



Contribution to the Theme Section 'Small pelagic fish: new research frontiers'

Estimating a thermal constant of spawning to explain spawning time of Pacific herring *Clupea pallasii* across space and time

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ABSTRACT: Explaining variation in life history phenology requires us to disentangle environmental-dependent variability from that caused by adaptive change across time and space. Here, we offer thermal time models (models measuring time in temperature units) as tools to understand the spawning dynamics of small pelagic fish, such as Pacific herring *Clupea pallasii*. We hypothesised that thermal time explains the annual timing of spawning of Pacific herring across space and time. By testing this hypothesis, we identified developmental constants (thermal constants of spawning) that can be used to make spawning time predictions. We examined spatio-temporal changes in Pacific herring spawning time over a 69 yr period (1941–2010) across 6 regions off British Columbia (BC), Canada. We estimated the degree-days (DD, °C-days) from the onset of gonadal maturation to spawning by combining spawning time estimates with distribution-specific temperature estimates. We then fitted models to explore how DD to spawning can be used to explain observed spawning time patterns across space and time and identified temperature-independent sources of variability (e.g. adaptive differences among regions, spawner size). We found that, even though Pacific herring often spawned ~5 d later with each increasing degree in latitude, the average thermal time in DD to spawning was ~1700°C-days. We also found that DD to spawning explains linear variation in spawning time across years for some regions of the BC Pacific herring. Thermal time models can aid in predictions of environmental responses and forecasts of life-history phenology in a changing climate.

KEY WORDS: Spawning time · Thermal time · Degree-days · Pacific herring · Climate change

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1. INTRODUCTION

Phenology, the study of reoccurring biological events, has proven to be a relevant and resilient proxy of the state of both terrestrial (Tang et al. 2016) and marine ecosystems (Platt et al. 2003, Ferreira et al. 2020, 2023). Studies focusing on phenology provide insight into the spatio-temporal dynamics of organisms, thus creating a great base from which to derive predictions about the impacts of future rising temperature (Asch et al. 2019). This is a concept that has played a crucial role in understanding fish recruitment dynamics, especially within critical early-life

phases of fishes, when the timing of first-feeding larvae needs to overlap with that of food availability in time and space (Neuheimer et al. 2018, Ferreira et al. 2020, 2023), as well as in understanding fish spawning dynamics (Otterlei et al. 1999, Trudgill et al. 2005, Neuheimer & Taggart 2007, Neuheimer & MacKenzie 2014, Neuheimer et al. 2018).

Fish spawning time is shaped by several factors, such as predator–prey dynamics influencing the survivorship at early life stages as in the match–mismatch hypothesis, which focuses on food availability to fish offspring (Cushing 1990, Neuheimer et al. 2018, Ferreira et al. 2020). Other factors affecting time

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to spawning are fish weight and age. Younger individuals will typically spawn later than the older individuals due to different levels of gonadal maturation (Lambert 1987, Arula et al. 2019). However, a key factor influencing fish spawning time is temperature (Trudgill et al. 2005) either directly (e.g. affecting development rates) or indirectly (e.g. influencing prey availability or spatial distribution of spawners). Specifically, increasing water temperatures accelerate the metabolism and thereby growth and development rates of fish, which in turn influences timing of spawning (Neuheimer & MacKenzie 2014). Because of accelerated development rates, the duration of the larval phase of a fish life cycle declines with increasing temperature (Duarte 2007). For example, Icelandic herring spawn at least 10 d later in colder temperatures (Óskarsson & Taggart 2009).

The influence of temperature on developmental rates is often described by a thermal performance curve where there is an increase in developmental rates over a mid-range in temperatures (Otterlei et al. 1999, Björnsson et al. 2001). The shape of the thermal performance curve may vary as a sign of adaptation across space (regions) or possibly time (years). As temperature affects physiology of all living organisms (Trudgill et al. 2005), it is worth investigating, especially when rising temperatures are disrupting the ecosystems at different levels and scales. Thermal time models are thus useful tools to explore changes in spawning dynamics of fish.

Pacific herring *Clupea pallasii*, hereafter herring, is an ecologically, economically, and culturally important species in the northeast Pacific Ocean. Commercial and traditional fishing communities in British Columbia (BC, west coast of Canada) target 5 major distinct stocks (Xu et al. 2019, Fisheries and Oceans Canada 2022). Herring fisheries in this area have been conducted by First Nations for over 500 generations and continue to be important, for commercial, food, social, and ceremonial purposes (Fisheries and Oceans Canada 2023). Herring feed on zooplankton (e.g. copepods, euphausiids) along the continental shelf in summer before spawning in nearshore areas from winter to spring with the first stocks beginning to spawn in the southern regions near San Francisco, California (USA), in the early winter months, and in the spring in the more northern regions off of BC and south-eastern Alaska (Haegeler & Schweigert 1985, Hay & Kronlund 1987, Hebert 2020). The spawn is deposited on marine vegetation and on bottom substrate near the coast, with these habitats having a major influence on egg survivorship (Shelton et al. 2014). The spawn represents a large seasonal influx of

energy to coastal ecosystems. Identifying the factors controlling herring spawning time is thus critical to explaining larval survival and therefore abundance (Ferreira et al. 2020, 2023), which impacts commercial and traditional fisheries as well as the ecosystem.

Here, we explored how a thermal constant can be used to explain variability in spawning time of Pacific herring both across time (years) and space (regional differences). We hypothesised that the thermal time from the onset of gonadal maturation to spawning represents a thermal constant that can be used to explain the spatio-temporal variability in spawning time. Finally, we investigated other factors, such as weight and age of spawners, and how they correlate with the timing of spawning.

2. MATERIALS AND METHODS

2.1. Data

Spawning time data were retrieved from Fisheries and Oceans Canada (DFO), who conducted herring spawning surveys in 6 regions in BC from 1941 to 2016. Extensive surface surveys were used until 1988, when diver surveys became common practice. The data on the absolute herring spawning biomass (in tonnes) were grouped by geographical section (areas smaller than region that are later grouped by region) and estimated through a modelling approach that considers age, size, size-specific fecundity, and width and intensity estimates based on observations from both the Fishery Officer and SCUBA diver surveys (Hay & Kronlund 1987), then averaged by region and year, and published on the DFO data portal. Our study uses the output, i.e. mean, minimum, and maximum dates of spawning, from DFO for the 6 main spawning regions in British Columbia, from south to north (increasing mean latitude): Strait of Georgia (SoG), West Coast Vancouver Island (WCVI), Johnstone Strait (JS), Central Coast (CC), Haida Gwaii (HG), and Prince Rupert District (PRD, Fig. 1).

