity at the organismal level to gain a cause-and-effect understanding of the

potential impacts of environmental changes at the population-level, and ii) accounting for thermal sensitivity across life-stages to identify the most vulnerable life-stages to make more robust projections of climate impacts.

The protocol used here to estimate key features of cardiac performance is less challenging than using respirometry to measure aerobic scope, particularly when examining embryos and larvae of fish. The protocol, however, has some caveats when used on early stages compared to larger juveniles and adults, such as i) the higher sensitivity of larvae to handling, ii) the inability to chemically induce a maximum heart rate (Drost et al., 2015), and iii) the potential changes in heart rate during early development (Barrionuevo and Burggren, 1999). Nevertheless, it is a promising tool to rapidly determine temperature thresholds (i.e. lower and upper thermal tolerance, optimal temperature) in early life stages of fish, especially in combination with other physiological measurements ideally at different organization levels. This latter aspect is important as some authors have suggested that further research is needed before using this method as a single screening tool of thermal tolerance in new fish species (Eliason and Anttila, 2017). In addition, this method provides estimates of the temperature at which arrhythmia is first induced, which could be a more precise (and physiologically more relevant) endpoint for critical thermal maximum assays than the righting reflex which has been criticized (e.g. Lutterschmidt and Hutchison, 1997a; Angilletta et al., 2013).

5. Conclusion

The present study demonstrates how short-term physiological measurements at the suborganismal- (i.e. cardiac system) and organismal- (i.e. growth) levels can be used to explain patterns in real-world, long-term performance at the population-level in an aquatic ectotherm. Comparing physiological indicators to long-term field data is rarely done in marine systems (Bartolini et al., 2013) despite its promise (Horodysky et al., 2015). Using Atlantic herring early stages as a case study, we identified the optimal temperature for cardiac function (16 °C) and relate this threshold to decreased annual productivity in the western Baltic. These results add to the growing body of evidence reporting phenological changes in the abundance and productivity of ectothermic organisms related to earlier, warmer springs in the Baltic Sea. Based on the work presented here, we encourage other researchers to consider the use of thermal sensitivity of cardiac performance as a screening tool to assess optimal and upper tolerance temperatures in early life stages of marine fish. Ideally, this indicator would be tested on all life stages and used in combination with indicators at other levels of biological organization (Cooke et al., 2014; Pérez-Ruzafa et al., 2018). This study highlights that physiological measurements can be used as indicators for population resilience (Filgueira et al., 2014; Harrington et al., 2019). The direct application of thermal threshold indices to support single-species assessment advice is often constrained by the absence of reliable seasonal climate forecasting in many areas. However, there are many recent developments in the realm of oceanographic predictive capacity, and seasonal forecasting is now used to provide advice at operational time-scales relevant to the fisheries industry in several areas of the world (Mills et al., 2017; Hobday et al., 2018). These indices may also be useful for identifying ecosystem-wide responses to phenological changes that are relevant for the assessment of ecosystem status but more work is needed before that can be realized.

CRedit authorship contribution statement

Marta Moyano: Conceptualization, Methodology, Investigation, Validation, Formal analysis, Data curation, Writing - original draft, Writing - review & editing, Visualization, Project administration, Funding acquisition. **Björn Illing:** Investigation, Writing - review &

editing. **Patrick Polte:** Conceptualization, Methodology, Resources, Formal analysis, Writing - review & editing. **Paul Kotterba:** Methodology, Writing - review & editing. **Yury Zablotski:** Methodology, Software, Formal analysis, Writing - review & editing. **Tomas Gröhsler:** Resources, Writing - review & editing. **Patricia Hüdelpohl:** Investigation, Writing - review & editing. **Steven J. Cooke:** Conceptualization, Writing - review & editing. **Myron A. Peck:** Conceptualization, Methodology, Resources, Writing - review & editing, Project administration, Funding acquisition.

Reference Data

Data available at the zenodo repository (<https://zenodo.org>) with DOI <https://doi.org/10.1016/j.ecolind.2020.106146>.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors would like to acknowledge Martina Wichmann and Philip Peschutter for their help rearing the herring larvae, and Fintan Burke for his help with the graphical abstract. High Resolution SST data were provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from their Web site at <https://www.esrl.noaa.gov/psd/>. The research was partially funded by the German Research Foundation (THRESHOLDS, MO 2873/3-1) and the European Union's Horizon 2020 research and innovation programme under grant agreement No 678193 (CERES, Climate Change and European Aquatic Resources) and No. 773713 (PANDORA, Paradigm for New Dynamic Ocean Resource Assessments and Exploitation).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2020.106146>.

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