

Post-settlement abundance, condition, and survival in a climate-stressed population of Pacific cod

Alisa A. Abookire, Michael A. Litzow, Michael J. Malick, and Benjamin J. Laurel

Abstract: The Pacific cod (*Gadus macrocephalus*) fishery recently collapsed in the Gulf of Alaska after a series of marine heatwaves that began in 2014. To gauge the likelihood of population recovery following these extreme warming events, we investigate potential thermal stress on age-0 cohorts through a comprehensive analysis of juvenile cod abundance, condition, growth, and survival data collected from 15 years of beach seine surveys. Abundance was strongly negatively related to ocean temperature during the egg and larval phase (winter–spring), but age-0 cod were larger in the early summer following warm winter–spring temperatures. Body condition indices suggest that warm summers may improve energetic reserves prior to the first winter; however, there was no summer temperature effect on post-settlement growth or survival. Spatial differences in abundance, condition, or growth were not detected, and density-dependent effects were either weak or positive. While the positive effects of increased summer temperatures on juvenile condition may benefit overwintering survival, they cannot compensate for high pre-settlement mortality from warming winter–spring temperatures. We conclude the critical thermal bottleneck for juvenile abundance occurs pre-settlement.

Résumé : La pêche à la morue du Pacifique (*Gadus macrocephalus*) s'est récemment effondrée dans le golfe d'Alaska après une série de vagues de chaleur marines qui ont débuté en 2014. Afin d'évaluer la probabilité d'un rétablissement de la population après ces épisodes de réchauffement extrême, nous examinons le stress thermique potentiel sur des cohortes de moins de 1 an par une analyse exhaustive de données sur l'abondance, l'embonpoint, la croissance et la survie de morues juvéniles obtenues de 15 années de levés à la seine de rivage. L'abondance présente une forte relation négative avec la température de l'océan durant la phase des œufs et des larves (hiver–printemps), mais les morues de moins de 1 an sont plus grandes au début d'étés suivant des températures hivernales–printanières élevées. Les indices d'embonpoint indiqueraient que des étés chauds pourraient améliorer les réserves d'énergie avant le premier hiver; aucun effet de la température estivale sur la croissance ou la survie après l'établissement n'est cependant relevé. Aucune variation spatiale de l'abondance, de l'embonpoint ou de la croissance n'est détectée, et les effets dépendants de la densité sont faibles ou positifs. Si les effets positifs de températures estivales plus élevées sur l'embonpoint des juvéniles pourraient améliorer la survie hivernale, ils ne peuvent pallier la mortalité élevée qui précède l'établissement, causée par la hausse des températures hivernales–printanières. Nous concluons que le goulot d'étranglement thermique critique pour l'abondance des morues juvéniles se produit avant l'établissement. [Traduit par la Rédaction]

Introduction

The recent collapse of the Pacific cod (*Gadus macrocephalus*) stock in the Gulf of Alaska has been directly linked to warming ocean temperatures in 2014–2016 (Barbeaux et al. 2020b) and highlights the need to understand the effects of climate change on fish populations (Brander 2015). The accelerated warming of the Gulf of Alaska (Bond et al. 2015; Walsh et al. 2018) has resulted in spatial shifts in the adult Pacific cod population, as seen with diminished spawning habitat and activity (Laurel and Rogers 2020) and recent movements northward into the Bering Sea (Spies et al. 2020). To assess potential stock recovery, it is necessary to determine species-specific thermal tolerances across life stages (Dahlke et al. 2020; Sunday 2020). While thermal effects on Pacific cod eggs and larvae are relatively well understood (Hurst et al. 2010; Laurel et al. 2011, 2016b), questions about the post-settlement stage remain — namely, do condition, growth,

and survival of age-0 cod display the same temperature sensitivities as observed in pre-settlement life stages? A mixture of environmental and anthropogenic drivers influence recruitment variability in gadid species world-wide (Stige et al. 2013; Laurel et al. 2017; Lunzmann-Cooke et al. 2021), and understanding thermal effects on the first year of life processes is necessary to evaluate sustainability of Pacific cod in the region (Litzow et al. 2021).

Pacific cod have a relatively complex early life history, where a single batch of negatively buoyant, semi-adhesive eggs (Alderdice and Forrester 1971) are spawned offshore during late winter and spring (Dunn and Matarese 1987; Doyle et al. 2009). After a period of 2–3 weeks on the bottom, eggs hatch and positively buoyant larvae rise through the water column (Hurst et al. 2009) where they are initially transported onshore by ocean currents to pelagic shelf habitats (Doyle et al. 2009; Laurel and Rogers 2020)

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before eventually settling in nearshore nurseries (Abookire et al. 2007; Laurel et al. 2007, 2009). Multiple early life history periods may limit recruitment for Pacific cod, including the egg stage and larval stage (Hurst et al. 2009; Laurel and Rogers 2020; Laurel et al. 2021), the transition from larval shelf habitat to juvenile coastal nursery areas (Hinckley et al. 2019), post-settlement survival in nursery areas (Laurel et al. 2016a), and survival through the first winter (Hurst 2007; Geissinger et al. 2021).

Pre-settlement survival is largely driven by oceanographic conditions such as temperature, timing of spring productivity, and currents (Laurel et al. 2011, 2021; Doyle et al. 2019). Pacific cod eggs exhibit a narrow thermal tolerance, with steep declines in hatch success outside an optimal temperature range of 4–5 °C (Laurel and Rogers 2020). Movement and survival of Pacific cod larvae are directly affected by temperature and light (Hurst et al. 2009), and larvae can experience high daily mortality rates before arriving to nearshore nurseries (Moss et al. 2016). Pacific cod may exhibit localized retention (Lewandoski et al. 2018; Hinckley et al. 2019) and spawning site fidelity (Neidetcher et al. 2014), and onshore delivery in the Gulf of Alaska is reliant on enhanced alongshore winds (Doyle et al. 2009) and reduced gyre circulation (Hinckley et al. 2019).

Transformation to the juvenile stage occurs at around 25–35 mm standard length (SL) (Dunn and Matarese 1987), and by July Pacific cod are settled in nearshore shallow coastal nursery areas (Abookire et al. 2007; Laurel et al. 2007, 2009). Newly settled age-0 cod have a preference for emergent structures such as eelgrass (*Zostera marina*) and brown macroalgae at depths of <5 m (Laurel et al. 2007) and expand to more diverse, deeper habitat (10–30 m) with sea cucumber mounds and invertebrate worm tube cover (Abookire et al. 2007) and even bare gravel (Laurel et al. 2009) as they increase in size. Habitat structure is important for both prey avoidance (Laurel et al. 2007) and also foraging opportunities (Abookire et al. 2007). Juvenile cod remain in nearshore habitats throughout the summer and into the fall when they migrate to deeper water (Laurel et al. 2009).

Once present in coastal nursery areas, age-0 *Gadus* spp. may be surveyed with beach seine gear (Ings et al. 1997; Laurel et al. 2007; Rogers et al. 2011). Beach seines are logistically easy to deploy, and their use has contributed important data to our understanding of juvenile habitat preferences, growth, and survival (Methven and Bajdik 1994; Grant and Brown 1998). While beach seines do not sample the eggs and larvae, the catches are useful for tracking post-settlement abundance and provide an early snapshot of the annual cohort (Laurel et al. 2007, 2016a). Furthermore, beach seines can be utilized to effectively forecast adult biomass for some gadid stocks in the North Pacific (Stige et al. 2013; Litzow et al. 2022) and North Atlantic (Lunzmann-Cooke et al. 2021).

Our current knowledge of coastal nursery dynamics for Pacific cod is based on a series of studies conducted in a narrow region of coastline along Kodiak Island (two bays over ~45 km coastline; Laurel et al. 2007, 2009). These studies occurred before a series of marine heatwaves that began in 2014 (Bond et al. 2015), and they did not capture the response of age-0 cod to the extreme temperature anomalies that characterize the post-2014 period. In addition, Gulf of Alaska temperatures decline from east to west (Stabeno et al. 2004), suggesting the potential for spatial patterns in temperature effects on cod that would not be detected by a small-scale survey. In this study, we examine temperature effects on juvenile cod condition, growth, and survival, using a combination of long-term data from a core survey area consisting of two Kodiak bays (2006–2020) and data from a recent, geographically expanded survey (13 additional bays over ~575 km coastline, 2018–2020). A previous analysis of these data showed that warm pre-settlement (winter–spring) temperatures are associated with very low age-0 abundance (Litzow et al. 2022). The current paper examines temperature effects on condition, growth, and survival

of age-0 cod, as well as spatial variability in age-0 response variables that might follow the east–west temperature gradient.

Our specific goals are to (1) test for effects of pre-settlement (winter–spring) temperatures on the abundance and early season size of juvenile cod; (2) examine the effects of summer temperature on post-settlement condition, growth, and survival; (3) test for spatial patterns in the abundance, condition, and survival of juvenile cod; and (4) test for density-dependent effects on growth and survival that might buffer the effects of low recruitment events.

