Stage-specific drivers of Pacific hake (*Merluccius productus*) recruitment in the California Current Ecosystem

Running title: Environmental drivers of Pacific hake recruitment

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ABSTRACT

Understanding environmental drivers of recruitment variability in marine fishes remains an important challenge in fish ecology and fisheries management. We developed a conceptual life-history model for Pacific hake (*Merluccius productus*) along the west coast of the U.S. and Canada to generate stage-specific and spatiotemporally-specific hypotheses regarding the oceanographic and biological variables that likely influence their recruitment. Our model included seven life stages from pre-spawning female conditioning through pelagic juvenile recruitment (age-0 fish) for the coastal Pacific hake stock. Model-estimated log recruitment deviations from the 2020 hake assessment were used as the dependent variable, with predictor variables drawn primarily from a regional ocean reanalysis for the California Current Ecosystem. Indices of prey and predator abundance were also included in our analysis, as were predictors of local- and basin-scale climate. Five variables explained 59% of the recruitment variability not accounted for by the stock-recruitment relationship in the hake assessment. Recruitment deviations were negatively correlated with May – September eddy kinetic energy between 34.5° and 42.5°N, the North Pacific Current Bifurcation Index, and Pacific herring (*Clupea pallasii*) biomass during the spawner preconditioning stage, alongshore transport during the yolk-sac larval stage, and the number of days between storm events during the first-feeding larval stage. Other important predictors included upwelling strength during the preconditioning stage, the number of calm periods during the first-feeding larval stage, and age-1 hake predation on age-0 pelagic juveniles. These findings suggest that multiple mechanisms affect Pacific hake survival across different life stages, leading to variability in population-level recruitment.

KEYWORDS

California Current, environmental drivers, *Merluccius productus*, Pacific hake, recruitment, ROMS, transport

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1 | INTRODUCTION

For over a century, there has been intense scientific interest and research effort to identify the factors that influence recruitment variability in marine fishes. Year-class strength is thought to be set during the early larval stage, with recruitment (defined herein as individuals reaching age-1) being linked to number of factors, including first-feeding success ('Critical Period' hypothesis, Hjort, 1914, 1926), transport of eggs and larvae by ocean currents ('Aberrant Drift' hypothesis, Hjort, 1914), match in the timing between larval production and prey resources ('Match-Mismatch' hypothesis, Cushing, 1974, 1990), aggregation of prey via vertical stratification ('Stable Ocean' hypothesis, Lasker, 1978, 1981), and size-based predation ('Stage-Duration' hypothesis, Houde, 1987; Anderson, 1988), among others. To this day, understanding the mechanisms underlying recruitment variability remains a challenge in fish ecology and fisheries management. However, it is clear that the processes and mechanisms that generate recruitment variability work across multiple life stages (Houde, 2008) and that multi-hypothesis, integrative, and interdisciplinary approaches are needed (Hare, 2014).

Pacific hake (*Merluccius productus*), also known as Pacific whiting, is an ecologically important species that plays a key trophic role as both predator and prey in the California Current Ecosystem (CCE) (Ressler et al., 2007). Pacific hake occur primarily from the Gulf of California

(~25°N) to the Gulf of Alaska (~55°N) (Figure 1), occupying southern waters during the winter spawning season and migrating northward to feed between northern California and northern British Columbia during the spring, summer, and fall when the fishery is conducted (Grandin et al., 2020). Since the stock spans U.S. and Canadian waters, the hake fishery has been cooperatively managed through a bilateral agreement between the two countries since 2011, with quotas based on a harvest control rule and a fixed allocation share of the annual total allowable catch to each country (Jacobsen et al., 2019). Pacific hake population dynamics are strongly influenced by the periodic appearance of strong cohorts that have occurred across a range of population sizes (Figure 2). The stock assessment suggests that recruitment is highly variable (Figure 2b), resulting in large and rapid biomass changes, but the mechanisms underlying this variability are poorly understood. As a result, estimates of stock status and stock trajectory projections for Pacific hake remain highly uncertain due to the variability and uncertainty in the recruitment estimates, as cohort strength is generally not well detected until age 3 or 4 (Berger et al., 2019). Given the weak stock-recruitment relationship estimated by the stock assessment model (Figure 2c), environmental factors that vary at multiple spatial and temporal scales, such as temperature and upwelling strength, are likely important (Bailey, 1981).

Understanding the linkage between Pacific hake population dynamics and environmental conditions has been identified as a high priority research need for improving stock assessments and hake management strategies (Berger et al., 2019). Focusing on the survival of early life-history stages may be especially informative, as recruitment variability is known to have a stronger influence on the performance of alternative management strategies than rates of movement or the spatial distribution of the population (Jacobsen et al., 2019).

Initial research into the causes of Pacific hake recruitment variability began in the 1980s. Bailey and Francis (1985) linked recruitment of age-3 Pacific hake to post-larval abundance off the California coast in spring, suggesting that year-class strength was set during the first year of life. During the 1970s, recruitment strength was negatively correlated with temperature and upwelling (Bailey, 1981). However, these relationships did not persist in the 1980s (Bailey and Francis, 1985). More recently, Horne and Smith (1997) noted that changes in larval hake biomass were dominated by mortality and drift with prevailing currents, while Lo (2007) found that decreased larval production was associated with increasing ocean temperature since the 1980s. Strong year classes of Pacific hake and several other gadoid stocks have been linked to conditions related to the El Niño-Southern Oscillation (ENSO), which suggests that large-scale climate drivers play an important role (Hollowed et al., 2001). Factors that regulate larval delivery to nursery habitats, such as variation in circulation and mortality of eggs and larvae, are known to influence year-class strength (Houde, 2008; Rijnsdorp et al., 1995; Van der Veer et al., 2000), and transport has been linked to year-class formation in several Northeast Pacific marine fishes (Bailey et al., 1982; Vestfals et al., 2014; Wilderbuer et al., 2002). Species like Pacific hake may be especially sensitive to variations in climate due to their spatially separated spawning locations, nursery areas, and adult feeding grounds, which require the active migration of adults and ocean currents to transport eggs and larvae to complete their life cycle ("Migration Triangle" hypothesis, Harden Jones, 1968).

Technological advances in the last several decades have increased our ability to explore relationships between oceanic and atmospheric processes and fish populations. For example, monthly composite satellite sea surface temperature (SST) and surface chlorophyll *a* data have been used to predict potential spawning habitat of northern anchovy (*Engraulis mordax*) and

131 Pacific sardine (*Sardinops sagax*) in the CCE (Reiss et al., 2008), while maps of sea surface
132 height (SSH) constructed from satellite observations of sea level anomaly have shown that white
133 sharks (*Carcharodon carcharias*) exhibit a clear affinity for mesoscale eddies (Gaube et al.,
134 2018). Atmospheric and oceanic reanalysis products and ocean circulation models have been
135 used to examine how oceanographic and atmospheric processes affected recruitment variability
136 and productivity in several Northeast Pacific marine fish populations (Haltuch et al., 2020;
137 Litzow et al., 2018; Malick et al., 2017; Tolimieri et al., 2018; Vestfals et al., 2014).
138 Technological developments such as these provide a unique opportunity to revisit hypotheses
139 about the physical and biological processes that determine Pacific hake year-class strength
140 developed in the 1980s, and can potentially help to identify earlier indicators of recruitment
141 strength (i.e., age-1) than are currently available (i.e., age-3 or -4).
142 In this study, we (i) developed a literature-based, conceptual life-history model for
143 Pacific hake in the CCE that included seven stages from the conditioning of pre-spawning
144 females through the pelagic juvenile phase (age-0 fish) for the U.S. west coast Pacific hake
145 stock; (ii) used our conceptual model to generate stage-, space-, and time-specific hypotheses
146 regarding the physical and biological variables that likely influence Pacific hake recruitment; and
147 (iii) developed and compared several linear models to predict Pacific hake recruitment using
148 oceanographic variables derived from a regional ocean reanalysis for the CCE (Neveu et al.,
149 2016). We also investigated how biological indices like predator and prey abundances and local-
150 and basin-scale climate drivers (as proxies for nutrient input or changes in ocean currents) might
151 affect Pacific hake recruitment. Our analysis re-examined existing hypotheses of where and
152 when year-class strength is determined and investigated the relationships between ocean
153 conditions and Pacific hake survival across early life-history stages leading to recruitment, with

154 the goal of improving our understanding of the drivers of hake recruitment variability.

155

156 **2 | METHODS**

157 To address our objectives, we applied the methodology used by Tolimieri et al. (2018) for
158 sablefish (*Anoplopoma fimbria*) and Haltuch et al. (2020) for petrale sole (*Eopsetta jordani*) to
159 the U.S. west coast Pacific hake stock. We used estimates of log recruitment deviations from the
160 2020 hake stock assessment (Grandin et al., 2020) and model output from a CCE configuration
161 of the Regional Ocean Modeling System (ROMS) with data assimilation (Neveu et al., 2016).
162 The stock assessment model is an age-structured model fit to an acoustic survey index of
163 biomass, annual catch data, and age-composition data from the survey and commercial fisheries
164 (more details can be found in Grandin et al., 2020). Recruitment is estimated using a Beverton-
165 Holt stock-recruitment relationship where the unexploited recruitment parameter is freely
166 estimated and steepness is estimated using a weakly informative prior. The year-specific
167 deviations are estimated using a fixed standard deviation of 1.4. Although recruitment estimates
168 from the Pacific hake stock assessment were available from 1966 – 2019, our analysis was
169 constrained to the 1980 – 2010 period for which a self-consistent, high-resolution regional ocean
170 reanalysis was available to provide three-dimensional oceanographic conditions (see Section
171 2.2.1). We focused on the reproductively-active portion of the stock (U.S. west coast) occurring
172 within the region encompassed by the ROMS model, although variables representing conditions
173 outside of this region were incorporated into our analysis from other sources. We considered the
174 time from pre-spawning female conditioning through age-0 pelagic juveniles. By using this
175 conceptual approach, we were able to generate stage-specific and spatiotemporally-specific
176 hypotheses regarding the physical and biological variables likely to influence Pacific hake

177 survival at each life stage leading to recruitment. We tested our hypotheses using linear
178 modeling, model selection, and model validation.
179
180 **2.1 | Pacific hake life history: Female preconditioning to age-0 recruits**
181 Our conceptual life-history model began by first identifying each stage in the life history
182 of Pacific hake where environmental drivers might impact the size of each year class, beginning
183 with female conditioning prior to the spawning season through age-0 pelagic juveniles (Tables 1
184 and A1). Female condition has generally been shown to influence whether or not an individual
185 spawns, the quality and number of eggs that are produced, as well as their hatching success
186 (Laine & Rajasilta, 1999; Rodgveller et al., 2016; Sogard et al., 2008). Adult Pacific hake are
187 found throughout the water column in association with the shelf break, typically over bottom
188 depths ranging between 100 m and 300 m (Bailey et al., 1982; Cooke et al., 2006; Ressler et al.,
189 2007). Their northward feeding migration is timed with the spring transition in ocean conditions
190 along the shelf edge (Benson et al., 2002; Thompson, 1981). Adult Pacific hake spend summers
191 feeding off the coasts of Oregon, Washington, and British Columbia before migrating southward
192 in autumn to their spawning grounds off central and southern California, and Baja California,
193 Mexico (Hollowed & Bailey, 1989). Thus, the feeding period from spring to fall (April to
194 October) prior to spawning was considered important for female preconditioning.
195 Pacific hake are believed to spawn during the winter months, mainly between December
196 and March (Smith, 1995), with the peak occurring in January and February (Bailey, 1980;
197 Stauffer, 1985; Woodbury et al., 1995). While the exact location is unknown, spawning is
198 thought to occur up to 400 km offshore of the southern California Bight at depths of 130 – 500 m
199 over the continental slope (Bailey et al., 1982; Nelson & Larkins, 1970; Tillman, 1968), though

several studies have noted that hake spawning grounds are not fixed, but rather variable in location (Agostini et al., 2006; Horne & Smith, 1997; Sakuma & Ralston 1997).

After spawning, eggs rise upwards to the depth of neutral buoyancy, usually to the base of the mixed layer (Bailey et al., 1982). Time to hatch varies with temperature, but is typically around 4 to 5 days (Bailey, 1982). Both eggs and larvae are often found aggregated near the base of the mixed layer, usually at about 40 – 60 m depth (Ahlstrom, 1959; Bailey et al., 1982). Most early-stage larvae are found between January and March, with a peak in February (Hollowed, 1992). Yolk-sac larvae are mostly found at depths between 50 – 100 m, with yolk sac absorption occurring at 4.0 mm (Cass-Calay, 1997), when larvae are approximately 10 days old (Bailey & Francis, 1985), though this may occur earlier at higher temperatures (Bailey, 1982). First-feeding larvae (> 4.0 mm) can be found from 50 – 200 m deep over the continental shelf and slope (Bailey 1981, 1982). Flexion occurs at 10 mm in length (Matarese et al., 1989) after which post-flexion larvae can be found deeper in the water column, between 200 – 500 m during the day, but close to the surface at night, between 25 – 50 m (Bailey, 1982). Transformation to pelagic juveniles occurs between 30 – 35 mm in length (Matarese et al., 1989), with age-0 fish caught in surveys from mid-May to mid-June in the upper mixed layer over the shelf, inshore of the 200-m isobath (Sakuma & Ralston, 1997).

2.2 | Generating hypotheses about potential recruitment drivers

We developed *a priori*, life-stage-specific and spatiotemporally-specific (considering time, depth, latitude, and longitude) hypotheses for environmental covariates that may drive recruitment variability in Pacific hake (Tables 1 and A1). Our analysis included covariates obtained from a ROMS model, predator and prey indices, as well as local- (e.g., storm and calm

events, SSH) and basin-scale indices representing the El Niño-Southern Oscillation (ENSO), the Pacific Decadal Oscillation (PDO) (Mantua et al., 1997), the North Pacific Gyre Oscillation (NPGO) (Di Lorenzo et al., 2008), and the North Pacific Current (NPC) Bifurcation Index (BI) (Malick et al., 2017). A number of hypotheses were represented by two or more predictors that represented different spatial regions (e.g., cross-shelf transport and upwelling north and south of Point Conception) and several predictors were hypothesized to act on multiple life stages (e.g., ENSO during the preconditioning, larval, and juvenile stages, euphausiid prey availability during the late larval and pelagic juvenile stages). Thus, a total of 88 predictors were tested.

For each hypothesis, we specified the time period, depth, and latitudinal and longitudinal extent of the potential predictor based on the traditional model of hake life history. For example, net cross-shelf transport between January and March, at 40 – 60 m depth, between 31°N and 34.5°N, and near the shelf break (defined as being between the 100- and 2,000-m isobaths) may affect the transport and distribution of Pacific hake eggs (Tables 1 and A1). In some cases, the literature suggested multiple potential depth ranges over which environmental variables might influence recruitment. For example, Ahlstrom and Counts (1955) reported that Pacific hake eggs were found between 27 and 140 m while Bailey et al. (1982) reported aggregations of eggs just below the base of the mixed layer, usually at about 40 – 60 m depth. When selecting which environmental predictors to include in model selection, we initially evaluated variables (e.g., net cross-shelf transport) over both the broader and the more restricted depth range. Preliminary analyses showed that these paired predictors were highly correlated (e.g., $r > 0.87$ for the egg stage). We chose to include the narrower depth range version of each in our analyses to reduce the number of predictors because we believed this range more accurately captured the position of eggs and larvae located at the base of the mixed layer. The resulting testable hypotheses fall into

six general categories, which may overlap life-history stages (Tables 1 and A1): temperature, transport, mixing, prey, predators, and bottom-up ecosystem processes.

2.2.1 | Regional Ocean Model

Oceanographic information

The majority of the predictors in our analysis were physical oceanographic parameters (e.g., temperature, alongshore and cross-shelf currents, and mixed layer depth), which were derived from the data-assimilative CCE ROMS output (Neveu et al., 2016). The CCE-ROMS model domain covers the region from 30°N – 48°N and from the coastline to 134°W at 0.1° (~10 km) horizontal resolution, with 42 terrain-following vertical levels. We used the 1980 – 2010 CCE reanalysis, which assimilates satellite observations (SST, SSH) and *in situ* data (temperature and salinity from ships, floats, moorings, gliders) into the model to more accurately represent the true ocean state. This reanalysis has been used extensively in the CCE to study climate-ocean dynamics (Jacox et al., 2014, 2015), bottom-up controls on primary production (Jacox et al., 2016), oceanographic influences on species distributions (Becker et al., 2019; Brodie et al., 2018), and recruitment (Haltuch et al., 2020; Tolimieri et al., 2018). All ROMS output was averaged in 4-day increments and then either averaged or summed over the appropriate period, latitude/longitude, and depth (as defined in Tables 1 and A1) for each of the 30 years (n = 30 for each time series in the analysis; see Section 2.4, below).

The paucity of subsurface oceanographic data was the motivation for using the CCE ROMS model output in this study. Despite our inability to validate the subsurface model transport, the output provides a physically consistent estimate of subsurface dynamics, though it likely deviates from nature more at the subsurface than at the surface. Data assimilation was used

to improve models that already capture the dynamics in the CCE without data assimilation. The model's skill has been extensively documented for applications with and without data assimilation (e.g., Jacox et al., 2015; Veneziani et al., 2009). The model exhibits realistic physical variability even in the absence of data assimilation, as it is forced by realistic winds, surface heat fluxes, and lateral boundary conditions. Further details on the impact of assimilated data on different metrics of the CCE can be found in Moore et al. (2017).

2.2.1.1 | Temperature

Temperature may affect Pacific hake recruitment through a number of mechanisms. For example, higher temperatures during the spawning female preconditioning stage (Tables 1 and A1, hypothesis 1 (H1)) may increase energetic demands, causing less energy to be allocated to reproduction, resulting in reduced egg production or potentially skipped spawning. Temperature can also influence the timing and location of spawning, as well as the growth, development, and survival of eggs, larvae, and juveniles through multiple mechanisms. For example, growth rates may be higher at warmer temperatures, which may reduce the time spent by slow-growing and small larvae in stages vulnerable to predation (e.g., the 'Stage-Duration' or 'bigger-is-better' hypotheses; Houde, 1987, 1997). However, metabolic demands may also increase with increasing temperature, making larvae more susceptible to starvation, especially if warmer waters are associated with poor feeding conditions (e.g., lower quality prey or less abundant prey). Modeled temperatures were obtained from the ROMS output. In most cases, we included temperature as degree days (cumulative temperature above a threshold value, Chezik et al., 2014), setting a standard threshold temperature of 5.0°C (Chezik et al., 2014).

2.2.1.2 | Transport

Marine species with pelagic eggs and larvae must rely on transport and their own behavior to move them toward and keep them within suitable nursery habitat for successful recruitment to the juvenile stage. Transport to nursery habitat was characterized by ROMS estimates of mean alongshore and cross-shelf transport at specific depths and times for each relevant Pacific hake life history stage (Tables 1 and A1).

Pacific hake eggs rise to the base of the mixed layer after spawning (Bailey et al., 1982). Thus, the mixed-layer depth (MLD) may influence how high eggs rise in the water column, which in turn, may affect their transport (Hinckley et al., 1996; Sundby, 1991) and access to food resources after hatching (Cushing, 1982). We included the mean MLD from January to April, during which time eggs and larvae are believed to aggregate at the base of the mixed layer (Ahlstrom, 1959; Bailey, 1982).

The distribution of Pacific hake may be related to poleward flow in the California Undercurrent (CU), with changes in flow aiding or impeding the poleward migration of adults (Agostini et al., 2006, 2008; Benson et al., 2002; Dorn, 1995; Smith et al., 1990; Woodbury et al., 1995). While Pacific hake spawn primarily over the continental slope, Bailey (1981) suggested that the location of spawning is related to the CU, which usually occurs over the continental slope at depths of 200 – 400 m. Flow in the undercurrent peaks during the spawning period (Agostini, 2005), thus we included a metric of transport in the poleward undercurrent (PU) from January to June to determine whether the transport of eggs and larvae might be affected by changes in this feature (Tables 1 and A1).

2.2.1.3 | Upwelling

Wind-driven upwelling in the CCE drives its high biological productivity, supplying nutrient-rich water to the surface layer and fueling the growth of phytoplankton that form the base of the marine food web. To examine the impact of upwelling on recruitment, we used two upwelling indices developed for the U.S. west coast: the Coastal Upwelling Transport Index (CUTI) and the Biologically Effective Upwelling Transport Index (BEUTI) (Jacox et al. 2018). CUTI and BEUTI provide estimates of the total volume of water and the total quantity of nitrate upwelled or downwelled in a given time period, respectively. While CUTI is a measure of physical upwelling transport, BEUTI is a measure of both the intensity of upwelling and the quality of upwelled waters in terms of their nutrient content, which can strongly influence productivity, independent of the surface wind strength (Jacox et al., 2016).

The input of nutrients and the timing of the spring transition from downwelling-favorable to upwelling-favorable winds each year is critical to phytoplankton productivity, especially in the northern CCE (Bograd et al., 2009). In addition to the two upwelling indices described above, we included the timing of the spring transition as a predictor of hake recruitment due to its link to hake production (Hollowed et al., 2009). The Julian day of the Mean Spring Transition Date (SPTR), calculated using the Columbia Basin Research (CBR) Mean Method (Van Holmes, 2007), was used in our analysis. Briefly, the CBR Mean method averages daily upwelling deviations from mean offshore transport at three sites along the Oregon and Washington coasts (see Tables 1 and A1). The smoothed cumulative upwelling deviation indices are then examined for spring minima, with the Julian day of this extreme listed as the CBR Mean Spring Transition Date (Van Holmes, 2007).

2.2.1.4 | Eddy kinetic energy

Coastal eddies are mesoscale features that can retain early life stages and may contribute to enhanced recruitment in marine fishes (Hare & Cowen, 1996; Owen, 1980; Sakuma & Ralston, 1997; Sanchez & Gil, 2000; Vastano et al., 1992). Eddy kinetic energy (EKE) provides a proxy for the intensity of mesoscale turbulence, which includes not only mesoscale eddies, but also features such as meanders and fronts that can concentrate prey and lead to improved feeding conditions. We included EKE as a predictor to investigate the effect of mesoscale variability on Pacific hake recruitment during the post-spawning (January – April) and summer feeding (May – September) periods from 31° – 34.5°N, 34.5 – 42.5°N, and 42.5° – 47°N.

2.2.1.5 | Sea-surface height

The collective expression of basin-scale processes (see Section 2.2.5 below) can result in local changes in SSH. Thus, indices of SSH were included in our analysis to aid in testing the consistency of mechanisms hypothesized to impact Pacific hake recruitment. Indices were derived for the post-spawning (January – April) and summer feeding (May – September) periods from the female preconditioning to the age-0 pelagic juvenile stage between 31° – 34.5°N, 34.5° – 42.5°N, and 42.5°– 47°N.

2.2.2 | Prey availability

Prey availability in the months prior to spawning (here April – September) may affect female condition, which, in turn, may affect the quality or number of eggs produced, or the probability of spawning in a given year. We included recruitment of age-2 Pacific herring (*Clupea pallasii*, $PREY_{pre.her}$) off the west coast of Vancouver Island (WCVI), representing summer feeding conditions in Canadian waters, and log-transformed biomass of age-0 and age-1 juvenile hake ($logPRED_{pre.juvhake}$), representing cannibalism by adults, from their most recent

stock assessments (Cleary et al., 2020; Grandin et al., 2020), as indices of prey abundance for the female preconditioning period. Although euphausiids are a main prey item for Pacific hake adults (Livingston & Bailey, 1985), there is no continuous time series available that represents euphausiid abundance on their summer feeding grounds for the years examined in our analysis. Thus, the link between hake recruitment and euphausiid abundance for this stage was not explored.

