Original Article

Multidecadal daily resolved growth increments reveal climate effect on the growth of a highly migratory shark in the North Atlantic

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Substantial progress has been made in identifying large-scale climate effect on somatic growth through the use of ageing-based methods in aquatic environments, yet their annual/seasonal temporal resolution seems too coarse for such a fast process. Temporal resolution is a missing dimension in our understanding of climate effects on growth. Here, an alternative source of high temporal resolution growth increments embedded within a multidecadal traditional tag-recapture database was analysed to identify climate signals in the somatic growth of blue sharks *Prionace glauca* in the North Atlantic. Results indicate the growth response of *P. glauca* to the NAO occurred at a daily scale with a time-lag. Non-parametric modelling reveals an optimal response curve around the historical average of the NAO, and a significant negative response for large positive NAO anomalies. Growth predictions show that the last four decades are mostly associated with negative responses compared to the historical average. The temporal resolution of this study is unprecedented among current ageing-based studies with a comparable temporal coverage. Integrating high temporal resolution into long-term climate effect studies can open new avenues for research on identifying climate effect on growth and provide detailed clues to its mechanisms of action.

Keywords: climate change, high temporal resolution, long-term study, somatic growth, tag recapture data

Introduction

Long-term observational data and historical records are important sources of information that allows us to measure the integrated impact of climate change on biological systems (Magnuson, 1990; Hughes, 2000; Malhi *et al.*, 2020) and to reveal significant shifts in the distribution, behaviour and somatic growth of wild animals under climate change (Parmesan and Yohe, 2003; Ozgul *et al.*, 2009; Sheridan and Bickford, 2011). Among these aspects, somatic growth is an ideal indicator of climate effect because it underpins individual fitness, but also has consequences for population- and community-level processes (DeLong *et al.*, 2015; Smoliński and Mirny, 2017; Stawitz and Essington, 2019; Morrongiello *et al.*, 2021).

In aquatic environments, ageing-based methods, such as bio-chronologies developed from calcified structures, have led to substantial progress in identifying the climate effect on somatic growth, e, g., Thresher *et al.* (2007), Rountrey *et al.* (2014), and Morrongiello *et al.* (2021), yet challenges and limitations of this approach cannot be overlooked, as reviewed in Campana and Neilson (1985) and more recently in Matić-Skoko *et al.* (2020). Through simulation, Smoliński *et al.* (2020) shows that even moderate ageing errors can substantially reduce the ability to extract climate signals from bio-chronologies. Along with other limitations, the sensitivity to ageing errors substantially limits the achievable temporal resolution of such studies. The higher the temporal resolution, the larger the number of growth band readings to perform on a single specimen, and hence, more random errors are likely to occur. Most

bio-chronology studies are annually resolved (Morrongiello *et al.*, 2012, and references therein) and some of more recent studies have a seasonal resolution (Izzo *et al.*, 2017; Martino *et al.*, 2019). A bio-chronology with an even finer temporal resolution, e.g. monthly or daily, may not outperform that of a much coarser but more reliable resolution, e.g. annual/seasonal, in identifying climate signals due to the sensitivity of this approach to ageing errors.

Temporal resolution is a missing dimension in the current long-term climate effect studies, and matching the temporal scales of the underlying biological process and the collected data can improve the understanding of climate effects on biological systems (Adrian *et al.*, 2012). Even for slow processes, such as recruitment or colonization, a sub-annual scale can help identify critical windows of action, e.g. Köster *et al.* (2003), and for relatively fast processes, such as somatic growth, an annual/seasonal resolution seems overly coarse, and may mask important climate signals due to excessive averaging. Not being able to adopt a sufficiently high temporal resolution greatly constrains the power to track animal growth under climate change.

To solve this problem, this study presents a novel modelling approach to track the growth of a highly migratory shark species in the North Atlantic under climate change with unprecedented temporal resolution by leveraging an alternative observational data source of multi-decadal daily resolved growth increments (GIs) embedded within a traditional tag-recapture database. Compared to ageing-based methods, this data type avoids the error-prone ageing process altogether as GIs are timestamped by the actual time, offering a direct measure of animal growth with unprecedented temporal resolution.

Tag-recapture is one of the oldest and most commonly used methods to track animal movement and study population dynamics across different taxa around the world both for terrestrial and aquatic species. Many of the tagging programs last for decades and track hundreds of thousands of tagged animals, e.g. the ongoing Cooperative Shark Tagging Program has tagged over 229000 pelagic sharks starting from 1960s (Kohler and Turner, 2020), and many commercially important fishery stocks are also subject to extensive tagging, e.g. yellow perch *Perca flavescens* and walleye *Sander vitreus* in a freshwater environment (Thomas and Haas, 2005; Bi *et al.*, 2020), and southern bluefin tuna *Thunnus maccoyii* in a marine environment (Majkowski, 1982). In addition to the data of primary interest, i.e. the geographical location of the tagged animal and the associated time/date, a tag-recapture study usually also records auxiliary data, such as sex, maturity, and body length, at tagging and recapture events. These timestamped GIs hold a remarkable amount of information on the effects of climate change on the fitness of wild animals.

