



Pacific cod in the Anthropocene: An early life history perspective under changing thermal habitats

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Abstract

The rapid decline in Pacific cod (*Gadus macrocephalus*, Gadidae) biomass following multiple Gulf of Alaska marine heatwaves (2014–2016 and 2019) may be one of the most dramatic documented changes in a sustainably managed marine fishery. As such, fisheries managers are exploring new recruitment paradigms for Pacific cod under novel environmental conditions. In this review, we address the challenges of managing and forecasting Pacific cod populations in the Eastern Pacific where thermal habitats for early life stages are undergoing varying rates of change across space and time. We use observational data to examine changes in distribution, abundance and demographics of the population from 1993 to 2020, and model contemporary and future changes of thermal habitat for both spawning success and age-0 juvenile growth potential. Results indicate that reduced spawning habitat and early life stage abundance may be a precursor to regional population decline, but the recent apparent increases in size-at-age of pre-recruits will have unknown impacts on future recruitment in these regions. We contend that continued monitoring of early life stages will be necessary to track changes in phenology and growth that likely determine size-at-age and the survival trajectories of year classes into the adult population. These include complex size- and temperature-dependent energetics spanning seasonal habitats through the first winter. Climate-ready management of Pacific cod will, therefore, require new process investigations beyond single-season surveys focused on one-life stage.

KEYWORDS

eggs, *Gadus macrocephalus*, juvenile fish, larvae, size-at-age, spawning

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1 | INTRODUCTION

Pacific cod support major fisheries throughout the North Pacific and are a key ecosystem component in the Gulf of Alaska (GOA). Pacific cod were first commercially harvested in Alaska in 1863 (Cobb, 1926) and beginning in the late 1970s, Pacific cod exhibited large increases in abundance following a period of warming and an accompanying community regime shift (Benson & Trites, 2002; Litzow, 2006). However, closely spaced marine heatwaves (2014–16, nicknamed “The Blob”, and 2019) corresponded with a range of ecological shifts (Suryan et al., 2021), including negative impacts on Pacific cod recruitment and adult biomass that eventually resulted in a complete closure of the directed Pacific cod federal fishery in the GOA (Barbeaux et al., 2019; Barbeaux et al., 2020; Laurel & Rogers, 2020). While environmental influences on population dynamics of cod are diverse and varied across regions (Drinkwater, 2005; Kristiansen et al., 2011; Planque & Frédou, 1999), the mechanisms underlying these relationships are often unknown or too poorly resolved to forecast population health in future climate scenarios. Similarly, these processes may be non-stationary (e.g., Litzow et al., 2019) and change over time as environmental drivers impact one life stage or the ecosystem shifts to a new regime (Anderson & Piatt, 1999). Improved understanding of the mechanisms through which environmental drivers impact fish stocks across a species' life history are key missing pieces to successful management. Understanding these processes could allow for improved monitoring and early warning metrics that better prepare stakeholders for recruitment failure or success under changing climate conditions (Litzow & Hunsicker, 2016).

Temperature influences the early life stages (ELS) of marine fish through a number of processes, beginning with the timing and magnitude of reproductive output to the successful growth, development and survival of eggs, larvae and juveniles through to reproductive age. Recruitment to the adult population is, therefore, likely determined by the cumulative ELS mortality resulting from direct or indirect thermal experience (e.g., size- and stage-dependent mortality; Houde, 1987; Pepin, 1991). The role of temperature on energy allocation (lipids) is particularly important as larvae and juveniles balance ontogenetic demands with habitat transitions and seasonal changes in productivity (Martin et al., 2017). While a robust theoretical framework of how temperature can regulate survival has been built over decades, species-specific investigations require characterization of these vital rates and life stage sensitivity (Dahlke et al., 2020) as well as temperature mosaics over a broad geographic range reflective of the life history (Morley et al., 2018). This is challenging, as both the physiological response of fish and their thermal experience are highly dynamic in their first year of life. However, improved regional downscaling of global climate models has opened up a trove of high-resolution temperature data (historical, contemporary and future) that when combined with field observations and parameterized laboratory experiments, can be used to identify regional climate vulnerability in marine fish populations (Dahlke et al., 2020; Fagundes et al., 2020).

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In this article, we examine the ELS processes of Pacific cod in the NE Pacific, focusing on well-studied populations in the GOA in the broader context of regional declines of cod populations at lower latitudes. Pacific cod populations appear to be rapidly responding to marine heatwave events in the GOA, despite weaker impacts on the ecosystem as a whole (Litzow et al., 2020). Our perspective focuses on changes in thermal habitat and its impact on survival, growth and lipid allocation across early life stages, with the overall goal of identifying emerging life history bottlenecks under future climate scenarios. It is not our goal to develop a single recruitment paradigm for Pacific cod facing the Anthropocene (the emerging period where human activity has increasing influence on the ocean environment) but rather to identify key environmental processes across multiple life stages ('critical periods') that are potentially linked. While our perspective draws heavily from data collected in the GOA, we recognize that behavioral and physiological traits of Pacific cod

from other systems may differ and/or are locally adapted to those environments.

Our study comprises several review and empirical components, which together allow us to examine the thermal sensitivity of Pacific cod across early life stages to understand their regional climate vulnerability. We first summarize historical fisheries observations and early life history biology of cod in the NE Pacific. We then examine how the distributions of cod populations have related to thermal habitat modeled at two early life stages (spawning and age-0 juvenile). Finally, we analyze ELS time series data to determine whether early life stage demographics have changed with warming and serve as precursors to recruitment failure. These components are finally summarized into a list of science and management recommendations for Pacific cod fisheries in the new climate era.

1.1 | Historical fishery

The commercial fishery for NE Pacific cod has experienced many changes since its onset in the late 19th century. In the late 1880s, following reduced imports of cod from Japan, an industrialized fishery emerged using hook and line in the southeastern Bering Sea and GOA along the Alaska Peninsula. For not fully understood reasons, landings in those regions began declining in the 1930s, and by the 1950s, the industry shifted to an otter trawl fishery off the Canadian and Washington coasts (Ketchen, 1961). Pacific cod appeared with greater frequency in the trawl fishery off the Canadian coast in the 1950s according to Ketchen (1961). However, even during this period, it was recognized that this was a 'relatively high water temperature' for the species that was likely to impact various life history characteristics including growth, sexual maturity and life span (Ketchen, 1961). Cod catches between Cape Flattery and Destruction Island were considered the southern limit of the range in the early 1960s, although incidental catches were reported as far south as Pt Piedras Blancas (35 degrees 33 min N Lat; Cobb, 1927).

Pacific cod along the continental United States may be locally extinct (Gustafson et al., 2000), and populations have generally shifted north following southerly declines, since the early 1990s (Figures 1 and 2). Puget Sound populations are now considered extirpated despite early management restrictions (Palsson, 1990; Palsson et al., 1998) and cod populations just slightly north in Hecate Strait and Queen Charlotte Sound regions show steep declines, since the mid-1990s (as illustrated in Figure 1 as 'Canadian West Coast'). All Canadian populations are currently estimated to be below historical average and are avoided by fishing vessels given the very low quota limits (Forrest et al., 2015). The 2018 survey index for Western Vancouver Island regions was only ~25% of the magnitude of the previous 2016 observation, and there has been a notable decline in commercial catch per unit effort (CPUE) in recent years (Forrest et al., 2020). In the GOA, the Pacific cod stock was in healthy status prior to the 2014 to 2016 marine heatwave (Figure 1) despite increased fishing mortality, since the 1980s (Barbeaux et al., 2017). In 2020, the federal fishery was closed for Pacific cod in the GOA, and

the spawning biomass level was assessed at the lowest of the time series (Barbeaux et al., 2020).

A notable observation has been cod's appearance and disappearance in the archaeological record, living up to the species' Aleut word *atxidax*, which translates to "the fish that stops" (West et al., 2020). Size-structure in the population has remained constant over 6 millennia across much of the region, although some evidence of size truncation in the Western GOA is found on Sanak Island over this time period (Betts et al., 2011). Cooler conditions of the Neoglacial phase (3500–2500 calyr BP) were initially linked to higher relative abundance of Pacific cod in the archaeological record, although a more comprehensive analysis of that record was unable to find spatial-temporal variation associated with any particular climate condition across these scales (Betts et al., 2011). The modern Alaskan fishery for Pacific cod arguably began in the late 1970s, when populations dramatically increased during a regime shift followed by a period of winter warming (Litzow, 2006). Analyses of $\delta^{18}\text{O}$ of otolith core carbonate from late 19th/early 20th century cod capture a 2–3°C rise in coastal marine sea surface temperatures in the GOA leading up to this regime shift (Helser et al., 2018). Pacific cod populations have, therefore, experienced large-magnitude fluctuations across varying levels of fishing pressure, ecosystem structure and climate conditions.

1.2 | Review of early life stages

Pacific cod ELS information is based on a combination of field and laboratory investigations across multiple populations and regions. Survey data are relatively rare and prone to high measurement error due to a complex sequence of seasonal habitat transitions in the first year of life (Figure 3). As with many marine fish species, each habitat and developmental transition ('critical period') can lead to variable survival, which cumulatively can impact year-class strength and recruitment to the adult population (Houde, 1997). In this study, we highlight several ELS critical periods for Pacific cod in the GOA (Figure 3). These include the 'egg stage', the 10–20 day period when embryos are encased in their chorion and are drawing from endogenous reserves provisioned by the mother in the yolk (Laurel et al., 2008). Upon hatch, Pacific cod embryos become 'yolk-sac larvae' for a 5–7 day period drawing upon yolk reserves, as they transition from the ocean floor to surface waters where they become available to ichthyoplankton survey gear (Figure 4). Yolk-sac larvae then become 'feeding larvae' when they successfully transition from endogenous to exogenous resources. Larvae will feed on zooplankton for 60–90 days, as they grow and develop fin rays and pigmentation. The larval feeding period is separated into pre- and post-flexion larval stages, flexion being a developmental milestone describing the bending of the notochord tip that also occurs with development of the caudal-fin rays and skeletal structures. The late larval stages are commonly called 'pelagic juveniles' (20–40 mm SL) before they transition from the water column to the ocean bottom and become 'settled juveniles.' Age-0

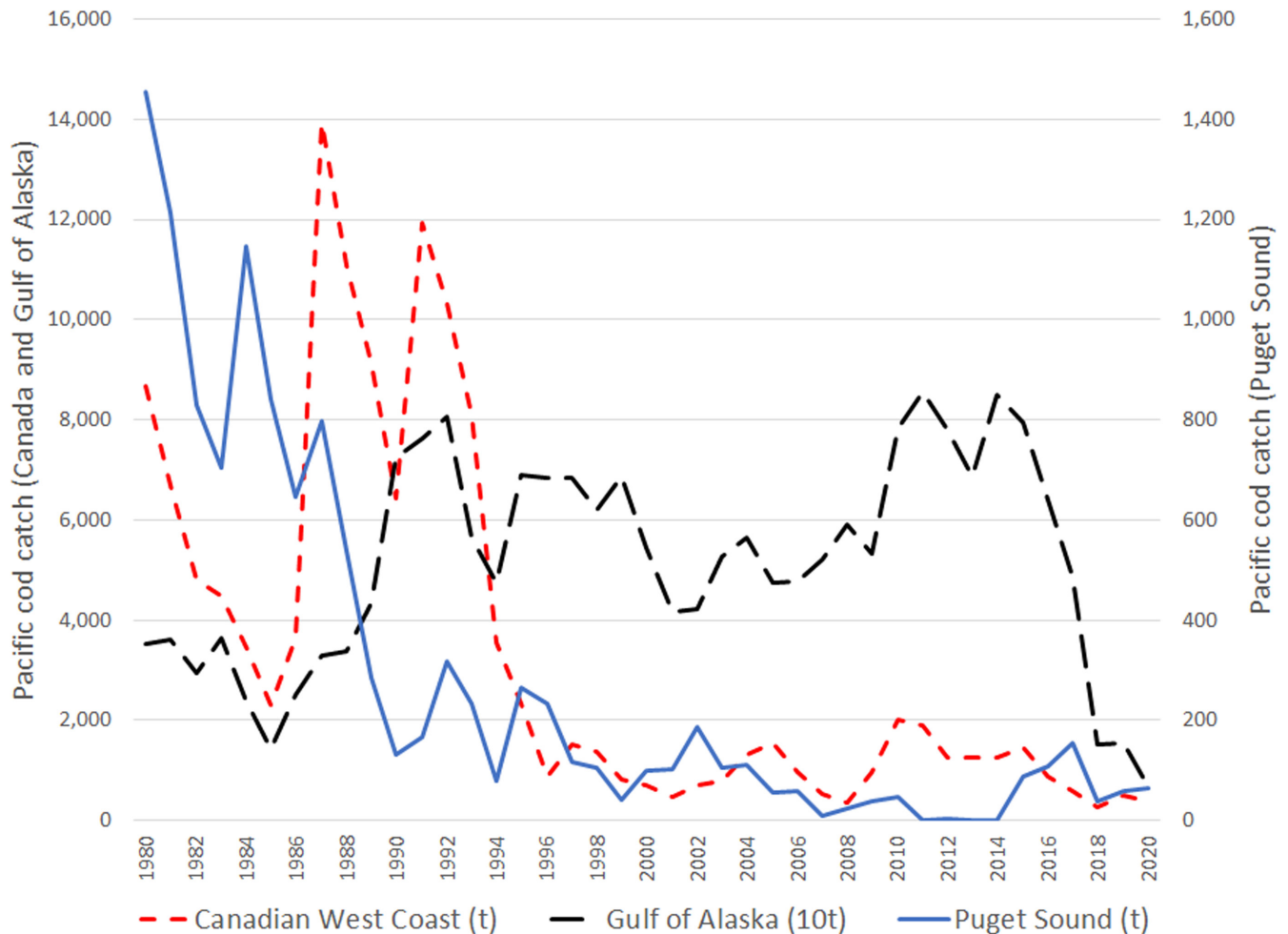


FIGURE 1 Decadal changes in Pacific cod catch (t) along the NE Pacific shelf regions. Catches dropped off in lower latitude regions of Puget Sound and the Canadian West coast during 1990 and 1996, respectively. The Gulf of Alaska (the focus region of this study) has experienced significant declines in catch following the onset of the 2014 marine heatwave period. Catch data were retrieved from the following sources: Puget Sound (Pacific Fisheries Information Network (PacFIN) and Recreational Fisheries Information Network (RecFIN) retrieval dated February 21, 2021, Pacific States Marine Fisheries Commission, Portland, Oregon (www.psmfc.org)), Canadian West Coast (Groundfish Fisheries Operations System (GFFOS) retrieval dated June 4, 2021, Fisheries and Oceans Canada (www.dfo-mpo.gc.ca)), and Gulf of Alaska (Alaska Fisheries Information Network (AKFIN) retrieval dated Mar. 52,021, Pacific States Marine Fisheries Commission, Portland, Oregon (www.psmfc.org)).

juveniles after settlement are available to beach seine gear in the summer (Figure 4) and have fully developed pigments and maintain a demersal lifestyle that continues to adulthood. And while each of these life stages or transitions may have lower or higher mortality potential, adult recruitment is a reflection of both the initial spawning effort (fecundity and 'spawning stock biomass'; SSB) and the cumulative mortality experienced across these early life history stages (e.g., Houde, 1997; Pepin, 1991).

