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Effects of climate and demography on reproductive phenology of a harvested marine fish population

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Abstract

Shifts in phenology are a well-documented ecological response to changes in climate, which may or may not be adaptive for a species depending on the climate sensitivity of other ecosystem processes. Furthermore, phenology may be affected by factors in addition to climate, which may accentuate or dampen climate-driven phenological responses. In this study, we investigate how climate and population demographic structure jointly affect spawning phenology of a fish species of major commercial importance: walleye pollock (Gadus chalcogrammus). We use 32 years of data from ichthyoplankton surveys to reconstruct timing of pollock reproduction in the Gulf of Alaska and find that the mean date of spawning has varied by over 3 weeks throughout the last >3 decades. Climate clearly drives variation in spawn timing, with warmer temperatures leading to an earlier and more protracted spawning period, consistent with expectations of advanced spring phenology under warming. However, the effects of temperature were nonlinear, such that additional warming above a threshold value had no additional effect on phenology. Population demographics were equally as important as temperature: An older and more age-diverse spawning stock tended to spawn earlier and over a longer duration than a younger stock. Our models suggest that demographic shifts associated with sustainable harvest rates could shift the mean spawning date 7 days later and shorten the spawning season by 9 days relative to an unfished population, independent of thermal conditions. Projections under climate change suggest that spawn timing will become more stable for walleye pollock in the future, but it is unknown what the consequences of this stabilization will be for the synchrony of first-feeding larvae with production of zooplankton prey in spring. With ongoing warming in the world's oceans, knowledge of the mechanisms underlying reproductive phenology can improve our ability to monitor and manage species under changing climate conditions.

KEYWORDS

age truncation, hatch dates, ichthyoplankton, larval fish, match-mismatch, recruitment, spawning, temperature, walleye pollock

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1 | INTRODUCTION

Shifts in phenology are among the most widely documented responses to changes in climate (Parmesan & Yohe, 2003; Poloczanska et al., 2013), with complex consequences for population, community, and ecosystem-level dynamics (Edwards & Richardson, 2004; Visser, Noordwijk, Tinbergen, & Lessells, 1998). Changes in the timing of reproductive events, in particular, can be critically important, as they determine conditions encountered during early life stages of offspring. In marine systems, many fish species exhibit strong seasonal patterns of spawning, often adapted such that first-feeding larvae overlap with the rapid increase in primary and secondary production in spring (Cushing, 1969). Variation in the timing of spawning relative to springtime conditions can have consequences for offspring survival. If larvae arrive too early, there may be insufficient zooplankton prey (match-mismatch dynamics: Cushing, 1990, Durant, Hjermann, Ottersen, & Stenseth, 2007) or unfavorable abiotic conditions, whereas if they arrive too late, larvae will be small relative to codeveloping predators and competitors (Bailey & Houde, 1989; Pope, Shepherd, & Webb, 1994). Changes in the timing of spawning can thus alter predator-prey dynamics, and, as the majority of lifetime mortality often occurs in the first weeks of life (Houde, 1987; Leggett & Deblois, 1994), can affect eventual recruitment success (Ohlberger, Thackeray, Winfield, Maberly, & Vollestad, 2014).

Spawning phenology has been shown to be sensitive to temperature in many fish species (Carscadden, Nakashima, & Frank, 1997; McQueen & Marshall, 2017). In general, warmer temperatures speed the rate of ovarian development and result in earlier onset of spawning in laboratory-held fish (Kjesbu et al., 2010); however, warmer than optimal temperatures may also delay spawning through delayed ovarian development (Tveiten & Johnsen, 1999; Wright, Orpwood, & Boulcott, 2017). While many studies have found relationships between temperature and spawn timing in the field, responses vary, even among populations of the same species. For instance, Hutchings and Myers (1994) found that two stocks of Atlantic cod (Gadus morhua) varied in their response to temperature, with one stock spawning earlier in warm years, and the other spawning earlier in cold years, with the latter presumably due to a temperature-induced delay in spawning migration from warmer waters. A further study found no effect of temperature on multiple stocks of Atlantic cod and haddock (Melanogrammus aeglefinus) (Morgan, Wright, & Rideout, 2013). The patterns and presumed mechanisms linking changing temperatures to spawn timing thus appear to differ among species and stocks, precluding general conclusions about thermal effects on spawn timing. Furthermore, organisms may have unique thresholds in their phenological responses related to physiological constraints, local adaptations, or behavioral plasticity, which could result in nonlinear thermal responses. Whether or not temperature-driven shifts in spawn timing are adaptive for a species will depend on the thermal sensitivity of other ecosystem processes (Thackeray et al., 2016), such as the onset and rapid increase in primary and secondary production during springtime, and resulting phenological synchrony or asynchrony of larval fishes with their prey (Kharouba et al., 2018).

While climate-related shifts in phenology are common, other factors may also play a role in determining the timing of life-cycle events. In the case of the spawning of fishes, demographic structure has been shown to be important in a number of species (Wright & Trippel, 2009), ranging from forage fishes such as herring (Clupea harengus; Lambert, 1987, Slotte, Johannessen, & Kjesbu, 2000) and capelin (Mallotus villosus; Carscadden et al., 1997), to gadids, including Atlantic cod and haddock (Hutchings & Myers, 1993; Morgan et al., 2013). In general, larger or older fish tend to spawn earlier, and over a longer duration, than smaller or younger fish; however, this is not true for all species (Morgan, 2003) or stocks (Hutchings & Myers, 1993; Morgan et al., 2013). Physiological and behavioral mechanisms may be responsible for age- or size-related differences in the timing and duration of spawning, which should ultimately reflect tradeoffs to maximize lifetime fitness. Changes in age- or size-structure can thus affect both the timing and duration of reproduction at the population level.

