Warming leads to opposite patterns in weight-at-age for young versus old age classes of Bering Sea walleye pollock

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Abstract

The temperature–size rule predicts that climate warming will lead to faster growth rates for juvenile fishes but lower adult body size. Testing this prediction is central to understanding the effects of climate change on population dynamics. We use fisheries-independent data (1999–2019) to test predictions of age-specific climate effects on body size in eastern Bering Sea walleye pollock (*Gadus chalcogrammus*). This stock supports one of the largest food fisheries in the world but is experiencing exceptionally rapid warming. Our results support the predictions that weight-at-age increases with temperature for young age classes (ages 1, 3, and 4) but decreases with temperature for old age classes (ages 7–15). Simultaneous demonstrations of larger juveniles and smaller adults with warming have thus far been rare, but pollock provide a striking example in a fish of exceptional ecological and commercial importance. The age-specific response to temperature was large enough (0.5–1 SD change in log weight-at-age) to have important implications for pollock management, which must estimate current and future weight-at-age to calculate allowable catch, and for the Bering Sea pollock fishery.

Résumé

La règle taille–température prédit que le réchauffement climatique se traduira par des taux de croissance accrus des poissons juvéniles, mais des tailles corporelles plus petites des poissons adultes. La validation de cette prédiction est d'importance centrale pour la compréhension des effets des changements climatiques sur la dynamique des populations. Nous utilisons des données indépendantes de la pêche (1999–2019) pour valider des prédictions d'effets du climat selon l'âge sur la taille du corps des goberges de l'Alaska (*Gadus chalcogrammus*) dans la mer de Behring. Ce stock qui supporte une des plus importantes pêches vivrières du monde est exposé à un réchauffement exceptionnellement rapide. Nos résultats appuient les prédictions voulant que la taille selon l'âge augmente avec la température pour les jeunes classes d'âge (1, 3 et 4 ans), mais diminue avec l'augmentation de la température pour les classes d'âge plus vieilles (7–15 ans). Si des observations simultanées de juvéniles plus grands et d'adultes plus petits accompagnant le réchauffement sont encore rares, le goberge en fournit un exemple frappant chez un poisson d'importance écologique et commerciale exceptionnelle. La réaction selon l'âge aux variations de température est suffisamment grande (variation de 0,5–1 ÉT du logarithme du poids selon l'âge) pour avoir une importante incidence sur la gestion du goberge, qui doit comprendre l'estimation du poids selon l'âge actuel et futur pour le calcul des prises permises, ainsi que sur la pêche au goberge de l'Alaska dans la mer de Behring. [Traduit par la Rédaction]

Introduction

Along with other high-latitude northern regions, the eastern Bering Sea (EBS; Fig. 1) is experiencing exceptionally rapid warming (Danielson et al. 2020). The EBS spans the boundary between the subarctic and arctic ecoregions and is home to species characteristic of both (Aydin and Mueter 2007; Mueter and Litzow 2008), and supports some of the largest and most valuable fisheries in the United States (Alaska Fisheries Science Center 2019). It is strongly influenced by seasonal ice cover and, until recently, a persistent cold pool of bottom temperatures below 2 °C. The spatial extent and seasonal timing of ice cover and the cold pool vary greatly among years and exert strong influence on the ecosystem (Walsh and Johnson 1979; Aydin and Mueter 2007). However, starting with a 2014–2016 marine heatwave, the EBS has been experiencing a prolonged warm period, characterized by unprecedented warm bottom and sea-surface temperatures (SSTs; Fig. 2), low sea ice extent, and a small or nonexistent cold pool (Di Lorenzo and Mantua 2016; Duffy-Anderson et al. 2019; Danielson et al. 2020; Huntington et al. 2020). These temperature anomalies are outside the range of preindustrial variability and have been attributed to human-induced causes with high confidence (Walsh et al. 2018; Laufkötter et al. 2020). These rapid changes have led to broad-

Fig. 1. Map of southeast Bering Sea (SEBS) showing sampling events as black circles. The bottom trawl survey samples a standard grid of stations each year, so sampling events from different years but the same station tend to cluster tightly in space. Map created using public domain data from Natural Earth accessed using packages *rnaturalearth* (South 2017*a*) and *rnaturalearthdata* (South 2017*b*). The map uses the Geographic projection and WGS84 coordinate system.

Fig. 2. April–June sea-surface temperature (SST) in the southeast Bering Sea.
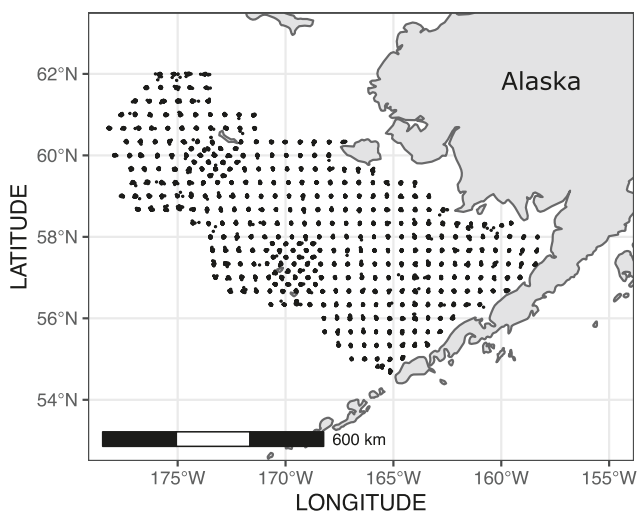
scale shifts in species distributions (Kotwicki and Lauth 2013; Alabia et al. 2018; Stevenson and Lauth 2019; Eisner et al. 2020; O'Leary et al. 2020), unusual mortality events (Duffy-Anderson et al. 2019; Siddon 2020), and an increasing dominance of subarctic taxa in the EBS (Duffy-Anderson et al. 2017; Stevenson and Lauth 2019; Marsh et al. 2020). However, temperature can also impact basic aspects of species' biology, such as growth rate and body size, that might be harder but equally important to monitor as the EBS ecosystem departs the envelope of temperatures under which much of our biological understanding of the system has been gained.

