

## ORIGINAL ARTICLE

# Oceanographic drivers of sablefish recruitment in the California Current

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## Abstract

Oceanographic processes and ecological interactions can strongly influence recruitment success in marine fishes. Here, we develop an environmental index of sablefish recruitment with the goal of elucidating recruitment-environment relationships and informing stock assessment. We start with a conceptual life-history model for sablefish *Anoplopoma fimbria* on the US west coast to generate stage- and spatio-temporally-specific hypotheses regarding the oceanographic and biological variables likely influencing sablefish recruitment. Our model includes seven stages from pre-spawn female condition through benthic recruitment (age-0 fish) for the northern portion of the west coast U.S. sablefish stock (40°N–50°N). We then fit linear models and use model comparison to select predictors. We use residuals from the stock-recruitment relationship in the 2015 sablefish assessment as the dependent variable (thus removing the effect of spawning stock biomass). Predictor variables were drawn primarily from ROMS model outputs for the California Current Ecosystem. We also include indices of prey and predator abundance and freshwater input. Five variables explained 57% of the variation in recruitment not accounted for by the stock-recruitment relationship in the sablefish assessment. Recruitment deviations were positively correlated with (i) colder conditions during the spawner pre-conditioning period, (ii) warmer water temperatures during the egg stage, (iii) stronger cross-shelf transport to near-shore nursery habitats during the egg stage, (iv) stronger long-shore transport to the north during the yolk-sac stage, and (v) cold surface water temperatures during the larval stage. This result suggests that multiple mechanisms likely affect sablefish recruitment at different points in their life history.

## KEYWORDS

*Anoplopoma fimbria*, California Current, oceanic drivers, recruitment, sablefish

## 1 | INTRODUCTION

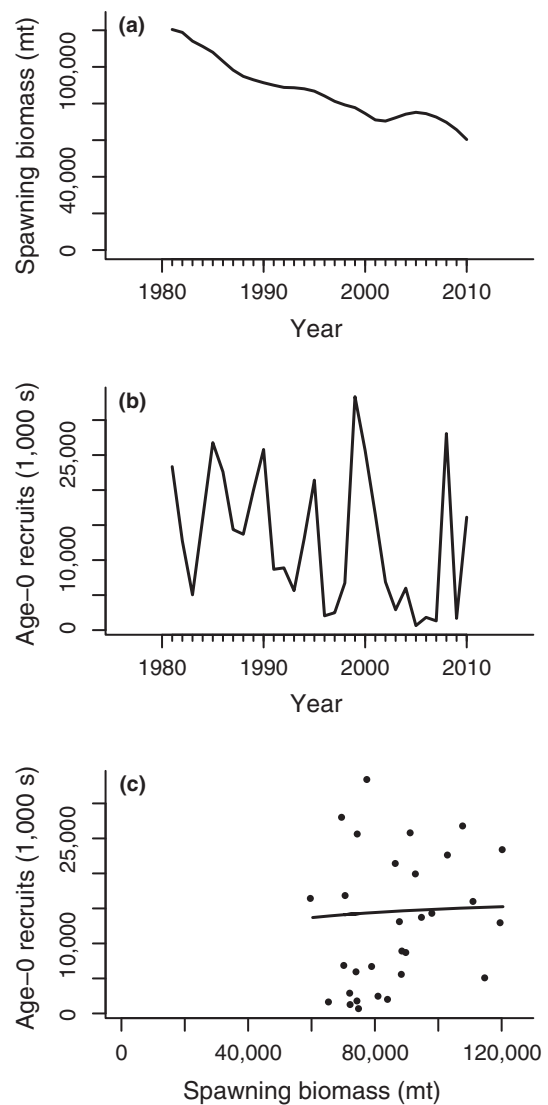
Climate plays an important role in coastal marine ecosystems, driving changes in horizontal and vertical transport that affect nutrient availability and primary production that, in turn, propagate through both lower and upper trophic levels (Chavez, Ryan, Lluch-Cota, & Niquen, 2003; Di Lorenzo, Mountain, Batchelder, Bond, & Hofmann, 2013; Hunt & McKinnell, 2006). In coastal upwelling systems the bottom-up forcing hypothesis has been the prevailing paradigm (Di Lorenzo

et al., 2013). However, recent synthesis by the Global Ecosystems Dynamics Program (GLOBEC) of four regions (Gulf of Alaska, Northern California Current, Northwest Atlantic and Southern Ocean) suggests that horizontal transport (cross-shelf, long-shore) is also highly important, providing the foundation for a new horizontal-advection bottom-up-forcing paradigm (Di Lorenzo et al., 2013). This new paradigm suggests that, in addition to the indirect effects of climate manifested through variability in primary production and the timing of the availability of food resources, horizontal transport directly

affects the reproductive success of taxa like fish by influencing their transport to suitable settlement habitat (reviewed by Di Lorenzo et al., 2013). At the same time, other oceanographic parameters such as temperature can affect growth, which can mediate an individual's vulnerability to predation and the susceptibility of larvae to starvation (Chezik, Lester, & Venturelli, 2014; Houde, 1987; Leggett & DeBlois, 1994; Litvak & Leggett, 1992). Likewise, ecological interactions such as prey availability, predator abundance and density dependence may also be important in determining reproductive success for marine fishes and other species (Field, Francis, & Aydin, 2006; Frank, Petrie, & Shackell, 2007; Hunt & McKinnell, 2006; Tolimieri, 2015). Recruitment, in turn, directly affects age structure and population size in marine fishes (Bailey, 1981; Hjort, 1914; Maunder & Watters, 2003; Myers, 1998). Therefore, it is important to understand the role of oceanographic processes and ecological interactions in determining recruitment success in marine fishes, both to gain a better understanding of their population dynamics and to better manage these species.