The rest of the article is as follows. First, a theory section is presented to show the validity and generality of this approach to study climate signals. Second, a brief summary of the tag-recapture database and the North Atlantic Oscillation (NAO) indices used in the case study is given, followed by the methodology to model growth variations from intrinsic non-climate factors and climate factors. Third, an examination of an adequate temporal scale to study the climate effect in this case study is also conducted. Fourth, the growth performance is predicted for the entire range where the NAO index is available. Finally, a comparison of the presented method and current ageing-based studies is presented with a discussion of pros and cons for both methods and recommendations for further research.

Material and methods
Validity and generality of the method
Somatic growth is usually expressed in the form of an ordinary differential equation (ODE),

$$\frac{dL}{dt} = f(L, \theta), \tag{1}$$

subject to the initial condition $L(t = 0) = L_0$, where $L(t)$ is the length of the animal at time t, the form of $f(.)$ may differ for different growth models, and θ is the set of growth parameters, which does not depend explicitly on the age of the individual. The commonly used growth equations, such as the von Bertalanffy equation, are solutions of the corresponding ODE model assuming a constant θ. Generally, when θ varies with time due to external forcing (climate), no closed-form solutions exist and numerical solutions are necessary. In view of Equation (1), the instantaneous growth rate is independent of age given L. In other words, the length increment (ΔL) between t_1 and t_2 does not depend on the age of the individual when the initial length $L(t_1)$ is known, and thus, the growth parameters θ can be estimated based on observations of segments of the growth trajectory and no age determination is required. Assuming the constancy of θ during a time interval Δt, the GI can be obtained by simply switching the initial condition from L_0 to $L(t_1)$.

In this study, the GI form of four somatic growth models was used as candidate baseline models, including the von Bertalanffy curve (Von Bertalanffy, 1957), a growth curve due to West *et al.* (2001), Gompertz curve (Gompertz, 1825), and logistic curve (Verhulst, 1845) with the equations provided in the Supplement. Generally, any growth model in the form of Equation (1) can be used to analyse timestamped GIs without the need for age determination.

Case study: daily resolved GIs and climate indices
A total of 7446 valid blue shark *Prionace glauca* GIs, spanning 55 years (1963–2017) were extracted from the NOAA NMFS Cooperative Shark Mark Recapture Database (Figure 1). A valid GI contains a pair of timestamped body length measurements, and in this particular case, it is fork length measured in centimetres. An increment is the difference in body length between subsequent measurements in time. Both positive and negative increments are valid due to measurement errors. A growth interval is the time interval between tagging and recapture events or between subsequent recapture events for individuals recaptured multiple times, and time is resolved to the day of the month.

Most growth intervals are less than 2 months, and the number of GIs declines substantially with increasing time at large. The average measured fork length at tagging is 162.3 cm, and the measured fork length at recapture is 189.4 cm with an average increment of 27.1 cm (Figure 2). Approximately, 20% of the increments are negative due to the combination of a short growth interval and stochastic measurement errors. The longest growth interval comes from an individual tagged on 22 August 1995 and after 191 months recaptured on 4 July 2011. Over 80% of the GIs come from individuals with an identified sex, with 32.77% female ($n = 2440$), 48.13% male ($n = 3584$) and the rest 19.10% ($n = 1422$) unknown. Most of the GIs come from a unique individual recaptured only once in the database (95.81%, $n = 7\,134$), and a small proportion comes from individuals recaptured multiple times (4.19%, $n = 312$).

