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Loss of spawning habitat and prerecruits of Pacific cod during a Gulf of Alaska heatwave

Benjamin J. Laurel and Lauren A. Rogers

Abstract: Pacific cod (*Gadus macrocephalus*) stocks in the Gulf of Alaska experienced steep, unexpected declines following an unprecedented 3-year marine heatwave (i.e., "warm blob") from 2014 to 2016. We contend that stock reproductive potential was reduced during this period, evidenced by a combination of new laboratory data demonstrating narrow thermal hatch success (3–6 °C), mechanistic-based models of spawning habitat, and correlations with prerecruit time series. With the exception of single-year El Niño events (1998, 2003), the recent 3-year heatwave (2014–2016) and return to similar conditions in 2019 were potentially the most negative impacts on spawning habitat for Pacific cod in the available time series (1994–2019). Continued warming will likely reduce the duration and spatial extent of Pacific cod spawning in the Gulf of Alaska.

Résumé : Les stocks de morue du Pacifique (*Gadus macrocephalus*) dans le golfe d'Alaska ont connu des déclins abrupts et inattendus à la suite d'une vague de chaleur marine (ou « warm blob ») sans précédent d'une durée de 3 ans, de 2014 à 2016. Nous soutenons que le potentiel de reproduction des stocks a diminué durant cette période, comme en fait foi une combinaison de nouvelles données de laboratoire qui démontrent une étroite fourchette de températures associée au succès d'éclosion (de 3 à 6 °C), des modèles mécanistes des habitats de frai et des corrélations avec des séries chronologiques pré-recrutement. À l'exception d'épisodes El Niño d'une seule année (1998, 2003), la vague de chaleur récente de trois ans (2014–2016) et le retour à des conditions semblables en 2019 constituent possiblement les impacts les plus importants sur les habitats de frai pour la morue du Pacifique dans les séries chronologiques disponibles (1994–2019). La poursuite du réchauffement réduira vraisemblablement la durée et l'étendue spatiale du frai des morues du Pacifique dans le golfe d'Alaska. [Traduit par la Rédaction]

Introduction

From late 2013 to 2016, the Gulf of Alaska (GOA) experienced 3–4 °C above average sea surface temperature anomalies (relative to 1980–2010) associated with a reduction in winter heat flux (i.e., "warm blob"; Bond et al. 2015) and the second strongest El Niño event on record between 2015 and 2016 (NOAA 2016). The 2014 to 2016 marine heatwave is currently considered the largest warm anomaly ever recorded in the North Pacific from 1880 to present (Di Lorenzo and Mantua 2016), and the broad-scale ecosystem response to this event is still being evaluated (Walsh et al. 2018). For the Pacific cod (*Gadus macrocephalus*) fishery, these impacts have already led to substantial economic loss by way of reduced biomass in the GOA (estimated 58% reduction in survey biomass from 2015 to 2017) and an 80% reduction in the recommended acceptable biological catch for 2018 (Barbeaux et al. 2017). Continued declines in 2019 led to the closure of the federal directed fishery for Pacific cod in the GOA for 2020. Such a dramatic change in the fishery has prompted fisheries managers to better examine the links between climate anomalies and reduced recruitment for Pacific cod in an effort to improve advice for timely management actions.

Temperature impacts every life history process in marine fish, but early life stages are generally considered more sensitive to environmental conditions than older, larger life stages (Houde 1987). Within the first year of life, the embryonic egg phase generally has the narrowest thermal range for survival, likely due to a finite supply of maternally provisioned heat shock proteins for cellular repair after thermal stress (Motani and Wainwright 2015). Eggs also lack the ability to behaviorally thermoregulate, unlike juveniles and adults (Kelsch and Neill 1990). As such, these early life stages may set biogeographic boundaries and limit productive capacity for fisheries impacted by climate change (Rijnsdorp et al. 2009), although comparatively few data are available to test these hypotheses.

Optimal thermal conditions for Pacific cod eggs in the GOA have been previously unknown, although eggs have been successfully incubated across a broad temperature range (0–8 °C; Laurel et al. 2008). In the western Pacific, temperature-dependent hatch rates have been quantified and indicate Pacific cod are highly temperature-sensitive, with highest hatch success occurring between 4 and 6 °C (Bian et al. 2016). Pacific cod are also rather atypical among gadids in that they are single-batch spawners and have demersal eggs that adhere to the bottom (Alderdice and Forrester 1971; Laurel et al. 2008). Pacific cod females can therefore place eggs in thermal habitats that optimize hatch success, unlike the pelagic eggs of Atlantic cod (*Gadus morhua*) that disperse in the water column and risk advection to suboptimal habitats during incubation (Bradbury et al. 2008). Spawning locations in the Gulf of Alaska have not been mapped, but spawning is generally thought to occur from January to June (with peak spawning between February and April), at depths of 100–200 m in Alaska (Stark 2007; Neidetcher et al. 2014).

Pacific cod undertake a variety of regional seasonal migrations between summer feeding and winter spawning grounds. In

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B.J. Laurel. Fisheries Behavioral Ecology Program, Resource Assessment and Conservation Engineering Division, Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, Hatfield Marine Science Center, Newport, OR 97365, USA.
L.A. Rogers. Recruitment Processes Program, Resource Assessment and Conservation Engineering Division, Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, Seattle, WA 98115, USA.
Corresponding author: Benjamin J. Laurel (email: ben.laurel@noaa.gov).

higher latitudes around Alaska and Canada, maturing individuals move to warmer, deeper water in the fall as inshore waters cool, before returning to warmer, shallower waters in the spring and summer to feed (Bakkala 1984; Ketchen 1961; Palsson 1990; Shimada and Kimura 1994). However, these migratory patterns are reversed (moving inshore in winter and offshore in summer) at the southern extent of their range where seasonal conditions are warmer (Karp 1983; Mishima 1984; Westrheim 1984; Zhang 1984), suggesting Pacific cod distributions may be more strongly linked to temperature than depth. There also appears to be some degree of spatial–temporal plasticity in spawning dynamics. Bering Sea populations appear to adjust spawning earlier in warmer years, and spawn timing tends to occur earlier at lower latitudes on both sides of the Pacific (Neidetcher et al. 2014). For example, spawning for Pacific cod starts in December along the west coast of the continental United States and shifts to February for Canadian stocks further north (Foucher and Westrheim 1990). In the GOA and eastern Bering Sea, Pacific cod spawn later in March and April (Neidetcher et al. 2014; Stark 2007). These observations of migration and phenology are consistent with the idea that thermal habitats play an important role in Pacific cod behavior and support the widely accepted view that marine fish place eggs and larvae in environments most optimal for successful hatch and early larval survival.