Sablefish (*Anoplopoma fimbria*) inhabit waters along the west coast of North America from the Baja California through Alaska and extend west (and south) to Japan (Allen & Smith, 1988; Hart, 1973; Johnson et al., 2016). Traditionally, two stocks have been recognized in the northeastern Pacific: (i) an Alaskan/British Columbian stock extending from the Bering Sea to Vancouver Island, and (ii) a U.S. west coast population extending from southwest Vancouver Island to Baja California (Johnson et al., 2016; Schirripa & Colbert, 2006), with each stock being subject to independent management. The spawning stock biomass (SSB) of the U.S. west coast sablefish stock (the focus of this work) has declined steadily since the 1980s (Figure 1a), concurrent with high landings during 1976–1990 (Johnson et al., 2016) and highly variable, but declining recruitment (Figure 1b). The stock-recruitment relationship appears weak (Figure 1c) suggesting that environmental factors are likely important.

Sablefish recruitment-environment investigations have generally focused on large-scale climate or oceanographic variables (Coffin & Mueter, 2015; Schirripa & Colbert, 2006; Schirripa, Goodyear, & Methot, 2009; Schirripa & Methot, 2001; Shotwell, Hanselman, & Belkin, 2014; Sogard, 2011). For example, in the California Current Ecosystem along the U.S. west coast, sablefish recruitment has been correlated with changes in sea surface height (SSH) and both northward and eastward Ekman transport (Schirripa & Colbert, 2006). Sea surface height has been used as an index of recruitment success in recent sablefish stock assessments (Johnson et al., 2016; Schirripa et al., 2009; Stewart & Forrest, 2011), in part as a proxy for abundance of copepods (Schirripa & Colbert, 2006; Schirripa & Methot, 2001; Schirripa et al., 2009), which are an important food source for larvae and juveniles (Grover & Olla, 1987; McFarlane & Beamish, 1992). Changes in SSH serve as a proxy for large-scale climate forcing that drives regional changes in alongshore and cross-shelf ocean transport. These changes directly impact the transport of water masses, nutrients, and organisms. SSH tracks these changes on a gross scale, explaining the weak but significant relationship with sablefish recruitment (Di Lorenzo et al., 2013; Schirripa & Colbert, 2006).



**FIGURE 1** Sablefish biological parameters from the 2015 stock assessment for 1981–2010. (a) spawning stock biomass (SSB) in metric tons (b) thousands of age-0 recruits, and (c) stock-recruitment relationship asserted in the assessment (line) versus observed data (points)

The relationship between sablefish recruitment and SSH is compelling from an ecological standpoint. However, the use of the index has not had a large effect on stock-assessment results because good data on year-class strength from fishery and fishery-independent survey data already inform the stock assessment regarding variability in recruitment (Stewart, Thorson, & Wetzel, 2011). While a significant predictor ( $r^2 \approx .3$ ), SSH provides too little additional information to lower uncertainty enough in the stock assessment to improve the precision of future recruitment predictions. To do so, an environmental index would need to explain more than 50% of the variability in recruitment unrelated to the stock-recruitment relationship and age structure (Basson, 1999; Johnson et al., 2016). Ideally, such an index should derive from environmental variables at scales relevant to the sablefish life history and be able to forecast into the future, potentially allowing managers and fishers to better respond

to probable shifts in sablefish recruitment. Given a robust environmental index with greater explanatory power, hind-casting recruitment strength on the basis of past environmental data can better inform recruitment estimates during time periods in which there is no information on fishery or survey length and age compositions.

Here, we (i) develop a literature-based, conceptual life-history model for sablefish that includes seven stages from female conditioning through benthic recruitment (age-0 fish) for the northern portion of the west coast U.S. sablefish stock (40°N–50°N); (ii) use this conceptual model to generate stage-specific and spatio-temporally-specific hypotheses regarding the physical and biological variables likely to influence sablefish recruitment and (iii) use linear models and model comparison to develop predictive models of sablefish recruitment using oceanographic drivers taken from a Regional Ocean Modeling System (ROMS) model of the California Current System (Neveu et al., 2016). We also evaluate support for biological indices like predator and prey abundance, temperature impacts on growth rates (e.g., Sogard & Olla, 2001), and freshwater input from the Columbia River as a proxy for nutrient input or effects on ocean currents. Our goal is to develop an ecologically meaningful, robust environment-recruitment relationship that has higher explanatory power than those developed in the past, with the end goal of enhancing the sablefish stock assessment and improving short term forecasts of sablefish recruitment required by fishery managers.

## 2 | MATERIALS AND METHODS

We investigate predictors of recruitment for the northern portion of the U.S. west coast stock from 40°N to 50°N. We focus on the northern portion of the stock because recruitment estimates from the coast-wide stock assessment model are most strongly informed by age and length composition data from the north (Johnson et al., 2016). Although the two stock definition for eastern Pacific sablefish (Alaskan/British Columbian and U.S. west coast) is commonly accepted, there is evidence that the dynamics of the U.S. west coast stock differs north and south of Cape Mendocino (~40.4°N). Head, Keller, and Bradburn (2014) concluded that the sablefish population south of Cape Mendocino may be a separate subpopulation based on differentiation in ages and lengths at 50% maturity, as well as potential differences in reproductive success. Maximum body size is larger and growth rates are slower north of Cape Mendocino. North of Cape Mendocino, the highest concentration of age-0 fishes observed in the West Coast Groundfish Bottom Trawl Survey (WCG BTS) is between 44°N and 45°N, just south of the Columbia River (Figure S1).

