Environ Biol Fish
https://doi.org/10.1007/s10641-022-01212-0

Temperature and the maturation of fish: a simple sine-wave model for predicting accelerated spring spawning

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Received: 28 April 2021 / Accepted: 7 January 2022

Abstract Global warming affects the phenology of the Earth's flora and fauna, notably by advancing the date at which many plants and animals tend to reproduce. We use fish, where this reproductive acceleration is well-documented, to present a simple approach based on sine curves to predict, in spring spawning fish, the minimum number of days (Δd_{min}) that spawning is advanced as the result of a given increase in water temperature (Δ°C). We show, via comparison with field estimates, that our simple model's robust predictions correspond to observed values of Δd_{min}/Δ°C, and discuss both the potential uses and the limitations of the model.

Supplementary information The online version contains supplementary material available at https://doi.org/10.1007/s10641-022-01212-0.

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Keywords Spring spawning in fish · Shifts in phenology · Temperature differences · Size at first maturity · Triggers for maturation · Amplitude of seasonal oscillations

Introduction

Global change, or more precisely, global warming, has modified much of the Earth's flora and fauna's reproductive phenology and can be expected to continue doing so for decades. These modifications take various forms, including earlier flowering in some trees and earlier migrations in birds (see, e.g., Ahas and Aasa 2006; Cohen et al. 2018), many due to sinusoid seasonal temperature oscillations with a higher annual mean (Fig. 1). In the past few decades, the temperatures of marine ecosystems have increased (Belkin 2009), as they have in freshwater bodies (Carpenter et al. 1992; Kangur et al. 2021). Increasing temperatures, on the other hand, will alter the physiology of fish, and particularly their reproduction, as can be expected in ectotherms (Alix et al. 2020).

The fact that ocean and freshwater warming is modifying the phenology of maturation and spawning in fishes, i.e., the timing of their reaching puberty, has been widely reported. A meta-analysis of observed phenological shifts suggested that seasonal events of marine species advanced by an average of 4.4 days per decade during the late twentieth century (Poloczanska et al. 2013). Also,

Published online: 08 February 2022

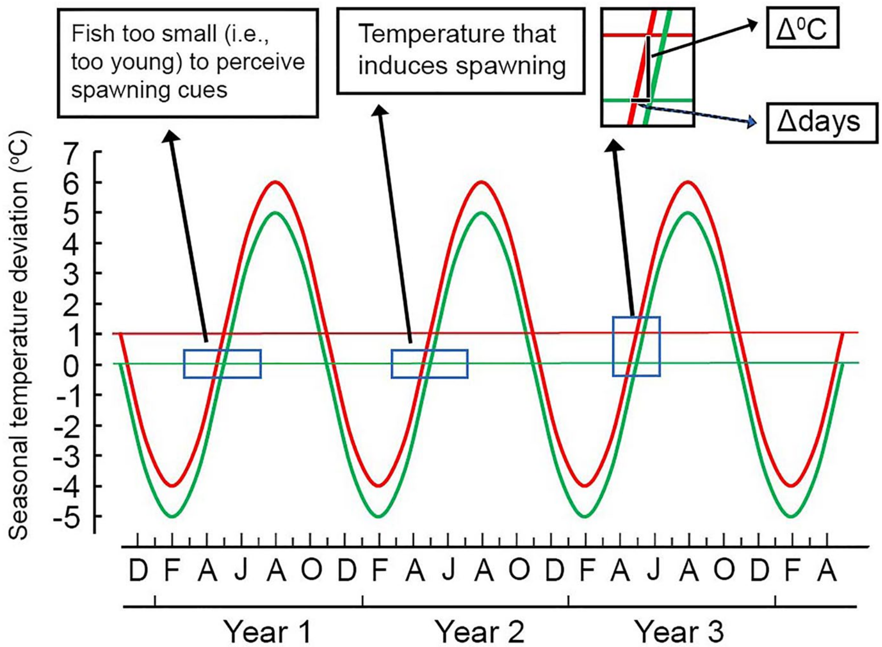


Fig. 1 Schematic representations of the effect of global warming on the phenology of spring spawning fish via the two sine curves. Here, the green one represents the baseline climate, with a temperature threshold in acting as an evolved trigger for maturation and spawning, while red curve represents the warmer climate, which leads to the trigger temperature being reached earlier

larvae of 17 of the 43 species of fish species in the California Current ecosystem occurred earlier in recent decades relative to the last 58 years (Asch 2015). However, zooplankton, being one of the main food items for these fishes, did not shift their phenology synchronously with most fishes (Asch 2015). Such a mismatch often disrupts the fine-tuned adaptation that usually results in fish larvae being hatched at the time where potential prey is abundant, and leads to high larval mortality due to starvation or increased predation on slower growing larvae (Cushing 1990; Asch et al. 2019).