In this study, we conducted new experimental work to parameterize the temperature-dependent hatch success of GOA Pacific cod and combine this relationship with seasonal water column temperature data to derive indices of spawning habitat suitability for Pacific cod over 26 years and spanning the recent marine heatwave. We then compared spawning habitat suitability with time series data on prerecruit abundance and adult recruitment over the same time range. Using this approach, we tested the following hypotheses: H_1: Pacific cod have experienced major shifts in the timing, depth, and extent of suitable spawning habitat in warm years; H_2: Pacific cod spawning habitat suitability was lower overall during extreme warm-water events (e.g., 1998, 2003 El Niño; 2014–2016 "warm blob"); H_3: Pacific cod spawning habitat suitability is a predictor of prerecruitment abundance and adult recruitment at age-3. These results are discussed in the context of spawning phenology and early warning management for Pacific cod fisheries facing future warming events in the GOA.

Methods

Laboratory experiment

An experiment testing the effects of temperature on Pacific cod eggs was conducted at the Alaska Fisheries Science Center (AFSC) laboratory in Newport, Oregon. The AFSC laboratory has captive adult brood stock collected from the GOA (Kodiak, Alaska: 57.882°N, 152.626°W) as age-0 juveniles in 2012 and 2013, as well as temperature-controlled laboratory space for incubation experiments. Environmental conditions for the mature brood stock were maintained at 7–9 °C during the summer and 2–6 °C during the spawning season.

Spawning of males (n = 3) and female (n = 1) brood stock was conducted in early March of 2016 at 4 °C to produce a fertilized egg batch following protocols described by Laurel et al. (2008). Eggs were then subdivided into incubation trays and acclimated to each temperature treatment (–1.1, 0.3, 1.9, 4.9, 9.0, 11.9, and 16.0 °C) at a rate of 1 °C·h^{-1}. After 24 h, the egg batch was divided across 21 replicate 1 L containers with 220 μm mesh bottom to track hatch success in an extended temperature incubation experiment. Eggs were volumetrically spread evenly across containers (0.5 mL per container at ~300 eggs). Estimated egg stocking densities for each beaker were adjusted to actual counts based on daily mortality and hatch counts at the end of the experiment. The mesh-bottom containers were suspended in a series of temperature-controlled, flow-through water baths (66 cm × 46 cm × 38 cm) maintained at each treatment temperature. Temperatures were maintained within 0.2 degrees of their nominal treatment during the course of the experiment. Three replicate containers were used for each temperature treatment (n = 7) for a total of 21 separate containers for egg incubation. Temperature-controlled seawater was supplied to each of the seawater baths at a rate of 2–3 L·min^{-1}. Water was exchanged daily by gently lifting and lowering containers in each seawater bath. Eggs from each replicate beaker were monitored daily thereafter to measure mortality and hatch. Eggs were considered dead when they were opaque in color. Dead eggs were counted and removed by pipette. As larvae hatched, individuals were transferred by pipette to a separate corresponding 1 L meshed beaker held at the same temperature in the same water bath. Replicate beakers of eggs continued to be checked daily until all embryos either hatched or died.

A nonlinear function was used to describe the relationship between hatch success (i.e., the proportion of eggs that successfully hatched) and incubation temperature. We considered two models with the desired properties of being dome-shaped and requiring relatively few parameters (only 3): the curve described by the Cauchy (Lorentzian) distribution, as well as a Gaussian curve (see Tsoukali et al. 2016 for a discussion of functional response). Each model was fit to observed hatch proportions within each replicate beaker, weighted by the total number of eggs in each beaker.

Spawning habitat index

The longest and most complete seasonal temperature record for the GOA exists at GAK1 (the innermost station on the Seward Line; see online Supplementary material, Fig. S1[1]), which has been maintained by the University of Alaska since 1970. Temperature measurements are taken from the surface to 200 or 250 m depth approximately monthly throughout the year and reported at discrete depths (0, 10, 20, 30, 50, 75, 100, 150, 200, 250 m). Comparison with available spring data from conductivity–temperature–depth (CTD) casts at Cape Kekurnoi in the Shelikof region (1986–1999) indicates the GAK1 measurements are similar to temperatures where prerecruit surveys were conducted (Stabeno et al. 2004). A further comparison with temperature profile data from March surveys in Shelikof Strait (2003–2019) confirms that GAK1 is capturing thermal conditions representative of a broader part of the GOA shelf (Fig. S2[1]). For this study, we use temperature data from GAK1 beginning in 1994, as measurements in January and February were uncommon prior to then. To account for variation in seasonal timing and frequency of measurements, temperature measurements were interpolated to a 1 m × 1 day grid using bivariate linear interpolation across depths and days, implemented using the Akima package in R (Akima and Gebhardt 2015).

Seasonal and depth-specific estimates of spawning habitat suitability were calculated using the interpolated temperature profiles at depth combined with experimentally derived temperature-dependent hatch success of Pacific cod eggs. An annual index was developed by taking the average of hatch success probability across depths of 100–250 m from January to April based on known spawning dynamics for Pacific cod in Alaska (Neidetcher et al 2014; Stark 2007). While water column and near-bottom temperatures at GAK1 may not precisely capture bottom temperatures for a given depth or area, this index integrates across depths and time to capture interannual variability in overall spawning habitat suitability. This index of spawning habitat suitability was then compared with subsequent measures of year-class abundance at larval, age-0, and age-3 stages, lagged as appropriate to correspond to year of hatching, as described below, using Pearson's correla-

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2019-0238.

tion coefficients. Time series were inspected for autocorrelation prior to analyses.

