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# ORIGINAL ARTICLE

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

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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 United States 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 prespawning 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 firstfeeding 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, Anderson, 1988; Houde, 1987), 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 ( $\sim$ 25°N) to the Gulf of Alaska ( $\sim$ 55°N) (Figure 1), occupying



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

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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). As the stock spans US 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 & 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 yearclass 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



**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 (RO) = 1,600, steepness (h) = .854, and unfished female spawning biomass (B0, thousand t) = 1,385 were obtained from Table 27 in the 2020 assessment

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 Pacific sardine (Sardinops sagax) in the CCE (Reiss et al., 2008), while maps of sea surface height (SSH) constructed from satellite observations of sea level anomaly have shown that white sharks (Carcharodon carcharias) exhibit a clear affinity for mesoscale eddies (Gaube et al., 2018). Atmospheric and oceanic reanalysis products and ocean circulation models have been used to examine how oceanographic and atmospheric processes affected recruitment variability and productivity in several Northeast Pacific marine fish populations (Haltuch et al., 2020; Litzow et al., 2018; Malick et al., 2017; Tolimieri et al., 2018; Vestfals et al., 2014). Technological developments such as these provide a unique opportunity to revisit hypotheses about the physical and biological processes that determine Pacific hake year-class strength developed in the 1980s and can potentially help to identify earlier indicators of recruitment strength (i.e., age 1) than are currently available (i.e., age 3 or 4).

In this study, we (i) developed a literature-based, conceptual lifehistory model for Pacific hake in the CCE that included seven stages from the conditioning of pre-spawning females through the pelagic juvenile phase (age-0 fish) for the US west coast Pacific hake stock; (ii) used our conceptual model to generate stage-, space-, and timespecific hypotheses regarding the physical and biological variables that likely influence Pacific hake recruitment; and (iii) developed and compared several linear models to predict Pacific hake recruitment using oceanographic variables derived from a regional ocean reanalysis for the CCE (Neveu et al., 2016). We also investigated how biological indices like predator and prey abundances and local- and basinscale climate drivers (as proxies for nutrient input or changes in ocean currents) might affect Pacific hake recruitment. Our analysis reexamined existing hypotheses of where and when year-class strength is determined and investigated the relationships between ocean conditions and Pacific hake survival across early life-history stages leading to recruitment, with the goal of improving our understanding of the drivers of hake recruitment variability.

# 2 | METHODS

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

# 2.1 | Pacific hake life history: Female preconditioning to age-0 recruits

Our conceptual life-history model began by first identifying each stage in the life history of Pacific hake where environmental drivers might impact the size of each year class, beginning with female conditioning prior to the spawning season through age-0 pelagic juveniles (Tables 1 and A1). Female condition has generally been shown to influence whether or not an individual spawns, the quality and number of eggs that are produced, and their hatching success (Laine & Rajasilta, 1999; Rodgveller et al., 2016; Sogard et al., 2008). Adult Pacific hake are found throughout the water column in association with the shelf break, typically over bottom depths ranging between 100 and 300 m (Bailey et al., 1982; Cooke et al., 2006; Ressler et al., 2007). Their northward feeding migration is timed with the spring transition in ocean conditions along the shelf edge (Benson et al., 2002; Thompson, 1981). Adult Pacific hake spend summers feeding off the coasts of Oregon, Washington, and British Columbia before migrating southward in autumn to their spawning grounds off central and southern California, and Baja California, Mexico (Hollowed & Bailey, 1989). Thus, the feeding period from spring to fall (April to October) prior to spawning was considered important for female preconditioning.

Pacific hake are believed to spawn during the winter months, mainly between December and March (Smith, 1995), with the peak occurring in January and February (Bailey, 1980; Stauffer, 1985; Woodbury et al., 1995). While the exact location is unknown, spawning is thought to occur up to 400 km offshore of the southern California Bight at depths of 130–500 m 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 FISHERIES OCEANOGRAPHY

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 and 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 to 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 and 500 m during the day, but close to the surface at night, between 25 and 50 m (Bailey, 1982). Transformation to pelagic juveniles occurs between 30 and 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 spatiotemporallyspecific (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, and local-(e.g., storm and calm events, SSH) and basin-scale indices representing the 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., crossshelf 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

TABLE	<ol> <li>Pacific hake</li> </ol>	e (Merluccius	s <i>productus</i> ) conceptual life history m	nodel showing	spatiotemporally explici	t hypothese:	s by life stage relate	d to factors (covariates) affe	cting survival
Р	Life-history	Time							
number	stage	period	Hypothesis	Stage	Covariates	Depth	Longitudinal extent	Latitudinal extent	Source
H	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 <sub>pre</sub>	Mean temperature	50-350 m	Shelf break, between 100 and 2,000 m isobaths	42°-47°N	ROMS
H2			(H2) As (H1), but degree days, not mean temperature	DD <sub>pre</sub>	Degree days	50-350 m	Shelf break, between 100 and 2,000 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	0–75 km offshore	41.5°-47.5°N	Jacox et al. (2018), oceanview.pfeg.noaa.gov
H4			(H4) As (H3), but biologically effective upwelling	UW <sub>pre.b</sub>	Biologically effective upwelling (BEUTI)	Base of mixed layer	0-75 km offshore	41.5°-47.5°N	Jacox et al. (2018), 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	PREV <sub>pre.her</sub> PREV <sub>pre.juvhake</sub>	Index of age-0 and age-1 Pacific hake biomass and age-2 Pacific herring biomass				Stock assessments
¥			(H6) Timing of availability of food affects energy allocation to reproduction with higher recruitment when more prey are available during the preconditioning period	SPTR <sub>pre</sub>	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), 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	TEMPspawn	Mean temperature	130-500 m	Shelf break, between 100 and 2,000 m isobaths	31°-36°N	ROMS
H8			(HB) As (H7), but degree days, not mean temperature	DD <sub>spawn</sub>	Degree days	130-500 m	Shelf break, between 100 and 2,000 m isobaths	31°-36°N	ROMS

Source	ROMS	ROMS	ROMS	ROMS	ROMS	ROMS	ROMS	ROMS	ROMS	ROMS
Latitudinal extent	31°-36°N	31°-34.5°N 34.5°-36°N	31°-36°N	32.5°−33.5°N	31°-36°N	31°-36°N	31°-34.5°N 34.5°-36°N		32.5°-33.5°N	31°−36°N
Longitudinal extent	Shelf break, between 100 and 2,000 m isobaths	Shelf break, between 100 and 2000 m isobaths	Shelf break, between 100 and 2000 m isobaths	Coast to 275 m isobath	Shelf break, between 100 and 2,000 m isobaths	Shelf break, between 100 and 2,000 m isobaths	Shelf break, between 100 and 2,000 m isobaths		Coast to 275 m isobath	
Depth		40-60 m	40-60 m	75-275 m	40-60 m		50-100 m		75-275 m	50-100 m
Covariates	Mean mixed layer depth (m)	Net cross-shelf transport	Net long-shore transport	Strength of the poleward undercurrent	Degree days	Mean mixed layer depth (m)	Net cross-shelf transport	Net long-shore transport	Strength of the poleward undercurrent	Degree days
Stage	MLD <sub>eggs</sub>	CST <sub>eggs.s</sub> CST <sub>eggs.n</sub>	AST <sub>eggs</sub>	PUeggs	DDeggs	MLD <sub>volk</sub>	CST <sub>yolk.s</sub> CST <sub>yolk.n</sub>	AST <sub>yolk</sub>	PU <sub>volk</sub>	DD <sub>yolk</sub>
Hypothesis	(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	(H10) Transport to settlement habitat affects recruitment (transport varies with latitude)	(H11) Increased northward advection away from juvenile nursery areas decreases recruitment	(H12) Increased northward advection away from juvenile nursery areas decreases recruitment	(H13) Growth/predation hypothesis: Growth rate is faster in warm water leading to reduced time vulnerable to predators	(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	(H15) Transport to settlement habitat affects recruitment (transport varies with latitude)	(H16) Increased northward advection away from juvenile nursery areas decreases recruitment	(H17) increased northward advection away from juvenile nursery areas decreases recruitment	(H18) Growth/predation hypothesis: Growth rate is faster in warm water leading to reduced time vulnerable to predators
Time period	Jan-Mar					Jan - Apr				
Life-history stage	Eggs					Yolk-sac larvae				
Ho number	6H	H10	H11	H12	H13	H14	H15	H16	H17	H18