Monthly, depth-stratified temperature data were collected from the Simple Ocean Data Assimilation (SODA, Carton et al. 2000a,b) from 1941 to 2016. The data were averaged within each of the spawning regions of Pacific herring (Fig. 1, Hay et al. 2009). Monthly-specific depths based on seasonal changes in depth distribution of Alaskan herring (Table 1; Sigler & Csepp 2007) as monthly and depth-specific estimates were unavailable for populations off BC. However, depth ranges for the Alaskan herring are in

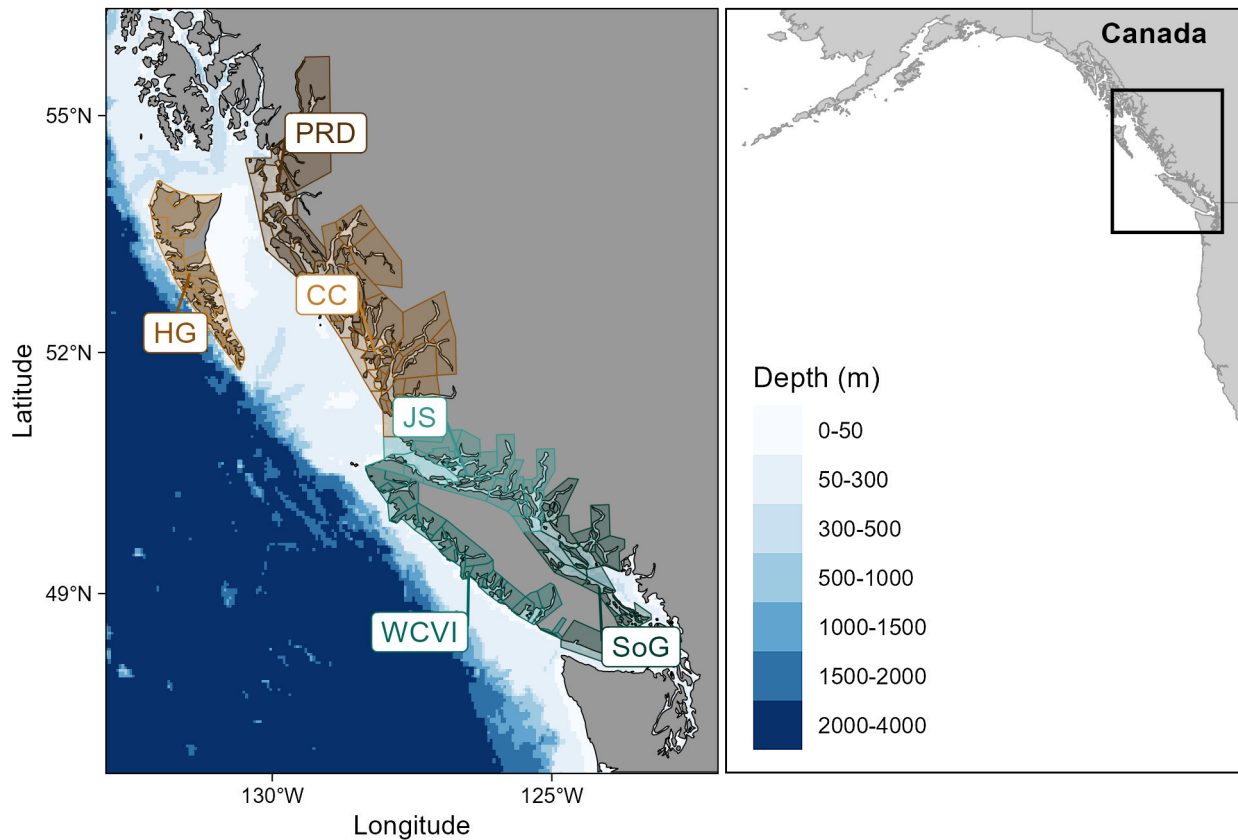


Fig. 1. Pacific herring spawning regions in British Columbia, Canada. SoG: Strait of Georgia; WCVI: West Coast Vancouver Island; JS: Johnstone Strait; CC: Central Coast; HG: Haida Gwaii; PRD: Prince Rupert District

Table 1. Seasonal depth distributions experienced by Pacific herring based on Sigler & Csepp (2007). DOY: day of the year

Month	Start day (DOY)	End day (DOY)	Shallow (m)	Deep (m)
Jan	1	31	90	110
Feb	31	59	100	140
Mar	60	90	80	110
Apr	91	120	5	50
May	121	151	5	50
Jun	152	181	5	50
Jul	182	212	10	65
Aug	213	243	10	110
Sep	244	273	30	100
Oct	274	304	30	110
Nov	305	334	40	110
Dec	335	365	65	110

accordance with what has been found for Pacific herring off BC (depths <185 m, Godefroid et al. 2019). We used linear interpolation to estimate the daily temperature time-series for each region by year (see the daily averages in Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m741p237_supp.pdf). The output resulted in a distribution-averaged

temperature data set representing the daily temperature experienced by Pacific herring. We compared the surface temperatures from SODA (5.01 m) with the lighthouse temperature data available at the DFO portal (Fig. S2). Even though we acknowledge that global reanalysis products (such as SODA) are limited in their ability to provide data with enough spatial resolution to use in studies such as ours, we chose to use SODA as it provides depth-specific temperatures, a factor we consider to be relevant in this study. Furthermore, the depth and spatial span of the lighthouse data would not allow us to use and compare results across the 6 spawning regions.