Demographic structure varies naturally with stochastic births and deaths, especially for species with high variation in recruitment, but age structure can also be shaped by human activities in the form of harvesting. In general, increased mortality reduces the mean age of a population, and this effect is strengthened if older individuals are targeted through size-selective harvesting (Barnett, Branch, Ranasinghe, & Essington, 2017). In addition to the pure effect of removals on age structure, there is potential for evolutionary change in spawner age structure through selection for maturation at earlier age or smaller size (reviewed in Wright & Trippel, 2009). Depending on the sensitivity of spawn timing to demography, demographic change could decouple spawn timing and larval first feeding from temperature-driven changes in the phenology of other spring events such as phytoplankton blooms and zooplankton production (Tillotson & Quinn, 2018). Furthermore, demography-induced reductions in spawning duration could increase the risk of a mismatch as firstfeeding larvae are delivered into the environment over a contracted period, which can increase variation in recruitment (McGilliard, Punt, Hilborn, & Essington, 2017; Mertz & Myers, 1994). A comprehensive understanding of how multiple processes affect reproductive phenology is necessary for forecasting shifts in spawn timing under future climate change, including potential interactions of warming with other factors such as harvesting.

In this study, we investigate how spawn timing has shifted over warm and cool periods, and through large demographic shifts in age structure in a commercially important marine fish, walleye pollock (*Gadus chalcogrammus*) in the Gulf of Alaska. Analyses are based on an exceptional 32-year time series of larval fish size, age, and abundance and validated with maturation data from spawning females. Using these data, we are able to test for effects of climate and demography on both mean spawn timing and duration of the spawning season, and produce forecasts of spawn timing under different scenarios of warming and fishing mortality rates. Finally, we discuss how shifts in spawn timing are relevant for both the biology and management of this species.

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2 | MATERIALS AND METHODS

2.1 | Study system

Walleve pollock (hereafter pollock) is a gadid of major commercial importance in the North Pacific Ocean. In the Gulf of Alaska (GOA), pollock support a \$30-40 million dollar fishery (ex-vessel value, Dorn et al., 2017), with a significant portion of the catch taken in winter as a roe fishery. The primary spawning ground for pollock in the Gulf of Alaska is Shelikof Strait, a deep channel between Kodiak Island and the Alaska Peninsula, where pollock congregate in late winter to spawn (Figure 1). Pollock mature at age 3-4 and can live up to 22 years, although individuals older than age 10 are uncommon (Dorn et al., 2017). Females are multiple-batch spawners, releasing roughly 10-20 batches of eggs over a period of 3 weeks or more (Hinckley, 1990). Eggs incubate at depths of 150-250 m for approximately 2 weeks before rising toward the upper 50 m of the water column as larvae (Kendall, Incze, Ortner, Cummings, & Brown, 1994). Larvae become entrained in the Alaska Coastal Current and drift toward the southwest as they develop, resulting in large patches of larvae downstream of Shelikof Strait in May.

2.2 | Larval data collection

Since 1979, researchers at the Alaska Fisheries Science Center's Ecosystems and Fisheries-Oceanography Coordinated Investigations (EcoFOCI, formerly FOCI) program have been studying the early life stages of pollock in the Gulf of Alaska. In the earlier years, 2–3 surveys were conducted each spring (April–June), targeting eggs, early larval stages, and late larval stages. Sampling targeted offspring from the Shelikof spawning stock and was thus spatially focused in the area to the southwest of Shelikof Strait, where larvae are advected by the Alaska Coastal Current. Since 2002, sampling has been restricted to the late larval period only (late May–early June). For

this study, we selected only samples taken during the late larval period (May 17–June 8), and from a standardized survey region (Figure 1) to ensure consistency across years (Table 1).

Larvae were sampled using paired 60 cm bongo nets with 505- μ m mesh towed obliquely to 100 m or 10 m off bottom at shallower stations. Flowmeters were mounted in the frame of each net to determine the amount of water filtered for each tow. The contents of one net were preserved in 5% formalin for later sorting and quantitative enumeration. From the other net, larval pollock were sorted and preserved in 95% ethanol for aging. The formalin-preserved samples were processed at the Polish Plankton Sorting Center in Szczecin, Poland, where pollock larvae were identified, counted, and up to 50 larvae from each station were measured for standard length. In 1988 and 1989 larvae were sampled using 1 m² Tucker trawls with 505- μ m mesh. A comparison of length-specific catch rates in the 1 m² Tucker and 60 cm bongo nets found no significant differences between the gears (Shima & Bailey, 1994).

A subset of ethanol-preserved larvae were selected for aging by sampling approximately 10 larvae from typically 8–12 stations distributed throughout the standard survey region. Larval otoliths were removed from ethanol-preserved fish using a dissection microscope equipped with polarized light. Sagittae otoliths were mounted in clear nail polish for reading and aged using a Zeiss compound microscope at 1,000× magnification. Interpretation of daily increments followed the protocol defined in Yoklavich and Bailey (1990).