Here we examine the effect of global warming on the onset of maturation and spawning in the spring-spawning freshwater and marine fish of temperate latitudes (roughly 24° N–67° N; 24° S–67° S), for which ample documentation exists. The paper aims to present a simple model that predicts how spawning in marine and freshwater fish can be predicted from temperature changes. Its use can stem the proliferation of adaptationist ad hoc hypotheses that are currently being proposed to explain why, given the warming of their surrounding water, spring-spawning fish now spawn earlier.

Conceptual background

The first concept addresses the conventional notion of the hormonal cascade that leads to maturation and spawning in fish, which is usually seen as being initiated when environmental stimuli trigger reproduction (see, e.g. Bhattacharya 1999; Pankhurst 2016; Taranger et al. 2010. This notion, as also noted by Thorpe (1986, 1990), overlooks the fact that prepuberty fish can experience several “spawning seasons” without perceiving the environmental stimuli that supposedly trigger reproduction (Pauly 2021a). Clearly, what is missing is an element causing an individual’s *internal* readiness to experience these environmental stimuli in the same manner that adult fish do. Thorpe (1990) suggested that this element is the growth performance of fish, i.e., “[e]xactly how the fish monitors its performance is unknown, but I have suggested elsewhere (Thorpe 1986) that it is physiologically aware of its growth rate through its rate of accumulation of surplus energy, and through hormone kinetics associated with storage of that energy.”

As proposed here, based on Pauly (1984), fish can monitor their growth performance, which is strongly dependent on their oxygen supply, by monitoring the ratio of their metabolic rate (Q) relative to their maintenance metabolism (Q_{maint}). Given the fact that the respiratory area of fish gills, as a 2-D surface, cannot keep up with the growth of the 3-D bodies that they supply with oxygen (Pauly 2019, 2021b), this ratio must decline and thus, as individual fish grow, reach a value (Q_m) at which maturation is triggered. The threshold value of the ratio Q_m/Q_{maint} for teleosts was estimated ~ 1.35, with a 95% confidence interval ranging from 1.2 to 1.5 (Pauly 1984, 2021a, b; Meyer and Schill 2020; Amarasinghe and Pauly 2021).

Thus, when fish are small (young), their Q_m/Q_{maint} » 1.35 and no maturation and spawning occur, even during the season that adult conspecifics perceive as spawning season. However, as the small fish grow, they will reach a size at which Q_m/Q_{maint} declines to 1.35, which triggers maturation and spawning. If this size coincides with a period of increasing temperature, as occurs in spring spawners, the increase will further reduce the Q_m/Q_{maint} ratio. Thus, if that increasing temperature occurs earlier, they will also mature and spawn earlier.

A simple sine wave model is presented here which allows the period by which maturation and spawning is advanced to be estimated.

Results

Figure 1 defines the problem for which we provide the solution, based on two sine curves. These sine curves represent typical seasonal oscillations of sea surface temperatures (SST) or the temperature oscillations in (northern) temperate freshwater bodies, where mean monthly temperature tends to oscillate with an amplitude (A) of about 10 °C (see, e.g., Fig. 5 in Genner et al. 2010). The curves require a shift by 6 months in the southern hemisphere.

The green (lower) sine curve represents the oscillation of the "baseline" climate, which usually exhibits minimum temperatures in February in the northern hemisphere (see e.g. Fig. 5 in Genner et al. 2010). The red (upper) sine curve represents a warmer climate, here with a temperature increase of 1 °C. The ascending parts of the red curve implies differences in the time various threshold temperature are reached. This difference has its annual minimum (Δd_{min}, with the subscript also referring to the "minus" sign of Δd) when the slope of the sine curve is highest; however, Δd does not change much within a range of 3–4 months.