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

We began our conceptual life-history model by first identifying each life-history stage that could potentially contribute to determining the

size of each sablefish year class, beginning with female condition prior to the start of the spawning season (Table 1). The energetic status of females may influence their propensity to spawn, and the quality and number of eggs produced (Rodgveller, Stark, Echave, & Hulson, 2016; Sogard, Berkeley, & Fisher, 2008). Thus, the summer and fall prior to spawning (June–December) may be important for female preconditioning. Spawning occurs from December to March with a peak in February. Most spawning takes place at the edge of the continental shelf at depths >300 m with eggs initially found from 200 m to >825 m (Hunter, Macewicz, & Kimbrell, 1989; Kendall & Matarese, 1987; Mason, Beamish, & McFarlane, 1983; Moser et al., 1994). Eggs are buoyant, rising to 200–300 m in the water column, but are most common between 240 m and 480 m, where they remain for approximately 12–17 days until hatching (Boehlert & Yoklavich, 1985; Kendall & Matarese, 1987; Mason et al., 1983; McFarlane & Beamish, 1992; Moser et al., 1994). Post hatch, larvae sink to 1,000–1,200 m where they can be found between February and May as yolk-sac larvae. By 14–17 days post-hatch larvae have consumed about 50% of their yolk sac and may show initial attempts at feeding approximately a week later. By 40 days post-hatch larvae are in surface waters from the 500 m isobath out to 150 nautical miles (277 km) from shore where they are found between February and May (Brock, 1940; McFarlane & Beamish, 1992; Moser et al., 1994). Pelagic juveniles are also found in these surface waters and are present from April through November (Kendall & Matarese, 1987; Mitchell & Hunter, 1970). Sablefish settle to the benthos as age-0 recruits between August and November with most fish likely settling to habitats 250 m or shallower.

### 2.2 | Regional ocean modeling system (ROMS)

The majority of our predictors were physical oceanographic parameters including temperature, long-shore and cross-shelf currents, and mixed layer depth. We derived these variables from a California Current System (CCS) configuration of the Regional Ocean Modeling System (ROMS) with four dimensional Variational (4D-Var) data assimilation (Neveu et al., 2016). The ROMS model domain covers the region 30°N–48°N and from the coast to 134°W at 0.1° (~10 km) horizontal resolution, with 42 terrain-following vertical levels. In the 1980–2010 CCS reanalysis used for this study, satellite observations (SST, SSH) and in situ data (temperature and salinity 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 spatial upwelling variability (Jacox, Moore, Edwards, & Fiechter, 2014), basin-scale climate influences (Jacox, Bograd, Hazen, & Fiechter, 2015; Jacox, Fiechter, Moore, & Edwards, 2015), and bottom-up controls on primary production (Jacox, Hazen, & Bograd, 2016) in the CCS. All ROMS output was averaged in 4 day increments and then either averaged or summed over the appropriate period (as defined in Table 1) for each of the 30 years ( $n = 30$  for each time series in the analysis). Additional predictors are described in relation to their specific hypotheses below.

**TABLE 1** Life history model. See the text for data sources

Life-history stage	Time period	Depth	Sablefish location	Hypothesis	Stage	Covariates	Depth extent	Longitudinal extent	Data source
Preconditioning	Jun-Dec (Year 0)	50–1,200 m	Bottom	(H1) Food availability affects energy allocation to reproduction with higher recruitment when more prey are available during the preconditioning period (H2) Higher temperature increases food demand resulting in lower egg production, egg quality, or probability of spawning resulting in lower recruitment	Pre <sub>Y<sub>hake</sub></sub> Pre <sub>Y<sub>lap</sub></sub>  DD <sub>pre</sub>	Index of age-0 hake and age-0 longspine thornyhead abundance  Degree days	50–1,200 m  (150–400 m)	50–1,200 m isobath  (150–400 m isobath)	Stock Assessments  ROMS
Spawning	Dec-Mar	300–500 m	Bottom	(H3) Temperature acts as a spawning cue with fish less likely to spawn at high temperature resulting in lower recruitment (H4) As H3 but degree days not mean temperature	Temp <sub>spawn</sub>  DD <sub>spawn</sub>	Mean temperature  Degree days	300–500 m  300–500 m	300–500 m isobath  300–500 m isobath	ROMS  ROMS
Eggs	Jan-Apr	300–825 m	Open water	(H5) Eggs are buoyant so Mixed Layer Depth may limit how far they rise in the water column affecting later transport (H6) Transport to settlement habitat affects recruitment (H7) Growth/Predation hypothesis: growth rate is faster in warm water leading to reduced time vulnerable to predators	MLD <sub>egg,mn</sub> MLD <sub>egg,sd</sub>  CST <sub>egg</sub>  DD <sub>egg</sub>	Location of mixed layer depth (m); mean and SD  Net cross-shelf transport  Degree days	300–825 m (240–480 m)  300–825 m (240–480 m)	Inshore limit: 500 m bottom depth, Seaward to 170 nmi  Inshore limit: 500 m bottom depth, Seaward to 170 nmi  Inshore limit: 500 m bottom depth, Seaward to 170 nmi	ROMS  ROMS  ROMS
Yolk-sack larvae	Feb-May	1,000–1,200 m	Open water	(H8) Longshore transport to settlement habitat affects recruitment (H9) Cross-shore transport to settlement habitat affects recruitment (H10) Growth/Predation hypothesis: growth rate is faster in warm water leading to reduced time vulnerable to predators	LST <sub>yolk</sub>  CST <sub>yolk</sub>  DD <sub>yolk</sub>	Net long-shore transport  Net cross-shelf transport  Degree days	1,000–1,200 m  1,000–1,200 m  1,000–1,200 m	1,000 m to 170 nmi  1,000 m to 170 nmi  1,000 m to 170 nmi	ROMS  ROMS  ROMS

(Continues)

TABLE 1 (Continued)