Materials and methods

Data collection

Beach seine sampling in the Gulf of Alaska is divided into two surveys conducted at fixed site locations. The longer time series (referred to as the “core survey”) has occurred at two Kodiak Island bays from 2006–2020 and an “expanded survey” has occurred from 2018–2020 at 13 additional bays on Kodiak Island, the Alaska Peninsula, and the Shumagin Islands ($n = 3–9$ fixed stations per bay, 95 total stations). Sampling for the core survey typically occurred twice in July and twice in August of each year (days of year 184–240). Sampling in the extended survey occurred during July and August during each year from 2018–2020; in 2018 sites on Kodiak Island and the Alaska Peninsula were sampled twice and in 2019 and 2020 each site was sampled once. There was a combined total of 1122 beach seine sets in both the core and expanded surveys (Fig. 1a).

At all sites, a 36 m long, negatively buoyant beach seine was deployed parallel to shore using a boat and retrieved by two people standing a fixed distance apart on shore (details in Laurel et al. 2007). Wings on the seine (13 mm mesh) were 1 m deep at the ends and 2.25 m in the middle with a 5 mm delta mesh cod end bag. The seine wings were attached to 25 m ropes for deployment and retrieval from shore, making the effective sampling area ~900 m² of bottom habitat.

In the field, all Pacific cod were counted and a subsample from each catch was measured for total length (± 1 mm). Length groups from these field measured cod ($n = 10\,296$ lengths from all bays and years combined) were used to differentiate age-0 (20–145 mm) from age-1 cod (>160 mm). In the extended survey (2018–2020) a subsample of age-0 cod (≈ 25 per bay, $n = 14$ bays) was frozen for condition analyses in the laboratory. Frozen cod ($n = 1010$) were thawed, dissected, and stomachs and livers were removed and weighed. After the otoliths were removed, the eviscerated fish were dried at 60 °C for 3 days to yield eviscerated dried body weight. Fulton’s condition index (K_{dry}) was calculated as

$$K_{dry} = \frac{1000W}{L^3}$$

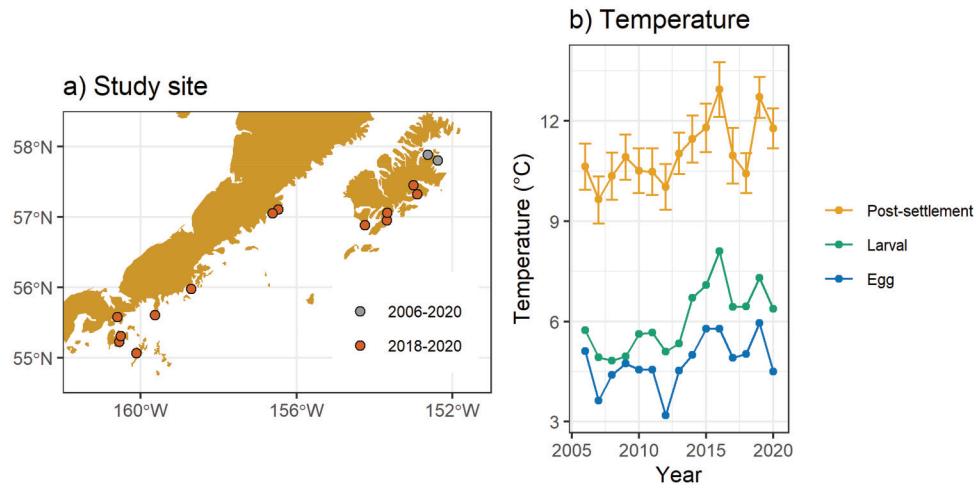
where W is eviscerated dry body weight (g), and L is total length (cm) (Grant and Brown 1999). The hepatosomatic index (HSI) was calculated as

$$HSI = \left(\frac{\text{wet liver weight (g)}}{\text{eviscerated dried fish weight (g)}} \right) \times 100$$

(Grant and Brown 1999). There was little correspondence between the two condition metrics (Fulton’s K_{dry} and HSI) when averaged by bay ($r = 0.38$) or for individual fish ($r = 0.20$, $n = 971$), and so they were analyzed independently.

Winter–spring (pre-settlement) temperatures were estimated with temperature data from the Global Ocean Data Assimilation System (GODAS) in times and depths representative of spawning (Laurel and Rogers 2020) and pelagic larval stages (Doyle et al. 2009). Temperatures during the egg stage were estimated with data for January–April at 105 m depth, and temperatures during

Fig. 1. (a) Study site (Kodiak Island and the Alaska Peninsula), indicating years of sampling for each bay. (b) Temperature for post-settlement cod (summer) and pre-settlement cod (egg or larval; winter–spring). Post-settlement data plotted with 95% CIs; pre-settlement plotted without error.



the larval stage were estimated with data for April–June at 15 m depth; both values spanned the area from the eastern extent of the Kodiak Archipelago to the western extent of the Shumagin Islands. Because mean temperatures for the egg and larval periods differed (Fig. 1b), each time series was standardized as zero mean, unit variance, and the two time series were then averaged to calculate a pre-settlement temperature anomaly for each year.

Post-settlement temperature was also measured at each beach seine set at 0.5 m depth with a YSI Professional Plus handheld meter. Observation error and differences in seasonal timing of sampling between years made these raw temperature measurements unsuitable for use in analyses of cod growth, survival, and condition. We therefore used a Bayesian regression model to estimate summer temperature as a function of year and bay identity (as categorical variables), and smooth effects of day of sampling (Bayesian $R^2 = 0.55$, 95% credible interval 0.52–0.58). Summer temperatures used in subsequent analyses were the predicted temperatures from this model for each bay-year combination, with the date of sampling held at the overall mean value for the study (day of year 213).

Data analysis

We began analysis by estimating annual means and 95% credible intervals (CIs) for juvenile cod abundance, length, and condition (K_{dry} and HSI). This initial step provides an overview of the data used in subsequent analysis and evaluates the ability of Bayesian regression models to provide precise annual-scale estimates of juvenile cod response variables from different bays and seasonal times of sampling in different years. The regression models for this step included year as a categorical variable, site nested within bay as a group-level (random) effect, and day of year of sampling as a continuous variable. The abundance model was fit with a zero-inflated negative binomial (ZINB) model (Yau et al. 2003; Zuur et al. 2009), and the condition models additionally included fish length as a continuous variable. All analyses in the study involving continuous terms used thin plate regression splines to account for nonlinear relationships (Wood 2003), and the number of basis functions was limited to 3 to avoid over-fitting data.

To analyze spatial (bay-level) differences in abundance we used a Bayesian ZINB model to estimate the effect of bay identity (as a categorical variable) on catch per unit effort per seine set (CPUE·set⁻¹). The mean temperature anomaly during the egg–larval pre-settlement phase, sampling day, and spawning stock biomass (estimated from the stock assessment model;

Barbeaux et al. 2020a) are accounted for in the model. Group-level (random) effects for site identity nested within bay were also included in this model. All terms were included in both the zero-inflated (binomial) and abundance (count) parts of the model. We used a logit link function for the zero-inflated component and log links for the abundance component and shape parameter. This model was based on a previous model selection process that evaluated temperature effects on age-0 abundance in Gulf of Alaska gadid stocks (Litzow et al. 2022). The abundance model in the current analysis adds a bay covariate to examine spatial effects, and no additional model selection was conducted.

Our analysis of length data was designed to distinguish the effects of pre-settlement temperature on early season size from the effect of post-settlement (summer) temperatures on summer growth. First, we estimated a mean growth trajectory through the sampling season, using a Bayesian regression model that included covariates for summer temperature, date of sampling, bay identity, and fourth-root transformed CPUE to account for density-dependent effects. To normalize CPUE data, the fourth-root transformation was used instead of log transformation due to the high number of zeros in the dataset (Field et al. 1982). Predicted size at date from this model (with all other effects held at their mean level) provides an estimate of average growth rates of age-0 cod across all bays and all years in the study. Next, we evaluated pre-settlement (winter–spring) temperature effects on early season size (defined as total length for age-0 cod sampled in all bays and all years during days of year 184–200) using a model selection process, comparing candidate models that invoked day of sampling, pre-settlement temperature, fourth-root transformed CPUE, and bay and site identity. Candidate models were evaluated with the expected log pointwise predictive density (ELPD), a measure of out-of-sample predictive skill (Vehtari et al. 2017). The effects of summer temperature on the two condition metrics (K_{dry} and HSI) from the extended survey during 2018–2020 were also analyzed with an ELPD model selection approach using summer temperature, fourth-root transformed CPUE (averaged across visits), and bay effects as candidate covariates.

The effect of summer temperatures on age-0 growth was evaluated using a subset of sites that were visited more than once a year, with each visit separated by at least 14 days ($n = 49$ site-year combinations from the core surveys and the 2018 extended survey). This analysis used the difference, in mm·day⁻¹ from the mean length at the first visit in the season as the response variable.