Across a wide variety of taxa and ecosystems, body size declines are very commonly linked to warming temperatures (Sheridan and Bickford 2011; Ohlberger 2013). Indeed, size declines have been proposed as a "universal" response to climate change (Daufresne et al. 2009; Gardner et al. 2011). Both the metabolic theory of ecology (MTE) (Brown et al. 2004) and the temperature–size rule (TSR) (Atkinson 1994; Kingsolver and Huey 2008) predict that warming should result in faster growth rates and reduced adult body sizes because growth rate and metabolic rate scale predictably with temperature (Gillooly et al. 2001). In fishes, reduced body size has multiple negative consequences, including reduced fecundity and productivity (Barneche et al. 2018), reduced population stability and climate resilience (Hsieh et al. 2010), and overall reduced survival probabilities (Audzijonyte et al. 2013). In addition, for some commercially harvested fishes, the relationship between temperature and body size could complicate stock assessment efforts.

Walleye pollock (*Gadus chalcogrammus*, henceforth "pollock") support one of the largest single-species fisheries in the world (2015–2019 mean annual first wholesale value US$1.4
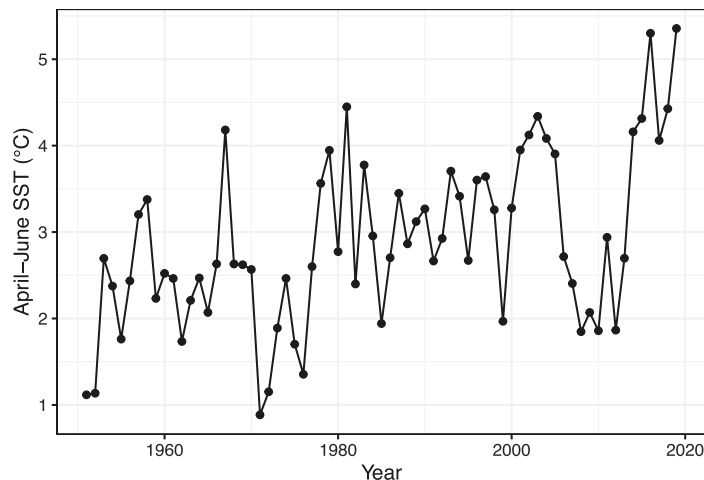
billion (Ianelli et al. 2020)). A relatively new fishery, the southeastern Bering Sea (SEBS) pollock fishery is often considered as an excellent example of sustainable management (Bailey 2013). However, pollock body size changes in response to warming could present a challenge for management of the fishery. The age-structured assessment model used to set management reference points estimates population size in numbers of fish, and these values must be converted to units of biomass (tons of fish) for quota setting (Ianelli et al. 2020). Catch-at-age estimates are only available from the previous year, so assessment authors must predict current and future pollock weight-at-age for biomass projections, potentially biasing weight-at-age estimates, which could result in a mismatch between expected and actual fishery mortalities (Ianelli et al. 2020). The pollock assessment already accounts for observed seasonal and spatial variations in weight-at-age (Ianelli et al. 2020), but temperature-related variations in weight-at-age among years could also be informative.

If body size varies predictably with temperature, weight-at-age predictions and short-term biomass projections could be improved using available temperature projections. However, this would require improved understanding of the relationship between pollock size and temperature. In particular, knowing whether the relationship between body size and temperature is strong or consistent among age groups could help to evaluate the potential benefits of incorporating temperature into the stock assessment.

The potential for temperature effects to vary among age classes might be especially important to consider in pollock. Juvenile and adult pollock differ in their spatial distributions and thus are likely exposed to different temperatures. For example, adult pollock show stronger avoidance of the cold pool than do juveniles (Bailey 1989; Wyllie-Echeverria and Wooster 1998). Moreover, the MTE and TSR predict smaller adult size but increased growth rates (Atkinson 1994; Brown et al. 2004; Kingsolver and Huey 2008), which should result in larger size-at-age in juveniles. A recent study on several Northeast Atlantic fishes supports predictions of differ-

Table 1. Annual sample sizes for each age class.

Year	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9	Age 10	Age 11	Age 12	Age 13	Age 14	Age 15
1999	135	216	167	104	48	64	200	91	76	78	34	18	14	28	21
2000	97	146	165	166	118	61	53	220	123	110	89	59	24	16	30
2001	135	241	150	72	112	131	68	44	158	143	93	98	44	19	9
2002	143	187	205	160	120	134	72	38	74	172	100	81	65	32	8
2003	161	134	205	149	111	85	113	84	40	80	180	107	56	29	16
2004	113	238	136	228	132	100	67	91	74	56	77	157	81	43	20
2005	186	157	176	117	174	133	92	57	70	57	26	67	117	66	50
2006	320	17	17	38	127	210	179	107	86	102	58	44	72	89	55
2007	562	19	19	25	73	135	148	129	75	54	49	44	31	33	43
2008	206	30	20	19	54	145	143	120	100	53	71	52	36	27	39
2009	373	65	65	51	34	55	99	96	83	70	55	38	50	28	25
2010	270	36	35	177	114	48	73	97	103	92	90	45	39	32	23
2011	274	51	61	39	282	182	78	66	130	129	135	113	56	34	32
2012	320	51	54	318	116	244	113	58	63	90	86	73	78	35	27
2013	431	34	49	65	449	162	182	88	38	49	77	60	60	39	27
2014	394	49	24	21	108	583	370	157	102	53	30	42	45	28	32
2015	385	93	179	49	115	260	721	273	109	58	10	12	17	10	10
2016	195	50	67	341	166	135	239	412	91	40	16	4	3	3	3
2017	170	41	50	216	313	169	152	155	241	68	31	9	2	1	2
2018	115	67	35	46	370	325	139	112	126	104	37	5	1	1	1
2019	162	47	42	39	123	559	292	89	68	49	28	15	5	28	21

ing body size responses to temperature among juveniles and adults (Ikpewe et al. 2020).

The overarching goal of this study is to determine whether and how temperature influences pollock body size. Our specific objectives are to use a 21-year long time series from a fisheries-independent bottom trawl survey to determine (1) whether and to what extent ocean warming influences pollock weight-at-age and (2) whether the effects of ocean warming on weight-at-age vary among age classes.