Starvation during the early life stages is thought to be an important regulator of recruitment in marine fishes, particularly at the time of first-feeding ('Critical Period' hypothesis, Hjort, 1914, 1926) and during the period of drift from spawning grounds to juvenile nursery areas, where the timing and abundance of food are important to survival ('Match-mismatch' hypothesis, Cushing, 1972). In years with near-average ocean conditions, the diet of early-juvenile Pacific hake transitions from copepods to euphausiids (Livingston & Bailey, 1985). We developed indices of copepod abundance (n m^{-2}) as prey for the early and late larval stages ($PREY_{larv.zp}$, $PREY_{latelarv.zp}$), and euphausiid abundance (n m^{-2}) as prey for the late larval and juvenile stages ($PREY_{latelarv.eup}$, $PREY_{age0.eup}$) from surveys conducted by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) off the coast of southern California. Weighted averages of copepod and euphausiid abundances from February to May were calculated for each year. Copepod data were obtained from the Zooplankton Database (https://oceaninformatics.ucsd.edu/zoodb/secure/login.php) and included pooled and unpooled samples of Copepoda (all genera and species, all phases and stages) from night tows conducted from February – May at lines 80 to 93 (Southern California). Euphausiid data were obtained from the Brinton and Townsend Euphausiid Database

384 (https://oceaninformatics.ucsd.edu/euphausiid/secure/login.php) and included all genera and
385 species, all phases and stages collected from Feb – May from lines 77 to 93 (Southern
386 California).
387
388 **2.2.3 | Predation on recruits**
389 Size-specific predation is a major source of mortality for the early life stages of marine
390 fishes (Bailey & Houde, 1989; Houde, 2008). We included several indices of predator abundance
391 to examine the effects of predation on recruitment. Pacific hake have been shown to be important
392 prey of California sea lions (*Zalophus californianus*), for example. In the late 1970s they were
393 the most abundant prey in the diet of sea lions from San Miguel Island, off southern California,
394 with almost 49% of scats examined containing Pacific hake, mostly 1-2 year old fish (Antonelis
395 et al., 1984; Livingston & Bailey, 1985). Scat samples collected seasonally on San Clemente and
396 San Nicolas islands in the Southern California Bight from 1981 – 2015 also show evidence of
397 sea lion predation on age-0 and age-1 Pacific hake (< 30 cm in length) (A. Curtis, NOAA,
398 personal communication). We used estimated pup abundances from Laake et al. (2018) as an
399 estimate of California sea lion predation on Pacific hake ($PRED_{age0.csl}$). Pup counts were used, as
400 they directly relate to predation on Pacific hake by females foraging around San Clemente and
401 San Nicolas islands (A. Curtis, NOAA, personal communication) by integrating both population
402 size and energetic demands of the population.
403 Arrowtooth flounder (*Atheresthes stomias*) is a highly piscivorous flatfish known to prey
404 on Pacific hake juveniles and adults (Buckley et al., 1999; Ressler et al., 2007; Sampson et al.,
405 2017). Pacific hake are the primary prey of arrowtooth flounder off Oregon and Washington
406 (Buckley et al., 1999). Although arrowtooth flounder are mostly found north of central California

(Best 1963), recent stomach content analysis work has found that young-of-the-year (YOY) fish are consumed as well where their distributions overlap (Draper, 2022). We included an index of arrowtooth flounder biomass from the most recent stock assessment (Sampson et al., 2017) as a predator of age-0 Pacific hake ($PRED_{age0.atf}$).

Studies have shown evidence of cannibalism by age-1 fish on YOY Pacific hake (Smith 1995; Buckley & Livingston, 1997). Thus, we included log-transformed age-1 biomass of Pacific hake from the 2020 stock assessment (Grandin et al., 2020) as an index of predation on age-0 juveniles ($logPRED_{age0.age1hake}$).

2.2.4 | Storm and calm periods

Wind-induced mixing can affect the vertical distribution of plankton in the upper water column, which, in turn, can influence feeding success and growth of larval fishes. Periods of calm are associated with vertical stratification of the water column, aggregating prey in sufficient concentrations to support successful foraging, growth, survival, and recruitment, while storm events can disperse both larvae and food patches, leading to lower foraging success ('Stable Ocean' hypothesis, Lasker, 1978, 1981). We included indices for the mean number of ($CALM_{larv}$, $STORM_{larv}$), duration of ($CALMD_{larv}$, $STORMD_{larv}$), and time between ($CALMB_{larv}$, $STORMB_{larv}$) distinct calm periods and storms events from February to May using the methodology outlined in Turley & Rykaczewski (2019). Wind events were identified using modeled wind output available from the NOAA National Centers for Environmental Prediction Climate Forecast System Reanalysis model (Saha et al., 2010) for the region between 28° and 36°N. Storm periods were identified as intervals when the wind speeds were equal to or greater than 10 m s^{-1} for a minimum of 18 h (and below this threshold for the preceding 96 h). A calm

period was identified when the wind speed was below 10 m s^{-1} for a minimum of 10 days and wind speeds were above the same threshold during the preceding 18 h. A minimum of 10 days was used because Pacific hake yolk-sac larvae must find food within this period, or irreversible starvation occurs (Bailey, 1982). Further methodological details can be found in Turley & Rykaczewski (2019).

2.2.5 | Basin-scale processes

Bifurcation Index

The NPC bifurcates into the poleward Alaska Current and the equatorward California Current in a transition zone that ranges from about 42° – 52° N (Freeland, 2006; Cummins and Freeland, 2007). Variability in the north-south location of this bifurcation has been linked to biological productivity in the CCE (Malick et al., 2017; Sydeman et al., 2011). We used an index of the location of the NPC bifurcation (BI, Malick et al., 2017) to examine whether Pacific hake recruitment was influenced by the positioning of the NPC, with the expectation that a northward-shifted NPC would lead to higher productivity in the CCE and higher recruitment.

El Niño-Southern Oscillation

Variability in Pacific hake year-class strength has been linked to conditions related to ENSO (Hollowed et al., 2001), which can cause warming of the upper ocean, depression of the thermocline, weakening of upwelling intensity, and intensification of the CU (Chelton & Davis, 1982; Hickey, 1998; Hollowed, 1992; Jacox et al., 2015). We used the Oceanic Niño Index (ONI), defined as the 3-month running average of sea surface temperature anomalies in the Niño 3.4 region (5°S – 5°N, 120° – 170°W) (Trenberth, 1997), to index variability associated with El

Niño and La Niña events from the female preconditioning period (ONI_{pre}), through the larval stages (ONI_{JA}), to summer feeding of age-0 pelagic juveniles (ONI_{AS}).

Pacific Decadal Oscillation

The Pacific Decadal Oscillation (PDO), defined as the leading principle component of monthly SST anomalies in the North Pacific poleward of 20°N (Mantua et al., 1997). The PDO been shown to be correlated with indices of salmon survival in the Northeast Pacific (Burke et al., 2013; Malick et al., 2009; Mantua et al., 1997) and the driver of inverse production regimes between Alaska and west coast salmon stocks (Hare et al., 1999). The PDO was included as a covariate for the female preconditioning period (PDO_{pre}), through the larval stages (PDO_{JA}), to summer feeding of age-0 pelagic juveniles (PDO_{AS}).

North Pacific Gyre Oscillation

The North Pacific Gyre Oscillation (NPGO) measures changes in the circulation of the North Pacific gyre and has been correlated with salinity, nutrient, and chlorophyll-a fluctuations measured in long-term observations in the California Current and Gulf of Alaska (Di Lorenzo et al., 2008). The NPGO has been linked to west coast salmon productivity (Malick et al., 2015, 2017) and may be important to the recruitment of Pacific hake. We included the NPGO as a covariate in our analysis across all stages in our conceptual life history model (preconditioning period, April – September; spawning to early larvae, January – April; late larvae to age-0 juveniles, April – September).

2.3 | Recruitment residuals

476 Model estimates of Pacific hake recruitment were taken from the most recent stock
477 assessment (here, Figure 3d, Figure 28 in Grandin et al., 2020). Specifically, we used the model-
478 estimated log deviations as the response variable, where the deviations were the annual
479 deviations from log median recruitment. Median recruitment was a function of the assumed
480 Beverton–Holt stock–recruitment relationship, aging error assumptions, and the data included in
481 the stock assessment model including the sampled age structure.
482 Our analysis covers recruitment residuals from 1981 – 2010, as the 1980 recruitment
483 deviation depends on the preconditioning period in 1979, which was not available in the CCE
484 ROMS output.
485
486 **2.4 | Model development**
487 Initial explorations of candidate variables led to a de facto reduction in the number of
488 models evaluated. Specifically, correlations among predictor variables and individual linear and
489 quadratic regressions for each predictor against recruitment deviations were calculated and
490 evaluated prior to model fitting and selection. Predictors that were strongly correlated (Figure
491 A2, $|r| > 0.70$) were not permitted in the same model (Dormann et al., 2013). Quadratic terms
492 were included in the main modeling exercise for individual hypothesized covariates where the
493 quadratic model fit better than the linear model (Akaike's Information Criterion, AIC (Akaike,
494 1998), was < 2.0 that of the linear model). Based on preliminary model explorations, the
495 following covariates were included as potential quadratic predictors during model selection:
496 BEUTI ($UW_{pre.beu}$) from 41.5° – 47.5°N during the adult female preconditioning stage, and
497 cross-shore transport during the first-feeding (CST_{larv}) and late larval stages ($CST_{latelarv}$).

Due to the large number of hypotheses generated about the drivers of Pacific hake recruitment, we used a three-step approach to model selection. First, a series of generalized linear models (GLMs) were fitted for each of the seven stages in our Pacific hake conceptual life history model, including all permutations of the ROMS covariates from our hypotheses and excluding highly correlated terms (Figure A2, $|r| > 0.70$) from the same model. To prevent overfitting, the number of ROMS predictors in a candidate model was limited to five (one covariate per six data points in the time series). Predictors that were identified as potentially quadratic were included in the models as a linear function and a quadratic function. The best-fit models with $\Delta AICc < 2.0$ were retained for further consideration (Burnham & Anderson, 1998). Second, generalized linear models (GLMs) were fit to all life stages combined and run with ROMS predictor variables from the best-fit model for each stage, along with those variables occurring in at least 3 of the stage-specific models with $\Delta AICc < 2.0$. Third, we retained all ROMS variables appearing in models with $\Delta AICc < 2.0$ from the previous step, added the predator, prey, and climate predictor variables, and re-evaluated the model selection for all life stages combined. In total, 117,439 models were considered.

All analyses were conducted using R statistical software version 3.6.1 (R Core Team, 2020) using the Multi-model inference package (MuMIn, Barton, 2020) for model selection. Due to a limit on the number of predictors allowed in the model fitting process (31), some covariates were not included in the final step of model fitting. Terms that were highly correlated with retained covariates (Figure A2, $PREY_{pre}$ with $PRED_{age0.age1hake}$ ($r = 0.88$); $CALMB_{larv}$ ($r = 0.76$) and $CALMD_{larv}$ ($r = 0.81$) with $CALM_{larv}$) or were correlated with a similar covariate ($NPGO_{JA}$ with both $NPGO_{pre}$ ($r = 0.73$) and $NPGO_{AS}$ ($r = 0.92$); ONI_{JA} with ONI_{pre} ($r = 0.76$)), were removed, although their hypothesized effects on recruitment were generally captured in the

521 analysis.

522

523 **2.5 | Model validation and testing**

524 The performance of the best-fit model for all stages in our conceptual life history model
525 was evaluated using (1) resampling with replacement of recruitment deviations to estimate R^2
526 values using 100 randomized data sets; (2) bootstrapping whole years with replacement to
527 estimate bias and calculate *SE* of the parameter estimates; (3) annual jackknife resampling to
528 determine the effect of any single year on the R^2; (4) resampling annual recruitment deviations
529 from a log-normal distribution using the annual mean and *SD* estimated from the assessment,
530 then recalculating recruitment residuals, and refitting the model 1,000 times; (5) refitting the
531 model using data for 1981 – 2005 and predicting recruitments deviations for 2006 – 2010; (6)
532 jackknife resampling to re-run the entire model-fitting and comparison exercise, to determine
533 whether removal of any individual year would change the selected predictor variables; and (7)
534 re-running the entire model fitting exercise 100 times using the re-sampled Pacific hake
535 recruitment deviations with error (from Step 4 above), comparing AICc-selected models from
536 each run. Finally, we used (8) jackknife resampling but fit only the years 1981 – 2005, compared
537 the resulting models to the best-fit model above, and used the 1981 – 2005 model to predict
538 recruitment deviations for 2006 – 2010.

539

540 **3 | RESULTS**

541 Model fitting identified a clear best-fit model for each stage in our conceptual life history
542 model for Pacific hake, with intercept-only models for the spawning, egg, and age-0 pelagic
543 juvenile stages (Table A2). The best-fit model for the adult female preconditioning stage, based

544 on the lowest AICc, included May – September eddy kinetic energy between 34.5° and 42.5°N
545 ($EKE_{pre.MS.c}$) and upwelling strength ($UW_{pre.cu}$), which together explained 31% of the
546 recruitment variability in Pacific hake. Alongshore transport (AST_{yolk}) and transport in the
547 poleward undercurrent (PU_{yolk}) during the yolk-sac stage explained 18% of the variability in
548 recruitment (Table A2). Cross-shelf transport north of Point Conception ($CST_{larv.n}$), along with
549 linear and quadratic predictors for cross-shelf transport south of Point Conception ($CST_{larv.s}$)
550 accounted for 16% of the recruitment variability for the first-feeding larval stage. Similarly,
551 linear and quadratic predictors for cross-shelf transport south of Point Conception during the late
552 larval stage ($CST_{latelarv.s}$) accounted for 22% of the variability in hake recruitment (Table A2).
553 All terms identified in the stage-specific best-fit models, along with those terms
554 appearing in three or more models with $\Delta AICc < 2.0$ (Table A3), were included in the next stage
555 of model fitting, where all life history stages were combined. Model fitting produced seven
556 candidate models with $\Delta AICc < 2.0$, which explained between 31% and 43% of the variability in
557 hake recruitment not accounted for by the stock-recruitment relationship in the assessment.
558 (Table A2). For the adult preconditioning stage, May – September EKE between 34.5° and
559 42.5°N ($EKE_{pre.MS.c}$) appeared in all seven models, while six models included upwelling strength
560 between 41.5° and 47.5°N ($UW_{pre.cu}$). Three models included alongshore transport during the
561 yolk-sac larval stage (AST_{yolk}) and two models included May – September EKE between 34.5°
562 and 42.5°N ($EKE_{MS.c}$). Linear and quadratic predictors for cross-shelf transport south of Point
563 Conception during the first-feeding larval stage ($CST_{larv.s}$, $CST^2_{larv.s}$) and the late larval stage
564 ($CST_{latelarv.s}$, $CST^2_{latelarv.s}$) each appeared in one model (Table A2). All terms appearing in the
565 seven models with $\Delta AICc < 2.0$ were carried over to the next step of model fitting.
566 The final step of model fitting, which combined the ROMS predictors identified in the

previous step with predator, prey, and climate predictors for all stages in our conceptual life history model, identified five candidate models with a ΔAICc < 2.0 (Table 2). The model with the lowest AIC included five covariates (Figures 3, A1 and A3, Table 2), which explained 59% of the variation in recruitment residuals from 1981 to 2010. Model predictions closely followed the estimated recruitments from the stock assessment in 23 out of 30 years, with the exceptions of 1984, 1989, 1990, 2000, 2005, 2007, and 2009 (Figure 4a). Recruitment deviations were negatively correlated with the NPC Bifurcation Index (BI_{pre}), May – September EKE between 34.5° and 42.5°N ($EKE_{pre.MS.c}$), and Pacific herring biomass off the WCVI ($PREY_{pre.her}$) during the female spawner preconditioning stage (Figure 5). Negative correlations were also found with northward alongshore transport between 50 – 100 m during the yolk-sac larval stage (AST_{yolk}) and the number of days between storm events during the first-feeding larval stage ($STORMB_{larv}$) (Figure 5, Table 3). Standardized coefficients suggested that $EKE_{pre.MS.c}$ and BI_{pre} had the strongest effect on recruitment, while the other predictors had relatively similar impacts (Table 3). All five ΔAICc < 2.0 models included the $EKE_{pre.MS.c}$ predictor. The remaining four models included combinations of the predictors described above, with additional terms including predation on age-0 pelagic juveniles by age-1 hake ($PRED_{age.0age1.hake}$), upwelling strength during the preconditioning stage ($UW_{pre.cu}$), which replaced the BI_{pre} predictor, and the number of calm periods during the first-feeding larval stage ($CALM_{larv}$) (Tables 2 and A2).

There was weak correlation among the covariates in the best-fit model (Table 4). Generalized variance inflation factor values (VIF), which measure how much the variance of the estimated regression coefficients is inflated as compared to when the predictor variables are not linearly related, were low (i.e., less than 2; Table 4). The diagnostics for the best-fit model show good model fit (Figure 5) with residuals that did not show signs of autocorrelation (Figure A1).

590

591 **3.1 | Model testing and validation: best-fit model**

592 Randomly resampling the recruitment deviations (bootstrap with replacement) and re-
593 running the AIC-best model resulted in a median expected $R^2 = 0.16$ (95% C.I. = 0.03–0.41),
594 suggesting that the observed value of $R^2 = 0.59$ was not likely to be observed at random.

595 After removing individual years and refitting the best-fit model (jackknifing), there was
596 little impact on the model fit (Figures 4 and 5, median $R^2 = 0.59$ (95% C.I. = 0.55 – 0.67)).
597 Predicting the missing year from any iteration produced estimates very similar to those for the
598 full model (Figure 4a). The years that showed the highest impact on the model's ability to explain
599 the data were 1990 (increased to $R^2 = 0.70$) and 2002 (decreased to $R^2 = 0.54$, Figure 6).

600 Resampling annual recruitment deviations with error produced a slight decline in model
601 performance (median $R^2 = 0.56$ (95% C.I. = 0.50 – 0.62)). This suggests that uncertainty in the
602 time series of recruitment deviations (given the current stock assessment parameters) results in a
603 somewhat lower ability to explain the variability in recruitment.

604 When the entire model-fitting process was re-run using the jackknife resampling, the
605 results were fairly consistent with the primary analysis (Table 5). May – September EKE
606 between 34.5° and 42.5°N, the NPC Bifurcation Index, and Pacific herring biomass during the
607 adult female preconditioning stage appeared in 95%, 55%, and 11% of the models, respectively.
608 Alongshore transport during the yolk-sac larval stage and the number of days between storm
609 events appeared in 40% and 21% of the models, respectively. Other predictors of note were
610 upwelling strength between 41.5° and 47.5°N during the adult female preconditioning stage and
611 the number of calm periods during the first-feeding larval stage, which appeared in 40% and
612 37% of the models, respectively.

Resampling the recruitment deviations (with error) and re-running the entire model-fitting exercise 100 times was mostly consistent with the AIC-best model from the primary analysis (Table 6). Three of the five predictors from the AIC-best model were the most commonly occurring predictors in the best-fit models from each iteration: $EKE_{pre.MS.c}$ (81% of models), BI_{pre} (46%), AST_{yolk} (41%). Additional predictors included $CALM_{larv}$ (44%) and $UW_{pre.cu}$ (40%). Other terms from the AIC-best model, $PREY_{pre.her}$ and $STORMB_{larv}$ occurred in 17% and 15% of the models, respectively.

Finally, jackknife resampling and re-running the entire model-fitting process for the 1981 – 2005 data supported the inclusion of only one term from the AIC-best model from the primary analysis. The predictor for the NPC Bifurcation Index during the preconditioning stage (BI_{pre}) appeared in 55% of the best-fit models given the exclusion of a given year (Table 7). Predictors representing predation on the early juvenile stages were important, with predation on age-0 fish by age-1 hake ($logPRED_{age0.age1.hake}$) and arrowtooth flounder predation on age-0 pelagic juveniles appearing in 98% and 33% of the best-fit models from 1981 – 2005, respectively. The linear and quadratic predictors for cross-shelf transport south of Point Conception during the first-feeding larval stage ($CST_{larv.s}$, $CST^2_{larv.s}$) appeared in 76% and 71% of models, respectively (Table 7). Other important predictors were the Ocean Niño Index during the adult female preconditioning stage (ONI_{pre}) and the number of calm periods during the first-feeding larval stage ($CALM_{larv}$), which appeared in 62% of and 24% the models, respectively. Surprisingly, the $EKE_{pre.MS.c}$ predictor, which was a strong predictor in the both the jackknife and resampling recruitment analyses, only appeared in 7% of the models, while $PREY_{pre.her}$ dropped to 2%. However, jackknife resampling using the AIC-best model from the primary analysis did a good job of predicting recruitment deviations for 1981 – 2005 ($R^2 = 0.63$, Figure 3b), although the

high recruitment events in 1990 and 2005 were underpredicted and recruitment in 1989 was overpredicted. Our five-term model predicted recruitment deviations well when used to forecast 2006 – 2010, although it overpredicted recruitment in 2006 and underpredicted recruitment in 2009 and 2010 (Figure 3b). The AIC-best model from the jackknife resampling (BI_{pre}, ONI_{pre}, $CST_{larv.s}$, $CST^2_{larv.s}$, and $logPRED_{age0.age1.hake}$) did a very good job of predicting recruitment deviations for 1981 – 2005 ($R^2 = 0.83$), yet only a marginal job for 1981 – 2010 ($R^2 = 0.44$). Thus, the five-term Model 1 from the primary analysis appears to be an effective predictor of Pacific hake recruitment variability.

4 | DISCUSSION

Our analyses revealed several potential drivers of recruitment variability in Pacific hake. The five variables in the AIC-best model explained 59% of the variability in Pacific hake recruitment not accounted for by estimates based exclusively on the spawning stock size. Recruitment deviations were negatively correlated with May – September eddy kinetic energy between 34.5° and 42.5°N, the location of the North Pacific Current bifurcation, and Pacific herring biomass during the female spawner preconditioning stage, northward alongshore transport during the yolk-sac larval stage, and the number of days between storm events during the first-feeding larval stage. Upwelling strength during the preconditioning stage, the number of calm periods during the first-feeding larval stage, and predation on age-0 pelagic juveniles by age-1 hake were also important predictors that were negatively correlated with recruitment (Table 2, A2). These findings suggest that multiple mechanisms likely affect Pacific hake recruitment at different stages in their early life history (Figure 7). Intercept-only models for the spawning, egg, and age-0 pelagic juvenile stages suggest that the hypotheses we evaluated for

659 these stages were not well explained by the ROMS data (Figure A2).

660 Eddy kinetic energy between May and September from Point Conception to Cape Blanco
661 during the female spawner preconditioning stage was the strongest driver of recruitment we
662 identified. Areas with higher mesoscale turbulence have energetic flow characterized by eddies,
663 meanders, and frontal structures, which are known to concentrate prey and improve feeding
664 opportunities for marine fishes (Logerwell & Smith, 2001; Bakun, 2006). As such, we expected
665 higher EKE to be associated with higher hake recruitment, yet the opposite relationship was
666 found. Decreasing recruitment with increasing EKE may be associated with its offshore
667 movement with the seasonal equatorward jet, which frequently separates from the coast at Cape
668 Blanco (Castelao et al., 2006; Strub & James, 2000). Fronts associated with upwelling filaments
669 may extend several hundred kilometers offshore (Castelao et al., 2006; Strub & James, 2000),
670 and while this could potentially benefit adult hake through expansion of their feeding habitat,
671 their movement offshore to less productive waters may result in poorer feeding conditions
672 overall, and greater energy expended on the return migration to their spawning grounds.
673 Similarly, Nieto et al. (2014) found that offshore transport had a negative effect on sardine
674 recruitment, despite the expansion of their spawning habitat farther offshore.