The derivation of an equation allowing for the computation of Δd_{min} is facilitated by shifting the time axis by 6 months, such it intercepts the ordinate in August (Fig. 2), with the curves now turned into cosine curves. The equation of the green (lower) curve in Fig. 2A is then:

$$Y_1 = (A/2) \cdot \cos(X) \tag{1}$$

with $A/2$ being half of the summer-winter amplitude.

When $Y_1=(A/2)\cdot\cos(X) = 0$ (g_1 and g_2 points in Fig. 2), then $\cos(X) = 0$, and $X = \arccos(0) = \pi/2$.

The equation of the red (upper) curve is:

$$Y_2 = (A/2) \cdot \cos(X) + B \tag{2}$$

with A being the amplitude of the oscillation, as defined above, and B being the temperature difference between the two cosine curves. We then have $Y_2 = (A/2)\cdot\cos(X) + B = 0$ (r_1 and r_2 points in Fig. 2A), then $\cos(X) = -2B/A$, and $X = \arccos(-2B/A)$.

Thus, the distance from r_1 to g_1 and from r_2 to g_2 on the X-axis (see Fig. 2A) is $[\arccos(-2B/A) - (\pi/2)]$. When the frequency of the sine curves is 1 year (365.24 days), each day corresponds to $2\pi/365.24$. Therefore, in areas where the spring spawning fish experience temperature changes between summer and winter, and the water temperature has become warmer by an average B, spawning should occur earlier, by a time predicted by.

$$\Delta_{min} = [\arccos(-2B/A) - (\pi/2)]/(2\pi/365.24) \tag{3a}$$

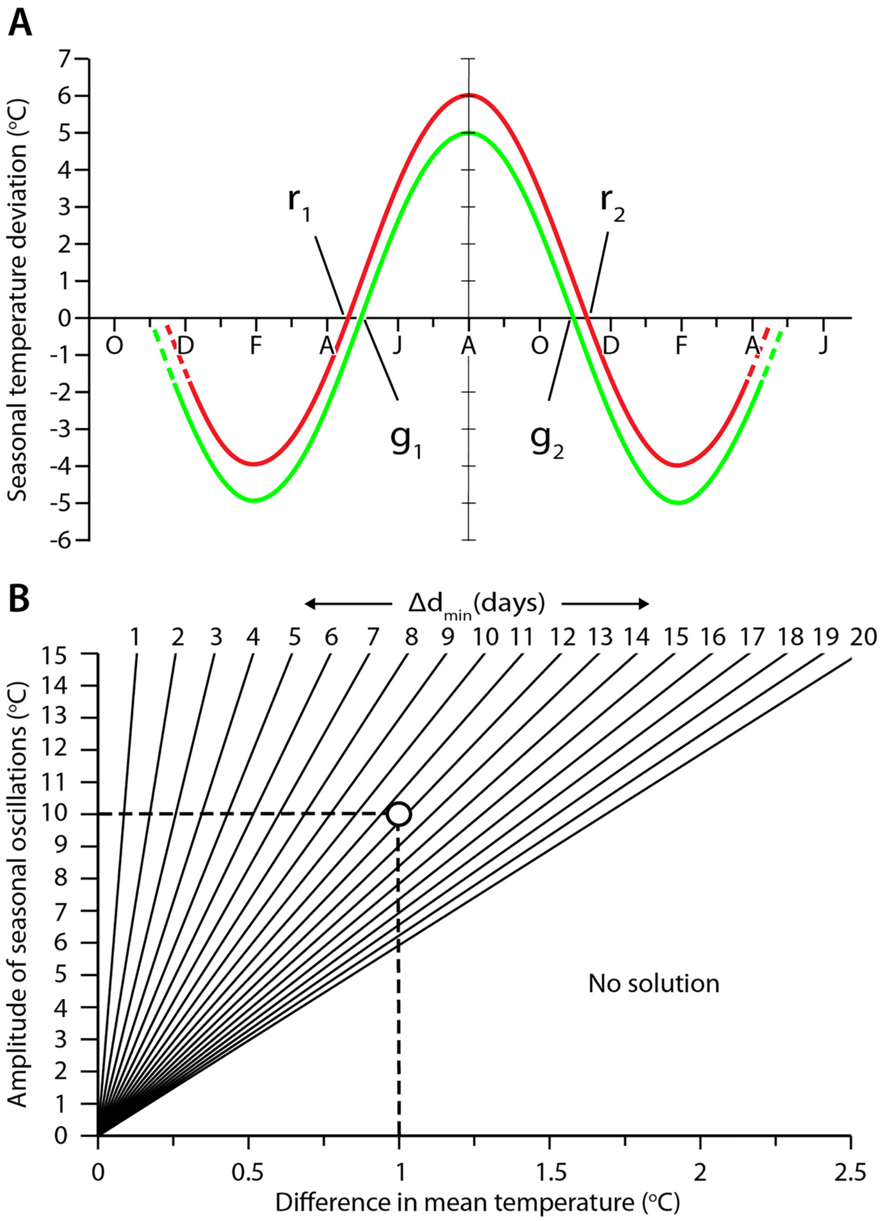
or simplified.