Methods

Study system

The EBS (Fig. 1) is characterized by a large, shallow shelf with nutrient-rich currents flowing northward over the shelf and exiting through the Bering Strait into the Chukchi Sea (for a general review of the EBS ecosystem, see Aydin and Mueter 2007). The SEBS is characterized by strong cross-shelf gradients defined by bathymetry and water column structure that are dominant drivers of the biogeography of fish on the shelf (Mueter and Litzow 2008) (Fig. 1). The ecology of the EBS ecosystem is dominated by demersal fishes and in particular has been dominated by pollock since the 1980s (Aydin and Mueter 2007).

Bottom trawl survey data

The National Oceanic and Atmospheric Administration (NOAA) conducts annual bottom trawl surveys of the SEBS from late-May to mid-August (with some variability in timing from year to year), which samples groundfish including pollock. The survey uses an 83–112 eastern otter trawl to sample 376 fixed stations on a 20 nautical mile (nmi) × 20 nmi (1 nmi = 1.852 km) grid each summer (for detailed methodology, see e.g., Lauth et al. 2019). Each year from 1999 to 2019, subsamples of commercially important fish species were measured (length and weight) and aged. Sample sizes for each age by year are provided in Table 1. Our study focuses on weight rather than length because weight-at-age is used in the assessment to convert numbers-at-age to biomass. Weights from before 1999 were judged to be unreliable because motion-compensated scales were not used. Older age classes had lower sample sizes, especially in recent years. Due to low sample sizes at older ages and for consistency with the pollock assessment, we used age classes from age 1 to age 15.

Statistical analyses

We used general additive mixed models (GAMMs) to model the response of weight-at-age to temperature. We used the logarithm of weight-at-age to account for right-skewedness in the data, and then scaled data (as z-scores) within a given age class to allow for comparisons among age classes. As a temperature metric, we used mean SST during spring/summer (April–June), the period prior to the annual bottom trawl survey, corresponding to the beginning of the ice-free season, the onset of stratification, and the spring bloom (Hunt et al. 2002). We expect that temperature effects will be most pronounced during the spring season, which could mediate pollock growth as they begin to grow post-winter, as well as the dynamics of pollock prey communities (Hunt et al. 2011). SST is correlated with a range of ecologically important climate variables in the system, including bottom temperature, cold pool extent, advection, surface salinity, wind mixing, and stratification (Hunt et al. 2002; Baker et al. 2020;

Danielson et al. 2020). Since these individual climate variables are collinear and share information, establishing the effect of individual physical covariates is difficult, so we treat SST as an index of overall climate conditions in the system, rather than concentrating on thermal effects exclusively. SST data were obtained from the ERSSTv5 data set (Huang et al. 2017), which measures mean monthly SST across a 2° latitude × 2° longitude grid. To calculate April–June SST, we averaged monthly means for April, May, and June for all measurements taken on the EBS shelf south of 64° latitude.

Each model also accounted for other factors that could influence weight-at-age but were not central to our objectives. First, pollock weight has been shown to vary through space (Ianelli et al. 2020), so we included a two-dimensional surface resulting from a tensor product interaction between latitude and longitude to account for the mean pattern of spatial variation in weight-at-age across years. Second, because growth continues through the spring and summer as sampling occurs and survey timing can vary somewhat from year to year, we accounted for the mean effect of sampling date by including a smoothed effect of day of year. Third, pollock body size is known to vary among cohorts (Ianelli et al. 2020). Although we expect that some among-cohort variation is due to the thermal regimes each cohort experiences, we also included a random intercept for cohort (year of birth) to account for the fact that some cohorts may be heavier, on average, due to factors other than temperature, especially density dependence and parental effects. Finally, we included a random effect of haul within year, to account for nonindependence of individuals sampled in the same haul as well as small-scale spatial variation within years. Each of these factors reflects our best understanding of our data structure; therefore, we did not subject them to model selection and instead include them to account for variation in pollock size resulting from the sampling and statistical designs.

Specifically, the model took the following form:

$$Y_{t,a,i} = \alpha + a_{h|t} + a_{\text{cohort}} + f_1\left(\text{SST}_t, \text{age class}\right) + f_2\left(x_i, y_i\right) + f_3\left(\text{doy}_{t,i}\right) + \varepsilon_{t,a,i}$$

where $Y_{t,a,i}$ is the scaled log(weight-at-age) of age a fish in year t at station i, α is the intercept, $a_{h|t}$ is the random effect of haul h nested within year t (see Table S1 for haul sample sizes), and a_{cohort} is the random effect of cohort, where both random effects are assumed to be independent and normally distributed with means zero and variances σ_h^2 and σ_c^2, respectively. SST_t is the April–June SST over the SEBS shelf in year t that interacts with the factor age class, x_i and y_i are the easting and northing, respectively, of station i, $\text{doy}_{t,i}$ is the day of year when station i was sampled in year t, and the $\varepsilon_{t,a,i}$ are independent, normally distributed residuals with mean zero and variance σ_ε^2.

We fit GAMMs using the package *gamm4* (Wood and Scheipl 2020). The latitude-by-longitude interaction was modeled as a tensor product interaction using the *t2()* function in *gamm4*. The random cohort effect was included as a simple random effect using *mgcv* syntax (specifically s(…, bs = "re")) for model efficiency (Wood 2017), whereas the more complex random

effect of haul nested in year was included using standard mixed model syntax for nested effects from the package *lme4* (Bates et al. 2015). For the day of year smoother and the smoothed interaction between SST and age class, the effective degrees of freedom were limited to three (basis dimension $k = 4$ for smooth term) to reduce the potential for overfitting to the limited number of annual SST measurements ($n = 21$) and because we considered more complex responses to be biologically unrealistic and likely to result in poor out-of-sample predictive skill.