675 Previous studies have linked a northward-shifted NPC bifurcation to higher biomass and
676 productivity in the CCE, which likely results from the advective transport of nutrients and large-
677 bodied, lipid-rich zooplankton from the sub-arctic domain into the CCE, leading to enhanced
678 production in higher trophic level species (Malick et al., 2017; Sydeman et al., 2011). We
679 expected a similar response with hake. In contrast, we found that a southward-shifted NPC
680 bifurcation during the adult female preconditioning stage was linked to higher recruitment the
681 following year. High productivity in the northern CCE has been attributed to several

682 mechanisms, including a persistent nutrient supply through the dynamics of the Strait of Juan de
683 Fuca and the Columbia River, local upwelling enhancement by submarine canyons (e.g., Juan de
684 Fuca and Astoria canyons), and physical features that allow for the development and retention of
685 phytoplankton blooms on the shelf (Hickey & Banas, 2008). During the summer, the Columbia
686 River plume typically flows southwestward offshore of the Oregon shelf, while during the
687 winter, it flows northward over the Washington shelf (Hickey, 1989, 1998). The plume can
688 become bi-directional from summer to early fall, depending on the direction of prevailing winds
689 (Hickey et al., 2005). With a southward shifted NPC bifurcation (e.g., south of the Columbia
690 River), the northward flowing Alaska Current could impede the southwesterly flow of the
691 Columbia plume, advecting the highly productive waters off the coasts of Washington and
692 southern British Columbia northward, leading to better feeding conditions for adult hake on their
693 summer feeding grounds. In contrast, a northward-shifted NPC bifurcation (e.g., off the coast of
694 southern Vancouver Island) would likely result in poorer conditions for hake on their summer
695 feeding grounds, as the high productivity off the coasts of Washington and southern British
696 Columbia would instead be advected southward, with enhanced southwestward offshore flow of
697 plume waters.

698 Hake recruitment was negatively correlated with northward transport during the yolk-sac
699 larval stage (AST_{yolk}, January to April at 50 – 100 m), which was similar to the findings of
700 Schirripa & Colbert (2006), who linked higher sablefish recruitment with stronger southward
701 transport of surface waters (50 – 100 m) in February. Tolimieri et al. (2018) found that
702 northward transport of sablefish yolk-sac larvae at 1,000 – 1,200 m was associated with higher
703 recruitment, likely because it increased their overlap with northern zooplankton once they moved
704 to surface waters and started feeding. Increased southward transport could potentially increase

the overlap of first-feeding hake larvae with boreal copepods, which are larger, higher in fatty acids, and provide a better food source than southern species (McFarlane & Beamish, 1992; Peterson, 2009; Peterson & Keister, 2003). Reduced northward transport likely maintains yolk-sac larvae in close proximity to their southern nursery grounds and may also improve survival by reducing the spatial overlap of larval and early juvenile stages with age-1 hake, thereby reducing cannibalism and competition for food resources (Buckley & Livingston, 1997; Smith, 1995).

We found that Pacific hake recruitment decreased as the number of days between storm events increased during the first-feeding larval stage. This result was somewhat unexpected, as calm periods in upwelling ecosystems are thought to facilitate vertical stratification of the water column, aggregating fish larvae and prey at concentrations that support successful feeding, survival, and recruitment (Lasker, 1978, 1981). For example, Peterman & Bradford (1987) found that the mortality rate of northern anchovy larvae declined as the frequency of calm periods with low wind speeds increased. However, Turley & Rykaczewski (2019) found that the number of hake recruits per spawning stock biomass was negatively correlated to the number of distinct calm periods per spawning season and that larval mortality significantly decreased as the number of storm events increased. While storm-induced mixing can disrupt or dilute patches of plankton, the authors suggested that these negative effects could be offset by increased contact rates between first-feeding larvae and their prey (e.g., MacKenzie & Leggett, 1991; MacKenzie et al., 1994). Turley & Rykaczewski (2019) also postulated that larval hake at the base of the mixed layer could benefit from turbulence avoidance behavior by prey in the mixed layer, with prey becoming more susceptible to predation as they swim downward (Franks, 2001). These mechanisms could also explain the negative correlation found between recruitment and the number of days between storm events in our study, as more frequent storm events would

maintain a downward flux of surface prey, leading to increased encounter rates, higher growth and survival of first-feeding hake larvae, and higher recruitment. While increased turbulence may initially improve feeding success by increasing encounter rates between predators and their prey, this may only be up to a certain point, akin to the "Optimal Environmental Window" hypothesis for upwelling (Cury & Roy, 1989). Research has shown that decreased ingestion rates may occur at higher levels of turbulence through disruption of feeding patches, with decreased reaction times of predators to increased prey velocities and decreased capture success also impacting the ability of larvae to feed successfully (Landry et al., 1995 and references therein). However, higher velocities of hake larvae and decreased capture success by their predators at higher levels of turbulence may also help hake early life stages elude their predators, leading to increased survival and higher recruitment.

Pacific herring biomass during the adult preconditioning stage was negatively correlated with hake recruitment. This result was surprising, as we expected higher herring biomass to lead to improved feeding conditions for adult hake, given that they become more piscivorous with age and are a primary predator of herring off the west coast of Canada (Schweigert et al., 2010; Ware and McFarlane, 1986, 1995). In a recent study, Godefroid et al. (2019) found that spatiotemporal densities of Pacific herring and Pacific hake off the WCVI in summer were negatively correlated, which the authors attributed to predation, although they noted this pattern might also reflect different responses to environmental conditions or prey availability. The negative relationship between hake recruitment and herring biomass during the adult preconditioning stage in our study might result from competitive interactions between the two species. Euphausiids are an important food source for Pacific hake across different life stages throughout their range (Livingston & Bailey, 1985), accounting for 80 – 90 % of prey consumed, although

751 they decrease in importance for larger fish on their northward migration (Stauffer, 1985). Still,
752 higher herring biomass on the hake summer feeding grounds may reduce the abundance of
753 euphausiids, which could lead to poorer feeding conditions for adult hake, reduced condition
754 prior to spawning, and lower recruitment.

755 Our analysis identified additional covariates that were less consistently correlated with
756 recruitment, but may be influential in some years. In particular, hake recruitment was linked to
757 the NPGO, PDO, and upwelling during the adult female preconditioning stage, the number of
758 calm periods and duration of storm events during the first-feeding larval stage, euphausiid
759 abundance during the late larval stage, predation by age-1 hake during the age-0 pelagic juvenile
760 stage, and timing of the spring transition (Table 2). When a new model was fit with these
761 additional covariates outside of our main analysis, almost 63% of the variability in Pacific hake
762 recruitment deviations was explained, compared to 59% in the AIC-best model. However, model
763 diagnostics for these models were poor, indicating that they were likely overfitting the data.
764 Increased storm duration and the number of calm periods were likely linked with higher
765 recruitment due to the previously described mechanisms, with enhanced feeding as prey are more
766 frequently mixed downwards or descend to avoid turbulence during storms (Turley &
767 Rykaczewski, 2019). An alternative mechanism could be that increased turbulence associated
768 with increased storm duration would disrupt potential predation on larval hake as contacts rates
769 decreased with high turbulence (Landry et al., 1995 and references therein). Atmospheric forcing
770 associated with both the PDO and NPGO controls decadal modulation of the upwelling cells,
771 resulting in spatially varying responses of coastal upwelling, with a strong PDO signal north of
772 38°N and a strong NPGO signal south of 38°N (Di Lorenzo et al., 2008). Chhak & DiLorenzo
773 (2007) found differences in modeled depth of the upwelling cell between “warm” and “cool”

774 phases of the PDO, likely impacting nutrient flux and biological productivity, though differences
775 were not as strong in southern regions of the CCE compared to northern regions. Thus, the PDO
776 and NPGO may impact recruitment in Pacific hake through upwelling-related changes in
777 productivity and horizontal advection in the CCE.

778 While upwelling was not a predictor in our AIC-best model, it often appeared in other
779 candidate models (Tables 2 and A2). Upwelling fuels the CCE's high biological productivity and
780 as such, we expected that higher upwelling would be linked to higher hake recruitment. Instead,
781 we found that weaker upwelling north of 42°N from April to October during the adult female
782 preconditioning stage was linked to higher recruitment. Upwelling may impact feeding adults in
783 a number of ways. First, strong poleward flow is thought to aid Pacific hake adults in their
784 northward migration to their summer feeding grounds (Agostini et al., 2006; Benson et al., 2002;
785 Dorn, 1995; Smith et al., 1990). However, the spring transition to upwelling-favorable winds
786 coincides with the onset of predominantly equatorward flow and a reduced California
787 Undercurrent (Siedlecki et al., 2015). Thus, upwelling may impede the northward movement of
788 hake, increasing the energy expended swimming against strong southward currents during their
789 northward migration (Ressler et al., 2007), resulting in lower condition of pre-spawning females.
790 Second, upwelling may impact Pacific hake recruitment through bottom-up processes that affect
791 prey abundance and availability. Upwelling off Oregon and Washington is usually episodic, with
792 events lasting from days to weeks followed by periods of relaxation (Huyer et al., 1979; Huyer,
793 1983; Barth et al., 2000). The shoreward advection of near-surface waters during relaxation or
794 downwelling events has been shown to control larval recruitment (Farrell et al. 1991; Mackas et
795 al., 2001; Roughgarden et al., 1991; Shanks & Morgan, 2018), including that of euphausiids,
796 which are an important prey item for Pacific hake throughout their range (Livingston & Bailey,

797 1985). Indeed, high euphausiid recruitment has been linked to periods of downwelling or below-
798 average upwelling, which maintains larvae on the continental shelf instead of being transported
799 offshore into less productive oceanic waters (Mackas et al., 2001). High abundances of hake
800 have often been found in close proximity to high abundance patches of euphausiids near the
801 shelf-break, but the overlap has been less obvious farther offshore (Swartzman et al., 2001;
802 Phillips et al., 2022). Thus, while strong and persistent upwelling can transport phytoplankton
803 blooms and zooplankton prey far from shore via strong Ekman transport (Botsford et al., 2006;
804 Mackas et al., 2001), periods of reduced upwelling may be beneficial to Pacific hake adults on
805 their summer feeding grounds by increasing the abundance of their euphausiid prey via enhanced
806 recruitment, and also by maintaining spatial overlap with them through reducing their offshore
807 transport.

808 The multiple model validation methods applied to these data suggest that the AIC-best
809 model predictions were robust. Recruitment residuals fell well outside of the predicted 95%
810 confidence interval in 1990, 2007, and 2009 (Figure 4a). The latter years coincide with an
811 increase in the abundance and distribution of the Humboldt squid (*Dosidicus gigas*), which are
812 voracious predators that are known to prey on Pacific hake (Field et al., 2007; Litz et al., 2011).
813 Oddly, hake recruitment was high in 2009, when lower densities of juvenile hake were
814 coincident with the presence of Humboldt squid (Litz et al., 2011). However, higher hake
815 recruitment in 2009 could be linked to weaker than normal upwelling and extended relaxation
816 events in summer 2009 (Bjorkstedt et al., 2010), which may have maintained larvae and early
817 juveniles in close proximity to nearshore nursery habitats, providing better feeding conditions
818 compared to those found offshore. The lack of a clear link between the covariates examined in
819 our study and high recruitment in 1990 suggests that other variables not included here may be

820 important drivers of recruitment. The AIC-best model predictions from a leave-one-year-out
821 jackknife analysis provided predictions that fell within the 95% confidence limits of the fitted
822 AIC-best model in all years (Figure 4a). The AIC-best model predictions that used the available
823 data through 2005 and then predicted 2006 – 2010 resulted in similar predictions to those from
824 1981 – 2010 (Figure 4b). However, two of the recruitment predictors in the AIC-best model
825 ($PREY_{pre.her}$ and $STORMB_{larv)}$ were no longer significant. This was likely due to higher values of
826 these predictors at the end of the time series, along with above average recruitment (except in
827 2007), which were removed when using the 1981 through 2005 training data set.
828 Predation on age-0 hake by the preceding cohort was an important predictor of hake
829 recruitment in our jackknife analysis. Previous studies have shown that year-class strength was
830 largely determined within the first few months of hatching (Bailey & Francis, 1985; Hollowed &
831 Bailey, 1989), but predation on juvenile hake was not considered to be a major source of
832 recruitment variability (Bailey & Francis, 1995). However, other studies have suggested that
833 recruitment may be affected by adjacent-cohort cannibalism (Buckley & Livingston, 1997;
834 Smith, 1995). Alternatively, increased competition for food may lead to reduced recruitment in a
835 cohort that follows a successful one (Buckley & Livingston, 1997; Smith, 1995).
836 Arrowtooth flounder biomass was also an important predictor during the model testing
837 and validation process. Pacific hake are the primary diet of arrowtooth flounder off the Oregon
838 and Washington coasts (Buckley et al., 1999). The positive relationship with recruitment could
839 potentially be explained by increased predation on older (age-2+) hake on their summer feeding
840 grounds when arrowtooth flounder biomass is high. Density-dependent mortality due to
841 cannibalism on age-0 and age-1 juvenile hake by older fishes is likely related to the amount of
842 spatial overlap between juvenile and adult fish (Buckley & Livingston, 1997). Thus, the higher

levels of recruitment seen when arrowtooth flounder biomass is high may reflect increased predation on adult hake, which would reduce the amount of adult cannibalism on age-1 and YOY fish (Buckley & Livingston, 1997). The arrowtooth flounder spawning biomass experienced a period of fairly rapid decline during the 1970s and subsequent increase through the 1980s, reaching a peak in 1991 (Sampson et al., 2017). Since then, spawning biomass has declined, reaching a low in 2010 (Sampson et al., 2017), which may explain the lack of relationship between recruitment and arrowtooth flounder predation in the 1981 – 2010 time series.

In comparison to recruitment drivers identified for other CCE species using the same approach, the lack of a temperature predictor in any of the models for Pacific hake is notable. Degree days during the female preconditioning period was found to be an important predictor of both sablefish (Tolimieri et al., 2018) and petrale sole recruitment (Haltuch et al., 2020). Pacific hake distribution is driven by interactions between age composition and temperature (Malick et al., 2020). However, temperature has a non-linear effect on the distribution of immature hake (i.e., age-2 fish) (Malick et al., 2020), and non-linearity could potentially explain the lack of a relationship between temperature and recruitment in our GLMs. Reproduction and early development in marine fishes are particularly sensitive to changes in temperature (Pepin, 1991; Pörtner et al., 2001; Van Der Kraak & Pankhurst, 1997) and temperature can affect growth and survival indirectly by altering the species composition, nutritional quality, and seasonal distribution of prey (Asch, 2015; Keister et al., 2011; Fietcher et al., 2015; Peterson, 2009; Peterson & Keister, 2003). Another potential explanation for the lack of relationship between temperature and recruitment may be that adult hake seek out a particular temperature or narrow range of temperatures and/or environmental conditions over which to spawn, though Agostini et al. (2006) found that Pacific hake habitat was associated with subsurface poleward flow rather

than a specific temperature range. If spawning is initiated when specific water mass properties or a particular temperature range is encountered, as suggested by Bailey et al. (1982), then a strong temperature response in post-spawning stages would not be expected. In addition, because hake spawn at depth where temperatures are cooler, their propagules are released into a relatively stable thermal environment that experiences less year-to-year variability compared to surface waters. Eggs and larvae are found in waters below the mixed layer, which are insulated to some extent from temperature fluctuations in the surface mixed layer above (Bailey, 1982). This relatively stable environment may explain why the early growth of hake larvae shows little variation from season to season (Bailey, 1982; Butler & Nishimoto, 1997). Thus, Pacific hake likely respond differently to climate variability compared to other species that occupy different parts of the water column during their life histories.

Based on the results of the current study, it appears that cohort strength is established between the larval and early juvenile stages, but conditions experienced by adult females prior to spawning are also important. Previous research has shown that the survival of larval Pacific hake is strongly influenced by the environmental conditions experienced during the first few months after spawning (Agostini, 2005; Bailey, 1981; Bailey & Francis, 1985; Bailey et al., 1986; Hollowed, 1992;), which suggests that year-class strength is set during the first year of life. Increased recruitment has been linked to weak offshore transport in early winter (Bailey 1980, 1981; Bailey & Francis, 1985; Hollowed & Bailey, 1989), warm January sea surface temperature (Bailey & Francis 1985; Hollowed & Bailey, 1989), and increased upwelling in March (Hollowed & Bailey, 1989). However, we did not find significant relationships between recruitment and covariates for temperature and upwelling during the early life stages, although upwelling during the preconditioning stage was important in two of the models with a ΔAICc <

889 2. One potential explanation for discrepancies between our analysis and past research findings
890 could be that earlier studies were limited by shorter time series (e.g., Bailey, 1981) and
891 previously observed relationships have not persisted over time. Indeed, associations between
892 environmental conditions and biological responses are often non-stationary in time (Myers,
893 1998). For example, regression models assuming stationary climate–salmon relationships were
894 found to be inappropriate over multidecadal time scales (1965 – 2012) in a recent study of
895 salmon (*Onchorynchus* spp.) productivity in the Gulf of Alaska (Litzow et al., 2018).
896 Relationships between recruitment, the prevalence of density dependence, and environmental
897 drivers have also been shown to differ between PDO regimes for bocaccio rockfish (*Sebastes*
898 *paucispinis*) (Tolimieri & Levin, 2005; Zabel et al., 2011). For Pacific hake, the changing
899 relationships between recruitment strength and temperature and upwelling during the 1970s
900 (Bailey, 1981) and the 1980s (Bailey & Francis, 1985) suggest that climate-recruitment
901 relationships may also be non-stationary. Another potential explanation for why our recruitment
902 predictors do not align with those found in previous studies is that different timeframes were
903 used to calculate the means for each predictor, obscuring conditions linked to high recruitment
904 events. For example, Hollowed & Bailey (1989) found that successful year-classes of Pacific
905 hake occurred after periods of low upwelling during early winter (either January or February)
906 followed by a period of intense upwelling in March. Our predictors for upwelling during the
907 yolk-sac and first-feeding larval stages were calculated over January – April and February –
908 May, respectively, thus, they likely would not capture specific upwelling events in March linked
909 to high recruitment.
910 One limitation of our study is that the CCE ROMS domain only covers the U.S. west
911 coast, thus we are unable to address oceanographic conditions in Canadian or Mexican waters

912 that might be important to Pacific hake recruitment. Several predictors did represent conditions
913 outside of the ROMS domain that could potentially affect hake recruitment. These included
914 basin-scale climate indices (e.g., ONI, PDO) and covariates representing the effects of storm
915 events and calm periods on first-feeding larvae off the coast of Baja California. Constraining the
916 spatial domain of the storm and calm covariates to that of the ROMS output (31° – 36°N vs. 28°
917 – 36°N) during exploratory analyses resulted in a change in model predictors, with predation on
918 age-0s by age-1 hake replacing the $CALM_{larv}$ predictor. This suggests that predation by the
919 preceding cohort may be an important driver of recruitment off southern California where
920 overlap between age-1 and YOY hake may be greater, while calm periods during the first-
921 feeding larval stage may be more important off Baja California. This finding underscores the fact
922 that environmental conditions outside of the ROMS region likely play an important role in hake
923 recruitment. Thus, regional ocean reanalyses with broader spatial coverage would be helpful to
924 include in future studies of recruitment drivers of species with distributions that cross
925 international boundaries.

926 Finally, while our analysis assumes that Pacific hake spawn off the coast of southern
927 California during the winter months, spawning has never been directly observed. Ressler et al.
928 (2007) suggest that the location of spawning is variable, with groups spawning in different
929 places, well north of where the classic model would suggest in some years (see their Figure 8).
930 Several studies have reported finding hake eggs and larvae in the northern region of the CCE in
931 some years (Auth et al., 2018; Brodeur et al., 2019; Hollowed, 1992; Phillips et al., 2007) and
932 future studies should consider alternative spawning grounds, as well as potential shifts in the
933 timing of spawning. Indeed, recent hake maturity work has shown that individuals may be
934 spawning outside of the traditional winter spawning season coast-wide (M. Head, NOAA,

935 personal communication).

936 Our work substantially updates the understanding of drivers of Pacific hake recruitment
937 in the CCE and has the potential to influence the stock assessment process, ecosystem
938 assessments, and management strategy evaluations (MSEs) (e.g., Hollowed et al., 2009). In the
939 current hake stock assessment, recruitment estimates in the current and previous years, and for 2-
940 3 year projections into the future are informed only by the stock-recruitment relationship and the
941 large standard deviation that is assumed for annual variability in recruitment. Empirical or
942 model-based information about the scale or direction of drivers of recruitment could reduce
943 uncertainty in recruitment in those years, which would reduce uncertainty in estimates of stock
944 status and allow the stock assessment scientists to provide more precise catch advice (Kaplan et
945 al., 2016; Siedlecki et al., 2016; Tommasi et al., 2017). Moreover, by annually updating
946 environmental predictors to inform recruitment forecasting based on both observed
947 oceanographic conditions and potentially sub-annual forecasts of environmental conditions
948 (Jacox et al., 2017; Siedlecki et al., 2016), managers and stakeholders could be provided with
949 leading environmental indicators of recruitment (Jacox et al., 2020). Recruitment indicators
950 could be used by stakeholders to reduce uncertainty in business planning, or more formally
951 within the management process by informing a risk assessment that could provide context for the
952 binational annual catch level negotiations (e.g., Dorn and Zador, 2020).

953 Our results can also inform assessments of hake's vulnerability to climate change and an
954 ongoing climate-informed MSE focused on hake. Several of the indicators of recruitment we
955 identified come from a ROMS product, and a related product has recently been forecasted to
956 2100 (Pozo Buil et al., 2021), meaning we can use forecasts of the drivers we identified to begin
957 to understand how recruitment variability could change under future ocean conditions.

Additionally, a management strategy evaluation for hake has shown that a northward distribution shift in the population could result in diminished ability of the U.S. fishery to catch fish in U.S. waters (Jacobsen et al., 2021). Our results identifying drivers of recruitment and the future ROMS projections together can be used to develop scenarios of future recruitment, which when combined with projecting movement, allow us to begin to understand the impacts of climate change on multiple aspects of Pacific hake life history and the consequences for the management of the binational fishery.

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CONFLICT OF INTEREST

The authors do not have any conflicts of interest, commercial or otherwise, that have influenced the findings of this research.

AUTHOR CONTRIBUTIONS

K.N.M., N.T., M.E.H., I.G.T, and A.M.B conceived the study. C.D.V. developed the conceptual life history model. N.T. developed and C.D.V. undertook statistical analyses. M.G.J. provided the oceanographic expertise and ROMS model outputs for the study. B.D.T. provided expertise and code for the storm and calm indices used in this study. C.D.V. drafted the manuscript with input and revisions from all authors.