An ELPD model selection approach was again used, with summer temperature, sampling day of the initial visit, fourth-root transformed CPUE (averaged across visits) and bay effects as additional candidate covariates. Our metric of survival was analyzed with the same approach used for growth, but in this case using the proportional change per day in fourth-root transformed CPUE as the response variable.

We report Bayes R^2 values for selected models, which are calculated from the model posteriors as

$$R^2 = \frac{\text{Var}_\mu}{\text{Var}_\mu + \text{Var}_{\text{res}}}$$

where Var_μ is the variance of modelled predictive means, and Var_{res} is the modelled residual variance (Gelman et al. 2019). Each regression model was fit using Stan 2.21.0 (Carpenter et al. 2017), R 4.0.2 (R Core Team 2018), and the brms packages (Buerkner 2017). Response variables for models of condition, growth, and survival were scaled as 0 mean, unit variance to aid model fitting. All estimated parameters had a potential scale reduction factor (R) less than 1.05, an effective sample size of at least 1000, and no divergent transitions were observed. We also assessed chain convergence and model fits using graphical methods (e.g., trace plots) and posterior predictive checks (Gabry et al. 2019). To aid interpretation of model results, scatter plots of raw observations against covariates are provided in an online Supplemental file¹. All data and code necessary for replicating the results of this study are available in the “GOA-cod” repository (<https://github.com/mikelitzow/GOA-cod>; permanent repository at <https://doi.org/10.5281/zenodo.5704064>).

Ethics approval

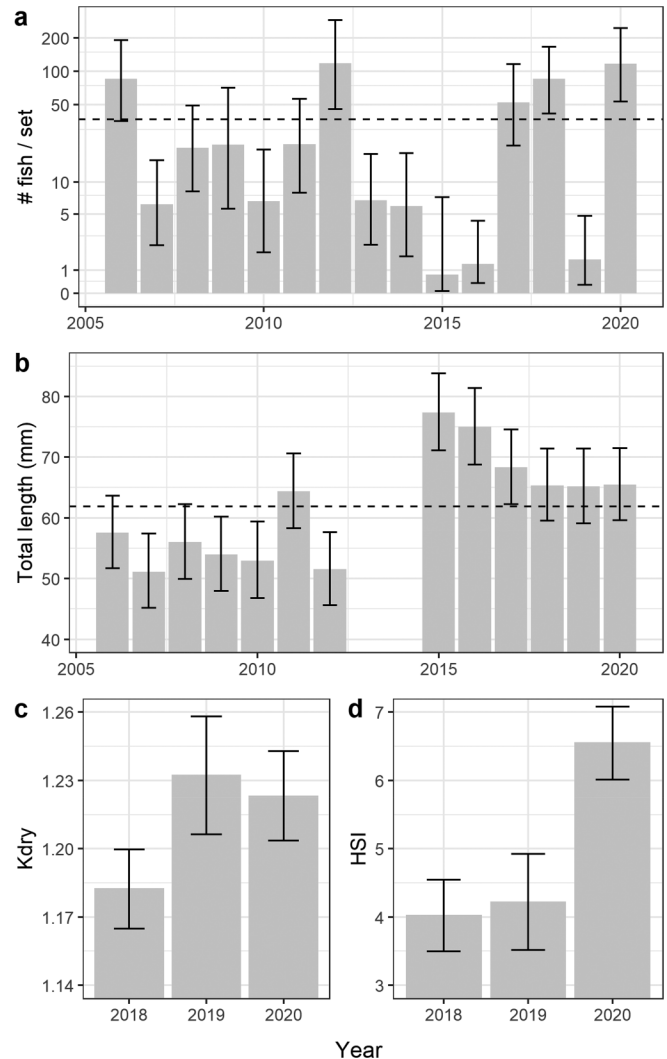
The collection of Pacific cod for condition analyses was conducted in accordance with all guidelines and regulations according to the State of Alaska, Department of Fish and Game. The specific permits obtained for collections were Aquatic Resources Permits CF-18-076, CF-19-083, and CF-20-073.

Results

The posterior means and 95% CIs from our initial models showed strong interannual variability in age-0 abundance (exceptionally low abundance in 2015, 2016, and 2019; Fig. 2a; model details in Table 1). Nonoverlapping 95% CIs for annual abundance, after accounting for spatial and temporal differences among years, indicated that estimates of annual abundance could be successfully derived based on combined information from the core and expanded surveys. We also found evidence for a step increase in average juvenile cod length, with greater predicted lengths in 2015–2020 than in 2006–2012 (no length data are available for 2013–2014; Fig. 2b). The two condition indices (K_{dry} and HSI; extended survey 2018–2020) showed distinct patterns of interannual variability (Figs. 2c, 2d).

The model for abundance variability showed strong negative effects of pre-settlement temperature on age-0 abundance, but spatial (bay) effects yielded no strong evidence for an east–west gradient in post-settlement abundance (Fig. 3; model details in Table 1). The spawning stock biomass effect indicated only a weak spawner–recruit relationship; however, we found a nonlinear declining trend in abundance with day of year (Fig. 3). The highest predicted abundance was on the earliest sampling day (day 184; Fig. 3c) with a nonlinear decline in abundance over time. Predicting abundance across different sampling days, while holding all covariates at their mean value, indicated that abundance on day 194 was 36% less than on sampling day 184. Correspondingly, abundance was reduced to $\approx 59\%$ on day 204 from the starting amount on

Fig. 2. Annual estimates of age-0 cod response variables from Bayesian regression models combining information from the core survey (2006–2020) and expanded survey (2018–2020): (a) abundance (fish per seine set); (b) total length (mm) at average day of sampling (day of year 213); (c) K_{dry} (Fulton’s condition index for eviscerated dry body weight); (d) hepatosomatic index (HSI). Plotted values are posterior means with 95% CI; dashed lines in panels (a) and (b) indicate interannual mean values.



day 184; followed by a slower decline afterwards ($\approx 71\%$ decline at day 214 and $\approx 76\%$ decline at day 224; Fig. 3c).

Early season size

The best exploratory model for cod length through the season invoked summer temperature, cod abundance, and bay effects in addition to seasonal (day of year) effects (Table 1). This model showed a sigmoidal growth pattern through the first summer post-settlement (Fig. 4), and predicted a growth rate of $\approx 0.81 \text{ mm}\cdot\text{day}^{-1}$ during the linear component of that curve (for days 205–225, corresponding to a predicted total length of 51–67 mm).

We evaluated the effects of winter–spring temperature on early-season length with analysis of a subset of length data collected over days 184–200. The best model invoked a spatial (bay) effect, day of sampling, and abundance in addition to winter–

¹Supplementary data are available with the article at <https://doi.org/10.1139/cjfas-2021-0224>.

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Table 1. Bayesian regression results.

Response variable	Figure	Covariate(s)	ELPD difference (SE)	Bayes R^2 (95% CI)
Abundance ^a	2a	DOY, year, site/bay	—	0.45 (0.32–0.57)
Length ^a	2b	DOY, year, site/bay	—	0.65 (0.64–0.65)
K_{dry} ^a	2c	DOY, year, length, site/bay	—	0.33 (0.28–0.37)
HSI ^a	2d	DOY, year, length, site/bay	—	0.25 (0.21–0.29)
Abundance ^b	3	DOY, winter–spring temp., spawning stock biomass, bay, site/bay	—	0.43 (0.27–0.56)
Length ^c	4	DOY, summer temp., fourth-root CPUE, bay	—	0.58 (0.57–0.58)
Early season size	5	DOY, winter–spring temp., fourth-root CPUE, bay	0 (0)	0.39 (0.37–0.41)
		DOY, winter–spring temp., fourth-root CPUE	–416.16 (32.60)	
		DOY, winter–spring temp.	–428.68 (33.07)	
K_{dry}	6	Length, summer temp., fourth-root abundance, bay	0 (0)	0.27 (0.23–0.31)
		Length, summer temp., fourth-root abundance	–6.87 (6.64)	
		Length, summer temp.	–12.17 (7.01)	
HSI	6	Length, summer temp., fourth-root CPUE, bay	0 (0)	0.15 (0.11–0.19)
		Length, summer temp., fourth-root CPUE	–27.99 (7.99)	
		Length, summer temp.	–35.12 (9.77)	
Growth	7	DOY, summer temp., fourth-root CPUE, site/bay	0 (0)	0.27 (0.25–0.30)
		DOY, summer temp., fourth-root CPUE, bay	–78.57 (19.90)	
		DOY, summer temp., bay	–82.25 (20.22)	
		DOY, bay	–86.35 (20.35)	
		Summer temp., fourth-root CPUE, bay	–108.90 (21.47)	
		Fourth-root CPUE, bay	–113.19 (21.51)	
		Summer temp., bay	–126.47 (22.35)	
Survival	8	DOY, summer temp., fourth-root CPUE, bay	0 (0)	0.33 (0.25–0.40)
		DOY, summer temp., fourth-root CPUE	–13.85 (6.32)	
		DOY, summer temp.	–28.05 (7.94)	
		DOY	–29.18 (8.75)	

Note: Response variables with multiple model formulations listed were subject to model selection by minimizing expected log pointwise predictive density (ELPD). ELPD difference = difference from best model, SE = standard error of difference, DOY = day of year, site/bay = site nested in bay (group-level, random term).