Geographically, tagged blue sharks cover major regions of the North Atlantic, and the majority of the records come from the
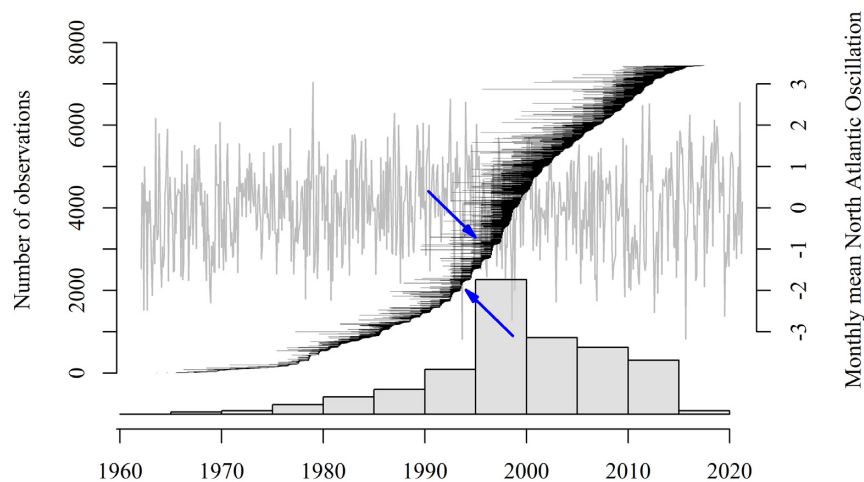
Figure 1. Temporal coverage of observed GIs (black horizontal segments) of blue sharks *Prionace glauca* under climate change. Monthly mean NAO index (grey) was plotted in the background, and the distribution of the observed GIs over time was plotted at the bottom. All three subfigures share the same *x*-axis. The staircase pattern (indicated by two blue arrows) seen in the GIs is due to the fact that most tagging and recapture events occurred in June through September. The histogram at the bottom was generated by stacking the GIs vertically, and its *y*-axis is not shown.
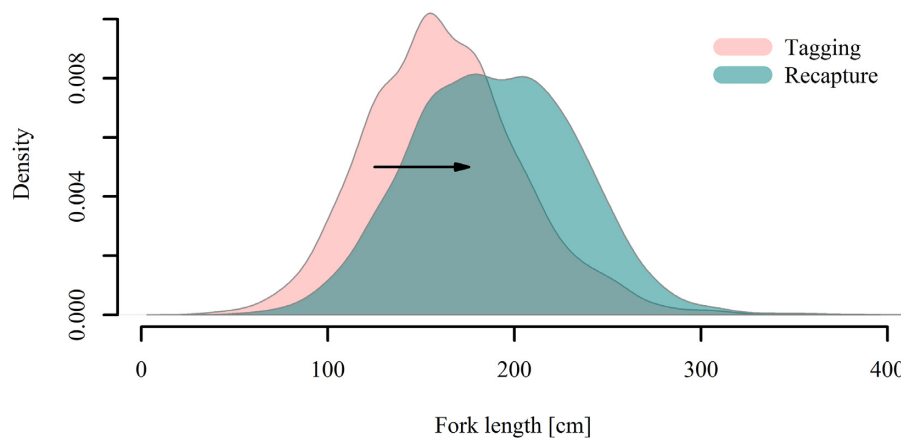

Figure 2. Density plots of recorded fork lengths of blue sharks at tagging (light pink) and recapture (teal). A bandwidth of 10 cm was used to generate these plots.

Western North Atlantic. The spatial distribution of the tagged individuals and the hypothesized movement between capture events are presented elsewhere (Kohler and Turner, 2020). Because of the use of traditional non-electronic tags, the actual movement trajectory between capture events is unknown.

Daily and monthly mean NAO time series were obtained from NOAA NWS Climate Prediction Center. Both time series were available from 1 January 1950 until 28 February 2021 at the time of this writing. As the dominant mode of atmospheric variability in the North Atlantic region, the NAO is associated with basin-wide changes in the intensity and location of the North Atlantic jet stream, in large-scale modulations of the normal patterns of heat and moisture transport (Olsen *et al.*, 2012), affecting various ecological processes through both direct and indirect pathways (Stenseth *et al.*, 2002, and the references therein).

Modelling intrinsic non-climate effects

Growth variations due to non-climate intrinsic factors were modelled before examining any climate factors. Examined covariates include monthly variation of growth rate (12 level categorical corresponding to the 12 months of the year), individual variation (7281 level categorical corresponding to the 7281 uniquely tagged individuals), sexual variation (three level categorical: male, female, and unknown). All the intrinsic effects were incorporated into the growth parameter(s) of the selected baseline model hierarchically (Table S1 in the Supplement).

Modelling climate effects

A tuneable dual-temporal-resolution incremental growth model has been developed to take into account both fine-scale daily resolved climate variations for shorter growth intervals and coarse-scale monthly resolved climate variations for longer growth intervals. This hybrid configuration allows the examination of climate effect at a finer temporal scale and also takes advantage of generally higher signal-to-noise ratio of a climate index at a coarser scale. Both linear and non-parametric climate effects were examined. For non-parametric models, independent cubic splines were incorporated into the growth function on the growth parameter(s).

Table 1. Select candidate models and model selection results. k^w and L_∞^w.are the growth parameters of the West growth curve. The selected model appears in bold. See Table S1 in the Supplement for a full list of candidate models.

Model	Description	$\triangle$AIC
B0.1	West growth curve	173.23
B1.3	B0.1 + effect of sex on k^w	112.58
N1.2	B1.3 + cubic spline of monthly NAO on k^w and L_∞^w	24.51
N2.2.30	N1.2 + daily NAO variation for GIs of less than 30 days	14.15
N3.7	**N2.2.30 + 7-day time lag**	**0.00**

Table 2. Parameter estimates for select models. k^w and L_∞^w.are the growth parameters of the West growth curve. Standard errors can be found in the parentheses after the point estimate, and units can be found in square brackets.