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DATA AVAILABILITY STATEMENT

The data associated with this manuscript are available through the NOAA Northwest Fisheries Science Center, Fishery Resource Analysis and Monitoring Division. The code used for the analysis is available on GitHub (https://github.com/pacific-hake/recruitment-index). Outputs from the regional ocean reanalysis are available from the UC Santa Cruz ocean modeling group (oceanmodeling.ucsc.edu).

REFERENCES

Agostini, V. N. (2005). Climate, ecology and productivity of Pacific sardine (*Sardinops sagax*) and hake (*Merluccius productus*). Doctoral dissertation, University of Washington, Seattle, WA.

Agostini, V. N., Francis, R. C., Hollowed, A. B., Pierce, S. D., Wilson, C., & Hendrix, A. N. (2006). The relationship between Pacific hake (*Merluccius productus*) distribution and poleward subsurface flow in the California Current System. *Canadian Journal of Fisheries and Aquatic Sciences*, *63*(12), 2648-2659. https://doi.org/10.1139/f06-139 © Canadian Science Publishing or its licensors.

Agostini, V. N., Hendrix, A. N., Hollowed, A. B., Wilson, C. D., Pierce, S. D., & Francis, R. C. (2008). Climate–ocean variability and Pacific hake: a geostatistical modeling approach. *Journal of marine systems*, *71*(3-4), 237-248. https://doi.org/10.1016/j.jmarsys.2007.01.010

Ahlstrom, E. H. (1959). Vertical distribution of pelagic fish egg and larvae off California and Baja California. *Fishery Bulletin*, *60*, 107-146.

Ahlstrom, E. H., & Counts, R. C. (1955). Eggs and larvae of the Pacific hake *Merluccius productus*. U.S. Government Printing Office.

Akaike, H. (1998). Information theory and an extension of the maximum likelihood principle. In: *Selected Papers of Hirotugu Akaike*. Springer, New York, NY

Antonelis, G. A., Fiscus, C. H., & DeLong, R. L. (1984). Spring and summer prey of California sea lions, *Zalophus californianus*, at San Miguel Island, California, 1978–79. *Fishery Bulletin*, *82*(1), 67-75.

Asch, R. G. (2015). Climate change and decadal shifts in the phenology of larval fishes in the California Current ecosystem. *Proceedings of the National Academy of Sciences*, *112*(30), E4065-E4074. https://doi.org/10.1073/pnas.1421946112

Auth, T. D., Daly, E. A., Brodeur, R. D., & Fisher, J. L. (2018). Phenological and distributional shifts in ichthyoplankton associated with recent warming in the northeast Pacific Ocean. *Global change biology*, *24*(1), 259-272. https://doi.org/10.1111/gcb.13872

Bailey, K. M. (1980). Recent changes in the distribution of hake larvae: causes and consequences. *California Cooperative Oceanic Fisheries Investigations Report, 21*, 167-171.

Bailey, K. M. (1981). Larval transport and recruitment of Pacific hake *Merluccius productus*. *Marine Ecology Progress Series*, *6*(1), 1-9. https://www.int-res.com/articles/meps/6/m006p001.pdf

Bailey, K. M. (1982). The early life history of the Pacific hake, *Merluccius productus*. *Fishery Bulletin*, *80*, 589-598.

Bailey, K. M., Francis, R. C., & Mais, K. F. (1986). Evaluating incidental catches of 0-age Pacific hake to forecast recruitment. *California Cooperative Oceanic Fisheries Investigations Report, 27*, 109-112.

Bailey, K. M., Francis, R. C., & Stevens, P. R. (1982). The life history and fishery of Pacific whiting, *Merluccius productus*. NWAFC Processed Report 82-03, 87 p.

Bailey, K.M. & Francis, R.C. (1985). Recruitment of Pacific Whiting, *Merluccius productus,* and the Ocean Environment. *Marine Fisheries Review*, *47*(2), 8-15. https://spo.nmfs.noaa.gov/sites/default/files/pdf-content/MFR/mfr472/mfr4723.pdf

Bailey, K. M., & Houde, E. D. (1989). Predation on eggs and larvae of marine fishes and the recruitment problem. In: *Advances in Marine Biology* (Vol. 25, pp. 1-83). Academic Press. https://doi.org/10.1016/S0065-2881(08)60187-X

Bakun, A. (2006). Fronts and eddies as key structures in the habitat of marine fish larvae: opportunity, adaptive response and competitive advantage. *Scientia Marina, 70*(A2), 105-122. https://doi.org/10.3989/scimar.2006.70s2105

Barth, J. A., Pierce, S. D., & Smith, R. L. (2000). A separating coastal upwelling jet at Cape Blanco, Oregon and its connection to the California Current System. *Deep Sea Research Part II: Topical Studies in Oceanography*, *47*(5-6), 783-810. https://doi.org/10.1016/S0967-0645(99)00127-7

Barton, K. (2020). MuMIn: multi-model inference. R package version 1.43.17.

Becker, E. A., Forney, K. A., Redfern, J. V., Barlow, J., Jacox, M. G., Roberts, J. J., & Palacios, D. M. (2019). Predicting cetacean abundance and distribution in a changing climate. *Diversity and Distributions*, *25*(4), 626-643. https://doi.org/10.1111/ddi.12867

Benson, A. J., McFarlane, G. A., Allen, S. E., & Dower, J. F. (2002). Changes in Pacific hake (*Merluccius productus*) migration patterns and juvenile growth related to the 1989 regime shift. *Canadian Journal of Fisheries and Aquatic Sciences*, *59*(12), 1969-1979. https://doi.org/10.1139/f02-156

Berger, A. M., Edwards, A. M., Grandin, C. J., & Johnson, K. F. (2019). Status of the Pacific Hake (whiting) stock in U.S. and Canadian waters in 2019. Prepared by the Joint Technical Committee of the U.S. and Canada Pacific Hake/Whiting Agreement, National Marine Fisheries Service and Fisheries and Oceans Canada. 249 p.

Best, E. A. (1963). Contribution to the biology of the Pacific hake, *Merluccius productus* (Ayres). *California Cooperative Oceanic Fisheries Investigations Report*, *9*, 51-56.

Bjorkstedt, E. P., Goericke, R., McClatchie, S., Weber, E., Watson, W., Lo, N., ... & Munger, L. M. (2010). State of the California Current 2009-2010: Regional variation persists through transition from La Niña to El Niño (and back?). *California Cooperative Oceanic Fisheries Investigations Report*, *51*, 39-69.

Burnham, K. P., & Anderson, D. R. (1998). Model selection and inference: A practical information-theoretic approach. New York, NY: Springer-Verlag.

Butler, J. L., & Nishimoto, R. N. (1997). Growth and cohort dynamics of larval Pacific hake (*Merluccius productus*). *California Cooperative Oceanic Fisheries Investigations Report*, *38*, 63-68.

Bograd, S. J., Schroeder, I., Sarkar, N., Qiu, X., Sydeman, W. J., & Schwing, F. B. (2009). Phenology of coastal upwelling in the California Current. *Geophysical Research Letters, 36*(1). https://doi.org/10.1029/2008GL035933

Botsford, L. W., Lawrence, C. A., Dever, E. P., Hastings, A., & Largier, J. (2006). Effects of variable winds on biological productivity on continental shelves in coastal upwelling systems. *Deep Sea Research Part II: Topical Studies in Oceanography*, *53*(25-26), 3116-3140. https://doi.org/10.1016/j.dsr2.2006.07.011

Brodeur, R. D., Auth, T. D., & Phillips, A. J. (2019). Major shifts in pelagic micronekton and macrozooplankton community structure in an upwelling ecosystem related to an unprecedented marine heatwave. *Frontiers in Marine Science*, *6*, 212. https://doi.org/10.3389/fmars.2019.00212

Brodie, S., Jacox, M. G., Bograd, S. J., Welch, H., Dewar, H., Scales, K. L., ... & Lewison, R. L. (2018). Integrating dynamic subsurface habitat metrics into species distribution models. *Frontiers in Marine Science*, *5*, 219. https://doi.org/10.3389/fmars.2018.00219

Buckley, T. W., & Livingston, P. A. (1997). Geographic variation in the diet of Pacific hake, with a note on cannibalism. *California Cooperative Oceanic Fisheries Investigations Report*, *38*, 53-62.

Buckley, T. W., Tyler, G. E., Smith, D. M., & Livingston, P. A. (1999). Food habits of some commercially important groundfish off the coasts of California, Oregon, Washington, and British Columbia. *NOAA Technical Memorandum NMFS-AFSC*, *102*, 173.

Burke, B. J., Peterson, W. T., Beckman, B. R., Morgan, C., Daly, E. A., & Litz, M. (2013). Multivariate models of adult Pacific salmon returns. *PloS ONE*, *8*(1), e54134. https://doi.org/10.1371/journal.pone.0054134

Burnham, K. P., & Anderson, D. R. (1998). Practical use of the information-theoretic approach. In: *Model selection and inference* (pp. 75-117). Springer, New York, NY.

Cass-Calay, S. L. (1997). Relation of mean growth rate to concentration of prey-sized particles for larvae of Pacific hake (*Merluccius productus*). *California Cooperative Oceanic Fisheries Investigations Report*, 69-76.

Castelao, R. M., Mavor, T. P., Barth, J. A., & Breaker, L. C. (2006). Sea surface temperature fronts in the California Current System from geostationary satellite observations. *Journal of Geophysical Research: Oceans*, *111*(C9). https://doi.org/10.1029/2006JC003541

Chelton, D. B., & Davis, R. E. (1982). Monthly mean sea-level variability along the west coast of North America. *Journal of Physical Oceanography*, *12*(8), 757-784. https://doi.org/10.1175/1520-0485(1982)012<0757:MMSLVA>2.0.CO;2

Chereskin, T. K., & Trunnell, M. (1996). Correlation scales, objective mapping, and absolute geostrophic flow in the California Current. *Journal of Geophysical Research: Oceans, 101*(C10), 22619-22629. https://doi.org/10.1029/96JC02004

Chezik, K. A., Lester, N. P., & Venturelli, P. A. (2014). Fish growth and degree-days I: selecting a base temperature for a within-population study. *Canadian Journal of Fisheries and Aquatic Sciences*, *71*(1), 47-55. https://doi.org/10.1139/cjfas-2013-0295

Chhak, K., & Di Lorenzo, E. (2007). Decadal variations in the California Current upwelling cells. *Geophysical Research Letters*, *34*(14).

Cleary, J., Hawkshaw, S., Grinnell, M., Grandin, C., Postlethwaite, V., Rusch, B., & Christensen, L. (2020). Stock status update with application of management procedures for Pacific herring (*Clupea pallasii*) in British Columbia: Status in 2020 and forecast for 2021. Canadian Science Advisory Secretariat. Pacific Region. Science Response 2021/001. https://waves-vagues.dfo-mpo.gc.ca/Library/40966264.pdf

Cooke, K. D., Holmes, J., Fleischer, G. W., Thomas, R. E., & Ressler, P. H. (2006). Distributional changes observed in the geographic range of Pacific hake (*Merluccius productus*) in association with ocean conditions off the Pacific coast of Canada and the United States. *ICES CM*, *2006*, 01. https://www.ices.dk/sites/pub/CM%20Doccuments/2006/B/B0106%20.pdf

Cummins, P. F., & Freeland, H. J. (2007). Variability of the North Pacific Current and its bifurcation. *Progress in Oceanography*, *75*(2), 253-265. https://doi.org/10.1016/j.pocean.2007.08.006

Cury, P., & Roy, C. (1989). Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Canadian Journal of Fisheries and Aquatic Sciences*, *46*(4), 670-680.

Cushing, D. H. (1972). The production cycle and the numbers of marine fish. In *Symposia of the Zoological Society of London*, *29*, 213-232.

Cushing, D. H. (1982). Climate and fisheries. London, UK: Academic Press.

Di Lorenzo, E. (2003). Seasonal dynamics of the surface circulation in the Southern California Current System. *Deep Sea Research Part II: Topical Studies in Oceanography*, *50*(14-16), 2371-2388. https://doi.org/10.1016/S0967-0645(03)00125-5

Di Lorenzo, E., Schneider, N., Cobb, K. M., Franks, P. J. S., Chhak, K., Miller, A. J., ... & Powell, T. M. (2008). North Pacific Gyre Oscillation links ocean climate and ecosystem change. *Geophysical Research Letters*, *35*(8). https://doi.org/10.1029/2007GL032838

Dong, C., Idica, E. Y., & McWilliams, J. C. (2009). Circulation and multiple-scale variability in the Southern California Bight. *Progress in Oceanography*, *82*(3), 168-190. https://doi.org/10.1016/j.pocean.2009.07.005

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., ... & Lautenbach, S. (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, *36*(1), 27-46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Dorn, M. W. (1995). The effects of age composition and oceanographic conditions on the annual migration of Pacific whiting, *Merluccius productus*. *California Cooperative Oceanic Fisheries Investigations Report*, *36*, 97-105.

Dorn, M.W. & Zador, S.G. (2020). A risk table to address concerns external to stock assessments when developing fisheries harvest recommendations. *Ecosystem Health and Sustainability*, *6*(1), p.1813634. https://doi.org/10.1080/20964129.2020.1813634

Draper, D. L. (2022). Food habit variability of arrowtooth flounder (*Atheresthes stomias*) along the US west coast. *Fisheries Research*, *248*, 106205. https://doi.org/10.1016/j.fishres.2021.106205

Farrell, T. M., Bracher, D., & Roughgarden, J. (1991). Cross-shelf transport causes recruitment to intertidal populations in central California. *Limnology and Oceanography*, *36*(2), 279-288. https://doi.org/10.4319/lo.1991.36.2.0279

Fiechter, J., Rose, K. A., Curchitser, E. N. & Hedstrom, K. S. (2015). The role of environmental controls in determining sardine and anchovy population cycles in the California Current: Analysis of an end-to-end model. *Progress in Oceanography*, *138*, 381-398. https://doi.org/10.1016/j.pocean.2014.11.013

Field, J. C., Baltz, K. E. N., Phillips, A. J., & Walker, W. A. (2007). Range expansion and trophic interactions of the jumbo squid, *Dosidicus gigas*, in the California Current. *California Cooperative Oceanic Fisheries Investigations Report*, *48*, 131-146.

Franks, P. J. (2001). Turbulence avoidance: An alternate explanation of turbulence-enhanced ingestion rates in the field. *Limnology and Oceanography*, *46*(4), 959-963. https://doi.org/10.4319/lo.2001.46.4.0959

Freeland, H. J. (2006). What proportion of the North Pacific Current finds its way into the Gulf of Alaska? *Atmosphere-Ocean*, *44*(4), 321-330. https://doi.org/10.3137/ao.440401

Gaube, P., Braun, C. D., Lawson, G. L., McGillicuddy, D. J., Della Penna, A., Skomal, G. B., ... & Thorrold, S. R. (2018). Mesoscale eddies influence the movements of mature female white sharks in the Gulf Stream and Sargasso Sea. *Scientific reports*, *8*(1), 1-8. https://doi.org/10.1038/s41598-018-25565-8

Godefroid, M., Boldt, J. L., Thorson, J. T., Forrest, R., Gauthier, S., Flostrand, L., ... & Galbraith, M. (2019). Spatio-temporal models provide new insights on the biotic and abiotic drivers shaping Pacific Herring (*Clupea pallasi*) distribution. *Progress in Oceanography*, *178*, 102198. https://doi.org/10.1016/j.pocean.2019.102198

Goericke, R., Venrick, E., Mantyla, A., Hoof, R., Collins, C., Gaxiola-Castro, G., ... & Sydeman, W. J. (2005). The state of the California Current, 2004-2005: still cool? *California Cooperative Oceanic Fisheries Investigations Report*, *46*, 32-71.

Grandin, C. J., Johnson, K. F., Edwards, A. M., & Berger, A. M. (2020). Status of the Pacific Hake (whiting) stock in U.S. and Canadian waters in 2020. Prepared by the Joint Technical Committee of the U.S. and Canada Pacific Hake/Whiting Agreement, National Marine Fisheries Service and Fisheries and Oceans Canada. 273 p.

Haltuch, M. A., Tolimieri, N., Lee, Q., & Jacox, M. G. (2020). Oceanographic drivers of petrale sole recruitment in the California Current Ecosystem. *Fisheries Oceanography*, *29*(2), 122-136. https://doi.org/10.1111/fog.12459

Harden Jones, F. R. (1968). Fish migration. St. Martin's Press, New York.

Hare, J. A. (2014). The future of fisheries oceanography lies in the pursuit of multiple hypotheses. *ICES Journal of Marine Science*, *71*(8), 2343-2356.

Hare, J. A., & Cowen, R. K. (1996). Transport mechanisms of larval and pelagic juvenile bluefish (*Pomatomus saltatrix*) from South Atlantic Bight spawning grounds to Middle Atlantic Bight nursery habitats. *Limnology and Oceanography*, *41*(6), 1264-1280. https://doi.org/10.4319/lo.1996.41.6.1264

Hare, S. R., Mantua, N. J. & Francis, R. C. (1999). Inverse production regimes: Alaska and west coast Pacific salmon. *Fisheries*, *24*(1), 6-14.

Hickey, B. M. (1989). Patterns and Processes of Circulation over the Washington Continental Shelf and Slope, 41-115. In: *Coastal Oceanography of Washington and Oregon*. Landry M. R., & Hickey, B. M. (Eds.), Elsevier Science, Amsterdam, The Netherlands.

https://doi.org/10.1016/S0422-9894(08)70346-5

Hickey, B. M. (1998). Coastal oceanography of western North America, from the tip of Baja California to Vancouver Island. *The sea*, *11*, 1062.

Hickey, B. M., & Banas, N. S. (2008). Why is the northern end of the California Current System so productive? *Oceanography*, *21*(4), 90-107. http://www.jstor.org/stable/24860012

Hickey, B., Geier, S., Kachel, N., & MacFadyen, A. (2005). A bi-directional river plume: The Columbia in summer. *Continental Shelf Research 25*(14): 1,631-1,656. https://doi.org/10.1016/j.csr.2005.04.010

Hinckley, S., Hermann, A. J., & Megrey, B. A. (1996). Development of a spatially explicit, individual-based model of marine fish early life history. *Marine Ecology Progress Series*, *139*, 47-68. doi:10.3354/meps139047

Hjort, J. (1914). Fluctuations in the great fisheries of Northern Europe. Rapports et Proces-verbaux des Reunions, Conseil International pour l'Exploration de la Mer, *20*, 1-13.

Hjort, J. (1926). Fluctuation in the year classes of important food fishes. Journal du Conseil/ Conseil Permanent International pour l'Exploration de la Mer**,** *1*, 5-38.

Hollowed, A. B. (1992). Spatial and temporal distributions of Pacific hake, *Merluccius productus*, larvae and estimates of survival during early life stages. *California Cooperative Oceanic Fisheries Investigations Report*, *33*, 100-123.

Hollowed, A. B., & Bailey, K. M. (1989). New perspectives on the relationship between recruitment of Pacific hake (*Merluccius productus*) and the ocean environment. In: Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models. Beamish R. J., & McFarlane, G. A. (Eds). *Canadian Special Publication of Fisheries and Aquatic Sciences*, *108*, 207-220.

Hollowed, A. B., Bond, N. A., Wilderbuer, T. K., Stockhausen, W. T., A'mar, Z. T., Beamish, R. J., ... & Schirripa, M. J. (2009). A framework for modelling fish and shellfish responses to future climate change. *ICES Journal of Marine Science*, *66*(7), 1584-1594. https://doi.org/10.1093/icesjms/fsp057

Hollowed, A. B., Hare, S. R., & Wooster, W. S. (2001). Pacific Basin climate variability and patterns of Northeast Pacific marine fish production. *Progress in Oceanography*, *49*(1-4), 257-282. https://doi.org/10.1016/S0079-6611(01)00026-X

Horne, J. K., & Smith, P. E. (1997). Space and time scales in Pacific hake recruitment processes: latitudinal variation over annual cycles. *California Cooperative Oceanic Fisheries Investigations Report*, *38*, 90-102.

Houde, E. D. (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. https://doi.org/10.1111/j.1095-8649.1997.tb06093.x

Huyer, A. (1983). Coastal upwelling in the California Current system. *Progress in Oceanography*, *12*(3), 259-284. https://doi.org/10.1016/0079-6611(83)90010-1

Huyer, A., Sobey, E. J. C., & R. L. Smith (1979). The spring transition in currents over the Oregon continental shelf. *Journal of Geophysical Research, 84,* 6995-7011. https://doi.org/10.1029/JC084iC11p06995

Jacobsen, N. S., Berger, A. M., Marshall, K. N., & Taylor, I. G. (2019). A management strategy evaluation of Pacific Hake: implications of spatial distribution and differentiated harvest control rules. DRAFT for submission to Scientific Review Group.

Jacobsen, N. S., Marshall, K. N., Berger, A. M., Grandin, C. J., & Taylor, I. G. (2021). Management Strategy Evaluation of Pacific Hake: Exploring the Robustness of the Current Harvest Policy to Spatial Stock Structure, Shifts in Fishery Selectivity, and Climate-Driven Distribution Shifts. NOAA Technical Memorandum NMFS-NWFSC-168. https://doi.org/10.25923/x9f9-9b20

Jacox, M. G., Alexander, M. A., Siedlecki, S., Chen, K., Kwon, Y. O., Brodie, S., ... & Capotondi, A. (2020). Seasonal-to-interannual prediction of North American coastal marine ecosystems: Forecast methods, mechanisms of predictability, and priority developments. *Progress in Oceanography*, *183*, 102307. https://doi.org/10.1016/j.pocean.2020.102307

Jacox, M. G., Alexander, M. A., Stock, C. A., & Hervieux, G. (2017). On the skill of seasonal sea surface temperature forecasts in the California Current System and its connection to ENSO variability. *Climate Dynamics*, 53, 7519–7533. https://doi.org/10.1007/s00382-017-3608-y

Jacox, M. G., Bograd, S. J., Hazen, E. L., & Fiechter, J. (2015). Sensitivity of the California Current nutrient supply to wind, heat, and remote ocean forcing. *Geophysical Research Letters*, 42, 5950-5957. https://doi.org/10.1002/2015GL065147

Jacox, M. G., Edwards, C. A., Hazen, E. L., & Bograd, S. J. (2018). Coastal upwelling revisited: Ekman, Bakun, and improved upwelling indices for the US West Coast. *Journal of Geophysical Research: Oceans*, *123*(10), 7332-7350. https://doi.org/10.1029/2018JC014187

Jacox, M. G., Fiechter, J., Moore, A. M., & Edwards, C. A. (2015). ENSO and the California Current coastal upwelling response. *Journal of Geophysical Research*: *Oceans*, 120, 1691-1702. https://doi.org/10.1002/2014JC010650

Jacox, M. G., Hazen, E. L., & Bograd, S. J. (2016). Optimal environmental conditions and anomalous ecosystem responses: Constraining bottom- up controls of phytoplankton biomass in the California current system. *Scientific Reports*, 6, 27612. https://doi.org/10.1038/srep27612

Jacox, M. G., Moore, A. M., Edwards, C. A., & Fiechter, J. (2014). Spatially resolved upwelling in the California Current System and its connections to climate variability. *Geophysical Research Letters*, 41, 3189–3196. https://doi.org/10.1002/2014GL059589

Kaplan, I. C., Williams, G. D., Bond, N. A., Hermann, A. J., & Siedlecki, S. A. (2016). Cloudy with a chance of sardines: Forecasting sardine distributions using regional climate models. *Fisheries Oceanography*, 25, 15–27. https://doi.org/10.1111/fog.12131

Keister, J. E., Di Lorenzo, E., Morgan, C. A., Combes, V. & Peterson, W. T. (2011). Zooplankton species composition is linked to ocean transport in the Northern California Current. *Global Change Biology*, *17*(7), 2498-2511.