Prerecruit–recruitment time series

Ichthyoplankton

The AFSC conducted ichthyoplankton surveys in the GOA, with annual surveys from 1981 to 2011 and biennial surveys thereafter. Larvae were sampled primarily using paired 60 cm bongo nets with 505 μm mesh. Oblique tows were carried out from 100 m depth to the surface or from 10 m off bottom in shallower water (Matarese et al. 2003; Ichthyoplankton Information System, https://access.afsc.noaa.gov/ichthyo/). 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 at the Polish Plankton Sorting Center in Szczecin, Poland. Historical sampling has been most intense in the vicinity of Shelikof Strait and the shelf southwest of Kodiak Island during mid-May through early June (Fig. S1[1]), a time frame when Pacific cod larvae are abundant in the water column (Doyle et al. 2009). From this area and time, a subset of data has been developed into a time series of larval Pacific cod abundance by calculating the area-weighted mean catch per 10 m^2 (after Doyle et al. 2009).

Age-0 juveniles

Newly settled age-0 juvenile cod were surveyed by a 36 m demersal beach seine along the Kodiak Island coast from 2006 to present (see Laurel et al. 2017 for details). The survey targets juvenile cod over a relatively small spatial extent, but represents the only age-0 time series spanning the before and after "warm blob" years in the GOA. Seine effort is restricted to 16 fixed-site locations spread equally across two embayments on the northeast portion of the island (Fig. S1[1]). Site locations are dominated by a mix of eelgrass (*Zostera marina*), *Laminaria saccharina*, or "bare" mineral substrates (sand–small cobble) at a mean depth of 2–4 m. Seine sites were surveyed twice on successive days during two summer sampling periods, 14–21 July and 21–28 August, in each year. A total of 14 years (2006–2019) of survey data were available for this study (n = 896 seine hauls). From these data, a time series of annual Pacific cod abundance was calculated based on the average catch of age-0 cod per haul across all sites.

Age-3 recruitment

Estimates of abundance at age-3 were taken from the stock assessment model for GOA Pacific cod, which is an age-structured model fit to survey and fishery data (Barbeaux et al. 2018). Recruitment to the fishery occurs at ages 3–4, and estimates of year-class strength in the assessment model are increasingly reliable from age-3.

Results

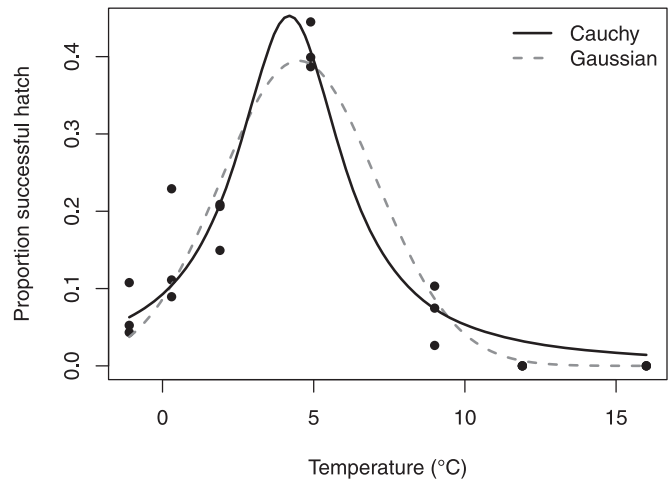
Experimental results

Hatch success in Pacific cod was highly temperature-sensitive, indicated by the narrow thermal range of proportionately higher hatch success at 5 °C and steep decline in the proportion of eggs that hatched at temperatures below 3 °C and above 7 °C (Fig. 1). Temperature (T) significantly impacted percent hatch success (H) in the statistical model (ANOVA; $F_{[6,14]}$ = 41.35, P < 0.001) and described 96% of the variation in hatch success as a continuous variable in the following Cauchy model:

$$H = \frac{0.453}{1 + \left(\frac{T - 4.192}{2.125}\right)^2}$$

A Gaussian model fit to the same data (Fig. 1) explained 95% of the variance in hatch success and had a greater residual standard error (0.74 compared with 0.67 for the Cauchy model). We used the Cauchy model to derive a spawning habitat suitability index, and the Gaussian model is presented for comparison.

Fig. 1. The effects of temperature on proportional hatch success of eggs batches from Gulf of Alaska Pacific cod (*Gadus macrocephalus*) incubated in the laboratory. Fitted lines are the results of three-parameter Cauchy (solid black) and Gaussian (dashed gray) model fits. Data are based on individual replicate 1 L beakers incubated across separate water baths (see Methods).