	Model B0.1	Model B1.3	Model N1.2	Model 2.2.30	Model N3.7
Fixed effects					
k^w [(30 days)$^{-1}$]	0.059 (0.002)	0.060 (0.005)	0.063 (0.005)	0.064 (0.005)	0.064 (0.005)
L_∞^w [cm$^{3/4}$]	60.93 (0.28)	60.72 (0.26)	60.96 (0.35)	60.91 (0.34)	60.92 (0.35)
SD of sex effect on k^w (log)	–	− 4.85 (0.43)	− 4.86 (0.43)	− 4.86 (0.43)	− 4.85 (0.43)
SD of NAO effect on k^w (log)	–	–	10.93 (1.21)	11.09 (1.18)	10.34 (1.34)
SD of NAO effect on L_∞^w (log)	–	–	4.43 (1.87)	4.56 (1.73)	4.33 (1.91)
SD of residual (log)	3.46 (0.008)	3.45 (0.008)	3.45 (0.008)	3.45 (0.008)	3.45 (0.008)
Random effects on k^w [(30 days)$^{-1}$]					
Female	–	− 0.0098 (0.005)	− 0.0096 (0.005)	− 0.0097 (0.005)	− 0.0098 (0.005)
Male	–	0.0086 (0.005)	0.0085 (0.005)	0.0084 (0.005)	0.0084 (0.005)
Unknown	–	0.0011 (0.005)	0.00074 (0.005)	0.0010 (0.005)	0.0011 (0.005)
No. of fixed parameters	3	4	6	6	6
−log(Likelihood)	36 315.3	36 283.98	36 237.94	36 232.76	36 225.68
$\triangle$AIC	173.23	112.58	24.51	14.15	0.00

A reference GI was used to compare the net growth response to climate variations among different models. The adopted reference GI comes from a female blue shark with an initial body length of 150 cm and the growth interval lasting for 30 days. Individuals with a body length of *c.* 150 cm are common in this database. Otherwise, this choice of the reference is arbitrary. Alternatively, any other combinations of sex category and body length could be used. Interested readers may use the source code provided with this article to compute the climate response of any other valid combinations of sex, body length, and growth interval. Note that the choice of the reference GI is only for prediction purposes, and it does not enter the likelihood function, and therefore does not affect parameter estimates.

Instead of showing the climate effect on growth parameters θ, the overall effect of climate on growth (ΔL over some time interval) was shown for the following reasons. First, growth models are justified primarily based on goodness of fit rather than on any biological mechanism (West *et al.*, 2001), and the biological meaning of the growth parameters from those models is usually unclear. Second, for those models that have a physiological interpretation, the effects on different growth parameters are usually not separable. For example, it is well known that the parameters of the von Bertalanffy growth are highly correlated, and inferences about the underlying source of growth variability based on model selection results can be erroneous (Eveson *et al.*, 2007). Third, growth parameters from different models usually are not directly comparable. On the other hand, the variation in growth offers a clear and unifying measure of climate effects.

Statistical analysis

All the analyses were conducted in R 4.0.3 statistical environment (R Core Team, 2020) with package TMB (Kristensen *et al.*, 2016). Model selection was based on AIC (Akaike, 1998). Prediction of the growth of a reference GI over Feb-1950 to Feb-2021 was based on model-averaged predictions from candidate models with $\triangle$AIC $\leq$ 10. Annotated source code is available from a public GitHub repository (https://github.com/HVoltBb/climate-change-01). See the Supplement for additional details.

Results

Intrinsic non-climate effects

Four baseline models with no covariate information were examined for fit to the observed GIs. The West curve (B0.1 in Table 1 and Table S1 in the Supplement) has the best fit based on AIC, followed by the von Bertalanffy curve ($\triangle$AIC = 176.80) and Gompertz curve ($\triangle$AIC = 193.34) with comparable performance; on the other hand, the logistic curve did not provide an adequate fit ($\triangle$AIC = 237.48). All the estimated coefficients of model B0.1 were significant at the 0.01 level. The estimated growth parameters of the West curve were k^w = 0.059 (SE = 0.002) [(30 days)$^{-1}$], L_∞^w = 60.93 (SE = 0.28) [cm$^{3/4}$] and residual standard deviation (SD) in log scale $\log(\sigma)$ = 3.46 (SE = 0.008) (Table 2, see the Supplement for the definition of the growth parameters). Model B0.1 provides a basis, on which all the subsequent models were built.