TABLE 1 (Continued)

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restricted depth range. Preliminary analyses showed that these paired predictors were highly correlated (e.g., *r* >.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 fell 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 dataassimilative CCE ROMS output (Neveu et al., 2016). The CCE-ROMS model domain covers the region from 30°-48°N and from the coastline to 134°W at .1° (~10 km) horizontal resolution, with 42 terrainfollowing vertical levels. We used the 1980-2010 CCE reanalysis, which assimilates satellite observations (SST and SSH) and in situ data (temperature and salinity from ships, floats, moorings, and 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; Jacox, Bograd, et al., 2015; Jacox, Fiechter, et al., 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, Bograd, 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).

#### 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).

#### 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).

#### 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 US 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 are 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).

#### 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; Sánchez & 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  $31^{\circ}$ – $34.5^{\circ}$ N,  $34.5^{\circ}$ – $42.5^{\circ}$ N, and  $42.5^{\circ}$ – $47^{\circ}$ N.

#### 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  $31^{\circ}$ – $34.5^{\circ}$ N,  $34.5^{\circ}$ – $42.5^{\circ}$ N, and  $42.5^{\circ}$ – $47^{\circ}$ 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<sub>pre.her</sub>) 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 (log-PRED<sub>pre.juvhake</sub>), 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<sub>larv.zp</sub>, PREY<sub>latelarv.zp</sub>) and euphausiid abundance (n  $m^{-2}$ ) as prey for the late larval and juvenile stages (PREY<sub>latelarv.eup</sub>, PREY<sub>age0.eup</sub>) 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 Data-(oceaninformatics.ucsd.edu/zoodb/secure/login.php) base 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 (oceaninformatics.ucsd.edu/euphausiid/secure/login.php) and included all genera and species, all phases and stages collected from February-May from lines 77 to 93 (Southern California).

#### 2.2.3 | Predation on recruits

Size-specific predation is a major source of mortality for the early life stages of marine fishes (Bailey & Houde, 1989; Houde, 2008). We included several indices of predator abundance to examine the effects of predation on recruitment. Pacific hake have been shown to be important prey of California sea lions (Zalophus californianus), for example. In the late 1970s, they were the most abundant prey in the diet of sea lions from San Miguel Island, off southern California, with almost 49% of scats examined containing Pacific hake, mostly 1-2 year old fish (Antonelis et al., 1984; Livingston & Bailey, 1985). Scat samples collected seasonally on San Clemente and San Nicolas islands in the Southern California Bight from 1981-2015 also show evidence of sea lion predation on age-0 and age-1 Pacific hake (< 30 cm in length) (A. Curtis, NOAA, personal communication). We used estimated pup abundances from Laake et al. (2018) as an estimate of California sea lion predation on Pacific hake (PRED<sub>age0.csl</sub>). Pup counts were used, as they directly relate to predation on Pacific hake by

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females foraging around San Clemente and San Nicolas islands (A. *Curtis*, NOAA, personal communication) by integrating both population size and energetic demands of the population.

Arrowtooth flounder (*Atheresthes stomias*) is a highly piscivorous flatfish known to prey on Pacific hake juveniles and adults (Buckley et al., 1999; Ressler et al., 2007; Sampson et al., 2017). Pacific hake are the primary prey of arrowtooth flounder off Oregon and Washington (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<sub>age0.atf</sub>).

Studies have shown evidence of cannibalism by age-1 fish on YOY Pacific hake (Buckley & Livingston, 1997; Smith, 1995). 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<sub>age0.age1hake</sub>).

# 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<sub>larv</sub>, STORM<sub>larv</sub>), duration of (CALMD<sub>larv</sub>, STORM-Dlary), and time between (CALMBlary, STORMBlary) distinct calm periods and storms events from February to May using the methodology outlined in Turley and 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<sup>-1</sup> 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<sup>-1</sup> 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 and 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 (Cummins & Freeland, 2007; Freeland, 2006). 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, Fiechter, et al., 2015). We used the Oceanic Niño Index (ONI), defined as the 3-month running average of SST 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<sub>pre</sub>), through the larval stages (ONI<sub>JA</sub>), to summer feeding of age-0 pelagic juveniles (ONI<sub>AS</sub>).

#### Pacific Decadal Oscillation

The PDO is defined as the leading principle component of monthly SST anomalies in the North Pacific poleward of  $20^{\circ}$ 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<sub>pre</sub>), through the larval stages (PDO<sub>JA</sub>), to summer feeding of age-0 pelagic juveniles (PDO<sub>AS</sub>).

#### North Pacific Gyre Oscillation

The 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

Model estimates of Pacific hake recruitment were taken from the most recent stock assessment (here, Figure 3d; Figure 28 in Grandin et al., 2020). Specifically, we used the model-estimated log deviations as the response variable, where the deviations were the annual deviations from log median recruitment. Median recruitment was a function of the assumed Beverton–Holt stock–recruitment relationship, aging



**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, (c) age-2 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*).

error assumptions, and the data included in the stock assessment model including the sampled age structure.

Our analysis covers recruitment residuals from 1981–2010, as the 1980 recruitment deviation depends on the preconditioning period in 1979, which was not available in the CCE ROMS output.

## 2.4 | Model development

Initial explorations of candidate variables led to a de facto reduction in the number of models evaluated. Specifically, correlations among predictor variables and individual linear and guadratic regressions for each predictor against recruitment deviations were calculated and evaluated prior to model fitting and selection. Predictors that were strongly correlated (Figure A1, |r| > .70) were not permitted in the same model (Dormann et al., 2013). Quadratic terms were included in the main modeling exercise for individual hypothesized covariates where the quadratic model fit better than model (Akaike's the linear Information Criterion. AIC [Akaike, 1998], was < 2.0 that of the linear model). Based on preliminary model explorations, the following covariates were included as potential quadratic predictors during model selection: BEUTI (UW<sub>pre,beu</sub>) from  $41.5^{\circ}-47.5^{\circ}N$  during the adult female preconditioning stage, and cross-shore transport during the first-feeding (CST<sub>larv</sub>) and late larval stages (CST<sub>latelarv</sub>).

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 A1, |r| > .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 guadratic were included in the models as a linear function and a quadratic function. The best-fit models with  $\triangle AICc < 2.0$  were retained for further consideration (Burnham & Anderson, 1998a, 1998b). Second, 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 three of the stage-specific models with  $\Delta AICc$ < 2.0. Third, we retained all ROMS variables appearing in models with  $\triangle AICc < 2.0$  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 A1, PREYpre with PREDage0.age1hake [r = .88]; CALMB<sub>lary</sub> [r = .76] and CALMD<sub>lary</sub> [r = .81] with CALM<sub>larv</sub>) or were correlated with a similar covariate (NPGO<sub>JA</sub> with both NPGO<sub>pre</sub> [r = .73] and NPGO<sub>AS</sub> [r = .92]; ONI<sub>JA</sub> with ONI<sub>pre</sub> [r = .76]) were removed, although their hypothesized effects on recruitment were generally captured in the analysis.

