

Regional warming exacerbates match/mismatch vulnerability for cod larvae in Alaska

Benjamin J. Laurel^{1*}, Mary E. Hunsicker^{2*}, Lorenzo Ciannelli³, Thomas P. Hurst¹, Janet Duffy-Anderson⁴, Robert O'Malley⁵ and Michael Behrenfeld⁵

¹ 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

² Estuarine and Ocean Ecology, Northwest Fisheries Science Center, National Marine Fisheries Service, NOAA, Hatfield Marine Science Center, Newport, OR 97365, USA

³ College of Earth, Ocean, and Atmospheric Sciences, Oregon State University, Corvallis, Oregon 97331, USA.

⁴ Recruitment Processes Program, Resource Assessment and Conservation Engineering Division, Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle, WA 98115, USA

⁵ Department of Botany and Plant Pathology, Oregon State University, Corvallis, Oregon 97331, USA.

*Corresponding author

Abstract

The match-mismatch hypothesis predicts that variability in spring primary production will increase starvation risk for marine fish populations. However, it is often unclear whether the synergic effects of temperature, phytoplankton phenology and metabolic demands of fish support these prediction within and across regions. In this study, we combine experimentally-derived rates of larval survival in relation to water temperature with satellite remote-sensing estimates of chlorophyll *a* and sea surface temperature to predict habitat quality of first feeding Pacific cod (*Gadus macrocephalus*) larvae in two adjacent large marine ecosystems; southeast Bering Sea (BS) and Gulf of Alaska (GOA). Predictions are made from 1998 to 2019, a period comprised of both warm and cool springs, followed by a series of extreme warming events (heatwaves) beginning in 2014. Model results indicate that the drivers of a mismatch between cod larvae and their food is fundamentally different between the two systems. In the GOA, larval habitat suitability is highly dependent on interannual fluctuations in sea surface temperature that regulate yolk reserves in embryos. In contrast, larval habitat suitability in the BS was more sensitive to the onset of the surface expression of Chl *a* production. The combined effects of changes in timing of Chl *a* and increased metabolic demands of larvae were captured by the model during the GOA marine heatwave (2014-16, 2019), which predicted significant loss of larval habitat across the entire region. These habitat models integrate important spatial, temporal and physiological components of match-mismatch theory that can be used to examine marine fish populations experiencing different rates of climate stress across regions.

KEYWORDS: Pacific cod, phenology, spawning dynamics, phytoplankton bloom, first-feeding larvae, marine heatwaves, *Gadus macrocephalus*

1. Introduction

Since the pioneering work of Johan Hjort (1914) on the importance of year-class strength as a major determinant of fish population abundance, the survival of fish early life stages has come to the forefront of fisheries ecology and resource management (Leggett & DeBlois, 1994; Bailey *et al.*, 2005; Houde, 2008). Avoiding predation, starvation, adverse habitats, diseases, and physiological stress are some of the natural challenges that fish need to overcome while developing from an egg to a reproductive individual. Many marine fish begin their development in the water column as weak swimming larvae and are considered to be more physiologically vulnerable to external physical and biological pressures than other life stages (Pörtner & Peck, 2010). At hatching, fish larvae have an undeveloped mouth and digestive system during their first days of life and hence feed on nutritional reserves – the yolk sac. Hjort (1914) postulated that high larval mortalities rates exist during the passage from endogenous to exogenous feeding at the end of the yolk-sac stage. At this time fish larvae are confronted with the need to find sufficient food resources or starve (Leggett & DeBlois, 1994).

Cushing (1975) hypothesized that the temporal match between the peak of larval production and prey availability is a key factor leading to higher larval survival. Cushing's hypothesis, known as the match-mismatch hypothesis (MM), was based on observations that the timing of larval production was seemingly relatively fixed in temperate and sub-arctic seas, whereas the timing of phytoplankton blooms was highly variable. Copepod egg and nauplii production, the suitable prey for many first-feeding marine fish larvae, is often linked to primary production (e.g., Fortier *et al.*, 1992), setting up the potential to generate mass mortalities in annual cohorts through temporal

mismatches between larvae and their food. The match-mismatch framework has also expanded to include spatial components of marine fish larvae and prey (e.g., Ferreira *et al.*, 2020; Brosset *et al.* 2020), drawing upon the notion that concentrated patches of larval abundance and prey production enhance feeding success at such locations (Lasker, 1978, 1981).

In light of current global warming trends, match-mismatch processes are likely to become more consequential as underlying environmental conditions continue to change (Durant *et al.*, 2007). Since Hjort's and Cushing's original hypotheses, marine and atmospheric scientists have increased our knowledge regarding the non-stationarity of earth-atmosphere ocean linkages and the phenology of marine populations (Litzow *et al.*, 2020). For example, water temperature can greatly influence the metabolism and nutritional demands of fish larvae in marine ecosystems, and thus can modulate the negative outcome of a mismatch (Beaugrand *et al.*, 2003). Warming can also influence the timing of spring phytoplankton blooms due to an alteration in water stratification (Behrenfeld *et al.*, 2006; Marinov *et al.*, 2013; Behrenfeld & Boss, 2018), and may influence phytoplankton biomass on a global scale (Behrenfeld *et al.*, 2006; but see Behrenfeld *et al.*, 2016). These changing environmental conditions and metabolic demands, all of which are indirectly tied to warming, could potentially result in "super mismatch events" (Laurel *et al.*, 2011) with low survival potential across an entire region.

In Alaska, major groundfish fisheries are supported by two large marine ecosystems with different physical environments, the southeastern Bering Sea (BS) and the Gulf of Alaska (GOA). The GOA has a narrow shelf, interspersed with canyons and troughs and is punctuated by several small islands (Figure 1). Apart from shallow regions

inside bays or fjords, the GOA shelf stays ice-free over the winter (Stabeno *et al.*, 2004). In contrast, the BS has a very wide and relatively shallow shelf region. Average width and depth of the BS shelf are about 300 km and 60 m, respectively (Coachman, 1986). Much of the BS shelf area has historically been covered by seasonal sea ice, but has remained largely ice-free in recent winters (Stabeno & Bell, 2019; Stevenson & Lauth, 2019). Loss of sea ice has corresponded with poleward shifts in multiple groundfish species (Barbeaux & Hollowed, 2018). In the GOA, warming has resulted in a wide range of measurable impacts across the entire ecosystem in the form of reduced energetic condition of individual fish and loss of population biomass of key groundfish (Barbeaux *et al.*, 2020). While spring bottom-up processes are hypothesized to play a central role ecosystem function (Sigler *et al.*, 2016; Kimmel *et al.*, 2018), the mechanistic frameworks by which temperature and food availability are impacting key fish species have generally been restricted to the post-larval summer/fall period e.g., age-0 juveniles through adults (Heintz *et al.*, 2013; Duffy-Anderson *et al.*, 2017; Zador & Yasumiishi, 2017; von Biela *et al.*, 2019; Yang *et al.*, 2019).

Pacific cod *Gadus macrocephalus* support major fisheries in the North Pacific and are key foodweb components of both the BS and GOA ecosystems. Unlike Atlantic cod (*Gadus morhua*), Pacific cod are single batch spawners and potentially at higher risk to prey mismatch due to a very narrow reproductive window in the spring. During the late 1970s and early 1980s, Pacific cod exhibited large increases in population in both the BS and GOA following a period of warming and community restructuring (Benson *et al.*, 2002; Litzow, 2006). However, recent unprecedented warming has corresponded with significant fisheries management challenges for each region. In the GOA, a complete

closure of the Pacific cod federal fishery was issued in 2020 following poor recruitment and a loss of adult biomass after two closely spaced marine heatwaves (2014-16, 2019) (Barbeaux *et al.*, 2019; Laurel & Rogers, 2020). In the BS, older stages of cod have shifted to deep water in the summer and extended their range outside the historical survey area to the north (Barbeaux & Hollowed, 2018; Stevenson & Lauth, 2019; Thompson & Thorson, 2019). While the realized impacts of warming on cod populations are varied across regions (Planque & Frédou, 1999; Drinkwater, 2005; Kristiansen *et al.*, 2011), a mechanistic understanding of how temperature impacts survival potential can be used to develop spatially relevant management strategy evaluations (MSE) and better preparedness for potential recruitment failure.

The objective of this study was to use mechanistic models to examine how match-mismatch dynamics may have impacted survival potential of larval Pacific cod and whether these processes differed between the GOA and BS. Our analysis takes into account the dynamic metabolic demands of Pacific cod larvae across space in relation to changes in the annual timing and magnitude of spring productivity in each region. The integration of physiological, temporal and spatial elements in a time-series analysis is an important and novel aspect of this study that could be applied to other species and regions. Conceivably, the synergistic interaction between temperature and timing may affect larval survival more than either factor in isolation. Our emphasis on predictions of early life stage survival also has important implications for the composition and population dynamics of these and other cod species globally.

2. Methods

2.1. Distribution and phenology of larval cod and phytoplankton production

The neighboring GOA and BS regions (Figure 1) have been surveyed for ichthyoplankton in the spring since the 1970's as part of the Alaska Fisheries Science Center's Ecosystems and Fisheries Oceanography Coordinated Investigations program (EcoFOCI, formerly FOCI). These collections were used to characterize the location of first feeding larval cod and to define their average phenology integrated across all years of the survey. First-feeding larvae (< 1 month old) were assigned by size in field collections (≥ 4.5 and ≤ 7.0 mm SL) based on known size-age relationships from laboratory experiments (Hurst *et al.*, 2010; Laurel *et al.*, 2011). However, we recognize that survey design, growth and mortality can all influence size-based estimates of spawn timing from larval samples (Rogers & Dougherty, 2019).