Average spawner weight and age were determined from weight-at-age and number-at-age data from 1951 to 2016 for 5 of the 6 regions (Johnstone Strait has no reported weight-at-age and number-at-age) from Cleary et al. (2017). These data were not available from the period 1941–1951. The weight-at-age data were estimated based on sampling using seine nets, due to the size selectivity of other gear types, such as gillnets. The number-at-age data were based on different gear types, specifically roe seine fishery, roe gillnet fishery and reduction, food, bait, and spe-

cial use fishery. We determined the average weight and average age of the spawners for each year. All herring under 2 yr old were removed from the data set, as these were not likely to be mature (Cleary et al. 2017). The spawners were grouped by year, and a weighted mean was found for age and weight, i.e. the weight and age were weighted by the number of fish at age (Figs. S3 & S4).

2.2. Analysis

Mean spawning time in calendar days (CD) was estimated by summing the days from the onset of gonadal maturation to the mean spawning day of the year in each year and spawning region. The onset of gonad maturation was estimated to be 1 September (day of year [DOY] 244; Fig. S5) based on reported changes in hormone levels and gonadosomatic index for Pacific herring off Nanaimo, BC (Hay & Outram 1981), and populations off Japan (Hay & Outram 1981, Koya et al. 2003). As region-specific dates for the onset of gonadal maturation are not available, the date of 1 September was used for all populations. This is similar to the procedure used for Atlantic cod *Gadus morhua* for which there was evidence that populations shared similar timing of the onset of gonadal maturation linked to light changes (Neuheimer & MacKenzie 2014).

Thermal time to mean spawning was estimated for each region and year as degree-days (DD, °C-days; Neuheimer & MacKenzie 2014). The region-specific temperature was used in the calculation of DD by summing the daily temperatures above a threshold temperature (T_{Th}) from the onset of gonadal maturation to the mean spawning time as in Neuheimer & MacKenzie (2014):

$$GDD(n) = \sum_{i=1}^n (T_{i,j} - T_{Th}) \cdot \Delta d, \quad T_{i,j} > T_{Th} \quad (1)$$

where $T_{i,j}$ is the interpolated mean daily temperature experienced by the year-class on day i in region j , where $i = 1$ at the onset of gonadal maturation (DOY 244, 1 September, Hay & Outram 1981, Koya et al. 2003), T_{Th} is the predetermined threshold temperature below which the fish experiences no gonadal development ($T_{Th} = 0^\circ\text{C}$; Neuheimer & Taggart 2007), and Δd is a set timestep (sampling frequency, i.e. 1 d). While no information on the T_{Th} of gonadal maturation development was available, we tested the effects of using $T_{Th} = 4^\circ\text{C}$ (vs. 0°C), as the lower limit of thermal tolerance of Pacific herring eggs once hatched is between 4 and 5°C (Alderdice & Velsen 1971). These results are found in Figs. S8 & S12.

We tested the hypothesis that spatial variability in time to spawning could be explained by thermal time. This involved comparing models fit to hypotheses:

$$\begin{aligned} CD_{i,j} &\sim \textit{Latitude} \\ &\text{vs.} \\ DD_{i,j} &\sim \textit{Latitude} \end{aligned} \quad (2)$$

where $CD_{i,j}$ and $DD_{i,j}$ are the year (i)- and location (j)-specific time to spawning as either calendar time (day) or thermal time (°C-days), and *Latitude* is the mean latitude of each of the 6 spawning regions (° N). For Eq. (2), the hypotheses were explored by fitting generalised linear models (GLMs) with gamma error distribution assumptions and a canonical inverse link function to reflect the positive, continuous nature of the response variable (either CD or DD). In all cases, model assumptions were assessed to ensure they were appropriate by inspection of scaled (quantile) residuals following methods in the 'DHARMA' package in R (Hartig 2022). These methods estimate model fit by testing the ability of the model to give rise to the data (observations). Quantile residuals are estimated by comparing observations to prediction distributions simulated from the fitted model, a method that is robust to model form and error distribution assumptions (Hartig 2022). We analysed the residuals of the model in Eq. (2) (Figs. S6 & S7) and used the same model for DD with $T_{Th} = 4^\circ\text{C}$ (Fig. S8). We also tested the effect of using different dates for the onset of gonadal maturation (Table S1). The decision was made to keep 1 September, as it is consistent with observed changes in gonadal development described above.

We tested the hypothesis that temporal variability in time to spawning could be explained by thermal time by comparing model fits to the hypotheses:

$$\begin{aligned} CD_{i,j} &\sim \textit{year} + \textit{region} + \textit{year:region} \\ &\text{vs.} \\ DD_{i,j} &\sim \textit{year} + \textit{region} + \textit{year:region} \end{aligned} \quad (3)$$

where *year* and *region* (categorical) are the observation year and region, and *year:region* indicates an interaction effect. For Eq. (3), the hypotheses were explored by fitting generalised least-squares models (GLSs) with an autocorrelation structure of order 1 to account for temporal autocorrelation. We compared the autocorrelation function for the same model structure with GLM and GLS to assess any residual temporal autocorrelation that may make inferences from model results harder to grasp (Fig. S9). We analysed the residuals of the model in Eq. (3) (Figs. S10 & S11) to determine the fit of the model. We also used the same model using DD estimated with $T_{Th} = 4$ vs. 0°C , as described above (Fig. S12).

Residuals from the models exploring temporal variability in spawning time were compared to mean weight and mean age of spawners in each year and location to consider the respective effects of fish size on spawning time (Figs. S13 & S14). Weight and age were not included in the initial models, as they are limited in the temporal and spatial coverage (see above).

Evidence for each hypothesis in both Eqs. (2) and (3) was determined by model selection, where models representing all possible covariate combinations (including the null hypothesis) were fit and compared to one another via corrected Akaike's information criteria (AIC corrected for small sample sizes: AICc). The best-specified model(s) was(were)determined as any model within 2 of the lowest AICc values (i.e. $\Delta\text{AICc} < 2$). All analyses were performed with R software (Hartig 2022), and p-values and total R^2 (based on the variance of the difference between the observed and predicted values) were estimated for each result. All analyses were run for the period 1941–2010. Results are reported as means \pm SD.

3. RESULTS

Pacific herring spawning time ranged between 3 January and 16 July, with average spawning between 27 February and 17 May (Fig. 2; Fig. S5). The decision to keep 1 September for the onset of gonadal maturation falls within the mean date of where DD explains latitudinal trends in spawning time (1 August to 1 October; Table S1).