2.3 | Hatch dates and spawn timing

The general procedure for determining hatch date distributions from the larval age, length, and abundance data was as follows: (a) An agelength regression was determined for each year, (b) ages were assigned to all larvae based on length samples and station-specific catches (standardized by effort), (c) hatch dates of sampled larvae were estimated based on age and sampling day, (d) a mortality correction





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TABLE 1 Summary of ichthyoplankton survey data used to estimate spawn timing from a core sampling period and region (Figure 1). Shown are dates, number of stations sampled, number of larval lengths measured, the range of lengths (converted to live SL) and the number of otoliths read for determining larval age/size relationships in each year

Year	Mean survey date (Range)	N Stations	N Lengths	Length range (mm SL)	N Ages
1979	19 May (17—20 May)	9	143	4.9–10.1	NA
1981	23 May (21– 27 May)	86	3,992	3.5–16.3	NA
1982	25 May (23–28 May)	25	297	4.4–12.6	NA
1983	24 May (21–28 May)	48	1879	4.9–22.1	109
1985	26 May (23–31 May)	36	330	4.4–15.9	25
1987	21 May (20–22 May)	40	1,321	3.4–12.6	176
1988	29 May (21 May–06 Jun)	152	5,718	3.1–21.1	279
1989	01 Jun (29 May–05 Jun)	93	4,146	3.4–18.5	220
1990	02 Jun (30 May–05 Jun)	101	3,242	3.6–25.2	145
1991	22 May (19–24 May)	62	550	4.6–13.4	113
1992	22 May (18–26 May)	93	2,954	3.4–12.8	219
1993	29 May (26 May–01 Jun)	64	1,486	3.4–20.4	140
1994	27 May (24–31 May)	95	1617	3.6–20.8	210
1995	25 May (22–28 May)	78	2,874	3.4–18.7	309
1996	28 May (25–30 May)	96	3,948	4.4–24	200
1997	27 May (24–29 May)	88	3,024	3.4–17.7	125
1998	26 May (22–28 May)	80	1,120	2.4–20.8	131
1999	28 May (25 May–01 Jun)	67	1,094	3.4–14.6	79
2000	30 May (27 May–01 Jun)	80	3,023	3.2–22.8	128
2001	29 May (27–31 May)	75	1674	3.4–20.8	77
2002	28 May (27–29 May)	41	883	3.4–12.6	107
2003	30 May (27–31 May)	69	1,439	3.9–16.7	99
2004	28 May (24–31 May)	58	305	3.9–14.6	78
2005	27 May (25–29 May)	74	955	3.9–21.8	94
2006	27 May (25–29 May)	80	2,623	4.2–19.7	93
2007	25 May (22–27 May)	76	1701	3.4–12	97
2008	26 May (24–30 May)	75	1987	3.2–16.9	103
2009	31 May (28 May–02 Jun)	73	1822	2.9–11.8	109
2010	25 May (23–27 May)	81	2,618	3.6–15.7	109
2011	05 Jun (01–06 Jun)	51	1,343	4.4–19.7	100
2013	22 May (18–25 May)	101	2,674	3.2–13.4	100
2015	22 May (17–25 May)	80	327	3.6–11.7	132

was applied to adjust for variable ages at sampling. Spawn timing was then determined by estimating temperature-dependent egg development timing based on experimental studies. Details follow.

An age–length relationship was developed by fitting a linear mixed effects model: Age ~ a + b * Length, with a random intercept and slope by station nested within year. The random effects model was used to assign ages to all larvae with measured lengths using predictions at the year level (when available) or at the population level for years with no age samples (1979–1982). Prior to analysis, all lengths were converted from preserved (ethanol or formalin) to live lengths, using (Porter, Brown, & Bailey, 2001; Theilacker & Porter, 1995):

LSL =	= 0.230	+ 1.02 >	PSL	(ethanol)) 1	а

$$LSL = 0.344 + 1.021 \times PSL \text{ (formalin)}$$
 1b

where LSL and PSL stand for live standard length and preserved standard length, respectively. Because only a subset of larvae at each station were measured for length, the estimated proportion of fish of each age at a station was multiplied by the standardized catch (larvae per 10 m^2) at that station. Population-level hatch date distributions were then determined by subtracting the age of each fish from the date sampled and aggregating across all stations.

Mortality rates during the larval stage are high (over 30% per day at 5 days old) and decrease with age (Bailey, Brodeur, &

Hollowed, 1996). Larvae sampled at 15 days old will have been reduced in abundance ~80% relative to if they had been sampled at 5 days old. Not accounting for larval mortality could bias estimates of hatch dates because of slight variation in the timing of the survey and ages of larvae sampled. We therefore used a mortality curve to adjust the abundance observed at each age to the predicted abundance at 5 days old: $M = 0.5488e^{-0.14Age}$, where M is the instantaneous mortality rate. This curve was estimated from 4 years of paired surveys during the larval period tracking the abundance and mortality of 3-day cohorts (Bailey et al., 1996). It is worth noting that considerable year-to-year variation in mortality rates is expected (Hjort, 1914) and has been observed (Bailey et al., 1996). We therefore also ran sensitivity tests using different assumptions about mortality to assess the importance of this correction for our estimates of spawn timing.

Spawning dates were determined by using temperature-dependent egg development rates to estimate time to hatch for each year. We compiled results from multiple laboratory rearing experiments (Blood, Matarese, & Yoklavich, 1994; Canino, 1994; Haynes & Ignell, 1983) to estimate a growing degree-day relationship for time to hatch (Neuheimer & Taggart, 2007). Results from incubations at 3.0-7.7°C were used to bracket the observed bottom temperatures in Shelikof Strait. Near-bottom temperatures measured in March-April were used to characterize the experienced thermal environment (see below).