To determine whether the effects of ocean warming on weight-at-age vary among age classes (objective 2), we compared the model described above to a model that included a single, global response to temperature, specifically:

$$Y_{t,a,i} = \alpha + a_{h|t} + a_{\text{cohort}} + f_1\left(\text{SST}_t\right) + f_2\left(x_i, y_i\right) + f3\left(\text{doy}_{t,i}\right) + \varepsilon t, a, i$$

Similarly, to determine whether and to what extent ocean warming influences pollock weight-at-age (objective 1), we compared our main model to a model without any SST term:

$$Y_{t,a,i} = \alpha + a_{h|t} + a_{\text{cohort}} + f_2\left(x_i, y_i\right) + f_3\left(\text{doy}_{t,i}\right) + \varepsilon_{t,a,i}$$

We compared the fit of these three alternative models using AIC$_c$(Sugiura 1978; Hurvich and Tsai 1991; Burnham and Anderson 2002). After considering the increase in AIC that would be expected from including extra parameters (Arnold 2010), we considered a $\Delta\text{AIC}_c > 4$ to represent an improvement in model fit. AIC$_c$ was obtained from models fitted using maximum likelihood using the function *AICc()* from the package MuMIn (Bartoń 2020). The model best supported by the data according to AIC$_c$ was refitted using restricted maximum likelihood and the strength of the SST effect was judged using p values and by comparing the gain in the amount of variance explained (whole model R^2) relative to the model without the SST term. Whole model R^2 was calculated following Xu (2003). All analyses were performed in R version 4.1.2 (R Core Team 2021).

To help interpret our results, we fit von Bertalanffy growth curves and simple linear models to the relationship between body length and weight separately to data collected during the cold 2006–2013 period and the warm 2014–2019 period. We then visually compared the fits to the warm and cold periods. Finally, we investigated whether estimated changes in pollock weight-at-age would have a meaningful impact on total biomass per recruit (BPR), spawning biomass per recruit (SBPR), or yield per recruit (YPR) under equilibrium conditions. We calculated per-recruit reference points under a fishing mortality rate ($F_{40\%}$) that reduces long-term SBPR to 40% of the unfished SBPR (SBPR$_{40\%}$). Calculations were based on age-specific natural mortalities, age-specific fishery selectivities, female maturity at age, and a 50% sex ratio as in Ianelli et al. (2021), together with temperature-dependent weight-at-age anomalies (Fig. 3, on the log scale) for converting numbers to biomass. The resulting weight-at-age anomalies at a given temperature were added to the long-term average log(weight-at-age) from the survey (Ianelli et al. 2021) and were back-

Fig. 3. Estimated smoothed effects of April–June sea-surface temperature (SST, °C) on scaled log(weight-at-age) by age class estimated by a General Additive Mixed Model (GAMM) that included an SST-by-age class interaction, conditional on all other variables (location and time of sampling) held constant. Rug along bottom axis shows SST observations, and grey band shows confidence interval. Figure created using package visreg (Breheny and Burchett 2017). [Colour online.]
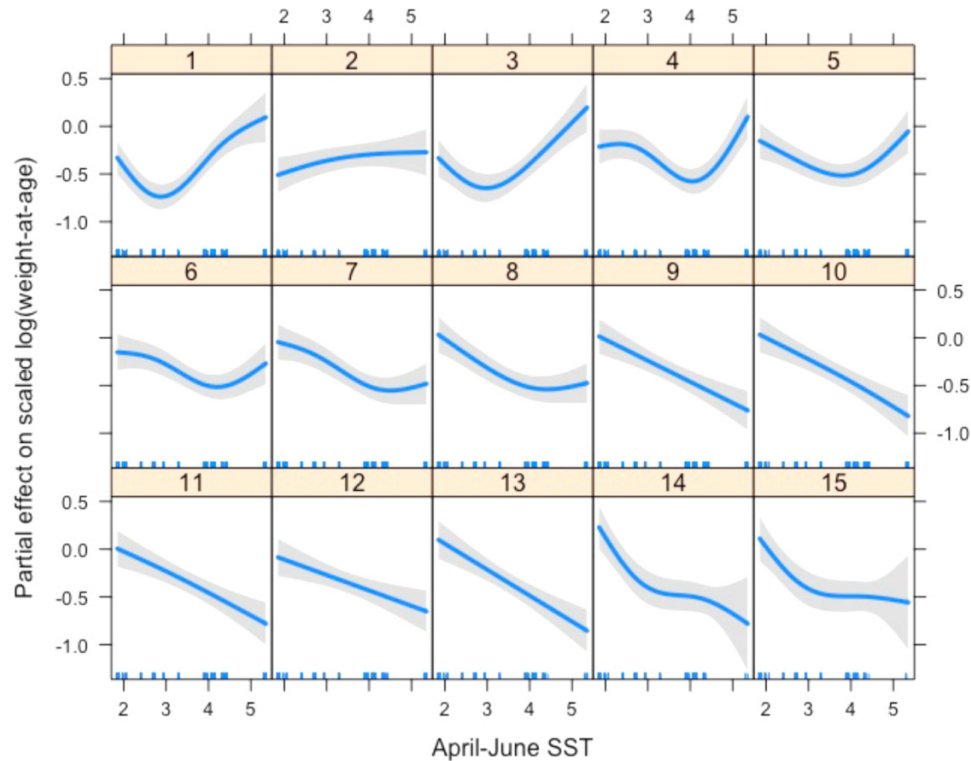
transformed to obtain a temperature-dependent weight-at-age for converting age-specific spawners per recruit to SBPR. To illustrate the effects of shifting weight-at-age, we computed proportional changes in each reference point at a given temperature, relative to the base case of assuming average weight-at-age, denoted as $\Delta BPR_{40\%}$, $\Delta SBPR_{40\%}$, and $\Delta YPR_{F40\%}$. We note that the $F_{40\%}$ rule approximates the current harvest control rule for pollock when the absolute biomass is above a spawning stock biomass threshold, but does not account for the sloping harvest control rule that reduces fishing mortality rates below the threshold (Ianelli et al. 2021). Moreover, we make the simplifying assumption that fishery weight-at-age is the same as survey weight-at-age because survey data were used to estimate weight at age anomalies. While this is unrealistic for EBS pollock due to differences in seasonal timing of the survey and fishery, among other factors (Ianelli et al. 2021), it has little impact on the relative changes in the reference points.