Laake, J. L., Lowry, M. S., DeLong, R. L., Melin, S. R., & Carretta, J. V. (2018). Population growth and status of California sea lions. *The Journal of Wildlife Management*, *82*(3), 583-595. https://doi.org/10.1002/jwmg.21405

Laine, P., & Rajasilta, M. (1999). The hatching success of Baltic herring eggs and its relation to female condition. *Journal of Experimental Marine Biology and Ecology*, *237*(1), 61-73. https://doi.org/10.1016/S0022-0981(98)00213-5

Landry, F., Miller, T. J. and Leggett, W. C. (1995). The effects of small-scale turbulence on the ingestion rate of fathead minnow (*Pimephales promelas*) larvae. *Canadian Journal of Fisheries and Aquatic Sciences*, *52*(8), 1714-1719.

Lasker, R. (1978). The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. Rapports et Proces-verbaux des Réunions. Conseil International pour l'Éxploration de la Mer, *173*, 212-230.

Lasker, R. (1981). The role of a stable ocean in larval fish survival and subsequent recruitment. *Marine fish larvae: morphology, ecology and relation to fisheries*, *1*, 80-89.

Litz, M. N., Phillips, A. J., Brodeur, R. D., & Emmett, R. L. (2011). Seasonal occurrences of Humboldt squid (*Dosidicus gigas*) in the northern California Current System. *California Cooperative Oceanic Fisheries Investigations Report*, *52*, 97-108.

Litzow, M. A., Ciannelli, L., Puerta, P., Wettstein, J. J., Rykaczewski, R. R., & Opiekun, M. (2018). Non-stationary climate–salmon relationships in the Gulf of Alaska. *Proceedings of the Royal Society B*, *285*(1890), 20181855. https://doi.org/10.1098/rspb.2018.1855

Livingston, P. A., & Bailey, K. M. (1985). Trophic role of the Pacific whiting, *Merluccius productus*. *Marine Fisheries Review*, *47*(2), 16-22.

Lo, N. C. (2007). Daily larval production of Pacific hake (*Merluccius productus*) off California in 1951-2006. *California Cooperative Oceanic Fisheries Investigations Report*, *48*, 147.

Logerwell, E. A., & Smith, P. E. (2001). Mesoscale eddies and survival of late stage Pacific sardine (*Sardinops sagax*) larvae. *Fisheries Oceanography*, *10*(1), 13-25. https://doi.org/10.1046/j.1365-2419.2001.00152.x

Lynn, R. J., & Simpson, J. J. (1987). The California Current System: The seasonal variability of its physical characteristics. *Journal of Geophysical Research: Oceans*, *92*(C12), 12947-12966. https://doi.org/10.1029/JC092iC12p12947

Mackas, D. L., Thomson, R. E., & Galbraith, M. (2001). Changes in the zooplankton community of the British Columbia continental margin, 1985-1999, and their covariation with oceanographic conditions. *Canadian Journal of Fisheries and Aquatic Sciences*, *58*(4), 685-702. https://doi.org/10.1139/f01-009

MacKenzie, B. R., & Leggett, W. C. (1991). Quantifying the contribution of small-scale turbulence to the encounter rates between larval fish and their zooplankton prey: effects of wind and tide. *Marine Ecology Progress Series*, *73*(2), 149-160. https://www.int-res.com/articles/meps/73/m073p149.pdf

MacKenzie, B. R., Miller, T. J., Cyr, S., & Leggett, W. C. (1994). Evidence for a dome-shaped relationship between turbulence and larval fish ingestion rates. *Limnology and Oceanography, 39*(8), 1790-1799. https://doi.org/10.4319/lo.1994.39.8.1790

Malick, M. J., Adkison, M. D., & Wertheimer, A. C. (2009). Variable effects of biological and environmental processes on coho salmon marine survival in Southeast Alaska. *Transactions of the American Fisheries Society*, *138*(4), 846-860. https://doi.org/10.1577/T08-177.1

Malick, M. J., Cox, S. P., Peterman, R. M., Wainwright, T. C., & Peterson, W. T. (2015). Accounting for multiple pathways in the connections among climate variability, ocean processes, and coho salmon recruitment in the Northern California Current. *Canadian Journal of Fisheries and Aquatic Sciences*, *72*(10), 1552-1564. https://doi.org/10.1139/cjfas-2014-0509

Malick, M. J., Cox, S. P., Mueter, F. J., Dorner, B., & Peterman, R. M. (2017). Effects of the North Pacific Current on the productivity of 163 Pacific salmon stocks. *Fisheries Oceanography*, *26*(3), 268-281. https://doi.org/10.1111/fog.12190

Malick, M. J., Hunsicker, M. E., Haltuch, M. A., Parker-Stetter, S. L., Berger, A. M., & Marshall, K. N. (2020). Relationships between temperature and Pacific hake distribution

vary across latitude and life-history stage. *Marine Ecology Progress Series*, *639*, 185-197. DOI: https://doi.org/10.3354/meps13286

Mantua, N. J., Hare, S. R., Zhang, Y., Wallace, J. M., & Francis, R. C. (1997). A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society*, *78*(6), 1069-1080. https://doi.org/10.1175/1520-0477(1997)078<1069:APICOW>2.0.CO;2

Matarese, A. C., Kendall Jr., A. W., Blood, D. M., & Vinter, B. M. (1989). Laboratory guide to early life history stages of northeast Pacific fishes. U.S. Department of Commerce, NOAA Technical Report. NMFS 80, 632 pp.

McFarlane, G. A., & Beamish, R. J. (1992). Climatic influence linking copepod production with strong year-classes in sablefish, *Anoplopoma fimbria*. Canadian Journal of Fisheries and Aquatic Sciences, 49, 743-753. https://doi.org/10.1139/f92-083

Mendelssohn, R., Schwing, F. B., & Bograd, S. J. (2003). Spatial structure of subsurface temperature variability in the California Current, 1950-1993. *Journal of Geophysical Research: Oceans*, *108*(C3). https://doi.org/10.1029/2002JC001568

Moore, A. M., Jacox, M. G., Crawford, W. J., Laughlin, B., Edwards, C. A., & Fiechter, J. (2017). The impact of the ocean observing system on estimates of the California Current Circulation spanning three decades. *Progress in Oceanography*, *156*, 41-60. https://doi.org/10.1016/j.pocean.2017.05.009

Myers, R. A. (1998). When do environment–recruitment correlations work? *Reviews in Fish Biology and Fisheries*, *8*(3), 285-305. https://doi.org/10.1023/A:1008828730759

Nelson, M. O., & Larkins, H. A. (1970). Distribution and biology of Pacific hake: a synopsis. In: Pacific hake, p. 23-33. U.S. Fish and Wildlife Service, Circular 332. https://spo.nmfs.noaa.gov/sites/default/files/legacy-pdfs/CIRC332.pdf

Neveu, E., Moore, A. M., Edwards, C. A., Fiechter, J., Drake, P., Crawford, W. J., ... & Nuss, E. (2016). An historical analysis of the California Current circulation using ROMS 4D-Var: System configuration and diagnostics. *Ocean Modelling*, *99*, 133-151. https://doi.org/10.1016/j.ocemod.2015.11.012

Owen, R. W. (1980). Eddies of the California Current System: Physical and Ecological Characteristics. In: *2nd California Islands Multidisciplinary Symposium*. 1978. 237-263. National Park Service. http://hdl.handle.net/10139/2881

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

Peterman, R. M., & Bradford, M. J. (1987). Wind speed and mortality rate of a marine fish, the northern anchovy (*Engraulis mordax*). *Science*, *235*(4786), 354-356.

DOI: 10.1126/science.235.4786.354

Peterson, W. T. (2009). Copepod species richness as an indicator of longterm changes in the coastal ecosystem of the northern *California Current. California Cooperative Oceanic Fisheries Investigations Reports*, *50*, 73-81.

Peterson, W. T., & Keister, J. E. (2003). Interannual variability in copepod community composition at a coastal station in the northern California Current: a multivariate approach. *Deep Sea Research Part II: Topical Studies in Oceanography*, *50*(14-16), 2499-2517.

Phillips, A. J., Ralston, S., Brodeur, R. D., Auth, T. D., Emmett, R. L., Johnson, C., & Wespestad, V. G. (2007). Recent pre-recruit Pacific hake (*Merluccius productus*) occurrences in the northern California Current suggest a northward expansion of their spawning area. *California Cooperative Oceanic Fisheries Investigations Report*, 48, 215-229.

Phillips, E. M. (2022). Spatiotemporal variability of euphausiids in the California Current Ecosystem: Insights from a recently developed time series. *ICES Journal of Marine Science*. https://doi.org/10.1093/icesjms/fsac055

Pörtner, H. O., Berdal, B., Blust, R., Brix, O., Colosimo, A., De Wachter, B., ... & Zakhartsev, M. (2001). Climate induced temperature effects on growth performance, fecundity and recruitment in marine fish: developing a hypothesis for cause and effect relationships in Atlantic cod (*Gadus morhua*) and common eelpout (*Zoarces viviparus*). *Continental Shelf Research*, *21*(18-19), 1975-1997. https://doi.org/10.1016/S0278-4343(01)00038-3

Pozo Buil, M., Jacox, M. G., Fiechter, J., Alexander, M. A., Bograd, S. J., Curchitser, E. N., Edwards, C. A., Rykaczewski, R. R., & Stock, C. A. (2021). A dynamically downscaled ensemble of future projections for the California Current System. *Frontiers in Marine Science*, *8*, p.324. https://doi.org/10.3389/fmars.2021.612874

Reiss, C. S., Checkley Jr, D. M., & Bograd, S. J. (2008). Remotely sensed spawning habitat of Pacific sardine (*Sardinops sagax*) and Northern anchovy (*Engraulis mordax*) within the California Current. *Fisheries Oceanography*, *17*(2), 126-136. https://doi.org/10.1111/j.1365-2419.2008.00469.x

Ressler, P. H., Holmes, J. A., Fleischer, G. W., Thomas, R. E., & Cooke, K. C. (2007). Pacific hake, *Merluccius productus*, Autecology: a timely review. *Marine Fisheries Review*, *69*(1), 1.

Rijnsdorp, A. D., Berghahn, R., Miller, J. M., & Van der Veer, H. W. (1995). Recruitment mechanisms in flatfish: what did we learn and where do we go? *Netherlands Journal of Sea Research*, *34*(1-3), 237-242. https://doi.org/10.1016/0077-7579(95)90031-4

Rodgveller, C. J., Stark, J. W., Echave, K. B. & Hulson, P. J. F. (2016). Age at maturity, skipped spawning, and fecundity of female sablefish (*Anoplopoma fimbria*) during the spawning season. *Fishery Bulletin*, *114*(1).

Roughgarden, J., Pennington, J. T., Stoner, D., Alexander, S., & Miller, K. (1991). Collisions of upwelling fronts with the interdidal zone: the cause of recruitment pulses in barnacle populations of central California. *Acta oecologica, 12*(1), 35-51.

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Saha, S., Moorthi, S., Pan, H. L., Wu, X., Wang, J., Nadiga, S., ... & Goldberg, M. (2010). The NCEP climate forecast system reanalysis. *Bulletin of the American Meteorological Society*, *91*(8), 1015-1058. https://doi.org/10.1175/2010BAMS3001.1

Sakuma, K. M., & Ralston, S. (1997). Vertical and horizontal distribution of juvenile Pacific whiting (*Merluccius productus*) in relation to hydrography off California. *California Cooperative Oceanic Fisheries Investigations Report*, *38*, 137-146.

Sampson, D. B., Hamel, O. S., Bosley, K., Budrick, J., Cronin-Fine, L., Hillier, L. K., Hinton, K. E., Krigbaum, M. J., Miller, S., Privitera-Johnson, K. M., Ramey, K., Rodomsky, B. T., Solinger, L. K., & Whitman, A. D. (2017). 2017 Assessment Update for the US West Coast Stock of Arrowtooth Flounder. Pacific Fishery Management Council, Portland, OR. Available from http://www.pcouncil.org/groundfish/stock-assessments/

Sánchez, F., & Gil, J. (2000). Hydrographic mesoscale structures and Poleward Current as a determinant of hake (*Merluccius merluccius*) recruitment in southern Bay of Biscay. *ICES journal of Marine Science*, *57*(1), 152-170. https://doi.org/10.1006/jmsc.1999.0566

Schirripa, M. J., & Colbert, J. J. (2006). Interannual changes in sablefish (*Anoplopoma fimbria*) recruitment in relation to oceanographic conditions within the California Current System. *Fisheries Oceanography*, 15, 25-36. https://doi.org/10.1111/j.1365-2419.2005.00352.x

Schweigert, J. F., Hay, D. E., Therriault, T. W., Thompson, M., & Haegele, C. W. (2009). Recruitment forecasting using indices of young-of-the-year Pacific herring (*Clupea pallasi*) abundance in the Strait of Georgia (BC). *ICES journal of Marine Science, 66*, 1681-1687. https://doi.org/10.1093/icesjms/fsp182

Shanks, A. L., & Morgan, S. G. (2018). Testing the intermittent upwelling hypothesis: upwelling, downwelling, and subsidies to the intertidal zone. *Ecological Monographs*, *88*(1), 22-35. https://doi.org/10.1002/ecm.1281

Siedlecki, S. A., Banas, N. S., Davis, K. A., Giddings, S., Hickey, B. M., MacCready, P., Connolly, T., & Geier, S. (2015). Seasonal and interannual oxygen variability on the Washington and Oregon continental shelves, *Journal of Geophysical Research: Oceans, 120,* 608-633. https://doi.org/10.1002/2014JC010254

Siedlecki, S. A., Kaplan, I. C., Hermann, A. J., Nguyen, T. T., Bond, N. A., Newton, J. A., … & Feely, R. A. (2016). Experiments with seasonal forecasts of ocean conditions for the northern region of the California Current upwelling system. *Scientific Reports*, *6*, 27203. https://doi.org/10.1038/srep27203

Smith, P. E. (1995). Development of the population biology of the Pacific hake, *Merluccius productus*. *California Cooperative Oceanic Fisheries Investigations Report*, *36*, 144-152.

Smith, B. D., McFarlane, G. A., & Saunders, M. W. (1990). Variation in Pacific hake (*Merluccius productus*) summer length-at-age near southern Vancouver Island and its relationship to fishing and oceanography. *Canadian Journal of Fisheries and Aquatic Sciences, 47*(11), 2195-2211. https://doi.org/10.1139/f90-244

Sogard, S. M., Berkeley, S. A., & Fisher, R. (2008). Maternal effects in rockfishes Sebastes spp.: a comparison among species. *Marine Ecology Progress Series*, *360*, 227-236. https://doi.org/10.3354/meps07468

Stauffer, G. D. (1985). Biology and life history of the coastal stock of Pacific whiting, *Merluccius productus*. *Marine Fisheries Review*, *47*(2), 2-7. https://spo.nmfs.noaa.gov/sites/default/files/pdf-content/MFR/mfr472/mfr4722.pdf

Strub, P. T., & James, C. (2000). Altimeter-derived variability of surface velocities in the California Current System: 2. Seasonal circulation and eddy statistics. *Deep Sea Research Part II: Topical Studies in Oceanography*, *47*(5-6), 831-870. https://doi.org/10.1016/S0967-0645(99)00129-0

Sumida, B. Y., & Moser, H. G. (1980). Food and feeding of Pacific hake larvae, *Merluccius productus*, off southern California and northern Baja California. *California Cooperative Oceanic Fisheries Investigations Report, 21,* 161-166. https://calcofi.com/publications/calcofireports/v21/Vol_21_Sumida___Moser.pdf

Sundby, S. (1991). Factors affecting the vertical distribution of eggs. *ICES Journal of Marine Science*, *192*, 33-38.

Swartzman, G. (2001). Spatial patterns of Pacific hake (*Merluccius productus*) shoals and euphausiid patches in the California Current ecosystem. *Spatial Processes and Management of Marine Populations*, 495-512.

Sydeman, W. J., Thompson, S. A., Field, J. C., Peterson, W. T., Tanasichuk, R. W., Freeland, H. J., Bograd, S. J., & Rykaczewski, R. R. (2011). Does positioning of the North Pacific Current affect downstream ecosystem productivity? *Geophysical Research Letters*, *38*(12). https://doi.org/10.1029/2011GL047212

Thompson, R. E. (1981). Oceanography of the British Columbia coast. *Canadian Special Publication of Fisheries and Aquatic Sciences*, *56*. 291 p.

Tillman, M. F. (1968). Tentative recommendations for management of the coastal fishery of Pacific hake, based on a simulation study of the effects of fishing upon a virgin population (Doctoral dissertation, MS thesis), University of Washington, Seattle, WA.

Tommasi, D., Stock, C. A., Pegion, K., Vecchi, G. A., Methot, R. D., Alexander, M. A. & Checkley Jr., D. M. (2017). Improved management of small pelagic fisheries through seasonal climate prediction. *Ecological Applications*, 27(2), 378-388. https://doi.org/10.1002/eap.1458

Tolimieri, N., & Levin, P. S. (2005). The Roles of Fishing and Climate in the Population Dynamics of Bocaccio Rockfish. *Ecological Applications*, 15, 458-468. https://doi.org/10.1890/03-5376

Tolimieri, N., Haltuch, M. A., Lee, Q., Jacox, M. G., & Bograd, S. J. (2018). Oceanographic drivers of sablefish recruitment in the California Current. *Fisheries Oceanography*, *27*(5), 458-474. https://doi.org/10.1111/fog.12266

Trenberth, K. E. (1997). The definition of El Niño. *Bulletin of the American Meteorological Society*, *78*(12), 2771-2778. https://doi.org/10.1175/1520-0477(1997)078<2771:TDOENO>2.0.CO;2

Turley, B. D., & Rykaczewski, R. R. (2019). Influence of wind events on larval fish mortality rates in the southern California Current Ecosystem. *Canadian Journal of Fisheries and Aquatic Sciences*, *76*(12), 2418-2432. https://doi.org/10.1139/cjfas-2018-0458

Van Der Kraak, G., & Pankhurst, N. W. (1997). Temperature effects on the reproductive performance of fish. In: '*Global Warming: Implications for Freshwater and Marine Fish*'. Wood, C. M., & McDonald, D. G. (Eds). pp. 159-176.

Van der Veer, H. W., Berghahn, R., Miller, J. M., & Rijnsdorp, A. D. (2000). Recruitment in flatfish, with special emphasis on North Atlantic species: progress made by the Flatfish Symposia. *ICES Journal of Marine Science*, *57*(2), 202-215. https://doi.org/10.1006/jmsc.1999.0523

Van Holmes, C. (2007). Mean Spring and Fall Upwelling Transition Dates off the Oregon and Washington Coasts. http://www.cbr.washington.edu/sites/default/files/papers/trans.cbrmean.pdf

Vastano, A. C., Incze, L. S., & Schumacher, J. D. (1992). Observation and analysis of fishery processes: larval pollock at Shelikof Strait, Alaska. *Fisheries Oceanography*, *1*(1), 20-31. https://doi.org/10.1111/j.1365-2419.1992.tb00022.x

Veneziani, M., Edwards, C. A., Doyle, J. D., & Foley, D. (2009). A central California coastal ocean modeling study: 1. Forward model and the influence of realistic versus climatological forcing. *Journal of Geophysical Research*, *114*, C04015.

https://doi.org/10.1029/2008JC004774

Venrick, E. L., Bograd, S. J., Checkley, D. A., Durazo, R. E., Gaxiola-Castro, G. I., Hunter, J. O., Huyer, A. D, Hyrenbach, K. D., Laveniegos, B. E., Mantyla, A. R., & Schwing, F. B. (2003). The state of the California Current, 2002-2003: Tropical and subarctic influences vie for dominance. *California Cooperative Oceanic Fisheries Investigations Report*, *44*, 28-60.

Vestfals, C. D., Ciannelli, L., Duffy-Anderson, J. T., & Ladd, C. (2014). Effects of seasonal and interannual variability in along-shelf and cross-shelf transport on groundfish recruitment in the eastern Bering Sea. *Deep Sea Research Part II: Topical Studies in Oceanography, 109*, 190-203. https://doi.org/10.1016/j.dsr2.2013.09.026

Ware, D. M., & McFarlane, G. A. (1986). Relative impact of Pacific hake, sablefish and Pacific cod on west coast of Vancouver Island herring stocks. *International North Pacific Fisheries Commission Bulletin*, *47*, 67-78.

Ware, D. M., & McFarlane, G. A. (1995). Pelagic community interactions in the Vancouver Island upwelling system. *Climate Change and Northern Fish Populations, 121*, 509-521. Beamish, R. J. (Ed.). NRC Research Press.

Wilderbuer, T. K., Hollowed, A. B., Ingraham Jr, W. J., Spencer, P. D., Conners, M. E., Bond, N. A., & Walters, G. E. (2002). Flatfish recruitment response to decadal climatic variability and ocean conditions in the eastern Bering Sea. *Progress in Oceanography, 55*(1-2), 235-247. https://doi.org/10.1016/S0079-6611(02)00081-2

Woodbury, D., Hollowed, A. B., & Pearce, J. A. (1995). Interannual variation in growth rates and back-calculated spawn dates of juvenile Pacific hake (*Merluccius productus*). *Belle W. Baruch Library in Marine Science*, *19*, 481-496.

Zabel, R. W., Levin, P. S., Tolimieri, N., & Mantua, N. J. (2011). Interactions between climate and population density in the episodic recruitment of bocaccio, *Sebastes paucispinis*, a Pacific rockfish. *Fisheries Oceanography* 20, 294-304. https://doi.org/10.1111/j.1365-2419.2011.00584.x

Tables and Figures

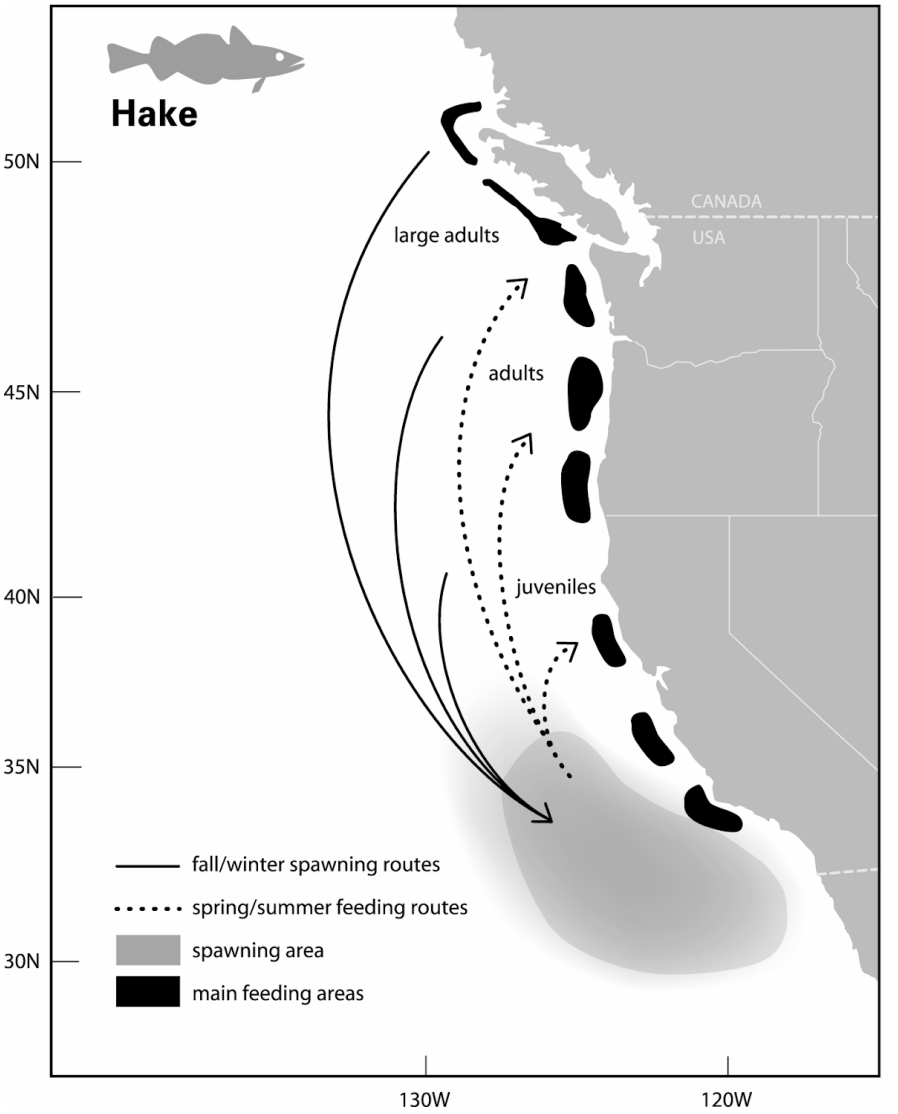


FIGURE 1: Hypothesized movement and spatial population structure of Pacific hake (*Merluccius productus*), reproduced from Agostini et al. (2006).