2.4 **Environmental conditions**

To characterize the thermal environment experienced by eggs in March-April of each year, we used temperature data from a Sea-Bird Electronics temperature-depth probe (SBE-39) mounted on the headrope of a trawl net used to survey spawning aggregations of pollock in Shelikof Strait (Stienessen, McCarthy, Jones, & Honkalehto, 2017). Data were collected from March 11-April 1 at 6-39 haul locations per year, all within the Shelikof Strait and Sea Valley. The temperature at maximum gear depth was averaged across stations for each year. Highest egg densities have been observed at depths >150 m (Kendall et al., 1994); thus, data were restricted to locations which were sampled to deeper than 150 m. For years when spawner surveys were not conducted or data were unavailable (1979, 1980, 1982, 1999, 2011), bottom temperatures were estimated based on a regression with March sea surface temperatures (SST) from the NCEP Reanalysis Project (Kalnay et al., 1996; linear regression $R^2 = 0.66, n = 31$).

In lieu of temperature data at depth, sea surface temperature data from the NCEP Reanalysis Project were used to characterize thermal conditions during the fall (mean Sept.-Dec.; FallT), and winter (mean Jan-Mar; WinterT) preceding spawning, as potential factors influencing ovarian maturation and spawn timing. March surface temperatures based on NCEP Reanalysis data (MarT) and bottom temperatures from trawls (TrawlT, with missing values modeled as described above) were also considered as covariates in spawn timing models.

2.5 Spawner demographics

The age structure of the spawning population was characterized based on results from an annual acoustic trawl survey in Shelikof Strait (Stienessen et al., 2017). We calculated the mean age of fish in the spawning population, with a lower cutoff of 3 years or 4 years of age (MeanAge3p, MeanAge4p), as well as the biomass-weighted mean age (MeanBAge3p, MeanBAge4p), which is essentially the mean age of a unit of spawner biomass. Data were not available from 1982, 1987, 1999, or 2011. For these years, we estimated age composition by progressing numbers at age from the previous year, incrementing the age by 1 and assuming constant mortality across age classes. Biomass at age was interpolated by multiplying the interpolated numbers at age by mean weight at age observed the previous year. We also tested models using mean age (3+ and 4+) based on abundance at age as estimated in the stock assessment for Gulf of Alaska pollock (MeanAge3p_SA, MeanAge4p_SA; Dorn et al., 2017). The age diversity of spawners was characterized using Shannon's diversity index (Shannon, 1948) applied to either numbers (Div3A, Div4A) or biomass (Div3B, Div4B) at age for ages 3+ or 4+ (see Stige et al., 2017).

2.6 Modeling changes in spawn timing and duration

We used linear regressions and generalized additive models (GAMs) to study the effects of climate conditions and spawner characteristics on mean spawn timing as well as duration of the spawning season. Mean spawn timing was calculated as the mean of the estimated spawn timing distribution in each year. The duration of spawning was calculated as four times the standard deviation (SD) of the spawn timing distribution, capturing the number of days over which approximately 95% of spawning occurred. We tested linear models with up to two terms, including one temperature term and one age composition term. We did not consider models with more than one temperature or age term due to collinearity within those sets of variables. Age diversity of spawners was considered as a potential predictor of spawning duration, but not of mean spawning. We also tested whether the mean day of sampling should be included in the models. All subsets of models with up to three terms (one temperature term, one demographic term, and the mean day of sampling) were compared using AICc. To test for nonlinear responses, we fit and compared GAMs with the same subsets of variables. All analyses were conducted in R (R Core Team, 2017).

2.7 | Validation of spawn timing with spawner maturity data

Historically, the pre-spawning survey for pollock in Shelikof Strait (late March) has collected information on gonad maturity of sampled fish (see Williams, Kruse, & Dorn, 2016 and Stienessen et al., 2017). WILEY- Global Change Biology

These data cannot be used to reconstruct the distribution of spawning times because sampling occurs over a short-time window (6-10 days) and macroscopic maturity classification is imprecise; however, a rough indication of relative spawn timing can be estimated from the proportion of fish that are in spawning or spent stages at the time of the survey. We use analysis of these data as an external validation of our approach, expecting that in years with early spawn timing, a higher proportion of fish would have been in spawning or spent stages during the late March survey. Rather than use raw proportions of fish in spawning and spent stages, we corrected for sampling day of year effects (later sampling is more likely to encounter spawning or spent fish), and geographic effects (e.g., due to spatial variation in the maturity status of fish; Williams et al., 2016). Only fish age 3 and older were included. Following Williams et al., 2016, we fit a GAM with a binomial response SP (0 = classified as immature, developing, or pre-spawning, 1 = classified as spawning or spent) of the following form:

$$SP = s(Lon, Lat) + s(Day) + Year + haul + \varepsilon$$
, 2

where s() indicates a smooth function of day of year or location. A random effect for haul was included to account for the nonindependence of samples within hauls. Year was modeled as a categorical variable. We then used this model to predict the proportion in spawning or spent stages in each year on April 1 in the core of the main spawning ground. Data were available for 16,962 females and from 1983 to 2013, excluding 1999 and 2011. We used only data sampled from March 12 to April 1 to ensure consistency among years. Note that Williams et al. (2016) model maturity, which includes fish in pre-spawning state, thus the response variable differs from this study.