Results

The model that allowed for age-specific relationships between weight-at-age and SST was much better supported by the data than the model with a single, global response to SST or the model without SST included (Table 2). The latter two models included far fewer parameters, but even accounting for the fact that each uninformative parameter can be expected to increase AIC by about 2 AIC units (Arnold 2010),

Table 2. Summary of model comparison for the three candidate models.

SST term	df	AIC_c	ΔAIC	R^2
SST-by-age class interaction	43	85 395.9	—	0.154
Global SST smooth	15	85 858.45	462.55	0.131
No SST	13	85 856.27	460.37	0.127

Note: R^2 is full model R^2 (for the fixed effect terms), and df is the degrees of freedom for each model obtained from the function $AICc()$ in package MuMIn. Both AIC_c and df are obtained from models fitted using maximum likelihood, whereas whole model R^2 is obtained from models fitted using restricted maximum likelihood.

the expected gain due to the greater number of parameters (~56 AIC units) was far less than the ΔAIC_c between the best supported and next best supported models ($\Delta AIC_c = 460.37$). This result suggests that temperature does impact pollock body size and that the relationship between pollock weight-at-age and temperature differed among ages (Fig. 3 and Table 3). Warm temperatures were associated with smaller weight-at-age in older age classes (ages 7–15). However, this relationship was reversed in most of the youngest age classes (ages 1, 3, and 4), which showed highest weight-at-age during warm years, lowest weight-at-age in intermediate years, and moderate weight-at-age during cool years. Age-2 pollock showed a slight increase in weight-at-age with increasing SST but the effect was not significant. Intermediate age classes (ages 5–6) showed an intermediate response with low weight-at-age at

Table 3. Summary of model results for the SST term from the model that was best supported by the data, which included an SST-by-age class interaction.

Age class	Effective degrees of freedom	F	p value
1	2.94	29.4	<0.0001
2	1.73	2.9	0.142
3	2.80	11.7	<0.0001
4	2.93	31.7	<0.0001
5	2.83	15.7	<0.0001
6	2.85	13.9	<0.0001
7	2.73	11.8	<0.0001
8	2.56	12.1	<0.0001
9	1.00	22.4	<0.0001
10	1.40	15.9	<0.0001
11	1.26	17.3	<0.0001
12	1.00	9.72	0.002
13	1.00	25.8	<0.0001
14	2.53	12.9	<0.0001
15	2.31	8.85	0.0001

Note: The effect of SST was significant for all age classes except age 2.

intermediate SSTs and high weight-at-age during the coldest and warmest years.

To illustrate the magnitude of observed changes, we estimated the expected change in weight-at-age due to SST, all else being equal, for young (age 3), intermediate (age 5), and old (age 8) pollock. The estimated effect of SST on log-transformed weight-at-age 3 resulted in an increase of about 0.44 standard deviations between 2 and 5 °C (Fig. 3), implying a roughly 1.2-fold increase in mean weight. At age 8, the same temperature differences resulted in a decrease of 0.49 standard deviations in log-transformed weight-at-age (Fig. 3), implying a 13.0% decrease in mean weight. SST had no effect on the weight-at-age of individuals of age 5 (Fig. 3).

The other terms included in the model, while not the focus of the current study, were also significant and worth noting. In general, weights at age were smaller to the northwest and larger to the south and southeast in nearshore areas ($F_{[13.7]}$ = 28.5, p < 0.0001; Fig. 4B). Weight-at-age increased over the sampling season, increasing quickly earlier in the year and slower later in the year ($F_{[2.40]}$ = 8.57, p = 1.28 × 10^{-4}; Fig. 4A). Weight-at-age varied among cohorts ($F_{[35.0]}$ = 29.4, p < 0.0001). The random effect of haul nested in year had a standard deviation of 0.28 and the residual standard deviation was 0.85.

The estimated changes in weight-at-age with temperature had a modest impact on SPR-based reference points under fishing at $F_{40\%}$ (Fig. 6). Compared to the base case, positive weight-at-age anomalies of older age classes at relatively low temperatures (Fig. 3) resulted in a 10% and 16% increase in $BPR_{40\%}$ and $SBPR_{40\%}$, respectively. At warm temperatures, $BPR_{40\%}$ and $SBPR_{40\%}$ also increased because positive weight-at-age anomalies of the highly abundant younger age classes compensated for the lost biomass resulting from smaller weight-at-age in the older age classes. Unlike at the coldest temperature, $\Delta SBPR_{40\%}$ was considerably smaller than

$\Delta BPR_{40\%}$. Both metrics decreased at intermediate temperatures (3.8–4 °C; Fig. 6). Proportional changes in YPR under fishing at $F_{40\%}$ were generally much smaller with the largest change, a 4.7% increase, occurring at the warmest temperature.

Discussion

Our results indicate that temperature influences pollock weight-at-age (Fig. 3), but the sign of that effect varies among age classes, with younger age classes positively influenced by temperature and older age classes negatively influenced. The observation that temperature influences size-at-age is consistent with observations from many taxa that warmer temperatures are associated with smaller adult body sizes (Daufresne et al. 2009; Gardner et al. 2011; Sheridan and Bickford 2011). Climate-associated body size declines have been observed in other marine fishes (Baudron et al. 2014; van Rijn et al. 2017; Shapiro Goldberg et al. 2019), though not all marine fish species get smaller with increasing temperature (Audzijonyte et al. 2020). Our results provide evidence for a negative impact of warm SSTs on the adult body size of a species of high commercial importance. Reduced weight-at-age of adult pollock may reflect smaller length-at-age, reduced body condition, or reduced reproductive investment, with potential implications for survival and reproductive capacity. If the Bering Sea continues to experience the exceptionally warm, low-ice conditions observed from 2014 to 2019, as has been predicted (Hermann et al. 2019), continued monitoring of trends in pollock body size and their implications for the fishery and ecosystem will be important.