Next, non-climate effects on growth were modelled. The incorporation of either monthly variation or individual effect on growth

rate led to inflated AIC with respect to the baseline (Table S1), and both factors were not further retained. The lack of significance of monthly variation is likely due to an insufficient coverage of the dataset over non-summer months as most tagging (*c.* 89%) and recapture (*c.* 71%) events occurred in June through September, and the lack of significance of the individual effect may be due to the small representation (4.19%) of repeatedly sampled individuals in the database. Sex type has a significant effect on the growth rate of blue sharks. Models incorporating sexual variation show substantially improved performance with respect to the baseline with AIC reductions over 50 units (Table S1). Among models with no-climate effect, the one with sexual variation on k^w (B1.3 in Table 1) has the lowest AIC, and the additional incorporation of sexual variation in L_∞^w did not further improve model performance. In model B1.3, the estimated fixed effect on growth parameters was similar to the baseline (Table 2). For the random effect on growth parameter k^w, female blue sharks have a lower growth rate ($v_0 = -0.0098$ [(30 days)$^{-1}$]) than males ($v_1 = 0.0086$ [(30 days)$^{-1}$]), and those without an identified sex have a growth rate ($v_2 = 0.0011$ [(30 days)$^{-1}$]) in between those with an identified sex (Table 2). Model B1.3 was further examined for any evidence of climate signal.

Climate effects

Models incorporating either linear or non-parametric climate effects were examined, but with contrasting results. Model selection results show that the linear climate effect model L1 did not improve upon model B1.3 (Table S1). In contrast, all non-parametric climate effect models substantially improved model performance with AIC reductions between 46 to 88 units against model B1.3 (Table S1). As will be shown below, the inability of the linear model to identify climate signal in this case is due to 1) the failure of the monthly NAO to capture growth variations at a daily scale, and 2) the bell shape of the optimal response curve (Figure 3b), i.e. a linear approximation to that curve is almost a flat line, and hence, the lack of statistical significance. The inclusion of non-parametric climate effect on either growth parameter k^w or L_∞^w of the West curve brought a similar reduction in AIC of *c.* 50 units, and the inclusion of climate effect in both parameters further reduced AIC by *c.* 40 units. The selected climate effect model under this category incorporated non-parametric monthly mean NAO effect on both parameters of the West curve.

The incorporation of daily climate variations and time lag brought further improvement to model performance. In particular, for the linear climate effect model (L1), the incorporation of daily NAO index alone helped reveal the climate signal while keeping other model components unchanged (Table S1), highlighting the significance of adopting a sufficiently high temporal resolution. However, the improvement is only limited to GIs with a short growth interval (< 30 days), and extending the daily resolved climate index to GIs less than 60 days did not bring further improvement, probably due to a higher signal-to-noise ratio of the monthly NAO index. Model N2.3.30, which incorporated daily NAO variation for GIs for less than 30 days, was further examined for any time lag in response. Fourteen time-lagged responses were modelled with an integer number of days of delay (from 1 to 14 days) between the climate index and the growth. Model selection results indicate substantial evidence for delayed responses at 7∼8 days (models N3.7–8 in Table S1) and also at 4 days (model N3.4).

Irrespective of the length of the time lag, an optimal curve response peaking slightly above the historical mean of the NAO re-emerges consistently with variations at the tail ends of the NAO index range (Figure 3 and Figures S1-12 in the Supplement). Other common features include the levelling of the slope at the NAO interval of $(-1.5, -1)$, and increased uncertainty towards both ends of the NAO range due to the low frequency of extreme climate events (Figure 3 and Figures S13-14 in the Supplement). The optimal curve at the centre of the NAO range peaks slightly above historical mean and declines on both sides. Additionally, an upward trend at the negative end of the NAO range is visible but with high levels of uncertainty with the 95% confidence band overlapping substantially with the horizontal line of no effect. At the positive range, despite increased uncertainty, the negative impact on growth is clear and significantly different from zero across all time lags examined.

Predicted growth performance

The predicted growth of blue sharks to climate variability shows a *regime* shift in response dynamics. To avoid any potential bias in picking a particular time lag, model-averaged predictions among all the candidate model with ΔAIC ≤ 10 were used to predict the climate response of a reference GI. Evident in the three-year moving average of the time series of the predicted growth response is a shift from large patches of positive growth interspersed by relatively short and shallow periods of negative growth in the early years (1950–1980) to two large patches of negative growth separated by fewer and smaller positive growth patches in the later years (1980–2020) (Figure 4). In later years, the negative growth period not only cut deeper but also lasted longer compared to earlier years, and additionally, the magnitude of the swing of the growth response also increased (Figure S15 in the Supplement).

Discussion and conclusions

Timestamped GIs complement the traditional ageing-based biochronology studies. Many fish species deposit daily growth rings, but only during larval and juvenile stages (Pannella, 1971; Brothers *et al.*, 1976; Campana and Neilson, 1985; Morales-Nin, 2000), making it impossible to reconstruct daily resolved chronologies for adults. Meanwhile, timestamped GIs are equally applicable to both juvenile and adult stages because they are timestamped by the actual time, offering effectively unlimited temporal resolution and a direct measure on somatic growth, not affected by ancillary processes, such as mineral deposition rates or resorption, which may obscure the interpretation of the results when a proxy is used instead. Timestamped GIs are also applicable to species with no seasonal marks, for which age-based methods cannot be used. On the other hand, calcified structures offer a richer set of biological data, including isotopic and elemental compositions, which can be used to track animal movement, e.g. Trueman *et al.* (2012), and variations in environmental conditions, e.g. Campana (1999) and Willmes *et al.* (2019).