We used Generalized Additive Models (GAM) to define the spatial and temporal features of larval production for both ecosystems. The GAM allows the regression of a dependent variable on a set of independent variables through the use of smoothing functions. Thus, there is no need to specify *a priori* the functional relationship between the response variable and the model covariates (Wood, 2017). In this application, station-by-station first feeding cod larval abundance was modeled as a function of location (latitude and longitude), water depth, day of year, and time of the day to develop an integrated average across all years. The day of the year effect is particularly important because it defines the larval production phenology.

Satellite remote sensing data spanning the SeaWiFS and MODIS eras were used to characterize the spatial and temporal features of surface chlorophyll *a* (Chl *a*) and sea surface temperature (SST) in the study area. The concentration of Chl *a* provides a first-

order index of phytoplankton biomass and net primary production [‘first order’ because Chl *a* also varies with physiological changes in response to nutrient and light availability (Behrenfeld et al. 2005, 2006, 2016). It is also important to note that cod larvae do not directly eat phytoplankton, but rather copepod nauplii that are at least one trophic level above algae. Incorporating a time lag with the timing of Chl *a* is a better indicator of the timing of secondary prey production (see below), but we recognize that spring primary production is just an index and can be out of phase with secondary production through other ecological processes not addressed in this study e.g., overwintering nauplii (Napp *et al.*, 1996). Satellite chlorophyll and 4-micron sea surface temperature data (SST4) estimated with MODIS-Aqua (years 2003-2019) were obtained from the NASA OceanColorWeb (<https://oceancolor.gsfc.nasa.gov>), while AVHRR SST and Chl *a* data corresponding to the SeaWiFS era (years 1998-2002) were obtained from the PO.DAAC (<https://podaac-www.jpl.nasa.gov>). Spatial resolution of the ocean color products was approximately 9 km (1/12 of a degree spacing in latitude and longitude for both MODIS and SeaWiFS, and AVHRR having a slightly broader spacing), while the temporal resolution used in this study were 8-day averages. The most recent processing was used for both SeaWiFS (R2014.0) and MODIS (R2018.0).

We limited Chl *a* and SST data analyses to the time window of the 57th (March 1st) to 209th (July 27th) day of the year, which is a broad period that encompasses the rise and fall of both the spring phytoplankton concentration and peaks of first feeding larval production (See Supplemental Figure S1.1 and S1.2). First, for each year and area within the two study regions (GOA and EBS) where cod larvae were present across all years (See Figure S2.1), we obtained a spatially-averaged time series of Chl *a* spanning March

1st to July 27th in 8-d time steps (corresponding to those of the remote sensing observations). The March-July time window is a broad period that encompasses the rise and fall of both the spring phytoplankton concentration and peaks of first feeding larval production. Then, a thin plate regression spline was fit to the yearly Chl *a* time series. The start and end of the surface expression of the phytoplankton concentration was assigned the day of the year at which the predicted Chl *a* biomass reached one-third and one-half of the yearly maximum, respectively. The duration of the subsequent high concentration was determined from the number of days between the pre- and post-thresholds of peak Chl *a* concentration. The highest yearly model predicted Chl *a* value within the March-July time window constituted the yearly amplitude (magnitude) of Chl *a* in the model. For both study systems, the pre peak Chl *a* biomass threshold was above the winter background level (Figure S1.1 and S1.2). Once the threshold was reached, Chl *a* values remained relatively elevated and in some cases above the one-third threshold throughout the summer, particularly in the GOA region. Therefore, the post peak Chl *a* biomass threshold was set at one half, rather than one third of the highest yearly Chl *a* observation.

2.2. Index of cod habitat quality

The influence of temperature on starvation resistance of newly hatched Pacific cod larvae was experimentally examined by Laurel *et al.* (2008) to define the “point-of-no-return”, approximated as the time at which larval abundance declines by 50% of its initial number. This physiological state is considered the point at which larvae are no longer strong enough to feed (Yin & Blaxter, 1987). Here we reanalyze the data from

that study for incorporation into our analysis of cod habitat quality. We used a GAM to fit the experimental logit-transformed survival data to predict larval survival in the field from observational data. The logit transformation was necessary as the survival data span from 0 to 1. For survival data corresponding to 0 (n=65 out of 499) or 1 (n=28 out of 499) we added and subtracted the lowest non-zero survival value, respectively. The GAM model estimated survival fraction as a function of time (days without food d), relative hatch time (h), and the interaction between temperature (T °C), and h . Relative hatch time (h) is a categorical variable and indicates the relative timing of egg hatching in the overall hatch cycle of an egg batch released by a female: *early* (~35% hatch), *middle* (~60% hatch) and *late* (>80% hatch). Typically, early hatching eggs result in larvae with larger yolk reserves enabling them to survive longer without food (Laurel *et al.* 2008). The interaction was necessary because the relationship between larval survival and days without food changed depending on the hatching type and water temperature. In addition, models without interaction terms were statistically inferior (based on the Generalized Cross Validation, gCV) and had aberrant residual patterns. The model formulation can be summarized as follows:

$$S_i = b_{j,k} + I_{j,k}g(d_i) + e_i \quad (1)$$

where S_i is larval survival measured at day d_i post hatch; j and k are indices for relative hatch time (3 levels) and temperature treatment (5 levels), respectively, $I_{j,k}$ are indicator variables with possible values being 0 or 1, depending on the level of the temperature treatment and hatching type (total of 8 indicator variables), b is the model intercept (also

assumed to change in relation to hatching and temperature treatment), and g is a univariate thin plate regression spline for the smooth effect of day (d_i).

For each spatial unit of Chl a satellite data (pixel) and for the two study areas, we derived an index of cod habitat quality from 1) the days of mismatch between first feeding cod production and onset of Chl a surface expression, 2) intervening SST, and 3) experimentally derived relationships between cod larval survival and days without food (i.e., food availability), and water temperature, assuming the survival function of the early egg hatch release which is a conservative estimate of larval survival in the absence of food (Figure 2). In line with what was done for describing the system-wide phenology of spring Chl a productivity, the start of surface spring Chl a production for each pixel occurred when the Chl a value of the pixel reached one-third of the yearly maximum. In addition, to estimate days of mismatch in each year, we added seven days to the predicted day of pre-peak Chl a concentration to account for the lag between production of phytoplankton and zooplankton, which are then consumed by larval Pacific cod (Ken Coyle pers. communication). The intervening water temperature was calculated as the average SST during the days that the larvae remained without food. The model assumed a ubiquitous distribution of larvae across the region given the incomplete sampling coverage across years.

Cod habitat quality was expressed as a percentage of cod larvae that survived from hatching to the encounter with food. The collection of all larval survival probabilities within each region forms a landscape of larval survival probabilities. We assume that once a habitat unit meets the Chl a onset criteria, the respective larval survival remains unchanged until the end of the simulation (i.e., July 27th). To condense

the spatially-explicit landscape of survival probabilities into a single metric, we established a yearly index of cod habitat quality, expressed as the percentage of total available habitat in which survival was equal or higher than 40%. We note that the specific threshold used has little impact on our interannual comparisons, as on a relative scale habitat quality would increase or decrease by a similar amount in each year.

To compare cod habitat quality within the GOA and EBS, we quantified the mean and variance of estimated habitat quality in defined sub-areas. We divided the GOA into three sub-areas: western (159-170°W), central (154-159°W), and eastern (147-154°W). The BS was divided into two sub-areas: north and south of 55°N. We tested for differences in habitat quality between subareas (and regions) using linear models, where the response variable was spatially explicit values of habitat quality and the explanatory variables included year and sub-area (or region). We used the same method to test for regional differences in the time series of onset, duration, and magnitude of peak Chl *a* concentration. Lastly, we tested for abrupt shifts in our derived time-series of habitat quality, Chl *a* concentration metrics (onset, duration, and magnitude), and SST for the GOA and BS regions. We applied segment regression models to the metrics and identified whether models with 0, 1 or more breakpoints best fit the time series. The best models were selected based on the F-statistic and the Bayesian Information Criteria (BIC) (Zeileis *et al.*, 2003). All statistical analyses were conducted in R (R Core Team 2020). Statistical tests for breakpoints were done using the ‘strucchange’ package (Zeileis *et al.*, 2003). The ‘mgcv’ package (Wood, 2017) was used to run the Generalized Additive Models.

3. Results

3.1. Experimental survival, distribution, and phenology of cod larvae

The survival of experimentally-reared and fasting cod larvae is considerably lower at higher water temperatures (Figure 2). In our analysis of the experimental data for Pacific cod, this period varied from about 17 days at 0°C, to about 7 days at 8°C (Figure 2). The GAM formulation used to model the experimental data (Eq. 1) explained 93.1% of the experimental survival variance. Residual patterns did not show signs of heteroscedasticity, outlying observations or departure from normality. Given the high percentage of variance explained and the robustness of the residual diagnostic, we felt confident in applying the specified model to predict the survival of first feeding cod larvae from ocean observation data.