Life-history stage	Time period	Depth	Sablefish location	Hypothesis	Stage	Covariates	Depth extent	Longitudinal extent	Data source
Larvae (start feeding)	Feb-May <sup>2</sup>	Surface waters	Open water	(H11) Longshore transport to settlement habitat affects recruitment	LST <sub>larv</sub>	Net long-shore transport	Surface waters	0–150 nautical nmi	ROMS
				(H12) Cross-shore transport to settlement habitat affects recruitment	CST <sub>larv</sub>	Net cross-shelf transport	Surface waters	0–150 nautical nmi	ROMS
				(H13) Growth/Predation hypothesis: growth rate is faster in warm water leading to reduced time vulnerable to predators	DD <sub>larv</sub>	Degree days	Surface waters	0–150 nautical nmi	ROMS
Pelagic juveniles (feeding pelagics)	Apr-Nov	Surface waters	Open water	(H14) Longshore transport to settlement habitat affects recruitment	LST <sub>pluv</sub>	Net long-shore transport	Surface waters	0–150 nautical nmi	ROMS
				(H15) Cross-shore transport to settlement habitat affects recruitment	CST <sub>pluv</sub>	Net cross-shelf transport	Surface waters	0–150 nautical nmi	ROMS
				(H17) Growth/Predation hypothesis: growth rate is faster in warm water leading to reduced time vulnerable to predators	DD <sub>pluv</sub>	Degree days	Surface waters	0–150 nautical nmi	ROMS
Benthic Juvenile (Age-0)	Aug-Nov	0–250 m	Bottom	(H17) Longshore transport to settlement habitat affects recruitment	LST <sub>bjuv</sub>	Net long-shore transport	to 250 m	0–250 m isobath	ROMS
				(H18) Cross-shore transport to settlement habitat affects recruitment	CST <sub>bjuv</sub>	Net cross-shelf transport	to 250 m	0–250 m isobath	ROMS
				(H19) Growth/Predation hypothesis: growth rate is faster in warm water leading to reduced time vulnerable to predators	DD <sub>bjuv</sub>	Degree days	to 250 m	0–250 m isobath	ROMS
				(H20) Predation	Pred <sub>bjuv</sub>	Some index of predator abundance	to 250 m	0–250 m isobath	Trawl Survey & Stock Assessments
				(H21) Nutrient input (fertilization) affects productivity, food availability and therefore survival or river discharge may affect currents.	FW <sub>bjuv</sub>	Annual discharge from Columbia River measured at The Dalles.	NA	NA	Columbia River DART
				(H22) Sea surface height as an indicator of basin- scale processes. Used in previous assessments.	SSH				Spring north coast SSH 44°N–50°N

Oceanographic data are scarcer at depth than at the surface. As a result, the ROMS output, which assimilates available data, is not as strongly constrained by observations at the subsurface as it is at the surface. It is therefore likely that the ROMS output deviates from nature more at the subsurface than it does at the surface, though the scarcity of subsurface measurements (or transport metrics at any depth) precludes a definitive model evaluation in this regard. The paucity of subsurface data, however, is the motivation for using model output in this study, and despite our inability to validate the subsurface transport in the model, there is reason to believe it provides useful information. First, the purpose of data assimilation is to further improve a model that already captures the dynamics of the California Current faithfully 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 is forced by realistic winds, surface heat fluxes, and lateral boundary conditions, which drive realistic physical variability even in the absence of data assimilation. Second, the data that are assimilated, even if only available at the ocean surface, can impact the subsurface dynamics. For example, assimilating sea surface height measurements constrains the geostrophic flow and therefore transport at the surface and in the subsurface. The impact of assimilated data on different metrics of the CCS circulation is discussed in detail in Moore et al. (2017). For a transport example, see Figure 4e in that paper.

### 2.3 | Hypotheses and additional data sources

We developed 21 a priori, life-stage-specific and space-specific (considering time, depth, and longitude) hypotheses for ecological and environmental covariates that may drive variation in sablefish recruitment (Table 1). Two hypotheses were represented by two predictors, and we included SSH for historical reasons (see below). Thus, we tested 24 total predictors. While the current sablefish stock assessment estimates coast-wide spawning biomass and recruitment time series, we limited the predictor time series to 40°N–48°N because a majority of the length and age composition data come from the northern California Current (Johnson et al., 2016). For each hypothesis, we specified the time period, depth and longitudinal extent of the potential predictor, for example, net cross-shelf transport between January and April at 300–825 m depth, between 40°N and 48°N and from the 500 m isobath to 170 nautical miles off shore may affect transport and distribution of sablefish eggs (Table 1).

We focused on hypotheses for which we had data (or model output) available for testing. We excluded some potential hypotheses for which data were not available rendering these hypotheses untestable. These hypotheses are not included in Table 1. The most obvious omission is food availability for larvae and pelagic juveniles (McFarlane & Beamish, 1992). Unfortunately, continuous data for northern copepod biomass anomaly begin in 1996 (<http://www.noaa.gov/iea/regions/california-current-region/indicators/climate-and-ocean-drivers.html>), long after recruitment estimates are available for sablefish. We also did not include potential mechanisms with indirect

effects such as upwelling, which might affect larval survival by influencing food availability. Note, however, that upwelling effects will likely be caught in many of the transport and temperature indices we did include. Finally, in some cases, the literature suggested multiple potential depth ranges over which environmental or biological variables might influence recruitment: one broad and one more restricted. For example, sablefish eggs are found between 240 and 825 m (Hunter et al., 1989; Kendall & Matarese, 1987; Mason et al., 1983; Moser et al., 1994) with the highest occurrence between 240 and 480 m (Moser et al., 1994). When selecting environmental predictors for inclusion in model selection, we initially evaluated variables (e.g., total cross shelf transport) for each depth range. However, preliminary analyses showed these paired predictors (i.e., net cross shelf transport between 300–825 m and 240–480 m) to be highly correlated ( $r > .88$ ), and we chose to include only the broader depth range version of each in our analyses to reduce the number of predictors. The resulting testable hypotheses fall into six general categories, which may overlap life-history stages (Table 1): temperature, transport, mixing, prey, predators, and nutrient fertilization or effects on oceanic currents from freshwater input from rivers.