^aInitial models for estimating annual mean values of response variables; no model selection conducted.

^bModel based on Litzow et al. (2022); no model selection conducted.

^cExploratory model for estimating mean seasonal growth trajectory; no model selection conducted.

spring temperature (Table 1). This model showed a strong positive temperature effect on early season size, a weak positive density-dependent effect, a seasonal effect showing an early season peak in size (suggesting possible early and late settlement pulses), and bay effects that did not show a strong longitudinal gradient, although the easternmost bays had the highest predicted early season size (Fig. 5). The conclusions about the nature of temperature, day of year, and density-dependent effects were qualitatively similar between this model and the best fit model, which did not invoke bay effects (Table 1). Hence, we presented results from the biologically relevant model that incorporated bay effects to evaluate the evidence for an east–west gradient in predicted length.

Condition

The best models for each body condition index (K_{dry} and HSI) showed strong positive summer temperature effects (Table 1; Fig. 6). There was also evidence of weak positive density-dependent effects and an absence of spatial effects among bays, with no evidence of east–west gradients in juvenile cod condition (Fig. 6).

Growth

Analysis for growth and survival used the same dataset consisting of the core survey (2006–2020; 2 bays) combined with one year of the extended survey (2018; 13 bays). For post-settlement growth the best model included date of sampling, summer temperature, cod abundance, and bay or site effects (Table 1). This model indicated that the effects of summer temperature and cod abundance on growth could not be distinguished from 0 (Fig. 7).

Survival

We used changes in abundance (proportional change per day in fourth-root CPUE) as our proxy for survival. The best model of

summer survival invoked day of sampling, summer temperature, cod abundance, and site identity nested within bay (Table 1). This model indicated little evidence of summer temperature effects on survival, some evidence of positive density-dependent effects, and no strong evidence of bay differences in survival (Fig. 8).

Discussion

As human-induced ocean warming yields annual ocean temperature extremes (Bond et al. 2015; Walsh et al. 2018) with strong effects on fish recruitment globally (Brander 2015), there is an urgent need to monitor climate change effects on various life stages of recruitment. The extended marine heatwave in 2014–2016 in the Gulf of Alaska (Bond et al. 2015) resulted in an 80% reduction in allowable catch in 2018 and a total fishery closure in 2020 (Barbeaux et al. 2020a) and was attributed to increased metabolic demands on adult cod combined with reduced prey supply (Barbeaux et al. 2020b). More recently, in 2019, extreme warming caused additional Pacific cod recruitment failure — but at a different life stage — with the age-0 cohort collapse (Laurel and Rogers 2020; Litzow et al. 2021; this study). Beach seine sampling of age-0 Pacific cod in inshore nursery areas provides some of the only direct observations of annual cohort strength before fish are available to the semi-annual offshore bottom trawl survey at age-2 (Barbeaux et al. 2020a), and the strong predictive ability of age-0 abundance estimates (Litzow et al. 2022) provide managers with a tool for earlier forecasting of adult year class strength and potential stock recovery.

Our expanded beach seine survey across the Central and Western Gulf of Alaska confirms earlier observations that pre-settlement ocean conditions are an important predictor of annual abundance for age-0 Pacific cod (Laurel et al. 2017; Laurel and Rogers 2020; Litzow et al. 2022). We build on this work by demonstrating that annual

Fig. 3. Predicted abundance as a function of (a) temperature during the egg or larval periods; (b) spawning stock biomass; (c) day of sampling; (d) bay effects (west–east). Posterior means are shown with 80%, 90%, and 95% CIs, except 95% CIs in panel (d).

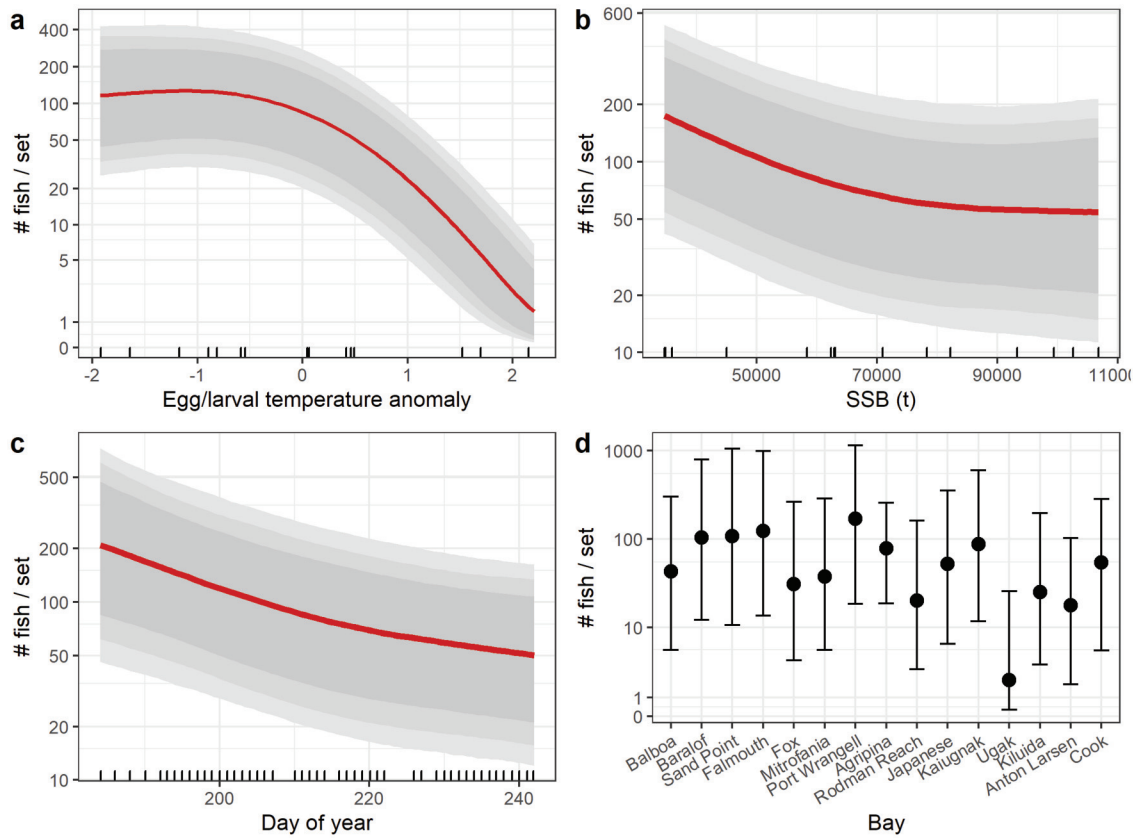
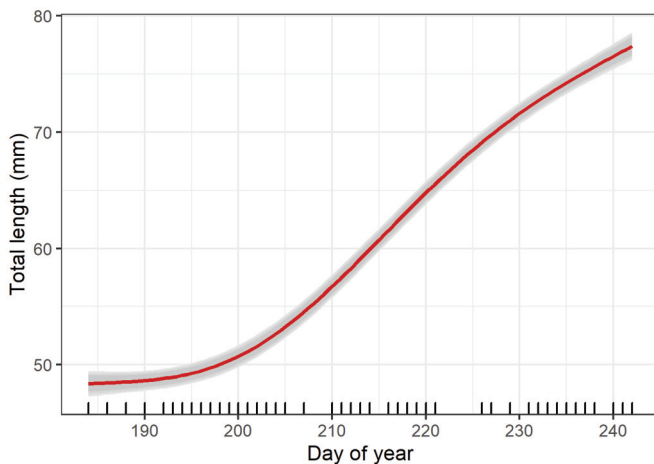


Fig. 4. Predicted age-0 cod total length as a function of day of year; posterior mean are shown with 80%, 90%, and 95% CIs.



abundance of cod is relatively constant across the region within a given year, and does not respond to the east–west gradient in temperature (Stabeno et al. 2004). We did not observe local scale structure governing age-0 cod abundance within any given year, as “large” and “small” annual cohort abundance was generally reflected throughout our entire survey of the Central and Western Gulf of Alaska. Additionally, the absence of strong spawning stock biomass effects on post-settlement abundance suggests that there currently remain a sufficient number of adult Pacific cod spawning (despite the recent fishery collapse; Barbeaux et al. 2020b) for successful age-0 recruitment.

Early season size

We observed a strong positive effect of pre-settlement temperatures on early season size; however, we are not able to distinguish between pre-settlement growth and spawning phenology. There is no fixed spawning date for Pacific cod in the Gulf of Alaska, as spawning females release a single batch of demersal eggs between mid-February and late April (Stark 2007). Therefore, the increase in pre-settlement size in certain years could be due to variation in spawning date (Laurel and Rogers 2020), variation in embryo development rate (Hurst et al. 2010), variation in larval growth rates (Hurst et al. 2010; Laurel et al. 2016b, 2021), or altered duration of coastal residency as a response to climate change (Langan et al. 2021).