The MTE and TSR both predict that warmer temperatures result in faster juvenile growth rates and smaller adult body sizes (Brown et al. 2004; Kingsolver and Huey 2008). Each of these predictions has been documented separately; that is, studies have reported either higher juvenile growth rates (e.g., Thresher et al. 2007; Rogers et al. 2011; Huss et al. 2019) or smaller adult body sizes (Gardner et al. 2011; Sheridan and Bickford 2011). Faster growth rates should logically result in larger juvenile body sizes (Huss et al. 2019). Interestingly, however, the simultaneous increase in body size of young individuals and decrease in body size of older individuals, as we observed for Bering Sea pollock, have not been widely documented. A recent study from the Northeast Atlantic states that it is the first to document both larger younger and smaller older individuals (Ikpewe et al. 2020). Our study provides evidence that warming is resulting in faster growth rates and smaller adult body sizes in one of the largest food fisheries in the world, with important implications both for fisheries management and for the response of boreal and subarctic fisheries to future climate conditions.

Identifying the mechanistic relationship between temperature and body size is beyond the scope of our study. The fact that we observed opposite responses to SST for young and old age classes could suggest that a direct effect of temperature on metabolism and growth is a more likely explanation than an indirect effect via shifting species interactions, but some role of shifting species interactions is hard to rule out. In addition to metabolism and growth, temperature influences

Fig. 4. (A) Effect of the tensor product interaction between latitude and longitude on weight-at-age. Strong positive effects (larger weight-at-age) are shown in warm colours (red and orange) and strong negative effects (smaller weight-at-age) in cool colours (blue and green). The outline of the coast is shown in black with land shown in white, and areas outside the survey area without data are shown in grey. (B) Partial effect of day of year on scaled log(weight-at-age). Rug along bottom axis shows SST observations, and grey band shows confidence interval. Figures created using package visreg (Breheny and Burchett 2017). Mapping details as for Fig. 1. [Colour online.]
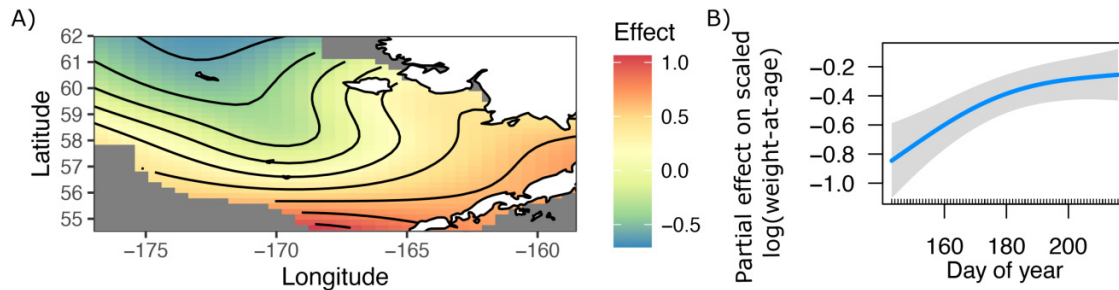
species interactions and prey availability and quality, making it difficult to tease apart their potentially interacting impacts on body size (Gardner et al. 2011; Ohlberger 2013). For example, warm temperatures can result in reduced young-of-year pollock body condition by increasing metabolism such that food requirements outpace prey availability and (or) quality (Rogers et al. 2020). The positive relationship between weight-at-age and temperature for younger age classes in this study suggests that prey availability for these age groups is generally sufficient to support both their increased metabolism and increased growth, whereas older fish may be unable to compensate for increased metabolic costs at higher temperatures. An explanation for how shifting species interactions could explain the opposite responses in young and old age classes is less obvious but cannot be ruled out. For example, different availabilities of forage fishes during warm versus cold conditions might impact adult pollock, which rely on piscivory to a greater extent than do juveniles (Dwyer et al. 1987). Given the potential for the many levels of temperature impacts to interact, the mechanistic explanation for the impacts of temperature on body size could be complex and contingent on the broader ecological context of any given warm period. Nonetheless, future work to determine the mechanisms underlying the patterns that we describe could help to predict how pollock will respond to future warming and is therefore likely prudent.

Our study focused on weight-at-age because of the potential for changing weight-at-age in response to warming to influence the accuracy of the conversion of the estimated number of pollock from the assessment model to allowable catch in biomass. However, changing weight-at-age could reflect changes in structural growth (i.e., length-at-age) or changing body condition (weight-at-length). Separate fits of a von Bertalanffy growth curve to data collected during the cold 2006–2013 period and the warm 2014–2019 period suggest that the growth rate, k, was higher during the warm period (0.235) than the cold period (0.195) and adult size, L_∞, was lower (621 mm in warm vs. 697 mm in cold) (Fig. 5A). In contrast, the relationship between pollock weight and length did not appear to differ meaningfully between the 2006–2013 cold

period and the 2014–2019 warm period (Fig. 5B). These patterns suggest that the observed effects for weight-at-age do not result from poor adult condition in warm years. In fact, pollock condition has been documented as being generally high during warm years (Boldt et al. 2015), including 2016–2019 (Grüss et al. 2020, 2021), so adult prey limitation in the warm period does not seem to explain their lower weight-at-age. Taken together, these lines of evidence suggest that a direct effect of temperature on growth seems a more likely explanation of the relationships that we observed between SST and weight-at-age, consistent with predictions from the MTE and TSR.

We account for spatial variation in weight-at-age by including a spatial term in our model, but given the relationship between age-specific distributions and temperature (Kotwicki et al. 2005; Thorson et al. 2017), it could be difficult to fully separate the effect of temperature from that of spatial variation. Previous work has shown that pollock distributions are influenced by temperature, for example, shifting northward and inshore during warm years (Kotwicki et al. 2005; Thorson et al. 2017). The spatial effect in our model was shared among all years in the study, so differences in distributions in warm versus cold years could result in the models overestimating the overall spatial variation in weight-at-age and underestimating interannual differences.