1.2.1 | Eggs

Pacific cod are single-batch spawners and release their eggs on the bottom during the winter–spring transition in the GOA (Stark, 2007). A key feature of Pacific cod eggs is that they are negatively buoyant

and semi-adhesive to the ocean bottom substrate during development (Alderdice & Forrester, 1971). It is, therefore, likely that eggs remain on the seafloor at their spawning location until hatch (Hinckley et al., 2019), which contrasts with the eggs of other commercially harvested gadids, such as Atlantic cod (*Gadus morhua*, Gadidae) and walleye pollock (*Gadus chalcogrammus*, Gadidae), which may be transported well away from their natal origin (Bradbury et al., 2008; Petrik et al., 2015). The egg development period varies from ~2 wks at 8°C to ~6 weeks at 0°C (Laurel et al., 2008), but optimal survival occurs within a narrow temperature range between 4 and 6°C (Bian et al., 2016; Laurel & Rogers, 2020) over a broad range of salinities (Alderdice & Forrester, 1971). The high temperature-sensitivity of Pacific cod eggs is another distinguishing characteristic from more thermally tolerant walleye pollock and Atlantic cod eggs (Dahlke et al., 2018; Laurel et al., 2018; See Figure 5).

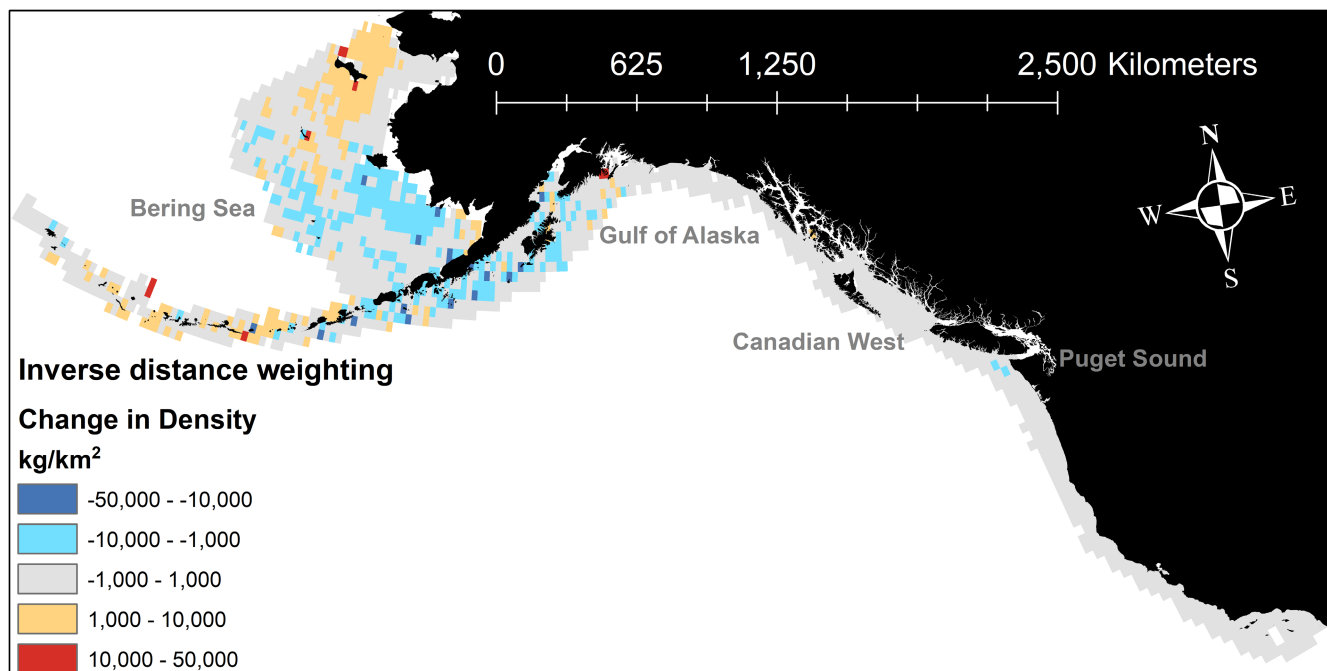


FIGURE 2 Recent spatial changes in Pacific cod catch per unit effort (CPUE; kg/km^2) along the United States and Canadian Eastern Pacific shelf regions from fisheries bottom trawl surveys. Data reflect the relative difference in average weighting during the 2010–2014 and 2017–2020 period, respectively. The Gulf of Alaska (the focus region of this study) has experienced significant declines in adult abundance following a series of heatwaves (2014–16, 2019) while cod in the Bering Sea appear to have shifted poleward. Pacific cod in SE Alaska and further south have maintained low abundance, since the 1990s (see Figure 1).

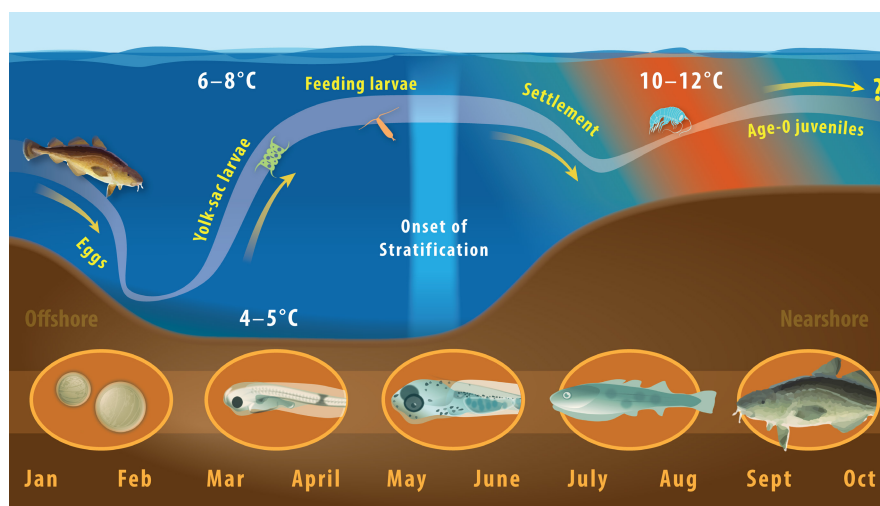


FIGURE 3 Conceptual model of the first year of life of Pacific cod in the Gulf of Alaska along with optimal temperatures for growth and survival at the egg¹, larval² and juvenile³ phases. Eggs are spawned in the spring on the bottom substrates and hatched larvae advect to surface layers in the spring. Larvae develop and feed on zooplankton in the water column as they are transported to coastal nursery habitats in the early summer. Post-settled juveniles shift to diverse epibenthic prey and gradually transition to deeper coastal waters through the early fall. Overwintering habitats have not been identified. ¹Laurel and Rogers (2020); ²Hurst et al. (2010); ³Laurel, Knoth et al. (2016), Hurst et al. (2012).

1.2.2 | Larvae

Eggs hatch into 4 mm larvae at ~3 wks at 4°C (Laurel et al., 2008) and become surface-oriented and available to pelagic ichthyoplankton nets during the spring (Doyle & Mier, 2016). During this period,

Pacific cod larvae consume eggs, nauplii and early copepodite stages of copepod prey <300 μm (Strasburger et al., 2014). The distribution of Pacific cod larvae shifts with ontogeny and is dependent on a number of behavioral and oceanographic processes. In GOA larval survey area (Figure 4), Pacific cod larvae are most abundant around

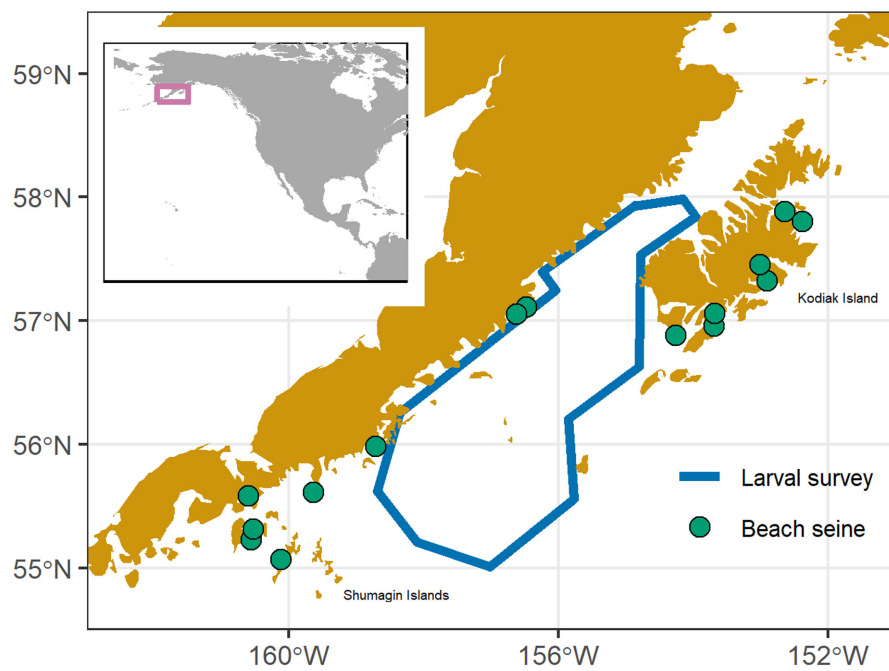


FIGURE 4 Annual survey locations for early life stages of Pacific cod (*Gadus macrocephalus*) in the Gulf of Alaska. Larval sampling occurs offshore in the spring (blue outline), whereas age-0 juvenile sampling (green circles) occurs in summer by beach seine. Inset shows relative location of full survey area within the NE Pacific (magenta box).

Kodiak Island in early April before concentrations shift downstream to the southwest in the Shumagin Islands in May and June (Doyle & Mier, 2016). Newly hatched larvae are surface oriented and make extended diel vertical migrations with increased size and development (Hurst et al., 2009). Larvae reach flexion between 10 and 15 mm and likely become more competent swimmers with increasing size (Voeselek et al., 2018). However, modelled transport pathways indicate that larvae do not disperse far from their spawning locations in the GOA (Hinckley et al., 2019).

Upper thermal tolerances on larval stages of Pacific cod have not been fully explored, but laboratory studies show growth accelerates linearly from 2 to 10°C when prey are abundant (Hurst et al., 2010). Mortality rates steadily increase above 10°C under laboratory conditions, although acute mortality does not occur until 19°C (K. Lavelle & T. Hurst unpub data). In the GOA, spring temperatures seldom approach 10°C, yet the larval abundance is lower during warm springs (Doyle et al., 2009; Doyle & Mier, 2016). Higher spring temperatures increase the vulnerability of Pacific cod larvae to prey mismatch (Laurel et al., 2011) and potentially reduce prey quality through relative shifts in the diatom and dinoflagellate community (Copeman & Laurel, 2010). A recent modeling study examined spring match-mismatch susceptibility of Pacific cod larvae in the GOA, and concluded larvae are indeed experiencing higher starvation risk following the onset of the marine heatwaves in 2014, whereas the Bering Sea ecosystem to north has remained relatively more stable under cooler conditions (Laurel et al., 2021).

1.2.3 | Age-0 juveniles

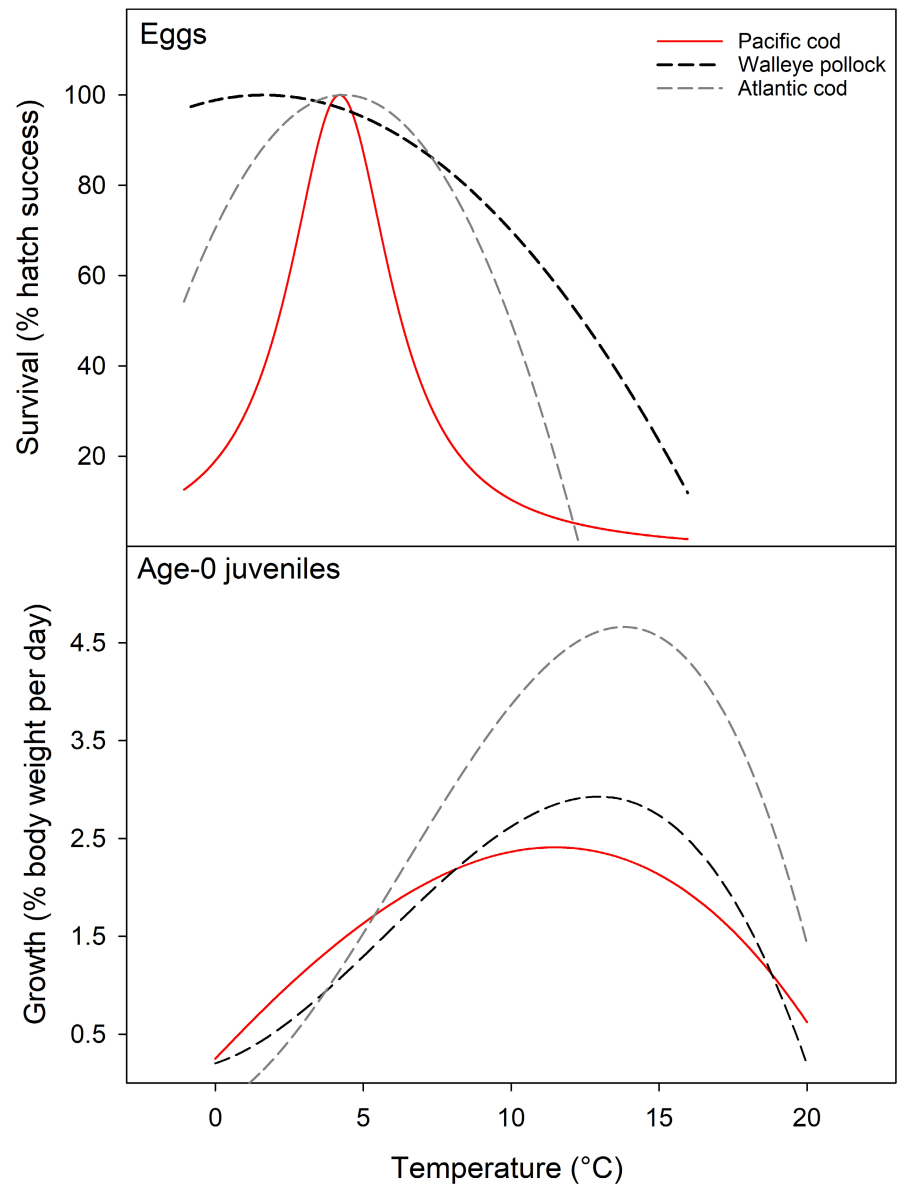
In early summer, juveniles ('pelagic juveniles') in the GOA transport into the nearshore and settle to the bottom around 30–40 mm where they remain through early fall (Laurel et al., 2017).