2.8 Fishing and climate change scenarios

The best model of mean spawn timing was used to predict how spawn timing could change under different scenarios of climate change and harvest mortality. Projected changes in the mean and variance of winter sea surface temperatures were taken from an ensemble average of CMIP5 models for RCP8.5, comparing the period 2006-2055 to 1956-2005 and accessed through NOAA's Climate Change Web Portal (https://www.esrl.noaa.gov/psd/ipcc/ accessed 5/23/2018; Scott, Alexander, Murray, Swales, & Eischeid, 2016). To estimate the effects of fishing on age structure of the population, we first used estimates of natural mortality and spawning weight at age from the 2017 stock assessment (Table 1.24 in Dorn et al., 2017) to estimate the stable unfished age and biomass at age distributions. We then compared these with the stable age distributions predicted under different levels of fishing mortality (F) given the age-specific fishery selectivity estimated in the stock assessment (the fishery primarily targets pollock age 4 and older, although younger fish are also harvested). Such scenarios do not capture yearto-year variation in age structure due to recruitment events but rather reflect the average long-term effect of fishing mortality on population age structure.

3 RESULTS

Data were available to reconstruct hatch dates and spawn timing of pollock in Shelikof Strait for 32 years between 1979 and 2015. Hatching of larvae typically began about April 15, peaked on May 3, and tapered off by May 18 (as measured by the 2.5%, mean, and 97.5% quantiles). Mean hatch dates varied by 24 days over the study time period (range: April 24-May 18). Including the larval mortality correction shifted mean hatch dates 0.4-2.2 days earlier relative to the mean of the uncorrected distributions.

We used a degree-day calculation to estimate temperature-dependent time to hatch of pollock eggs based on results from three laboratory studies. The best model indicated that it takes 97.9 degree-days to reach 50% hatch, with degree-days calculated using a base temperature of -2.16°C (Supporting Information Figure S1). This corresponded to incubation periods ranging from 12 to 16 days under the observed mean March bottom temperatures of 3.9-5.8°C.

By subtracting the egg incubation time from the hatch date distributions, we were able to estimate the date that pollock were spawned (Figure 2). Our data show that, on average, spawning began around April 2 (2.5% quantile), peaked on April 19, and tapered off by May 4 (97.5% quantile). The spawning period lasted just over a month on average; however, there was considerable variation from year to year in the duration of the spawning season (range: 17-57 days). Results also indicate variation in the mean date of spawning, varying by 24 days (April 10-May 4) over the period of the study. The years with earliest spawning were 1996-1997, and the years with latest spawning were 2007-2009. In general, in years when the mean timing of spawning was earlier, the spawning duration was greater (r = -0.55). Estimates of mean and duration of spawning were relatively insensitive to changes in the larval mortality rate (Supporting Information Figure S2).

Statistical models indicated that interannual variation in mean spawn timing was associated with shifts in temperature as well as shifts in spawner age structure. The best linear model of mean spawn timing included sea surface temperature in March and the mean biomass-weighted age of the spawning stock (age 3+; Table 2). A 1°C increase in March SST corresponded to a shift in the mean date of spawning by 5.0 days, with warmer temperatures leading to earlier spawning. A 1-year increase in the mean biomass-weighted age of the spawning stock led to a similar (4.5 day) advancement in mean spawn date. Together, the two terms explained 57% of the variance in mean spawn date (Supporting Information Figure S3). Models with alternative temperature and age structure covariates also explained significant amounts of variance, with the exception of FallT, which was not a significant predictor of spawn timing. To explore whether the effects of temperature or age structure might be nonlinear, we refit models using GAMs. The best model included the same terms, this time with a nonlinear effect of temperature on spawn timing, showing that the effect of temperature is strongest at low temperatures and has little additional effect above 4°C (Figure 3a,b). This model explained 70% of the variance, a significant improvement over the linear model ($\Delta AICc = 7.80$). We did not find



TABLE 2 Results of linear models (LM) and generalized additive models (GAM) of mean spawn date and spawning duration. No GAM results are shown for spawning duration as GAMs were outperformed by linear models. Values for each term are given as either estimated coefficients (linear terms) or estimated degrees of freedom (GAM smooth terms indicated by *s*()). The Δ AlCc is the difference in AlCc between the given model and the best-fitted model for that response variable. Only the top three models for each response variable and model type are shown

Model rank	MAR		MeanAge3p	MeanAge3p_SA	Med	nBAge3p	R ²		AICc	ΔAICc
Mean spawn date-Generalized additive models										
1	s(2.20	00)			-4.0	07	0.70		176.8	0.0
2	s(2.13	37)		-4.81			0.66		180.8	4.0
3	s(2.04	48)	-3.50				0.63		182.6	5.8
Mean spawn date-Linear models										
1	-5.00)			-4.4	45	0.57		184.6	7.8
2	-4.52	2	-3.96				0.54		186.9	10.1
3	-5.43	3		-5.34			0.53		187.0	10.2
Model rank	MAR	TrawlT	MeanBAge3p	MeanAge4p	Div3A	MeanSurveyDa	ite	R ²	AICc	ΔAICc
Spawning duration-Linear models										
1	9.00		5.49			2.03		0.59	220.0	0.0
2	8.60				11.05	1.76		0.56	222.2	2.2
3		12.37		7.94		2.51		0.55	222.7	2.7





FIGURE 3 Estimated effects of (a) mean spawner age and (b) March sea surface temperature (SST) on mean day of spawning from a GAM, explaining 70% of the variance

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evidence for a significant interaction between spawner age and temperature. Estimated mean time of spawning did not vary with survey timing (linear regression, p > 0.1), and including mean survey date in the best linear model selected above changed the estimated effect sizes by <5%.