$$\Delta_{min} = \left[\arccos(-2B/A) - (\pi/2)\right]/0.0172 \tag{3b}$$

which allows Δd_{min} to be calculated for spring spawners, given A and B, or the ratio A/B. Figure 2B shows the range of values can take, given different amplitudes of seasonal growth oscillations (A) and warming-induced increases of mean annual temperature (B).

Table 1 shows that the empirical estimates of $\Delta d/\Delta$°C that can be computed from the numbers in various explicit statements in the literature (see Supplementary Materials) correspond, on the average, to the theoretical estimates of Δd_{min} derived from Eq. 3.

Fig. 2 How the shift toward earlier temperature-induces spawning is estimated and can be evaluated. **A** Using trigonometry, with the variables g_1 and g_2 referring to the green, lower curve and r_1 and r_2 to the red, upper (see also Eqs. 1-3 and text); **B** the nomogram illustrates that the solutions of Eq. 3 are robust, but only within a limited warming range, and becomes useless when the mean annual temperature increase exceeds 2 °C. The dotted lines and the open circle refer to the example in panel **A**, which describes a case where $\Delta d_{min} = 11.7$ days



Discussion

The sinusoidal model presented here and Eq. 3 derived from it are simplifications of complex phenomena. However, we are not helpless in the face of this complexity. We know that seasonal temperature oscillations, driven by the Earth's highly regular movements around the Sun, and its angle of obliquity, generate and maintain the sinusoidal oscillations of many natural phenomena, including seasonal change in the temperature of water bodies. We also know that baseline temperatures have increased throughout much of the world. Combining these two facts with the knowledge that increasing temperature triggers maturation and spawning in spring-spawning fish (Fig. 3) should lead to a robust model for predicting the extent to which spawning will be shifted back in time, as long as the warming under consideration does not exceed 2 °C when the amplitude of the seasonal oscillation is < 10 °C.

Table 1 Instances of fish maturing and spawning earlier in the "spring" reproductive season, due to higher water temperature

No.	Species	Location	Years	Δ°C	Δ*d*	Δ*d*/Δ°C	Remarks and source
1	*Abramis brama*	Tjeukemeer Lake, Netherlands	1961–2006	1.94	20	10.3	Mooij et al. (2008)
2	*Acipenser schrenckii*	Aquaculture ponds, China	2011	3 vs. 6	30/50	8.3–10.0	Zhang et al. (2012)
3	*Gadus chalcogrammus*	Gulf of Alaska	1979–2015	---	---	5.0	Rogers and Dougherty (2019)
4	*Gadus morhua*	Northern and Central North and Irish Seas	1985–2015	1.1-1.4	---	8.1–27.4	McQueen and Marshall (2017)
5	*Gymnocyprisselincuoensis*	Selincuo Lake, Tibetan Plateau	1970–2000s	~1	11.7	11.7	Tao et al. (2018)
6	*Rutilus rutilus*	Meuse River, downstream of a nuclear power plant	1977	3	21	7	Mattheuws et al. (1981)
7	*Rutilus rutilus*	Lake Geneva (Switzerland/France)	1983–2001	~1	14	14	Gillet and Quétin (2006)
8	*Scomber scombrus*	North Sea	1968–2008	--	--	7.4–11.4	Jansen and Gislason (2011)
9	*Solea solea*	North and Irish Seas	1970–2010	1.72	40	23.3	Fincham et al. (2013)
10	*Tachysurus fulvidraco*	Aquaculture ponds, China	2013	5	25–30	5-6	You (2015)
11	13 marine spp.	English Channel, spring and summer spawners only	1975 vs. 1987	1.0	17	17	Genner et al. (2010)
12	Multiple spp. (larvae)	Southern California, USA	1949–2000	1.3	---	17.9	Ash (2015)
13	10 freshwater spp.	Estonian waters	1951–1998	2.65	10-30	3.8–11.3	Ahas and Aasa (2006)
14	All previous spp.	Freshwater and marine fish in temperate regions	--	--	--	12.7±1.6	Mean of above estimates, with st. dev. = 6.2 days[a]
15	Spring spawning fish	Freshwater and marine fish in temperate regions	--	--	--	11.7	Δd_{min} predicted by new model for A = 10 °C and B = 1 °C