Shallow, coastal nursery areas provide age-0 juvenile Pacific cod ideal conditions for rapid growth and refuge from predators (Laurel et al., 2007). Settled juvenile cod associate with structural bottom habitats (e.g., macrophytes) and remain close to shore through the summer (< 10 m depth) before shifting into deeper water in the fall, as they approach 90 mm (Laurel et al., 2007; Laurel et al., 2009). Age-0 juveniles become patchier due to schooling behavior, as they transition into deeper water (~10–20 m) while feeding on small calanoid copepods, mysids and gammarid amphipods during this period (Abookire et al., 2007).

1.2.4 | Lipids and ontogeny

Lipids are the densest form of energy in marine ecosystems (Parrish, 2013), and the ability of fish to acquire and store lipids in their body increases their likelihood for survival across periods of unfavorable feeding conditions, e.g., the first winter (Copeman et al., 2022; Hurst, 2007). As such, lipid energy has become an increasingly important metric to track annually in both single-species management (Heintz et al., 2013) and ecosystem status (Parrish, 2013). However, lipids in cod species fluctuate independently of environmental stress, especially across early life stages, necessitating that lipid and proxy metrics of fish condition be tailored to the appropriate life stage and time of year. For example, lipids may initially be elevated in larvae for the purposes of buoyancy (Laurel et al., 2008) and surviving first feeding (Houde, 2008; Laurel et al., 2011) before balancing later energetic demands for fast growth (Copeman et al., 2008). At earlier life stages, lipid content can be further constrained by maternal provisioning (Bogevik et al., 2012) and storage limitations in developing tissues (e.g., muscle vs liver; Copeman et al., 2017). Eventually, lipid density is dependent on seasonal food availability and the metabolic demands

FIGURE 5 Comparison of temperature-dependent egg survival (hatch success; top panel) and age-0 juvenile growth (% body weight per day; bottom panel) for Pacific cod (*Gadus macrocephalus*, red line plots), walleye pollock (*G. chalcogrammus*, black dashed line plots) and Atlantic cod (*G. morhua*, gray dashed line plots). Thermal conditions change across life stages for each species, but Pacific cod have a much narrower thermal tolerance for egg survival followed by a broad thermal tolerance at the juvenile stage. Egg models are normalized for comparison, based on Laurel and Rogers (2020) and Laurel et al. (2018) for Pacific cod and walleye pollock respectively, and Dahlke et al. (2018) for Atlantic cod. Juvenile growth data are based on models reported by Laurel, Knoth et al. (2016) for Pacific cod and walleye pollock, respectively, and Cote et al. (2021) for Atlantic cod.



on lipid stores that may contribute to successful overwintering (Copeman et al., 2022; Sogard & Olla, 2000). Temperature can play an indirect or direct role in all of these processes leading up to and through winter but must be considered in the broader context of development, allometry and other environmental drivers (Martin et al., 2017).

2 | METHODS

2.1 | Observation and sample data for Pacific cod

Surveys of pelagic age-0 Pacific cod have been conducted in some years (Moss et al., 2016) but may be prone to significant measurement error as fish transition to demersal habitats (Mukhina et al., 2003). Therefore, pre-recruit assessments of Pacific cod in the GOA are conducted separately, first during the spring larval period

and later in the summer during the post-settled juvenile stages (Figure 4). The primary surveys consist of: (1) an ichthyoplankton survey in the western GOA (1979–2021; <https://apps-afsc.fisheries.noaa.gov/ichthyo/index.php>), and (2) the a nearshore beach seine survey in Kodiak (2006–2021) with spatial expansion through the Central and Western GOA (2018–2021). Temporal details of these and other surveys by NOAA are listed in Table 1.

The EcoFOCI ichthyoplankton survey is focused in the vicinity of Kodiak Island, Shelikof Strait and Shelikof Sea Valley and captures Pacific cod larvae primarily in May when they are 5–8mm in size (Matarese et al., 2003). Larvae are sampled using oblique tows of a 60cm diameter bongo net (333 or 505µm mesh) from 10m off bottom (or 100m depth maximum) to the surface. Calibrated flowmeters in each net estimate the volume filtered. A random subsample of up to 50 Pacific cod larvae per station are measured for total length. Larval time series data used in this study were based on historical sampling focused in the vicinity of Shelikof Strait and

TABLE 1 Collections of the various life stages of Pacific cod in the Gulf of Alaska (GOA). All life stages have been monitored in the GOA with the exception of eggs (which are demersal). Program abbreviations within the NOAA Alaska Fisheries Science Center are as follows: FBEP=Fisheries Behavioral Ecology Program, EMA=Ecosystem Monitoring and Assessment, Eco-FOCI=Ecosystems and Fisheries Oceanography Coordinated Investigations, and MACE=Midwater Assessment and Conservation Engineering. Outside program abbreviations include the following: UAF=University of Alaska Fairbanks and ACOR=Alaska Coastal Observations and Research.

Life stage	Program	Years	Season	Sampling gear
Eggs	na	na	na	na
Larvae	Eco-FOCI	1981–2021	Spring	Bongo nets
Pelagic juveniles	ABL	2012	Summer	Surface trawl
Age 0–1 juveniles (Kodiak region)	FBEP	2006–2021	Summer	Beach seine
Age 0–1 juveniles (Expanded region)	FBEP/Kodiak lab/UAF/ACOR	2018–2021	Summer	Beach seine
Age-2+	RACE	1991–2019	Summer	Bottom trawl

the shelf southwest of Kodiak Island during mid-May through early June (Figure 4), a period when Pacific cod larvae have been observed to be abundant in the water column (Doyle et al., 2009). This subset of data was used to develop a time-series of larval Pacific cod abundance by calculating the area-weighted mean catch per 10 m².

The juvenile beach seine survey occurs in two bays (Cook Bay, CB and Anton Larsen Bay, ALB) using a 36 m long, negatively buoyant beach seine (details in Laurel et al., 2007). The beach seine targets settled age-0 juveniles in mid-July and late August when fish are 40–100 mm in length (Laurel, Knoth, et al., 2016). In the Kodiak region, sampling occurs multiple times a summer at fixed-site locations in each bay ($n=8$ stations per bay, 16 total stations sampled 2–4 times/year). An additional 13 bays on Kodiak Island, the Alaska Peninsula, and the Shumagin Islands were sampled during 2018–2021 during the same summer period (days of year 184–240, $n=3–9$ fixed stations per bay, 79 total stations). All juvenile cod are identified to species, counted and measured for total length (± 1 mm) to differentiate age-0 (20–145 mm) from age-1 fish (>160 mm) collected in the survey. Year-class strength was estimated from a zero-inflated negative binomial Bayesian regression model considering date of sampling controlled for as a smooth effect with nested site-bay effects as group-level/random term (See Litzow et al., 2022).

Data on adult distributions and abundance are from bottom trawl surveys conducted by the Alaska Fisheries Science Center in the Eastern and Northern Bering Sea (annual 2010–2019; Lauth et al., 2019); Aleutian Islands (biannual 2010–2018; von Szalay & Raring, 2020) and GOA (biannual 2011–2019; Von Szalay & Raring, 2018), by the Department of Fisheries and Oceans for the West Coast Vancouver Island (biannual 2010–2018; Williams et al., 2020b), West Coast Haida Gwaii (biannual 2010–2018; Williams et al., 2020a), Hecate Strait (biannual 2011–2019; Williams, 2018), West Coast Queen Charlotte Islands (biannual 2011–2019; Workman et al., 2008), and Strait of Georgia (2012 and 2015; Olsen & Workman, 2013), and by the Northwest Fisheries Science Center for the west coast of the continental United States (annual 2010–2019; Keller et al., 2017). The catch per unit effort was calculated for area swept as kg per km² for all surveys. For spatial visualizations, inverse distance weighting was applied across the surveys in aggregate using the ARCGIS (Version 10.6.0.8321) and

shown as the relative change between two averaged time periods (2010–2014 and 2017–2020). Spatial Analyst IDW function was shown with a cell size of 0.4° × 0.4° with maximum neighbors of five for each time period. Note, surveys were not standardized to reflect differences in fishing power for spatial visualization.

Data for ontogenetic studies of growth and energy (lipid) allocation were sourced from tissues and live age-0 cod collected in Kodiak and shipped to NOAA's seawater laboratory in Newport, OR.

2.2 | Thermal habitat models

Thermal habitat suitability models were developed by combining stage-specific biological models with bottom temperature data made available by the high-resolution global reanalysis GLORYS12V1 (Lellouche et al., 2018). The GLORYS12V1 reanalysis is a state-of-the-art global hydrodynamic model at 1/12 degrees resolution and 50 vertical depth levels that assimilates available observations (CTD, XBT, floats, satellite data) for the period 1993–2019. Temperature data were extracted at the vertical grid points closest to the seafloor, filtered to include depths shallower than 250 m, and averaged between both the February–April (spawning) and July–September (age-0 juvenile) periods. February–April was chosen based on known spawning dynamics for Pacific cod in Alaska (Neidetcher et al., 2014; Stark, 2007) and July–September was chosen based on period when juveniles are abundant in the nearshore (Laurel et al., 2009). Daily extreme values were averaged and smoothed to match the monthly temporal resolution of GLORYS temperature data. Statistically bias-corrected and downscaled climate projections were calculated in two steps: (i) bias correction of CMIP6 data at their original resolution, and (ii) statistical downscaling of the bias-corrected data to the 1/12th degree resolution grid of the GLORYS model. For the downscaling presented here, we use the GLORYS12V1 global reanalysis (Drévilion et al., 2021) as “observations” for bottom temperature. A total of eight CMIP6 models were individually downscaled and averaged to create a climate ensemble. The CMIP6 models include MIROC-ES2L, MPI-ESM1-2-LR, CMCC-ESM2, IPSL-CM6A-LR, CMCC-CM2-SR5, CanESM56-CanOE, UKESM1-0-LL and GFDL-ESM4. For these models, expected global greenhouse gas

concentrations (emerging from the Representative Concentration Pathways – RCPs) under different shared socioeconomic pathways (SSPs) up to the year 2100 (O'Neill et al., 2016) are used as input. For the 6th Intergovernmental Panel on Climate Change (IPCC) report, five narratives provide alternative socio-economic developments for the world including sustainable development (SSP1), regional rivalry (SSP3), inequality (SSP3, SSP4), fossil fueled development (SSP5) and middle-of-the-road development (SSP2). Here, we focus on the combinations SSP1-RCP2.6, SSP2-RCP4.5 and SSP5-RCP8.5. These scenarios provide us with the full envelope of climate futures to be expected for the GOA ranging from an optimistic future to a more pessimistic fossil-driven one, allowing us to consider the consequences on Pacific cod habitat.

For spawning, thermal habitat suitability was defined as the temperature-dependent hatch success of eggs of GOA Pacific cod described by Laurel and Rogers (2020) and scaled to range from 0 to 1. For juveniles, thermal habitat suitability was defined as the temperature-dependent growth potential of GOA age-0 juvenile cod under food replete conditions (Laurel, Knoth, et al., 2016). These stage-specific thermal response curves for Pacific cod are shown in Figure 5 alongside walleye pollock and Atlantic cod, two other important gadid fisheries in the Pacific and Atlantic, respectively. Habitat suitability maps were then projected from 40 to 62 degrees N along the west coast of the North American continent, near the reported historical limit of the commercial fishery (Cobb, 1926). Additional habitat maps were created comparing the relative difference in spawning and juvenile habitats between the 1993–2013 and the 2014–2020 time periods, coarsely representing the 'pre-' and 'post-heatwave' era, respectively. Future habitat projections under climate scenarios SSP1-RCP2.6, SSP2-RCP4.5 and SSP5-RCP8.5 were created comparing the relative differences in habitat between the 1993–2013 and 2021–2040 time periods.

2.3 | Time series trends

Year class strength data for both larvae and juveniles were plotted with the annually updated NOAA-AFSC Pacific cod spawning habitat index based on the observed temperatures for GOA at GAK1 (see Laurel & Rogers, 2020; Shotwell et al., 2022). Time series were inspected for autocorrelation prior to analyses and examined by way of Pearson's correlation coefficients.

An annual marine heatwave index was developed from the daily sea surface temperatures record of the NOAA High-resolution Blended Analysis Data database (National Oceanic and Atmospheric Administration, 2017) and filtered to only include data from the central GOA between 145 and 160°W longitude for waters less than 300m in depth. Daily mean sea surface temperatures were then calculated by averaging across all points for the entire region. The daily mean sea surface temperature data were processed through the R package *heatwaveR* (Schlegel & Smit, 2018) to obtain the marine heatwave cumulative intensity (MHCI) value (Hobday et al., 2016), where we defined a heatwave as 5 days or more with daily mean

sea surface temperatures greater than the 90th percentile of the time series. MHCI was then summed for each year for the months of January through March, November, and December to create an annual winter marine heatwave cumulative index (WMHCI) to compare with annual indices of spawning habitat and larval and juvenile CPUE in the GOA.

2.4 | Demographic patterns

Demographic analyses on larvae and juvenile cod were conducted to determine whether thermal conditions in the spring have: (1) corresponded with changes in size and (2) carry across larval and juvenile stages.