In the GOA first feeding cod larvae were found throughout the sampled regions with peak densities north and east of Kodiak Island and in various high density pockets from the Shumagin Islands to Unimak Pass (Figure 3). In the BS, first feeding cod larvae distribution had a clear center of aggregation in the Unimak region. Cod larvae were also found around the Pribilof Islands and along the shelf edge of the BS, but at lower density. It should be noted that the intensity of ichthyoplankton sampling in the BS is very limited compared to that in the GOA (with inconsistent effort along the shelf edge and Pribilof Islands regions), and therefore spatial patterns are incomplete and less accurate in their reconstruction (Figure 3). While the habitat model was not weighted by larval density, we recognize that model outputs in these aggregation areas may be more significant than areas where few larvae were observed.

Day of year had a significant effect on first feeding larval abundance (Table 1), confirming the existence of strong seasonality in cod larval production. Peak larval production in the BS averaged about 4-5 days earlier than in the GOA across all years (Figure S2.1), but the shape of the production curve in the BS was dependent on the inclusion of the extended spatial survey further north (Figure S2.2). The abundance peak estimates were similar for both BS surveys (May 12th vs May 13th), but slightly earlier than the May 17th estimated for the GOA. In the GOA, the spread of the cod larvae phenology curve was greater than that of the BS, with possible additional but minor peaks of larval abundance found on April 29th and June 8th. This higher phenological variability of the GOA may be due to sampling artifacts from the survey or an indication of more complex stock structure in the region.

3.2. SST phenology and chlorophyll *a* in BS and GOA

Within the observed distribution of first-feeding larval cod, interannual water temperature was 1.5 to 3°C warmer in the GOA than in the BS (Figure 4). The derived SST climatology steadily increased in both basins from 1999 to 2019 by an overall amount of about 3.5°C and 3.0°C in the GOA and BS, respectively. Based on our climatology, 2016 was the warmest year for cod larvae in the time series of each region, but was briefly surpassed by 2019 in the BS time series during the spring, March to May (Figure S3.1 and S3.2).

There were also notable differences in the time series of the averaged Chl *a* concentration estimates between the GOA and BS (Figure 4). In the GOA, Chl *a* concentration was less variable than the BS in the early part of time series, which is

expected since vast regions of the BS experience variable (albeit declining) annual sea ice extent during spring. After 2015, we detected a significant shift to early increases in Chl *a* concentration following some of the warmest years on records for both the GOA and BS ($p < 0.01$, Table S4.1). Prior to 2015, the pre-peak Chl *a* biomass threshold in the GOA historically occurred within the month of April, while in the BS it ranged in start times from early March to as late as the second half of May. In the GOA, the duration of peak Chl *a* concentration ranged from about 30 – 100 days (in 2004 and 2011, respectively) compared to 20 – 80 days in the BS (in 1998 and 2001, respectively). The magnitude (amplitude) of Chl *a* concentration ranged from $\sim 2 \text{ mg m}^{-3}$ (1998, 2008) to $\sim 7.5 \text{ mg m}^{-3}$ (2000) in the GOA, and from $\sim 2 \text{ mg m}^{-3}$ (2011) to $\sim 6.7 \text{ mg m}^{-3}$ (2004) in the BS. There was no significant difference in the mean duration or magnitude of peak Chl *a* concentration between the two systems ($p > 0.05$), nor did we detect temporal shifts in these time series (Figure 4; Table S4.1). Overall, we did not find evidence of an effect of incumbent SSTs on the pre-peak threshold, duration, or magnitude of peak Chl *a* concentration in either the BS or GOA.

Peak larval cod production in the GOA occurred between the pre- and post-peak Chl *a* concentration thresholds in the time series (Figure 4; Figure S1.1). In contrast, the BS pre-peak Chl *a* concentration threshold was closer in time to the peak of larval production, and in some years (e.g., 2006-07), the spring bloom was just beginning during larval peak abundance (Figure 4; Figure S1.2). From the observed trends, two inferences can be made. One is that food mismatches in both systems are more likely to occur as a consequence of a late pre-peak in Chl *a* concentration, rather than an early one. Following the onset of Chl *a*, concentrations remained elevated for a sufficient duration

to overlap with larval production timing, even in early bloom years (Figure 4). The other inference is that Bering Sea cod may be more vulnerable to temporal mismatches than the GOA cod if the Bering Sea onset of Chl *a* occurs later in the year or if Pacific cod spawn phenology shifts to earlier times in the spring as baseline conditions continue to warm (Figure 4). Both interpretations would be further amplified if and when Pacific cod spawn timing shifts to earlier times in the spring as baseline conditions continue to warm.

3.3. Habitat quality

The index of habitat quality for larval cod, calculated from the statistical survival model in Eq. 1 applied to the field data, was considerably higher in the BS than in the GOA (Figure 4; Figure 5). As an average of all years inspected, larval cod had modeled survival probability equal or above 40% on 59.3% of the BS habitat compared to only 34.6% of the GOA habitat. In the BS, cod habitat quality has maintained relatively high through the recent period of warming (after 2013), and the system experienced slight shifts downward in habitat quality following 2007 (Figure 4; Figure 5). BS cod habitat quality also appears to remain high during periods with early Chl *a* onset (e.g., 2000 to 2005) as well as recent years characterized by later onset. In contrast, GOA larval habitat appears to be much more sensitive to temperature, with poorest quality occurring during both warm periods (1998 – 2005 and 2014-2019; although habitat quality in 1999 was anomalously high for that period) and highest occurring during the cool period (2006-2013). On an annual basis, we found that in the GOA there is a significant inverse relationship between the regional average of SST in the two weeks that precedes the

phytoplankton bloom and the predicted habitat quality index ($R^2 = 0.70$, $p < 0.001$). This was not found to be the case for the BS ($R^2 = 0.01$, $p = 0.655$).

Our within-regional spatial examination of habitat quality revealed some additional trends. In the GOA, during warm years (e.g. 2016), the spatial representation of habitat quality predictions showed areas with particularly low indices in the east (Figure S6.1), which are also the warmest areas of the GOA (Figure S5.1 – S5.8). Western regions of the GOA were higher in habitat quality ($p < 0.001$), but were more variable year-to-year (Figure S6.2). In the BS, however, the spatial representations of habitat quality were more directly reflecting patterns of Chl *a* phenology, with highest survival areas characterized by early peaks in Chl *a* concentration (Exemplified in Figure 6, but also see Figure S5.1 – S5.8)). The spatial analysis suggested higher habitat quality north of 55°N compared to the southern part of the BS region, most notably in more recent, warm years (Figure S6.3). There were no clear patterns in the spatial variance of habitat within regions in the BS (Figure S6.4).

As a test of the survival predictions of the model, we correlated the larval cod habitat quality with independent estimates of year class strength for each region. In particular, we first obtained estimates of age-0 cod annual recruitment (numbers of individuals) and adult female spawning biomass (thousands tonnes) from the most current stock assessment reports (BS, Thompson & Thorson, 2019; GOA, Barbeaux *et al.*, 2019), and then calculated an annual recruits per spawner index (natural log of the ratio between recruits and spawners). This index is also representative of the eggs that survive into recruitment age (Ricker, 1954). The analysis showed no correlation between

habitat quality and recruitment per spawner index in the BS ($p = 0.96$), whereas a significant correlation did appear in the GOA ($p < 0.05$; Figure 7).

4. Discussion

4.1. Regional annual variability

Our study predicts warming has increased the relative risk of trophic mismatch for cod larvae, and these risks are more apparent in the GOA compared to the BS. A novel finding from our study is the mechanistic role of temperature in each regions. In the GOA, the degree of mismatch (i.e., days to encounter prey) is relatively more sensitive to temperature effects on the metabolic rates of cod larvae (i.e., duration of yolk reserves), which in turn can amplify vulnerability prey mismatch when warming also results in a shift in these onset of Chl *a* onset. In the BS, cooler temperatures reduce metabolic demands of larvae which in turn buffer the longer temporal separation between peak Chl *a* and larval production. These results demonstrate how temperature can play both constructive and destructive interference in the underlying match-mismatch vulnerability of marine fish larvae experiencing changes in prey phenology.

Based on the experimental data, the warmer on average thermal conditions of the GOA mean larvae have ~50% less time to encounter sufficient prey to initiate feeding compared to larvae in the BS. Conditions were particularly warm for cod larvae in the central GOA (Cook Inlet area) where larvae had < 1 week of yolk reserves and were potentially exposed to thermal conditions sub-optimal for growth (Hurst *et al.*, 2010). Lacking compensatory changes in primary productivity, the habitat index for the GOA abruptly shifted to a low-threshold state following the onset of the marine heatwaves

beginning in 2014 e.g., <50% of the lowest average observed in the Bering Sea. These habitat indices were linked to annual recruitment estimates in the GOA, but were not considered in the context of other temperature-dependent processes regulating survival at different life history stages such as egg survival ((Bian *et al.*, 2016; Laurel & Rogers, 2020), size-at-hatch (Laurel *et al.*, 2008) and changing metabolic demands for older life stages (Holsman & Aydin, 2015; Barbeaux *et al.*, 2020). We also did not consider the potential trophic links of chlorophyll *a* on older life stages that might impact recruitment through fluctuations in parental condition (Freidland *et al.* 2015). Therefore, match-mismatch dynamics of first-feeding larvae are likely just one of several mechanisms contributing to poor recruitment and loss of biomass in the GOA Pacific cod fishery following the recent marine heatwaves in the time series (Barbeaux *et al.*, 2019).