#### 2.3.1 | Temperature

Ambient temperature may affect the production of recruits through multiple mechanisms. During the preconditioning period for spawning females (Table 1, hypothesis 2, hereafter, H2) warmer temperatures may increase energy demands (H2), forcing female sablefish to allocate less energy to reproduction, reducing the production of eggs. Temperature may also act as a spawning cue (H4). For eggs and larvae, temperature may also affect growth, development, survival, and susceptibility to predation through multiple mechanisms, among which we cannot distinguish (H7, H10, H13, H17 and H19). For example, warmer temperatures allow for faster growth allowing larvae to 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. Temperature data were obtained from ROMS outputs. In most cases, we include temperature as degree days (cumulative temperature above a threshold value, Chezik et al., 2014), setting a slightly conservative threshold temperature of 3.5°C (Alderdice, Jensen, & Velzen, 1988; Sogard & Spencer, 2004).

#### 2.3.2 | Transport

Transport to, or advection 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 ROMS estimates of net long-shore transport (LST: H8, H11, H14 & H17) and net cross-shelf transport (CST: H6, H9, H12, H15 & H18) at specific depths and time periods for each sablefish life-history stage.



Sablefish spawn at depth, but eggs are initially buoyant, rising in the water column. The mixed-layer depth (MLD) may influence how high eggs rise in the water column, thereby affecting transport (H5). We included the ROMS estimates of MLD (mean depth and SD) from January–April when eggs are in the water column.

### 2.3.3 | Prey availability and female condition

Prey availability (H1) during the months prior to spawning (June–December) may affect female condition and in turn, egg quality, egg production or even the probability of spawning in a given year. For example, given poor prey availability, individual sablefish in Alaskan waters may skip spawning in some years (Rodgveller et al., 2016). We included the abundance of age-0 hake *Merluccius productus* ( $\text{Prey}_{\text{hake}}$ ) and age-0 longspine thornyhead *Sebastolobus altivelis* ( $\text{Prey}_{\text{sp}}$ ) from their most recent stock assessments (Stephens & Taylor, 2014; Taylor, Grandin, Hicks, Teylor, & Cox, 2015) as indices of prey abundance for female sablefish. Both species make up substantial proportions of the sablefish diet (Laidig, Adams, & Samiere, 1997). We included them as separate indices because hake were much more abundant than thornyheads and a combined index was highly correlated with  $\text{Prey}_{\text{Hake}}$  ( $r = .99$ ).

### 2.3.4 | Predation on recruits

Predation (H20) in the period immediately following settlement can strongly affect population size and structure for benthic fishes (Hixon & Jones, 2005; Tolimieri, 2015). Therefore, an index of predator abundance was developed based on known sablefish predators including: lingcod *Ophiodon elongatus*, arrowtooth flounder *Atheresthes stomias*, Pacific halibut *Hippoglossus stenolepis*, widow rockfish *Sebastes entomelas*, yelloweye rockfish *Sebastes ruberrimus* and black rockfish *Sebastes melanops*. Data were drawn from two sources: (i) stock assessments for each species (Hamel, Sethi, & Wadsworth, 2009; He et al., 2011; Kaplan & Helser, 2007; Stewart, Monnahan, & Martel, 2015; Taylor & Wetzel, 2011; Wallace, Cheng, & Tsou, 2008), and (ii) West Coast Groundfish Bottom Trawl Survey (Keller et al., 2008). Stock assessments for some of these species did not cover the period under investigation (1980–2010). Therefore, we used multivariate autoregressive state-space (MARSS) models to combine the stock assessment and trawl time series for each species into one population trend. We then summed the trends for each species and year to create a single index of sablefish predator abundance (Holmes, Ward, & Scheuerell, 2014; Holmes, Ward, & Wills, 2012; Tolimieri, Holmes, Williams, Pacunski, & Lowry, 2017; see Supporting information for more detail).

### 2.3.5 | Freshwater input effects on nutrient fertilization and circulation

Freshwater outflow (H21) from major rivers influence the nearby marine environment. For example, freshwater discharge from the Fraser River appears to play a role in sablefish recruitment in the

Gulf of Alaska, possibly through its influence on nearshore currents (Coffin & Mueter, 2015). While total catch was low for age-0 fishes, preliminary analysis of the West Coast Groundfish Bottom Trawl Survey data showed a preponderance individuals in the vicinity of the mouth of the Columbia River suggesting a similar effect and the possibility of nutrient fertilization (Figure S1). Annual discharge from the Columbia River measured at The Dalles ([www.cbr.washington.edu/dart/query/streamflow\\_daily](http://www.cbr.washington.edu/dart/query/streamflow_daily)), Oregon is included as an index of potential fertilization or influence on currents.

### 2.3.6 | Sea-surface height

Finally, for historical purposes we include an index of north coast spring sea surface height (SSH, H22), which has been evaluated in recent stock assessments (Johnson et al., 2016; Taylor et al., 2015). While not spatio-temporally specific like the other predictor variables, including the SSH index aids in testing the consistency of mechanisms hypothesized to impact sablefish recruitment and whether or not the more specific mechanistic variables identified in this study allow for better recruitment prediction. For 1980–1992 the index is derived from tide-gauge data and is the average of monthly SSH at Neah Bay and Toke Point, Washington and Astoria and Newport, Oregon from April–June. From 1993 onwards, the data come from JASON and TOPEX satellites and represents a north coast spring index of SSH for 44°N–50°N (Schirripa, 2007).