Thermal effects on size were examined for larval and newly settled juvenile cod. Mean size of larvae was standardized to May 25 (median date of larval sampling) by fitting a mixed effects model to the larval length data, with categorical year and day of year as fixed effects and haul as a random effect. The day of year term accounted for variation in sampling day both within and between years, which varied up to 24 days. Mean size of age-0 juveniles sampled during mid-July in Kodiak was calculated for each year for each bay. All sampling occurring within 1 week of July 14 in each year were included in the analysis. This period approximates the time juveniles are first arriving to nearshore nurseries, that is, 'size-at-settlement'. Model-predicted length of larvae on May 25 for each year was plotted as a function of mean April–May SST for the Central GOA area (as described earlier), and a linear regression was used to test for effects of temperature on mean annual size obtained by May 25. Effects of spring temperature and larval size on mean size-at-settlement were tested in separate linear mixed effects model, each with a random effect for bay.

Lipid density was examined across life stages (egg to juvenile) and across years within a life stage (August age-0 juveniles) to illustrate ontogenetic and environmental effects on energy allocation. Data for the ontogenetic development of lipid storage were sourced from both published and unpublished samples analyzed at the 'Marine Lipid Ecology Lab' at the Hatfield Marine Science Center. These include data from the egg stage ($n=6-9$ samples per stage from Laurel et al., 2010), yolk-sac larval stage ($n=28$ pooled samples from Laurel et al., 2010; Copeman & Laurel, 2010; Hurst et al., 2019), first-feeding larval stage ($n=4-6$ samples per week from Copeman & Laurel, 2010; Hurst et al., 2019), pelagic juvenile stage from the laboratory ($n=7$ samples from Hurst et al., 2019) and settled juveniles collected by beach seine from Kodiak ($n=20$ samples per month; A. Abookire and L. Copeman unpub. data). Data were expressed as total fatty acids per DWT or total fatty acids per individual at a given developmental stage. Triacylglycerols are 95% by mass composed of fatty acids and therefore, fatty acids per weight reflects much of the variability in the major storage lipid class. All data were presented as the average value for samples within that the month or developmental stage for that study with exception of newly hatched larvae which were averaged across all studies.

All reported lipid data represent the whole fish, based on either composite samples of whole eggs, yolk-sac and feeding larvae, or reconstructions of sub-samples of tissues from juveniles that were pre-weighed for wet weight (WWT). Total lipids of wet tissues (100 to 300 mg) were extracted in chloroform and methanol according to Parrish (1987). Conversions between WWT and dry weight (DWT) were completed on composite samples of the same batches of eggs and larvae that were used for lipid analyses. Subsamples of juvenile tissues used in lipid analyses were dried to determine a WWT to DWT conversion factor. Wet tissues were dried for at least 72 h at 65°C to a constant weight. Total lipid extracts were derivatized using acid catalyzed methylation and H₂SO₄ (Budge et al., 2006) or HCL (Meier et al., 2006). An internal standard, 23:0 methyl ester, was added to samples prior to derivatization in order to express total fatty acids (µg) per weight of tissue extracted (mg) or per individual fish in relation to standard length (mm). Fatty acids were analyzed on a gas chromatographer with flame ionization detection using chromatographic methods and identification standards as described in Copeman et al. (2020).

3 | RESULTS

3.1 | Thermal habitat and distribution

The highest spawning habitat suitability for Pacific cod remains in the central and western GOA region of our NE Pacific map projection (Figure 6a). Our spawning habitat model predicted low egg survival potential (<50%) where relatively few fish are currently landed in the

commercial fishery and observed in summer trawl surveys (Figure 2). Notably, high-spawning habitat suitability was indicated in the Cook Inlet and other nearshore regions of the GOA (Figure 6a), but these predictions may be artificially high due to underestimated water temperatures associated with spring freshwater input and complex tidal mixing in that region (Dobbins et al., 2009).

Juvenile summer habitats are predicted to be highly suitable in coastal areas of the GOA where fish can meet >90% of their growth potential (Figure 6d). In Canadian waters farther south, suitable habitat for age-0 juvenile appears to be less restricted to coastal areas, and more widely extended into the offshore shelf where it is predicted juveniles can achieve >75% of the growth potential (Figure 6d). Unlike spawning habitat, juvenile habitat availability does not appear to be restricting the current abundance and distribution patterns of the adult population shown in Figures 1 and 2.

Both spawning and juvenile habitat suitability changed over time according to the models. Spawning habitat suitability declined across the projected region, with the exceptions of some patchy increases in the Western GOA and Aleutian Islands (Figure 6b). In contrast, models predicted a relative increase and shift in juvenile habitat suitability towards the offshore shelf regions (Figure 6e). These patterns are magnified into the future (2021–2040) under varying future climate scenarios, illustrated in Figure 6c and Figure 6f under SSP2-RCP4.5 and Figures S1 and S2 under SSP1-RCP2.6 and SSP5-RCP8.5, respectively. The models did not indicate widespread upper thermal stress in the nearshore, although temperature predictions at the coastal interface may be underestimated where juveniles are typically most abundant during peak summer; for example <2 m depth (Laurel et al., 2007). Overall,

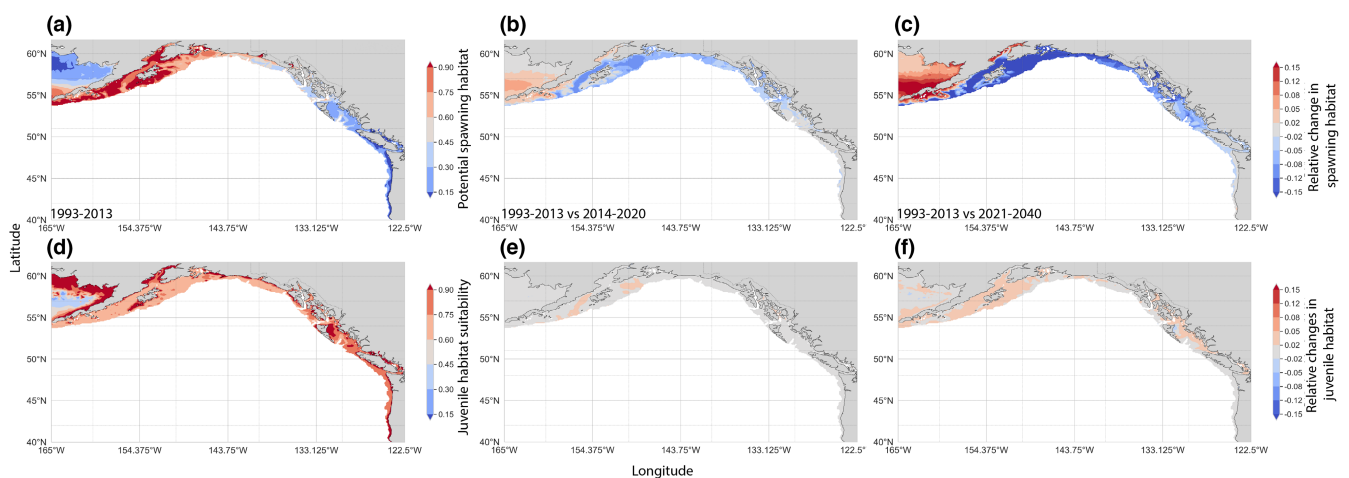


FIGURE 6 Habitat maps of Pacific cod (*Gadus macrocephalus*) in the NE Pacific based on annually averaged temperature-dependent spring spawning (a) and age-0 juvenile summer growth (d) from 1993–2013. Relative changes in habitat suitability from 1993–2013 to 2014–2020 are shown for spring spawning (b) and age-0 juvenile summer growth (e). Future relative changes in habitat suitability from 1993–2013 to 2021–2040 are shown for spawning (c) and juvenile summer growth (f) under a future climate scenario (SSP2-RCP4.5). See Figures S1 and S2 for similar habitat projections under future climate scenarios SSP1-RCP2.6 and SSP5-RCP8.5, respectively. Thermal conditions for spawning potential are spatially restricted to the GOA and declining over time and into the future. Thermal conditions for juvenile cod growth potential remain relatively ubiquitous throughout the historical distribution of Pacific cod and show recent and future gains into the offshore. Habitat maps are based on monthly bottom temperatures from GLORYS12V1 reanalysis averaged seasonally (Feb–Apr) for the spawning period and summer (Jul–Sept) for the juvenile growth period (See Methods).

thermal conditions in the GOA fell within optimal conditions for both egg and juvenile life stages of Pacific cod over a ~20-year period from 1993 but are currently on the higher side of optimal across most of the GOA since 2012 (Figure S3). In contrast, thermal conditions outside the GOA have been sub-optimal for both egg survival and juvenile growth over the same time period. For example, juvenile growth potential is lower to the west of the GOA due to cooler summer temperatures, whereas regions to the south and farther east are too warm for optimal spawning success (Figure S3). Figures S4 and S5 illustrate overall uncertainty in spatially averaged habitat trends under future climate scenarios SSP1-RCP2.6, SSP2-RCP4.5 and SSP5-RCP8.5.

3.2 | Time series analyses

Annual abundance of age-0 cod in the GOA was highly variable, with notable negative anomalies corresponding with extremely low-spawning habitat suitability during marine heatwave periods of 2015, 2016 and 2019 (Figure 7). The GOA spawning habitat suitability index was initially correlated with larval CPUE ($R^2=58\%$, $p<0.001$), but it did not explain annual variation in age-0 juvenile CPUE above the 0.25 index threshold (Figure 8). Juvenile abundance measured by the beach seine was historically correlated with age-1 abundance the following year (Laurel et al., 2017), but recent abundant age-0-year classes have not been observed the following year in the post-heatwave period (Figure 9).

3.3 | Demographic analyses

Ontogenetic differences in lipid density were highly apparent across life stages of Pacific cod, beginning with increasing lipid in the late egg stages (lipogenesis) followed by a decline as fish grow and settle into the coastal nurseries (Figure 10). By August and early fall, ELS Pacific cod have their lowest lipid content before switching back to increasing lipid storage preceding winter.

The size of ELS Pacific cod (mm SL) has increased as the GOA has warmed in recent years. The estimated mean size of larvae on May 25 was over 10mm in 2017, larger than any other year in the time-series, and also well-above average in 2015, the only other year larvae were sampled since the onset of the heatwave period. Larval length was significantly associated with spring sea surface temperatures in April–May ($\beta=1.2$, $F_{1,30}=17.2$, $p<0.001$), with larger larvae in warmer springs. A similar pattern was found for size-at-settlement in July ($\beta=8.4$, $F_{1,23}=29.9$, $p<0.001$). Annual variation in the size at the larval stage correlated with size at juvenile settlement, explaining 69% of the variance in size in mid-July. Juvenile cod sampled in mid-July were ~50% larger in length since the onset of the marine heatwave period beginning in 2014 (Figure 11).

4 | DISCUSSION

Our review of early life history and changes in habitat, abundance and demographics of Pacific cod indicates several significant

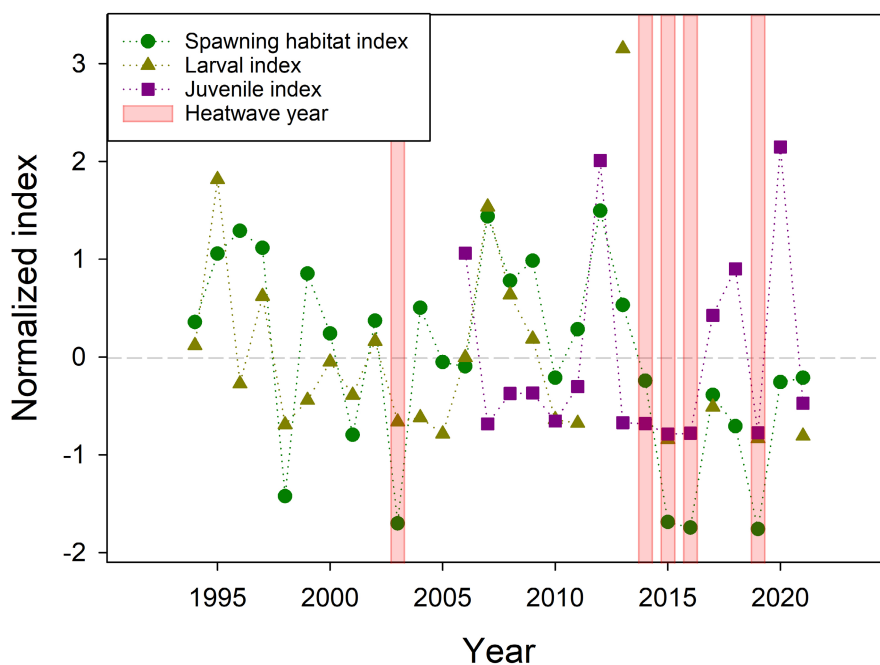


FIGURE 7 Gulf of Alaska winter marine heatwave index compared to available indices of Pacific cod spawning habitat, larval abundance and age-0 juvenile abundance from 1995–2021. The spawning habitat index is based on integrated bottom temperature data at depths and times of potential spawning and the temperature-dependent hatch success of Pacific cod eggs (see Laurel & Rogers 2020). The larval index is based on relative abundance of Pacific cod larvae collected during the RACE EcoFOCI ichthyoplankton survey in the western GOA. The juvenile index is derived from age-0 catch data from the Kodiak beach seine survey (2006–2021; ~64 hauls/yr) and 13 western GOA bays (2018–2021; 78–102 hauls/yr; see Methods). Annual values are normalized within each index for comparative visualization.