Spring Chl *a* biomass was highly variable in the Bering Sea time series, but the habitat models indicated cod larvae were less vulnerable to prey mismatches than the GOA. Bering Sea productivity was characterized by a low-intensity, short duration surface expression with a highly variable onset among years. Our analysis did detect a significant shift to earlier more prolonged Chl *a* presence during the 2016-18 warm period, followed by a return to historical patterns in 2019. While warming can result in earlier phytoplankton blooms (Hjerne *et al.*, 2019), our observations run somewhat counter to expectations that, due to delayed water column stratification sea-ice, bloom timing should be later when seasonal sea ice is absent (Sigler *et al.*, 2014). Regardless, the high year-to-year variation of Chl *a* onset in the BS would assumingly amplify the risk of prey mismatches for cod larvae. However, the metabolic demands of cod larvae are largely buffered by the cooler spring conditions of the Bering Sea which has allowed

average larval habitat suitability to remain higher and more stable across time than that of the GOA. The BS habitat model appeared stable even in years when the peak observed Chl *a* biomass was extremely early (2007, 2016-18) or very delayed (2006, 2009, 2011).

It is important to note that we did not consider whether early Chl *a* onset, and thus potentially increase in spring primary production, indeed remains available to pelagic grazers or sinks to the bottom to support the benthic community (sensu Hunt & Stabeno, 2002). Such processes are hypothesized to be important for successful feeding of cod independent of the larval stage, and lagged in time for older life stages in the form of increased benthic prey production (Aydin & Mueter, 2007). These trophic mechanisms are described under the Oscillating Control Hypothesis (OCH; Hunt *et al.*, 2002) and have been updated to include for more complex seasonal zooplankton dynamics and juvenile feeding success (Hunt *et al.*, 2011; Kimmel *et al.*, 2018). A future step will be to consider these broader mechanisms of energy flow in the models of larval cod habitat from this study, especially as the Bering Sea continues to warm and potentially increase vulnerability of cod larvae to prey mismatches in time and space.

4.2. Sub-regional annual variability

Although habitat suitability was highly correlated across sub-regions of the BS and GOA, the survival potential of larvae ultimately depend on their distribution across these habitat mosaics. Unlike older life stages, larvae of cod species have limited swimming ability to move and select favorable habitats across large scales (Leis, 2006; Peck *et al.*, 2006). Shelf-wide distributions of cod larvae are more determined by complicated extrinsic factors such as advective transport, predation (differential

mortality) and source spawning locations (e.g., Bradbury *et al.*, 2008). While patchy habitat areas in the northern region of our BS study area are likely due to variable ice-retreat, we lack sufficient ichthyoplankton data to examine spatial overlap and validate survival predictions in other areas of interest identified in the model. In the GOA, where ichthyoplankton survey coverage is more consistent, there is evidence suggesting larval cod abundance was indeed lower in the eastern GOA where habitat suitability declined in recent years of the time series. As with the BS, these patterns in habitat suitability would be best validated with additional field observations on larval distributions before attempting to address mechanisms of regional composition and survival variability of cod subpopulations. However, the physical and biological factors that regulate larval retention into and out of these habitats may be more tractable in the GOA using biophysical models that can track and simulate the small-scale behavior of Pacific cod larvae that is currently unavailable in conventional field sampling (Hinckley *et al.*, 2019).

4.3. Assumptions, uncertainty and model improvement

We emphasize that our larval survival model is best used as a mechanistic framework to show how temperature regulates metabolic demands differently across ecosystems in a key marine fish species. For management and recruitment forecasting, these model should always be considered alongside other processes. These include temperature-dependent hatch success (Laurel & Rogers, 2020), connectivity to nearshore nurseries (Hinckley *et al.*, 2019), post-settlement growth (Laurel *et al.*, 2016), predation (Bailey *et al.* 2000; Ciannelli *et al.* 2005) and overwintering stress (Heintz *et al.*, 2013; Farley *et al.*, 2016). In light of these mechanisms, we should be cautious in attributing

causation to any current or future recruitment relationships that emerge in these time series. These habitat models may be capturing multiple temperature mechanisms, and in the case of the GOA, accelerating the system towards a threshold state where such processes collectively limit recruitment potential.

Further validation on timing of spring events in both ecosystems will improve confidence in these model projections. We assumed that Chl *a* values provide a first-order index on the timing of phytoplankton bloom events and zooplankton abundance, and while this can be a valid assumption (Platt *et al.*, 2003), we fully recognize that surface expressions of Chl *a* do not capture sub-surface phytoplankton dynamics and that a host of other factors can modify peak plankton abundance in time and space (See Methods) and its connection to fish larvae through zooplankton (Ji *et al.*, 2010). Therefore, we only consider the Chl *a* metrics used in this study as proxies for overall system productivity. We also recognize that the phytoplankton blooms are comprised of mixed taxon (dinoflagellates, diatom, etc), which could contribute to variable nutritional quality for Pacific cod larvae (Copeman & Laurel, 2010). For the timing of Pacific cod larval production, while we applied different phenologies in the BS and GOA, our analyses assumed a consistent phenology across years and sub-regions within each system. It is possible that within a certain limit, larval phenology shifts earlier with warming as a consequence of ovary maturation or faster egg development time. These changes have been observed in co-occurring walleye pollock stocks using spawn timing reconstructions in the same region as our study (Rogers & Doherty, 2019), and if also detected in Pacific cod, have the potential to further amplify risk of prey mismatch.

5. Conclusions

Warming projections will likely further increase prey mismatch vulnerability for cod larvae by decreasing the time window for first-feeding, which may be further amplified by temperature-associated changes in spring productivity. Our study shows how these processes are manifested differently in two adjacent ecosystems. In the GOA, warming has resulted in a significant reduction of favorable habitat for cod larvae while conditions in the BS have remained relatively favorable. The closure of the GOA Pacific cod Federal fishery in 2020 was preceded by consecutive years of extensive pelagic habitat loss for cod larvae, where larval survival probabilities were 50% lower than the lowest average time period ever observed in the BS time series. With annual updates, these larval habitat models have potential to improve ecosystem-based fisheries management by providing early warning indicators and process understanding for Pacific cod and other species facing regional climate stress. Alone or combined with mechanistic information on other critical life stages and processes, they can improve the ability of management strategy evaluations to provide critical data to ensure the sustainable harvest of this economically important species during periods of ecosystem change.

Acknowledgements:

We thank B. Knoth and A. Abookire who assisted with Pacific cod egg field collections around Kodiak, AK. We also thank L. Copeman, S. Haines and P. Iseri who contributed to husbandry and experimental work at the NOAA-AFSC laboratory at the Hatfield Marine Science Center. Boat charters were kindly provided by Tim Tripp aboard the F/V Miss O. We thank J. Napp, M. Sigler and J. Neilsen for reviewing earlier drafts of this

manuscript. This study was supported by the North Pacific Research Board (NPRB) grant #R0605, NOAA's Fisheries Behavioral Ecology Program and NOAA's Ecosystems and Fisheries Oceanography Coordinated Investigations Program. The findings and conclusions in the paper are those of the authors and do not necessarily represent the views of the National Marine Fisheries Service, NOAA.

References:

- Aydin, K., & Mueter, F. (2007). The Bering Sea - A dynamic food web perspective. *Deep-Sea Research Part II -Topical Studies in Oceanography*, 54(23-26), 2501-2525. doi:10.1016/j.dsr2.2007.08.022
- Bailey, K. M., Ciannelli, L., Bond, N. A., Belgrano, A., & Stenseth, N. C. (2005). Recruitment of walleye pollock in a physically and biologically complex ecosystem: a new perspective. *Progress in Oceanography*, 67(1), 24-42.
- Barbeaux, S. J., Aydin, K., Fissel, B., Holsman, K., Laurel, B. J., Palsson, W., . . . Zador, S. (2019). Assessment of the Pacific cod stock in the Gulf of Alaska. *North Pacific Fisheries Management Council*.
- Barbeaux, S. J., & Hollowed, A. B. (2018). Ontogeny matters: Climate variability and effects on fish distribution in the eastern Bering Sea. *J Fisheries Oceanography*, 27(1), 1-15.
- Barbeaux, S. J., Holsman, K., & Zador, S. (2020). Marine heatwave stress test of ecosystem-based fisheries management in the Gulf of Alaska Pacific cod fishery. *Frontiers in Marine Science*, 7, 703.
- Beaugrand, G., Brander, K. M., Lindley, J. A., Souissi, S., & Reid, P. C. (2003). Plankton effect on cod recruitment in the North Sea. *Nature*, 426(6967), 661-664.
- Behrenfeld, M. J., & Boss, E. S. (2018). Student's tutorial on bloom hypotheses in the context of phytoplankton annual cycles. *Global Change Biology*, 24(1), 55-77.
- Behrenfeld, M. J., O'Malley, R. T., Boss, E. S., Westberry, T. K., Graff, J. R., Halsey, K. H., . . . Brown, M. B. (2016). Revaluating ocean warming impacts on global phytoplankton. *Nature Climate Change*, 6(3), 323-330. doi:10.1038/nclimate2838
- Behrenfeld, M. J., O'Malley, R. T., Siegel, D. A., McClain, C. R., Sarmiento, J. L., Feldman, G. C., . . . Boss, E. S. (2006). Climate-driven trends in contemporary ocean productivity. *Nature*, 444(7120), 752-755.
- Benson, A. J., Trites, A. W. J. F., & Fisheries. (2002). Ecological effects of regime shifts in the Bering Sea and eastern North Pacific Ocean. 3(2), 95-113.
- Bian, X. D., Zhang, X. M., Sakurai, Y., Jin, X. S., Wan, R. J., Gao, T. X., & Yamamoto, J. (2016). Interactive effects of incubation temperature and salinity on the early life stages of pacific cod *Gadus macrocephalus*. *Deep-Sea Research Part II - Topical Studies in Oceanography*, 124, 117-128. doi:10.1016/j.dsr2.2015.01.019
- Bradbury, I., Laurel, B., Robichaud, D., Rose, G., Snelgrove, P., Gregory, R., . . . Windle, M. (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. *Fisheries Research (Amsterdam)*, 91(2), 299-309.
- Brosset, P., Smith, A.D., Plourde, S. et al. (2020). A fine-scale multi-step approach to understand fish recruitment variability. *Scientific Reports*, 10, 16064 (2020). <https://doi.org/10.1038/s41598-020-73025-z>
- Coachman, L. J. C. S. R. (1986). Circulation, water masses, and fluxes on the southeastern Bering Sea shelf. 5(1-2), 23-108.