The measured duration of spawning was, however, influenced by survey timing, such that years with earlier larval surveys corresponded to shorter estimated spawning durations, likely due to not sampling the latest hatched larvae. Mean survey date was thus included in all spawn duration models. The best model of spawning duration included March SST and mean biomass-weighted age of spawners (3+), and explained 59% of the variance (Table 2 and Supporting Information Figure S3). This model suggests that spawning duration is 9 days longer when surface temperatures are 1°C warmer and that a 1-year increase in mean spawner age extends the spawning duration by at least 5 days. Models that included age diversity of spawners and temperature at depth were also well supported (Table 2), with an increase in spawner age diversity corresponding to longer spawning duration. Using GAMs did not improve model fits for spawning duration models.

As an external validation, we compared our estimates of mean spawn timing to spawning status of pollock sampled during late March. In most years, only a small fraction of sampled fish were in spawning or spent stages (mean proportion *SP* across years = 0.079). In general, years with higher proportions of fish in spawning or spent stages on April 1 (as estimated from a GAM model incorporating day of year and latitude/longitude) corresponded to years with earlier estimated spawn timing based on the larval sampling (Figure 4). While the spawner data gives us only a coarse indication of the



FIGURE 4 Comparison of estimates of mean spawning date derived from larval data with the proportion of sampled fish in spawning or spent stages during the late March acoustic trawl survey. Proportions are corrected for day of year and location by using predictions from a binomial GAM fitted with those terms (see Methods), and presented as logit-transformed proportions (i.e., the transformation used in the binomial GAM). Pearson's correlation coefficient r is indicated

progression of the spawning season in a given year, interannual variation in the proportion spawned or spent during the March survey is consistent with our estimates of interannual variation in mean spawning date based on larval data (Pearson's r = -0.68, p < 0.001).

Using the best GAM, we generated predictions for mean spawn timing under different climate conditions and levels of fishing mortality (Figure 5). Under projected climate warming of 1.1°C for the western Gulf of Alaska in winter by mid-century (https://www.esrl. noaa.gov/psd/ipcc/), mean spawning date is projected to advance by only 1–2 days relative to the historical average due to the nonlinear temperature response above ~4°C. Interannual variation in temperature is expected to remain similar to historical, which means that spawn timing is likely to stabilize as temperatures warm, becoming less variable from year to year (Figure 5). Population age structure is thus likely to become relatively more important as a driver of interannual variation in spawn timing.

Variation in age structure is primarily driven by year-to-year variation in year-class strength (Supporting Information Figure S4); however, fishing mortality also alters the mean demographics. Assuming a stable age distribution, an unfished population of pollock would have a mean biomass-weighted age (3+) of 7.3 years, based on basic life-history parameters. Historically (1980-2017), fishing mortality has averaged F = 0.14/year (M. Dorn, AFSC, personal communication), which gives an estimated mean biomass-weighted age (3+) of 6.2 years, assuming a stable age distribution. The level of fishing mortality estimated to give maximum Acceptable Biological Catch (ABC) under the current management scheme results in a mean biomass-weighted age (3+) of 5.6 years, a 1.7-year reduction relative to an unfished population. Our models suggest that demographic shifts associated with sustainable harvest rates could shift mean spawn date 7 days later, and shorten the spawning season by 9 days relative to an unfished population, independent of thermal conditions (Figure 5).

4 DISCUSSION

We found clear evidence that both climate conditions and population demographics have led to changes in the reproductive phenology of pollock in Shelikof Strait, the primary spawning grounds for this commercially important species in the Gulf of Alaska. In addition to affecting the mean timing of spawning, both age structure and water temperature affected the duration of the spawning season: Spawning started earlier and lasted longer when temperatures were warmer and the spawning stock older. Based on analysis of over three decades of field data on pollock early life stages, we found that the response to temperature was nonlinear, with strong effects of cold temperatures on timing of reproduction, but relatively little effect of warming above the long-term average. While shifts in phenology are one of the most widely documented responses to changes in climate (Poloczanska et al., 2013), our study highlights nonlinearities in phenological responses, as well as the importance of factors beyond climate which affect phenological traits.

This study presents the first comprehensive analysis of variable spawning phenology for pollock. Previous studies focused in the

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Bering Sea have suggested that pollock spawn timing may be sensitive to temperature (Haynie & Pfeiffer, 2013; Smart, Duffy-Anderson, & Horne, 2012) and documented geographic variation in spawn timing among spawning groups experiencing different thermal regimes (Bacheler, Ciannelli, Bailey, & Duffy-Anderson, 2010; Jung, Kang, Kim, & Kendall, 2006), but the degree and form of thermal sensitivity was not quantified, and other (e.g., demographic) effects were not considered. In the Gulf of Alaska, some evidence for variation in spawn timing among years has been presented (Ciannelli, Bailey, Chan, & Stenseth, 2007; Yoklavich & Bailey, 1990); however, consideration of mechanisms has fallen outside the scope of previous studies. Often spawn timing has been assumed to be fixed in time due to lack of data (Picquelle & Megrey, 1993). The strength of our study is that we used comprehensive information gained from over three decades of surveys, at-sea process studies, laboratory experiments, and analyses on early life-history stages. These allowed us to account for variable growth, egg development rates, mortality by age, and sampling dates, to reconstruct distributions of spawn dates across a range of climatic and demographic conditions.