Our study, which focuses on SST in the important spring–early summer period prior to the start of the bottom trawl survey, is largely consistent with recent work showing that young age classes of pollock have elevated growth rates during warm years. Previous work on age-0 pollock in the EBS has shown that production of larvae is strong during spring in warm years (Hunt et al. 2011) but that the availability of high-quality prey tends to be low during the late summer and fall of warm years (Coyle et al. 2011), which leads ultimately to lower overwinter survival (Moss et al. 2009; Heintz et al. 2013) and lower recruitment (Mueter et al. 2011). The positive association between weight-at-age and spring–early summer SST in young age classes (Fig. 3) suggests that ages 1, 3, and 4 pollock also have higher growth rates in warm years. Whether the survival of young pollock will be similarly con-

Fig. 5. (A) von Bertalanffy growth curves (solid lines) fitted to data collected during either the cold 2006–2013 period (black) or the warm 2014–2019 period (grey). Growth rate, k, was 0.195 in the cold period and 0.235 in the warm period, while adult size, L_∞, was 697 mm in the cold period and 621 mm in the warm period. Individual points are jittered within an age along the x axis to allow for better visualization. (B) The linear relationship (solid line) between the logarithms of pollock weight (g) and length (mm) for data collected during either the cold 2006–2013 period (black) or the warm 2014–2019 period (grey). The slopes and intercepts were similar for both periods: -12.4 and 3.08 for the cold versus -12.0 and 3.00 for the warm. Points show individual data points in both panels A and B.
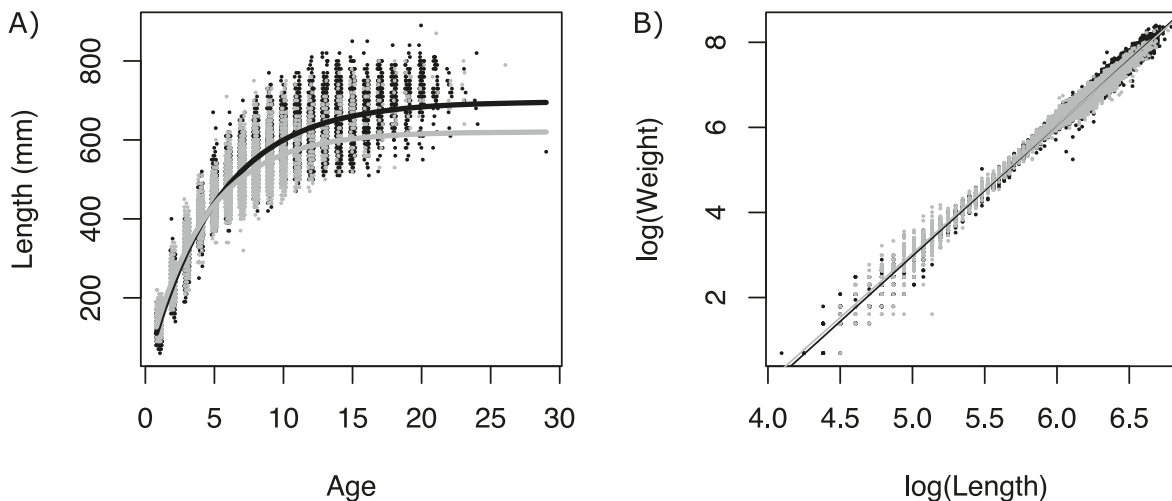
strained by food availability in warm years could determine the implications of elevated growth rates at the population level. Nonetheless, our results suggest that warm temperatures that induce high juvenile growth rates also result in smaller adult sizes. This differing response among age classes in the same population highlights the complex consequences that climate change is currently having on fishes and the fisheries they support.

Smaller adult body sizes in fishes can have negative consequences for ecosystem services, including reduced productivity and fisheries yield and (or) profit (Law 2000; Ohlberger et al. 2020; Oke et al. 2020), reduced population stability and climate resilience (Hsieh et al. 2010), shifting species interactions (Audzijonyte et al. 2013), and increased susceptibility to predators (Audzijonyte et al. 2013). In our study period, the most dramatic warming occurred only in the final five years (2014–2019), which were preceded by a cool period. Yet, the changes observed were already substantial; all else being equal, we estimated that at 5 °C young (age 3) individuals were 124% the weight they would be at 2 °C, whereas old (age 8) individuals were 86.9% their weight at 2 °C (Fig. 3). As warming continues and cold periods become less frequent, the negative relationship between temperature and adult body size might become more pronounced. Already, the reduced weight-at-age of older age classes could have important ecological or economic implications. Unusually, small pollock were a concern noted by fishers in the 2020 B-season (Ianelli et al. 2020). Interestingly, a recent study by Wootton et al. (2022) showed that in experimentally warmed zebrafish (*Danio rerio*) populations maintained for six generations, increased reproductive allocation at earlier ages in faster growing individuals was a better explanation for smaller adult body sizes than increased metabolism, which was elevated

only in early generations. If smaller adult body size in pollock is also associated with increased reproductive investment at earlier ages (Angilletta et al. 2004), estimates of biological reference points linked to spawning biomass could be affected.

The magnitude of the effect of SST on weight-at-age can also be demonstrated from the raw data. Our dataset included four years with April–June SST below 2 °C (1999, 2008, 2010, and 2012) and two years above 5 °C (2016 and 2019). Mean weights at age 3 were 220.1 g when April–June SST was below 2 °C and 283.9 g above 5 °C, whereas at age 8 mean weights were 1089 g below 2 °C and 851.4 g above 5 °C. The loss of weight-at-age was even more dramatic for ages 9–15 than for age 8 (Fig. 3). Although older age classes tend to make up a relatively small proportion of the catch compared to intermediate ages that showed little influence of SST on weight-at-age (ages 8–11 are on average 13% of the catch compared to 72% for ages 4–7 (Ianelli et al. 2020)), a per-fish loss of over 200 g in older age classes could result in considerable foregone biomass in the fishery or potentially influence the types of products that can be made from smaller fish. Critically, body size and life span both generally decline with warming (Gillooly et al. 2001; Munch and Salinas 2009), so the loss of per-fish biomass could be compounded by a decline in the proportion of older, larger fish, though the assessment does not currently show evidence of declining age in the surveys or fishery (Ianelli et al. 2020).