To validate our model, we inspected the residuals of the model in Eq. (2), CD and latitude (Fig. S6). The distribution of the residuals followed the expected distribution (Kolmogorov-Smirnov $p = 0.11$, dispersion test $p = 0.39$, outlier test $p = 0.05$). The distribution of the residuals for the Eq. (2) model with DD and latitude (Fig. S7) followed the expected distribution (Kolmogorov-Smirnov $p = 0.89$, dispersion test $p = 0.92$, outlier test $p = 1$). There was a pattern in the residuals vs. fitted values assessed via quantile regression. Changes to the link function (e.g. using log link) or error distribution assumption (Gaussian) made no improvement, and we used the inverse link function for Eq. (2). Overall, these departures from well-behaved

residuals reflect the low sample size (6 regions) and that processes within each region across years differ, which is explored in our analysis of temporal variability in spawning time.

Time to spawning measured in CD (Eq. 2) increased with increasing mean latitude at a rate of 5.20 ± 0.15 d per degree of latitude ($R^2 = 0.53$, $p < 0.001$, Fig. 3A). The mean spawning time for herring was as early as DOY 73.6 (14–15 March) in the southernmost region (SoG), and as late as DOY 95.9 (5–6 April) in the northernmost region (PRD). Both minimum and maximum mean spawning dates also significantly increased with latitude (minimum: 6.91 ± 0.25 d per degree of latitude, $R^2 = 0.14$, $p < 0.001$; maximum: 5.14 ± 0.37 d per degree of latitude, $R^2 = 0.47$, $p < 0.001$; Fig. 3A).

In contrast, the time to spawning measured in DD showed no change in DD with latitude ($R^2 = 0$, $p = 0.76$, Fig. 3B). The thermal constant of spawning (i.e. thermal time needed from onset of gonadal maturation to spawning) was estimated at $1709 \pm 16^\circ\text{C-days}$. Analysis of thermal time using $T_{\text{Th}} = 4^\circ\text{C}$ showed a slight decline in DD to spawning with mean latitude ($R^2 = 0.11$, $p < 0.001$; Fig. S8). DD to the maximum spawning time was also constant over latitude with a thermal constant of $1957 \pm 28^\circ\text{C-days}$ ($R^2 = 0$, $p = 0.22$, Fig. 3B), while DD to the minimum spawning time showed a significant increase with latitude of $18.92 \pm 2.23^\circ\text{C-days}$ per degree of latitude ($R^2 = 0.05$, $p < 0.001$; Fig. 3B).

We validated our model Eq. (3), CD vs. year and region (Fig. S10), by inspecting the normalised residuals which showed a slight increase in variability with

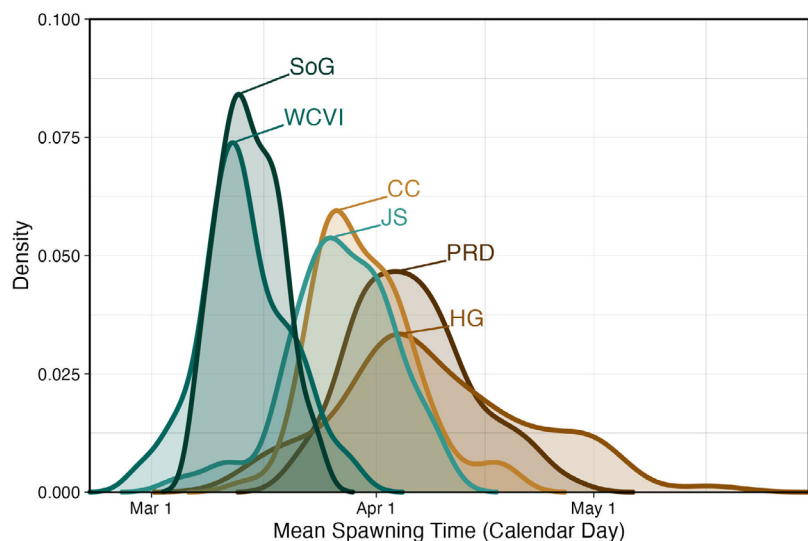


Fig. 2. Seasonal distribution of mean spawning time of Pacific herring. Site abbreviations and colours for the spawning regions as in Fig. 1