- Copeman, L. A., & Laurel, B. J. (2010). Experimental evidence of fatty acid limited growth and survival in Pacific cod larvae. *Marine Ecology Progress Series*, 412, 259-272. doi:10.3354/meps08661
- Cushing, D. H. (1975). *Marine ecology and fisheries*: Cambridge University Press Archive.
- Drinkwater, K. F. (2005). The response of Atlantic cod (*Gadus morhua*) to future climate change. *ICES Journal of Marine Science*, 62(7), 1327-1337. doi:10.1016/j.icesjms.2005.05.015
- Duffy-Anderson, J. T., Stabeno, P. J., Siddon, E. C., Andrews, A. G., Cooper, D. W., Eisner, L. B., . . . Kimmel, D. G. (2017). Return of warm conditions in the southeastern Bering Sea: Phytoplankton-Fish. *PLoS One*, 12(6).
- Durant, J. M., Hjermann, D. Ø., Ottersen, G., & Stenseth, N. C. (2007). Climate and the match or mismatch between predator requirements and resource availability. *Climate Research*, 33(3), 271-283.
- Farley, E. V., Heintz, R. A., Andrews, A. G., & Hurst, T. P. (2016). Size, diet, and condition of age-0 Pacific cod (*Gadus macrocephalus*) during warm and cool climate states in the eastern Bering sea. *Deep-Sea Research Part II -Topical Studies in Oceanography*, 134, 247-254. doi:10.1016/j.dsr2.2014.12.011
- Ferreira, A. S. A., Stige, L. C., Neuheimer, A. B., Bogstad, B., Yaragina, N., Prokopchuk, I., & Durant, J. M. (2020). Match– mismatch dynamics in the Norwegian– Barents Sea system. *Marine Ecology Progress Series*. 650, 81-94.
- Fortier, L., Levasseur, M. E., Drolet, R., & Therriault, J.-C. (1992). Export production and the distribution of fish larvae and their prey in a coastal jet frontal region. *Marine Ecology Progress Series*, 85, 203-218.
- Friedland, Kevin D., Robert T. Leaf, Trond Kristiansen, and Scott I. Large. 2015. "Layered Effects of Parental Condition and Larval Survival on the Recruitment of Neighboring Haddock Stocks." *Canadian Journal of Fisheries and Aquatic Sciences*. 72 (11): 1672-81
- Heintz, R. A., Siddon, E. C., Farley, E. V., & Napp, J. M. (2013). Correlation between recruitment and fall condition of age-0 pollock (*Theragra chalcogramma*) from the eastern Bering Sea under varying climate conditions. *Deep Sea Research (Part II, Topical Studies in Oceanography)*, 94, 150-156. doi:DOI 10.1016/j.dsr2.2013.04.006
- Hinckley, S., Stockhausen, W. T., Coyle, K. O., Laurel, B. J., Gibson, G. A., Parada, C., . . . Ladd, C. (2019). Connectivity between spawning and nursery areas for Pacific cod (*Gadus macrocephalus*) in the Gulf of Alaska. *Deep-Sea Research Part II - Topical Studies in Oceanography*, 165, 113-126. doi:10.1016/j.dsr2.2019.05.007
- Hjerne, O., Hajdu, S., Larsson, U., Downing, A. S., & Winder, M. (2019). Climate Driven Changes in Timing, Composition and Magnitude of the Baltic Sea Phytoplankton Spring Bloom. *Frontiers in Marine Science*, 6(482). doi:10.3389/fmars.2019.00482
- Hjort, J. (1914). Fluctuations in the great fisheries of northern Europe, viewed in the light of biological research. *Rapports et Proces-Verbaux des Reunions du Conseil Permanent International pour l'Exploration de la Mer*, 20, 1–228.

- Holsman, K. K., & Aydin, K. (2015). Comparative methods for evaluating climate change impacts on the foraging ecology of Alaskan groundfish. *Marine Ecology Progress Series*, 521, 217-235.
- Houde, E. D. (2008). Emerging from Hjort's shadow. *Journal of Northwest Atlantic fishery science*, 41, 53-70.
- Hunt, G. L., Coyle, K. O., Eisner, L. B., Farley, E. V., Heintz, R. A., Mueter, F., . . . Salo, S. (2011). Climate impacts on eastern Bering Sea foodwebs: a synthesis of new data and an assessment of the Oscillating Control Hypothesis. *JICES Journal of Marine Science*, 68(6), 1230-1243.
- Hunt, G. L., Stabeno, P., Walters, G., Sinclair, E., Brodeur, R. D., Napp, J. M., & Bond, N. A. (2002). Climate change and control of the southeastern Bering Sea pelagic ecosystem. *J Deep Sea Research Part II: Topical Studies in Oceanography*, 49(26), 5821-5853.
- Hunt, G. L., & Stabeno, P. J. (2002). Climate change and the control of energy flow in the southeastern Bering Sea. *Progress in Oceanography*, 55(1-2), 5-22.
- Hurst, T. P., Laurel, B. J., & Ciannelli, L. (2010). Ontogenetic patterns and temperature-dependent growth rates in early life stages of Pacific cod (*Gadus macrocephalus*). *Fishery Bulletin*, 108(4), 382-392.
- Ji, R., Edwards, M., Mackas, D. L., Runge, J. A., & Thomas, A. C. (2010). Marine plankton phenology and life history in a changing climate: current research and future directions. *Journal of Plankton Research*, 32(10), 1355-1368.
doi:10.1093/plankt/fbq062
- Kimmel, D. G., Eisner, L. B., Wilson, M. T., & Duffy-Anderson, J. T. (2018). Copepod dynamics across warm and cold periods in the eastern Bering Sea: Implications for walleye pollock (*Gadus chalcogrammus*) and the Oscillating Control Hypothesis. *J Fisheries Oceanography*, 27(2), 143-158.
- Kristiansen, T., Drinkwater, K. F., Lough, R. G., & Sundby, S. (2011). Recruitment variability in North Atlantic cod and match-mismatch dynamics. *PLoS One*, 6(3).
- Lasker, R. (1978). The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. *Rapp. P.-V. Reun. Cons. Int. Explor. Mer.*, 173, 212-230.
- Lasker, R. (1981). Factors contributing to variable recruitment of the northern anchovy (*Engraulis mordax*) in the California Current: contrasting years, 1975 through 1978. *Rapp. pv Reun. Cons. Int. Expl. Mer.*, 178, 375-388.
- Laurel, B. J., Hurst, T. P., & Ciannelli, L. (2011). An experimental examination of temperature interactions in the match-mismatch hypothesis for Pacific cod larvae. *Canadian Journal of Fisheries and Aquatic Sciences*, 68(1), 51-61.
doi:10.1139/F10-130
- Laurel, B. J., Hurst, T. P., Copeman, L. A., & Davis, M. W. (2008). The role of temperature on the growth and survival of early and late hatching Pacific cod larvae (*Gadus macrocephalus*). *Journal of Plankton Research*, 30(9), 1051-1060.
doi:10.1093/plankt/fbn057
- Laurel, B. J., & Rogers, L. A. (2020). Loss of spawning habitat and pre-recruits of Pacific cod during a Gulf of Alaska heatwave. *Canadian Journal of Fisheries and Aquatic Sciences*(ja). doi:dx.doi.org/10.1139/cjfas-2019-0238