Spawning habitat suitability

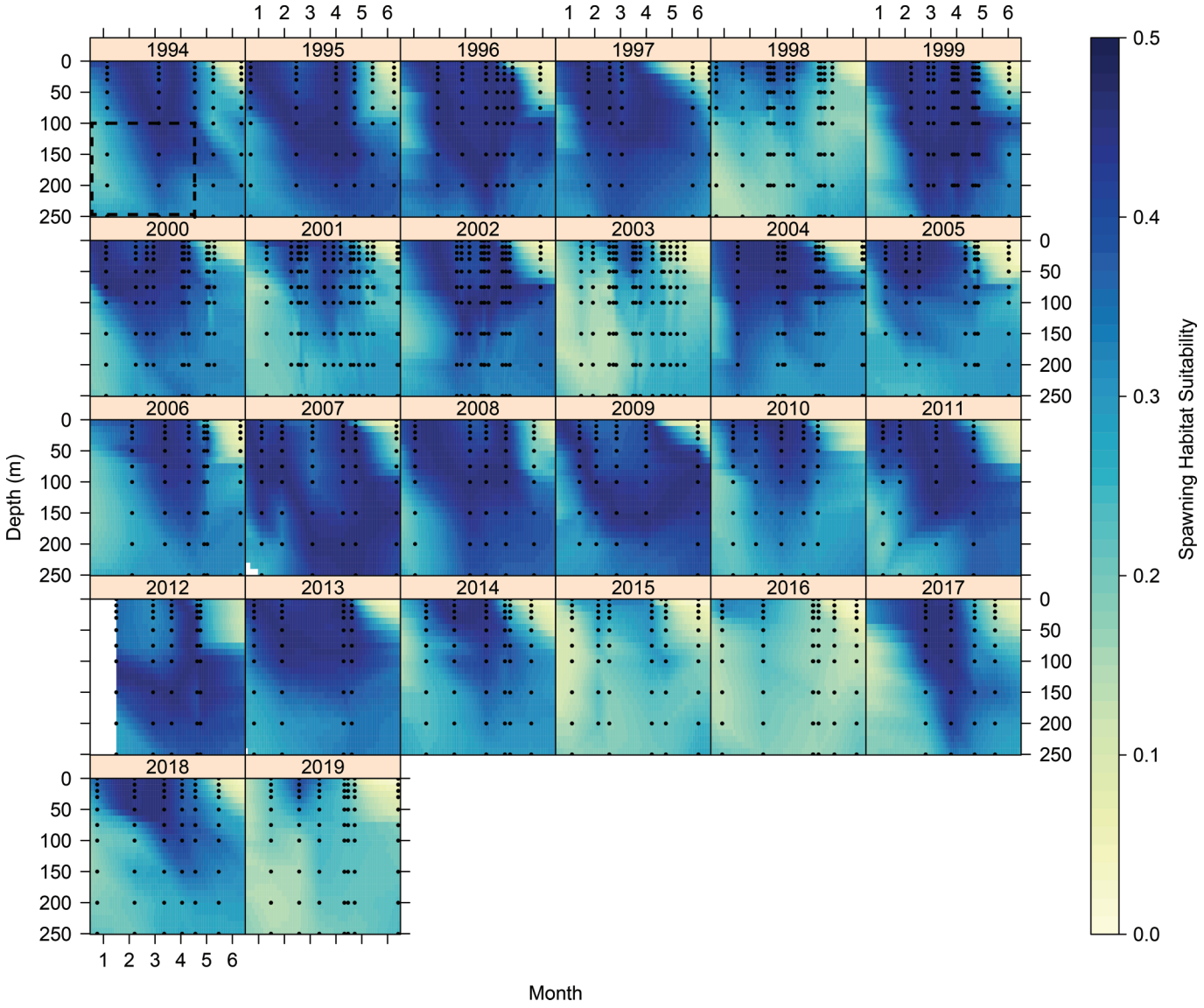
Thermal habitat for successful hatching of Pacific cod eggs has been plentiful in most years during the months of January to April in the Gulf of Alaska (Fig. 2). On average, in January, the most suitable habitat is in shallower waters down to 50 m, while deeper regions remain warmer than optimal for successful hatching. From February to April, suitable habitat extends through the water column down to 250 m. By May, the surface begins to warm and suitable habitat is restricted to only deeper waters (Figs. 2 and S3[1]).

In 2015, 2016, and 2019, suitable habitat was substantially reduced due to warm temperatures throughout the water column (Fig. 2). Based on temperatures from January to April in waters > 100 m, the probability of successful hatch in these recent warm years was 57%–59% that of an average non-heatwave year and less than half that observed in 2012, the year with the highest habitat index (Fig. 3*a*). The years 1998 and 2003 also showed reductions in habitat due to warm events, but these events were more limited in their depth (1998) or temporal extent (2003) (Figs. 2 and 3*a*). In most years, the limiting factor for hatch success was the presence of warmer-than-optimal waters, but in a few years (e.g., 2007, 2009, 2012), shallower waters in late winter were colder than the optimum for hatch success. In 2019, a return of warm conditions again reduced suitable habitat for Pacific cod eggs in the GOA. Spawning habitat suitability based on a Gaussian model fit was highly correlated (ρ = 0.98) with suitability based on the Cauchy model.

Prerecruitment abundance

Interannual variation in ln-transformed abundance of Pacific cod larvae was significantly correlated with the index of spawning habitat suitability (ρ = 0.76, p < 0.001), with fewer larvae in years when the thermal habitat was less suitable for successful hatching of eggs (Fig. 3*b*). This relationship continued to hold for subsequent life stages, including the abundance of age-0 cod measured in nearshore nursery habitats during their first summer (ρ = 0.50, p < 0.05; Fig. 3*c*) and subsequent estimated numbers of age-3 recruits to the population (ρ = 0.57, p < 0.01; Fig. 3*d*). The habitat suitability, larval, and age-0 time series did not have significant

Fig. 2. Habitat suitability for Pacific cod spawning based on temperature profiles at depth combined with experimentally derived, temperature-dependent hatch success of eggs (Fig. 1). Panels are based on temperature data interpolated to a 1 m × 1 day grid using bivariate linear interpolation across depths and days. Points indicate the time and depth of actual temperature measurements, although note that temperature measurements from 1 month prior to and 1 month beyond the period shown were used for interpolations. Temperatures were measured at the GAK1 oceanographic station near Seward, Alaska. Dashed box in upper left panel indicates the months and depths over which habitat suitability was averaged to create an index of spawning habitat suitability. Habitat suitability for all months of the year is shown in Fig. S3[1]. [Colour online.]