We also noted that early season juveniles were slightly larger in the easternmost bays (Cook Bay and Anton Larsen Bay; Fig. 4), and the east–west spatial variation may indicate that different, earlier spawning events contribute to those bays as opposed to the bays along the Alaska Peninsula and near the Shumagin Islands. Given that the peak spawning season spans three months (Stark 2007), it is possible that pulses of cod settle to the nearshore with the later recruitment pulses giving rise to smaller early season juveniles, either due to a shortened duration of time in which to grow or a mismatch with prey (Doyle et al. 2009, 2019; Laurel et al. 2021). Given that smaller individuals are more susceptible to starvation in warm environments (Jobling 1988; Sogard 1997; Laurel et al. 2021), it is unlikely that these shifts in size are simply due to increased growth (Laurel et al. 2016b).

We observed greater predicted length of juvenile cod following a series of marine heatwaves that began in 2014 (Bond et al. 2015), which could be due to earlier spawning prompted by warmer ocean temperatures (Laurel and Rogers 2020). Reproductive phenology for the congener walleye pollock (*Gadus chalcogrammus*)

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Fig. 5. Early season size (predicted length from samples during days of year 184–200): effects of (a) temperature during the egg or larval periods; (b) cod abundance (catch per unit effort, CPUE); (c) day of sampling; (d) bay effects (west–east). Posterior means are shown with 80%, 90%, and 95% CIs, except 95% CIs in panel (d).

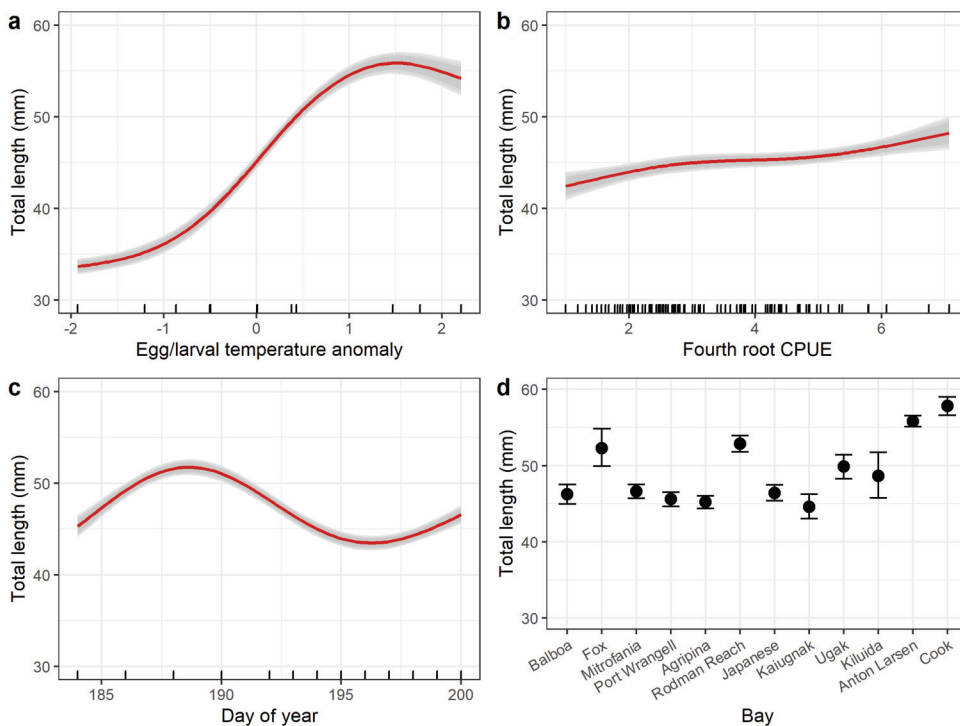


Fig. 6. Cod condition: predicted values of K_{dry} and HSI as functions of (a, d) summer temperature; (b, e) cod abundance; and (c, f) bay (west–east). Posterior means are shown with 80%, 90%, and 95% CIs, or 95% CIs for bay effects; response variables are scaled as zero mean, unit variance.

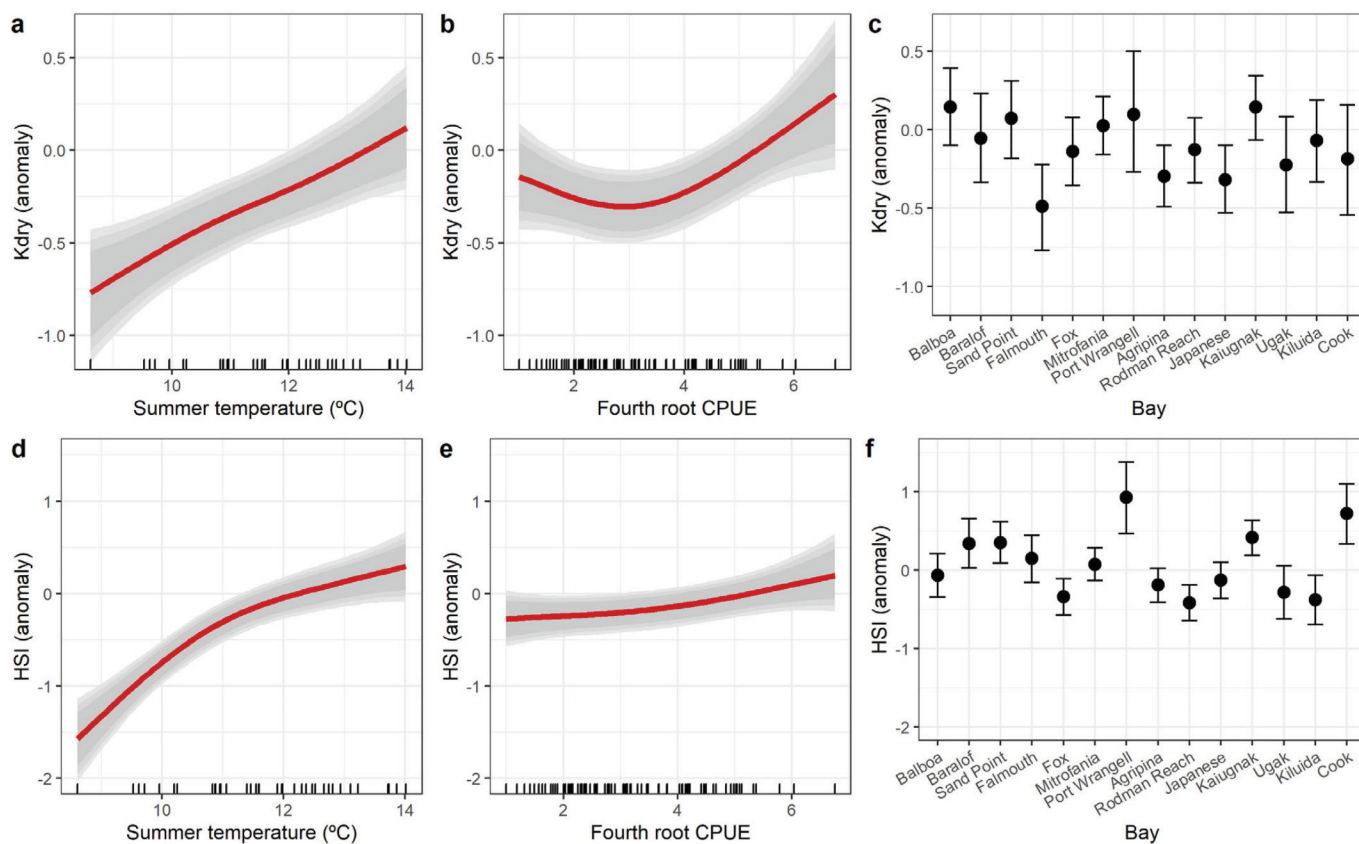


Fig. 7. Estimated effects of (a) summer temperature and (b) cod abundance (catch per unit effort, CPUE) on age-0 cod growth; posterior means are shown with 80%, 90%, and 95% CIs. Growth ($\text{mm}\cdot\text{day}^{-1}$) is scaled as mean 0, unit variance.