Since, in this analysis, the 1980 recruitment deviation depends upon data on the preconditioning period in 1979, our analysis covers recruitment residuals from 1981 to 2010.

## 2.4 | Preliminary analyses

We conducted two sets of preliminary analyses prior to model fitting. First, we evaluated correlations among predictor variables (Tables S1 and S2). As noted above, paired predictors that were the same variable but with different spatial extents were highly correlated (Table S1), and we eliminated the smaller-scale version from the model fitting to reduce the number of potential predictors. Some of the remaining predictors showed strong correlation (Table S2,  $r > .75$ ), and we required both correlated variables not appear together in any model under consideration.

Next, we ran individual linear and quadratic regressions for each predictor against recruitment deviations to determine if the data supported non-linear relationships. Quadratic terms were included in the main modeling exercise for those terms where, in these preliminary analyses, the individual quadratic model fit 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 long-shore transport during the benthic juvenile stage ( $\text{LST}_{\text{bjuv}}$ ) was included as a potential predictor in the final model selection. Additionally, SSH was included as a potential quadratic term based on the observed relationship in Schirripa and Colbert (2006).

## 2.5 | Recruitment residuals

Estimates of sablefish recruitment and spawning stock biomass (SSB) were taken from the most recent stock-assessment (Figure 1c, Johnson et al., 2016). The recruitment time-series from the stock assessment is generated, in part, by an asserted stock-recruitment relationship (asserted because the form is assumed to be Beverton-Holt; steepness, unfished spawning biomass, and recruitment at unfished biomass are fixed; and the data are derived data from the stock assessment process, see Equations 1–3 below). If the environmental indices are to be useful for prediction within the stock assessment, it is necessary to remove this relationship to avoid double counting the effect of SSB on recruitment. Moreover, the stock-recruitment relationship is known, and we want to predict the variability in recruitment unaccounted for by the SSB. In order to remove the effect of the asserted stock-recruitment relationship, recruitment residuals for this study were calculated as the difference between the estimated recruitments from the stock assessment and the assumed stock-recruitment relationship, and are given by:

$$\text{Recruitment residuals} = R_{\text{assessment}} - R_{\text{sr,curve}}, \quad (1)$$

where  $R_{\text{assessment}}$  are the estimated recruitments from the stock assessment and  $R_{\text{sr,curve}}$  are the predicted recruitments from the stock-recruitment relationship. Note that the recruitment residuals calculated for this study are not the same as the estimated recruitment deviations from the stock assessment, which are constrained to sum to zero over the time period during which recruitments are estimated in the stock assessment model.  $R_{\text{sr,curve}}$  is calculated as:

$$R_{\text{sr,curve}} = \frac{R_0 * S}{(b + S)}, \quad (2)$$

where  $R_0$  is recruitment at unfished biomass (equilibrium recruitment),  $S$  is the spawning biomass, and  $b$  is:

$$b = \frac{(R_0 * 0.2 * S_0)}{(h - R_0) - (0.2 * S_0)}, \quad (3)$$

where,  $S_0$  is unfished biomass and  $h$  is steepness (the ratio of recruitment at 20% versus 100% of unfished biomass). From the 2015 assessment,  $R_0 = 115,622$  thousand age-0 fish,  $S_0 = 17,198$  metric tons, and  $h = 0.6$ .

## 2.6 | Model selection

We fit a series of generalized linear models (GLMs) including all possible permutations of the 24 covariates ( $n = 27,191$  models) with the above restrictions for total number of parameters and exclusion of highly correlated terms ( $|r| > .75$ ) from the same model. Each covariate matched a specific hypothesis in Table 1 with the exceptions of  $\text{Prey}_{\text{hake}}$  and  $\text{Prey}_{\text{lsb}}$ , which both mapped to H1, prey availability. The number of predictors in a candidate model was limited to five (one covariate per six data points in the time series) to prevent over-fitting. The two potentially quadratic predictors ( $\text{LST}_{\text{bjuv}}$  and  $\text{SSH}$ ) were allowed to enter the models as linear, quadratic only, or linear + quadratic forms. The best-

fit model(s) was selected using  $\Delta\text{AICc}$  values, retaining models with  $\Delta\text{AICc} < 2.0$  (Burnham & Anderson, 1998).

## 2.7 | Model validation and testing

We conducted additional analyses to evaluate the performance of the best-fit models. First, recruitment deviations were resampled with replacement to estimate  $r^2$  values for randomized data (1,000 permutations) for the final, best-fit model. Second, standard bootstrapping (resampled whole years with replacement) was used to estimate bias and calculate SE of the parameter estimates. Third, jackknife resampling was used to determine the effect of any single year on the  $r^2$  of the best-fit model. Fourth, since the dependent variable was based on estimated recruitments from a stock-assessment, there is error for each recruitment residual that is not accounted for in the best-fit model. Therefore, we resampled the recruitment values for each year from a log-normal distribution where the mean was the value for that year and recruitment SD for each year was taken from the sablefish stock assessment (Johnson et al., 2016, table 15). We then recalculated the recruitment residuals and refit the best-fit model repeating the process 1,000 times. Fifth, we refit the best-supported model using data for 1981–2005 and used this model to predict recruitments for 2006–2010. Sixth, jackknife resampling was used to re-run the entire model fitting and comparison exercise, rather than re-fitting only the best-fit model, to determine if removal of any individual year would change the oceanographic/biological variables in the final model. Finally, we re-ran the entire model fitting exercise 100 times using the re-sampled sablefish recruitments with error (from Step 4 above) and compared top models from each run.