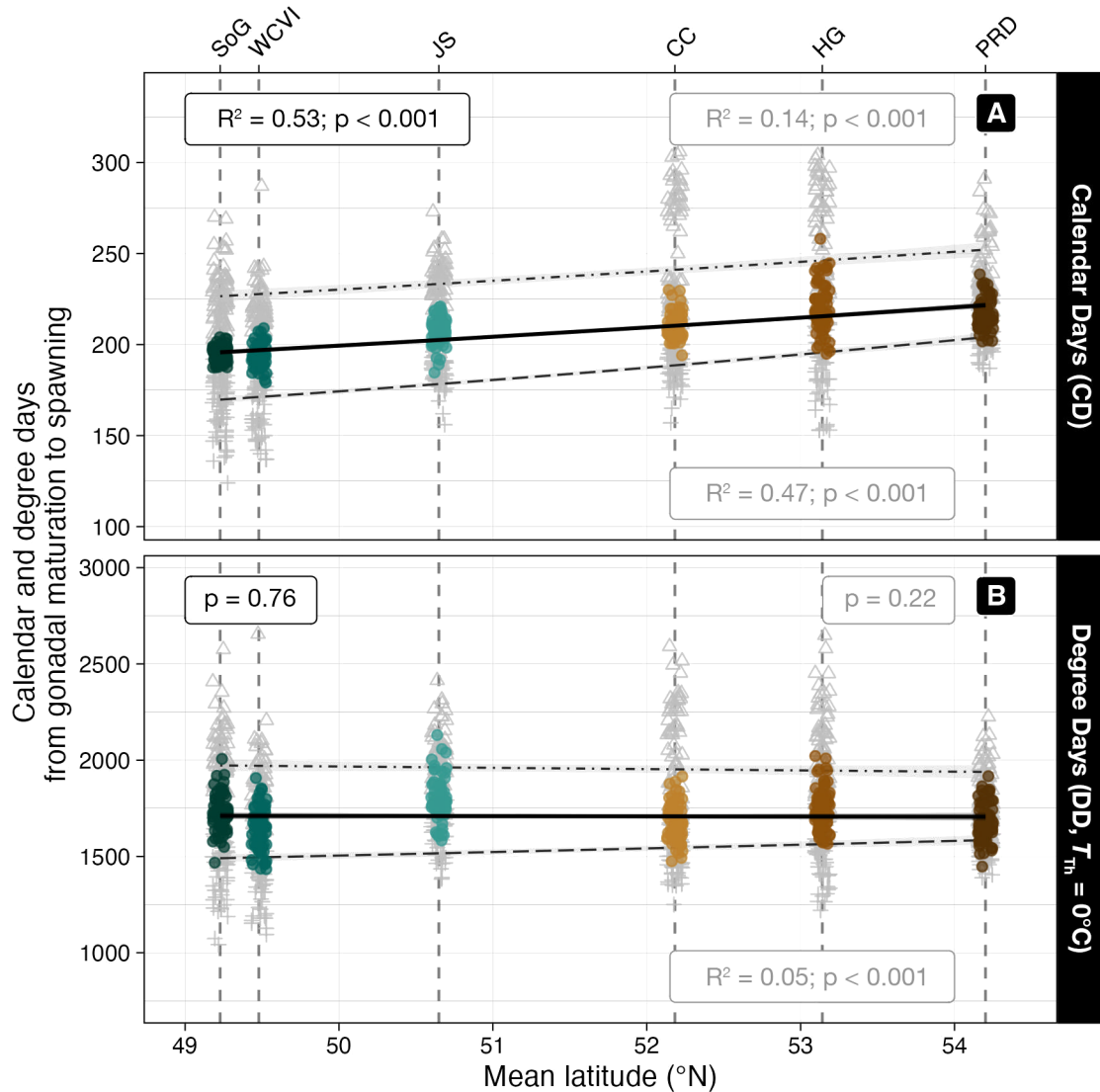


Fig. 3. Spatial variation in spawning. A comparison of time to mean spawning as (A) calendar days (CD), and (B) degree-days (DD) with mean latitude of each of the 6 spawning regions (abbreviations as in Fig. 1), using 1 September as the gonadal maturation start-date (see Table S1 in the Supplement for the effect of using different dates). Horizontal black, solid and dashed lines show a significant linear trend in CD but not in DD to spawning with year; grey areas show the 95% confidence interval around the prediction. The horizontal black, dashed-dotted line with the grey triangles corresponds to the model in Eq. (2) run for the maximum recorded spawning dates, whereas the horizontal black, dashed line with the plus signs corresponds to the model with minimum spawning dates. Jittering has been applied on the x-axis of the data (0.3°) to facilitate the reading of the plot. T_{th} : threshold temperature. The colours correspond to the spawning regions as in Fig. 1

fitted values. In contrast, residuals for the model in Eq. (3), DD vs. year and region, showed no heteroskedasticity with a uniform cloud (Fig. S11). Analysis of the autocorrelation function for both models showed that the correlation structure was well captured with no significant temporal autocorrelation remaining (Fig. S9).

Patterns in temporal variability in CD to spawning varied by region. No linear trend in region-specific CD to spawning was evident over time for 3 regions (SoG, CC, and PRD), with an average CD of 195 ± 4.14 , 210 ± 6.93 , and 217 ± 8.19 , respectively

(DOYs = 73.6, 89.4, and 95.9), ranging from 187 (DOY = 66.4, 1945) and 239 (DOY = 118, 1977) (Fig. 4). CD to spawning increased over the study period for 1 region (Fig. 4B): WCVI increased 0.19 ± 0.03 CD per year ($R^2 = 0.78$, $p = 0.003$), with average CD to spawning ranging from 179 (DOY = 58.1, 1944) to 209 (DOY = 88, 1971). In contrast, time to spawning decreased in 2 regions (Fig. 4C,F): JS decreased 0.21 ± 0.04 CD per year ($R^2 = 0.78$, $p = 0.001$), with CD to spawning ranging from 185 (DOY = 63.6, 2005) to 221 (DOY = 99.9, 1956); and HG decreased 0.38 ± 0.03 CD per year ($R^2 = 0.78$, $p < 0.001$) with CD to