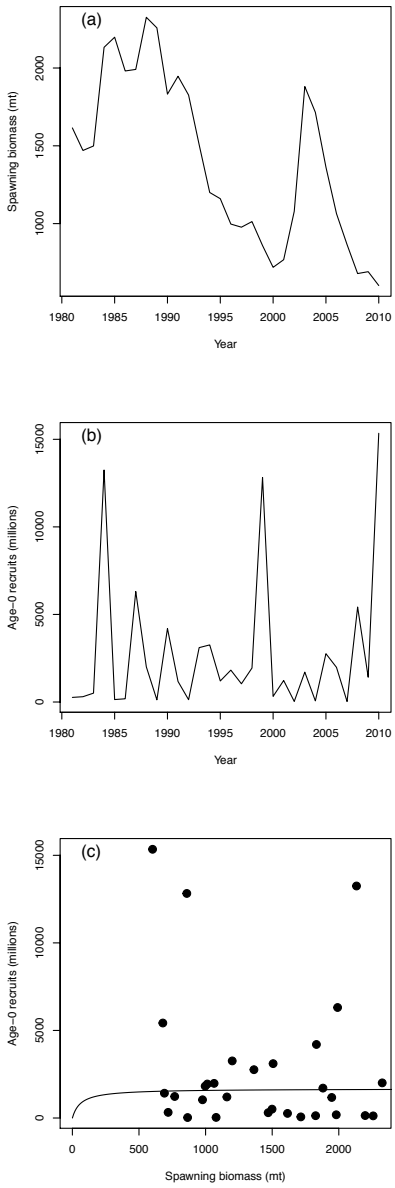


FIGURE 2: Derived quantities of Pacific hake (*Merluccius productus*) from the 2020 stock assessment (Grandin et al., 2020) for 1981 – 2010: (a) spawning stock biomass (SSB) in metric tons (mt), (b) age-0 recruits in millions, and (c) the stock-recruitment relationship supported in the assessment (line) versus observed data (points). Values for unfished recruitment (*R0*) = 1600, steepness (*h*) = 0.854, and unfished female spawning biomass (*B0*, thousand t) = 1,385 were obtained from Table 27 in the 2020 assessment.

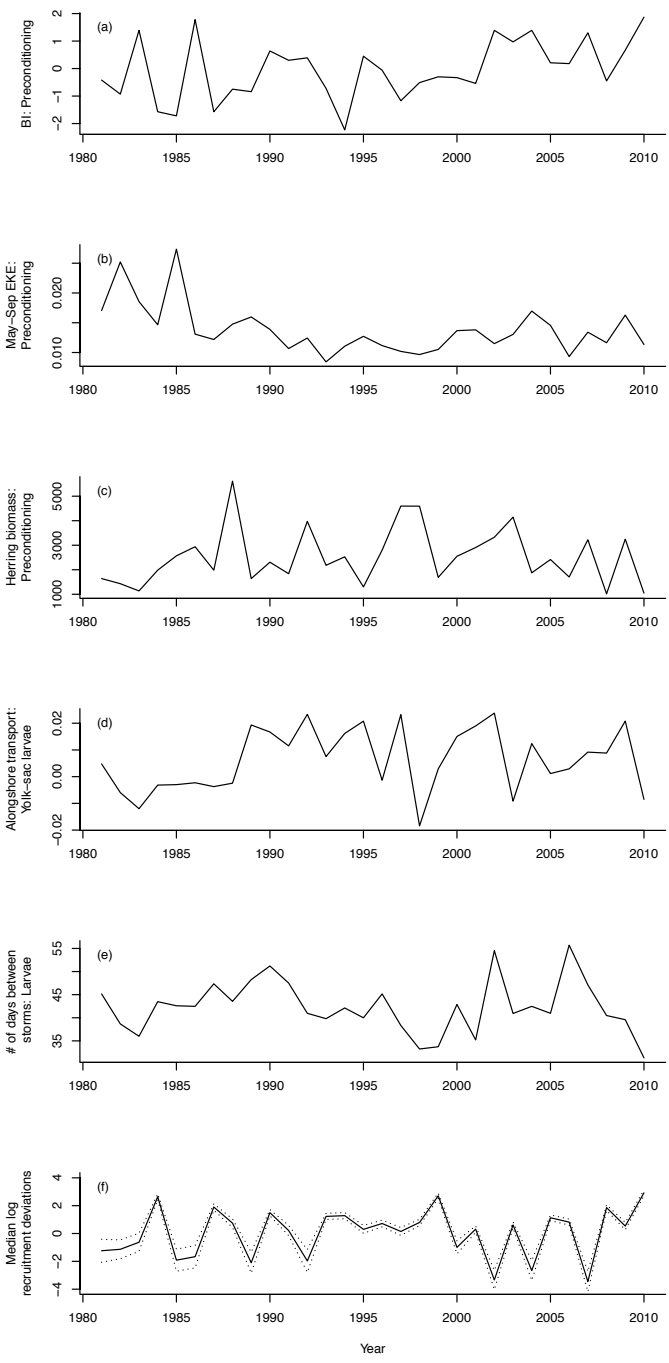
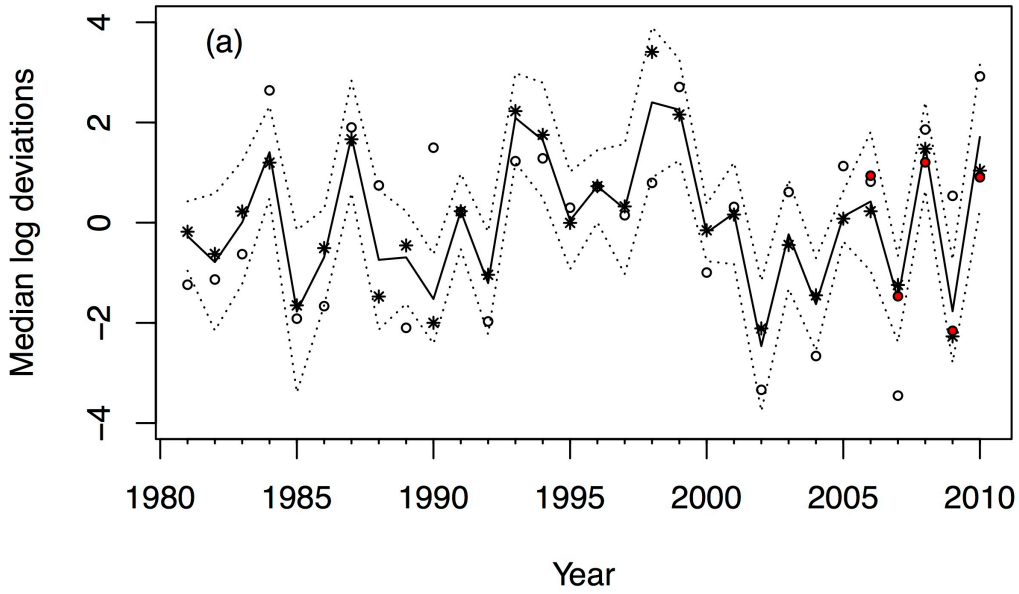


FIGURE 3: Time series of independent predictor variables in the AIC-best model of Pacific hake (*Merluccius productus*) recruitment: (a) bifurcation index (BI), (b) May – September eddy kinetic energy (EKE) between 34.5° and 42.5°N, and (c) Pacific herring (*Clupea pallasii*) biomass off the west coast of Canada during the adult female preconditioning stage, (d) alongshore transport during the yolk-sac larval stage, and (e) number of days between storm events during the first-feeding larval stage compared to (f) median log recruitment deviations from the 2020 Pacific hake stock assessment (Grandin et al., 2020). Dotted lines are ±1.0 standard deviation (*SD*).



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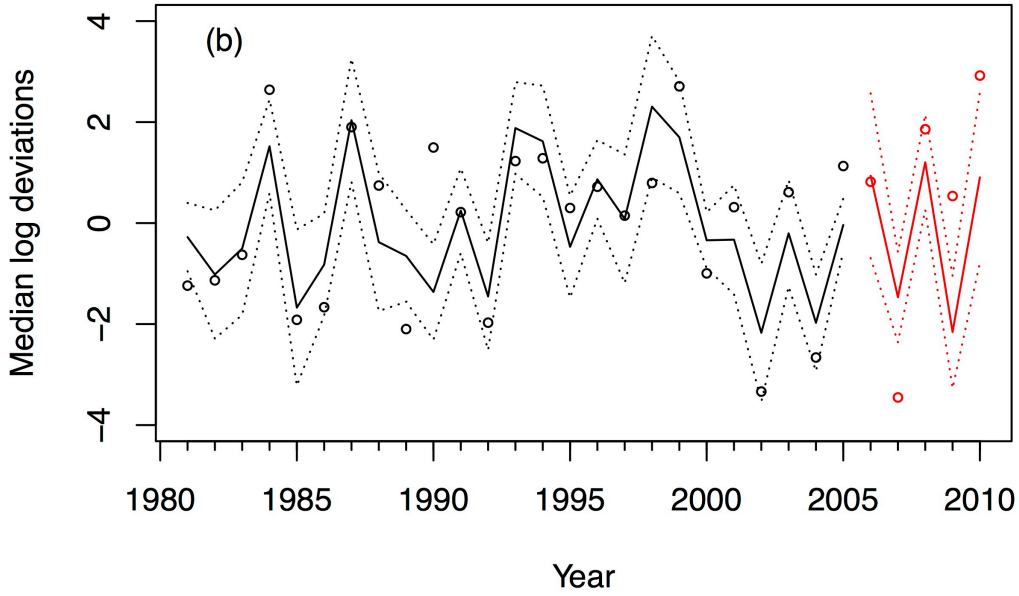

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1765 FIGURE 4: (a) Fit of the AIC-best model (R^2 = 0.59) to the estimated median log recruitment
1766 deviations from the 2020 Pacific hake (*Merluccius productus*) stock assessment. Solid line is the
1767 predicted recruitment deviations from the full time series. Dotted lines = 95% confidence limits.
1768 Open circles are the median log recruitment deviations from the 2020 Pacific hake assessment.
1769 Stars are predicted values from jackknife analysis removing individual years one at a time. Red
1770 points are predictions from fitting the AIC-best model to 1981–2005 and then predicting 2006–
1771 2010. (b) Fit of the AIC-best model from jackknife-refitting the 1981–2005 data (R^2 = 0.63).
1772 Open circles are the log recruitment deviations from the 2020 Pacific hake assessment. Solid
1773 black line is the predicted recruitment deviations from the model for 1981–2005; solid red line is
1774 the predicted recruitment deviations for 2006–2010 based on the model for 1981–2005. Dotted
1775 lines = 95% confidence limits.

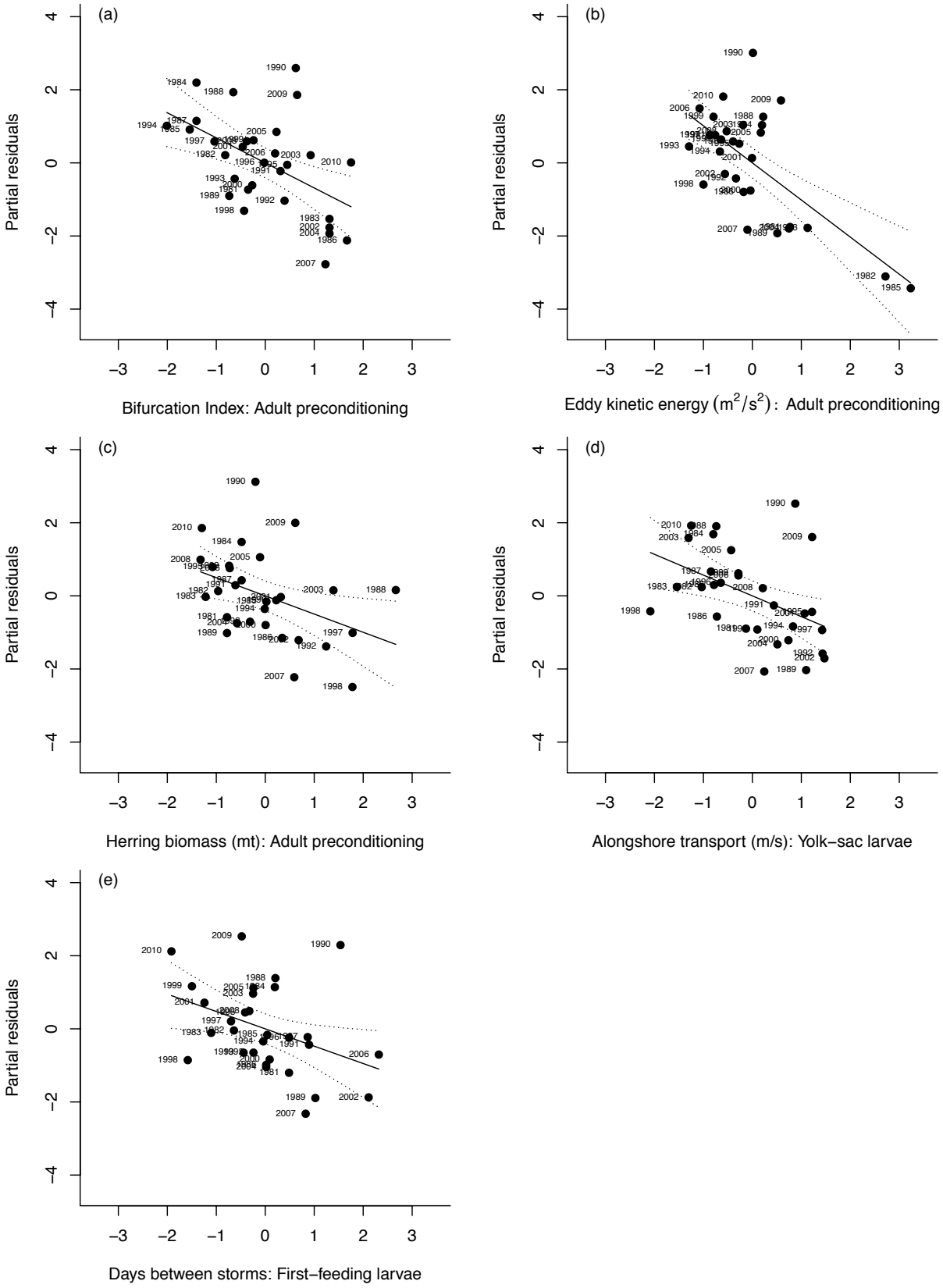
(a)
Partial residuals
Bifurcation Index: Adult preconditioning
(b)
Partial residuals
Eddy kinetic energy (m²/s²): Adult preconditioning
(c)
Partial residuals
Herring biomass (mt): Adult preconditioning
(d)
Partial residuals
Alongshore transport (m/s): Yolk−sac larvae
(e)
Partial residuals
Days between storms: First−feeding larvae

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FIGURE 5: Partial residual plots of predictor variables in the the AIC-best model of Pacific hake (*Merluccius productus*) recruitment: (a) the bifurcation index, (b) May – September eddy kinetic energy (EKE) between 34.5° and 42.5°N, and (c) Pacific herring (*Clupea pallasii*) biomass off the west coast of Canada during the adult female preconditioning stage, (d) alongshore transport during the yolk-sac larval stage, and (e) number of days between storm events during the first-feeding larval stage.

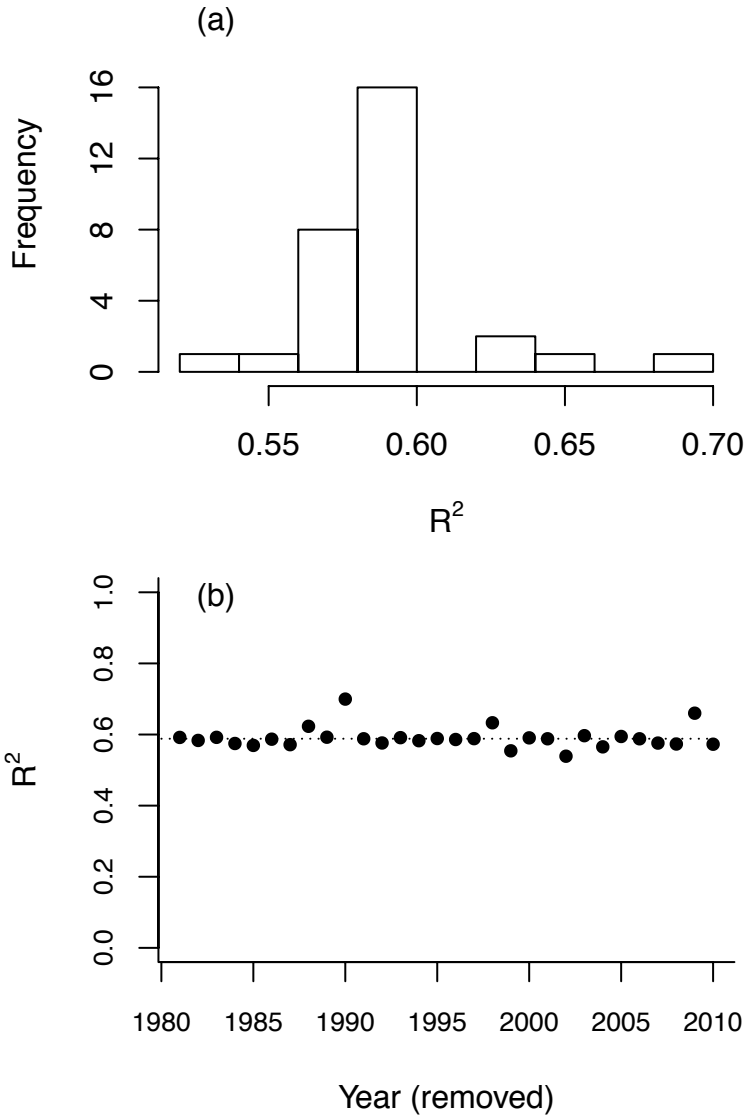

FIGURE 6: Results of jackknife resampling showing the distribution of R^2 values. (a) Frequency distribution of R^2 values, and (b) R^2 for when the indicated year was removed from the model.

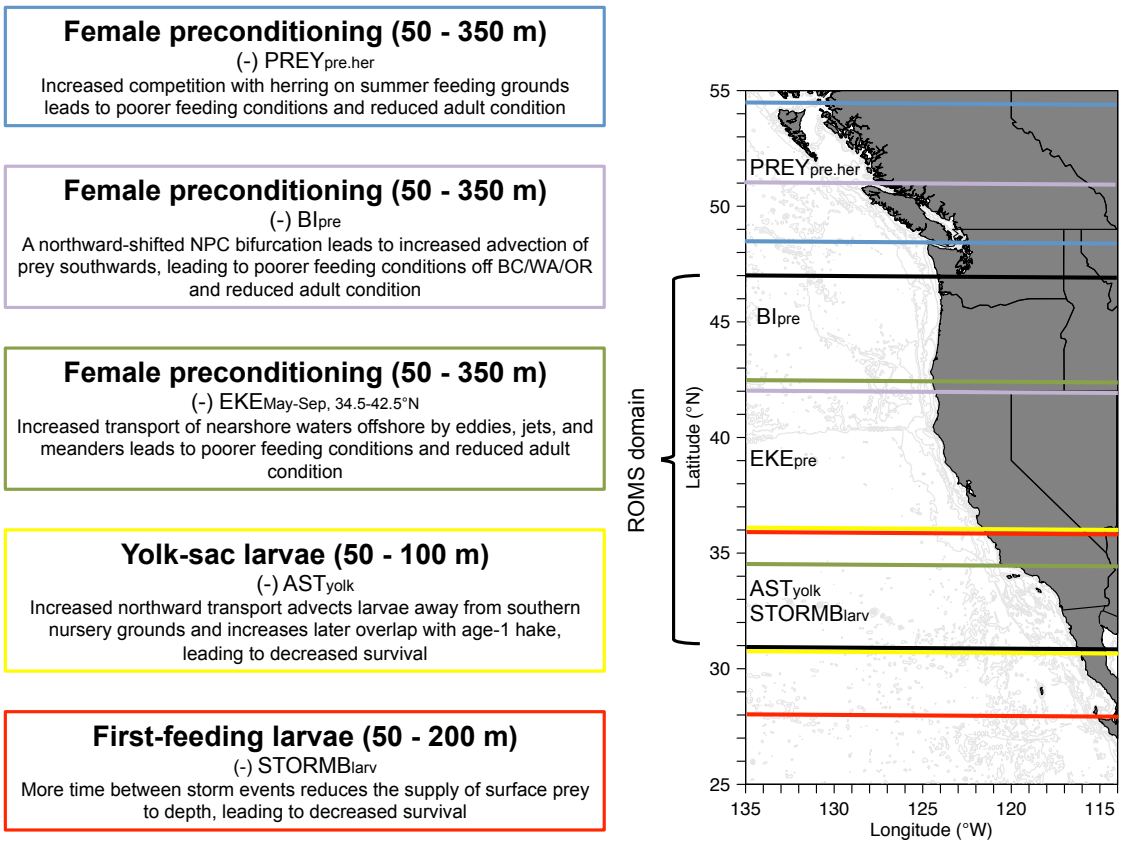

FIGURE 7: Conceptual model for Pacific hake (*Merluccius productus*) showing the environmental drivers at specific life-history stages that lead to higher recruitment. Signs in parentheses indicate the partial correlation of each term with residuals from the Pacific hake stock-recruitment relationship. See Figure 4 for plots of these relationships. Boundary lines correspond to the region over which the predictor was calculated.

TABLE 1: Pacific hake (*Merluccius productus*) conceptual life history model showing spatiotemporally-explicit hypotheses by life stage related to factors (covariates) affecting survival. The adult female preconditioning through yolk-sac larval stages are shown here. For full conceptual life history model, see TABLE A1.