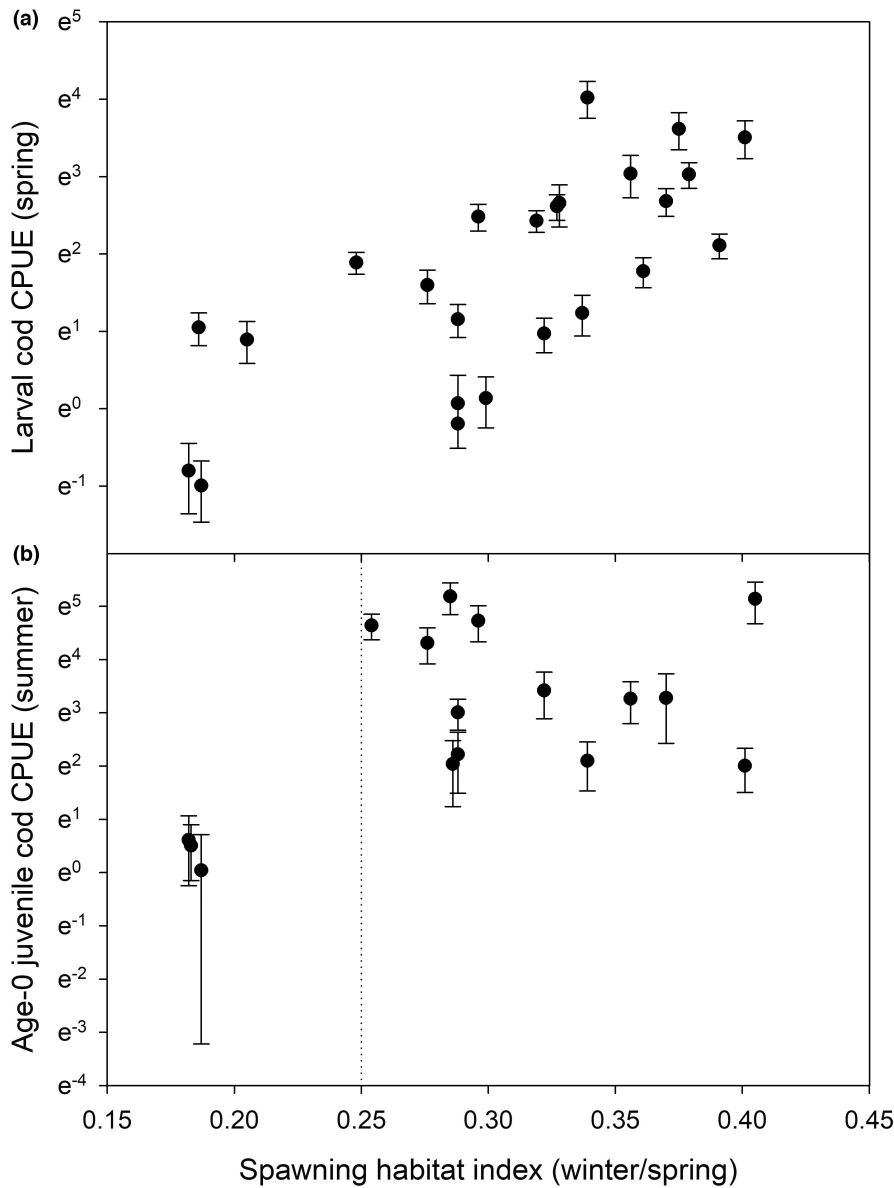


FIGURE 8 Spawning habitat suitability is correlated with initial reproductive output of larvae (a) $R^2 = 58\%$, $p < 0.001$, but does not explain variation in juvenile abundance (b) above the 0.25 index threshold. The spawning habitat index is based on integrated bottom temperature data at depths and times of potential spawning and the temperature-dependent hatch success of Pacific cod eggs (Laurel & Rogers, 2020). Age-0 data are combined data from 2 Kodiak bays (2006–2021; ~64 hauls/yr) and 13 western GOA bays (2018–2021; 78–102 hauls/yr). Year-class strength estimated from zero-inflated negative binomial Bayesian regression model considering date of sampling controlled for as smooth effect with nested site – bay effects as group-level/random term (See Litzow et al., 2022). Note, all points to the left of the dotted reference line (0.25) occurred during marine heatwave years (2015, 2016, and 2019).

patterns relevant for immediate and long-term management consideration. Here, we discuss the nature of these changes and how continued monitoring of thermal habitat and pre-recruits serve as valuable early warning metrics for cod populations in the GOA, the region that currently defines the southern edge of the fishery in the NE Pacific.

4.1 | Spawning habitat

The hatch success models indicate contemporary spawning habitat is largely restricted to shelf areas of the GOA with increasing declines in suitability to the southeast towards Canadian waters and the Washington coast. The regions with more areal extent and high-spawning habitat suitability also appear to reflect areas of highest catch in the current fishery (Figure 2). While fishing effort on spawning aggregations in the spring is not surprising, this observation

provides some validation for the spawning habitat model and its potential relevance to regional population dynamics for cod. The recent and projected loss of spawning habitat throughout most of the study region is therefore concerning (Figure 6). While spawning habitat suitability depends on factors beyond temperature, such as favorable feeding and retention conditions for larvae and juveniles (Hinckley et al., 2019), thermal conditions for egg survival is a prerequisite.

It is possible Pacific cod will shift their spawning behavior to place eggs in more favorable habitats in the future. In Canadian waters, peak spawning historically occurred earlier in February at depths between 100 and 120m near Hecate Strait and ~8wks later (April) in shallower waters (75m) farther north (Ketchen, 1961). In the GOA, gonadal condition of mature females suggests spawning occurs between March and early April (Smith et al., 1990). These latitudinal differences indicate an increasingly later spawn timing from south to north. The bathymetric migration cycle of Pacific cod also

FIGURE 9 Both age-0 recruitment and overwintering survival appears to have declined, since the onset of the Gulf of Alaska heatwave era beginning in 2014. Data are average annual catch per unit effort (CPUE) of the age-0 and age-1 cohort (lagged by 1 year) as surveyed by beach seine in Kodiak Alaska. It is unclear if these changing relationships reflect changes in post-settlement survival or habitat shifts to deeper water, i.e., measurement error in the beach seine. Data points reflect 64 seine hauls conducted between July to August across 16 sites in each year ± 1 S.E. (See Methods). Dotted line reflects a significant linear regression ($R^2 = 62\%$) between age-0 and age-1 lagged abundance in the GOA pre-heatwave era.

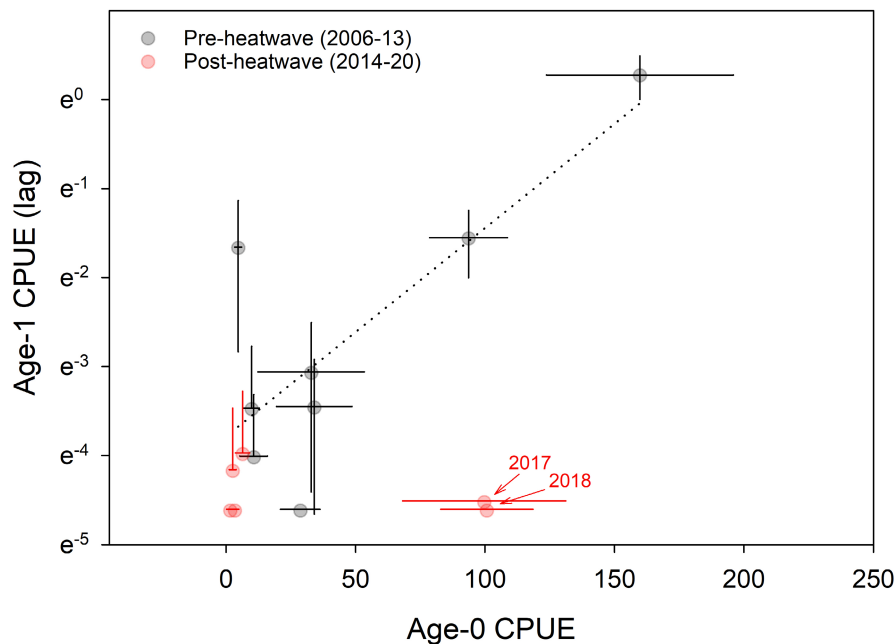
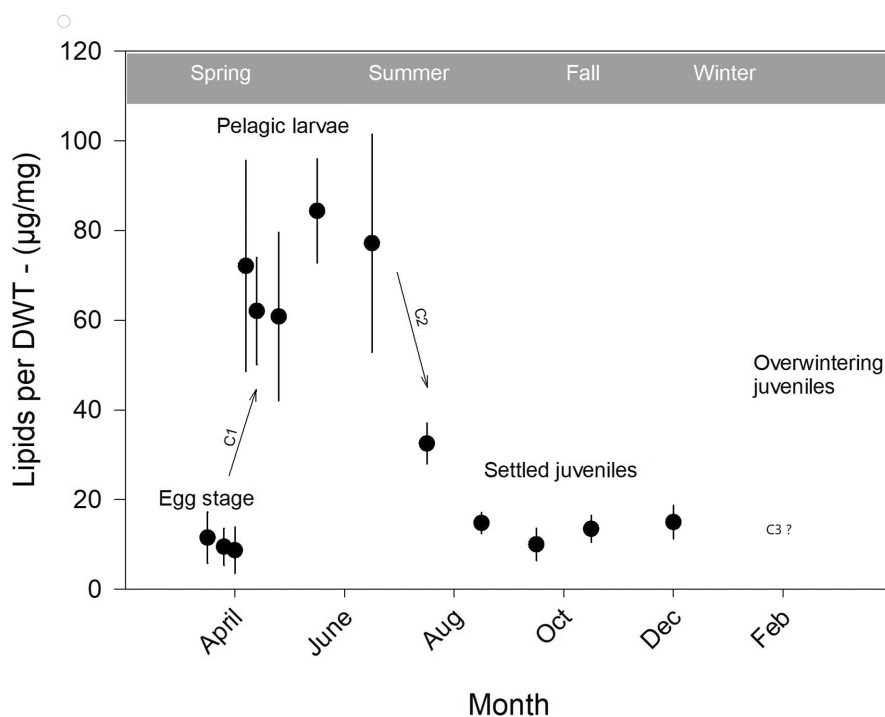


FIGURE 10 Average lipid density of Pacific cod at varying early life stages changes in the Gulf of Alaska. Patterns are influenced by a combination of ontogeny (means), individual phenotypic expression under environmental conditions (error bars), and potential energy transfer across life stages, i.e. “carry over effects” (c1, c2 etc) represented by arrows. Lipid density may have a role in survival across ontogenetic stages but is unlikely to fully carry over into the next ontogenetic stage due to other life history constraints. Data are mean values of total fatty acids by dry weight (mg) of 5–20 pooled individual Pacific cod from the Gulf of Alaska ± 1 SD. Data sources represent a combination published and unpublished field and laboratory studies indicated by footnote (See Methods).



suggests there is strong thermal preference for certain feeding and spawning conditions. For example, cod in the northern part of the Canadian coast occupy the coldest available water ($6\text{--}7^\circ\text{C}$) during spawning and throughout most of the year (Ketchen, 1961), resulting in a deeper winter distribution followed by a transition to shallow regions in early summer. Figure 6 confirms that deeper slope waters in that region are the only areas currently suitable for spawning. At lower latitudes around Puget Sound, cod are reported to make an opposite migration to track cold water masses, beginning with shallow winter waters to spawn followed by movement to cooler deeper waters in the summer to feed (Karp, 1983). Winter and spring bottom

temperatures throughout the Puget Sound appear to be currently too warm to support high egg survival, which may explain why cod appear extirpated from the region (Figure 1). However, the degree to which cod populations can shift their spawn timing and location to match suitable thermal habitats remains unclear.

4.2 | Juvenile habitat

Unlike spawning habitat, thermally suitable juvenile nursery habitat was abundant throughout the study region and actually appears to

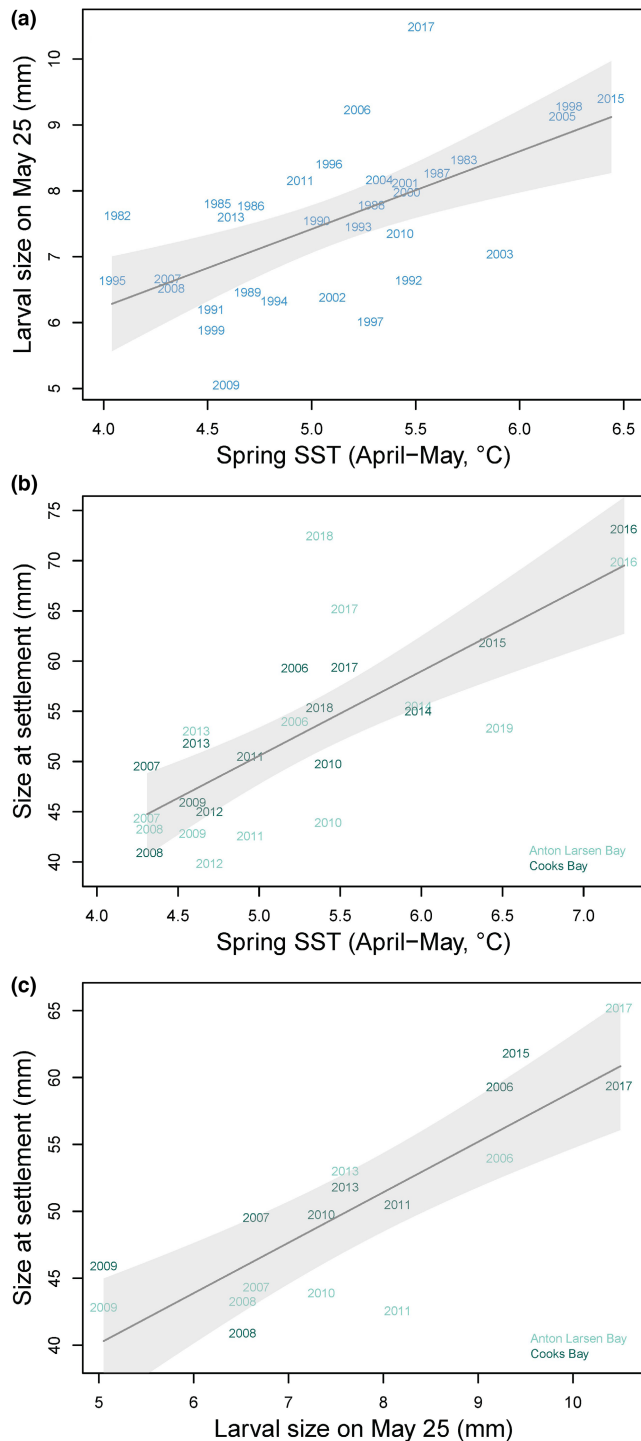


FIGURE 11 Sea surface temperatures in spring (April–May) are a significant predictor of (a) the size of larvae in May ($\beta = 1.2$, $p < 0.001$) and (b) the size of juveniles arriving to coastal nurseries in mid-July ($\beta = 8.4$, $p < 0.001$), which have increased in recent years. The size of larvae in May is also highly predictive of juvenile size in any given year (c; $\beta = 3.7$, $p < 0.001$). Temperatures reflect the 145–160 °W Gulf of Alaska shelf domain. Size data for juveniles were based on collections from two bay locations (hence two values per year reported).

have increased in recent years with increasing expansion projected into 2040 (Figure 6, bottom panels). The highest habitat suitability in the GOA was predicted in nearshore regions where age-0 cod are currently surveyed annually by beach seine (Abookire et al., 2021; Laurel, Spencer, et al., 2016), although recent and future warming indicates increased growth potential in deeper waters of the GOA region. In contrast, deeper offshore regions were more suitable for age-0 cod in lower latitudes across the entire time period. Growth potential in the nearshore is likely an important component of successful recruitment to the adult population in the Central GOA (Laurel et al., 2017). However, there are several limitations in these habitat models to consider. First, the GLORYS12V1 model is not expected to resolve extreme nearshore temperatures where age-0 cod can be abundant in summer. For example, actual temperature measurements from summer beach seine locations approached ~16°C during a marine heatwave (2014–2016, 2019), and while not lethal, would be sub-optimal for growth even when food is plentiful (Laurel, Spencer, et al., 2016). Second, these juvenile habitat models assume sufficient food is available in the regions identified as areas of high growth potential, which is a particular concern if warming is also associated with lower prey biomass. Surprisingly, however, the abundance of offshore cold water zooplankton community in the water column did not notably decline during 2014–16 GOA heatwave period (Suryan et al., 2021). In the Kodiak nearshore, stomach fullness of juvenile age-0 Pacific cod has remained consistent from 2006–2019, but there is evidence of changes in prey types during marine heatwave years that could potentially impact fish condition (Thalman et al., unpublished data).