Nonlinearity in the response of reproductive phenology to temperature suggests that warmer waters advance the date of spawning, but a threshold is reached, whereby increased warming has no additional effect on spawn timing. This threshold could reflect a physiological constraint, such as a minimum number of days needed for maturation, or could indicate a temperature cue for initiation of spawning. Unlike its congener, Atlantic cod, for which spawning date has been shown to be a function of degree-days since the autumn equinox (Kjesbu et al., 2010), it is not known what the cues are for spawning in pollock. We found that March sea surface temperature was the best thermal predictor of both mean spawn timing and spawn duration, outperforming models with measures of thermal exposure in the fall and winter prior to spawning. This suggests that it is temperatures during the final stages of maturation that most strongly determine the spawning time and duration. Surprisingly, measured March temperatures at the depths where spawning occurs were a poorer predictor of spawn timing than SST from a global reanalysis, maybe due to interannual variation in timing and location of measured thermal profiles that are not accounted for here.

We found differences in spawn timing related to the mean age of the stock, with spawning occurring earlier and lasting longer on average when the mean age was older. This likely represents agespecific differences in spawn timing, with older fish initiating spawning earlier and continuing to spawn over a longer period than younger fish. This would be consistent with findings for Atlantic cod, also a multiple-batch spawner (Kjesbu, Solemdal, Bratland, & Fonn, 1996), and haddock, for which spawning duration increases by 4-5 weeks in older fish relative to first-time spawners (Wright & Gibb, 2005). Given age-specific differences in spawn timing, a more diverse age composition would also result in a longer spawning season due to greater variance among individuals in the day that spawning is initiated, a result that is consistent with our spawning duration model. This means that changes in the demographic structure of the population can shift spawn timing and spawning duration, and subsequently alter the timing of when first-feeding larvae are in the water column.

Variability in age structure in pollock is primarily driven by occasional large year classes which dominate the biomass for successive years. For instance, the stock is currently (in 2018) dominated by the large 2012 year class, which made up 64% of the total biomass at age 5 (Dorn et al., 2017). However, fishing mortality tends to reduce the abundance of older age classes and thus the mean age (Barnett et al., 2017). For pollock, increased fishing mortality is projected to shift spawn timing to later in the season, on average, as well as contract the spawning season to a shorter time period. It is unknown to what extent spawn timing may have evolved or be evolving due to selection from fisheries (see Tillotson & Quinn, 2018), but fishing-induced shifts -WILEY- Global Change Biology

in spawn timing through demographic truncation could alter the relationship between spawning phenology and subsequent ecological conditions conducive to offspring survival (Wright & Trippel, 2009). Such consequences of shifting phenology may extend beyond the larval stage, as size at end of summer is also linked to hatch date (Cargnelli & Gross, 1996; Dougherty, Bailey, Vance, & Cheng, 2012), and may be important for size-dependent overwinter survival (Sogard, 1997), although this mechanism has not been investigated for pollock in the Gulf of Alaska.

This study illustrates one mechanism by which old, large females may be disproportionately important for recruitment success (Berkeley, Hixon, Larson, & Love, 2004; Hixon, Johnson, & Sogard, 2014; Longhurst, 2002): by increasing the length of the spawning season. By spawning over a longer duration, older spawners ensure their offspring are hatching over a broader temporal window. In environments with high variability in spring production dynamics, this bethedging strategy is hypothesized to lead to more stable recruitment dynamics (McGilliard et al., 2017; Mertz & Myers, 1994), although empirical evidence for this is so far not strong. An increase in spawning duration should also result in offspring spread over a broader geographic range (Stige et al., 2017), hedging bets in a spatial as well as temporal dimension. Given the relatively fast speed of the Alaska Coastal Current (Stabeno et al., 2016), pollock larvae are rapidly displaced from the Shelikof Strait region upon hatching to become dispersed over the GOA shelf (Hermann, Rugen, Stabeno, & Bond, 1996; Hinckley, Hermann, Mier, & Megrey, 2001); increased variance in spawn date should increase this dispersion, thus increasing the likelihood that some offspring are delivered to suitable nursery habitats given variable local oceanographic conditions across seasons and years. Finally, increased spawning duration has the potential to increase intracohort variation in offspring body size. which may also constitute a form of bet-hedging (Marshall, Bonduriansky, & Bussière, 2008): depending on the size-spectrum of predators and prey throughout the first growing season, survival of smaller or larger offspring may be favored (Pope et al., 1994). Further work is needed to determine whether changes in spawning duration through reduced mean age or age diversity may be linked to recruitment success or variation through any of these mechanisms.