Ho Number	Life-history stage	Time period	Hypothesis	Stage	Covariates	Depth	Longitudinal extent	Latitudinal extent	Source
H1	Preconditioning	Apr - Oct (Year 0)	(H1) Higher temperature increases food demand resulting in lower egg production, egg quality, or probability of spawning and lowers recruitment	$TEMP_{pre}$	Mean temperature	50 - 350 m	Shelf break, between 100 - 2000 m isobaths	42° - 47°N	ROMS
H2			(H2) As (H1), but degree days, not mean temperature	DD_{pre}	Degree days	50 - 350 m	Shelf break, between 100 - 2000 m isobaths	42° - 47°N	ROMS
H3			(H3) Higher coastal upwelling leads to increased productivity, better condition, higher egg production, egg quality, or probability of spawning and increases recruitment	$UW_{pre.c}$	Coastal upwelling (CUTI)	Base of mixed layer		41.5° - 47.5°N	Jacox et al. (2018), https://oceanview.pfeg.noaa.gov
H4			(H4) As (H3), but biologically effective upwelling	$UW_{pre.b}$	Biologicially effective upwelling (BEUTI)	Base of mixed layer	0 - 75 km offshore	41.5° - 47.5°N	Jacox et al. (2018), https://oceanview.pfeg.noaa.gov
H5			(H5) Food availability affects energy allocation to reproduction with higher recruitment when more prey are available during the preconditioning period	$PREY_{pre.her}$ $PREY_{pre.juvhake}$	Index of age-0 and age-1 Pacific hake biomass, and age-2 Pacific herring biomass				Stock assessments
H6			(H6) Timing of availability of food affects energy allocation to reproduction with higher recruitment when more prey are available during the preconditioning period	$SPTR_{pre}$	Mean date of the spring transition from downwelling-favorable southerly winds to upwelling-favorable northerly winds		125°W	42°N (West of OR/CA border) 45°N (West of Siletz Bay, OR) 48°N (West of La Push, WA)	CBR Mean Method, Van Holmes (2007), http://www.cbr.washington.edu/status/trans
H7	Spawning	Jan - Mar	(H7) Temperature acts as a spawning cue with fish less likely to spawn at high temperature resulting in lower recruitment	$TEMP_{spawn}$	Mean temperature	130 - 500 m	Shelf break, between 100 - 2000 m isobaths	31° - 36°N	ROMS
H8			(H8) As (H7), but degree days, not mean temperature	DD_{spawn}	Degree days	130 - 500 m	Shelf break, between 100 - 2000 m isobaths	31° - 36°N	ROMS
H9	Eggs	Jan - Mar	(H9) Eggs aggregate at base of mixed layer so Mixed Layer Depth may limit how far they rise in the water column affecting later transport	MLD_{eggs}	Mean mixed layer depth (m)		Shelf break, between 100 - 2000 m isobaths	31° - 36°N	ROMS
H10			(H10) Transport to settlement habitat affects recruitment (transport varies with latitude)	$CST_{eggs.s}$ $CST_{eggs.n}$	Net cross-shelf transport	40 - 60 m	Shelf break, between 100 - 2000 m isobaths	31° - 34.5°N 34.5° - 36°N	ROMS
H11			(H11) Increased northward advection away from juvenile nursery areas decreases recruitment	ASTeggs	Net alongshore transport	40 - 60 m	Shelf break, between 100 - 2000 m isobaths	31° - 36°N	ROMS
H12			(H12) Increased northward advection away from juvenile nursery areas decreases recruitment	PU_{eggs}	Strength of the poleward undercurrent	75 - 275 m	Coast to 275 m isobath	32.5° - 33.5°N	ROMS
H13			(H13) Growth/Predation hypothesis: growth rate is faster in warm water leading to reduced time vulnerable to predators	DD_{eggs}	Degree days	40 - 60 m	Shelf break, between 100 - 2000 m isobaths	31° - 36°N	ROMS
H14	Yolk-sac larvae	Jan - Apr	(H14) Larvae aggregate at base of mixed layer so Mixed Layer Depth may limit how far they rise in the water column affecting later transport	MLD_{yolk}	Mean mixed layer depth (m)		Shelf break, between 100 - 2000 m isobaths	31° - 36°N	ROMS
H15			(H15) Transport to settlement habitat affects recruitment (transport varies with latitude)	$CST_{yolk.s}$ $CST_{yolk.n}$	Net cross-shelf transport	50 - 100 m	Shelf break, between 100 - 2000 m isobaths	31° - 34.5°N 34.5° - 36°N	ROMS
H16			(H16) Increased northward advection away from juvenile nursery areas decreases recruitment	ASTyolk	Net alongshore transport				ROMS
H17			(H17) Increased northward advection away from juvenile nursery areas decreases recruitment	PU_{yolk}	Strength of the poleward undercurrent	75 - 275 m	Coast to 275 m isobath	32.5° - 33.5°N	ROMS
H18			(H18) Growth/Predation hypothesis: growth rate is faster in warm water leading to reduced time vulnerable to predators	DD_{yolk}	Degree days	50 - 100 m		31° - 36°N	ROMS

TABLE 2: The set of top candidate models (those with ΔAICc < 3.0) that were used to identify factors influencing Pacific hake (*Merluccius productus*) early life history survival and recruitment. Models are ordered by ΔAICc, so the overall best model, as supported by the data, is identified as Model 1.

Model															R^2	ΔAICc
1	AST_{yolk}	BI_{pre}	-	$EKE_{pre.MS.c}$	-	-	-	-	$PREY_{pre.her}$	-	-	$STORMB_{larv}$	-	-	0.59	0.00
2	AST_{yolk}	BI_{pre}	-	$EKE_{pre.MS.c}$	-	-	-	-	$PREY_{pre.her}$	-	-	-	-	-	0.52	1.03
3	-	-	$CALM_{larv}$	$EKE_{pre.MS.c}$	$PRED_{age0.age1.hake}$	-	-	-	-	-	-	-	-	$UW_{pre.cu}$	0.51	1.70
4	AST_{yolk}	BI_{pre}	-	$EKE_{pre.MS.c}$	-	-	-	-	-	-	-	$STORMB_{larv}$	-	-	0.51	1.75
5	-	-	$CALM_{larv}$	$EKE_{pre.MS.c}$	-	-	-	-	-	-	-	-	-	$UW_{pre.cu}$	0.46	1.79
6	AST_{yolk}	BI_{pre}	-	$EKE_{pre.MS.c}$	-	-	PDO_{pre}	-	$PREY_{pre.her}$	-	-	-	-	-	0.56	2.05
7	AST_{yolk}	Bipre	-	$EKE_{pre.MS.c}$	-	-	-	-	-	-	-	-	-	-	0.45	2.17
8	AST_{yolk}	BI_{pre}	-	$EKE_{pre.MS.c}$	-	$NPGO_{pre.AS}$	-	-	$PREY_{pre.her}$	-	-	-	-	-	0.56	2.19
9	-	-	$CALM_{larv}$	$EKE_{pre.MS.c}$	$PRED_{age0.age1.hake}$	-	-	-	-	-	-	-	$STORMD_{larv}$	$UW_{pre.cu}$	0.56	2.20
10	AST_{yolk}	BI_{pre}	-	$EKE_{pre.MS.c}$	-	-	PDO_{pre}	-	-	-	-	-	-	-	0.50	2.23
11	AST_{yolk}	BI_{pre}	-	$EKE_{pre.MS.c}$	-	-	-	-	$PREY_{pre.her}$	-	$SPTR_{pre}$	-	-	-	0.55	2.41
12	-	BI_{pre}	-	$EKE_{pre.MS.c}$	-	-	-	-	$PREY_{pre.her}$	-	-	$STORMB_{larv}$	-	-	0.50	2.59
13	AST_{yolk}	BI_{pre}	-	$EKE_{pre.MS.c}$	-	-	-	-	$PREY_{pre.her}$	-	-	-	$STORMD_{larv}$	-	0.55	2.59
14	AST_{yolk}	BI_{pre}	$CALM_{larv}$	$EKE_{pre.MS.c}$	-	-	-	-	$PREY_{pre.her}$	-	-	-	-	-	0.55	2.61
15	-	-	-	$EKE_{pre.MS.c}$	-	-	-	$PREY_{latelarv.eup}$	-	-	-	$STORMB_{larv}$	$STORMD_{larv}$	$UW_{pre.cu}$	0.55	2.88
16	-	-	$CALM_{larv}$	$EKE_{pre.MS.c}$	-	-	-	-	-	SPTR	-	-	-	$UW_{pre.cu}$	0.49	2.94

Note: Abbreviations: AS, April – September; AST, alongshore transport; BI, bifurcation index; c, central region from 34.5 – 42.5°N; CALM, number of calm periods; cu, Coastal Upwelling Transport Index (CUTI); EKE, eddy kinetic energy; larv, first-feeding larval stage; latelarv, late larval stage; MS, May – September; NPGO, North Pacific Gyre Oscillation; PDO, Pacific Decadal Oscillation; pre, preconditioning stage; PREDage0.age1hake, log-transformed predation of age-0 Pacific hake (*Merluccius productus)* by age-1 hake; PREYeup, euphausiids as prey for late larval stages; PREYher, Pacific herring (*Clupea pallasii*) as prey for adult female preconditioning stage; SPTR, timing of spring transition; STORMB, number of days between storm events; STORMD, duration of storm events; UW, upwelling; yolk, yolk-sac larval stage.

TABLE 3: Coefficients for the AIC-best model of Pacific hake (*Merluccius productus*) recruitment (Model 1 in Table 2) showing both raw and standardized (beta) coefficients.

	Coefficient	Bias	SE	Standardized Coefficient	Std Bias	Std SE
Intercept	8.26	0.03	2.05	0.04	0.00	0.23
BI_{pre}	-0.63	-0.02	0.21	-0.69	-0.03	0.23
$EKE_{pre.MS.c}$	-242.70	-0.65	57.34	-1.02	0.00	0.24
$PREY_{pre.her}$	0.00	0.00	0.00	-0.50	0.02	0.23
AST_{yolk}	-47.88	-1.68	20.72	-0.57	-0.02	0.25
$STORMB_{larv}$	-0.08	0.00	0.04	-0.47	-0.01	0.24

Note: Bias and standard error (*SE*) are from bootstrap resampling. Abbreviations: AST, alongshore transport; BI, bifurcation index; c, central region from 34.5 - 42.5°N; CALM, number of calm periods; EKE, eddy kinetic energy; larv, first-feeding larval stage; MS, May – September; pre, preconditioning stage; PREYher, Pacific herring (*Clupea pallasii*) as prey during preconditioning stage; STORMB, number of days between storm events.

TABLE 4: Correlations among variables in the AIC-best model of Pacific hake (*Merluccius productus*) recruitment.

	BI_{pre}	$EKE_{pre.MS.c}$	$PREY_{pre.her}$	AST_{yolk}	$STORMB_{larv}$	VIF
BI_{pre}	-					1.03
$EKE_{pre.MS.c}$	-0.14	-				1.09
$PREY_{pre.her}$	-0.06	-0.17	-			1.04
AST_{yolk}	-0.01	-0.19	0.04	-		1.15
$STORMB_{larv}$	0.02	-0.06	-0.02	0.31	-	1.11

Note: Abbreviations: Abbreviations: AST, alongshore transport; BI, bifurcation index; c, central region from 34.5 - 42.5°N; CALM, number of calm periods; EKE, eddy kinetic energy; larv, first-feeding larval stage; MS, May – September; pre, preconditioning stage; PREYher, Pacific herring (*Clupea pallasii*) as prey during preconditioning stage; STORMB, number of days between storm events; VIF, variance inflation factor.

TABLE 5: Variables included in all candidate models of Pacific hake (*Merluccius productus*) recruitment from jackknife refits of the entire model-fitting process. Bolded variables were those found in the AIC-best model.

Predictor	**Number of times included**	**%**
AST_{yolk}	**25**	**40**
BI	1	2
BI_{pre}	**34**	**55**
$CALM_{larv}$	**23**	**37**
$CST_{larv.s}$	0	0
$CST^2_{larv.s}$	0	0
$CST_{latelarv.s}$	1	2
$CST^2_{latelarv.s}$	1	2
$EKE_{MS.c}$	1	2
$EKE_{pre.MS.c}$	**59**	**95**
$logPRED_{age0.age1.hake}$	5	8
ONI_{AS}	0	0
ONI_{pre}	0	0
$NPGO_{AS}$	1	2
$NPGO_{pre.AS}$	1	2
PDO_{JA}	0	0
PDO_{AS}	0	0
PDO_{pre}	1	2
$PRED_{age0.atf}$	0	0
$PRED_{age0.csl}$	0	0
$PREY_{larv.zp}$	0	0
$PREY_{latelarv.eup}$	6	10
$PREY_{pre.her}$	7	11
SPTR	1	2
$SPTR_{pre}$	0	0
$STORM_{larv}$	1	2
$STORMB_{larv}$	**13**	**21**
$STORMD_{larv}$	4	6
$UW_{pre.cu}$	25	40
Total number of models	62	

Note: Results are the number of years a specific predictor was in the best-fit model (lowest AICc and fewest parameters). Individual years could have more than one candidate model.

Abbreviations: age-0, age-0 pelagic juvenile stage; age1, age-1 pelagic juvenile stage; AS, April – September; AST, alongshore transport; BI, bifurcation index; c, central region from 34.5 - 42.5°N; CALM, number of calm events; CALMB, number of days between calm events; CALMD, duration of calm events; CST, cross-shelf transport at depths of 50 – 300 m; EKE, eddy kinetic energy; eup, euphausiids; JA, January – April; larv, first-feeding larval stage; latelarv, late larval stage; NPGO, North Pacific Gyre Oscillation; ONI, Ocean Niño Index; PDO, Pacific Decadal Oscillation; pre, preconditioning stage; PREDage0.age1.hake; predation of age-0 hake by age-1 hake; PREDage0.atf, predation of age-0 hake by arrowtooth flounder; PREDage0.csl, predation of age-0 hake by California sea lions; PREYlarv.zp, copepods as prey for first-feeding (and late) larvae; PREYlatelarv.eup, euphausiids as prey for late larvae; PREYpre.her, Pacific herring as prey for adult female preconditioning stage; s, southern region from 31.0 °- 34.5°N; SPTR, Julian day of spring transition; STORM, number of storm events; STORMB, number of days between storm events; STORMD, duration of storm events; UW, coastal upwelling; yolk, yolk-sac larval stage; zp, copepod zooplankton.

TABLE 6: Results from completely refitting the model 100 times while jackknife resampling median recruitment deviations from a log-normal distribution using the recruitment deviations and *SD*s from the 2020 Pacific hake (*Merluccius productus*) stock assessment.

Predictor	**Number of jackknifes**	**Number of models**	**%**
AST_{yolk}	**48**	**65**	**41**
BI	0	0	0
BI_{pre}	**54**	**72**	**46**
$CALM_{larv}$	52	70	44
$CST_{larv.s}$	2	2	1
$CST^2_{larv.s}$	1	1	1
$CST_{latelarv.s}$	7	7	4
$CST^2_{latelarv.s}$	3	3	2
$EKE_{MS.c}$	1	1	1
$EKE_{pre.MS.c}$	**87**	**128**	**81**
$logPRED_{age0.age1.hake}$	19	21	13
ONI_{AS}	0	0	0
ONI_{pre}	0	0	0
$NPGO_{AS}$	0	0	0
$NPGO_{pre.AS}$	4	4	3
PDO_{JA}	8	12	8
PDO_{AS}	2	3	2
PDO_{pre}	10	10	6
$PRED_{age0.atf}$	1	1	1
$PRED_{age0.csl}$	0	0	0
$PREY_{larv.zp}$	3	3	2
$PREY_{latelarv.eup}$	7	8	5
$PREY_{pre.her}$	23	27	17
SPTR	9	13	8
$SPTR_{pre}$	2	2	1
$STORM_{larv}$	0	0	0
$STORMB_{larv}$	**21**	**23**	**15**
$STORMD_{larv}$	4	5	3
$UW_{pre.cu}$	48	63	40
Total	100	158	

Note: Each refit iteration could include multiple candidate models (with AICc < 2.0 and the fewest included parameters). Number of jackknives is the number of times the variable was included in one of the candidate models for any jackknife iteration. Number of models is the total number of times the variable was included in a model across all candidate models. Total is the total number of jackknife iterations and the total number of models fit. See Table 5 for an explanation of ROMS parameters. Bold text indicates variables from the AIC-best model.

TABLE 7: The number of times each predictor variable was included in model fits of data (1981 – 2005) across the jackknife resampling procedure.

Predictor	**Times included**	**%**
AST_{yolk}	2	5
BI	0	0
BI_{pre}	23	55
$CALM_{larv}$	10	24
$CST_{larv.s}$	32	76
$CST^2_{larv.s}$	30	71
$CST_{latelarv.s}$	0	0
$CST^2_{latelarv.s}$	0	0
$EKE_{MS.c}$	0	0
$EKE_{pre.MS.c}$	3	7
$logPRED_{age0.age1.hake}$	41	98
ONI_{AS}	4	10
ONI_{pre}	26	62
$NPGO_{AS}$	2	5
$NPGO_{pre.AS}$	4	10
PDO_{JA}	2	5
PDO_{AS}	0	0
PDO_{pre}	1	2
$PRED_{age0.atf}$	14	33
$PRED_{age0.csl}$	2	5
$PREY_{larv.zp}$	0	0
$PREY_{latelarv.eup}$	3	7
$PREY_{pre.her}$	1	2
SPTR	0	0
$SPTR_{pre}$	0	0
$STORM_{larv}$	1	2
$STORMB_{larv}$	0	0
$STORMD_{larv}$	0	0
$UW_{pre.cu}$	6	14

Note: Times included is the number of times the AIC-best model (AICc < 2.0, fewest parameters) included the term. There was only one AIC-best model for each year iteration. See Table 5 for an explanation of ROMS parameters.

Appendices

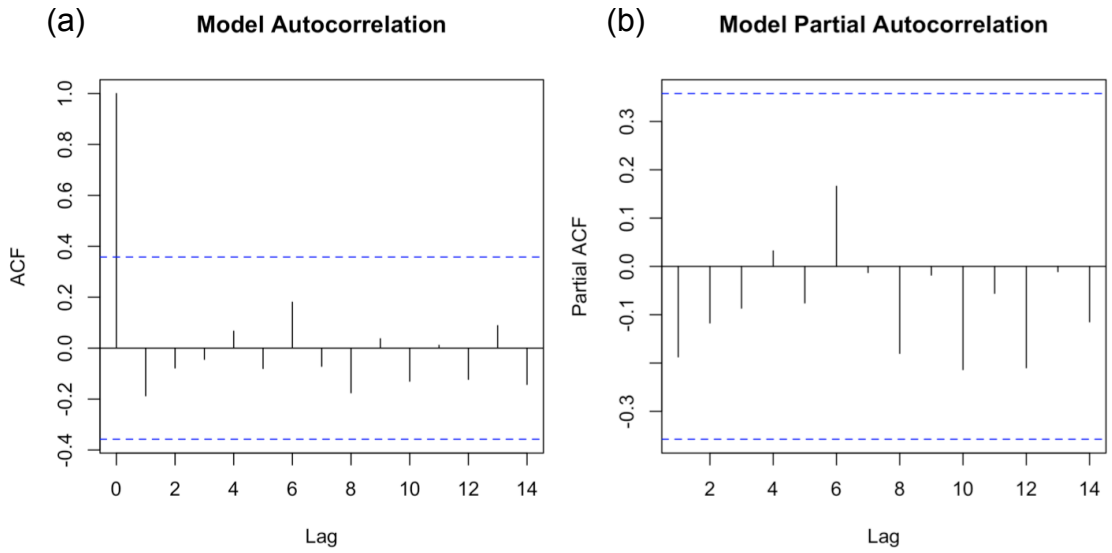

FIGURE A1: Autocorrelation Function (ACF) and Partial Autocorrelation Function (PACF) plots of the residuals for the AIC-best model of Pacific hake (*Merluccius productus*) recruitment. Blue dashed lines indicate the 95% confidence intervals.

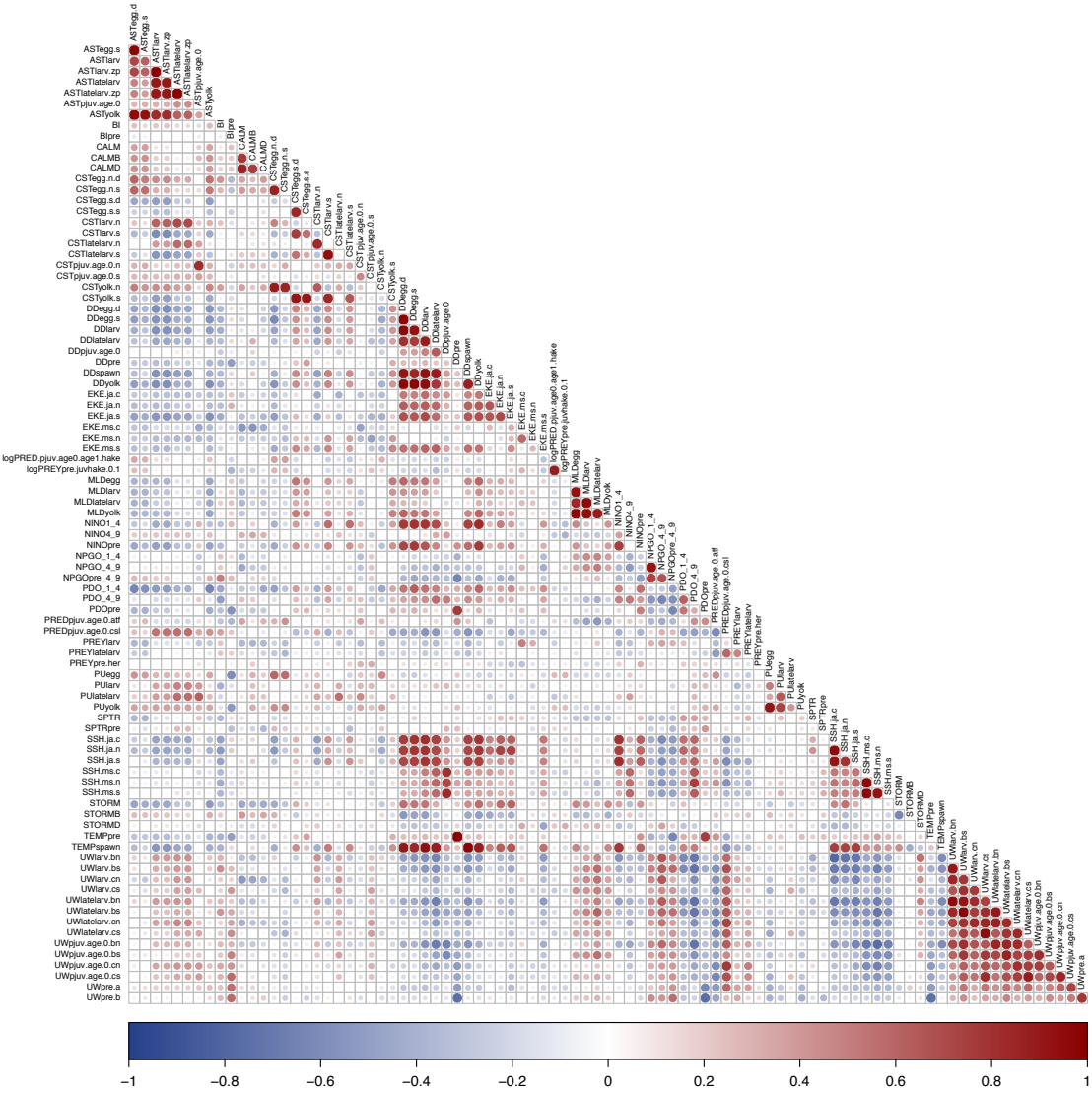

FIGURE A2: Correlations among predictor variables hypothesized to affect Pacific hake (*Merluccius productus*) recruitment. The size and color of the circle represents the strength and sign of the correlation, respectively.