It is unclear whether spatial shifts in thermal habitat will influence age-0 cod survival, distribution or recruitment to the adult population. Juvenile habitat use is dependent on a host of processes independent of behavior, including those occurring pre-settlement (e.g., larval supply, transport, mortality; Hinckley et al., 2019) coupled with state-dependent variables occurring post-settlement (predator avoidance, food availability, etc.; Juanes, 2007). Under laboratory conditions, age-0 and age-1+ Pacific cod are reluctant to move from warmer, high-growth conditions (9°C) into cooler waters (3°C), but will eventually make this transition when food is more available in these colder habitats (Davis & Ottmar, 2009). Age-0 Atlantic cod also experience higher predation risk in deeper water (Linehan et al., 2001) and may be reluctant to move across risky habitats (Stanley et al., 2012). Ideal thermal habitats may therefore go unexploited by juvenile Pacific cod or result in new behavioral or physiological phenotypes. These include increased schooling behavior (Laurel et al., 2007) or shifts in metabolic thermal performance; that is, 'reaction norms' (Hutchings et al., 2007; Neubauer & Andersen, 2019). For example, cohorts of age-0 Pacific cod collected in warm years grow faster at warmer temperature than age-0 cohorts collected in colder years (Hurst et al., 2012), and recent genetic studies suggest strong

directional selection among the ZP3 haplotype which has functional links to antifreeze glycoproteins and low-thermal tolerance (Spies et al., 2021). These and other potential thermal adaptations are significant knowledge gaps for Pacific cod at every life stage and will have important bearing on how shifting thermal habitats affect Pacific cod under future climate change.

Juvenile overwintering habitats will be important to characterize as the GOA winters continue to warm. Winter processes in general are poorly captured in marine systems due to the lack of sampling, and where examined, tend to focus on the physiological limits of lower temperature combined with lower productivity (Hurst, 2007). In the GOA, winter temperatures have seldom dropped below 2°C, since 1993 (Figure S3), and it is not likely age-0 juvenile cod experience low temperature stress like other cod in sub-Arctic systems (Laurel et al., 2017). Rather, the impact of warming winters has the potential to increase starvation rates and size-dependent predation through reduced growth and condition (Sogard & Olla, 2000). Winter surface conditions appear to be warming at faster rate than other times of the year in the GOA (Figure S3). Under cooler winter conditions (e.g., 0°C), age-0 gadids can survive for >2 months in the absence of food (Copeman et al., 2022; Sogard & Olla, 2000), although Pacific cod have much higher metabolic demands than other Arctic gadids like polar cod (*Boreogadus saida*, Gadidae) at warmer temperatures (Laurel et al., 2016a). Forage fish may also have lower energy densities as a consequence of these metabolic demands in winter, leading to mortality across a range of trophic levels and taxa ("ectothermic vise"; Piatt et al., 2020). During the marine heatwave period in 2015, stomach fullness of adult Pacific cod (40–80 cm) was the lowest on record at the same time preferred prey were notably absent, including Tanner crab (*Chionoecetes bairdi*, Oregoniidae) and capelin (*Mallotus villosus*, Osmeridae) (Barbeaux et al., 2019). Bioenergetic models indicated that the sustained demand for prey through the winter months was unlikely met, especially for fish in the 10 cm size range (age-0s) as well as older life stages (>40 cm) requiring additional energy for reproduction (Barbeaux et al., 2020).

4.3 | Shifting mortality schedules and demographics

Warming appears to be negatively impacting early life stages of cod in the GOA, with an almost complete absence of pre-recruits observed in the major heatwave years of 2015, 2016 and 2019. Historically, spring temperature had little predictive value on recruitment dynamics of cod, suggesting a non-stationarity in this relationship (Litzow et al., 2022). Mechanistically, these temperature-associated sources of mortality are understood through upper thermal stress on eggs (Laurel & Rogers, 2020) and higher potential for starvation in first-feeding larvae (Laurel et al., 2021). Reproductive potential was also likely reduced during this period through metabolic stress on older life stages (Barbeaux et al., 2019).

Despite these negative impacts of warming, we observed a positive influence of winter–spring temperatures on the annual size of larvae and juveniles. While these observations conform to expectations (the temperature–size rule, Atkinson, 1994), it is unclear whether these demographic shifts are buffering or amplifying early sources of mortality. The processes driving these size shifts are also uncertain, as they could reflect temperature-dependent changes in spawning time (Rogers & Dougherty, 2019), size-at-hatch (Laurel et al., 2008), pre-settlement growth (Abookire et al., 2021), post-settlement growth (Hurst et al., 2010), size-selective mortality or some combination of all these processes (e.g., Pepin et al., 2015). All of these factors can work alone or together to impact the size and timing of settlement in nursery grounds, but disentangling these processes will require refined information on age and growth of larvae and juveniles. Additional diet information will also be needed to measure consequences of early spawning for first-feeding larvae in the spring (e.g., match-mismatch dynamics; Laurel et al., 2021), increased metabolic demands and shifts in prey-size spectra (Munk, 1997). And finally, accounting for these cumulative temperature impacts through and beyond the first year of life (e.g., 'carry over effects'; O'Connor et al., 2014; Pechenik, 2018) will require modeling frameworks that track demographic changes in cohorts over space and time, e.g. Individual Based Models (IBMs) (Hinckley et al., 2019; Kristiansen et al., 2009).

4.4 | Temperature and energy reserves

The ontogenetic changes in lipid energy in Pacific cod reveal a series of changing energy allocation strategies as eggs, larvae and juveniles transition and shift to new habitats. Eggs and newly hatched larvae rely on yolk energy stores before first feeding and then appear to build lipid density at pelagic stages prior to settlement. The rapid decline in lipid energy after settlement may reflect an ontogenetic process (e.g., energy allocation to growth) and/or trophic stress resulting from the habitat transition (e.g., prey quality, capture, availability, etc; Copeman et al., 2009; Nunn et al., 2012). The ability to store lipid energy from these summer growth environments may be important for future survival (Weinig & Delph, 2001). For example, age-0 juvenile Atlantic cod must grow rapidly in the summer to escape gape-limited predation (Linehan et al., 2001), but consequently enter their first winter with very low-lipid reserves (Copeman et al., 2008). Age-0 juvenile Pacific cod are also in relatively low-lipid condition during the summer in the GOA nearshore (Budge et al., 2022) and laboratory experiments show lipid allocation rates in age-0 Pacific cod declining further as temperatures exceed 10°C (Copeman et al., 2017). Interestingly, an analysis of age-0 cod collected throughout the Central and Western GOA in 2018–20 indicated fish in 2019 (a heatwave year) had higher hepatosomatic values compared to fish collected in cooler adjacent years (Abookire et al., 2021). However, the 2019 observation is confounded by significant concurrent changes in average fish size (larger) and cohort density (lower) for that year. In addition, lipids are difficult to

estimate using gravimetric proxies due to their high-energetic density (Copeman et al., 2022). These challenges coupled with seasonal, ontogenetic and environmental constraints on lipid energy storage make it difficult to develop and interpret condition-based survival trajectories for Pacific cod early in the year.

Despite missing mechanistic information, condition metrics for early life stages (e.g., lipids, size-at-age, total energy density) are used in fisheries management of Alaska gadids (Shotwell et al., 2022). The implicit understanding is that larger or faster growing members of a cohort have a survival advantage during the winter, because they are less vulnerable to predators (Hurst, 2007) and can carry more fall energy reserves through the winter period of low productivity (Byström et al., 2006; Post & Evans, 1989; Thompson et al., 1991). These principles support a current recruitment paradigm for walleye pollock in the Bering Sea, where size and condition of juveniles in the fall preceding their first winter is a recruitment indicator (Heintz et al., 2013). There are currently no surveys in Alaska to track age-0 cod condition in the fall, but such information may determine whether missing age-1 cohorts (e.g., 2017 and 2018; Figure 9) are due to older juvenile stages shifting to the offshore or the result of winter bioenergetic stress.

4.5 | Science and management recommendations

Pacific cod in the GOA exemplify the new challenges of managing fisheries in a climate era without historical precedent. Management targets (e.g., spawning stock biomass) and assumptions in stock assessment (e.g., ELS natural mortality) remain misaligned with new climate-driven processes, leading to unanticipated impacts on local populations. Recruitment forecasts based on historical statistical relationships will, therefore, be unreliable for Pacific cod populations experiencing rapid warming conditions. We describe several processes by which seasonal warming negatively impacts ELS cohorts of Pacific cod in the GOA that have only become evident in the most recent part of our time series. Determining the downstream effects of these ELS impacts will continue to be challenging for fisheries management, especially as shifts in habitat and size-at-age could lead to new mortality and maturity schedules. However, models that can utilize time series data from multiple life history stages are most likely to have the highest predictive skill for stock assessment (Litzow et al., 2022) while providing mechanistic understanding for declining stocks attributed to anthropogenic ocean warming (Litzow et al., 2021).

One of the challenges for fisheries managers will be to decide on where to direct limited resources to monitor Pacific cod populations experiencing climate stress. For example, surveys of early life stages can provide early warnings of recruitment failure but may perform poorly at predicting strong year classes when they precede later critical periods. This includes measurements of fish condition (e.g., lipid density) taken during a time/ontogenetic period of low environmental influence or too early in advance of winter when these energetic reserves are required. At the same time, late-stage

monitoring will provide less lead-time for management and miss emergent climate drivers acting on sensitive early life stages needed for decadal forecasts. Both approaches are needed in management for climate stressed fisheries like Pacific cod. Furthermore, climate-driven changes in phenology (e.g., spawn timing, ontogenetic habitat shifts) can complicate efforts to monitor early life stages, and need to be tracked and accounted for. Predictions based on physiological and biological sensitivity (e.g., thermal habitat models) can fill these knowledge gaps as more comprehensive monitoring programs are built.

We, therefore, advocate a synoptic approach that integrates ecosystem and ELS monitoring across multiple life stages while improving seasonal thermal habitat metrics for use in short-term and long-term forecasting. Pre-recruit monitoring should be conducted annually to fill in gaps in the adult bottom trawl survey (currently conducted biennially; Barbeaux et al., 2019) and spatially extended along an east to west gradient (warm to cool) to capture climate stress before impacts are apparent across the entire region. Increased spatial coverage is also necessary to span genetic breaks recently discovered in the Central GOA region (Spies et al., 2021). We also recommend occasional integrated ecosystem surveys with laboratory and oceanographic support to lend improved mechanistic interpretation towards emerging patterns of redistribution, size structure and abundance in the Pacific cod population. An example of such effort occurred through the Bering Sea Integrated Ecosystem Research Project (BSIERP) which developed new recruitment paradigms for several focal species, including walleye pollock (Heintz et al., 2013). While more modest ecosystem surveys have been conducted in the GOA (Ormseth & Norcross, 2009), they need to be repeated as continued warming exceeds historical observations and early life stages are exposed to novel environmental conditions. These recommendations apply more broadly to other marine species given the rapid changes occurring in most marine ecosystems (Smale et al., 2019). Collectively, these tools and approaches can provide some climate resiliency for stakeholders in the Pacific cod fishery, both by increasing lead times for early detection of recruitment failure, and by providing the mechanistic underpinning necessary to produce medium- to long-term stock outlooks to guide proactive planning.

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DATA AVAILABILITY STATEMENT

The majority of data for this study are from published sources, all of which are identified and cited in the article's reference list. Access to demographic data are available upon reasonable request to Benjamin Laurel (ben.laurel@noaa.gov). Inquiries on habitat models and climate projections should be directed to Trond Kristiansen (trondkr@faralloninstitute.org).