"°C" refers to difference in temperature between the years and "days" refers to the time difference in maturation and/or spawning[a]. The standard deviation and standard error are underestimates, as only the midrange of the *d*/°C were used

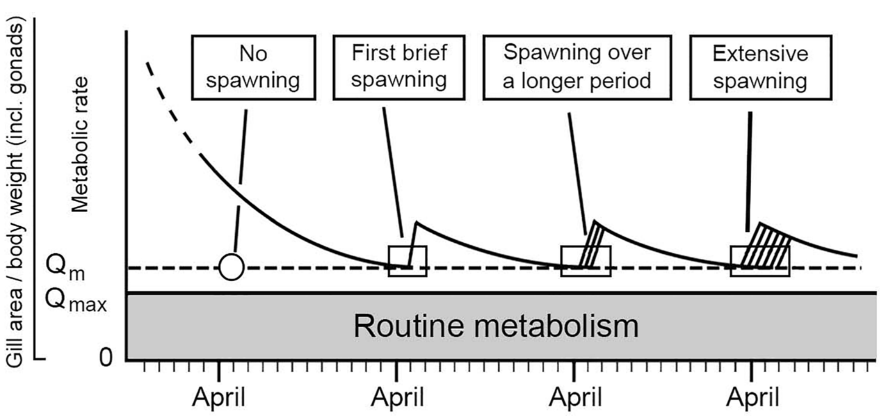


Fig. 3 Illustrating that a trigger temperature being reached is only the *sufficient* condition for maturation and spawning, the *necessary* condition being that the fish has reached a weight at which its metabolic rate is equivalent to ~1.35 times their routine metabolic rate (i.e., Q_m/Q_{maint} ~1.35; Pauly 1984, 2021a). Note that once the fish have spawned, their weight declines, and the ratio Q_m/Q_{maint} returns to being > 1.35; also note that the spawning season of large/old adults is longer than for small/young ones. This schema is not to scale and does not consider seasonal growth oscillations (but see Pauly 2019)

The model may thus be used to assess whether an observed change in the phenology of spawning is small or large compared to a prediction from Eq. 3. Another potential use of the model would be to allow assessing whether it is justified to evoke the match-mismatch hypothesis (Cushing 1990) or other complex hypotheses often presented to explain temporal shift of spawning in terms of adaptation to temporal shifts of the emergence of prey species.

Acknowledgements We thank Ms. Elaine Chu for drafting our figures.

Author contribution The work described has not been published before and is not under consideration for publication anywhere else. Its publication has been approved by both co-authors, as well as tacitly by the responsible authorities at the institutes where the work has been carried out. Both authors contributed equally, and reviewed and approved the final draft.

Funding DP thanks the *Sea Around Us*, a research initiative supported by philanthropic foundations, notably the Marisla, MAVA, Minderoo, Oak, David and Lucille Packard, and Rockefeller Foundations, as well as the Pew Charitable Trusts and the WWF. CL thanks financial support by the Open Fund of CAS Key Laboratory of Marine Ecology and Environmental Sciences, Institute of Oceanology, Chinese Academy of Sciences (KLMEES202004).

Data availability All data generated or analyzed during this study are included in this published article.

Code availability All the data used here are presented in the text and figures; no code was used.

Declarations

Human and animal rights The research reported herein did not involve human subject and/ or live animals or cell lines.

Conflict of interest The authors declare no competing interests.

Ethics approval Not applicable.

Consent to participate Not applicable.

References

Ahas R, Aasa A (2006) The effects of climate change on the phenology of selected Estonian plant, bird and fish populations. Int J Biometeorol 51(1):17–26. https://doi.org/10.1007/s00484-006-0041-z

Alix M, Kjesbu OS, Anderson KC (2020) From gametogenesis to spawning: how climate-driven warming affects teleost reproductive biology. J Fish Biol 97:607–632. https://doi.org/10.1111/jfb.144396

Amarasinghe US, Pauly D (2021) The relationship between size at maturity and maximum size in cichlid populations corroborates the Gill-Oxygen Limitation Theory (GOLT). Asian Fish Sci 34:14–22. https://doi.org/10.33997/j.afs.2021.34.1.002

Asch RG (2015) Climate change and decadal shifts in the phenology of larval fishes in the California Current ecosystem. Proc Natl Acad Sci 112(30):E4065-E4074. https://doi.org/10.1073/pnas.1421946112

Asch RG, Stock CA, Sarmiento JL (2019) Climate change impacts on mismatches between phytoplankton blooms and fish spawning phenology. Glob Change Biol 25:2544–2559. https://doi.org/10.1111/gcb.14650

Bhattacharya S (1999) Recent advances in the hormonal regulation of gonadal maturation and spawning in fish. Curr Sci 76:342–349

Belkin IM (2009) Rapid warming of large marine ecosystems. Prog Oceanogr 81:207–213. https://doi.org/10.1016/j.pocean.2009.04.011

Carpenter SR, Fisher SG, Grimm NB, Kitchell JF (1992) Global change and freshwater ecosystems. Annu Rev Ecol Syst 23(1):119–139

Cohen JM, Lajeunesse MJ, Rohr JR (2018) A global synthesis of animal phenological responses to climate change. Nat Clim Chang 8:224–228. https://doi.org/10.1038/s41558-018-0067-3

Cushing DH (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Adv Mar Biol 26:249–293. https://doi.org/10.1016/S0065-2881(08)60202-3

Fincham JI, Rijnsdorp AD, Engelhard GH (2013) Shifts in the timing of spawning in sole linked to warming sea temperatures. J Sea Res 75:69–76. https://doi.org/10.1016/j.seares.2012.07.004

Genner MJ, Halliday NC, Simpson SD, Southward AJ, Hawkins SJ, Sims DW (2010) Temperature-driven phenological changes within a marine larval fish assemblage. J Plankton Res 32(5):699–708. https://doi.org/10.1093/plankt/fbp082

Gillet C, Quétin P (2006) Effect of temperature changes on the reproductive cycle of roach in Lake Geneva from 1983 to 2001. J Fish Biol 69(2):518–534. https://doi.org/10.1111/j.1095-8649.2006.01123.x

Jansen T, Gislason H (2011) Temperature affects the timing of spawning and migration of North Sea mackerel. Cont Shelf Res 31(1):64–72. https://doi.org/10.1016/j.csr.2010.11.003

Kangur K, Tammiksaar E, Pauly D (2021) A reflection of global warming in the long-term fisheries catch of a large north-temperate lake: insights from the ´Mean Temperature of the Catch´ concept. Environ Biol Fish. https://doi.org/10.1007/s10641-021-01114-7

Mattheeuws A, Genin M, Detollenaere A, Micha J -C, avec la collaboration technique de Y. Mine. (1981) Etude de la reproduction du gardon (*Rutilus rutilus*) et des effets d'une élévation provoquée de la température en Meuse sur

cette reproduction. Hydrobiologia 85(3):271–282. https://doi.org/10.1007/BF00017615
McQueen K, Marshall CT (2017) Shifts in spawning phenology of cod linked to rising sea temperatures. ICES J Mar Sci 74(6):1561–1573. https://doi.org/10.1093/icesjms/fsx025
Meyer KA, Schill DJ (2020) The Gill-Oxygen Limitation Theory and size at maturity/maximum size relationships for salmonid populations occupying flowing waters. J Fish Biol 98:44–49. https://doi.org/10.1111/jfb.14555
Mooij WM, De Senerpont Domis LN, Hülsmann S (2008) The impact of climate warming on water temperature, timing of hatching and young-of-the-year growth of fish in shallow lakes in the Netherlands. J Sea Res 60(1):32–43. https://doi.org/10.1016/j.seares.2008.03.002
Pankhurst NW (2016) Reproduction and development. Fish Physiol 35:295–331
Pauly D (2021a) Why do fish reach first maturity when they do? J Fish Biol. https://doi.org/10.1111/jfb.14902
Pauly D (2021b) The Gill-Oxygen Limitation Theory (GOLT) and its critics. Sci Adv 7(2). https://doi.org/10.1126/sciadv.abc6050
Pauly D (2019) Gasping fish and panting squids: oxygen temperature and the growth of water breathing animals (2nd edn). International Ecology Institute
Pauly D (1984) A mechanism for the juvenile-to-adult transition in fishes. ICES J Mar Sci 41(3):280–284. https://doi.org/10.1093/icesjms/41.3.280
Poloczanska ES, Brown CJ, Sydeman WJ, Kiessling W, Schoeman DS, Moore PJ, Brander K, Bruno JF, Buckley LB, Burrows MT, Duarte CM, Halpern BS, Holding J, Kappel CV, O'Connor MI, Pandolfi JM, Parmesan C, Schwing F, Thompson SA, Richardson AJ (2013) Global imprint of climate change on marine life. Nat Clim Chang 3(10):919–925. https://doi.org/10.1038/nclimate1958
Rogers LA, Dougherty AB (2019) Effects of climate and demography on reproductive phenology of a harvested marine fish population. Glob Change Biol 25(2):708–720. https://doi.org/10.1111/gcb.14483
Tao J, He D, Kennard MJ, Ding C, Bunn SE, Liu C, Jia Y, Che R, Chen Y (2018) Strong evidence for changing fish reproductive phenology under climate warming on the Tibetan Plateau. Glob Change Biol 24(5):2093–2104. https://doi.org/10.1111/gcb.14050
Taranger GL, Carrillo M, Schulz RW, Fontaine P, Zanuy S, Felip A, Hansen T (2010) Control of puberty in farmed fish. Gen Comp Endocrinol 165:483–515
Thorpe JE (1986) Age at first maturity in Atlantic salmon, *Salmo salar*: freshwater period influences and conflicts with smolting. Can Spec Publ Fish Aquat Sci 89:7–14
Thorpe JE (1990) Variation in life-history strategy in salmonids. Polish Arch Hidrobiol 37:3–12
You X (2015) The effect of temperature on sex differentiation, sex steroid hormones and growth in yellow catfish, *Pseudobagrus fulvidraco* Richardson. [Master's thesis]. Huazhong Agriculture University, Wuhan
Zhang Y, Sun HW, Liu XY, Qu QZ, Sun DJ (2012) Histological observation of gonadal differentiation and effect of rearing temperature on sex differentiation in Amur sturgeon *Acipenser schrenckii*. J Fish Sci China 19(6):1008–1017. https://doi.org/10.3724/SP.J.1118.2012.01008

Supplementary Materials

to

Temperature and the maturation of fish:
a simple sine-wave model for predicting accelerated spring spawning

by

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The Δ^0C and Δday values in Table 1 can be verified though the information provided below. These values were extracted from papers that explicitly provided summary values of Δ^0C and Δdays in their text or the captions of their figures, or showed trend lines from which these values could be inferred. We cite below the words and numbers pertaining to the entries of Table 1, including the page and/or figures where they can be found:

1) Mooij et al. (2008) wrote in the caption of Figure 4, which shows increasing temperature trends in 4 Dutch lakes, including Lake Tjeukemeer: "The 4 lines have equal slopes with a value of 0.042 ^{0}C yr^{-1}. For the whole period of 46 years this results in a warming of 1.94 ^{0}C." Also, on p. 38, they wrote: "The increase of water temperature during the past decades results in the onset of growth of larval bream to occur 20 days over the period 1971-2006."

2) Zhang et al. (2012), with regard to Amur sturgeon, wrote in their abstract that "Temperature can affect the time of gonadal differentiation of juvenile *Acipenser schrenckii*. High temperature (24 ^{0}C and 27 ^{0}C) can lead to earlier gonadal differentiation. Sex differentiation of individuals reared at 27 ^{0}C and 24 ^{0}C occurred 50 days and 30 days earlier than the control group (21 ^{0}C), respectively." Translated form" 温度可影响施氏鲟幼鱼性腺分化的时间…高温(24 ^{0}C 和 27 ^{0}C)可使施氏鲟幼鱼提前性腺分化，其中 27 ^{0}C 组较对照组(21 ^{0}C)提前 50 天, 24 ^{0}C 组提前 30 天。"

3) Rogers and Dougherty (2019) wrote: "A 1^{0}C increase in March SST corresponded to a shift in the mean date of spawning by 5.0 days, with warmer temperatures leading to earlier spawning."