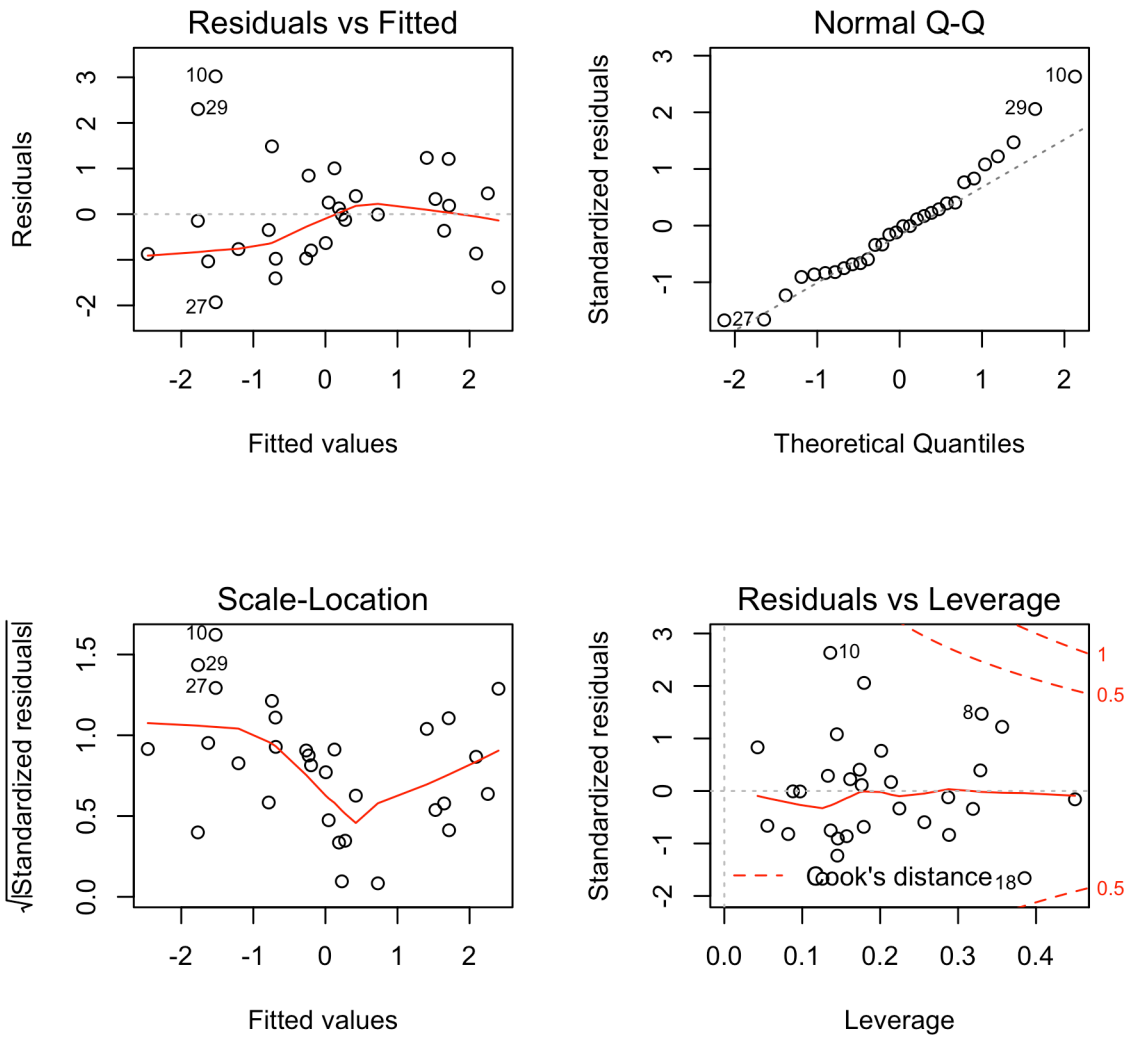

FIGURE A3: AIC-best model diagnostic plots showing (a) residuals vs. fitted values, (b) normal Q-Q plot, (c) scale-location, and (d) residuals vs. leverage.

TABLE A1: Pacific hake (*Merluccius productus*) conceptual life history model showing spatiotemporally-explicit hypotheses by life stage related to factors (covariates) affecting survival.

See TableA1_Stage_Hypotheses.pdf

TABLE A2: Models with ΔAICc < 2.0 for each stage (pre-pawning female conditioning to age-0 pelagic juveniles) in the Pacific hake (*Merluccius productus*) conceptual life history model, all stages combined, and all stages with predator, prey, and climate indices.

See TableA2_R_Table_Delta2.hake_all_stages_models pre_to_age0_FO_Revision.xlsx

TABLE A1: Pacific hake (*Merluccius productus*) conceptual life history model showing spatiotemporally-explicit hypotheses by life stage related to factors (covariates) affecting survival.

Ho Number	Life-history stage	Time period	Hypothesis	Stage	Covariates	Depth	Longitudinal extent	Latitudinal extent	Source
H1	Preconditioning	Apr - Oct (Year 0)	(H1) Higher temperature increases food demand resulting in lower egg production, egg quality, or probability of spawning and lowers recruitment	$TEMP_{pre}$	Mean temperature	50 - 350 m	Shelf break, between 100 - 2000 m isobaths	42° - 47°N	ROMS
H2			(H2) As (H1), but degree days, not mean temperature	DD_{pre}	Degree days	50 - 350 m	Shelf break, between 100 - 2000 m isobaths	42° - 47°N	ROMS
H3			(H3) Higher coastal upwelling leads to increased productivity, better condition, higher egg production, egg quality, or probability of spawning and increases recruitment	$UW_{pre.c}$	Coastal upwelling (CUTI)	Base of mixed layer		41.5° - 47.5°N	Jacox et al. (2018), https://oceanview.pfeg.noaa.gov
H4			(H4) As (H3), but biologically effective upwelling	$UW_{pre.b}$	Biologicially effective upwelling (BEUTI)	Base of mixed layer	0 - 75 km offshore	41.5° - 47.5°N	Jacox et al. (2018), https://oceanview.pfeg.noaa.gov
H5			(H5) Food availability affects energy allocation to reproduction with higher recruitment when more prey are available during the preconditioning period	$PREY_{pre.her}$ $PREY_{pre.juvhake}$	Index of age-0 and age-1 Pacific hake biomass, and age-2 Pacific herring biomass				Stock assessments
H6			(H6) Timing of availability of food affects energy allocation to reproduction with higher recruitment when more prey are available during the preconditioning period	$SPTR_{pre}$	Mean date of the spring transition from downwelling-favorable southerly winds to upwelling-favorable northerly winds		125°W	42°N (West of OR/CA border) 45°N (West of Siletz Bay, OR) 48°N (West of La Push, WA)	CBR Mean Method, Van Holmes (2007), http://www.cbr.washington.edu/status/trans
H7	Spawning	Jan - Mar	(H7) Temperature acts as a spawning cue with fish less likely to spawn at high temperature resulting in lower recruitment	$TEMP_{spawn}$	Mean temperature	130 - 500 m	Shelf break, between 100 - 2000 m isobaths	31° - 36°N	ROMS
H8			(H8) As (H7), but degree days, not mean temperature	DD_{spawn}	Degree days	130 - 500 m	Shelf break, between 100 - 2000 m isobaths	31° - 36°N	ROMS
H9	Eggs	Jan - Mar	(H9) Eggs aggregate at base of mixed layer so Mixed Layer Depth may limit how far they rise in the water column affecting later transport	MLD_{eggs}	Mean mixed layer depth (m)		Shelf break, between 100 - 2000 m isobaths	31° - 36°N	ROMS
H10			(H10) Transport to settlement habitat affects recruitment (transport varies with latitude)	$CST_{eggs.s}$ $CST_{eggs.n}$	Net cross-shelf transport	40 - 60 m	Shelf break, between 100 - 2000 m isobaths	31° - 34.5°N 34.5° - 36°N	ROMS
H11			(H11) Increased northward advection away from juvenile nursery areas decreases recruitment	ASTeggs	Net alongshore transport	40 - 60 m	Shelf break, between 100 - 2000 m isobaths	31° - 36°N	ROMS
H12			(H12) Increased northward advection away from juvenile nursery areas decreases recruitment	PU_{eggs}	Strength of the poleward undercurrent	75 - 275 m	Coast to 275 m isobath	32.5° - 33.5°N	ROMS
H13			(H13) Growth/Predation hypothesis: growth rate is faster in warm water leading to reduced time vulnerable to predators	DD_{eggs}	Degree days	40 - 60 m	Shelf break, between 100 - 2000 m isobaths	31° - 36°N	ROMS
H14	Yolk-sac larvae	Jan - Apr	(H14) Larvae aggregate at base of mixed layer so Mixed Layer Depth may limit how far they rise in the water column affecting later transport	MLD_{yolk}	Mean mixed layer depth (m)		Shelf break, between 100 - 2000 m isobaths	31° - 36°N	ROMS
H15			(H15) Transport to settlement habitat affects recruitment (transport varies with latitude)	$CST_{yolk.s}$ $CST_{yolk.n}$	Net cross-shelf transport	50 - 100 m	Shelf break, between 100 - 2000 m isobaths	31° - 34.5°N 34.5° - 36°N	ROMS
H16			(H16) Increased northward advection away from juvenile nursery areas decreases recruitment	ASTyolk	Net alongshore transport				ROMS
H17			(H17) Increased northward advection away from juvenile nursery areas decreases recruitment	PU_{yolk}	Strength of the poleward undercurrent	75 - 275 m	Coast to 275 m isobath	32.5° - 33.5°N	ROMS
H18			(H18) Growth/Predation hypothesis: growth rate is faster in warm water leading to reduced time vulnerable to predators	DD_{yolk}	Degree days	50 - 100 m		31° - 36°N	ROMS
H19	First-feeding larvae	Feb - May	(H19) Larvae aggregate at base of mixed layer so Mixed Layer Depth may limit how far they rise in the water column affecting later transport	MLD_{larv}	Mean mixed layer depth (m)		Shelf break, between 100 - 2000 m isobaths	31° - 36°N	ROMS
H20			(H20) Transport to settlement habitat affects recruitment (transport varies with latitude)	$CSTlarv.s$ $CSTlarv.n$	Net cross-shelf transport	50 - 200 m	Shelf break, between 100 - 2000 m isobaths	31° - 34.5°N 34.5° - 36°N	ROMS
H21			(H21) North to south transport brings northern zooplankton and leads to higher survival and recruitment, Transport to settlement habitat affects recruitment	ASTlarv	Net alongshore transport	50 - 200 m	Shelf break, between 100 - 2000 m isobaths	31° - 36°N	ROMS

TABLE A1 (cont'd): Pacific hake (*Merluccius productus*) conceptual life history model showing spatiotemporally-explicit hypotheses by life stage related to factors (covariates) affecting survival.

H_0 Number	Life-history stage	Time period	Hypothesis	Stage	Covariates	Depth	Longitudinal extent	Latitudinal extent	Source
H22	First-feeding larvae	Feb - May	(H22) Increased northward advection away from juvenile nursery areas decreases recruitment	PU_{larv}	Strength of the poleward undercurrent	75 - 275 m	Coast to 275 m isobath	32.5° - 33.5°N	
H23			(H23) Higher coastal upwelling leads to increased productivity, better condition, higher survival and increased recruitment	$UW_{larv.cs}$ $UW_{larv.cn}$	Coastal upwelling (CUTI)	base of mixed layer	0 - 75 km offshore	30.5° - 34.5°N 34.5° - 36.5°N	Jacox et al. (2018), https://oceanview.pfeg.noaa.gov/
H24			(H24) As (H23), but biologically effective upwelling	$UW_{larv.bs}$ $UW_{larv.bn}$	Biologicially effective upwelling (BEUTI)	base of mixed layer	0 - 75 km offshore	30.5° - 34.5°N 34.5° - 36.5°N	Jacox et al. (2018), https://oceanview.pfeg.noaa.gov/
H25			(H25) Growth/Predation hypothesis: growth rate	DD_{larv}	Degree days	50 - 200 m	Shelf break, between 100 - 2000 m isobaths	31° - 36°N	ROMS
H26			(H26) Higher zooplankton abundance leads to higher survival and recruitment	$PREY_{larv.zp}$	Index of copepod abundance	0 - 210 m	117.4 - 121.9°W	31.5° - 34.5°N	Zooplankton Database, Scripps Institute of Oceanography https://oceaninformatics.ucsd.edu/zoodb/secure/login.php
H27			(H27) Critical period hypothesis: more frequent storm events lead to poorer feeding conditions,	$STORM_{larv}$	Mean number of storm events		Coast to 126°W	28° - 36°N	Turley and Rykaczewski (2019) NOAA National Centers for Environmental Prediction Climate Forecast System Reanalysis model (CFSR, Saha et al., 2010)
H28			(H28) Critical period hypothesis: extended storm events lead to poorer feeding conditions, lower	$STORMD_{larv}$	Mean duration of storm events		Coast to 126°W	28° - 36°N	Turley and Rykaczewski (2019), CFSR, Saha et al. (2010)
H29			(H29) Critical period hypothesis: fewer days between storm events lead to poorer feeding	$STORMB_{larv}$	Mean number of days between storm events		Coast to 126°W	28° - 36°N	Turley and Rykaczewski (2019), CFSR, Saha et al. (2010)
H30			(H30) Critical period hypothesis: more frequent calm events lead to better feeding conditions,	$CALM_{larv}$	Mean number of calm events		Coast to 126°W	28° - 36°N	Turley and Rykaczewski (2019), CFSR, Saha et al. (2010)
H31			(H31) Critical period hypothesis: extended periods of calm lead to poorer feeding conditions,	$CALMD_{larv}$	Mean duration of calm events		Coast to 126°W	28° - 36°N	Turley and Rykaczewski (2019), CFSR, Saha et al. (2010)
H32			(H32) Critical period hypothesis: shorter intervals between calm events lead to better feeding	$CALMB_{larv}$	Mean number of days between calm events		Coast to 126°W	28° - 36°N	Turley and Rykaczewski (2019), CFSR, Saha et al. (2010)
H33	Late larvae	Mar - Jun	(H33) Larvae aggregate at base of mixed layer so Mixed Layer Depth may limit how far they rise in the water column affecting later transport	$MLD_{latelarv}$	Mean location of mixed layer depth (m)		Shelf break, between 100 - 2000 m isobaths	31° - 37°N	ROMS
H34			(H34) Transport to settlement habitat affects recruitment (transport varies with latitude)	$CST_{latelarv.s}$ $CST_{latelarv.n}$	Net cross-shelf transport	50 - 300 m	Shelf break, between 100 - 2000 m isobaths	31° - 34.5°N 34.5° - 37°N	ROMS
H35			(H35) North to south transport brings northern zooplankton and leads to higher survival and recruitment, Transport to settlement habitat affects recruitment	$AST_{latelarv}$	Net alongshore transport	50 - 300 m	Shelf break, between 100 - 2000 m isobaths	31° - 37°N	ROMS
H36			(H36) Increased northward advection away from juvenile nursery areas decreases recruitment	$PU_{latelarv}$	Strength of the poleward undercurrent	75 - 275 m	Coast to 275 m isobath	33.5° - 34.5°N	ROMS
H37			(H37) Higher coastal upwelling leads to increased productivity, better condition, higher survival and increased recruitment	$UW_{latelarv.cs}$ $UW_{latelarv.cn}$	Coastal upwelling (CUTI)	base of mixed layer	0 - 75 km offshore	30.5° - 34.5°N 34.5° - 37.5°N	Jacox et al. (2018), https://oceanview.pfeg.noaa.gov
H38			(H38) As (H37), but biologically effective upwelling	$UW_{latelarv.bs}$ $UW_{latelarv.bn}$	Biologicially effective upwelling (BEUTI)	base of mixed layer	0 - 75 km offshore	30.5° - 34.5°N 34.5° - 37.5°N	Jacox et al. (2018), https://oceanview.pfeg.noaa.gov
H39			(H39) Growth/Predation hypothesis: growth rate is faster in warm water leading to reduced time vulnerable to predators	$DD_{latelarv}$	Degree days	50 - 300 m	Shelf break, between 100 - 2000 m isobaths	31° - 37°N	ROMS
H40			(H40) Timing of availability of food affects condition, leading to higher survival and increased recruitment	$SPTR_{latelarv}$	Mean date of the spring transition from downwelling-favorable southerly winds to upwelling-favorable northerly winds		125°W	42°N (West of OR/CA border) 45°N (West of Siletz Bay, OR) 48°N (West of La Push, WA)	CBR Mean Method, Van Holmes (2007) http://www.cbr.washington.edu/status/trans
H41			(H41) Higher prey abundance leads to higher survival and recruitment	$PREY_{latelarv.zp}$	Index of copepod abundance	0 - 210 m	117.4 - 121.9°W	31.5° - 34.5°N	Zooplankton Database, Scripps Institute of Oceanography (SIO) https://oceaninformatics.ucsd.edu/zoodb/secure/login.php
				$PREY_{latelarv.eup}$	Index of euphausiid abundance	0 - 210 m	117.3 - 125.0°W	29.9° - 35.1°N	Brinton and Townsend Euphausiid Database, SIO https://oceaninformatics.ucsd.edu/euphausiid/secure/login.php

TABLE A1 (cont'd): Pacific hake (*Merluccius productus*) conceptual life history model showing spatiotemporally-explicit hypotheses by life stage related to factors (covariates) affecting survival.

H_0 Number	Life-history stage	Time period	Hypothesis	Stage	Covariates	Depth	Longitudinal extent	Latitudinal extent	Source
H42	Pelagic juveniles (age-0)	Apr - Sep	(H42) Transport to settlement habitat affects recruitment (transport varies with latitude)	$CST_{age0.s}$ $CST_{age0.n}$	Net cross-shelf transport	0 - 50 m	inshore of 200 m isobath	31° - 34.5°N 34.5° - 38°N	ROMS
H43			(H43) North to south transport brings northern zooplankton and leads to higher survival and recruitment, Transport to settlement habitat affects recruitment	$ASTage0$	Net alongshore transport	0 - 50 m	inshore of 200 m isobath	31° - 38°N	ROMS
H44			(H44) Higher coastal upwelling leads to increased productivity, better condition, higher survival and increased recruitment (upwelling varies with latitude)	$UW_{age0.cs}$ $UW_{age0.cn}$	Coastal upwelling (CUTI)	base of mixed layer	0 - 75 km offshore	30.5° - 34.5°N 34.5° - 38.5°N	Jacox et al. (2018), https://oceanview.pfeg.noaa.gov
H45			(H45) As (H44), but biologically effective upwelling	$UW_{age0.bs}$ $UW_{age0.bn}$	Biologicially effective upwelling (BEUTI)	base of mixed layer	0 - 75 km offshore	30.5° - 34.5°N 34.5° - 38.5°N	Jacox et al. (2018), https://oceanview.pfeg.noaa.gov
H46			(H46) Growth/Predation hypothesis: growth rate is faster in warm water leading to reduced time vulnerable to predators	DD_{age0}	Degree days	0 - 50 m	inshore of 200 m isobath	31° - 38°N	ROMS
H47			(H47) Timing of availability of food affects condition, leading to higher survival and increased recruitment	$SPTR_{age0}$	Mean date of the spring transition from downwelling-favorable southerly winds to upwelling-favorable northerly winds		125°W	42°N (West of OR/CA border) 45°N (West of Siletz Bay, OR) 48°N (West of La Push, WA)	CBR Mean Method, Van Holmes (2007) http://www.cbr.washington.edu/status/trans
H48			(H48) Increased food availablility leads to better feeding conditions, leading to higher survival and recruitment	$PREY_{age0.eup}$	Index of euphausiid abundance	0 - 210 m	117.3 - 125.0°W	29.9° - 35.1°N	Brinton and Townsend Euphausiid Database, SIO https://oceaninformatics.ucsd.edu/euphausiid/secure/login.php
H49			(H49) Higher predation leads to lower survival and recruitment	$PRED_{age0.age1hake}$ $PRED_{age0.atf}$ $PRED_{age0.csl}$	Index of age-1 Pacific hake biomass, arrowtooth flounder biomass, California sea lion pup counts				Stock assessments, Laake et al. (2017)
H50	Preconditioning Egg to late larvae First feeding larvae to age-0	Jan - Apr May - Sep Jan - Apr May - Sep	(H50) Sea surface height as an indicator of basin-scale processes	$SSH_{pre.JA.s}$ $SSH_{pre.JA.c}$ $SSH_{pre.MS.c}$ $SSH_{pre.MS.n}$ $SSH_{JA.s}$ $SSH_{JA.c}$ $SSH_{MS.s}$ $SSH_{MS.c}$	Sea surface height	Surface	0 - 30 km offshore	31° - 34.5°N 34.5° - 42.5°N 34.5° - 42.5°N 42.5° - 47°N 31° - 34.5°N 34.5° - 42.5°N 31° - 34.5°N 34.5° - 42.5°N	ROMS
H51	Preconditioning First feeding larvae to age-0 Late larvae to age-0	Jan - Apr May - Sep Jan - Apr May - Sep	(H51) Eddy kinetic energy as a proxy for the intensity of mesoscale turbulence - higher EKE, with more meanders, fronts, and eddies, leads to better feeding conditions, higher survival and recruitment	$EKE_{pre.JA.s}$ $EKE_{pre.JA.c}$ $EKE_{pre.MS.c}$ $EKE_{pre.MS.n}$ $EKE_{JA.s}$ $EKE_{JA.c}$ $EKE_{MS.s}$ $EKE_{MS.c}$	Eddy kinetic energy	Surface	0 - 30 km offshore	34.5° - 42.5°N 42.5° - 47°N 34.5° - 42.5°N 42.5° - 47°N 31° - 34.5°N 34.5° - 42.5°N 31° - 34.5°N 34.5° - 42.5°N	ROMS
H52	Preconditioning	Apr - Sep Jan - Apr Apr - Sep	(H52) Pacific Decadal Oscillation as an indicator of basin-scale processes; negative phase linked to higher productivity, better feeding conditions, better condition, higher survival and recruitment	PDO_{pre} PDO_{JA} PDO_{AS}	Pacific Decadal Oscillation				Mantua (1999), http://research.jisao.washington.edu/pdo/
H53	Preconditioning	Apr - Sep Jan - Apr Apr - Sep	(H53) North Pacific Gyre Oscillation as an indicator of basin-scale processes; postive phase linked to higher nutrient concentrations, higher productivity, better feeding conditions, better condition, higher survival and recruitment	$NPGO_{pre}$ $NPGO_{JA}$ $NPGO_{AS}$	North Pacific Gyre Oscillation				Di Lorenzo et al. (2008), http://www.o3d.org/npgo/
H54	Preconditioning First-feeding larvae to age-0		(H54) More northward shifted bifurcation of the North Pacific Current leads to increased transport of enriched subarctic waters to the south, higher productivity, better feeding conditions, better condition, higher survival and recruitment	BI_{pre} BI	Bifurcation Index				Malick et al. (2017)