# 2.5 | Model validation and testing

The performance of the best-fit model for all stages in our conceptual life history model was evaluated using (1) resampling with replacement of recruitment deviations to estimate  $R^2$  values using 100 randomized data sets; (2) bootstrapping whole years with replacement to estimate bias and calculate SE of the parameter estimates; (3) annual jackknife resampling to determine the effect of any single year on the  $R^2$ ; (4) resampling annual recruitment deviations from a log-normal distribution using the annual mean and SD estimated from the assessment, then recalculating recruitment residuals, and refitting the model 1000 times; (5) refitting the model using data for 1981-2005 and predicting recruitments deviations for 2006-2010; (6) jackknife resampling to re-run the entire model-fitting and comparison exercise, to determine whether removal of any individual year would change the selected predictor variables; and (7) re-running the entire model fitting exercise 100 times using the re-sampled Pacific hake recruitment deviations with error (from Step 4 above), comparing AICc-selected models from each run. Finally, we used (8) jackknife resampling but fit only the years 1981-2005, compared the resulting models to the best-fit model above, and used the 1981-2005 model to predict recruitment deviations for 2006-2010.

# 3 | RESULTS

Model fitting identified a clear best-fit model for each stage in our conceptual life history model for Pacific hake, with intercept-only models for the spawning, egg, and age-0 pelagic juvenile stages (Table A2). The best-fit model for the adult female preconditioning stage, based on the lowest AICc, included May-September EKE between 34.5° and 42.5°N (EKE\_{pre.MS.c}) and upwelling strength (UWpre,cu), which together explained 31% of the recruitment variability in Pacific hake. Alongshore transport (AST<sub>yolk</sub>) and transport in the poleward undercurrent (PUyolk) during the yolk-sac stage explained 18% of the variability in recruitment (Table A2). Cross-shelf transport north of Point Conception (CST<sub>larv.n</sub>), along with linear and quadratic predictors for cross-shelf transport south of Point Conception (CST<sub>larv</sub>s), accounted for 16% of the recruitment variability for the first-feeding larval stage. Similarly, linear and quadratic predictors for cross-shelf transport south of Point Conception during the late larval stage (CST<sub>latelary.s</sub>) accounted for 22% of the variability in hake recruitment (Table A2).

All terms identified in the stage-specific best-fit models, along with those terms appearing in three or more models with  $\Delta$ AlCc < 2.0 (Table A2), were included in the next stage of model fitting, where all life history stages were combined. Model fitting produced seven candidate models with  $\Delta$ AlCc < 2.0, which explained between 31% and 43% of the variability in hake recruitment not accounted for by the stock-recruitment relationship in the assessment (Table A2). For the adult preconditioning stage, May–September EKE between 34.5° and 42.5°N (EKE<sub>pre.MS.c</sub>) appeared in all seven models, while six models included upwelling strength between 41.5° and 47.5°N (UW<sub>pre.cu</sub>).

Three models included alongshore transport during the yolk-sac larval stage (AST<sub>yolk</sub>) and two models included May–September EKE between 34.5° and 42.5°N (EKE<sub>MS.c</sub>). Linear and quadratic predictors for cross-shelf transport south of Point Conception during the first-feeding larval stage (CST<sub>larv.s</sub>, CST<sup>2</sup><sub>larv.s</sub>) and the late larval stage (CST<sub>latelarv.s</sub>, CST<sup>2</sup><sub>larv.s</sub>) and the late larval stage (CST<sub>latelarv.s</sub>, CST<sup>2</sup><sub>latelarv.s</sub>) each appeared in one model (Table A2). All terms appearing in the seven models with  $\Delta$ AICc < 2.0 were carried over to the next step of model fitting.

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  $\triangle AICc < 2.0$  (Table 2). The model with the lowest AIC included five covariates (Figures 3, A2, 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 BI (BIpre), May-September EKE between 34.5° and 42.5°N (EKEpreMS.c), and age-2 Pacific herring biomass off the WCVI (PREY<sub>pre.her</sub>) during the female spawner preconditioning stage (Figure 5). Negative correlations were also found with northward alongshore transport between 50 and 100 m during the yolk-sac larval stage (AST<sub>yolk</sub>) and the number of days between storm events during the first-feeding larval stage (STORMB<sub>larv</sub>) (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  $\triangle AICc < 2.0$  models included the EKE<sub>pre.MS.c</sub> 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<sub>age.0age1.hake</sub>), upwelling strength during the preconditioning stage (UW<sub>pre.cu</sub>), which replaced the BI<sub>pre</sub> predictor, and the number of calm periods during the first-feeding larval stage (CALM<sub>larv</sub>) (Tables 2 and A2).

There was weak correlation among the covariates in the best-fit model (Table 4). Generalized variance inflation factor (VIF) values, 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 A2) with residuals that did not show signs of autocorrelation (Figure A3).

# 3.1 | Model testing and validation: Best-fit model

Randomly resampling the recruitment deviations (bootstrap with replacement) and re-running the AIC-best model resulted in a median expected  $R^2 = .16$  (95% C.I. = .03-.41), suggesting that the observed value of  $R^2 = .59$  was not likely to be observed at random.

After removing individual years and refitting the best-fit model (jackknifing), there was little impact on the model fit (Figures 4 and 5, median  $R^2 = .59$  [95% C.I. = .55-.67]). Predicting the missing year

R <sup>2</sup> ΔAICc
STORMB <sub>larv</sub> -
- STOR
PREY <sub>pre.her</sub>
έξ.
EKEpre.MS.c -
. 9
i

transformed predation of age-O Pacific hake (*Merluccius productus*) by age-1 hake; PREY<sub>eup</sub> euphausiids as prey for late larval stages; PREY<sub>hen</sub>, age-2 Pacific herring (*Clupea pallasii*) as prey for adult female preconditioning 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; PRED<sub>age0.age1hake</sub>, logstage; SPTR, timing of spring transition; STORMB, number of days between storm events; STORMD, duration of storm events; UW, upwelling; yolk, yolk-sac larval stage. 363



**FIGURE 4** (a) Fit of the AIC-best model ( $R^2 = .59$ ) to the estimated median log recruitment deviations from the 2020 Pacific hake (*Merluccius productus*) stock assessment. Solid line is the predicted recruitment deviations from the full time series. Dotted lines = 95% confidence limits. Open circles are the median log recruitment deviations from the 2020 Pacific hake assessment. Stars are predicted values from jackknife analysis removing individual years one at a time. Red points are predicting 2006–2010. (b) Fit of the AIC-best model from jackknife-refitting the 1981–2005 data ( $R^2 = .63$ ). Open circles are the log recruitment deviations from the 2020 Pacific hake assessment. Solid black line is the predicted recruitment deviations for 2006–2010 based on the model for 1981–2005. Dotted lines = 95% confidence limits

from any iteration produced estimates very similar to those for the full model (Figure 4a). The years that showed the highest impact on the model's ability to explain the data were 1990 (increased to  $R^2 = .70$ ) and 2002 (decreased to  $R^2 = .54$ , Figure 6).

Resampling annual recruitment deviations with error produced a slight decline in model performance (median  $R^2 = .56$  [95% C.I. = .50-.62]). This suggests that uncertainty in the time series of recruitment deviations (given the current stock assessment parameters) results in a somewhat lower ability to explain the variability in recruitment.

When the entire model-fitting process was re-run using the jackknife resampling, the results were fairly consistent with the primary analysis (Table 5). May–September EKE between 34.5° and 42.5°N, the NPC BI, and Pacific herring biomass during the adult female preconditioning stage appeared in 95%, 55%, and 11% of the models, respectively. Alongshore transport during the yolk-sac larval stage and the number of days between storm events appeared in 40% and 21% of the models, respectively. Other predictors of note were upwelling strength between 41.5° and 47.5°N during the adult female preconditioning stage and the number of calm periods during the first-feeding larval stage, which appeared in 40% and 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<sub>pre.</sub> MS.c (81% of models), BI<sub>pre</sub> (46%), AST<sub>yolk</sub> (41%). Additional predictors included CALM<sub>larv</sub> (44%) and UW<sub>pre.cu</sub> (40%). Other terms from the AIC-best model, PREY<sub>pre.her</sub> and STORMB<sub>larv</sub> occurred in 17% and 15% of the models, respectively.