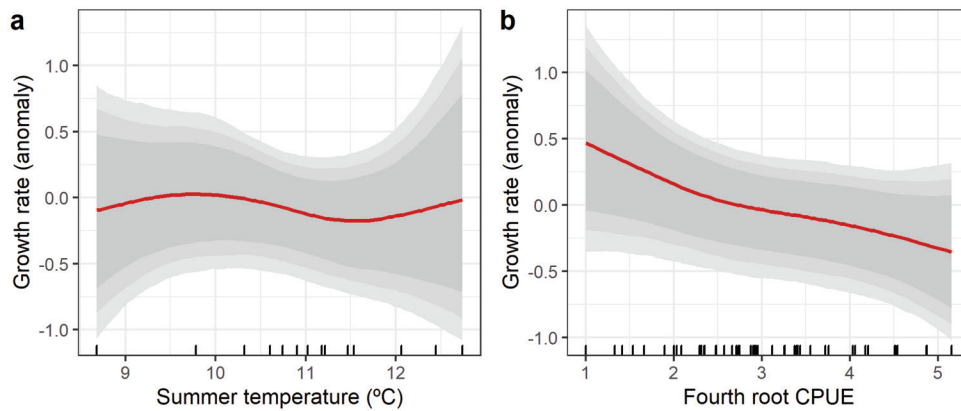
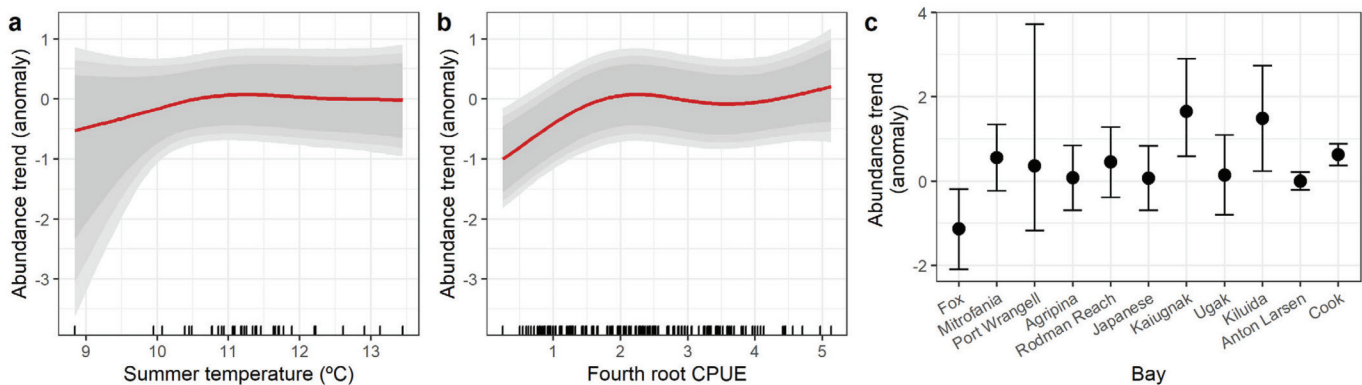


Fig. 8. Changes in age-0 cod abundance as a proxy for survival. Trend is calculated as proportional change in fourth-root transformed CPUE per day, scaled as zero mean, unit variance. Estimated effects of (a) summer temperature, (b) mean abundance (catch per unit effort, CPUE), and (c) bay effects (west-east); posterior means are shown with 80%, 90%, and 95% CIs (a, b), or 95% CI (c).



has shifted earlier in the year in response to warmer winter temperatures (Rogers and Dougherty 2019). Identifying the mechanisms driving temperature-dependent size effects will require additional age and growth data (e.g., otolith analysis), and the cohorts will have to be tracked further in time to determine how these size effects impact survival potential into later age classes.

Condition

We observed large recruitment events since the onset of extreme temperatures in 2014 (Fig. 2); however, it is uncertain whether these cohorts observed at age-0 will successfully overwinter to join the adult population, especially as warming winters may increase the potential for metabolic stress in older juveniles (Geissinger et al. 2021). In this context, our finding that the two condition indices increased with summer temperatures (Fig. 6) suggests the potential for positive effects on overwinter survival and eventual recruitment to the adult population.

The increase in morphological measures of fish condition (K_{dry} and HSI) in this study indicate that increased summer temperatures may improve cod health. Proteins and lipids comprise the major energy reserves in fish, and measures of the tissues containing these reserves provides an indication of the fish’s physiological health (“condition”; Wuenschel et al. 2019). Because lipid analysis of juvenile Pacific cod tissues have not been documented, we apply the well-established relationships documented for age-0 Atlantic cod (*Gadus morhua*), where most of the lipids are stored in the liver (Grant et al. 1998) and the body musculature is

composed largely of proteins (Lambert and Dutil 1997). Hence, liver and fish muscle together represent the bulk of the energy reserves and when examined together can provide a relatively accurate measure of the physiological health of a juvenile cod (Grant and Brown 1999). Fish condition increases with optimal food intake and decreases during periods of food limitation, when energy reserves from both the liver and muscle are catabolized (Lambert and Dutil 1997; Grant and Brown 1999).

Juvenile fish may partition resources to either increase somatic growth or energy reserves (Booth and Keast 1986), with differences in allocation likely dependent on life stage (Copeman et al. 2020; Post and Parkinson 2001). It is likely that warmer summer temperatures allow juvenile Pacific cod to allocate energy to lipid storage without any apparent decrease in somatic growth (i.e., length). While more detailed lipid analyses are required to test this hypothesis, the Fulton’s condition factor (K_{dry}) used in this study provides a relatively accurate measure of protein content compared to standard wet condition measures that can be confounded by water in muscle tissues (Lambert and Dutil 1997; Geissinger et al. 2021). Additional dietary information may help interpret these findings, as it is unclear how food availability and quality may be shifting with varying environmental conditions. For example, in age-0 walleye pollock from the Bering Sea, juveniles were in poorer condition when ocean temperatures were warmer due to a prey shift from lipid-rich to lipid-poor zooplankton in the summer (Siddon et al. 2013). Studies on juvenile Atlantic cod indicate that ingesting high

lipid prey increases lipid storage and body condition (Grant et al. 1998; Grant and Brown 1998, 1999), confirming the importance of prey quality and potential long-term survival benefits (e.g., overwintering success; Geissinger et al. 2021). Given that age-0 Pacific cod eat a wide range of prey items (Abookire et al. 2007), and as there was no effect of bay or density on cod condition, we conclude that food is unlikely to be a limiting resource for juvenile cod in this study area.

Growth

Post-settlement growth did not appear to be related to summer temperature in the nurseries, and this is likely because temperature-dependent growth is nonlinear (Laurel et al. 2016b). Moreover, maximum growth potential for juvenile Pacific cod peaks at ~11.5 °C, and then rapidly declines at laboratory temperatures above 15 °C (Laurel et al. 2016b). Temperature effects on growth were not observed in earlier studies in the Kodiak region (Laurel et al. 2017) or in this study probably because summer temperatures in the years we measured growth ranged slightly below and above this asymptote (9–12.5 °C; Laurel et al. 2016b). Additionally, prey quality or quantity could account for the discrepancy in wild and laboratory growth rates as metabolic costs are higher in the field due to predator avoidance and foraging activity (Jobling 1988; Hurst et al. 2010; Laurel et al. 2016b). While growth response to summer temperatures was not detected in our study, extreme pre-settlement thermal conditions have been associated with alternate thermal reaction norm growth curves in juvenile Pacific cod sampled from the Kodiak region (Hurst et al. 2012). It is therefore possible that growth sensitivity in the summer is buffered by cross life stage acclimatization to thermal conditions set up earlier in the year.

Survival

Survival of juvenile Atlantic cod in nursery areas has been negatively associated with high fish density stemming from increased predator exposure when refuge habitats are overcrowded and therefore unavailable (Gotceitas and Brown 1993; Tupper and Boutilier 1995; Robichaud and Rose 2006). Structured habitat has also been linked to survival of various-sized age-0 Pacific cod (Laurel et al. 2007). However, in our study, we observed a weak positive effect of cod density on post-settlement survival. One explanation is that schooling behavior exhibited by early juveniles (Laurel et al. 2007) may result in substantive benefits such as decreased predation (Laurel et al. 2004), thereby reducing the leading cause of post-settlement mortality (as seen with Atlantic cod; Grabowski et al. 2018).

We were able to detect weak positive density-dependent impacts on early season size, fish condition, and survival, likely due to our fish collections across multiple years of both high and low abundance. In a 90+ year time series analysis of beach seine data in Norway, Rogers et al. (2011) found that density-dependent effects for size in juvenile Atlantic cod were detectable only at very high densities and when using fine-scale bay effects for abundance rather than the larger fjord scale. In the Kodiak region, Laurel et al. (2016a) detected a weak (negative) density-dependent impact on juvenile Pacific cod growth when sites were pooled for each embayment and compared to annual cohort strength. Because our study incorporates the years analyzed by Laurel et al. (2016a; years 2006–2013) and adds years 2014–2020 along with the broader spatial sampling from the extended survey (2018–2020; Fig. 1a) to analyze abundance by site within bay, the combined data allowed for a more robust analysis from which we find no evidence of negative density-dependent effects on survival in the broader Gulf of Alaska.