Many of the long-term large-scale tag-recapture programs are administered by government agencies, the operations of which bears no direct cost to researchers studying climate change effects. This removes the financial and logistic barriers for data collection and management aspects of a climate effect study (Matić-Skoko *et al.*, 2020), and can stimulate new research from a broader community of researchers. With respect to historical records, although the body of existing tag-recapture databases with timestamped GIs is large, e.g. Mejuto *et al.* (2005), Kohler and Turner (2020), and Thomas and Haas (2005) among others, the total amount of records is fixed; on the other hand, historical growth patterns embedded in the hard parts from either museum specimens or living organ-
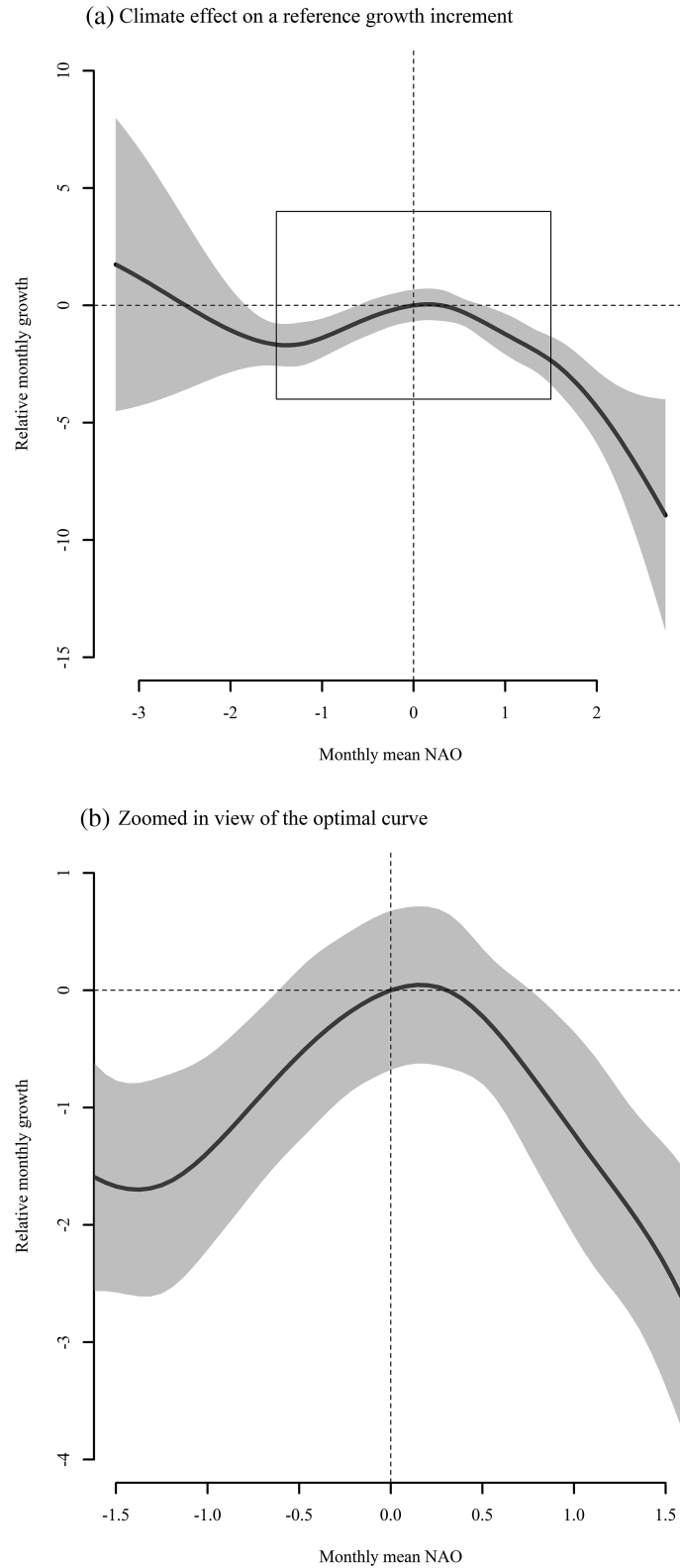
(a) Climate effect on a reference growth increment