## 2.8 | Northern copepod biomass anomaly

Previous work has suggested that recruitment success in sablefish is influenced by the abundance of northern copepods (McFarlane & Beamish, 1992), which are larger and fattier than southern species. Sablefish stock assessments have included zooplankton indices as environmental predictors (Schirripa, 2002, 2007). We could not test the northern copepod biomass anomaly directly in our main analyses because the continuous time series begins in 1996 (although there are some earlier data). However, after selecting a best-fit model from the main analysis, we refit this model for years 1996–2010 both with and without this index. Data were the northern copepod biomass anomaly,  $\log_{10}(\text{mg C/m}^3)$ , taken from the California Integrated Ecosystem Assessment (<https://www.integratedecosystemassessment.noaa.gov/regions/california-current-region/indicators/ecological-integrity.html>). We averaged monthly values over the summer months (July–September) in each year.

## 3 | RESULTS

Model fitting produced a clear best-fit model, with no other candidate models with a  $\Delta\text{AICc} < 2.0$  (Table 2, Table 3). In fact, the next



**TABLE 2** Results of model selection showing models with a  $\Delta AICc < 6.0$ 

Model							$R^2$	$\Delta AIC$
Model 1	DD <sub>pre</sub>	CST <sub>egg</sub>	DD <sub>egg</sub>	LST <sub>yolk</sub>	DD <sub>larv</sub>		.57	0
Model 2			DD <sub>egg</sub>	LST <sub>yolk</sub>		LST <sub>pjuv</sub>	SSH <sup>2</sup>	3.92
Model 3	Prey <sub>hake</sub>		DD <sub>egg</sub>	LST <sub>yolk</sub>		LST <sub>pjuv</sub>	SSH <sup>2</sup>	3.94
Model 4	DD <sub>Pre</sub>	CST <sub>egg</sub>	DD <sub>egg</sub>	LST <sub>yolk</sub>			SSH	3.95

CST, cross-shelf transport; LST, long-shore transport; DD, degree days; Prey, prey index; pre, preconditioning; egg, egg stage; yolk, yolk sac larvae; larv, larval stage; pjuv, pelagic juvenile; bjuv, benthic juveniles. AICc, Akaike's information criterion adjusted for small sample size.

**TABLE 3** Coefficients for the best-fit model (Model 1 from Table 2) showing both raw and standardized (beta) coefficients

	Coefficient	Bias	SE	Standardized coefficient	Bias	SE
Intercept	6973.8	-888.9	18216.9	-1534.3	38.1	1288.1
DD <sub>pre</sub>	-523.2	8.2	147.4	-6149.0	103.1	1753.2
CST <sub>egg</sub>	112489.8	33,44.9	26593.2	6607.4	107.3	1641.2
DD <sub>egg</sub>	1308.52	12.8	250.1	11126.9	-91.2	2100.1
LST <sub>yolk</sub>	44813.1	209.9	15348.5	4920.7	-48.4	1669.3
DD <sub>larvae</sub>	-231.3	-9.3	84.3	-5,012.8	-134.7	1987.8

Bias and standard error (SE) are from bootstrap resampling. DD, degree days; CST, cross-shelf transport; LST, long-shore transport; pre, preconditioning; egg, egg stage; yolk, yolk sac larvae; larvae, larval stage.

best model had a  $\Delta AICc > 3.9$ . The best-fit model included five covariates (Figure 2) related to temperature and transport, which explained 57% of the variation in recruitment residuals (from the stock-recruitment relationship) during 1981–2010. Model predictions closely followed the estimated recruitments from the stock assessment with the exception of 2006–2009 when the model over or under-predicted recruitment (Figure 3). Recruitment residuals were negatively correlated with degree days during the period of female preconditioning (DD<sub>pre</sub>) and larval stage (DD<sub>larv</sub>). Conversely, cross-shelf transport during the egg stage (CST<sub>egg</sub>), degree days during the egg stage (DD<sub>egg</sub>), and long-shore transport during the yolk-sac stage (LST<sub>yolk</sub>) were positively correlated with recruitment residual (Figure 4, Table 3). Standardized coefficients suggest that DD<sub>egg</sub> had the strongest effect on recruitment deviations, while the other predictors had similar impact (Table 3).

Only three additional models had  $\Delta AICc < 4.0$  and all had  $\Delta AICc > 3.9$ . These models were generally consistent in structure with the best-fit model (Table 2). The terms DD<sub>egg</sub> and LST<sub>yolk</sub> occurred in all three models, and DD<sub>pre</sub> and DD<sub>egg</sub> in two. Model 4 was a subset of Model 1 minus the DD<sub>larv</sub> term ( $r^2 = .43$ ). The other two models included alternate terms that had less support from the data including prey abundance, long-shore transport during the pelagic juvenile stage and SSH.

There was some moderate correlation between the covariates with the highest being for DD<sub>pre</sub> and DD<sub>egg</sub> ( $r = .62$ , Table 4). Generalized variance inflation factor values (VIF; which measure how much the variance of the estimated regression coefficients are inflated as compared to when the predictor variables are not linearly related) were low to moderate with the exception of DD<sub>egg</sub>, which was moderate (Table 4). Because there was