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REFERENCES

- Abookire, A. A., Duffy-Anderson, J. T., & Jump, C. M. (2007). Habitat associations and diet of young-of-the-year Pacific cod (*Gadus macrocephalus*) near Kodiak, Alaska. *Marine Biology*, 150(4), 713–726.
- Abookire, A. A., Litzow, M. A., Malick, M. J., & Laurel, B. J. (2021). Post-settlement abundance, condition, and survival in a climate-stressed population of Pacific cod. *Canadian Journal of Fisheries and Aquatic Sciences*, 79(6), 958–968. <https://doi.org/10.1139/cjfas-2021-0224>
- Alderdice, D. F., & Forrester, C. R. (1971). Effects of salinity, temperature, and dissolved oxygen on early development of Pacific cod (*Gadus macrocephalus*). *Journal of the Fisheries Research Board of Canada*, 28(6), 883–902. <https://doi.org/10.1139/F71-130>
- Anderson, P. J., & Piatt, J. F. (1999). Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Marine Ecology Progress Series*, 189, 117–123.
- Atkinson, D. (1994). Temperature and organism size—a biological law for ectotherms? *Advances in Ecological Research*, 25, 1–58.
- Barbeaux, S., 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.
- Barbeaux, S. J., Aydin, K., Fissel, B., Holsman, K., Laurel, B. J., Palsson, W., Shotwell, K., Spies, I., & Zador, S. (2019). *Assessment of the Pacific cod stock in the Gulf of Alaska*. North Pacific Fisheries Management Council.
- Barbeaux, S., Aydin, K., Fissel, B., Holsman, K., Palsson, W., Shotwell, K., Yang, Q., & Zador, S. (2017). *Chapter 2: Assessment of the Pacific cod stock in the Gulf of Alaska*. North Pacific Fishery Management Council.
- Benson, A. J., & Trites, A. W. (2002). Ecological effects of regime shifts in the Bering Sea and eastern North Pacific Ocean. *Fish and Fisheries*, 3(2), 95–113.
- Betts, M. W., Maschner, H. D., & Lech, V. (2011). A 4500-year time-series of otariid abundance on Sanak Island, western Gulf of Alaska. In *Human impacts on seals, sea lions, and sea otters: Integrating archaeology and ecology in the northeast Pacific* (pp. 93–110). University of California Press.
- 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. <https://doi.org/10.1016/j.dsr2.2015.01.019>
- Bogevik, A., Natário, S., Karlsen, Ø., Thorsen, A., Hamre, K., Rosenlund, G., & Norberg, B. (2012). The effect of dietary lipid content and stress on egg quality in farmed Atlantic cod *Gadus morhua*. *Journal of Fish Biology*, 81(4), 1391–1405.
- Bradbury, I., Laurel, B., Robichaud, D., Rose, G., Snelgrove, P., Gregory, R., Cote, D., & 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.
- Budge, S. M., Iverson, S. J., & Koopman, H. N. (2006). Studying trophic ecology in marine ecosystems using fatty acids: A primer on analysis and interpretation. *Marine Mammal Science*, 22(4), 759–801.
- Budge, S. M., Wang, S. W., Ormseth, O. A., & Rand, K. M. (2022). Foraging ecology of nearshore fishes in the Gulf of Alaska. *Deep Sea Research Part II: Topical Studies in Oceanography*, 195, 105013.
- Byström, P., Andersson, J., Kiessling, A., & Eriksson, L. O. (2006). Size and temperature dependent foraging capacities and metabolism: Consequences for winter starvation mortality in fish. *Oikos*, 115(1), 43–52.
- Cobb, J. N. (1926). *Pacific cod fisheries*. US Government Printing Office.
- Cobb, J. N. (1927). *Pacific cod fisheries (No. 1014)*. US Government Printing Office.
- Copeman, L. A., Laurel, B. J., Spencer, M., & Sremba, A. (2017). Temperature impacts on lipid allocation among juvenile gadid species at the Pacific Arctic-Boreal interface: an experimental laboratory approach. *Marine Ecology Progress Series*, 566, 183–198.
- Copeman, L., Parrish, C. C., Gregory, R., Jamieson, R., Wells, J., & Whitticar, M. (2009). Fatty acid biomarkers in Coldwater eelgrass meadows: Elevated terrestrial input to the food web of age-0 Atlantic cod *Gadus morhua*. *Marine Ecology Progress Series*, 386, 237–251.
- Copeman, L., Spencer, M., Heintz, R., Vollenweider, J., Sremba, A., Helsler, T., Logerwell, L., Sousa, L., Danielson, S., Pinchuk, A. I., & Laurel, B. (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 Biology*, 43(8), 1121–1140.
- 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. <https://doi.org/10.3354/meps08661>
- Copeman, L. A., Parrish, C. C., Gregory, R. S., & Wells, J. S. (2008). Decreased lipid storage in juvenile Atlantic cod (*Gadus morhua*) during settlement in cold-water eelgrass habitat. *Marine Biology*, 154(5), 823–832. <https://doi.org/10.1007/s00227-008-0975-2>
- Copeman, L. A., Stowell, M. A., Salant, C. D., Ottmar, M. L., Spencer, M. L., Iseri, P. J., & Laurel, B. J. (2022). The role of temperature on over-winter survival, condition metrics and lipid loss in juvenile polar cod (*Boreogadus saida*): A laboratory experiment. *Deep Sea Research Part II: Topical Studies in Oceanography*, 205, 105177.
- Cote, D., Konecny, C. A., Seiden, J., Hauser, T., Kristiansen, T., & Laurel, B. J. (2021). Forecasted shifts in thermal habitat for cod species in the northwest Atlantic and Eastern Canadian Arctic. *Frontiers in Marine Science*, 8, 764072.
- Dahlke, F. T., Butzin, M., Nahrung, J., Puvanendran, V., Mortensen, A., Pörtner, H.-O., & Storch, D. (2018). Northern cod species face spawning habitat losses if global warming exceeds 1.5°C. *Science Advances*, 4(11), eaas8821. <https://doi.org/10.1126/sciadv.aas8821>
- Dahlke, F. T., Wohlrab, S., Butzin, M., & Pörtner, H.-O. (2020). Thermal bottlenecks in the life cycle define climate vulnerability of fish. *Science*, 369(6499), 65–70.
- Davis, M. W., & Ottmar, M. L. (2009). Vertical distribution of juvenile Pacific cod *Gadus macrocephalus*: Potential role of light, temperature, food, and age. *Aquatic Biology*, 8(1), 29–37. <https://doi.org/10.3354/ab00209>

- Dobbins, E. L., Hermann, A. J., Stabeno, P., Bond, N. A., & Steed, R. C. (2009). Modeled transport of freshwater from a line-source in the coastal Gulf of Alaska. *Deep Sea Research Part II: Topical Studies in Oceanography*, 56(24), 2409–2426.
- Doyle, M. J., & Mier, K. L. (2016). Early life history pelagic exposure profiles of selected commercially important fish species in the Gulf of Alaska. *Deep-Sea Research Part II-Topical Studies in Oceanography*, 132, 162–193. <https://doi.org/10.1016/j.dsr2.2015.06.019>
- Doyle, M. J., Picquelle, S. J., Mier, K. L., Spillane, M. C., & Bond, N. A. (2009). Larval fish abundance and physical forcing in the Gulf of Alaska, 1981–2003. *Progress in Oceanography*, 80(3–4), 163–187. <https://doi.org/10.1016/j.pocean.2009.03.002>
- Drévilion, M., Lellouche, J.-M., Régnier, C., Garric, G., Bricaud, C., Hernandez, O., & Bourdallé-Badie, R. (2021). QUID for Global Ocean reanalysis products GLOBALREANALYSIS-PHY-001-030. Copernicus.eu <https://catalogue.marine.copernicus.eu/documents/QUID/CMEMS-GLO-QUID-001-030.pdf>
- Drinkwater, K. F. (2005). The response of Atlantic cod (*Gadus morhua*) to future climate change. *ICES Journal of Marine Science*, 62(7), 1327–1337. <https://doi.org/10.1016/j.icesjms.2005.05.015>
- Fagundes, M., Litvin, S., Micheli, F., De Leo, G., Boch, C., Barry, J., Omidvar, S., & Woodson, C. (2020). Downscaling global ocean climate models improves estimates of exposure regimes in coastal environments. *Scientific Reports*, 10(1), 1–11.
- Forrest, R., Rutherford, K., Lacko, L., Kronlund, A., Starr, P., & McClelland, E. (2015). Assessment of Pacific cod (*Gadus macrocephalus*) for Hecate Strait (5CD) and queen Charlotte sound (5AB) in 2013. Canadian science advisory secretariat (CSAS).
- Forrest, R. E., Anderson, S. C., Grandin, C. J., & Starr, P. J. (2020). Canadian science advisory secretariat (CSAS) research document 2020/070 Pacific region.
- Gustafson, R. G., Lenarz, W. H., McCain, B. B., Schmitt, C. C., Grant, W. S., Builder, T. L., & Methot, R. D. (2000). Status review of Pacific hake, Pacific cod, and walleyepollock from Puget Sound, Washington.
- 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. <https://doi.org/10.1016/j.dsr2.2013.04.006>
- Helser, T., Kastle, C., Crowell, A., Ushikubo, T., Orland, I. J., Kozdon, R., & Valley, J. W. (2018). A 200-year archaeozoological record of Pacific cod (*Gadus macrocephalus*) life history as revealed through ion microprobe oxygen isotope ratios in otoliths. *Journal of Archaeological Science: Reports*, 21, 1236–1246.
- 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. <https://doi.org/10.1016/j.dsr2.2019.05.007>
- Hobday, A. J., Alexander, L. V., Perkins, S. E., Smale, D. A., Straub, S. C., Oliver, E. C., ... Feng, M. (2016). A hierarchical approach to defining marine heatwaves. *Progress in Oceanography*, 141, 227–238.
- Houde, E. (1987). Fish early life dynamics and recruitment variability. *American Fisheries Society Symposium*, 2, 17–29.
- Houde, E. D. (1997). Patterns and trends in larval-stage growth and mortality of teleost fish. *Journal of Fish Biology*, 51, 52–83.
- Houde, E. D. (2008). Emerging from Hjort's shadow. *Journal of Northwest Atlantic Fishery Science*, 41, 53–70.
- Hurst, T. P. (2007). Causes and consequences of winter mortality in fishes. *Journal of Fish Biology*, 71(2), 315–345. <https://doi.org/10.1111/j.1095-8649.2007.01596.x>
- Hurst, T. P., Cooper, D. W., Scheingross, J. S., Seale, E. M., Laurel, B. J., & Spencer, M. L. (2009). Effects of ontogeny, temperature, and light on vertical movements of larval Pacific cod (*Gadus macrocephalus*). *Fisheries Oceanography*, 18(5), 301–311. <https://doi.org/10.1111/j.1365-2419.2009.00512.x>
- Hurst, T. P., Copeman, L. A., Haines, S. A., Meredith, S. D., Daniels, K., & Hubbard, K. M. (2019). Elevated CO₂ alters behavior, growth, and lipid composition of Pacific cod larvae. *Marine Environmental Research*, 145, 52–65.
- 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.
- Hurst, T. P., Munch, S. B., & Lavelle, K. A. (2012). Thermal reaction norms for growth among cohorts of Pacific cod (*Gadus macrocephalus*). *Marine Biology*, 159, 2173–2183.
- Hutchings, J. A., Swain, D. P., Rowe, S., Eddington, J. D., Puvanendran, V., & Brown, J. A. (2007). Genetic variation in life-history reaction norms in a marine fish. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 274(1619), 1693–1699.
- Juanes, F. (2007). Role of habitat in mediating mortality during the post-settlement transition phase of temperate marine fishes. *Journal of Fish Biology*, 70(3), 661–677.
- Karp, W. A. (1983). *Biology and management of Pacific cod (Gadus macrocephalus tulesius) in Port Townsend, Washington*. (Ph. D.). University of Washington.
- Keller, A. A., Wallace, J. R., & Methot, R. D. (2017). The northwest fisheries science Center's West coast Groundfish bottom trawl survey: History, design, and description.
- Ketchen, K. (1961). Observations on the ecology of the Pacific cod (*Gadus macrocephalus*) in Canadian waters. *Journal of the Fisheries Board of Canada*, 18(4), 513–558.
- 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), e17456.
- Kristiansen, T., Vikebø, F., Sundby, S., Huse, G., & Fiksen, Ø. (2009). Modeling growth of larval cod (*Gadus morhua*) in large-scale seasonal and latitudinal environmental gradients. *Deep Sea Research Part II: Topical Studies in Oceanography*, 56(21–22), 2001–2011.
- Laurel, B., Spencer, M., Iseri, P., & Copeman, L. (2016). Temperature-dependent growth and behavior of juvenile Arctic cod (*Boreogadus saida*) and co-occurring North Pacific gadids. *Polar Biology*, 39(6), 1127–1135. <https://doi.org/10.1007/s00300-015-1761-5>
- Laurel, B. J., Copeman, L. A., Hurst, T. P., & Parrish, C. C. (2010). The ecological significance of lipid/fatty acid synthesis in developing eggs and newly hatched larvae of Pacific cod (*Gadus macrocephalus*). *Marine Biology*, 157(8), 1713–1724. <https://doi.org/10.1007/s00227-010-1445-1>
- Laurel, B. J., Copeman, L. A., Spencer, M., & Iseri, P. (2018). Comparative effects of temperature on rates of development and survival of eggs and yolk-sac larvae of Arctic cod (*Boreogadus saida*) and walleye Pollock (*Gadus chalcogrammus*). *ICES Journal of Marine Science*, 2403–2412, 2403–2412. <https://doi.org/10.1093/icesjms/fsy042>
- Laurel, B. J., Cote, D., Gregory, R. S., Rogers, L., Knutsen, H., & Olsen, E. M. (2017). Recruitment signals in juvenile cod surveys depend on thermal growth conditions. *Canadian Journal of Fisheries and Aquatic Sciences*, 74(4), 511–523. <https://doi.org/10.1139/cjfas-2016-0035>
- Laurel, B. J., Hunsicker, M. E., Ciannelli, L., Hurst, T. P., Duffy-Anderson, J., O'Malley, R., & Behrenfeld, M. (2021). Regional warming exacerbates match/mismatch vulnerability for cod larvae in Alaska. *Progress in Oceanography*, 193, 102555.
- 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. <https://doi.org/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. <https://doi.org/10.1093/plankt/fbn057>
- Laurel, B. J., Knoth, B. A., & Ryer, C. H. (2016). Growth, mortality, and recruitment signals in age-0 gadids settling in coastal Gulf of Alaska. *ICES Journal of Marine Science*, 73(9), 2227–2237.
- 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*, 77(4), 644–650. <https://doi.org/10.1139/cjfas-2019-0238>
- Laurel, B. J., Ryer, C. H., Knoth, B., & Stoner, A. W. (2009). Temporal and ontogenetic shifts in habitat use of juvenile Pacific cod (*Gadus macrocephalus*). *Journal of Experimental Marine Biology and Ecology*, 377(1), 28–35. <https://doi.org/10.1016/j.jembe.2009.06.010>
- Laurel, J., Stoner, A. W., Ryer, C. H., Hurst, T. P., & Abookire, A. A. (2007). Comparative habitat associations in juvenile Pacific cod and other gadids using seines, baited cameras and laboratory techniques. *Journal of Experimental Marine Biology and Ecology*, 351(1–2), 42–55. <https://doi.org/10.1016/j.jembe.2007.06.005>
- Lauth, R. R., Dawson, E. J., & Conner, J. (2019). Results of the 2017 eastern and northern Bering Sea continental shelf bottom trawl survey of groundfish and invertebrate fauna. <https://doi.org/10.25923/h118-nw41>
- Lellouche, J.-M., Le Galloudec, O., Greiner, E., Garric, G., Regnier, C., Drevillon, M., Bourdallé-Badie, R., Bricaud, C., Drillet, Y., & Le Traon, P.-Y. (2018). The Copernicus marine environment monitoring service global ocean 1/12 physical reanalysis GLORYS12V1: Description and quality assessment. Paper presented at the EGU General Assembly Conference Abstracts.
- Linehan, J. E., Gregory, R. S., & Schneider, D. C. (2001). Predation risk of age-0 cod (*Gadus*) relative to depth and substrate in coastal waters. *Journal of Experimental Marine Biology and Ecology*, 263(1), 25–44.
- 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., Abookire, A. A., Duffy-Anderson, J. T., Laurel, B. J., Malick, M. J., & Rogers, L. A. (2022). Predicting year class strength for climate-stressed gadid stocks in the Gulf of Alaska. *Fisheries Research (Amsterdam)*, 249, 106250.
- Litzow, M. A., Ciannelli, L., Puerta, P., Wettstein, J. J., Rykaczewski, R. R., & Opiekun, M. (2019). Nonstationary environmental and community relationships in the North Pacific Ocean. *Ecology*, 100(8), 1–8.
- Litzow, M. A., & Hunsicker, M. E. (2016). Early warning signals, nonlinearity, and signs of hysteresis in real ecosystems. *Ecosphere*, 7(12), e01614.
- Litzow, M. A., Hunsicker, M. E., Ward, E. J., Anderson, S. C., Gao, J., Zador, S. G., Batten, S., Dressel, S. C., Duffy-Anderson, J., Fergusson, E., & Hopcroft, R. R. (2020). Evaluating ecosystem change as Gulf of Alaska temperature exceeds the limits of preindustrial variability. *Progress in Oceanography*, 186, 102393.
- Litzow, M. A., Malick, M. J., Abookire, A. A., Duffy-Anderson, J., Laurel, B. J., Ressler, P. H., & Rogers, L. A. (2021). Using a climate attribution statistic to inform judgments about changing fisheries sustainability. *Scientific Reports*, 11(1), 1–12.
- Martin, B. T., Heintz, R., Danner, E. M., & Nisbet, R. M. (2017). Integrating lipid storage into general representations of fish energetics. *Journal of Animal Ecology*, 86(4), 812–825.
- Matarese, A. C., Blood, D. M., Picquelle, S. J., & Benson, J. L. (2003). Atlas of abundance and distribution patterns of ichthyoplankton from the Northeast Pacific Ocean and Bering Sea ecosystems: Based on research conducted by the Alaska fisheries science center (1972–1996). *NOAA Technical Report*.
- Meier, S., Mjøs, S. A., Joensen, H., & Grahl-Nielsen, O. (2006). Validation of a one-step extraction/methylation method for determination of fatty acids and cholesterol in marine tissues. *Journal of Chromatography A*, 1104(1–2), 291–298.
- Morley, J. W., Selden, R. L., Latour, R. J., Frölicher, T. L., Seagraves, R. J., & Pinsky, M. L. (2018). Projecting shifts in thermal habitat for 686 species on the north American continental shelf. *PLoS One*, 13(5), e0196127.
- Moss, J. H., Zaleski, M. F., & 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 Research Part II: Topical Studies in Oceanography*, 132, 146–153.
- Mukhina, N. V., Marshall, C. T., & Yaragina, N. A. (2003). Tracking the signal in year-class strength of Northeast Arctic cod through multiple survey estimates of egg, larval and juvenile abundance. *Journal of Sea Research*, 50(1), 57–75.
- Munk, P. (1997). Prey size spectra and prey availability of larval and small juvenile cod. *Journal of Fish Biology*, 51, 340–351.
- National Oceanic and Atmospheric Administration. (2017). *ESRL: PSD: Visualize NOAA high-resolution blended analysis data*. National Oceanic and Atmospheric Administration.
- Neidetcher, S. K., Hurst, T. P., Ciannelli, L., & Logerwell, E. A. (2014). Spawning phenology and geography of Aleutian Islands and eastern Bering Sea Pacific cod (*Gadus macrocephalus*). *Deep Sea Research Part II: Topical Studies in Oceanography*, 109, 204–214.
- Neubauer, P., & Andersen, K. H. (2019). Thermal performance of fish is explained by an interplay between physiology, behaviour and ecology. *Conservation Physiology*, 7(1), coz025.
- Nunn, A. D., Tewson, L. H., & Cowx, I. G. (2012). The foraging ecology of larval and juvenile fishes. *Reviews in Fish Biology and Fisheries*, 22(2), 377–408. <https://doi.org/10.1007/s11160-011-9240-8>
- O'Connor, C. M., Norris, D. R., Crossin, G. T., & Cooke, S. J. (2014). Biological carryover effects: Linking common concepts and mechanisms in ecology and evolution. *Ecosphere*, 5(3), 1–11.
- Olsen, N., & Workman, G. (2013). Strait of Georgia Groundfish bottom trawl survey, March 14–24, 2012.
- O'Neill, B. C., Tebaldi, C., Van Vuuren, D. P., Eyring, V., Friedlingstein, P., Hurtt, G., Knutti, R., Kriegler, E., Lamarque, J.-F., Lowe, J., Meehl, G. A., Moss, R., Riahi, K., & Sanderson, B. M. (2016). The scenario model intercomparison project (ScenarioMIP) for CMIP6. *Geoscientific Model Development*, 9(9), 3461–3482.
- Ormseth, O. A., & Norcross, B. L. (2009). Causes and consequences of life-history variation in north American stocks of Pacific cod. *ICES Journal of Marine Science*, 66(2), 349–357. <https://doi.org/10.1093/icesjms/fsn156>
- Palsson, W. A. (1990). *Pacific cod (Gadus macrocephalus) in Puget Sound and adjacent waters: Biology and stock assessment*. Department of fish and wildlife.
- Palsson, W. A., Northrup, T. J., & Barker, M. W. (1998). *Puget Sound groundfish management plan: Washington Department of Fish and Wildlife, fish management program, marine ...*
- Parrish, C. C. (1987). Separation of aquatic lipid classes by chromarod thin-layer chromatography with measurement by latroscan flame ionization detection. *Canadian Journal of Fisheries and Aquatic Sciences*, 44(4), 722–731. <https://doi.org/10.1139/F87-087>
- Parrish, C. C. (2013). Lipids in marine ecosystems. *International Scholarly Research Notices*, 2013, 604045.
- Pechenik, J. (2018). Latent effects: Surprising consequences of embryonic and larval experience on life after metamorphosis. In *Evolutionary ecology of marine invertebrate larvae* (pp. 208–225). Oxford University Press.
- Pepin, P. (1991). Effect of temperature and size on development, mortality, and survival rates of the pelagic early life-history stages of marine fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 48(3), 503–518. <https://doi.org/10.1139/F91-065>