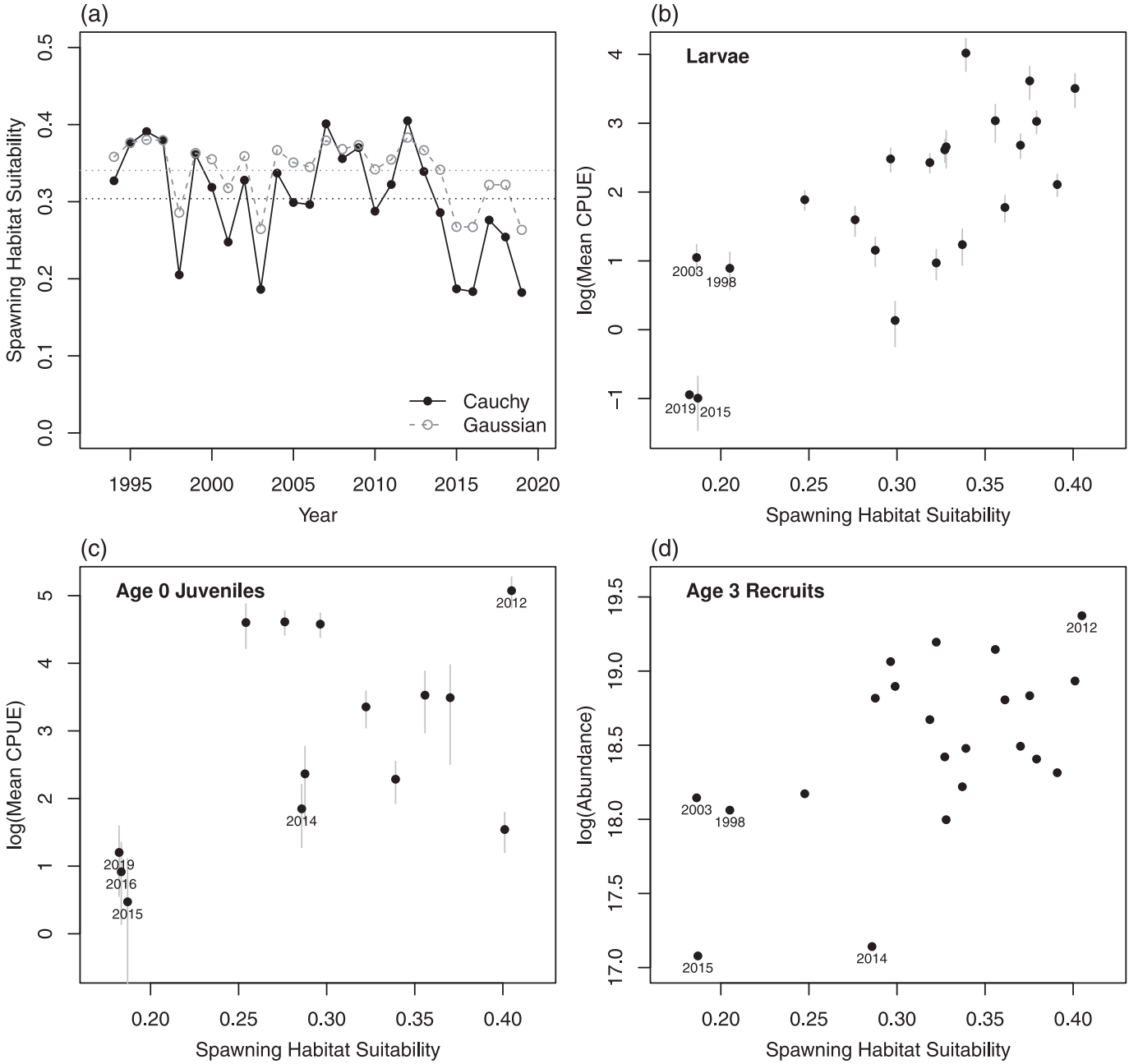
autocorrelation; however, the age-3 time series was significantly autocorrelated at lag 1 ($p < 0.05$). The years 2015, 2016, and 2019 had the lowest observed abundance of larvae and age-0 juveniles in the time series (Figs. 3*b*, 3*c*, S4[1]). Estimated recruitment to age-3 has not yet been observed for the 2016 and 2019 year classes, but was record low in 2015 (Figs. 3*d*, S4[1]).

Discussion

Our study suggests that poor hatch success due to a reduction in thermal habitat suitability may have contributed to low recruitment during the recent marine heat wave in the GOA. Experimental results show narrow thermal tolerance of Pacific cod eggs, with an optimum around 4–5 °C and rapid decline at warmer and cooler temperatures. The precipitous drop in hatch success above and below 5 °C is consistent with experimental data from the Strait of Georgia, British Columbia (Alderdice and Forrester 1971) and southwest Japan (Bian et al 2016), which collectively suggest Pacific cod have much higher temperature sensitivity than other gadids with pelagic eggs (e.g., Atlantic cod, Geffen et al. 2006; walleye pollock (*Gadus chalcogrammus*), Laurel et al. 2018; Tsoukali et al. 2016). Such narrow thermal tolerance may reflect the relatively stable thermal conditions encountered by demersal eggs under normal conditions and the ability of females to select spawning habitat to optimize fitness for offspring. A characteristic feature of the recent GOA marine heatwaves was the presence and persistence of warm waters even at depth, which drastically reduced the availability of thermal habitat conducive to offspring survival. Pacific cod appear to have a narrow thermal tolerance at the egg stage that leaves them especially vulnerable to warming.

While the GOA heatwave likely imparted bioenergetic stress across the full life history of Pacific cod (Zador and Yasumiishi 2017), this study demonstrates one mechanism by which warm

Fig. 3. Spawning habitat suitability index (*a*), calculated as the mean habitat suitability from January to April at depths greater than 100 m. Spawning habitat suitability is based on temperature profiles at depth combined with experimentally derived, temperature-dependent hatch success of eggs. Results using both the Cauchy and Gaussian response curves are shown. Horizontal dotted lines show the time-series averages. Spawning habitat suitability is positively correlated with relative abundance of (*b*) larvae (±1 SE), (*c*) age-0 juveniles (±1 SE), and (*d*) estimates of abundance at age-3 (±1 SD). Larval and juvenile CPUE are based on biannual and annual surveys in the western Gulf of Alaska (Fig. S1[1]), whereas age-3 estimates are based on an age-structured stock assessment model fit to survey and fishery data (see Fig. S4[1] for time series). Years are labeled to highlight heatwave (2014–2016, 2019) and El Nino (1998, 2003) years, as well as the year with highest spawning habitat index (2012). Missing labels in individual panels indicate no observation or available estimate for that year.



temperatures may limit recruitment to the fishery: stock reproductive potential. A constriction in the duration of suitable hatching temperatures has similarly been hypothesized to be the cause for a decline in Baltic spring-spawning herring (*Clupea harengus*; Dodson et al. 2018), another stock with demersal eggs. However, other mechanisms may link warmer temperatures to reduced recruitment. In spring-spawning marine fish, temperature-dependent metabolic demand can impact surplus energy available for reproduction that is already depleted from overwintering (Pankhurst 1997). For example, Atlantic cod will skip spawning when there is insufficient energy (liver stores) to support gonad development (Rideout et al. 2006), and other species may fail to make migrations to spawning grounds (Milton and Chenery 2005). Thus, it is possible that warm temperatures may additionally lead to reduced reproductive output through effects on maternal conditions and spawning activity.