(b) Zoomed in view of the optimal curve

Figure 3. Climate effect of the NAO on a reference GI based on the selected model N3.7 (a) and a zoomed in view of the optimal curve around the historical mean of the NAO (b). The reference GI comes from a female blue shark starting with a body length of 150 cm, and the growth interval lasted for 30 days. Model N3.7 used the West growth curve as the baseline. For intrinsic factors, it incorporated sex effect on growth parameter k^w. For climate effects, it incorporated independent cubic splines on both growth parameters of the West curve (k^w and L_∞^w). GIs of less than 30 days were modelled using the daily NAO index, and GIs of 30 + days were modelled using the monthly NAO index. In addition, a time lag of 7 days was introduced between climate indices and the growth response. The 95% confidence band is shaded.
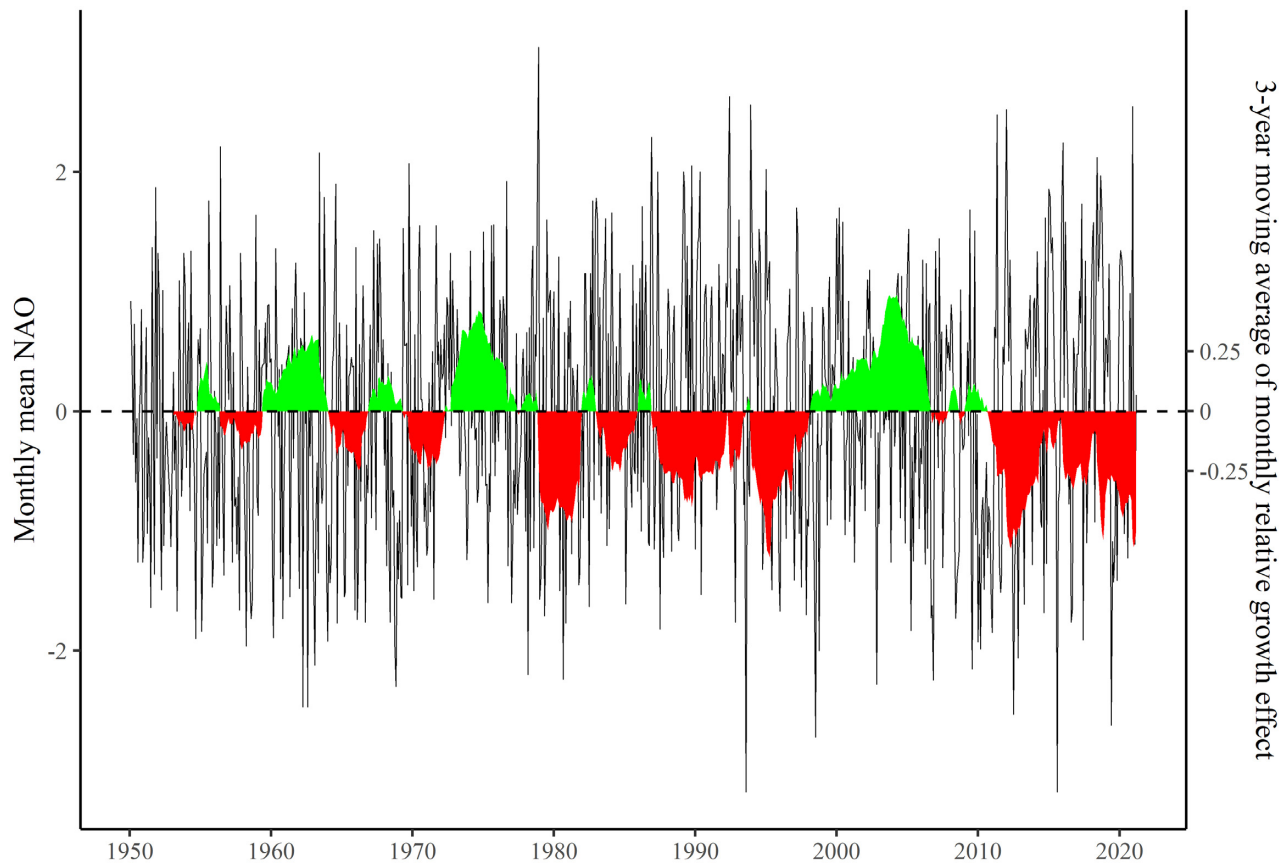
Figure 4. The monthly mean NAO index (black) and a three-year moving average of model-averaged predicted monthly relative growth of a reference growth increment (GI). The reference GI comes from a female blue shark starting with a body length of 150 cm at the first day of each month from February 1950 to February 2021, and each growth interval lasted for one calendar month. The mean GI from the first 30 years were subtracted to produce the relative growth. Positive deviations from the historical mean appear in green, and negative deviations appear in red.

isms can still be extracted. With respect to future records, ongoing tag-recapture programs will continue to generate unparalleled high-temporal-resolution GI records.