Despite substantial changes in individual weight-at-age, the effects of changing temperatures on per recruit reference points were relatively moderate (Fig. 6) due to the opposite effects of temperature on the weights of younger and older age classes (Fig. 3). The largest change from the base case was associated with spawning biomass at the coldest temperature, increasing $\mathrm{SBPR}_{40\%}$ by 16% compared to a 10% increase

Fig. 6. Proportional changes in biomass per recruit (ΔBPR), spawning biomass per recruit (ΔSBPR), and yield per recruit (ΔYPR) under an $F_{40\%}$ harvest control rule that reduces spawning biomass to 40% of the unfished spawning biomass. Changes reflect the impact of temperature on age-specific weight-at-age anomalies relative to the base case of average weight-at-age (Base) and are shown over the observed range of mean April–June sea-surface temperatures (SSTs, °C) in the eastern Bering Sea. [Colour online.]
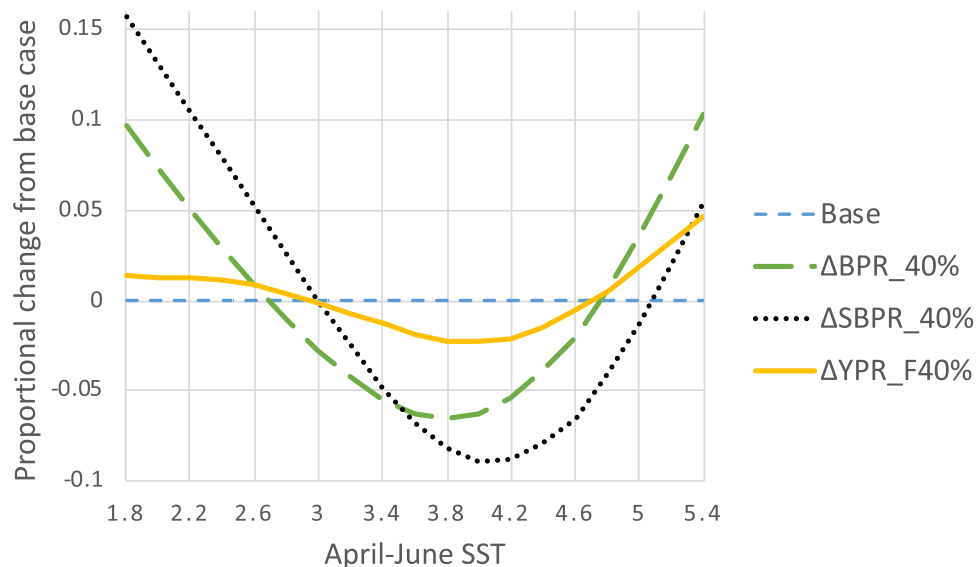
in $BPR_{40\%}$. The former was more strongly affected by above average weights of older age classes because older age classes make up a much larger proportion of spawning biomass compared to total biomass. At warm temperatures, positive anomalies in weight-at-age of younger fish resulted in a larger increase in $BPR_{40\%}$ compared to $SBPR_{40\%}$. The effects of changing weight-at-age on YPR were considerably dampened compared to the effects on biomass reference points. This can be attributed to compensatory changes in $F_{40\%}$ resulting from changes in the age-specific biomass composition. For example, at the coldest temperature, $F_{40\%}$ was much lower than under the base case to allow more fish to reach older ages, which make up a larger proportion of the spawning biomass than under the base case. The effect on $YPR_{40\%}$ was highest at the warmest temperatures, when more of the biomass consists of younger fish and the population can be fished at a higher rate.

The magnitude of shifts in weight-at-age observed during the study period is substantial enough that taking the age-specific impacts of temperature on weight-at-age into consideration could influence management decisions, although the changes in YPR were all under 5%. Our analysis made several simplifying assumptions that may limit its real-world utility. In particular, the population is not at equilibrium and has indeed a highly variable age structure (Ianelli et al. 2021). Moreover, temperatures fluctuate from year to year and on longer time scales, which can result in strong cohort effects, as well as effects on weight-at-age across ages in a given year. In addition, temperature variations are likely to affect other age-specific processes such as mortality (Gislason et al. 2010) and maturity (Berrigan and Charnov 1994), thereby further modifying the effects of temperature on pollock biomass and potential yield.

Our period of study was only 21 years and would have captured a limited number of pollock generations. Pollock begin to mature around age 3, with a majority of individuals mature by age 4 (Ianelli et al. 2020), so the maximum possible number of generations in our study period would be around 6.5. Any long-term or evolutionary impacts of prolonged warm periods thus remain unclear. Moreover, our study period included a series of cool years from roughly 2006 to 2012, so many of the individuals in our study would have experienced at least some cool years, especially those in older age classes. It remains to be seen whether the patterns that we observed will continue or become more pronounced in future generations experiencing warmer or exclusively warm conditions.

Conclusions

Our results have implications for fisheries management in the EBS as well as other boreal and subarctic ecosystems. The pollock stock assessment requires assumptions about future pollock body size to convert allowable catches from abundance to biomass and to assess stock status under different fishing scenarios (Ianelli et al. 2020). The relationships identified here, along with projections of future SST, could provide improved predictions of future weights-at-age beyond the current use of recent averages (Ianelli et al. 2020). An important caveat arises due to the seasonal differences in pollock weight-at-age (Ianelli et al. 2020), which also complicate the conversion from abundance to biomass. Our study focused on weight-at-age estimated during the summer bottom trawl survey, which differs from weight-at-age in the fishery as the fishery is prosecuted over an extended period and targets spawning aggregations in the spring. An important next step in accounting for the relationship between body size

and temperature could be improved understanding of age-specific responses to temperature across seasons and sampling designs.

Given that the estimated relationships between SST and body size were age-specific, the effects of temperature on future biomass will critically depend on age structure. Therefore, the consequences of changing temperatures on pollock biomass dynamics are best evaluated within the context of an age-structured assessment model. A fuller understanding of how temperature and body size interact in pollock and other species could help inform expectations of how stocks and fisheries will respond to future climate conditions in the changing Bering Sea ecosystem, where warming and loss of sea ice are expected to continue (Hermann et al. 2019).

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Data availability

All data used in the current manuscript were obtained from publicly available sources. An archived version of data and code is available at https://doi.org/10.5281/zenodo.7063333.

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