- Leggett, W., & DeBlois, E. (1994). Recruitment in marine fishes: is it regulated by starvation and predation in the egg and larval stages? *Netherlands Journal of Sea Research*, 32(2), 119-134.
- Leis, J. M. (2006). Are larvae of demersal fishes plankton or nekton? *Advances in Marine Biology*, 51, 57-141.
- Litzow, M. A. (2006). Climate regime shifts and community reorganization in the Gulf of Alaska: how do recent shifts compare with 1976/1977? *ICES Journal of Marine Science*, 63(8), 1386-1396.
- Litzow, M. A., Hunsicker, M. E., Ward, E. J., Anderson, S. C., Gao, J., Zador, S. G., . . . Fergusson, E. (2020). Evaluating ecosystem change as Gulf of Alaska temperature exceeds the limits of preindustrial variability. *Progress in Oceanography*, 186, 102393.
- Marinov, I., Doney, S. C., Lima, I. D., Lindsay, K., Moore, J., & Mahowald, N. (2013). North-South asymmetry in the modeled phytoplankton community response to climate change over the 21st century. *Global Biogeochemical Cycles*, 27(4), 1274-1290.
- Napp, J. M., Incze, L. S., Ortner, P. B., Siefert, D. L., & Britt, L. (1996). The plankton of Shelikof Strait, Alaska: standing stock, production, mesoscale variability and their relevance to larval fish survival. *Fisheries Oceanography*, 5, 19-38.
- Peck, M. A., Buckley, L. J., & Bengston, D. A. (2006) Effects of Temperature and Body Size on the Swimming Speed of Larval and Juvenile Atlantic Cod (*Gadus Morhua*): Implications for Individual-Based Modelling. *Environmental Biology of Fishes* 75 (4): 419-29.
- Planque, B., & Frédou, T. (1999). Temperature and the recruitment of Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* 56(11), 2069-2077.
- Platt, T., Fuentes-Yaco, C., & Frank, K. T. (2003). Spring algal bloom and larval fish survival. *Nature*, 423(6938), 398-399.
- Pörtner, H.-O., & Peck, M. (2010). Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. *Journal of Fish Biology*, 77(8), 1745-1779.
- Ricker, W. E. (1954). Stock and recruitment. *Journal of the Fisheries Board of Canada*, 11(5), 559-623.
- Rogers, L. A., & Dougherty, A. B. (2019). Effects of climate and demography on reproductive phenology of a harvested marine fish population. *Global Change Biology*, 25(2), 708-720.
- Sigler, M. F., Napp, J. M., Stabeno, P. J., Heintz, R. A., Lomas, M. W., & Hunt, G. L. (2016). Variation in annual production of copepods, euphausiids, and juvenile walleye pollock in the southeastern Bering Sea. *Deep Sea Research Part II: Topical Studies in Oceanography*.
- Sigler, M. F., Stabeno, P. J., Eisner, L. B., Napp, J. M., & Mueter, F. (2014). Spring and fall phytoplankton blooms in a productive subarctic ecosystem, the eastern Bering Sea, during 1995–2011. *Deep Sea Research Part II: Topical Studies in Oceanography*, 109, 71-83.

- Stabeno, P. J., & Bell, S. W. (2019). Extreme Conditions in the Bering Sea (2017–2018): Record-Breaking Low Sea-Ice Extent. *Geophysical Research Letters*, *46*(15), 8952-8959.
- Stabeno, P. J., Bond, N. A., Hermann, A. J., Kachel, N. B., Mordy, C. W., & Overland, J. E. (2004). Meteorology and oceanography of the Northern Gulf of Alaska. *Continental Shelf Research*, *24*(7), 859-897.
doi:<https://doi.org/10.1016/j.csr.2004.02.007>
- Stevenson, D. E., & Lauth, R. R. (2019). Bottom trawl surveys in the northern Bering Sea indicate recent shifts in the distribution of marine species. *Polar Biology*, *42*(2), 407-421.
- Thompson, G., & Thorson, J. T. (2019). Assessment of the Pacific cod stock in the Eastern Bering Sea. *North Pacific Fisheries Management Council*.
- von Biela, V. R., Arimitsu, M. L., Piatt, J. F., Heflin, B., Schoen, S. K., Trowbridge, J. L., & Clawson, C. M. (2019). Extreme reduction in nutritional value of a key forage fish during the Pacific marine heatwave of 2014-2016. *Marine Ecology Progress Series*, *613*, 171-182.
- Wood, S. N. (2017). *Generalized additive models: an introduction with R*: CRC press.
- Yang, Q., Cokelet, E. D., Stabeno, P. J., Li, L., Hollowed, A. B., Palsson, W. A., . . . Barbeaux, S. J. (2019). How “The Blob” affected groundfish distributions in the Gulf of Alaska. *Fisheries Oceanography*.
- Yin, M., & Blaxter, J. (1987). Feeding ability and survival during starvation of marine fish larvae reared in the laboratory. *Journal of Experimental Marine Biology and Ecology*, *105*(1), 73-83.
- Zador, S., & Yasumiishi, E. M. (2017). Ecosystem Considerations 2017 Status of the Gulf of Alaska Marine Ecosystem.
- Zeileis, A., Kleiber, C., Krämer, W., Hornik, K., & Analysis, D. (2003). Testing and dating of structural changes in practice. *Computational Statistics & Data Analysis*, *44*(1-2), 109-123.

Figure Captions:

Figure 1: Map of the two focal regions in Alaska, the Bering Sea (BS) and Gulf of Alaska (GOA), including place names referenced in the paper.

Figure 2: Experimentally derived cod larval survival (points) and GAM model fit (lines) for the three different timings of cod egg hatches (early = ~35% of hatches; mid = ~60% of hatches; late = > 80% hatches). Data reanalyzed from Laurel et al. (2008)

Figure 3: Model predicted distribution of Pacific cod first feeding larvae from available ichthyoplankton survey years in the western Gulf of Alaska (GOA; 1972 - 2015) and the southeastern Bering Sea (BS; 1979 -2016). The black points indicate areas of sampling effort by NOAA Fisheries Oceanography Coordinated Investigations (FOCI, Matarese et al. 2003).

Figure 4: Time series of Chl *a* metrics (start, duration, amplitude), incumbent sea surface (SST, °C) and larval habitat suitability for the Bering Sea (BS, left panels) and Gulf of Alaska (GOA, right panels). Chl *a* metrics were estimated from the satellite imagery based on SeaWiifs (1998-2002) and Modis-Aqua (2003-2019). Larval habitat suitability is based on the proportion of Pacific cod larvae that survived from hatching to the encounter with food, estimated from the start of Chl *a* and the incumbent sea surface (SST, °C) in the western Gulf of Alaska (GOA) and the southeastern Bering Sea (BS). For each year and both study regions we calculated the incumbent SST as the average temperature during the week leading up to the peak of cod larval abundance (i.e., from day 129 to day

137, Fig S3). Horizontal dashed lines indicate days of peak larval production. Vertical dashed lines indicate significant breakpoints in the time series identified using the 'strucchange' R package (Zeileis 2006). The breakpoints were determined based on lowest BIC score and p values < 0.05.

Figure 5: Annual characterization of Pacific cod larval habitat suitability in the Gulf of Alaska (GOA) and Bering Sea (BS) based on spring patterns in phytoplankton productivity and sea surface temperatures (See Methods and Fig. 4 for additional details). The GOA has undergone large annual fluctuations in larval habitat that have historically been driven by variability in the Central and Eastern GOA but have now occurred across the Gulf with recent warming events (2014-16, 2019). The BS continues to remain relatively suitable for survival overall with possible exception along the inner-middle shelf domain in recent years.

Figure 6: Demonstration of how Pacific cod larval habitat suitability is regionally impacted in a cold year (2007, top panels) and warm year (2016, bottom panel) in the Gulf of Alaska (GOA) and Bering Sea (BS). From left to right, panels indicate days of mismatch from phytoplankton bloom (quantified as days of separation between the peak of larval production and the start of the phytoplankton bloom), average sea surface temperature during days of mismatch (SST, °C) and the predicted index of habitat quality for first feeding larval cod based on these annual environmental conditions (See Fig. 2). In general, larval habitat suitability in the BS is more sensitive to phytoplankton

productivity timing whereas in the GOA, habitat suitability is more sensitive to temperature.

Figure 7: Relationship between the Gulf of Alaska (GOA) annual index of larval cod habitat suitability (See Methods and Fig. 4 for additional details) and estimates of year class strength derived from the GOA Pacific cod stock assessment model (Barbeaux et al. 2019).

Table 1. Results from a Generalized Additive Model (GAM) fitted to the abundance data of first feeding cod larvae. Overall explained variances (and deviance) were 36.4% (39%) and 30.2% (40.5%) for the western Gulf of Alaska (GOA) and southeastern Bering Sea (BS), respectively. EDF, estimated degrees of freedom.