Our first and second hypotheses were supported by the annual habitat suitability model outputs, indicating that optimal spawn-

ing habitat was reduced (H_1) and spatiotemporally restricted (H_2) to shallower regions and earlier times in the year in the warmest years (1998, 2003, 2015, 2016, 2019). However, adapting the timing and location of spawning to match changes in optimal spawning habitat will depend on a number of physiological and behavioral factors. Temporal plasticity in spawn timing (phenology), while potentially favorable for maximizing hatch success, may result in larvae hatching into a poor foraging environment, that is, "match–mismatch" processes (Durant et al. 2007). Spring spawn timing may also be constrained by bioenergetics, hormone secretion, and gametogenesis that are regulated by preceding fall and winter environments (Pankhurst 1997). Warm years are indeed associated with accelerated gonad maturation and early spawning in Pacific cod in the Bering Sea (Neidetcher et al. 2014). Behavioral thermoregulation of the spatial and temporal release of eggs would be highly adaptive for a thermally sensitive, single-batch spawner like Pacific cod, although no spring data are available to confirm earlier shifts in spawning during the marine heatwaves. Spatial heterogeneity in thermal habitats within the GOA may provide opportunities for spawners to select suitable microhabitats even when mean temperatures are above optimal. Indeed, observations of adult Pacific cod shifting to deeper, cooler regions during the summer in response to warming suggests this species can cue to preferred thermal feeding habitats when they are available (Yang et al. 2019). Improved knowledge of Pacific cod spawning locations and behavior in the GOA could lead to better characterization of spawning habitat suitability and its importance as a limiting factor for recruitment success.

The low numbers of larval and age-0 juvenile stages observed during the marine heatwave may suggest spawning output was lower (supporting H_3), but may also be the result of increased posthatch mortality. Although larvae and juvenile Pacific cod can grow and survive over a broad range of temperatures (2–11 °C; Hurst et al. 2010), the thermal conditions during the 2014–2016 period would be metabolically demanding for larvae if prey densities were low (Laurel et al. 2011) and potentially impactful on growth following settlement into shallow nursery areas (Laurel et al. 2017). Temperature can also impact larval survival indirectly through trophic links, for instance through changes in prey quality or by altering the timing and magnitude of zooplankton prey production (Durant et al. 2007). Disentangling these indirect effects of temperature are challenging. However, even given considerable uncertainty in abundance indices, including stock assessment estimates of abundance at age-3, we were able to detect a clear relationship between thermal conditions during spawning and eventual year-class size, pointing to the importance of processes occurring during the egg stage.

Pacific cod recruitment is characterized by occasional strong year classes, and multiple consecutive years of low recruitment are not unprecedented (Barbeaux et al. 2018). Early indications based on age-0 abundance estimates suggest that the 2017 and 2018 year classes may be strong (B. Laurel, unpublished data). However, long-term warming in the GOA and predicted increased frequency of heatwaves means thermal conditions will become increasingly unfavorable for Pacific cod. Projections under Representative Concentration Pathway 8.5 (i.e., "business as usual") indicate mean winter sea surface temperature in the GOA increasing at least 3 °C in the next century (Scott et al. 2016). Indeed, heatwave conditions have returned to the western GOA in 2019 after only a 2-year hiatus, and sea surface temperatures are forecasted to remain 0.5 to 2 °C above average into 2020 (http://www.cpc.ncep.noaa.gov/products/NMME/seasanom.shtml). Complex bathymetry and its interaction with currents and on-shelf flow may provide some local thermal refugia for spawning Pacific cod even in warm years, but large-scale population-level shifts in spawning area are unlikely. Regions in the far western GOA are typically cooler than central and eastern GOA, but these regions are downstream of important coastal nursery areas identified for juveniles in the central GOA (Fig. S1[1]; Stabeno et al. 2016; Laurel et al. 2017) and at the edge of a narrow shelf where there is high risk of off-shelf larval advection (Doyle et al 2009; Hinckley et al. 2019). Like the extreme western GOA, nearby spawning areas in the Aleutian Islands (Unimak Pass) and Bering Sea shelf may remain thermally suitable for Pacific cod with continued warming, but these populations are genetically distinct (Spies 2012) and also downstream of ocean currents that could potentially seed the GOA with larvae and juveniles. Tagging studies also suggest very limited movement of Pacific cod between the Aleutian–Bering region and the central GOA (Rand et al. 2014). Although distinct east-to-west genetic structure and reduced gene flow within the GOA (Drinan et al. 2018) will increase selection pressure on local populations to adapt to changing thermal habitats, the natural adaptation rates in longer-lived species like cod will likely fall behind projected rates of medium- to long-term climate warming (Reed et al. 2011).

Conclusion

Our study suggests that loss of spawning habitat from extreme warming events contributes to poor recruitment for Pacific cod in the GOA. The most recent warming events (2014–2016, 2019) corresponded with multiple years of sustained, below average habitat suitability. We also contend that the spatial–temporal extent of suitable spawning habitat for Pacific cod will continue to decline as conditions continue to warm. As single-batch, seasonal spawners, the offspring of Pacific cod have an inherently high exposure risk to environmental conditions for growth and survival (Lowerre-Barbieri et al. 2011). A further narrowing or shift in spawning activity could exacerbate larval mismatch with spring productivity (Durant et al. 2007) or place larvae outside key advective pathways for transport to critical juvenile nearshore nursery areas (Hinckley et al. 2019). While these processes merit further study, the direct impact of temperature on egg survival, coupled with the apparent loss of both adults and prerecruits in the Gulf of Alaska, is strong evidence that spawning output by Pacific cod will be substantially reduced with continued regional warming.

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References

Akima, H., and Gebhardt, A. 2015. akima: interpolation of irregularly and regularly spaced data. R package version 0.5-12 [online]. Available from https://CRAN.R-project.org/package=akima.

Alderdice, D.F., and Forrester, C.R. 1971. Effects of salinity, temperature, and dissolved oxygen on early development of the Pacific cod (*Gadus macrocephalus*). J. Fish. Res. Board Can. **28**(6): 883–902. doi:10.1139/f71-130.

Bakkala, R. 1984. Pacific cod of the eastern Bering Sea. J. Int. North Pac. Fish. Comm. Bull. **42**: 157–179.

Barbeaux, S.J., Aydin, K., Fissel, B., Holsman, K., Palsson, W., Shotwell, S.K., et al. 2017. Assessment of the Pacific cod stock in the Gulf of Alaska. North Pacific Fisheries Management Council.

Barbeaux, S.J., Aydin, K., Fissel, B., Holsman, K., Laurel, B., Palsson, W., et al. 2018. Assessment of the Pacific cod stock in the Gulf of Alaska. North Pacific Fisheries Management Council.

Bian, X.D., Zhang, X.M., Sakurai, Y., Jin, X.S., Wan, R.J., Gao, T.X., and Yamamoto, J. 2016. Interactive effects of incubation temperature and salinity on the early life stages of Pacific cod *Gadus macrocephalus*. Deep Sea Res Part II Top. Stud. Oceanogr. **124**: 117–128. doi:10.1016/j.dsr2.2015.01.019.

Bond, N.A., Cronin, M.F., Freeland, H., and Mantua, N. 2015. Causes and impacts of the 2014 warm anomaly in the NE Pacific. Geophys. Res. Lett. **42**(9): 3414–3420. doi:10.1002/2015GL063306.

Bradbury, I., Laurel, B., Robichaud, D., Rose, G., Snelgrove, P., Gregory, R., et al. 2008. Discrete spatial dynamics in a marine broadcast spawner: re-evaluating scales of connectivity and habitat associations in Atlantic cod (*Gadus morhua* L.) in coastal Newfoundland. Fish. Res. **91**(2): 299–309. doi:10.1016/j.fishres.2007.12.006.

Di Lorenzo, E., and Mantua, N. 2016. Multi-year persistence of the 2014/15 North Pacific marine heatwave. Nat. Clim. Change, **6**(11): 1042–1047. doi:10.1038/nclimate3082.

Dodson, J.J., Daigle, G., Hammer, C., Polte, P., Kotterba, P., Winkler, G., and Zimmermann, C. 2018. Environmental determinants of larval herring (*Clupea harengus*) abundance and distribution in the western Baltic Sea. Limnol. Oceanogr. **64**(1): 317–329. doi:10.1002/lno.11042.

Doyle, M.J., Picquelle, S.J., Mier, K.L., Spillane, M.C., and Bond, N.A. 2009. Larval fish abundance and physical forcing in the Gulf of Alaska, 1981–2003. Prog. Oceanogr. **80**(3–4): 163–187. doi:10.1016/j.pocean.2009.03.002.

Drinan, D.P., Gruenthal, K.M., Canino, M.F., Lowry, D., Fisher, M.C., and Hauser, L. 2018. Population assignment and local adaptation along an isolation-by-distance gradient in Pacific cod (*Gadus macrocephalus*). Evol. Appl. **11**(8): 1448–1464. doi:10.1111/eva.12639.

Durant, J.M., Hjermann, D.Ø., Ottersen, G., and Stenseth, N.C. 2007. Climate and the match or mismatch between predator requirements and resource availability. Clim. Res. **33**(3): 271–283. doi:10.3354/cr033271.

Foucher, R., and Westrheim, S. 1990. The spawning season of Pacific cod on the west coast of Canada. Department of Fisheries and Oceans, Biological Sciences Branch.

Geffen, A.J., Fox, C.J., and Nash, R.D.M. 2006. Temperature-dependent development rates of cod *Gadus morhua* eggs. J. Fish Biol. **69**(4): 1060–1080. doi:10.1111/j.1095-8649.2006.01181.x.

Hinckley, S., Stockhausen, W.T., Coyle, K.O., Laurel, B.J., Gibson, G.A., Parada, C., et al. 2019. Connectivity between spawning and nursery areas for Pacific cod (*Gadus macrocephalus*) in the Gulf of Alaska. Deep-Sea Res Part II Trop. Stud. Oceanogr. **165**: 113–126. doi:10.1016/j.dsr2.2019.05.007.

Houde, E. 1987. Fish early life dynamics and recruitment variability. Am. Fish. Soc. Symp. **2**: 17–29.

Hurst, T.P., Laurel, B.J., and Ciannelli, L. 2010. Ontogenetic patterns and temperature-dependent growth rates in early life stages of Pacific cod (*Gadus macrocephalus*). Fish. Bull. **108**(4): 382–392.

Karp, W.A. 1983. Biology and management of Pacific cod (*Gadus macrocephalus tilesius*) in Port Townsend, Washington. Thesis, University of Washington, Seattle, Wash.

Kelsch, S.W., and Neill, W.H. 1990. Temperature preference versus acclimation in fishes: selection for changing metabolic optima. Trans. Am. Fish. Soc. **119**(4): 601–610. doi:10.1577/1548-8659(1990)119<0601:TPVAIF>2.3.CO;2.

Ketchen, K.S. 1961. Observations on the ecology of the Pacific cod (*Gadus macrocephalus*) in Canadian waters. J. Fish. Board Can. **18**(4): 513–558. doi:10.1139/f61-044.

Laurel, B.J., Hurst, T.P., Copeman, L.A., and Davis, M.W. 2008. The role of temperature on the growth and survival of early and late hatching Pacific cod larvae (*Gadus macrocephalus*). J. Plankton Res. **30**(9): 1051–1060. doi:10.1093/plankt/fbn057.

Laurel, B.J., Hurst, T.P., and Ciannelli, L. 2011. An experimental examination of temperature interactions in the match–mismatch hypothesis for Pacific cod larvae. Can. J. Fish. Aquat. Sci. **68**(1): 51–61. doi:10.1139/F10-130.

Laurel, B.J., Cote, D., Gregory, R.S., Rogers, L., Knutsen, H., and Olsen, E.M. 2017. Recruitment signals in juvenile cod surveys depend on thermal growth conditions. Can. J. Fish. Aquat. Sci. **74**(4): 511–523. doi:10.1139/cjfas-2016-0035.

Laurel, B.J., Copeman, L.A., Spencer, M., and Iseri, P. 2018. Comparative effects of temperature on rates of development and survival of eggs and yolk-sac larvae of Arctic cod (*Boreogadus saida*) and walleye pollock (*Gadus chalcogrammus*). ICES J. Mar. Sci. **75**(7): 2403–2412. [fsy042.] doi:10.1093/icesjms/fsy042.

Lowerre-Barbieri, S.K., Ganias, K., Saborido-Rey, F., Murua, H., and Hunter, J.R. 2011. Reproductive timing in marine fishes: variability, temporal scales, and methods. Mar. Coast. Fish. **3**(1): 71–91. doi:10.1080/19425120.2011.556932.

Matarese, A.C., Blood, D.M., Picquelle, S.J., and Benson, J.L. 2003. Atlas of abundance and distribution patterns of ichthyoplankton from the Northeast Pacific Ocean and Bering Sea ecosystems: based on research conducted by the Alaska Fisheries Science Center (1972–1996). NOAA Technical Report.