Finally, jackknife resampling and re-running the entire modelfitting 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 BI during the preconditioning stage (BIpre) 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 (logPRE-Dage0.age1.bake) and arrowtooth flounder predation on age-0 pelagic juveniles appearing in 98% and 33% of the best-fit models from 1981 to 2005, respectively. The linear and guadratic predictors for crossshelf transport south of Point Conception during the first-feeding larval stage (CST<sub>larv.s</sub>, CST<sup>2</sup><sub>larv.s</sub>) 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<sub>pre</sub>) and the number of calm periods during the first-feeding larval stage (CALM<sub>larv</sub>), which appeared in 62% of and 24% the models, respectively. Surprisingly, the EKE<sub>pre.MS.c</sub> predictor, which was a strong predictor in the both the jackknife and resampling recruitment analyses, only appeared in 7% of the models, while PREY<sub>pre,her</sub> 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 ( $R^2 = .63$ , 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 (Blpre, ONIpre, CST<sub>larv.s</sub>, CST<sup>2</sup><sub>larv.s</sub>, and logPRED<sub>age0.age1.hake</sub>) did a very good job of predicting recruitment deviations for 1981-2005 ( $R^2 = .83$ ), yet only a marginal job for 1981-2010 ( $R^2 = .44$ ). 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 **FIGURE 5** Partial residual plots of predictor variables in 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, (c) age-2 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



Days between storms: First-feeding larvae

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 EKE between 34.5° and 42.5°N, the location of the NPC bifurcation, and age-2 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 (Tables 2 and 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 these stages were not well explained by the ROMS data (Table A2).

EKE between May and September from Point Conception to Cape Blanco during the female spawner preconditioning stage was the strongest driver of recruitment we identified. Areas with higher mesoscale turbulence have energetic flow characterized by eddies, meanders, and frontal structures, which are known to concentrate prey and improve feeding opportunities for marine fishes (Bakun, 2006; Logerwell & Smith, 2001). As such, we expected higher EKE to be associated with higher hake recruitment, yet the opposite relationship was found. Decreasing recruitment with increasing EKE may be associated with its offshore movement with the seasonal equatorward jet, which frequently separates from the coast at Cape Blanco (Castelao et al., 2006; Strub & James, 2000). Fronts associated with upwelling filaments may extend several hundred kilometers

	Coefficient	Bias	SE	Standardized coefficient	Std bias	Std SE
Intercept	8.26	.03	2.05	.04	.00	.23
$BI_{pre}$	63	02	.21	69	03	.23
EKE <sub>pre.MS.c</sub>	-242.70	65	57.34	-1.02	.00	.24
$PREY_{pre.her}$	.00	.00	.00	50	.02	.23
AST <sub>yolk</sub>	-47.88	-1.68	20.72	57	02	.25
STORMB <sub>larv</sub>	08	.00	.04	47	01	.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; PREY here age-2 Pacific herring (Clupea pallasii) as prey during preconditioning stage; STORMB, number of days between storm events.

	Blpre	EKE <sub>pre.MS.c</sub>	PREY <sub>pre.her</sub>	$AST_{yolk}$	STORMB <sub>larv</sub>	VIF
Bl <sub>pre</sub>	-					1.03
EKE <sub>pre.MS.c</sub>	14	-				1.09
$PREY_{pre.her}$	06	17	-			1.04
AST <sub>yolk</sub>	01	19	.04	-		1.15
STORMB <sub>larv</sub>	.02	06	02	.31	-	1.11

TABLE 3 Coefficients for the AICbest model of Pacific hake (Merluccius productus) recruitment (Model 1 in Table 2) showing both raw and standardized (beta) coefficients

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

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; PREY<sub>her</sub>, age-2 Pacific herring (Clupea pallasii) as prey during preconditioning stage; STORMB, number of days between storm events; VIF, variance inflation factor.

offshore (Castelao et al., 2006; Strub & James, 2000), and while this could potentially benefit adult hake through expansion of their feeding habitat, their movement offshore to less productive waters may result in poorer feeding conditions overall, and greater energy expended on the return migration to their spawning grounds. Similarly, Nieto et al. (2014) found that offshore transport had a negative effect on sardine recruitment, despite the expansion of their spawning habitat farther offshore.

Previous studies have linked a northward-shifted NPC bifurcation to higher biomass and productivity in the CCE, which likely results from the advective transport of nutrients and large-bodied, lipid-rich zooplankton from the sub-arctic domain into the CCE, leading to enhanced production in higher trophic level species (Malick et al., 2017; Sydeman et al., 2011). We expected a similar response with hake. In contrast, we found that a southward-shifted NPC bifurcation during the adult female preconditioning stage was linked to higher recruitment the following year. High productivity in the northern CCE has been attributed to several mechanisms, including a persistent nutrient supply through the dynamics of the Strait of Juan de Fuca and the Columbia River, local upwelling enhancement by submarine canyons (e.g., Juan de Fuca and Astoria canyons), and physical features that allow for the development and retention of phytoplankton blooms on the shelf (Hickey & Banas, 2008). During the summer, the Columbia River plume typically flows southwestward offshore of the Oregon shelf, while during the winter, it flows northward over the Washington shelf (Hickey, 1989, 1998). The plume can become bidirectional from summer to early fall, depending on the direction of

prevailing winds (Hickey et al., 2005). With a southward shifted NPC bifurcation (e.g., south of the Columbia River), the northward flowing Alaska Current could impede the southwesterly flow of the Columbia plume, advecting the highly productive waters off the coasts of Washington and southern British Columbia northward, leading to better feeding conditions for adult hake on their summer feeding grounds. In contrast, a northward-shifted NPC bifurcation (e.g., off the coast of southern Vancouver Island) would likely result in poorer conditions for hake on their summer feeding grounds, as the high productivity off the coasts of Washington and southern British Columbia would instead be advected southward, with enhanced southwestward offshore flow of plume waters.

Hake recruitment was negatively correlated with northward transport during the yolk-sac larval stage (AST<sub>volk</sub>, January to April at 50-100 m), which was similar to the findings of Schirripa and Colbert (2006), who linked higher sablefish recruitment with stronger southward transport of surface waters (50-100 m) in February. Tolimieri et al. (2018) found that northward transport of sablefish yolk-sac larvae at 1,000-1,200 m was associated with higher recruitment, likely because it increased their overlap with northern zooplankton once they moved 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

![](_page_15_Figure_1.jpeg)

![](_page_15_Figure_2.jpeg)

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 and 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 and 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 et al., 1994; MacKenzie & Leggett, 1991).

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**TABLE 5** Variables included in all candidate models of Pacific hake (*Merluccius productus*) recruitment from jackknife refits of the entire model-fitting process

Predictor	Number of times inclu	uded %
AST <sub>yolk</sub>	25	40
BI	1	2
Bl <sub>pre</sub>	34	55
CALM <sub>larv</sub>	23	37
CST <sub>larv.s</sub>	0	0
CST <sup>2</sup> <sub>larv.s</sub>	0	0
CST <sub>latelarv.s</sub>	1	2
CST <sup>2</sup> <sub>latelarv.s</sub>	1	2
EKE <sub>MS.c</sub>	1	2
EKE <sub>pre.MS.c</sub>	59	95
$logPRED_{age0.age1.hake}$	5	8
ONI <sub>AS</sub>	0	0
ONI <sub>pre</sub>	0	0
NPGO <sub>AS</sub>	1	2
NPGO <sub>pre.AS</sub>	1	2
PDO <sub>JA</sub>	0	0
PDO <sub>AS</sub>	0	0
PDO <sub>pre</sub>	1	2
PRED <sub>age0.atf</sub>	0	0
PRED <sub>age0.csl</sub>	0	0
PREY <sub>larv.zp</sub>	0	0
PREY <sub>latelarv.eup</sub>	6	10
PREY <sub>pre.her</sub>	7	11
SPTR	1	2
SPTR <sub>pre</sub>	0	0
STORM <sub>larv</sub>	1	2
STORMB <sub>larv</sub>	13	21
STORMD <sub>larv</sub>	4	6
UW <sub>pre.cu</sub>	25	40
Total number of models	62	

*Note*: Bolded variables were those found in the AIC-best model. 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, firstfeeding larval stage; latelarv, late larval stage; NPGO, North Pacific Gyre Oscillation: ONI, Ocean Niño Index: PDO, Pacific Decadal Oscillation: pre. preconditioning stage;  $PRED_{age0.age1.hake}$ ; predation of age-0 hake by age-1 hake; PRED<sub>age0.atf</sub>, predation of age-0 hake by arrowtooth flounder; PRED<sub>age0.csl</sub>, predation of age-0 hake by California sea lions; PREY<sub>larv.zp</sub>, copepods as prey for first-feeding (and late) larvae; PREY<sub>latelarv.eup</sub>, euphausiids as prey for late larvae;  $\mathsf{PREY}_{\mathsf{pre.her}}$ , age-2 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.

Predictor

 $\mathsf{AST}_{\mathsf{yolk}}$ 

BI

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48

^

Number of jackknifes

Number of models

65

^

%

41

Λ

**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 *SDs* from the 2020 Pacific hake (*Merluccius productus*) stock assessment

ы	0	Ŭ	0
Bl <sub>pre</sub>	54	72	46
CALM <sub>larv</sub>	52	70	44
CST <sub>larv.s</sub>	2	2	1
CST <sup>2</sup> <sub>larv.s</sub>	1	1	1
CST <sub>latelarv.s</sub>	7	7	4
CST <sup>2</sup> <sub>latelarv.s</sub>	3	3	2
EKE <sub>MS.c</sub>	1	1	1
EKE <sub>pre.MS.c</sub>	87	128	81
$logPRED_{age0.age1.hake}$	19	21	13
ONI <sub>AS</sub>	0	0	0
ONI <sub>pre</sub>	0	0	0
NPGO <sub>AS</sub>	0	0	0
NPGO <sub>pre.AS</sub>	4	4	3
PDO <sub>JA</sub>	8	12	8
PDO <sub>AS</sub>	2	3	2
PDO <sub>pre</sub>	10	10	6
$PRED_{age0.atf}$	1	1	1
PRED <sub>age0.csl</sub>	0	0	0
PREY <sub>larv.zp</sub>	3	3	2
PREY <sub>latelarv.eup</sub>	7	8	5
<b>PREY</b> <sub>pre.her</sub>	23	27	17
SPTR	9	13	8
SPTR <sub>pre</sub>	2	2	1
STORM <sub>larv</sub>	0	0	0
	21	23	15
STORMD <sub>larv</sub>	4	5	3
UW <sub>pre.cu</sub>	48	63	40
Total	100	158	

*Note*: Each refit iteration could include multiple candidate models (with AICc < 2.0 and the fewest included parameters). The number of jackknives is the number of times the variable was included in one of the candidate models for any jackknife iteration. The 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.

Turley and 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

 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 <sub>yolk</sub>	2	5
BI	0	0
BI <sub>pre</sub>	23	55
CALM <sub>larv</sub>	10	24
CST <sub>larv.s</sub>	32	76
CST <sup>2</sup> <sub>larv.s</sub>	30	71
CST <sub>latelarv.s</sub>	0	0
CST <sup>2</sup> <sub>latelarv.s</sub>	0	0
EKE <sub>MS.c</sub>	0	0
EKE <sub>pre.MS.c</sub>	3	7
logPRED <sub>age0.age1.hake</sub>	41	98
ONI <sub>AS</sub>	4	10
ONI <sub>pre</sub>	26	62
NPGO <sub>AS</sub>	2	5
NPGO <sub>pre.AS</sub>	4	10
PDO <sub>JA</sub>	2	5
PDO <sub>AS</sub>	0	0
PDO <sub>pre</sub>	1	2
PRED <sub>age0.atf</sub>	14	33
PRED <sub>age0.csl</sub>	2	5
PREY <sub>larv.zp</sub>	0	0
PREY <sub>latelarv.eup</sub>	3	7
PREY <sub>pre.her</sub>	1	2
SPTR	0	0
SPTR <sub>pre</sub>	0	0
STORM <sub>larv</sub>	1	2
STORMB <sub>larv</sub>	0	0
STORMD <sub>larv</sub>	0	0
UW <sub>pre.cu</sub>	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.

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 & 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

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

Our analysis identified additional covariates that were less consistently correlated with recruitment but may be influential in some years. In particular, hake recruitment was linked to the NPGO, PDO, and upwelling during the adult female preconditioning stage, the number of calm periods and duration of storm events during the firstfeeding larval stage, euphausiid abundance during the late larval stage, predation by age-1 hake during the age-0 pelagic juvenile stage, and timing of the spring transition (Table 2). When a new model was fit with these additional covariates outside of our main analysis, almost 63% of the variability in Pacific hake recruitment deviations was explained, compared to 59% in the AIC-best model. However, model diagnostics for these models were poor, indicating that they were likely overfitting the data. Increased storm duration and the number of calm periods were likely linked with higher recruitment due to the previously described mechanisms, with enhanced feeding as prey are more frequently mixed downwards or descend to avoid turbulence during storms (Turley & Rykaczewski, 2019). An alternative mechanism could be that increased turbulence associated with increased storm duration would disrupt potential predation on larval hake as contacts rates decreased with high turbulence (Landry et al., 1995, and references therein). Atmospheric forcing associated with both the PDO and NPGO controls decadal modulation of the upwelling cells. resulting in spatially varying responses of coastal upwelling, with a strong PDO signal north of 38°N and a strong NPGO signal south of 38°N (Di Lorenzo et al., 2008). Chhak and Di Lorenzo (2007) found differences in modeled depth of the upwelling cell between "warm" and "cool" phases of the PDO, likely impacting nutrient flux and biological productivity, though differences were not as strong in southern regions of the CCE compared to northern regions. Thus, the PDO and NPGO may impact recruitment in Pacific hake through upwellingrelated changes in productivity and horizontal advection in the CCE.

While upwelling was not a predictor in our AIC-best model, it often appeared in other candidate models (Tables 2 and A2). Upwelling fuels the CCE's high biological productivity, and as such, we expected that higher upwelling would be linked to higher hake recruitment. Instead, we found that weaker upwelling north of 42°N from April to October during the adult female preconditioning stage was linked to higher recruitment. Upwelling may impact feeding adults in a number of ways. First, strong poleward flow is thought to aid Pacific hake adults in their northward migration to their summer feeding grounds (Agostini et al., 2006; Benson et al., 2002; Dorn, 1995; Smith et al., 1990). However, the spring transition to upwelling-favorable winds coincides with the onset of predominantly equatorward flow and a reduced California Undercurrent (Siedlecki et al., 2015). Thus, upwelling may impede the northward movement of hake, increasing

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**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.

the energy expended swimming against strong southward currents during their northward migration (Ressler et al., 2007), resulting in lower condition of pre-spawning females. Second, upwelling may impact Pacific hake recruitment through bottom-up processes that affect prey abundance and availability. Upwelling off Oregon and Washington is usually episodic, with events lasting from days to weeks followed by periods of relaxation (Barth et al., 2000; Huver, 1983; Huver et al., 1979). The shoreward advection of nearsurface waters during relaxation or downwelling events has been shown to control larval recruitment (Farrell et al., 1991; Mackas et al., 2001; Roughgarden et al., 1991; Shanks & Morgan, 2018), including that of euphausiids, which are an important prey item for Pacific hake throughout their range (Livingston & Bailey, 1985). Indeed, high euphausiid recruitment has been linked to periods of downwelling or below-average upwelling, which maintains larvae on the continental shelf instead of being transported offshore into less productive oceanic waters (Mackas et al., 2001). High abundances of hake have often been found in close proximity to high abundance patches of euphausiids near the shelf-break, but the overlap has been less obvious farther offshore (Phillips et al., 2022; Swartzman, 2001). Thus, while strong and persistent upwelling can transport phytoplankton blooms and zooplankton prey far from shore via strong Ekman transport (Botsford et al., 2006; Mackas et al., 2001), periods of reduced upwelling may be beneficial to Pacific hake adults on their summer feeding grounds by increasing the abundance of their euphausiid prey via enhanced recruitment, and also by maintaining spatial overlap with them through reducing their offshore transport.

The multiple model validation methods applied to these data suggest that the AIC-best model predictions were robust. Recruitment residuals fell well outside of the predicted 95% confidence interval in 1990, 2007, and 2009 (Figure 4a). The latter years coincide with an increase in the abundance and distribution of the Humboldt squid (Dosidicus gigas), which are voracious predators that are known to prey on Pacific hake (Field et al., 2007; Litz et al., 2011). Oddly, hake recruitment was high in 2009, when lower densities of juvenile hake were coincident with the presence of Humboldt squid (Litz et al., 2011). However, higher hake recruitment in 2009 could be linked to weaker than normal upwelling and extended relaxation events in summer 2009 (Biorkstedt et al., 2010), which may have maintained larvae and early juveniles in close proximity to nearshore nursery habitats, providing better feeding conditions compared to those found offshore. The lack of a clear link between the covariates examined in our study and high recruitment in 1990 suggests that other variables not included here may be important drivers of recruitment. The AIC-best model predictions from a leave-1-year-out jackknife analysis provided predictions that fell within the 95% confidence limits of the fitted AIC-best model in all years (Figure 4a). The AIC-best model predictions that used the available data through 2005 and then predicted 2006-2010 resulted in similar predictions to those from 1981 to 2010 (Figure 4b). However, two of the recruitment predictors in the AIC-best model (PREYpre,her and STORMBlary) were no longer significant. This was likely due to higher values of these predictors at the end of the time series, along with above average recruitment (except in 2007), which were removed when using the 1981 through 2005 training data set.

Predation on age-0 hake by the preceding cohort was an important predictor of hake recruitment in our jackknife analysis. Previous studies have shown that year-class strength was largely determined within the first few months of hatching (Bailey & Francis, 1985; Hollowed & Bailey, 1989), but predation on juvenile hake was not considered to be a major source of recruitment variability (Bailey & Francis, 1985). However, other studies have suggested that recruitment may be affected by adjacent-cohort cannibalism (Buckley & Livingston, 1997; Smith, 1995). Alternatively, increased competition for food may lead to reduced recruitment in a cohort that follows a successful one (Buckley & Livingston, 1997; Smith, 1995).

Arrowtooth flounder biomass was also an important predictor during the model testing and validation process. Pacific hake are the primary diet of arrowtooth flounder off the Oregon and Washington coasts (Buckley et al., 1999). The positive relationship with recruitment could potentially be explained by increased predation on older (age-2+) hake on their summer feeding grounds when arrowtooth flounder biomass is high. Density-dependent mortality due to cannibalism on age-0 and age-1 juvenile hake by older fishes is likely related to the amount of 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; Fiechter 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

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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 SST (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  $\triangle$ AICc < 2.0 One potential explanation for discrepancies between our analysis and past research findings could be that earlier studies were limited by shorter time series (e.g., Bailey, 1981) and previously observed relationships have not persisted over time. Indeed, associations between environmental conditions and biological responses are often non-stationary in time (Myers, 1998). For example, regression models assuming stationary climate-salmon relationships were found to be inappropriate over multidecadal time scales (1965-2012) in a recent study of salmon (Onchorynchus spp.) productivity in the Gulf of Alaska (Litzow et al., 2018). Relationships between recruitment, the prevalence of density dependence, and environmental drivers have also been shown to differ between PDO regimes for bocaccio rockfish (Sebastes paucispinis) (Tolimieri & Levin, 2005; Zabel et al., 2011). For Pacific hake, the changing relationships between recruitment strength and temperature and upwelling during the 1970s (Bailey, 1981) and the 1980s (Bailey & Francis, 1985) suggest that climate-recruitment relationships may also be non-stationary. Another potential explanation for why our recruitment predictors do not align with those found in previous studies is that different time frames were used to calculate the means for each predictor, obscuring conditions linked to high recruitment events. For example, Hollowed and Bailey (1989) found that successful year-classes of Pacific hake occurred after periods of low upwelling during early winter (either January or February) followed by a period of intense upwelling in March. Our predictors for upwelling during the yolk-sac and firstfeeding larval stages were calculated over January-April and February-May, respectively; thus, they likely would not capture specific upwelling events in March linked to high recruitment.

One limitation of our study is that the CCE ROMS domain only covers the US west coast; thus, we are unable to address oceanographic conditions in Canadian or Mexican waters that might be important to Pacific hake recruitment. Several predictors did represent

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

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

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

Our results can also inform assessments of hake's vulnerability to climate change and an ongoing climate-informed MSE focused on hake. Several of the indicators of recruitment we identified come from a ROMS product, and a related product has recently been forecasted to 2100 (Pozo Buil et al., 2021), meaning we can use forecasts of the drivers we identified to begin to understand how recruitment variability could change under future ocean conditions. Additionally, an MSE for hake has shown that a northward distribution shift in the population could result in diminished ability of the US fishery to catch fish in US 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 fisherv.

#### 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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#### CONFLICT OF INTEREST STATEMENT

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

#### 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 (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).

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#### SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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![](_page_27_Figure_2.jpeg)

**FIGURE A1** 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.

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![](_page_28_Figure_0.jpeg)

FIGURE A3 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.

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þ	Source	ROMS	ROMS	Jacox et al. (2018), oceanview.pfeg.noaa.gc	Jacox et al. (2018), https://oceanview. pfeg.noaa.gov	Stock assessments	CBR Mean Method, Van Holmes (2007), cbr.washington.edu/ status/trans	(Conti
	atitudinal ctent	2° −47° N	2° -47° N	1.5°-47.5°N	1.5°-47.5°N		2°N (west of OR/CA border) 5°N (west of Siletz Bay, OR) 3°N (west of La Push, WA)	
)	Longitudinal L. extent e:	Shelf break, 4 between 100 and 2,000 m isobaths	Shelf break, 4 between 100 and 2,000 m isobaths	0–75 km dfshore	0–75 km d offshore		125°W 4	
-	Depth	50-350 m	50-350 m	Base of mixed layer	Base of mixed layer			
-	Covariates	Mean temperature	Degree days	Coastal upwelling (CUTI)	Biologicially effective upwelling (BEUTI)	Index of age-0 and age-1 Pacific hake biomass and age-2 Pacific herring biomass	Mean date of the spring transition from downwelling- favorable southerly winds to upwelling- favorable northerly winds	
-	Stage	TEMP <sub>pre</sub>	DD <sub>pre</sub>	UWpre.c	UW <sub>pre.b</sub>	PREY <sub>pre-her</sub> PREY <sub>pre-juv</sub> hake	SPTRpre	
-	Hypothesis	(H1) Higher temperature increases food demand resulting in lower egg production, egg quality, or probability of spawning and lowers recruitment	(H2) As (H1), but degree days, not mean temperature	(H3) Higher coastal upwelling leads to increased productivity, better condition, higher egg production, egg quality, or probability of spawning and increases recruitment	(H4) As (H3), but biologically effective upwelling	(H5) Food availability affects energy allocation to reproduction with higher recruitment when more prey are available during the preconditioning period	(H6) Timing of availability of food affects energy allocation to reproduction with higher recruitment when more prey are available during the preconditioning period	
	Time period	Apr-Oct (year 0)						
	Life-history stage	Preconditioning						
	Ho number	H H	H2	Н3 Н	H4	H5	9H	

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

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Source	ROMS	ROMS	ROMS	ROMS	ROMS	ROMS	ROMS	ROMS
						z		
Latitudinal extent	31°-36°N	31°-36°N	31°-36°N	31°-34.5° N 34.5° -36° N	31°-36°N	32.5° -33.5°	31°-36°N	31°-36°N
Longitudinal extent	Shelf break, between 100 and 2,000 m isobaths	Shelf break, between 100 and 2,000 m isobaths	Shelf break, between 100 and 2,000 m isobaths	Shelf break, between 100 and 2,000 m isobaths	Shelf break, between 100 and 2,000 m isobaths	Coast to 275 m isobath	Shelf break, between 100 and 2,000 m isobaths	Shelf break, between 100 and 2,000 m isobaths
Depth	130-500 m	130-500 m		40-60 m	40-60 m	75-275 m	40-60 m	
Covariates	Mean temperature	Degree days	Mean mixed layer depth (m)	Net cross-shelf transport	Net along-shore transport	Strength of the poleward undercurrent	Degree days	Mean mixed layer depth (m)
Stage	TEMP <sub>spawn</sub>	DD <sub>spawn</sub>	MLD <sub>eggs</sub>	CST <sub>eggs.n</sub> CST <sub>eggs.n</sub>	ASTeggs	PUeses	DDeges	MLD <sub>volk</sub>
Hypothesis	(H7) Temperature acts as a spawning cue with fish less likely to spawn at high temperature resulting in lower recruitment	(H8) As (H7), but degree days, not mean temperature	(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	(H10) Transport to settlement habitat affects recruitment (transport varies with latitude)	(H11) Increased northward advection away from juvenile nursery areas decreases recruitment	(H12) Increased northward advection away from juvenile nursery areas decreases recruitment	(H13) Growth/predation hypothesis: Growth rate is faster in warm water leading to reduced time vulnerable to predators	(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
Time period	Jan-Mar		Jan-Mar					Jan-Apr
Life-history stage	Spawning		Eggs					Yolk-sac larvae
Ho number	H H	H8	£	H10	H11	H12	H13	H14

TABLE A	11 (Continued)								
Ho number	Life-history stage	Time period	Hypothesis	Stage	Covariates	Depth	Longitudinal extent	Latitudinal extent	Source
H15			(H15) Transport to settlement habitat affects recruitment (transport varies with latitude)	CST <sub>yolk.s</sub> CST <sub>yolk.n</sub>	Net cross-shelf transport	50-100 m	Shelf break, between 100 and 2,000 m isobaths	31°-34.5° N 34.5°-36° N	ROMS
H16			(H16) Increased northward advection away from juvenile nursery areas decreases recruitment	AST <sub>yolk</sub>	Net along-shore transport				ROMS
H17			(H17) Increased northward advection away from juvenile nursery areas decreases recruitment	PU <sub>volk</sub>	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 <sub>volk</sub>	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 <sub>arv</sub>	Mean mixed layer depth (m)		Shelf break, between 100 and 2,000 m isobaths	31°36°N	ROMS
H20			(H20) Transport to settlement habitat affects recruitment (transport varies with latitude)	CST <sub>larv.s</sub> CST <sub>larv.n</sub>	Net cross-shelf transport	50-200 m	Shelf break, between 100 and 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 survivaland recruitment, transport to settlementhabitat affects recruitment	ASTIarv	Net along-shore transport	50-200 m	Shelf break, between 100 and 2,000 m isobaths	31°-36°N	ROMS
H22			(H22) Increased northward advection away from juvenile nursery areas decreases recruitment	PU <sub>larv</sub>	Strength of the poleward undercurrent	75-275 m	Coast to 275 m isobath	32.5°-33.5°N	ROMS

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Ho number	Life-history stage	Time period	Hypothesis	Stage	Covariates	Depth	Longitudinal extent	Latitudinal extent	Source
H23			(H23) Higher coastal upwelling leads to increased productivity, better condition, higher survival and increased recruitment	UW <sub>larv.cs</sub> UW <sub>larv.cn</sub>	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), oceanview.pfeg.noaa.gov/
H24			(H24) As (H23), but biologically effective upwelling	UW <sub>larv.bs</sub> UW <sub>larv.bn</sub>	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 is faster in warm water leading to reduced time vulnerable to predators	DD <sub>larv</sub>	Degree days	50-200 m	Shelf break, between 100 and 2,000 m isobaths	31°-36°N	ROMS
H26			(H26) Higher zooplankton abundance leads to higher survival and recruitment	PREV <sub>larv.zp</sub>	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
Н27			(H27) Critical period hypothesis: More frequent storm events lead to poorer feeding conditions, lower survival and recruitment	STORMarv	Mean number of storm events		Coast to 126°W	28°-30° 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 survival and recruitment	STORMD <sub>iarv</sub>	Mean duration of storm events		Coast to 126°W	28° –36° N	Turley and Rykaczewski (2019), CFSR, Saha et al. (2010)
Н29			(H29) Critical period hypothesis: Fewer days between storm events lead to poorer feeding conditions, lower survival and recruitment	STORMB <sub>larv</sub>	Mean number of days between storm events		Coast to 126°W	28°-34° N	Turley and Rykaczewski (2019), CFSR, Saha et al. (2010)

TABLE A1 (Continued)

TABLE A	1 (Continued)								
Ho number	Life-history stage	Time period	Hypothesis	Stage	Covariates	Depth	Longitudinal extent	Latitudinal extent	Source
Н30			(H30) Critical period hypothesis: More frequent calm events lead to better feeding conditions, higher survival and recruitment	CALM <sub>larv</sub>	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, lower survival and recruitment	CALMD <sub>larv</sub>	Mean duration of calm events		Coast to 126°W	28°-36°N	Turley and Rykaczewski (2019), CFSR, Saha et al. (2010)
Н32			(H32) Critical period hypothesis: Shorter intervals between calm events lead to better feeding conditions, higher survival and recruitment	CALMB <sub>larv</sub>	Mean number of days between calm events		Coast to 126°W	28°-36°N	Turley and Rykaczewski (2019), CFSR, Saha et al. (2010)
Н33	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 <sub>latelarv</sub>	Mean location of mixed layer depth (m)		Shelf break, between 100 and 2,000 m isobaths	N°-37° N°	ROMS
H34			(H34) Transport to settlement habitat affects recruitment (transport varies with latitude)	CST <sub>latelarv.s</sub> CST <sub>latelarv.n</sub>	Net cross-shelf transport	50-300 m	Shelf break, between 100 and 2,000 m isobaths	31°-34.5°N 34.5°-37°N	ROMS
Н35			(H35) North to south transport brings northern zooplankton and leads to higher survivaland recruitment, transport to settlementhabitat affects recruitment	AST <sub>latelarv</sub>	Net along-shore transport	50-300 m	Shelf break, between 100 and 2,000 m isobaths	N∘75-∘15	ROMS
Н36			(H36) Increased northward advection away from juvenile nursery areas decreases recruitment	PU <sub>latelarv</sub>	Strength of the poleward undercurrent	75-275 m	Coast to 275 m isobath	33.5°34.5°N	ROMS
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	Source	Jacox et al. (2018), oceanview.pfeg.noaa.gov	Jacox et al. (2018), https://oceanview. pfeg.noaa.gov	SOMS	CBR Mean Method, Van Holmes (2007) http:// www.cbr.washington.edu/ status/trans	Zooplankton database, Scripps Institute of Oceanography (SIO) https://oceaninformatics. ucsd.edu/zoodb/secure/ login.php	Brinton and Townsend Euphausiid database, SIO https://oceaninformatics. ucsd.edu/euphausiid/ secure/login.php	ROMS	ROMS
	Latitudinal extent	30.5° – 34.5° N 34.5° – 37.5° N	30.5° –34.5° N 34.5° –37.5° N	31°-37°N	42° N (west of OR/CA border) 45° N (west of Siletz Bay, OR) 48° N (west of La Push, WA)	31.5°-34.5°N	29.9°-35.1°N	31°-34.5°N 34.5°-38°N	31°-38°N
	Longitudinal extent	0-75 km offshore	0–75 km offshore	Shelf break, between 100 and 2,000 m isobaths	125°W	117.4-121.9°W	117.3° - 125.0°W	Inshore of 200 m isobath	Inshore of 200 m isobath
	Depth	Base of mixed layer	Base of mixed layer	50-300 m		0-210 m	0-210 m	0-50 m	0-50 m
	Covariates	Coastal upwelling (CUTI)	Biologicially effective upwelling (BEUTI)	Degree days	Mean date of the spring transition from downwelling- favorable southerly winds to upwelling- favorable northerly winds	Index of copepod abundance	Index of euphausiid abundance	Net cross-shelf transport	Net along-shore transport
	Stage	UW latelarv.cs UW latelarv.cn	UW <sub>latelarv.bs</sub> UW <sub>latelarv.bn</sub>	DD <sub>latelarv</sub>	SPTR <sub>latelarv</sub>	PREY <sub>latelarv zp</sub>	PREY <sub>latelarv.eup</sub>	CST <sub>age0.s</sub> CST <sub>age0.n</sub>	AST <sub>aeo</sub>
	Hypothesis	(H37) Higher coastal upwelling leads to increased productivity, better condition, higher survival and increased recruitment	(H38) As (H37), but biologically effective upwelling	(H39) Growth/predation hypothesis: Growth rate is faster in warm water leading to reduced time vulnerable to predators	(H40) Timing of availability of food affects condition, leading to higher survival and increased recruitment	(H41) Higher prey abundance leads to higher survival and recruitment		(H42) Transport to settlement habitat affects recruitment (transport varies with latitude)	(H43) North to south transport brings northem zooplankton and leads to higher survivaland recruitment, transport to
	Time period							Apr - Sep	
1 (Continued)	Life-history stage							Pelagic juveniles (age-0)	
TABLE A	Ho number	Н37	H38	НЗ9	Н40	H41		H42	H43

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Source		Jacox et al. (2018), oceanview.pfeg.noaa.gov		Jacox et al. (2018), oceanview.pfeg.noaa.gov		ROMS	CBR Mean Method, Van Holmes (2007) cbr. washington.edu/status/ trans		Brinton and Townsend Euphausiid database, SIO https://oceaninformatics. ucsd.edu/euphausiid/ secure/login.php	Stock assessments, Laake et al. (2018)	(Continues)
Latitudinal extent		30.5° −34.5° N	34.5° -38.5° N	30.5° – 34.5° N	34.5°-38.5°N	31°-38°N	42°N (west of OR/CA border) 45°N (west of Siletz Bay, OR) 48°N (west of La Push, WA)		29.9°-35.1°N		
Longitudinal		0-75 km offshore		0-75 km offshore		Inshore of 200 m isobath	125°W		117.3°-125.0°W		
Denth	-	Base of mixed layer		Base of mixed layer		0-50 m			0-210 m		
Covariates		Coastal upwelling (CUTI)		Biologicially effective upwelling (BEUTI)		Degree days	Mean date of the spring transition from downwelling- favorable southerly winds to upwelling-	favorable northerly winds	Index of euphausiid abundance	Index of age-1 Pacific hake biomass, arrowtooth flounder biomass,	
Stage	0	UW <sub>age0.cs</sub> UW <sub>age0.cn</sub>		UW <sub>age0.bs</sub> UW <sub>age0.bn</sub>		DD <sub>ageo</sub>	SPTRageo		PREV <sub>age0.eup</sub>	PRED <sub>age0.age1</sub> hake PRED <sub>age0.atf</sub> PRED <sub>age0.cs1</sub>	
Hvnothesis	settlementhabitat affects recruitment	(H44) Higher coastal upwelling leads to	increased productivity, better condition, higher survival and increased recruitment (upwelling varies with latitude)	(H45) As (H44), but biologically effective upwelling		(H46) Growth/predation hypothesis: Growth rate is faster in warm water leading to reduced time vulnerable to predators	(H47) Timing of availability of food affects condition, leading to higher survival and increased recruitment		(H48) Increased food availability leads to better feeding conditions, leading to higher survival and recruitment	(H49) Higher predation leads to lower survival and recruitment	
Time	L										
Life-history stage	0										
Ho number		H44		H45		H46	H47		H48	H49	

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ource		SMOS		SMOS	√antua et al. (1997), esearch.jisao. vashington.edu/pdo/
Latitudinal extent		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°N	34.5°-42.5°N 42.5°-47°N 34.5°-47°N 31°-34.5°N 31°-34.5°N 31°-34.5°N 31°-34.5°N	
Longitudinal extent		0-30 km offshore		0-30 km offshore	
Depth		Surface		Surface	
Covariates	California sea lion pup counts	Sea surface height		Eddy kinetic energy	Pacific Decadal Oscillation
Stage		SSH pre.JA.s SSH pre.JA.c SSH pre.MS.c SSH pre.MS.n	SSH <sub>JAs</sub> SSH <sub>JAc</sub> SSH <sub>MSs</sub>	EKE <sub>pre-Jas</sub> EKE <sub>pre-Jac</sub> EKE <sub>pre-MS,n</sub> EKE <sub>Jas</sub> EKE <sub>Jas</sub> EKE <sub>Jas</sub>	PDO <sub>Pre</sub> PDO <sub>JA</sub>
Hypothesis		(H50) Sea surface height as an indicator of basin- scale processes		(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 to better feeding conditions, higher survival and recruitment	(H52) Pacific Decadal Oscillation as an indicator of basin-scale processes; negative phase linked to higher productivity, better feeding conditions, better
Time period		Jan-Apr May - Sep	Jan-Apr May-Sep	Jan-Apr May-Sep May-Sep	Apr-Sep Jan-Apr Apr-Sep
Life-history stage		Preconditioning	Egg to late larvae First feeding larvae to age-0	Preconditioning First feeding larvae to age-0 Late larvae to age-0	Preconditioning
Ho number		H50		H51	H52

# TABLE A1 (Continued)

			FISHERIES FOCEANOGRAPHY	-WILEY
Source		Di Lorenzo et al. (2008), o3d.org/npgo/	Malick et al. (2017)	
Latitudinal extent				
Longitudinal extent				
Depth				
Covariates		North Pacific Gyre Oscillation	Bifurcation Index	
Stage		NPGO <sub>pre</sub> NPGO <sub>AS</sub>	BI BI	
Hypothesis	condition, higher survival and recruitment	(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	(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	
Time period		Apr-Sep Jan - Apr Apr - Sep		
Life-history stage		Preconditioning	Preconditioning First-feeding larvae to age-0	
Ho number		H53	H54	