Conclusions

It is uncertain whether healthy cohorts of Pacific cod seen in recent years following the 2014–2016 recruitment failure will successfully overwinter to join the adult populations, especially as winters warm and increase the potential for metabolic stress in

older juveniles. Our results indicate that ocean warming creates potential tradeoffs for juvenile cod survival in the Gulf of Alaska. Warm winter–spring conditions are associated with very low age-0 abundance, but warm summer temperatures are associated with improved age-0 body condition. Overwinter survival is an important consideration for juvenile (age-0 to age-1) recruitment, and increased condition during warmer summers has potentially positive implications for survival through the first winter (as observed with Atlantic cod; Geissinger et al. 2021). Eventually, future research will elucidate if warming ocean temperatures yield positive implications for first winter survival through increased fish condition (this study) or negative implications due to either increased metabolic demands (Sogard and Olla 2000) or shortened coastal residency (Langan et al. 2021). However, if the trajectory of Pacific cod mirrors that of fish worldwide (Dahlke et al. 2020; Sunday 2020), then the combination of strong thermal sensitivity in cod eggs (Hurst et al. 2010; Laurel and Rogers 2020) and rapid anthropogenic warming of the Gulf of Alaska (Walsh et al. 2018) suggest that any positive thermal effects on juvenile condition will unlikely outweigh the negative effects on year class strength at the pre-settlement life stage.

Competing interests statement

The authors declare there are no competing interests.

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References

- Abookire, A.A., Duffy-Anderson, J.R., and Jump, C.M. 2007. Habitat associations and diet of young-of-the-year Pacific cod near Kodiak, Alaska. *Mar. Biol.* **150**: 713–726. doi:10.1007/s00227-006-0391-4.
- Alderdice, D.F., and Forrester, C.R. 1971. Effect of salinity, temperature, and dissolved oxygen on early development of the Pacific cod (*Gadus macrocephalus*). *J. Fish. Res. Bd. Can.* **28**(6): 883–902. doi:10.1139/f71-130.
- Barbeaux, S., Ferriss, B., Palsson, W., Shotwell, K., Spies, I., Wang, M., and Zador, S. 2020a. Chapter 2: assessment of the Pacific cod stock in the Gulf of Alaska. In *Gulf of Alaska Stock Assessment and Fishery Evaluation report*. North Pacific Fishery Management Council, 1007 West Third, Suite 400, Anchorage, AK 99501, USA. pp. 1–181.
- Barbeaux, S.J., Holsman, K., and Zador, S. 2020b. Marine heatwave stress test of ecosystem-based fisheries management in the Gulf of Alaska Pacific cod fishery. *Front. Mar. Sci.* **7**(703): 1–21. doi:10.3389/fmars.2020.00703. PMID:32802822.
- 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**: 3414–3420. doi:10.1002/2015GL063306.
- Booth, D.J., and Keast, J.A. 1986. Growth energy partitioning by juvenile bluegill sunfish, *Lepomis macrochirus* Rafinesque. *J. Fish Biol.* **28**: 37–45. doi:10.1111/j.1095-8649.1986.tb05139.x.
- Brander, K. 2015. Improving the reliability of fishery predictions under climate change. *Curr. Clim. Change Rep.* **1**: 40–48. doi:10.1007/s40641-015-0005-7.
- Buerkner, P.C. 2017. brms: an R Package for Bayesian multilevel models using Stan. *J. Stat. Softw.* **80**: 1–28. doi:10.18637/jss.v080.i01.
- Carpenter, B., Gelman, A., Hoffman, M.D., Lee, D., Goodrich, B., Betancourt, M., et al. 2017. Stan: a probabilistic programming language. *J. Stat. Softw.* **76**(1): 1–32. doi:10.18637/jss.v076.i01.
- Copeman, L., Spencer, M., Heintz, R., Vollenweider, J., Sremba, A., Helser, T., et al. 2020. Ontogenetic patterns in lipid and fatty acid biomarkers of juvenile polar cod (*Boreogadus saida*) and saffron cod (*Eleginus gracilis*) from across the Alaska Arctic. *Polar Biol.* **43**: 1121–1140. doi:10.1007/s00300-020-02648-9.
- Dahlke, F.T., Wohrlab, S., Butzin, M., and Pörtner, H.-O. 2020. Thermal bottlenecks in the life cycle define climate vulnerability of fish. *Science*, **369**(6499): 65–70. doi:10.1126/science.aaz3658. PMID:32631888.
- 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**: 163–187. doi:10.1016/j.pocan.2009.03.002.