- Pepin, P., Robert, D., Bouchard, C., Dower, J. F., Falardeau, M., Fortier, L., Jenkins, G. P., Leclerc, V., Levesque, K., Llopiz, J. K., Meekan, M. G., Murphy, H. M., Ringuette, M., Sirois, P., & Sponaugle, S. (2015). Once upon a larva: Revisiting the relationship between feeding success and growth in fish larvae. *ICES Journal of Marine Science*, 72(2), 359–373. <https://doi.org/10.1093/icesjms/fsu201>
- Petrik, C. M., Duffy-Anderson, J. T., Mueter, F., Hedstrom, K., & Curchitser, E. N. (2015). Biophysical transport model suggests climate variability determines distribution of walleye Pollock early life stages in the eastern Bering Sea through effects on spawning. *Progress in Oceanography*, 138, 459–474. <https://doi.org/10.1016/j.pcean.2014.06.004>
- Piatt, J. F., Parrish, J. K., Renner, H. M., Schoen, S. K., Jones, T. T., Arimitsu, M. L., Kuletz, K. J., Bodenstein, B., Garcia-Reyes, M., Duerr, R. S., Corcoran, R. M., Kaler, R. S. A., McChesney, G. J., Golightly, R. T., Coletti, H. A., Suryan, R. M., Burgess, H. K., Lindsey, J., Lindquist, K., ... Sydeman, W. J. (2020). Extreme mortality and reproductive failure of common murrelets resulting from the Northeast Pacific marine heatwave of 2014–2016. *PLoS One*, 15(1), e0226087.
- Planque, B., & Frédo, T. (1999). Temperature and the recruitment of Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, 56(11), 2069–2077.
- Post, J. R., & Evans, D. (1989). Size-dependent overwinter mortality of young-of-the-year yellow perch (*Perca flavescens*): Laboratory, in situ enclosure, and field experiments. *Canadian Journal of Fisheries and Aquatic Sciences*, 46(11), 1958–1968.
- 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.
- Schlegel, R. W., & Smit, A. J. (2018). heatwaver: A central algorithm for the detection of heatwaves and cold-spells. *Journal of Open Source Software*, 3(27), 821.
- Shotwell, S., Pirtle, J., Watson, J., Deary, A., Doyle, M., Barbeaux, S., Dorn, M. W., Gibson, G. A., Goldstein, E. D., Hanselman, D. H., Hermann, A. J., Hulson, P. J. F., Laurel, B. J., Moss, J. H., Ormseth, O. A., Robinson, D., Rogers, L. A., Rooper, C. N., Spies, I., ... Vollenweider, J. J. (2022). Synthesizing integrated ecosystem research to create informed stock-specific indicators for next generation stock assessments. *Deep Sea Research Part II: Topical Studies in Oceanography*, 198, 105070.
- Smale, D. A., Wernberg, T., Oliver, E. C. J., Thomsen, M., Harvey, B. P., Straub, S. C., Burrows, M. T., Alexander, L. V., Benthuyens, J. A., Donat, M. G., Feng, M., Hobday, A. J., Holbrook, N. J., Perkins-Kirkpatrick, S. E., Scannell, H. A., Gupta, A. S., Payne, B. L., & Moore, P. J. (2019). Marine heatwaves threaten global biodiversity and the provision of ecosystem services. *Nature Climate Change*, 9(4), 306–312. <https://doi.org/10.1038/s41558-019-0412-1>
- Smith, R. L., Paul, A. J., & Paul, J. M. (1990). Seasonal-changes in energy and the energy-cost of spawning in Gulf of Alaska Pacific cod. *Journal of Fish Biology*, 36(3), 307–316. <https://doi.org/10.1111/j.1095-8649.1990.tb05611.x>
- Sogard, S. M., & Olla, B. L. (2000). Endurance of simulated winter conditions by age-0 walleye Pollock: Effects of body size, water temperature and energy stores. *Journal of Fish Biology*, 56(1), 1–21.
- Spies, I., Drinan, D. P., Petrou, E. L., Spurr, R., Tarpey, C., Hartinger, T., Larson, W., & Hauser, L. (2021). Evidence for selection and spatially distinct patterns found in a putative zona pellucida gene in Pacific cod, and implications for management. *Ecology and Evolution*, 11(23), 16661–16679.
- Stanley, R., Snelgrove, P. V., & Gregory, R. S. (2012). Dispersal patterns, active behaviour, and flow environment during early life history of coastal cold water fishes. *PLoS One*, 7(9), e46266. <https://doi.org/10.1371/journal.pone.0046266>
- 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. *Fishery Bulletin*, 105(3), 396–407.
- Strasburger, W. W., Hillgruber, N., Pinchuk, A. I., & Mueter, F. J. (2014). Feeding ecology of age-0 walleye Pollock (*Gadus chalcogrammus*) and Pacific cod (*Gadus macrocephalus*) in the southeastern Bering Sea. *Deep-Sea Research Part II-Topical Studies in Oceanography*, 109, 172–180. <https://doi.org/10.1016/j.dsr2.2013.10.007>
- Suryan, R. M., Arimitsu, M. L., Coletti, H. A., Hopcroft, R. R., Lindeberg, M. R., Barbeaux, S. J., Batten, S. D., Burt, W. J., Bishop, M. A., Bodkin, J. L., Brenner, R., Campbell, R. W., Cushing, D. A., Danielson, S. L., Dorn, M. W., Drummond, B., Esler, D., Gelatt, T., Hanselman, D. H., ... Zador, S. G. (2021). Ecosystem response persists after a prolonged marine heatwave. *Scientific Reports*, 11(1), 1–17.
- Thompson, J. M., Bergersen, E. P., Carlson, C. A., & Kaeding, L. R. (1991). Role of size, condition, and lipid content in the overwinter survival of age-0 Colorado squawfish. *Transactions of the American Fisheries Society*, 120(3), 346–353.
- Voesenek, C. J., Muijres, F. T., & van Leeuwen, J. L. (2018). Biomechanics of swimming in developing larval fish. *Journal of Experimental Biology*, 221(1), jeb149583. <https://doi.org/10.1242/jeb.149583>
- Von Szalay, P. G., & Raring, N. W. (2018). Data report: 2017 Gulf of Alaska bottom trawl survey. <https://doi.org/10.7289/V5/TM-AFSC-374>
- von Szalay, P. G., & Raring, N. W. (2020). Data report: 2018 Aleutian Islands bottom trawl survey. <https://doi.org/10.25923/qe5v-fz70>
- Weinig, C., & Delph, L. F. (2001). Phenotypic plasticity early in life constrains developmental responses later. *Evolution*, 55(5), 930–936.
- West, C. F., Etnier, M. A., Barbeaux, S., Partlow, M. A., & Orlov, A. M. (2020). Size distribution of Pacific cod (*Gadus macrocephalus*) in the North Pacific Ocean over 6 millennia. *Quaternary Research*, 108, 43–63. <https://doi.org/10.1017/qua.2020.70>
- Williams, D., Olsen, N., & Wyeth, M. R. (2020a). Summary of the West Coast Haida Gwaii Synoptic Bottom Trawl Survey, September 2–24, 2018. Canadian Manuscript Report of Fisheries and Aquatic Sciences/Rapport Manuscrit Canadien Des Sciences Halieutiques et Aquatiques, 3196: viii, 54 p.
- Williams, D., Olsen, N., & Wyeth, M. R. (2020b). Summary of the West coast Vancouver Island synoptic bottom trawl survey, May 18–June 14, 2018. Canadian Manuscript Report of Fisheries and Aquatic Sciences/Rapport Manuscrit Canadien Des Sciences Halieutiques et Aquatiques, 3195: viii 60 p.
- Williams, D. C. (2018). Summary of the Hecate Strait synoptic bottom trawl survey, may 19–June 15, 2017. Department of Fisheries and Oceans.
- Workman, G., Stanley, R., Olsen, N., & Rutherford, K. (2008). West coast Queen Charlotte Islands groundfish bottom trawl survey, September 11th to October 17th, 2007. Canadian Manuscript Report of Fisheries and Aquatic Sciences/Rapport Manuscrit Canadien Des Sciences Halieutiques et Aquatiques, 2823.

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