4) McQueen and Marshall (2017) wrote: "The rate of change in spawning time in relation to autumn temperature rise ranged from 1.16 weeks per 1 ^{0}C change in autumn SST in IVa, to 3.92 weeks per 1 ^{0}C rise in autumn SST in VIIa."

5) Tao et al. (2018) wrote: "the reproduction date of *G. selincuoensis* would have occurred an average of 2.9 days (11.7 days divided by four) per decade on average from the 1970s to 2000s". The temperature difference of ~1 ^{0}C was read off from their figure 3 using the Origin 8.5 software.

6) Mattheuws et al. (1981) wrote in their abstract: "The thermal pollution of the Tihange Nuclear Power Plant increases the temperature (+ 3 ^{0}C) of the river Meuse and has precise effects on the reproductive cycle of the roach (*Rutilus rutilus*) downstream: well-defined, ovarial development, acceleration of maturation, and earlier laying of eggs (3 weeks)."

7) Gillet and Quétin (2006) wrote about roach (*Rutilus rutilus*) in Lake Geneva: "The increase in the mean annual temperature was c.1 ^{0}C from 1983 to 2000" (p. 521) and "Over the 19 years surveyed, the date of the spawning period has advanced by 2 weeks" (p. 522).

8) Jansen and Gislason (2011, p. 68) wrote: "The estimated average effect of SST [on larval occurrence] on the beginning was – 11.4 +/- 7.8 days/^{0}C and 7.5+/- 4.2 days/^{0}C on the peak."

9) Fincham et al. (2013) wrote: "Further, the overall increase in SST was significant, and amounted to 0.043 ^{0}C for all areas combined (equivalent to a 1 ^{0}C increase in 23 years)." They also wrote: "the long-term trend towards earlier spawning for all stocks combined (Fig. 3h) was significant… This amounts to a rate of advancement in timing of 1.50 weeks per decade, or very approximately 1 day each year."

10) You (2015) wrote: "The gonadal differentiation process of *Pelteobagrus fulvidraco* reared at different temperature is similar, while the development speed is quite different, and the development speed increases with the increase of temperature. The gonadal differentiation of *Pelteobagrus fulvidraco* of the 22±1 ^{0}C group occurred 25-30 days later than that of 27±1 ^{0}C group". Translated from "培育温度不同黄颡鱼性腺分化进程相似但发育速度差异较大，随着温度升高发育速度加快。(22±1)^{0}C 组黄颡鱼性腺分化进程比(27±1) ^{0}C 组晚 25-30 d." Note that *Pelteobagrus fulvidraco* is considered of synonym of a *Tachysurus fulvidraco* (see FishBase; www.fishbase.org).

11) Genner et al. (2009) wrote: "After correction for temporal trends, the observed temperature changes of 1 ^{0}C were associated with annual phenological change of 17 days."

12) From Ash, (2015, p.): "In the southern [California] Current Ecosystem, fishes that spawn earlier during warm conditions advanced their phenology at a mean rate of 6.4 d/decade, whereas other species experienced mean delays of 5.1 d/decade. Assuming that temperature is a primary factor affecting fish phenology, the mean temperature sensitivity would be

24.6/^{0}C for the earlier phenophases (range: 10.8–d/^{0}C) and 19.6 d/^{0}C for later phenophases (range: 11.5–27.7 d/^{0}C), because this region warmed by 1.3 ^{0}C between 1949 and 2000 […]. When examining all phenology groups jointly using absolute values of phenological change, a mean of 4.7 ± 3.3 SD d/decade or 17.9 ± 12.8 SD d/^{0}C was obtained. These rates were comparable to results from other studies of the phenology of marine and freshwater fishes."

13) Ahas and Aasa (2006) wrote in their abstract that "Significant values on plant and bird phases have advanced 5-20 days, and fish phases have advanced 10-30 days in the spring period". They also wrote on p. 22-23: "Significant trends are also detected in spring (March-May) when the linear trend shows an increase of 2.0-3.3 ^{0}C."

14) The standard deviation (6.2 days) and the standard error (1.6 days are underestimates, because only the midrange of the Δday/Δ^0C values were used.

15) Δd_{min} predicted by Equation 3 of new model, for an amplitude of seasonal temperature (A) of 10 ^{0}C and increase due to warming (B) of 1 ^{0}C.