As with much of the world's oceans, the Gulf of Alaska is projected to warm under climate change (https://www.esrl.noaa.gov/ psd/ipcc/). Given the nonlinear response of spawn timing to warming, we can expect that if cold years become less frequent, spawn timing will become more stable. A key uncertainty is what this will mean for larval survival. As of now, it is unknown to what extent the timing and amount of primary and secondary production will shift under climate change in the Gulf of Alaska. The western Gulf of Alaska is a downwelling system in general, and initiation of the spring phytoplankton bloom depends on stratification of the water column and solar radiation (Napp, Incze, Ortner, Siefert, & Britt, 1996). Stratification is driven not only by temperature, but also by freshwater runoff and the timing of spring storms (Napp et al., 1996; Stabeno et al., 2004). Warming can be expected to speed the development of zooplankton in spring (McLaren, 1978) and thus advance the availability of early life stages (e.g., nauplii) as prey for larval fishes; however, different zooplankton taxa differ in their lifehistory strategies and production dynamics, likely resulting in different sensitivity to warming. For instance, Neocalanus depends solely on stored lipid reserves to fuel reproduction in late winter (Miller & Clemons, 1988), whereas Calanus and Pseudocalanus also depend on spring phytoplankton production to provide energy for reproduction (Napp et al., 1996). Beyond match-mismatch dynamics with prey, the timing and intensity of spring storms may be an important factor for larval survival, as intense wind mixing during the first-feeding period has been associated with poor survival (Bailey & Macklin, 1994). Thus, whether or not the nonlinear thermal response of pollock spawn timing is adaptive will depend on the thermal sensitivity of other processes, including primary and secondary production, for which there are likely to be species-specific differences in thermal responses and thresholds.

Our estimates of spawn timing based on sampled larvae depend on a number of assumptions which could potentially bias our estimates. First, our larval sampling in late May could be underestimating the abundance of the oldest larvae, either because the oldest larvae are advected out of the study area prior to sampling, or because larger larvae are able to avoid the sampling gear. While previous work suggests that larvae up to 18 mm (approx. 66 days old) are sufficiently well sampled by both the 60 cm bongo and 1 m² Tucker nets (Shima & Bailey, 1994), catchability likely decreases with size as larval swimming abilities develop, meaning that older larvae may be able to evade the nets. We are also likely undersampling the latest hatched larvae, as larvae continue to hatch during, and likely after the survey. Possible undersampling of the earliest and latest spawned individuals, and subsequent truncation of estimated spawn timing distributions, means that we may be underestimating the interannual variation in mean spawn timing as well as spawning duration. The correspondence of our mean spawn timing estimates with shifts in the proportion of fish spawning or spent on April 1 (from the pre-spawning survey) indicates that we are capturing meaningful year-to-year variation in spawn timing.

Our models assume that egg mortality rates are constant through the season, and across years, which is clearly an oversimplification given the dynamic ocean environment. Based on a series of surveys in 1981, Kim and Gunderson (1989) found that egg mortality decreased through the season, being highest for eggs spawned before peak spawning, but it is not known whether this finding applies to other years. Presumably, egg and larval mortality rates vary throughout the season and across years as a function of predation pressure, advection, wind mixing, and the production and quality of zooplankton prey. Despite this unaccounted for variation in mortality, our results suggest that by sampling surviving larvae over a consistent temporal and spatial extent, variation in the spawning dynamics of pollock can be reconstructed.

While it is unclear how shifts in spawn timing affect pollock recruitment, there are clear implications of shifting spawn timing for the assessment and management of the pollock stock in the Gulf of

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Alaska. One of the main surveys informing the stock assessment of pollock targets the stock during the pre-spawning season. Pollock are aggregated on spawning grounds during this time and thus can be surveyed in a smaller geographic area relative to other times of the year. Currently, the pre-spawning survey takes place in the second half of March, with the aim of sampling the pollock as they mature, but prior to peak spawning (Wilson, 1994). When a majority of the fish sampled are spawning or post-spawning individuals, the abundance tends to decrease, suggesting that fish leave the spawning grounds soon after spawning (Wilson, 1994). Changes in spawn timing relative to the pre-spawning survey could thus affect our ability to accurately survey the spawning stock, biasing estimates of abundance. Such a situation may call for adjusting survey timing adaptively if a preseason forecast of spawn timing were available. The high R^2 value of our spawn timing model suggests that spawn timing could be forecast in advance using predictions of age composition and winter temperatures. The first is possible using simple demographic modeling based on age-specific natural and fishing mortality rates (Dorn et al., 2017), whereas the second could be produced by seasonal oceanographic forecasts (e.g., Siedlecki et al., 2016). Thus, the basic ecological understanding we have gained of processes underlying changes in spawn timing could be used to improve our ability to survey and assess the stock, contributing to sustainable management of this stock under climate change.

Climate change projections for marine species often focus on geographic range shifts as well as shifts in recruitment, body size, or growth. However, shifts in reproductive phenology are likely to play an important role in determining future predator-prey interactions and survival rates of early life stages. Here, we provide a model for projecting reproductive phenology for a commercially important marine fish species under future climate and fishing scenarios. The consequences of the projected changes in phenology will depend on cooccurring shifts in other ecosystem components including production of predators and prey, which are so far poorly understood. Furthermore, nonlinearities in thermal responses and co-occurring changes in phenology due to harvesting exemplify the complexities associated with anticipating future ecosystem states under climate warming. While the consequences of changes in pollock reproductive phenology are as of yet unknown, knowledge of the underlying drivers of spawn timing can improve our ability to monitor and manage species under changing climate conditions.

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SUPPORTING INFORMATION

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Graphical Abstract

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We investigate how climate and population age structure jointly affect spawning phenology of a fish species of major commercial importance: walleye pollock (*Gadus chalcogrammus*). Using data from historical larval surveys dating back to 1979, we find evidence that the timing and duration of spawning have shifted in response to changes in temperature as well as population age structure. In general, spawning occurs earlier and over a longer duration when spawners are older and temperatures are warmer.