Basin	Covariate	P-value	EDF
GOA	Julian day	<< 0.0001	7.083
	Location (lat, lon)	<< 0.0001	22.498
	Bottom depth	0.00569	7.385
	Time of day	0.33966	5.378
BS	Julian day	0.0299	3.766
	Location (lat, lon)	<<0.0001	13.473
	Bottom depth	0.4469	4.297
	Time of day	0.1260	1

Figure 1:

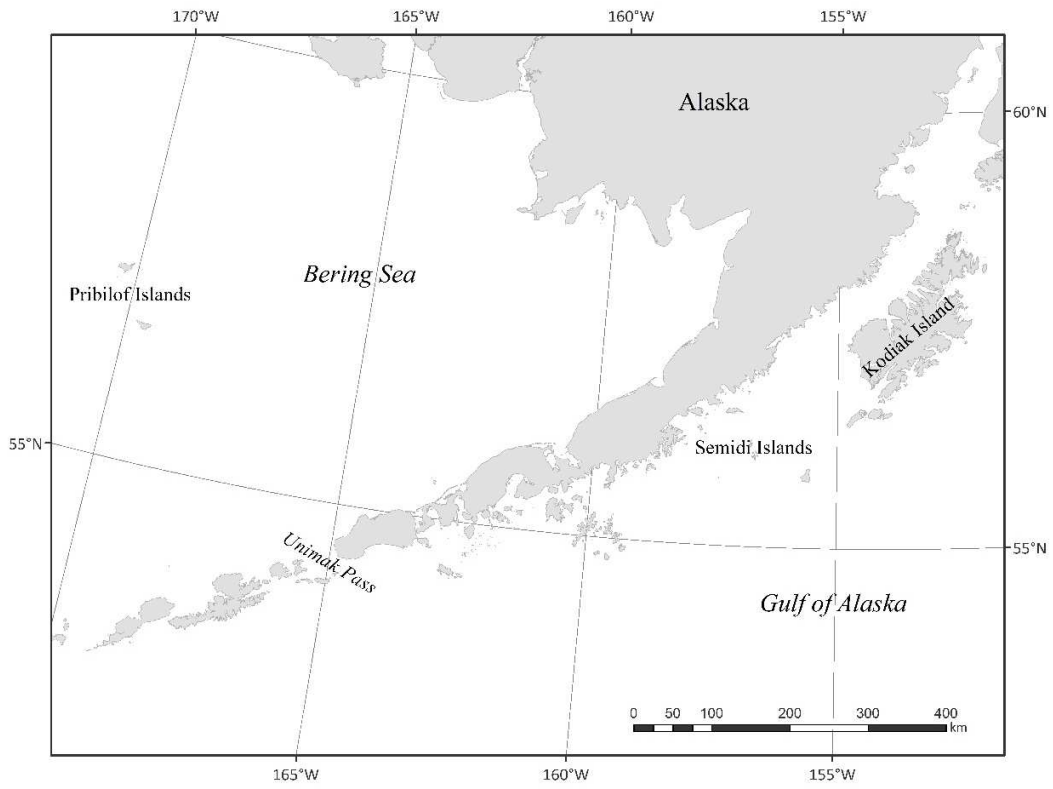


Figure 2:

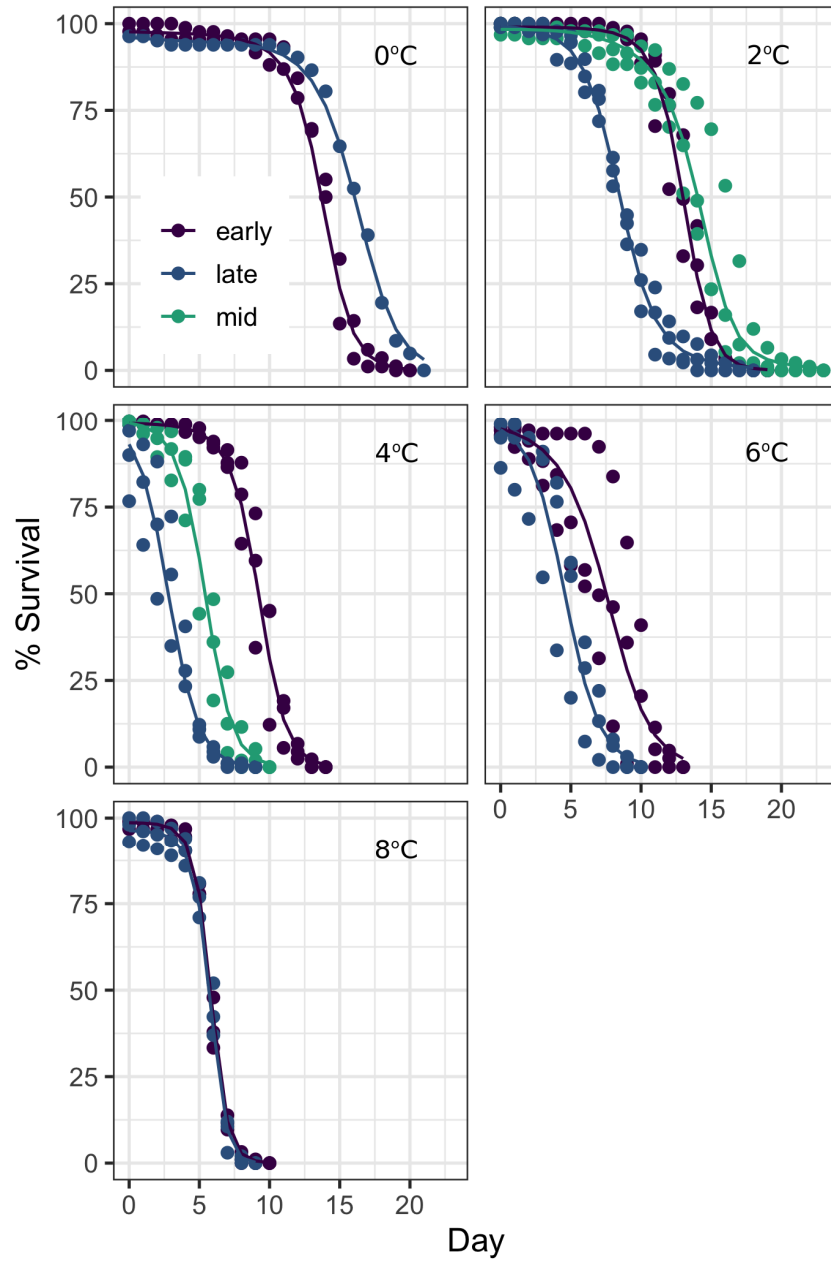


Figure 3:

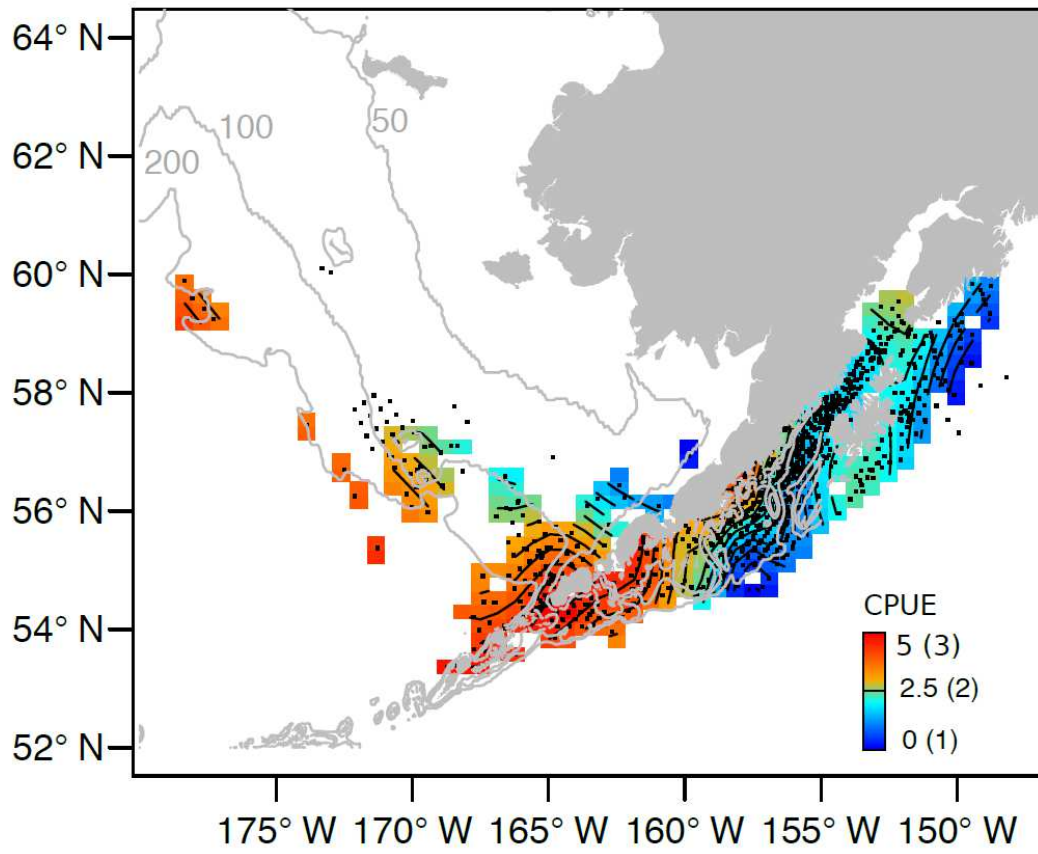


Figure 4:

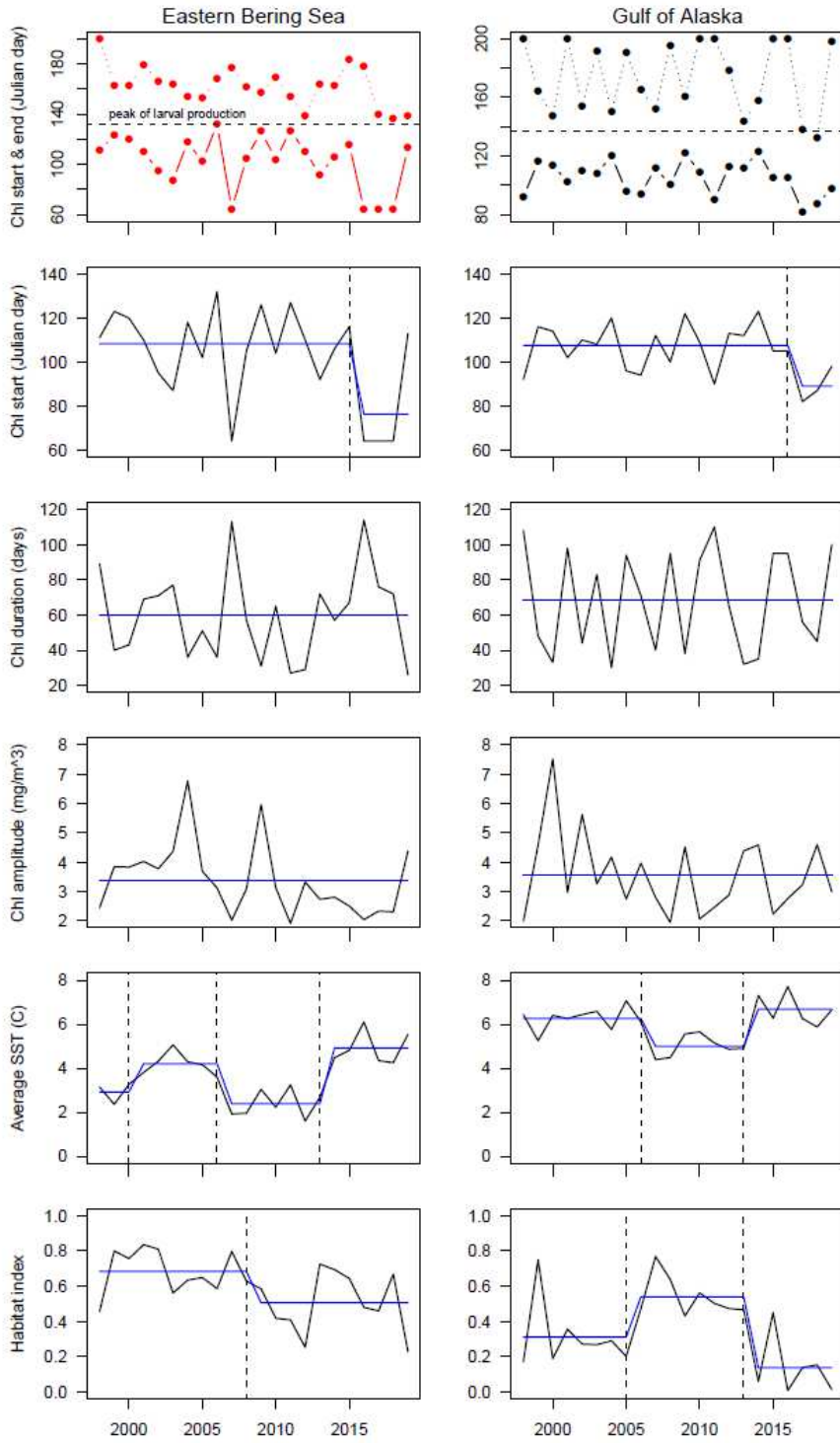


Figure 5:

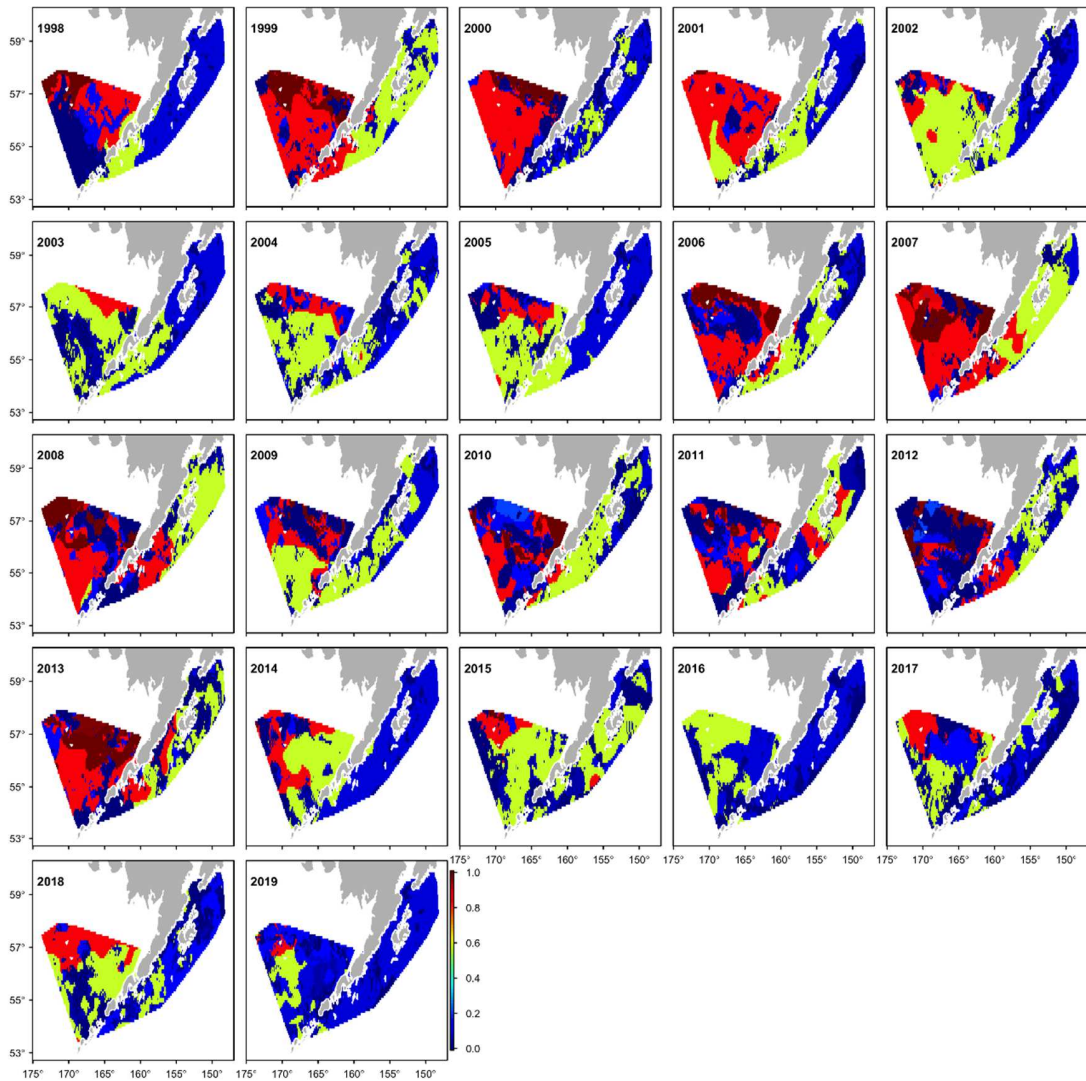


Figure 6:

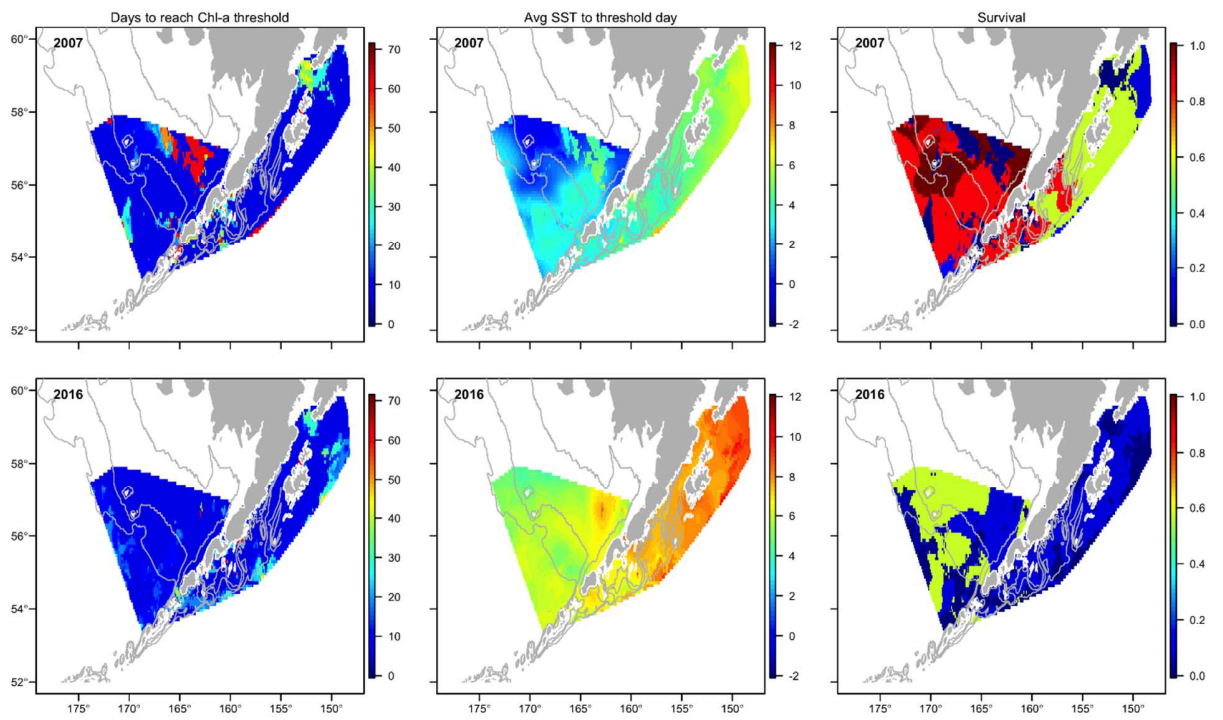


Figure 7:

