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Oceanographic drivers of petrale sole recruitment in the **California Current Ecosystem**

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Abstract

This paper investigates environmental drivers of U.S. West Coast petrale sole (Eopsetta jordani) recruitment as an initial step toward developing an environmental recruitment index that can inform the stock assessment in the absence of survey observations of age-0 and age-1 fish. First, a conceptual life history approach is used to generate life-stage-specific and spatio-temporally specific mechanistic hypotheses regarding oceanographic variables that likely influence survival at each life stage. Seven life history stages are considered, from female spawner condition through benthic recruitment as observed in the Northwest Fisheries Science Center West Coast Groundfish Bottom Trawl Survey (age-2 fish). The study area encompasses the region from 40 to 48°N in the California Current Ecosystem. Hypotheses are tested using output from a regional ocean reanalysis model outputs and model selection techniques. Four oceanographic variables explained 73% of the variation in recruitment not accounted for by estimates based exclusively on the spawning stock size. Recruitment deviations were (a) positively correlated with degree days during the female precondition period, (b) positively correlated with mixed-layer depth during the egg stage, (c) negatively correlated with cross-shelf transport during the larval stage, and (d) negatively correlated with cross-shelf transport during the benthic juvenile stage. While multiple mechanisms likely affect petrale sole recruitment at different points during their life history, the strength of the relationship is promising for stock assessment and integrated ecosystem assessment applications.

KEYWORDS

California Current, Eopsetta jordani, oceanic drivers, petrale sole, recruitment

1 | INTRODUCTION

Petrale sole (Family: Pleuronectidae, Eopsetta jordani) has consistently been the most commercially valuable flatfish targeted in the California Current Ecosystem. During the 1980s through the 2000s, the petrale sole spawning biomass was around or below 10% of the unexploited stock size (Haltuch, Ono, & Valero, 2013). More recently, the fishery has depended on infrequent above average recruitments, generally followed by several years of low recruitments, that drive fluctuations in the spawning biomass (Figure 1; Haltuch et

al., 2013). This dependence of the fishery on relatively few strong recruitment events makes understanding the drivers of petrale sole recruitment a priority.

The horizontal-advection bottom-up forcing paradigm provided a mechanistic framework for testing the hypothesis that climate-driven changes in cross-shelf and alongshore advection drive petrale sole recruitment strength (Di Lorenzo, Mountain, Batchelder, Bond, & Hofmann, 2013; Parrish, Nelson, & Bakun, 1981). This paradigm suggested that large-scale climate forcing drives regional changes in alongshore and cross-shelf ocean transport that directly

impact ecosystem functions such as productivity, species composition, and spatial connectivity. Oceanographic studies illustrated the influence of large-scale climate drivers on mesoscale processes in the California Current Ecosystem that drive cross-shelf and alongshore transport at local scales (Chelton, Bernal, & Mcgowan, 1982; Combes et al., 2013; Di Lorenzo et al., 2013; Hickey, 1979; Keister, Lorenzo, Morgan, Combes, & Peterson, 2011). Variability in crossshelf transport in the California Current Ecosystem was important for understanding population and ecosystem dynamics because of variable offshore and northward transport of nutrients, mass, and organisms (Combes et al., 2013; Di Lorenzo et al., 2013; Jacox, Hazen, & Bograd, 2016). Additionally, fish life cycles and population connectivity patterns can be impacted via the transport of larvae by either coastal upwelling or offshore advection of water from the poleward flowing California Undercurrent (Combes et al., 2013; Di Lorenzo et al., 2013). Research has suggested that horizontal advection affects density-independent survival during early life stages, specifically that offshore transport of eggs and larvae results in poor recruitment (Castillo, 1995; Castillo, Li, & Golden, 1994). Furthermore, decadal-scale variability in wind-driven cross-shelf transport of early life stages of other flatfish species toward favorable nursery areas influenced recruitment strength (Hollowed et al., 2009; Wilderbuer et al., 2002; Wilderbuer, Stockhausen, & Bond, 2013). Concurrently, temperature can influence growth rates of early life history stages, mediating larval vulnerability to predation and the likelihood of starvation (Chezik, Lester, & Venturelli, 2014; Houde, 1987; Leggett & DeBlois, 1994; Litvak & Leggett, 1992).

This study leveraged recruitment estimates from an information-rich stock assessment for the California Current Ecosystem petrale sole stock (Stawitz et al., 2016) to build a mechanistic ISHEKIES ICEANOGRAPHY

framework for investigating oceanographic drivers of survival using a conceptual life history approach to frame hypotheses regarding factors that affect survival at each early life history stage. Petrale sole were an excellent candidate for investigations into oceanographic drivers of recruitment strength for multiple reasons. First, the petrale sole data set were likely the most information-rich groundfish data set due to the large amount of age and length data that spans multiple generations (compared to <1 generation for most rockfishes). Next, multiple stock assessment models and model sensitivity runs, and thus historical recruitment estimates, produced highly similar results. Finally, previous fisheries and oceanographic research suggested potential mechanisms for oceanographic drivers of petrale sole recruitment. However, prior to using oceanographic recruitment drivers to forecast recruitment for either near-term tactical management or long-term strategic decision-making, statistical models must be built and evaluated. Our goal was to develop a statistically robust environment-recruitment relationship to explain variability in recruitment (Basson, 1999) for use in both near-term and long-term petrale sole recruitment forecasting. We developed and tested a series of generalized linear models (GLMs) to explore the influence of oceanographic drivers on petrale sole survival at different life stages, from female spawner condition through benthic recruitment.

2 | METHODS

This study applied the methodology implemented by Tolimieri, Haltuch, Lee, Jacox, and Bograd (2018) for sablefish to the U.S. West Coast petrale sole stock using estimates of log recruitment

FIGURE 1 Biological parameters from the 2015 petrale sole stock assessment for 1981–2010: (a) spawning stock biomass (SSB) in metric tons, (b) thousands of age-0 recruits, (c) stock-recruitment relationship (line) versus observed data (points), and (d) the log recruitment deviations from the stock assessment. Dotted lines are ±1.0SD



TABLE 1 Conceptual life history model

116	Maar	Stage	Channe da untile	Ho	the state of	
Preconditioning	Year 0, May- October	uuration	Bottom depths of 50–200 m	1	Higher bottom water temperatures in- creases food demand resulting in lower egg production, egg quality, or probabil- ity of spawning and lowers recruitment (likely a bell-shaped relationship)	Mean bottom water tempera- ture (°C, 4 days)
Spawning	Year 1, November– March		Bottom depths of 250–500 m	2	Bottom water temperature acts as a spawning cue with fish less likely to spawn at high temperature resulting in lower recruitment	Mean bottom water tempera- ture (°C, 4 days)
			Bottom depths of 250–500 m	3	Water column temperature acts as a spawning cue with fish less likely to spawn at high temperature resulting in lower recruitment	Mean water column tempera- ture (°C, 4 days)
Egg, surface	Year 1, November- April	6-14 days	Water column from surface to MLD	4	Eggs are buoyant so mixed-layer depth limits how far they rise in the water column affecting later transport	Mean mixed-layer depth (m)
			Water column from surface to MLD	5	Transport in the water column above the MLD to settlement habitat affects recruitment	Mean long-shore transport between the surface and MLD (m/s, 4 days cumulative)
			Water column from surface to MLD	6	Transport in the water column above the MLD to settlement habitat affects recruitment (aka Advection reduces recruitment while retention enhances recruitment)	Mean cross-shelf transport between the surface and MLD (m/s, 4 days cumulative)
			Water column from surface to MLD	7	Growth/Predation hypothesis: growth rate is faster in warm water leading to reduced time vulnerable to predators	Degree days in the water column calculated from mean water column temperature between the surface and MLD (days, 4 days)
Egg, sinking	Year 1, November– April	6-14 days	Water column from MLD to 400 m	8	Transport in the water column to settle- ment habitat affects recruitment (aka Advection reduces recruitment while retention enhances recruitment)	Mean long-shore transport from the MLD to 400 m (m/s, 4 days cumulative)
			Water column from MLD to 400 m	9	Transport in the water column to settle- ment habitat affects recruitment	Mean cross-shelf transport from the MLD to 400 m (m/s, 4 days cumulative)
			Water column from MLD to 400 m	10	Growth/Predation hypothesis: growth rate is faster in warm water leading to reduced time vulnerable to predators	Degree days in the water column calculated from mean water column temperature between the MLD and 400 m (days, 4 days)
Larvae (both yolk sac and feeding)	Year 1, December- May	~5 months for all pelagic stages	Water column from 0 to 50 m	11	North to south transport in the water col- umn brings northern zooplankton and leads to higher survival and recruitment	Mean long-shore transport in the water column at 50– 150 km offshore (m/s, 4 days cumulative)
			Water column from 0–50 m	12	Transport in the water column to settle- ment habitat affects recruitment (aka Advection reduces recruitment while retention enhances recruitment)	Mean cross-shelf transport in the water column at 50– 150 km offshore (m/s, 4 days cumulative)
			Water column from 0 to 50 m	13	Growth/Predation hypothesis: growth rate is faster in warm water leading to reduced time vulnerable to predators	Degree days in the water column calculated from mean water column temperature at 50 – 150 km offshore (days, 4 days)

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Life stage	Year	Stage duration	Stage depth	Ho Number	Hypothesis	ROMS covariates (40°N-48°N)
Pelagic juveniles (feeding pelagics)	Year 1, March-June	I, ~5 months n-June for all pelagic stages	Water column from 0 to 150 m	14	North to south transport brings northern zooplankton and leads to higher survival and recruitment, Transport to settle- ment habitat affects recruitment	Mean long-shore transport in the water column at 80– 120 km offshore (m/s, 4 days cumulative)
			Water column from 0 to 150 m	15	Transport in the water column to settle- ment habitat affects recruitment (aka Advection reduces recruitment while retention enhances recruitment)	Mean cross-shelf transport in the water column at 80– 120 km offshore (m/s, 4 days cumulative)
			Water column from 0 to 150 m	16	Growth/Predation hypothesis: growth rate is faster in warm water leading to reduced time vulnerable to predators	Degree days in the water column calculated from mean water column temperature at 80- 120 km offshore (days, 4 days)
Benthic Juvenile (Age-0)	Year 1, April- October		Bottom depths from 50–150 m AND 150–500 m	17	Bottom water transport to settlement habitat affects recruitment (Advection reduces recruitment while retention enhances recruitment)	Mean long-shore transport at bottom depths of 50–150 m and 150 – 500 m (m/s, 4 days cumulative); Two depth ranges are considered due to uncertainty regarding juvenile distributions
			Bottom depths from 50-150 m AND 150-500 m	18	Bottom water transport to settle- ment habitat affects recruitment (aka Advection reduces recruitment while retention enhances recruitment)	Mean cross-shelf transport at bottom depths of 50–150 m and 150–500 m (m/s, 4 days cu- mulative); Two depth ranges are considered due to uncertainty regarding iuvenile distributions

Note: Bold text indicates covariates extracted from the ROMs model or derived from ROMs model covariates for the recruitment modeling component of this study.

deviations from the petrale stock assessment (Stawitz et al., 2016) from 1981 to 2010 and model output from a California Current Ecosystem configuration of the Regional Ocean Modeling System (ROMS) with data assimilation (Neveu et al., 2016). While reliable recruitment estimates from the petrale sole stock assessment ranged from 1945, due to earlier collections of length and age composition data, through 2013, the ROMS model outputs did not span the full time series of recruitment estimates. ROMS model outputs were available from 1981 through 2010. We focused on the northern portion of the stock (40-48°N) because a majority of the spawning biomass and spawning grounds were distributed in the north and recruitment estimates from the coast-wide stock assessment model were most strongly informed by age and length composition data from the north (Stawitz et al., 2016). Petrale sole stock assessments prior to 2009 were conducted separately for northern and southern regions of the California Current Ecosystem (Lai, Haltuch, Punt, & Cope, 2005). However, due to strong similarities in both spawning biomass and recruitment trends the regional stock assessments were combined into a single coast-wide stock assessment during 2009 (Haltuch & Hicks, 2009). We considered the time from female pre-spawning condition through benthic recruitment (age-0 fish). This conceptual approach allowed for the generation of life-stagespecific and spatio-temporally specific hypotheses regarding the physical variables likely to influence petrale sole survival at each life stage leading to recruitment. Hypotheses were tested using linear modeling, model selection, and model validation.

2.1 | Petrale sole life history: female preconditioning to age-0 recruits

The conceptual life history approach tracked each life stage beginning with female condition prior to the spawning season through recruitment at age 0 (Table 1). Research on rockfishes and sablefish has shown that female condition may influence whether or not an individual spawns, and the quality and number of eggs produced by female fishes (Rodgveller, Stark, Echave, & Hulson, 2016; Sogard, Berkeley, & Fisher, 2008). While petrale sole may have the potential for skip spawning, currently available data are inconclusive (Pers. Comm. M. Head). Petrale sole spawn during the winter; thus, the summer and fall prior to spawning (May to October) were important for female preconditioning.

Spawning occurred from November to March with a peak during December to January (Cleaver, 1949; DiDonato & Pasquale, 1970; Harry, 1959; Pedersen, 1975). Petrale sole form deepwater spawning aggregations (270–460 m) at localized sites along the shelf break, with most spawning taking place at depths ranging from 250 to 500 m (Best, 1960; Casillas et al., 1998; Castillo, 1995; Castillo et al., 1994; Gregory & Jow, 1976; Harry, 1959; Love, 1996; Moser, 1996). Females spawn once each year and fecundity varies allometrically with fish size, with one large female laying as many as 1.5 million eggs (Porter, 1964). Eggs rise to the surface between November and April, remaining in surface waters for 6–14 days (Alderdice & Forrester, 1971; Casillas et al., 1998; Hart, 1973; Love, 1996), and WILEY-FISHERIES

then sink to approximately 400 m depth before hatching (Hunter, Macewicz, & Kimbrell, 1989; Kendall & Matarese, 1987; Mason, Beamish, & McFarlane, 1983; Moser et al., 1994) as yolk-sac larvae. After hatching, the larvae rise to the upper 50 m of the water column and remain there for approximately 5 months, through the feeding larval stage (Alderdice & Forrester, 1971; Casillas et al., 1998; Hart, 1973; Love, 1996; Pearcy, Hosie, & Richardson, 1977). Planktonic petrale sole larvae range in size from approximately 3-20 mm and were found up to 150 km offshore foraging upon copepod eggs and nauplii (Casillas et al., 1998; Hart, 1973; MBC Applied Environmental Sciences, 1987; Moser, 1996). At about 2.2 cm in length, petrale sole larvae settle to the benthos as age-0 recruits on the inner continental shelf (Pearcy et al., 1977). Benthic juveniles inhabit sandy or sand-mud bottoms (Eschmeyer, Herald, & Hammann, 1983; MBC Applied Environmental Sciences, 1987), ranging in size from approximately 2.2 cm to the size at maturity. Fifty percent of the population was mature at approximately 38 and 41 cm for males and females, respectively (Casillas et al., 1998). Specific nursery areas for juvenile petrale sole have not been identified. Due to a lack of sampling of newly settled petrale sole, this study evaluated two alternative hypotheses regarding settlement depths, from 50 to 150 m depth and from 150 to 500 m depth.

In northern and central California, petrale sole were found primarily on the middle and outer continental shelf (Allen, Pondella, & Horn, 2006). Pacific Fisheries Information Network (PacFIN) fishery logbook data showed that a majority of the adult petrale sole catch off the U.S. West Coast takes place between 70 and 220 m during March through October and between 290 and 440 m from November through February.

Juveniles show little coast-wide or bathymetric movement, while studies suggested that adults generally move inshore and northward to the continental shelf feeding grounds during the spring and summer and offshore and southward to deepwater spawning grounds during the fall and winter (Hart, 1973; Horton, 1989; Love, 1996; MBC Applied Environmental Sciences, 1987).

2.2 | Regional ocean modeling system (ROMS)

Predictors considered here were physical oceanographic parameters including temperature, long-shore and cross-shelf currents, and mixed-layer depth (Table 1). Variables were obtained from a California Current Ecosystem configuration of the Regional Ocean Modeling System (ROMS) of the California Current Ecosystem with 4-Dimensional Variational (4D-Var) data assimilation (Neveu et al., 2016). The ROMS model domain covered the region 30–48°N and from the coast to 134°W at 0.1° (~10 km) horizontal resolution, with 42 terrain-following vertical levels. For the 1980–2010 California Current Ecosystem reanalysis used for this study, satellite observations (SST, SSH) and in situ data (temperature and salinity measurements from ships, floats, moorings) are assimilated into the model to improve its representation of the true ocean state. This reanalysis has been used extensively to study physical and biogeochemical dynamics in the California Current Ecosystem (Jacox, Bograd, Hazen, & Fiechter, 2015; Jacox, Fiechter, Moore, & Edwards, 2015; Jacox, Moore, Edwards, & Fiechter, 2014) and to develop models of marine species recruitment (Tolimieri et al., 2018) and distribution (e.g., Brodie et al., 2018). All ROMS outputs for the study region were obtained as 4-day averages, and then either averaged or summed over the appropriate life history time period (as defined in Table 1) within each of the 30 years (1980–2010) for each time series in the analysis. Specific hypotheses for each predictor below are described below.

Oceanographic data were scarcer at depth than at the surface. As a result, the ROMS output that assimilates available data was less constrained by observations at the subsurface than at the surface. Therefore, the ROMS output likely deviates from nature more at the subsurface than at the surface. However, the paucity of subsurface data was the motivation for using model output in this study; the model output was useful despite the inability to validate the subsurface model transport. Data assimilation was used to improve models that already capture the California Current Ecosystem dynamics without data assimilation. The fidelity of this model to nature has been documented extensively for applications with and without data assimilation (e.g., Jacox, Bograd, et al., 2015; Veneziani, Edwards, Doyle, & Foley, 2009). The model was forced by realistic winds, surface heat fluxes, and lateral boundary conditions, which drive realistic physical variability even in the absence of data assimilation. Assimilated data, even if only available at the surface, can influence the subsurface dynamics. For example, assimilating sea surface height measurements constrains the geostrophic flow and therefore transport at both the surface and subsurface. The impact of assimilated data on different metrics of the California Current Ecosystem circulation is discussed in detail in Moore et al. (2017).

2.3 | Hypotheses and additional data sources

We developed 18 a priori, life-stage-specific and space-specific (considering time, depth, and longitude) hypotheses for environmental covariates that may drive variation in petrale sole recruitment (Table 1). Hypotheses for age-0 benthic juveniles were tested using two depth ranges given the uncertainty and lack of literature regarding the depth range of newly settled to age-2 juvenile petrale sole. Given the 18 hypotheses, three of which had two covariates, 21 total predictors were tested. Each hypothesis tested had specific temporal, longitudinal, and depth ranges (Table 1).

Only hypotheses that had ROMS model outputs available were tested (Table 1), thus excluding potential hypotheses such as food availability for larvae and pelagic juveniles (McFarlane & Beamish, 1992), which remain untestable due to insufficient data. This study did not test mechanisms with potential indirect effects on survival at each life stage such as drivers of food availability (e.g., upwelling). However, some of these effects are implicit in the transport and temperature indices that are included (e.g., upwelling cools surface waters and drivers offshore transport).

2.4 | Temperature

Temperature may affect recruitment through multiple mechanisms. During spawner preconditioning (Table 1, hypothesis 1, hereafter, H1), warmer temperatures may increase energy demands (H1), forcing female petrale sole to allocate less energy to reproduction by reducing egg production or aborting spawning. Temperature may also act as a spawning cue (H2 and H3) or affect growth, development, survival, and susceptibility to predation of eggs and pelagic larvae through multiple mechanisms, among which we cannot distinguish (H7, H10, H13, and H16). For example, warmer temperatures allow for faster growth and may help larvae to transition through developmental stages (e.g., egg stage) or outgrow potential predators (e.g., stage duration or "bigger-is-better" hypotheses; Houde, 1987, 1997), but warm waters may also increase energy demands making larvae more susceptible to starvation, especially if warmer waters bring poor feeding conditions. In most cases, temperature data were included as degree days (cumulative temperature above a threshold value, Chezik et al., 2014). There is limited information on the effects of temperature on the development of petrale eggs and larvae. Alderdice and Forrester (1971) saw slight curvature and an increase in the rate of development from 4 to 8.5°C. Therefore, we set the cumulative threshold to 3.5°C in this study.

2.5 | Transport

Transport to or away from appropriate settlement habitat can strongly affect larval supply and settlement of marine species with pelagic eggs and larvae (Montgomery, Tolimieri, & Haine, 2001; Schirripa & Colbert, 2006). Transport to settlement habitat was characterized by estimates of mean long-shore (LST: H5, H9, H11, H14, and H17) and cross-shelf transport (CST: H6, H8, H12, H15, and H18) at specific depths and times for each petrale sole life history stage.

Petrale sole spawn at depth but eggs rise in the water column. The mixed-layer depth (MLD) may influence how high eggs rise in the water column, thereby affecting transport (H4) (Hinckley, Hermann, & Megrey, 1996; Sundby, 1991) and available food resources post-egg hatch (Cushing, 1982). Therefore, the mean MLD from November to April, when eggs are in the water column, was included.

2.6 | Preliminary analyses

The correlations among predictor variables and individual linear and quadratic regressions for each predictor against recruitment deviations were calculated (Tables S1 and S2) and evaluated prior to model fitting and selection. Strongly correlated predictors (Table S1, r > .70) were not permitted in the same model (Dormann et al., 2013). Quadratic terms were included in the main modeling exercise, in addition to linear terms, if the individual quadratic model fits SHERIES DEANOGRAPHY

better than the individual linear model (Akiake's information criterion, AIC, was <2.0 that of the linear model, see Table S1, Burnham & Anderson, 1998). Based on preliminary analyses, a quadratic term for degree days during the egg stage (DD_{egg}) and degree days during the larval stage (DD_{larv}) was included as potential predictors in the final model selection.

2.7 | Recruitment deviations

Model estimates of petrale sole recruitment were taken from the most recent stock assessment (Figure 1c here, fig. C in Johnson et al., 2016, Stawitz et al., 2016). Specifically, the model-estimated log deviations where the deviations were the annual deviations from log-mean recruitment were used. Mean recruitment was a function of the assumed Beverton–Holt stock–recruitment relationship, aging error assumptions, and the data included in the stock assessment model.

2.8 | Model selection

A series of generalized linear models (GLMs) were run including all possible permutations of the 21 covariates (n = 11,611 models) excluding highly correlated terms (|r| > 0.7) from the same model. Each covariate matched a specific hypothesis in Table 1. The number of predictors in a candidate model was limited to five (one covariate per six data points in the time series) to prevent overfitting. The potentially quadratic predictors were allowed to enter the models as linear, or linear + quadratic forms. The best-fit models were selected using Δ AICc values, retaining models with Δ AICc < 2.0 (Burnham & Anderson, 1998).

2.9 | Model validation and testing

Performance of the best-fit 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 (Figure 1c here, Stawitz et al., 2016, fig c.), then recalculating recruitment residuals, and refitting the model 1,000 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 oceanographic variables; and (7) the entire modelfitting exercise was re-run 100 times using the re-sampled petrale recruitment deviations with error (from Step 4 above), comparing AICc selected models from each run. Finally, (8) we used jackknife resampling but fit only the years 1981-2005, compared the resulting

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	Weight	0.32	0.17	0.14	0.13	0.12	
	AICc		.19	.67	.76	.87	

-0.38 0.82

R² 0.73 0.72 0.75 0.75 0.74 0.74

AICc

LSTegg

DDlarv

DDegg1

LSTbjuv.a

CSTbjuv.a

CSTlarv

MLDegg

DDpre 0.012 0.012

Intercept

-38.526

-41.815 -39.178 -47.960 -47.763 -39.673 -46.850

0.041

-3.779 -4.043

> Model.2 Model.3

Model .1

0.038 0.041 0.038 0.036

0.012

0.013

-4.272 -4.459

Model.4

-3.632 -4.737

Model.5 Model.6

0.012

0.12

2.00

1.38 1.49 1.62

-1.640

0.002

0.003

-43.688

-44.831 -43.993

11.778

1.3

Note: Abbreviations: AICc, Akaike's information criterion adjusted for small sample size; bjuv.a, benthic juveniles at depths of 50–150 m; CST, cross-shelf transport; DD, degree days; egg1, surface egg stage; egg2, sinking egg stage; larv, larval stage; LST, long-shore transport

0.004

14.671

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models to the best-fit model above, and used the 1981–2005 model to predict recruitment deviations for 2006–2010.

3 | RESULTS

There were six candidate models with a Δ AlCc < 2.0. All of these models had the same three core terms (Table 2): degree days during the female preconditioning stage (DDpre), mixed-layer depth during the egg stage (MLDegg), and cross-shelf transport during the larval stage (CSTlarv) (Figure 2). Two of these models (Model 1 and Model 2) included four total predictors, while the remaining models included five. The fourth terms for Model 1 and Model 2 were highly correlated and essentially indistinguishable: cross-shelf transport during the benthic juvenile stage (CSTbjuv.a) and long-shore transport during the same stage (LSTbjuv.a; Figure 2). We chose Model 1 as the best-fit model because it had the lowest AlCc, highest weight, and fewest parameters. However, we note that CSTbjuv.a and LSTbjuv.a are highly correlated with several other variables and distinguishing between them was not possible.

Predictions of recruitment deviations from the best-fit model closely followed those estimated within the stock assessment (r^2 = .73, Figure 3a). Analysis of partial residuals showed that recruitment deviations were positively correlated with degree days during the female preconditioning period and mixed-layer depth during the egg stages. Recruitment deviations were negatively correlated with cross-shelf transport during both the larval stage and benthic juvenile stages (Figure 4, Table 3). Standardized coefficients suggested roughly similar effects of the three core variables on recruitment deviations with cross-shelf transport during the benthic juvenile stage having the smallest effect (Table 3). Including only the three core terms in the model resulted in a moderate decrease in fit (r^2 = .64, Table S3).

There was weak correlation among the covariates in the bestfit model with the highest being -0.58 for the correlation between mixed-depth layer and cross-shelf transport during the benthic juvenile stage (Table 4). The variance inflation factor values (VIF), which measure how much the variance of the estimated regression coefficients is inflated as compared to when the predictor variables are not linearly related, were low (Table 4). The diagnostics for the best-fit model show good model fit (Figure 4 and Figure S1) with residuals that did not show signs of autocorrelation (Figure S2).

3.1 | Model testing and validation: core-fit model

Randomly resampling the recruitment deviations (bootstrap with replacement) gave a median expected r^2 = .14 (95% C.I. = 0.02–0.33) for the core model suggesting that the observed value of r^2 = .73 was unlikely to be observed at random.

Removing individual years and refitting the best-fit model (jackknifing) had little impact on the model fit (Figures 3 and 5, median $r^2 = .73$ (95% C.I. = 0.70–0.76). Predicting the missing year from any iteration produced estimates very similar to those for the full model

TABLE 2 Results of model selection showing models with $\Delta AICc < 2.0$

FIGURE 2 Time series of independent variables in the best-fit core model: (a) degree days during female preconditioning stage, (b) mixed-layer depth during the egg stage, (c) cross-shelf transport during the larval stage, and (d) cross-shelf transport during the benthic juvenile stage for the "a" option in Table 1





FIGURE 3 (a) Fit of the best-fit model ($r^2 = 0.73$) to the estimated recruitment residuals from the stock assessment. Solid line is the predicted recruitment deviations from the full time series. Dotted lines = 95% confidence limits. Open circles are the log recruitment deviations from the 2015 sablefish assessment. Stars are predicted values from jackknife analysis removing individual years one at a time. Red points are predictions from fitting best-fit model to 1981-2005 and then predicting 2006-2010. (b) Fit of the core model from jackknife-refitting the 1981-2005 data ($r^2 = 0.64$). Open circles are the log recruitment deviations from the 2015 sablefish assessment. Solid black line is the predicted recruitment deviations for the core model for 1981-2005, solid red line is the predicted recruitment deviations for 2006-2010 based on the model for 1981-2005. Dotted lines = 95% confidence limits

(Figure 3a). The years that showed the highest impact on the model's ability to explain the data were 1991 (increased to r^2 = .77) and 2008 (decreased to r^2 = .69; Figure 5).

Resampling annual recruitment deviations with error produced a modest decline in model performance (median $r^2 = 0.62$ [95% C.I. = 0.48–0.75]). This suggests that uncertainty in the time series of recruitment deviations (given the current assessment parameters) results in a somewhat lower ability to explain the variability in recruitment.

Using the jackknife resampling and re-running the entire model-fitting process produced results consistent with the primary analysis (Table 5). Degree days during preconditioning, mixed-layer depth, and cross-shelf transport during the larval stage appeared in all models, while cross-shelf transport and long-shore transport during the benthic juvenile stage alternated in appearance.

Resampling the recruitment deviations (with error) and re-running the entire model-fitting exercise 100 times were generally consistent with the core model from the primary analysis (Table 6). The three core terms appeared in the majority of models and years.

Finally, jackknife resampling and re-running the entire model-fitting process for the 1981–2005 data supported the inclusion of the three core terms, which appeared in all best-fit models given the exclusion of a given year (Table 7). The only exception was crossshelf transport during the larval stage, which appeared in 24 out of 25 years. Predicting recruitment deviations for 1981–2005 generally did a good job of predicting recruitment deviations ($r^2 = 0.61$, Figure 3b). This three-term model did not predict the high recruitment deviations in 2006–2008 when used to forecast recruitment (Figure 3b) but did forecast increases in recruitment for these years and closely forecast recruitment deviations for 2009 and 2010. Thus, Model 1 appears to be an effective yet conservative predictor.



FIGURE 4 Partial residual plots for (a) degree days during female preconditioning stage, (b) mixed-layer depth during the egg stage, (c) cross-shelf transport during the larval stage, and (d) cross-shelf transport during the benthic juvenile stage for the "a" option in Table 1

TABLE 3 Coefficients for the core-fit model (Table 2) showing both raw and standardized (beta) coefficients

Predictor	Coefficient	Bias	SE	Standardized coefficient	Std bias	Std SE
Intercept	-3.779	-0.010	0.499	0.006	0.002	0.038
DDpre	0.012	0.000	0.002	0.237	-0.005	0.040
MLDegg	0.041	0.001	0.008	0.212	0.006	0.047
CSTlarv	-41.815	-0.119	7.801	-0.292	0.001	0.055
CSTbjuv.a	-38.526	1.392	15.075	-0.153	0.008	0.062

Note: Bias and standard error (SE) are from bootstrap resampling.

Abbreviations: bjuv.a, benthic juvenile stage; CST, cross-shelf transport; DD, degree days; egg, surface egg stage; larv, larval stage; MLD, mixed-layer depth.

 TABLE 4
 Correlations among variables included in the core model

Parameter	DDpre	MLDegg	CSTlarv	VIF
DDpre	-			1.48
MLDegg	0.13	-		1.91
CSTlarv	0.31	0.54	-	1.65
CSTbjuv.a	0.28	-0.58	-0.38	2.02

Note: Abbreviations: bjuv.a, benthic juveniles; CST, cross-shelf transport; DD, degree days; egg, surface egg stage; larv, larval stage; VIF, generalized variance inflation factor.

4 | DISCUSSION

The four oceanographic variables in the best-fit model explained 73% of the variation in petrale sole recruitment not accounted for by estimates based exclusively on the spawning stock size. Recruitment deviations were positively correlated with: (a) degree days at the female preconditioning stage and (b) mixed-layer depth at the egg stage, but negatively correlated with (c) cross-shelf transport during the larval stage and (d) cross-shelf transport during the benthic juvenile stage. These results suggest that petrale sole recruitments were a product of multiple mechanisms acting at different early life history life stages (Figure 6). Notably, although the time spans and depth ranges for each life stage were different, both the core model relationships for petrale sole and the best-fit model from a similar study for California Current sablefish (Tolimieri et al., 2018) share some of the same linear covariates that suggested spawner condition and horizontal transport impact recruitment success for both species.

The best-fit model (Model 1) fits the recruitment deviations from the stock-recruitment relationship well. During the spawner preconditioning stage, degree days from May through October impacted subsequent recruitments, with better recruitment when females experienced warmer conditions prior to spawning. Some species like Atlantic cod (Pedersen & Jobling, 1989) and bullhead (Abdoli, Pont, & Sagnes, 2005) showed positive correlations between growth or egg production and water temperature. Presumably, warmer water



FIGURE 5 Results of jackknife resampling showing distribution of r^2 values. (a) Frequency distribution of r^2 values, (b) r^2 for when the indicated year was removed from the model

temperatures allowed for higher metabolism and more rapid conversion of energy into eggs resulting in higher growth and fecundity given sufficient food resources. Earlier work by Castillo et al., 1994 also concluded that warmer water temperatures were associated with increased egg and larval survival, which may be influenced by increased egg production.

During the egg stage, mixed-layer depth from November through April was an important driver of recruitment. Specifically, water below the MLD was denser than that above, thus petrale sole eggs that are positively buoyant at spawning depths below the MLD were neutrally buoyant at or above the MLD (Alderdice & Forrester, 1971). The vertical distribution of fish eggs in the water column affected horizontal transport of eggs and larvae (Hinckley et al., 1996; Sundby, 1991). A shallower MLD may allow eggs to rise and be transported into more productive waters, resulting in higher larval survival due to better feeding conditions (Cushing, 1982).

At both the larval (from December through May) and benthic juvenile (from April to October) stages, cross-shelf transport was an important driver of recruitment. Similarly, Castillo et al. (1994) found that winter horizontal transport played an important role in determining petrale sole year-class strength, describing over half SHERIES

 TABLE 5
 ROMS predictors included in the candidate models

 from jackknife refits of the entire model-fitting process

ROMS predictor	Times included
CSTbjuv.a	29
CSTbjuv.b	4
CSTegg1	0
CSTegg2	0
CSTlarv	66
CSTpjuv	0
DDegg1	3
DDegg1 ²	0
DDegg2	0
DDlarv	0
DDlarv ²	0
DDpjuv	0
DDpre	66
LSTbjuv.a	28
LSTbjuv.b	4
LSTegg	0
LSTegg2	0
LSTlarv	0
LSTpjuv	0
MLDegg	66
Tpre.a	0
Tpre.b	0
Total models	66

Note: Results are 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: bjuv.a, benthic juveniles at depths of 50–150 m; bjuv.b, benthic juveniles at depths of 150–500 m; CST, cross-shelf transport; DD, degree days; egg1, surface egg stage; egg2, sinking egg stage; larv, larval stage; LST, long-shore transport; MLD, mixed-layer depth; pjuv, pelagic juvenile stage; pre, spawner preconditioning; pre.a, spawner preconditioning using bottom water temperature; pre.b, spawner precondition using water column temperature; T, temperature.

recruitment variability estimated at that time. Stronger cross-shelf transport from deepwater spawning locations to shallower continental shelf waters transported and retained individuals in near-shore settlement habitat, resulting in higher recruitment and reduced advection of larvae and juveniles offshore, potentially important for match-mismatch dynamics with prey resources (Peck, Huebert, & Llopiz, 2012).

Hypotheses regarding recruitment drivers at other life stages including spawning, the sinking egg stage, and pelagic juvenile stage were not included in the core model. However, the AICc selected suite of models (Table 2) includes additional covariates that appear to be occasional recruitment drivers including long-shore transport during the surface egg and benthic juvenile stages, and degree days during the surface egg and larval stages. The cross-shore transport and long-shore transport at the benthic juvenile stages, as well as WILEY-

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TABLE 6Results from completely refitting the recruitment-
environment model 100 times while resampling recruitment
deviations from a log-normal distribution using the recruitment
deviations and SDs from the 2015 assessment

ROMS	Number of jackknives	Number of models
CSTbjuv.a	56	88
CSTbjuv.b	21	24
CSTegg1	13	21
CSTegg2	12	17
CSTlarv	81	161
CSTpjuv	29	50
DDegg1	13	23
DDegg2	7	10
DDlarv	3	4
DDpjuv	0	0
DDpre	100	218
DDegg1 ²	1	3
DDlarv ²	0	0
LSTbjuv.a	35	42
LSTbjuv.b	31	36
LSTegg	11	19
LSTegg2	18	29
LSTlarv	5	5
LSTpjuv	11	20
MLDegg	81	164
Tpre.a	4	6
Tpre.b	4	6
Total	100	227

Note: Each refit iteration could include multiple candidate models (with AICc < 2.0 and the fewest included parameters). Number of jackknives is the number of times the term was included in one the candidate models for any jackknife iteration. Number of models is total number of times the term 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 covariates from the best fit model.

degree days at the surface egg and larval stages, were highly correlated (Table S1). Including these additional covariates explained up to about 75% of the variability in petrale sole recruitment deviations. However, model diagnostics for these models were poor, indicating that they were likely overfitting the data. The negative relationship with cross-shore transport and the positive relationship with longshore transport during the benthic juvenile stage may indicate that if benthic juveniles were transported offshore and to the south, then recruitment is lower, possibly due to relatively poor food resources in this region. The positive relationship with warm conditions during the surface egg and larval stages may indicate faster development in warmer waters, thus decreased predation pressure (Chavez, Ryan, Lluch-Cota, & Niquen, 2003; Harvey, 2005; Peterson, 2009; Sydeman et al., 2011).

TABLE 7 Results from jackknife fits of 1981–2005

ROMS parameter	Time included
CSTbjuv.a	0
CSTbjuv.b	0
CSTegg1	0
CSTegg2	1
CSTlarv	24
CSTpjuv	1
DDegg1	0
DDegg1 ²	0
DDegg2	0
DDlarv	0
DDlarv ²	0
DDpjuv	0
DDpre	25
LSTbjuv.a	0
LSTbjuv.b	0
LSTegg	1
LSTegg2	0
LSTlarv	0
LSTpjuv	0
MLDegg	25
Tpre.a	0
Tpre.b	0

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

Bold text indicates covariates from the best fit model.

The multiple model validation methods applied to these data suggest that the core model predictions were robust. Recruitment residuals from the Beverton-Holt stock-recruitment relationship, based on the 2015 petrale sole stock assessment, fell within the core model 95% confidence interval during 24 years, below during 3 years (1986, 2001, and 2005), and above during 3 years (1989, 1990, and 2008) (Figure 3a). The years in which recruitment residuals fell outside of the predicted 95% confidence interval did not clearly align with large-scale climate oscillations in the north Pacific, such as the El Niño-Southern Oscillation (ENSO). The core model predictions from a leave-one-year-out jackknife analysis provided predictions within the 95% confidence limits of the fitted core model for all years, 1981 through 2010 (Figure 3a). Core model predictions that used the available data through 2005 and then predicting 2006-2010 resulted in underpredicting three out of five years that were among the largest recruitment deviations in the time series (Figure 3b). These underpredictions were likely due to increases in the spawning biomass at the end of the time series that were removed from the 1981 through 2005 training data set.

This study provides the basis for understanding and forecasting the implications of climate change and climate variability on petrale



FIGURE 6 Petrale sole conceptual model of environmental drivers at specific life history stages. Bold text indicates core model covariates. See Figure 4 for plots of these relationships

sole recruitment within the stock assessment process, ecosystem assessments, and MSEs (e.g., Hollowed et al., 2009). The stock assessment uses the Northwest Fisheries Science Center West Coast Groundfish Bottom Trawl Survey data, which initially samples petrale sole as age-2 fishes. However, petrale sole are not 50% selected until approximately age 6 (Stawitz et al., 2016). The ability to predict recruitment more than one year ahead would allow the stock assessment to provide better catch advice based on improved estimates of the recruitments likely to be entering the fishery in the near term, prior these recruitments being well sampled by the survey (Kaplan, Williams, Bond, Hermann, & Siedlecki, 2016; Siedlecki et al., 2016). Annually updating environmental predictors to inform recruitment forecasting based on both observed oceanographic conditions and potentially sub-annual forecasts of environmental conditions (Jacox, Alexander, Stock, & Hervieux, 2017; Siedlecki et al., 2016) could provide leading environmental indicators of recruitment for managers and fishers. Additionally, long-term stock productivity projections based on oceanographic output from global climate models or regional ocean models could be useful for fishery stakeholders and for evaluating the robustness of harvest control rules (HCRs) to changes in long-term stock productivity evaluation via management strategy evaluation (MSE). Of course, given concerns about nonstationarity in environment-recruitment relationships (Myers, 1998), periodic re-evaluations any environmental drivers of recruitment are necessary and are dependent upon the continuation of both oceanographic and biological monitoring programs.

This work can also inform the selection of historical environmental data sets for hindcasting petrale sole recruitment in the absence of age and length composition data, rather than assuming some level of

average recruitment into the past based on more recently observed recruitment variability. Using environmental indicators of what early recruitment might have been could reduce stock assessment uncertainty and provide better estimates of management reference points. Stock assessments estimate age-0 recruitment conditioned on the available data, a majority of which may come from only one environmental regime. Using stock-recruitment data from only one environmental regime may result in over- or underestimating past recruitment, pro-

in the California Current Ecosystem where many age and length time series are short relative to the timescales of low frequency environmental variability (e.g., the Pacific Decadal Oscillation, Berger, 2019). Transitioning the environmental drivers of petrale sole recruitment from this research to an operational product for both stock assessments and ecosystem assessments for fishery managers ideally requires the extension of ocean reanalyses both forward and backwards in time; this study uses data from 1980 through 2010. Alternatively, more easily available observational data sets could

ducing bias in the calculation of fishery reference points, particularly

serve as proxies for the selected covariates. Finally, if available, skillful, short-term oceanographic model forecasts of relevant oceanographic covariates could be used to inform recruitment estimation prior to survey data availability.

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CONFLICT OF INTEREST

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

AUTHOR CONTRIBUTIONS

M.A.H. and N.T. conceived the study. L.Q., M.A.H, and N.T. developed the conceptual life history model. N.T. and M.A.H. developed and undertook statistical analyses. M.G.J. provided the oceanographic expertise and ROMs model outputs for the study. M.A.H. and N.T. drafted the manuscript with input and revisions from all authors.

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DATA AVAILABILITY STATEMENT

The data associated with this manuscript are available through the NOAA Northwest Fisheries Science Center, Fishery Resource Analysis and Monitoring Division.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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