Biological processes take time, and examining them at an appropriate temporal scale improves the understanding of climate change on biological systems (Adrian *et al.*, 2012). The somatic growth of an individual involves a chain of events, from searching for prey items, ingestion, digestion, and up to the synthesis of new body materials. Any of these processes could be affected by large-scale climate variations either directly or indirectly, and when examined in sufficient temporal resolution, time lags will emerge. Blue sharks are opportunistic feeders on a wide range of teleosts and cephalopods (Clarke and Stevens, 1974; Clarke *et al.*, 1996; McCord and Campana, 2003; Mendonça, 2009). Climate signal observed in the GI of blue sharks could be bio-accumulated through different trophic pathways in a food web, with each pathway having a signature time lag due to the unique chain of processes involved. In this study, the NAO was used as a so-called "package of weather" (Stenseth and Mysterud, 2005) in lieu of direct impacting factors. Future investigations into the relation among the time-lag of the climate response, the diet of the species, and the food web structure may offer further insight into how climate signal is transmitted at an ecosystem scale, and elucidate direct impacting factors. While the data-driven approach adopted here can be helpful in the identification of potential predictors of individual's responses and can also serve in the generation of new hypotheses, testing a large number of potential

environmental signals, e.g. with different time lags, and the application of flexible non-parametric splines in the analysis may lead to spurious results. Further research is needed to investigate this issue, for example, through simulation as in Smoliński (2019).

Obtaining longer time series is crucial in identifying consistent and more understandable climate signals from biological systems (Magnuson, 1990). The predicted growth performance of a reference GI over 1950 to 2020 shows clustered phases (*c*. 10–20 years) with opposite signs, especially after 1980 until present (Figure 4). This is caused by the low frequency (decadal) fluctuation of the NAO (Hurrell, 1995), and the negative response of blue shark somatic growth to moderate NAO anomalies in either direction. For shorter time series, one of the growth phases (either positive or negative) may dominate the observed climate effect, and a simple extrapolation may draw seemingly contradictory conclusions on the climate effect on growth, reinforcing the idea that a shorter-term time series (10–20 years in this case) is subject to serious misinterpretation if not situated in its long-term ecological context (Magnuson, 1990). Worse still, when the temporal extent of the dataset covers two growth phases of opposite signs, a linear climate effect may not even be identifiable due to the bell-shaped response curve, underscoring the importance of routinely assessing nonlinearity in climate effect studies (Mysterud *et al.*, 2001).

The case study examined here contributes to the growing line of evidence of the shrinking effect of climate change (Sheridan and Bickford, 2011; Cheung *et al.*, 2013; Baudron *et al.*, 2014). Previ-

ous studies have mainly focused on the effect of a warning climate, and this study shows that moderate anomalies of the climate index in both directions reduce growth, although the shrinkage in response to positive anomalies is more striking (Figure 3a). The last 40 years have been dominated by negative growth relative to the historical mean (Figure 4). Currently, the NAO is in its positive phase (Weisheimer *et al.*, 2017), and this negative growth trend is likely to continue in the near future. For large negative NAO anomalies (< -2), although the estimated climate response is trending up, the result is inconclusive due to insufficient coverage of observed GIs over those extreme climate events (Figures S13-14 in the Supplement). Other tag-recapture databases, e.g. those reviewed in Mejuto *et al.* (2005), and bio-chronology based on hard parts may offer further insights.

In parallel with developing higher quality GIs, it is equally important to improve the quality of climate indices. As shown in this study, the temporal resolution of GIs is so high that the quality of the NAO index became inadequate. Even though strong signals of the daily NAO index were identified, the monthly NAO index has a much stronger signal for GIs with longer growth intervals (1 month and more). Many NAO indices exist. Station-based indices measure the sea-level pressure (SLP) difference between Iceland and Azores. Although easy to calculate and usually available for a longer time period, e.g. the Hurrell index (Hurrell, 1995) extends back to 1864, these indices do not represent sub-annual variations of the NAO due to their fixed station design (Jones *et al.*, 1997). Analysis-based indices are calculated based on gridded SLP. These indices provide a more optimal representation of the full NAO spatial variation. In this study, analysis-based indices from NOAA NWS Climate Prediction Center calculated based on a rotated EOF (Barnston and Livezey, 1987) were used to represent sub-annual variations of the NAO. These indices have widespread usage in climate effect studies, e.g. Stenseth *et al.* (2003) and Tabari and Willems (2018). A newer analysis-based NAO index based on differences of normalized regionally zonal-averaged SLP has shown superior signal-to-noise ratio at monthly to annual scales (Li and Wang, 2003), but its performance at a daily scale has not been evaluated. Adopting an NAO index with a higher signal-to-noise ratio has the potential to improve the detection of climate effect and therefore warrants further investigation.

An alternative source of high temporal resolution GIs embedded in a multi-decadal traditional tag-recapture database has been modelled in this study to identify climate signals on the somatic growth of a highly migratory shark in the North Atlantic. The methodology presented here is broadly applicable to other species, either in a terrestrial or aquatic environment, as long as timestamped GIs are available. To the best of my knowledge, the temporal resolution of this study is unprecedented among current bio-chronology studies with a comparable temporal coverage. Combining a fine temporal resolution with long-term coverage enables us to examine climate signals on a time scale on which biological systems act. It is expected that climate effect studies with a daily temporal resolution will become common when researchers tap into the potential of timestamped GIs embedded within a large body of existing tag-recapture databases.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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