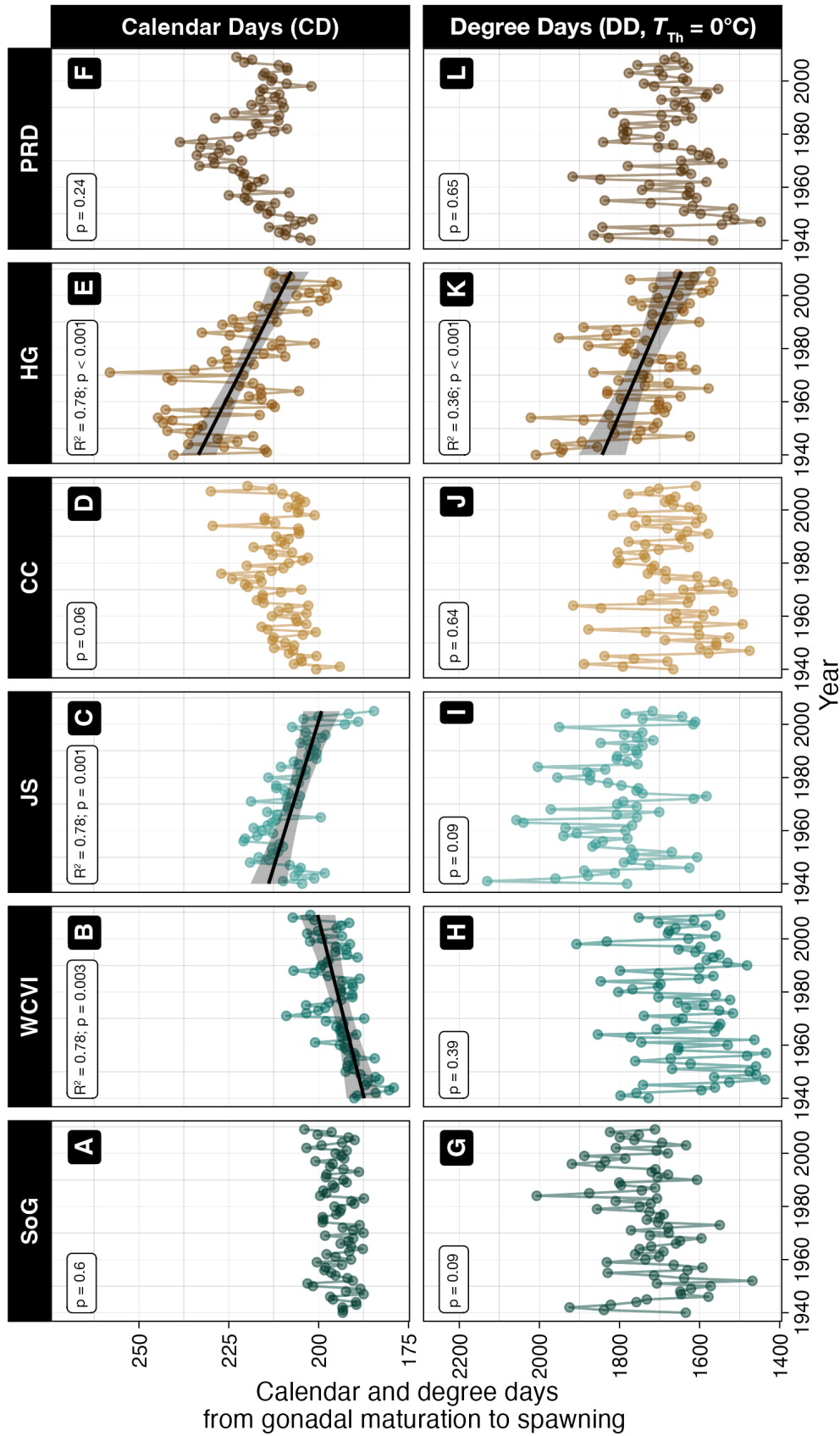


Fig. 4. Temporal variation in spawning. A comparison of yearly time to mean spawning as (A–F) calendar days (CD), and (G–L) degree-days (DD), using 1 September as the gonadal maturation start-date, for each of the 6 spawning regions. Black lines show significant linear trends in CD and DD to spawning with year; grey areas show the 95% confidence interval around the prediction. T_{Th} : threshold temperature. Abbreviations of the spawning regions as in Fig. 1

spawning ranging from 195 (DOY = 73.9, 2004) to 258 (DOY = 137.1, 1971). Please note that the R^2 relating to Eq. (3) are not possible to compute per region.

For 2 of 3 regions showing significant linear trends in CD, the trends in spawning time were not present in the thermal time models. Increasing CD to spawning for the WCVI region disappeared when examined in thermal time (Fig. 4H, $p = 0.39$), where the region-specific thermal constant of spawning was $1634 \pm 41^\circ\text{C-days}$ for WCVI. The pattern of decreasing time to spawning with year disappeared for JS (Fig. 4I, $p = 0.09$), where the region-specific thermal constant of spawning was $1802 \pm 42^\circ\text{C-days}$ for JS. The pattern of decreasing time to spawning with year remained in the HG region with a decline of $2.86 \pm 0.42^\circ\text{C-days}$ per year ($R^2 = 0.36$, $p < 0.001$) over the study period (Fig. 4K). Finally, there were no trends in time to spawning for the SoG, CC, and PRD regions when examined as DD to spawning (Fig. 4G,J,L, $p = 0.09$, 0.64, and 0.65, respectively). Analysis of region-specific thermal time to spawning over years using a T_{Th} of 4°C showed similar patterns, except for the HG region, where the thermal time can also explain the pattern of decreasing time to spawning with year (Fig. S12K).

In 1 out of 5 regions, there was a significant increase in residuals from the CD model with time associated with higher spawner weight. This indicates that later CD to spawning was associated with heavier spawners in the PRD region ($R^2 = 0.18$, $p = 0.0015$; Fig. S13E; note: no weight information for JS). Patterns between the residuals of the DD to spawning vs. year model (Eq. 3) and the average weight of spawners were not significant for any of the regions tested ($p > 0.29$; Fig. S13).

The residuals from the model explaining time (CD or DD) to spawning with year and region (Eq. 3) were not correlated to average age of spawners in any of the regions ($p > 0.18$; Fig. S14; note: no age information for JS).

4. DISCUSSION

We used an integrated temperature metric to explain temperature-dependent variation in spawning time for Pacific herring off BC, Canada. Location and timing of spawning are crucial for determining pelagic fish survival. For example, the collapse of Pacific herring in Prince William Sound in 1993 has been linked to abrupt shifts in spawning distribution in both space and time leading to poor recruitment and ultimately survival (McGowan et al. 2021, Dias et al. 2022).

In this study, we explored how a thermal constant can be used to explain temperature-dependent variability in spawning time. Such a thermal constant of spawning assumes the herring are experiencing temperatures within their thermal tolerance range where a change in development rate with temperature is near linear. By applying such a metric of thermal time, we can see how monotonic (linear) trends in spawning time can be explained, and how remaining variability in spawning time might be explained by temperatures outside tolerance limits and/or other factors such as spawner size. Following this motivation, we used linear shape assumptions in our modelling and explored any remaining variability (including non-linearity) in our model results in the residuals. We feel this method is appropriate given (1) the limited knowledge of the shape of the thermal performance curves associated with development rate, (2) the coarseness of the resolution in latitude, and (3) the necessary assumptions regarding ambient temperature.

4.1. Explaining spawning variation in space

We found that measures of thermal time (DD to spawning) explain variation in spawning time across space, allowing us to estimate a thermal constant of spawning for BC Pacific herring. We found that, even though Pacific herring off BC spawned ~ 5 d later with each increasing degree in latitude, the average thermal time to spawning was $\sim 1700^\circ\text{C-days}$ (Fig. 3) across regions. This thermal constant can be used to make predictions for future herring spawning time, i.e. by estimating the number of days it will take to accumulate $\sim 1700^\circ\text{C-days}$ from the onset of gonadal maturation to spawning. In this way, the thermal constant offers a predictive tool to explain future spawning time for the region which can be used to inform management strategies across the study region (e.g. decisions about fishery season opening).