- Doyle, M.J., Strom, S.L., Coyle, K.O., Hermann, A.J., Ladd, C., Matarese, A.C., et al. 2019. Early life history phenology among Gulf of Alaska fish species: strategies, synchronies, and sensitivities. *Deep-Sea Res. Part II*, **165**: 41–73. doi:10.1016/j.dsr2.2019.06.005.
- Dunn, J.R., and Matarese, A.C. 1987. A review of the early life history of northeast Pacific gadoid fishes. *Fish. Res.* **5**: 163–184. doi:10.1016/0165-7836(87)90038-5.
- Field, J.G., Clark, K.R., and Warwick, R.M. 1982. A practical strategy for analyzing multispecies distribution patterns. *Mar. Ecol. Prog. Ser.* **8**: 37–52. doi:10.3354/meps008037.
- Gabry, J., Simpson, D., Vehtari, A., Betancourt, M., and Gelman, A. 2019. Visualization in Bayesian workflow. *J. R. Stat. Soc. Ser. A*, **182**: 389–402. doi:10.1111/rssa.12378.
- Geissinger, E.A., Gregory, R.S., Laurel, B.J., and Snelgrove, P.V.R. 2021. Food and initial size influence overwinter survival and condition of a juvenile marine fish (age-0 Atlantic cod). *Can. J. Fish. Aquat. Sci.* **78**(4): 472–482. doi:10.1139/cjfas-2020-0142.
- Gelman, A., Goodrich, B., Gabry, J., and Vehtari, A. 2019. R-squared for Bayesian regression models. *Am. Stat.* **73**: 307–309. doi:10.1080/00031305.2018.1549100.
- Goteceitas, V., and Brown, J.A. 1993. Substrate selection by juvenile Atlantic cod (*Gadus morhua*): effects of predation risk. *Oecologia*, **93**: 31–37. doi:10.1007/BF00321187. PMID:28313770.
- Grabowski, J.H., Conroy, C.W., Gittman, R.K., Kelley, J.T., Sherman, S., Sherwood, G.D., and Wipplhauser, G. 2018. Habitat associations of juvenile cod in nearshore waters. *Rev. Fish. Sci. Aquacult.* **26**(1): 1–14. doi:10.1080/23308249.2017.1328660.
- Grant, S.M., and Brown, J.A. 1998. Nearshore settlement and localized populations of age 0 Atlantic cod (*Gadus morhua*) in shallow coastal waters of Newfoundland. *Can. J. Fish. Aquat. Sci.* **55**(6): 1317–1327. doi:10.1139/f97-310.
- Grant, S.M., and Brown, J.A. 1999. Variation in condition of coastal Newfoundland 0-group Atlantic cod (*Gadus morhua*): field and laboratory studies using simple condition indices. *Mar. Biol.* **133**: 611–620. doi:10.1007/s002270050501.
- Grant, S.M., Brown, J.A., and Boyce, D.L. 1998. Enlarged fatty livers of small juvenile cod (*Gadus morhua* L.): a comparison of laboratory cultured and wild juveniles. *J. Fish. Biol.* **52**: 1105–1114. doi:10.1111/j.1095-8649.1998.tb00958.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*, **165**: 113–126. doi:10.1016/j.dsr2.2019.05.007.
- Hurst, T.P. 2007. Causes and consequences of winter mortality in fishes. *J. Fish Biol.* **71**: 315–345. doi:10.1111/j.1095-8649.2007.01596.x.
- Hurst, T.P., Cooper, D.W., Scheingross, J.S., Seale, E.M., Laurel, B.J., and Spencer, M.L. 2009. Effects of ontogeny, temperature, and light on vertical movements of larval Pacific cod (*Gadus macrocephalus*). *Fish. Oceanogr.* **18**: 301–311. doi:10.1111/j.1365-2419.2009.00512.x.
- 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**: 382–392.
- Hurst, T.P., Munch, S.B., and Lavelle, K.A. 2012. Thermal reaction norms for growth vary among cohorts of Pacific cod (*Gadus macrocephalus*). *Mar. Biol.* **159**: 2173–2183. doi:10.1007/s00227-012-2003-9.
- Ings, D.W., Schneider, D.C., and Methven, D.A. 1997. Detection of a recruitment signal in juvenile Atlantic cod (*Gadus morhua*) in coastal nursery areas. *Can. J. Fish. Aquat. Sci.* **54**(S1): 25–29. doi:10.1139/f96-152.
- Jobling, M. 1988. A review of the physiological and nutritional energetics of cod, *Gadus morhua* L., with particular reference to growth under farmed conditions. *Aquaculture*, **70**(1): 1–19. doi:10.1016/0044-8486(88)90002-6.
- Lambert, Y., and Dutil, J.D. 1997. Can simple condition indices be used to monitor and quantify seasonal changes in the energy reserves of cod (*Gadus morhua*)? *Can. J. Fish. Aquat. Sci.* **54**(S1): 104–112. doi:10.1139/f96-149.
- Langan, J.A., Puggioni, G., Oviatt, C.A., Henderson, M.E., and Collie, J.S. 2021. Climate alters the migration phenology of coastal marine species. *Mar. Ecol. Prog. Ser.* **660**: 1–18. doi:10.3354/meps13612.
- Laurel, B.J., and Rogers, L.A. 2020. Loss of spawning habitat and prerecruits of Pacific cod during a Gulf of Alaska heatwave. *Can. J. Fish. Aquat. Sci.* **77**(4): 644–650. doi:10.1139/cjfas-2019-0238.
- Laurel, B.J., Gregory, R.S., Brown, J.A., Hancock, J., and Schneider, D.S. 2004. Behavioural consequences of density-dependent habitat use in juvenile cod (*Gadus morhua*): Role of movement and aggregation. *Mar. Ecol. Prog. Ser.* **272**: 257–270. doi:10.3354/meps272257.
- Laurel, B.J., Stoner, A.W., Ryer, C.H., Hurst, T.P., and Abookire, A.A. 2007. Comparative habitat associations in juvenile Pacific cod and other gadids using seines, baited cameras and laboratory techniques. *J. Exp. Mar. Biol. Ecol.* **351**: 42–55. doi:10.1016/j.jembe.2007.06.005.
- Laurel, B.J., Ryer, C.H., Knoth, B., and Stoner, A.W. 2009. Temporal and ontogenetic shifts in habitat use of juvenile Pacific cod (*Gadus macrocephalus*). *J. Exp. Mar. Biol. Ecol.* **377**: 28–35. doi:10.1016/j.jembe.2009.06.010.
- 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., Knoth, B.A., and Ryer, C.H. 2016a. Growth, mortality, and recruitment signals in age-0 gadids settling in coastal Gulf of Alaska. *ICES J. Mar. Sci.* **73**(9): 2227–2237. doi:10.1093/icesjms/fsw039.
- Laurel, B.J., Spencer, M., Iseri, P., and Copeman, L.A. 2016b. Temperature-dependent growth and behavior of juvenile Arctic cod (*Boreogadus saida*) and co-occurring North Pacific gadids. *Polar Biol.* **39**: 1127–1135. doi:10.1007/s00300-015-1761-5.
- 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., Hunsicker, M.E., Ciannelli, L., Hurst, T.P., Duffy-Anderson, J., O'Malley, R., and Behrenfeld, M. 2021. Regional warming exacerbates match/mismatch vulnerability for cod larvae in Alaska. *Progr. Oceanogr.* **193**: 1–11. doi:10.1016/j.pocean.2021.102555.
- Lewandoski, S.A., Bishop, M.A., and McKinzie, M.K. 2018. Evaluating Pacific cod migratory behavior and site fidelity in a fjord environment using acoustic telemetry. *Can. J. Fish. Aquat. Sci.* **75**(11): 2084–2095. doi:10.1139/cjfas-2017-0432.
- Litzow, M.A., Abookire, A.A., Duffy-Anderson, J.T., Laurel, B.J., Malick, M.J., and Rogers, L.A. 2022. Predicting year class strength for climate-stressed gadid stocks in the Gulf of Alaska. *Fish. Res.* **249**: 106250. doi:10.1016/j.fishres.2022.106250.
- Litzow, M.A., Malick, M.J., Abookire, A.A., Duffy-Anderson, J., Laurel, B.J., Ressler, P.H., and Rogers, L.A. 2021. Using climate attribution statistic to inform judgments about changing fisheries sustainability. *Sci. Rep.* **11**, 23924. doi:10.1038/s41598-021-03405-6.
- Lunzmann-Cooke, E.L., Gregory, R.S., Snelgrove, P.V.R., Cote, D., and Fuentes-Yaco, C. 2021. Spatial, temporal, and environmental influences on Atlantic cod *Gadus morhua* offshore recruitment signals in Newfoundland. *Mar. Ecol. Prog. Ser.* **673**: 151–164. doi:10.3354/meps13806.
- Methven, D.A., and Bajdik, C. 1994. Temporal variation in size and abundance of juvenile Atlantic cod (*Gadus morhua*) at an inshore site off eastern Newfoundland. *Can. J. Fish. Aquat. Sci.* **51**(1): 78–90. doi:10.1139/f94-010.
- Moss, J.H., Zaleski, M.F., and Heintz, R.A. 2016. Distribution, diet, and energetic condition of age-0 walleye pollock (*Gadus chalcogrammus*) and Pacific cod (*Gadus macrocephalus*) inhabiting the Gulf of Alaska. *Deep-Sea Res. II*, **132**: 146–153. doi:10.1016/j.dsr2.2015.03.014.
- 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. II*, **109**: 204–214. doi:10.1016/j.dsr2.2013.12.006.
- Post, J.R., and Parkinson, E.A. 2001. Energy allocation strategy in young fish: allometry and survival. *Ecology*, **82**: 1040–1051. doi:10.1890/0012-9658(2001)082[1040:EASIFY]2.0.CO;2.
- R Core Team. 2018. R: a language and environment for statistical computing. vol. 3.4.3. R Foundation for Statistical Computing, Vienna, Austria. Available from <https://www.R-project.org>.
- Robichaud, D., and Rose, G.A. 2006. Density-dependent distribution of demersal juvenile Atlantic cod (*Gadus morhua*) in Placentia Bay, Newfoundland. *ICES J. Mar. Sci.* **63**: 766–774. doi:10.1016/j.icesjms.2005.12.002.
- Rogers, L.A., and Dougherty, A.B. 2019. Effects of climate and demography on reproductive phenology of a harvested marine fish population. *Global Change Biol.* **25**: 708–720. doi:10.1111/gcb.14483.
- Rogers, L.A., Stige, L.C., Olsen, E.M., Knutsen, H., Chan, K.S., and Stenseth, N.C. 2011. Climate and population density drive changes in cod body size throughout a century on the Norwegian coast. *Proc. Natl. Acad. Sci. U.S.A.* **108**(5): 1961–1966. doi:10.1073/pnas.1010314108. PMID:21245301.
- Siddon, E.C., Heintz, R.A., and Mueter, F.J. 2013. Conceptual model of energy allocation in walleye pollock (*Theragra chalcogramma*) from age-0 to age-1 in the southeastern Bering Sea. *Deep-Sea Res. II*, **94**: 140–149. doi:10.1016/j.dsr2.2012.12.007.
- Sogard, S.M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bull. Mar. Sci.* **60**: 1129–1157.
- Sogard, S.M., and Olla, B.L. 2000. Endurance of simulated winter conditions by age-0 walleye pollock: effects of body size, water temperature and energy stores. *J. Fish Biol.* **56**(1): 1–21. doi:10.1111/j.1095-8649.2000.tb02083.x.
- Spies, I., Gruenthal, K.M., Drinan, D.P., Hollowed, A.B., Stevenson, D.E., Tarpey, C.M., and Hauser, L. 2020. Genetic evidence of a northward range expansion in the eastern Bering Sea stock of Pacific cod. *Evol. Appl.* **13**(2): 362–375. doi:10.1111/eva.12874.
- 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**: 859–897. doi:10.1016/j.csr.2004.02.007.
- 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**: 396–407.
- Stige, L.C., Hunsicker, M.E., Bailey, K.M., Yaragina, N.A., and Hunt, G.L., Jr. 2013. Predicting fish recruitment from juvenile abundance and environmental indices. *Mar. Ecol. Prog. Ser.* **480**: 245–261. doi:10.3354/meps10246.
- Sunday, J. 2020. When do fish succumb to heat? *Science*, **369**(6499): 35–36. doi:10.1126/science.abd1272. PMID:32631884.
- Tupper, M., and Boutilier, R.G. 1995. Effects of habitat on settlement, growth, and postsettlement survival of Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* **52**(9): 1834–1841. doi:10.1139/f95-176.
- Vehtari, A., Gelman, A., and Gabry, J. 2017. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Stat. Comput.* **27**(5): 1413–1432. doi:10.1007/s11222-016-9696-4.

- 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](https://doi.org/10.1175/BAMS-D-17-0105.1).
- Wood, S.N. 2003. Thin plate regression splines. *J. R. Stat. Soc. Ser. B Stat. Methodol.* **65**: 95–114. doi:[10.1111/1467-9868.00374](https://doi.org/10.1111/1467-9868.00374).
- Wuenschel, M.J., McElroy, W.D., Oliveira, K., and McBride, R.S. 2019. Measuring fish condition: an evaluation of new and old metrics for three species with contrasting life histories. *Can. J. Fish. Aquat. Sci.* **76**(6): 886–903. doi:[10.1139/cjfas-2018-0076](https://doi.org/10.1139/cjfas-2018-0076).
- Yau, K.K.W., Wang, K., and Lee, A.H. 2003. Zero-inflated negative binomial mixed regression modeling of over-dispersed count data with extra zeros. *Biom. J.* **45**: 437–452. doi:[10.1002/bimj.200390024](https://doi.org/10.1002/bimj.200390024).
- Zuur, A.F., Ieno, N., Walker, N., Saveliev, A.A., and Smith, G.M. 2009. *Mixed effects models and extensions in ecology with R*. Springer.