Milton, D.A., and Chenery, S.R. 2005. Movement patterns of barramundi *Lates calcarifer*, inferred from $^{87}Sr/^{86}Sr$ and Sr/Ca ratios in otoliths, indicate non-participation in spawning. Mar. Ecol. Prog. Ser. **301**: 279–291. doi:10.3354/meps301279.

Mishima, S. 1984. Stock assessment and biological aspects of Pacific cod (*Gadus macrocephalus* Tilesius) in Japanese waters. Bull. Int. North Pac. Fish. Comm. **42**: 180–188.

Motani, R., and Wainwright, P.C. 2015. How warm is too warm for the life cycle of actinopterygian fishes? Sci. Rep. (U.K.), **5**: 11597. doi:10.1038/srep11597.

Neidetcher, S.K., Hurst, T.P., Ciannelli, L., and Logerwell, E.A. 2014. Spawning phenology and geography of Aleutian Islands and eastern Bering Sea Pacific cod (*Gadus macrocephalus*). Deep Sea Res. Part II Top. Stud. Oceanogr. **109**: 204–214. doi:10.1016/j.dsr2.2013.12.006.

NOAA. 2016. El Niño/Southern Oscillation (ENSO) Diagnostic Discussion [online]. NOAA/National Weather Service, Camp Springs, Maryland. Available from http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/enso_disc_jan2016/ensodisc.pdf.

Palsson, W.A. 1990. Pacific cod (*Gadus macrocephalus*) in Puget Sound and adjacent waters: biology and stock assessment. Department of Fish and Wildlife.

Pankhurst, N. 1997. Effect of stress on reproduction and growth of fish. *In* Fish stress and health in aquaculture. *Edited by* G.K. Iwama, A.D. Pickering, J.P. Sumpter, and C.B. Schreck. Cambridge University Press, Cambridge, UK. pp. 73–93.

Rand, K.M., Munro, P., Neidetcher, S.K., and Nichol, D.G. 2014. Observations of seasonal movement from a single tag release group of Pacific cod in the Eastern Bering Sea. Mar. Coast. Fish. **6**(1): 287–296. doi:10.1080/19425120.2014.976680.

Reed, T.E., Schindler, D.E., and Waples, R.S. 2011. Interacting effects of phenotypic plasticity and evolution on population persistence in a changing climate. Conserv. Biol. **25**(1): 56–63. doi:10.1111/j.1523-1739.2010.01552.x.

Rideout, R.M., Morgan, M.J., and Lilly, G.R. 2006. Variation in the frequency of skipped spawning in Atlantic cod (*Gadus morhua*) off Newfoundland and Labrador. ICES J. Mar. Sci. **63**(6): 1101–1110. doi:10.1016/j.icesjms.2006.04.014.

Rijnsdorp, A.D., Peck, M.A., Engelhard, G.H., Mollmann, C., and Pinnegar, J.K. 2009. Resolving the effect of climate change on fish populations. ICES J. Mar. Sci. **66**(7): 1570–1583. doi:10.1093/icesjms/fsp056.

Scott, J.D., Alexander, M.A., Murray, D.R., Swales, D., and Eischeid, J. 2016. The Climate Change Web Portal: a system to access and display climate and earth system model output from the CMIP5 archive. Bull. Am. Meteor. Soc. **97**(4): 523–530. doi:10.1175/BAMS-D-15-00035.1.

Shimada, A.M., and Kimura, D.K. 1994. Seasonal movements of Pacific cod, *Gadus macrocephalus*, in the Eastern Bering Sea and adjacent waters based on tag-recapture data. Fish. Bull. **92**(4): 800–816. Available from https://spo.nmfs.noaa.gov/content/seasonal-movements-pacific-cod-gadus-macrocephalus-eastern-bering-sea-and-adjacent-waters.

Spies, I. 2012. Landscape Genetics Reveals Population Subdivision in Bering Sea and Aleutian Islands Pacific Cod. Trans. Am. Fish. Soc. **141**(6): 1557–1573. doi:10.1080/00028487.2012.711265.

Stabeno, P.J., Bond, N.A., Hermann, A.J., Kachel, N.B., Mordy, C.W., and Overland, J.E. 2004. Meteorology and oceanography of the Northern Gulf of Alaska. Cont. Shelf Res. **24**(7): 859–897. doi:10.1016/j.csr.2004.02.007.

Stabeno, P.J., Bell, S., Cheng, W., Danielson, S., Kachel, N.B., and Mordy, C.W. 2016. Long-term observations of Alaska Coastal Current in the northern Gulf of Alaska. Deep Sea Res. Part II Top. Stud. Oceanogr. **132**: 24–40. doi:10.1016/j.dsr2.2015.12.016.

Stark, J.W. 2007. Geographic and seasonal variations in maturation and growth of female Pacific cod (*Gadus macrocephalus*) in the Gulf of Alaska and Bering Sea. Fish. Bull. **105**(3): 396–407. Available from https://spo.nmfs.noaa.gov/content/geographic-and-seasonal-variations-maturation-and-growth-female-pacific-cod-gadus.

Tsoukali, S., Visser, A.W., and MacKenzie, B.R. 2016. Functional responses of North Atlantic fish eggs to increasing temperature. Mar. Ecol. Prog. Ser. **555**: 151–165. doi:10.3354/meps11758.

Walsh, J.E., Thoman, R.L., Bhatt, U.S., Bieniek, P.A., Brettschneider, B., Brubaker, M., et al. 2018. The high latitude marine heat wave of 2016 and its impacts on Alaska. Bull. Am. Meteor. Soc. **99**(1): S39–S43. doi:10.1175/BAMS-D-17-0105.1.

Westrheim, S. 1984. Migration of Pacific cod (*Gadus macrocephalus*) in British Columbia and nearby waters. Int. North Pac. Fish. Comm. Bull. **42**: 214–222.

Yang, Q., Cokelet, E.D., Stabeno, P.J., Li, L., Hollowed, A.B., Palsson, W.A., et al. 2019. How "The Blob" affected groundfish distributions in the Gulf of Alaska. Fish. Oceanogr. **28**(4): 434–453. doi:10.1111/fog.12422.

Zador, S., and Yasumiishi, E.M. 2017. Ecosystem considerations 2017: Status of the Gulf of Alaska Marine Ecosystem. Gulf of Alaska Ecosystem Status Report.

Zhang, C. 1984. Pacific cod of South Korean waters. Int. North Pac. Fish Comm. Bull. **42**: 116–129.