Shifts in spawning location may lead to poor recruitment (McGowan et al. 2021), thus considering space (latitude in this study) is a necessity. The spawning populations off BC overlap considerably in latitude, and adult populations of herring are known to mix in the feeding grounds (Beacham et al. 2008), even though Rooper et al. (2024 in this Theme Section) found that herring off BC tend to spawn at the same locations over time. Therefore, our results may be affected by a spatial mismatch between the temperature values used to determine DD (represented by the polygons in Fig. 1) and the spawning populations. Nevertheless, assuming our spatial locations are represen-

tative of the spawning populations, it would be interesting to compare the thermal constant measured here to those for other populations of herring across the species' range. Neuheimer & MacKenzie (2014) found that the thermal constant for Atlantic cod *Gadus morhua* declined with latitude, meaning that cod at higher latitudes need fewer DD to spawn than cod at lower latitudes. This was shown to be consistent with adaptive variability in spawning time that allowed the first-feeding cod to match their prey across space and time (Neuheimer et al. 2018). Here, we found the same thermal constant for all latitudes in the study region, which may be a result of this range of latitudes being too small (49.23–54.20° N) compared to that in the Atlantic cod study (40–80° N). Future work should investigate if the ~1700°C-days thermal constant can be applied to other areas. Future work should also consider using the raw survey data (daily data with latitude and longitude coordinates), as in Rooper et al. (2024), to extract more robust thermal constant(s).

Other studies may find it useful to include daylength (closely linked to latitude) in their analyses. The data we used in this study have latitudinal differences ranging a maximum of 10°. This difference, at the latitudes the data are at (48–56° N) corresponds to a maximum of 1.5 h difference in day light. We believe this difference would not impact our results, since we are looking at average spawning time and the original daily spawning data are not available. However, future studies may find that daylength and temperature may play an even more important role.

4.2. Explaining spawning variation in time

Temporal trends in spawning timing patterns varied by region with spawning time increasing, decreasing, or showing no linear change over years (Fig. 4). In 2 out of 3 regions, the linear trends in spawning time were explained by thermal time (WCVI and JS, Fig. 4B,C, respectively), i.e. a thermal constant can be used to predict the spawning timing of these populations across years. These results are similar to those of Neuheimer & MacKenzie (2014), who found linear trends showing that both delayed and advanced spawning time for cod were explained by DD. However, it is important to note that an important factor that may have led to spurious increasing trends in the spawning time is survey methodology. An organisational shift in the 1990s led to a decrease in operational staff responsible for sampling the more remote coastal locations (Fisheries and Oceans Canada 2023). The loss of this observational capacity may

have resulted in missing reports of the very early small spawning events, thus contributing to the apparent increase in spawning time. Moreover, using the raw survey data (see, for instance, Rooper et al. 2024) would have allowed for more representative spawning events in both time and space.

No significant linear relationship was found for the annual variation in spawning timing in CD for the southern-most region (SoG), CC, and the northern-most region (PRD) (Fig. 4A,D,F, respectively). In the northern-most region, there is a non-linear variability in CD to spawning, with peak CD to spawning in 1977 (Fig. 4F). When viewed on thermal time, this non-linear pattern disappears and herring in the PRD region show a thermal constant of $1675 \pm 41^\circ\text{C-days}$ to spawning. In contrast, both SoG and CC showed very small (not significant) increases in time to spawning as CD, a pattern which also disappears in DD to spawning (Fig. 4G,J, respectively). The spawning of Pacific herring in these regions can thus be explained by a thermal constant.

The JS region showed a significant decrease in CD over time, indicating earlier spawning when viewed in calendar time. This linear pattern disappeared when viewed in thermal time (cf. Fig. 4C,I), suggesting that earlier spawning time can be explained by temperature, i.e. JS herring reach their thermal constant of spawning (approximately $1802 \pm 42^\circ\text{C-days}$ to spawning) earlier in later years.

The HG region showed a decreasing trend in both CD and DD over time, identifying remaining variability in spawning time for this population that may indicate the influence of other factors (e.g. spawner size or age), or limitations to our DD model (see Section 4.3). We would expect an earlier spawning time in HG due to global ocean warming reaching ~1700°C-days to spawning sooner. However, the decreasing trend in spawning time is rather steep, and remains significant on thermal (DD) time, thus indicating that there may be factors other than temperature leading to this trend (Fig. 4K).

4.3. Remaining patterns in time to spawning over the years

We found one linear trend in thermal time to spawning over years (i.e. patterns unexplained by our DD to spawning estimate). HG showed a decrease in DD to spawning over years which can be explained as follows: (1) our thermal time model assumptions were not valid for this population/region, possibly because the temperature data are not representative of those

experienced by the fish, or our linear approximation of the thermal performance curve is not correct; or (2) other factors are influencing the spawning time (e.g. adaptation or weight or age of spawners).

With respect to (1), violations of our assumptions regarding our thermal time model may explain the spawning time pattern remaining in thermal time (i.e. linear trend in DD to spawning in Fig. 4K). An accurate estimate of thermal time requires temperatures experienced by the fish during gonadal maturation. Here, we used season- and depth-defined temperatures according to Sigler & Csepp (2007) for Alaskan herring as in Table 1 for the polygons defined in Fig. 1. Variations in the vertical distribution of BC vs. Alaskan herring as well as spatio-temporal variations in distributions are not included in our model of thermal time. A more detailed vertical distribution is particularly important because herring are known to perform diel vertical migrations as they feed on zooplankton in the Atlantic (Ferreira et al. 2012), as well as in the Pacific (Blaxter & Parrish 1965, Bollens et al. 1992, Mackinson 1999). Furthermore, the polygons within which we averaged the temperature (Fig. 1) may not only be varying in time, but they may even not be representative of the total range of temperatures experienced by these fish. Hay et al. (2009) suggested that smaller spatial units (area $<0.1 \text{ km}^2$) are more suited to explaining the spatial diversity in spawning as it was significantly correlated with spawning stock biomass. More accurate horizontal and vertical distribution information that is region-specific would lead to more accurate thermal time metrics. For example, the decreasing trend in time to spawning that remains in DD may be a sign that the temperature we used was not representative of the temperature experienced by the HG fishes, as this region is more exposed to highly variable oceanographic conditions (Haegle & Schweigert 1985), and thus may experience a higher thermal range.

In addition, we based the start date of our thermal integral (onset of gonadal maturation) on hormone levels and gonadosomatic index. The estimate comes from populations off BC (Hay & Outram 1981) and Japan (Hay & Outram 1981, Koya et al. 2003), indicating the timing may be consistent across populations (as found for cod, Neuheimer & MacKenzie 2014). Still, any variation in the onset of gonadal maturation across regions may explain the remaining patterns in spawning time.

Another reason that our DD estimate may not be appropriate is that the threshold temperature below which fishes experience no gonadal development (T_{Th}) is incorrect or varies across regions. We reanal-

ysed our data with a higher T_{Th} based on the observation that the lower thermal tolerance limit of Pacific herring eggs post-spawning is between 4 and 5°C (Alderdice & Velsen 1971). Note that this T_{Th} is relevant for herring egg development post-spawning and may not be appropriate for the T_{Th} associated with gonadal maturation. Our results differed in 2 ways when using $T_{Th} = 4$ vs. 0°C to calculate DD to spawning. First, a decreasing trend in DD to spawning was found with increasing latitude when using $T_{Th} = 4^\circ\text{C}$ ($-1.55 \pm 0.10^\circ\text{C-days per year}$, $R^2 = 0.11$, $p < 0.001$; Fig. S12) vs. no trend with $T_{Th} = 0^\circ\text{C}$ (Fig. 3). A decreasing thermal constant with increasing latitude is similar to what was found for Atlantic cod by Neuheimer & MacKenzie (2014). Second, the trend toward decreasing DD to spawning with year found for the HG region when using $T_{Th} = 0^\circ\text{C}$ ($-2.86 \pm 0.42^\circ\text{C-days per year}$, $R^2 = 0.36$, $p < 0.001$; Fig. 4K) disappears when using $T_{Th} = 4^\circ\text{C}$ ($p = 0.09$; Fig. S12K). More generally, information about the non-linear thermal performance curve describing temperature-dependent gonadal development would negate the need for a T_{Th} parameter and the simple DD assumption we use here (e.g. Neuheimer et al. 2018). This includes spatial and/or temporal variability in the thermal performance curve. Some populations may be adapting to increasing temperatures, i.e. their thermal constant of spawning is shifting. Evidence of adaptive behaviour has been found for Pacific herring in terms of reproductive strategies (Hay et al. 2008, dos Santos Schmidt et al. 2021). Moreover, Atlantic herring populations with Pacific ancestry show signs of adaptation in their life history (Mikkelsen et al. 2018). Again, region-specific estimates of the thermal performance curves for development would help explain these trends. Overall, refining our formulation of the thermal time measure would lead to a more accurate thermal time metric that would allow us to identify any remaining temperature-dependent spawning time variability.

Regarding (2), temperature-independent factors affecting spawning time, we explored the effects of weight and age of spawners on spatio-temporal spawning variation over the years (Figs. S13 & S14, respectively). We found that the residuals of the model in Eq. (3) using CD as the response variable for the PRD region increased with increasing average weight of spawners (Fig. S13E). This indicates that larger fish may be spawning later in calendar time. Older (and perhaps larger) fish spawning later is not a common pattern but has been found previously (Hutchings & Myers 1993, Morgan et al. 2013). Note that this pattern in PRD of spawning time variability

with weight of the fish is explained by thermal time (i.e. no trend; Fig. S13J). Older and larger fish may travel to more distant feeding grounds and, thus, have a longer return migration to their spawning area (Callihan et al. 2015). Other fish species (such as gadoid fishes) show signs that, besides water temperature, changes in the age structure of the stock can also have an impact on spawning timing during the period of gonadal maturation (Wieland et al. 2000, Morgan et al. 2013). For herring off BC, the literature reports later spawning timings for younger fish (Ware & Tanasichuk 1989). However, that evidence may be outdated, perhaps due to the aforementioned reasons, such as changes in age structure. In our results, age did not show significant linear patterns with spawning time (Fig. S14).

4.4. Implications

Thermal time models use information about temperature-dependent development rates to define thermal constants that can be used to estimate the seasonal timing (e.g. spawning time). These thermal constants can also be used as a strategy to tease apart expected environmental responses from potential tipping points (e.g. adaptive change, regime shifts), and to make forecasts of life-history phenology in a changing climate.

With the observed global warming patterns, it is likely that the $\sim 1700^{\circ}\text{C}\text{-day}$ threshold needed to spawn will be reached earlier in coming years, and this will be observed as earlier spawning by Pacific herring in the future. Spatial variability in warming trends may mean that spawning time variability differs across regions. As temperatures are expected to rise at faster rates than previously observed (IPCC 2022), *in situ* temperatures may eventually exceed the thermal tolerance limits of development. This could result in distribution changes by the herring (to maintain environmental temperatures within tolerance limits), and/or adaptation of the thermal performance curve to compensate for the increased temperatures. It is unclear if such adaptation could keep pace with the expected rate of temperature increase.

Our findings identifying thermal constants for BC herring spawning time are particularly relevant for the roe fishery in this region. The lethal portion of the Pacific herring roe fishery is timed for when most fish in the stock have ovulated but before mass spawning (Gillis et al. 1990). This requires repeated sampling of stocks to check ovulation status. In some cases, the fishery is opened within hours of the sufficient

roe status being identified. Thermal constants of spawning time can help better predict the timing of the fishery opening, aiding both the lethal portion of the roe fishery, as well as the non-lethal spawn-on-kelp fishery by limiting the need for sampling to check ovulation status and better plan resources with more precise fishery timing. By adopting a DD approach, we are able to better predict when Pacific herring will spawn each year, depending on the temperature experienced since 1 September. Moreover, these results can be used to identify other factors driving interannual variations in herring spawning time (e.g. size and demographics) that can be used to improve long-term predictions of timing and production in the future.

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