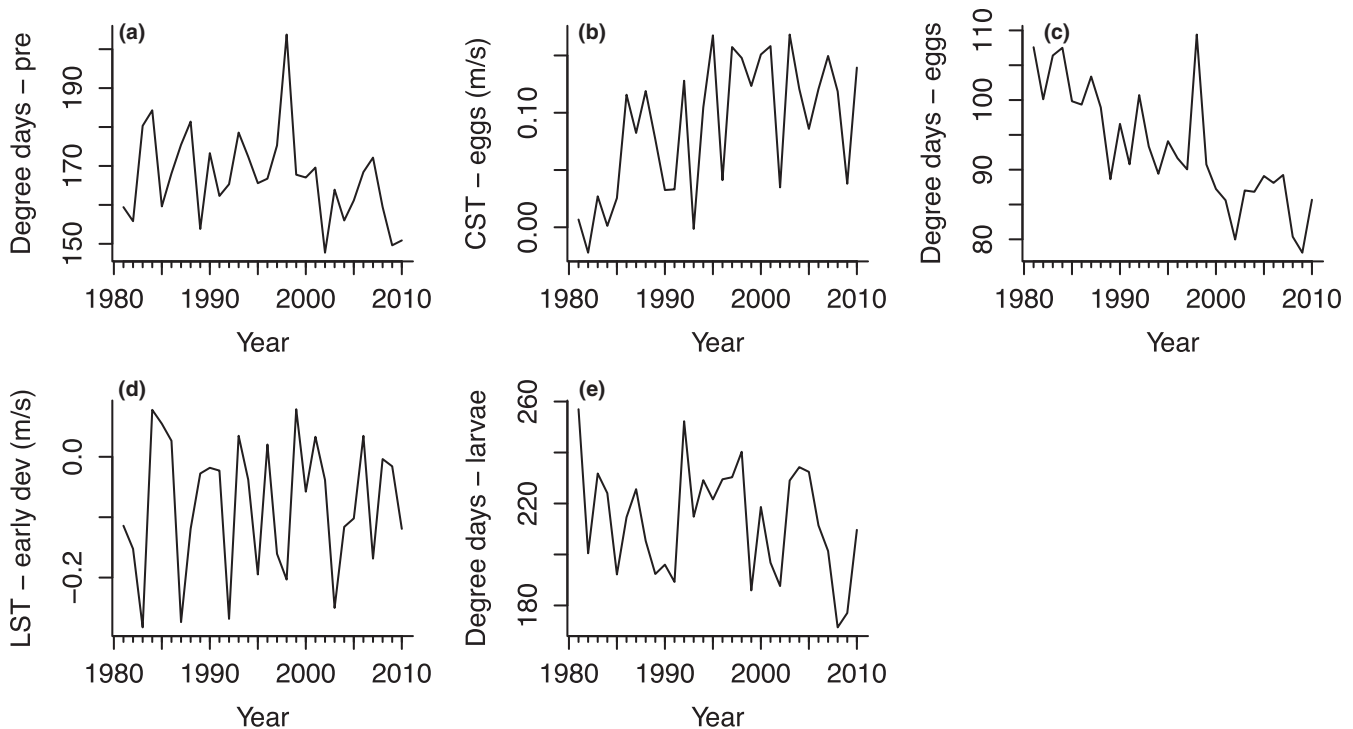
moderate correlation between DD<sub>egg</sub> and the other two DD terms, we refit the best-fit model adding interactions between DD<sub>egg</sub> and the other two DD terms. These additional models included all nested possibilities from an individual interaction term to all interaction terms including a three-way interaction. Adding interactions increased AICc values by 2.99–14.78 points for all models suggesting that non-interaction model best fit the data. Residuals from the best-fit model did not show signs of autocorrelation (Figure S2).

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

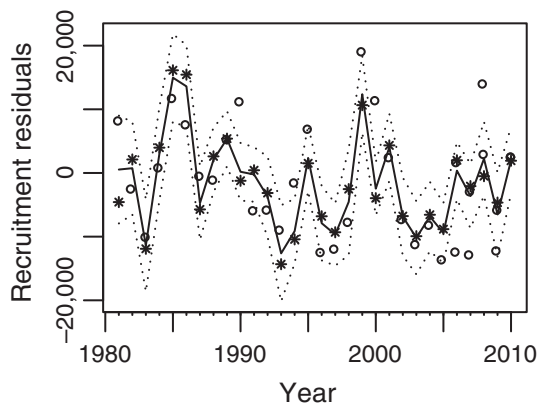
Randomly resampling the recruitment deviations (with replacement) gave a median expected  $r^2 = .17$  (95% confidence limits of 0.03–0.40) for a five parameter model suggesting that the observed value of  $r^2 = .57$  was unlikely to be observed at random.

Removing individual years and refitting the best-fit model (jack-knifing) had little impact on the model fit (Figures 3 and 5, median  $r^2 = .57$ ). Predicting the missing year from any iteration produced estimates very similar to those for the full model (Figure 3). The three years that showed the highest impact on the model's ability to explain the data were 1999, 2000 and 2006. Removing 1999 reduced the explained variance the most ( $r^2 = .51$ ), while removing 2000 or 2006 increased the  $r^2$  to .63. Recruitment was higher than predicted in 1999 and 2000 but lower than predicted in 2006. Predicting recruitments for 2006–2010 based on a 1981–2005 model produced estimates very close to those for the 1981–2010 model (Figure 3).

Resampling individual recruitments with error had little effect on the model's predictive power with median  $r^2 = .55$  (95% CI = 0.59–



**FIGURE 2** Time-series of independent variables in the best-fit model. (a) degree days during female preconditioning, (b) net cross-shelf transport during the egg stage, (c) degree days during the yolk-sac stage, (d) long-shore transport during the yolk-sac stage, and (e) degree days during the larval stage



**FIGURE 3** Fit of the best-supported model ( $r^2 = .57$ ) to the estimated recruitment residuals from the stock assessment. Solid line is the predicted recruitment residuals from the full time series. Dotted lines = 95% confidence limits. Black points are recruitment residuals from the Beverton-Holt stock recruitment relationship from the 2015 sablefish assessment. Stars are predicted values from jackknife analysis removing individual years one at a time. Grey points are predicted values for the retrospective analysis of the last five years. Note, all three points overlap in 2010

0.70) across all trials. This result suggests that uncertainty in the recruitment time series (given the current assessment parameters) did not greatly affect the results.

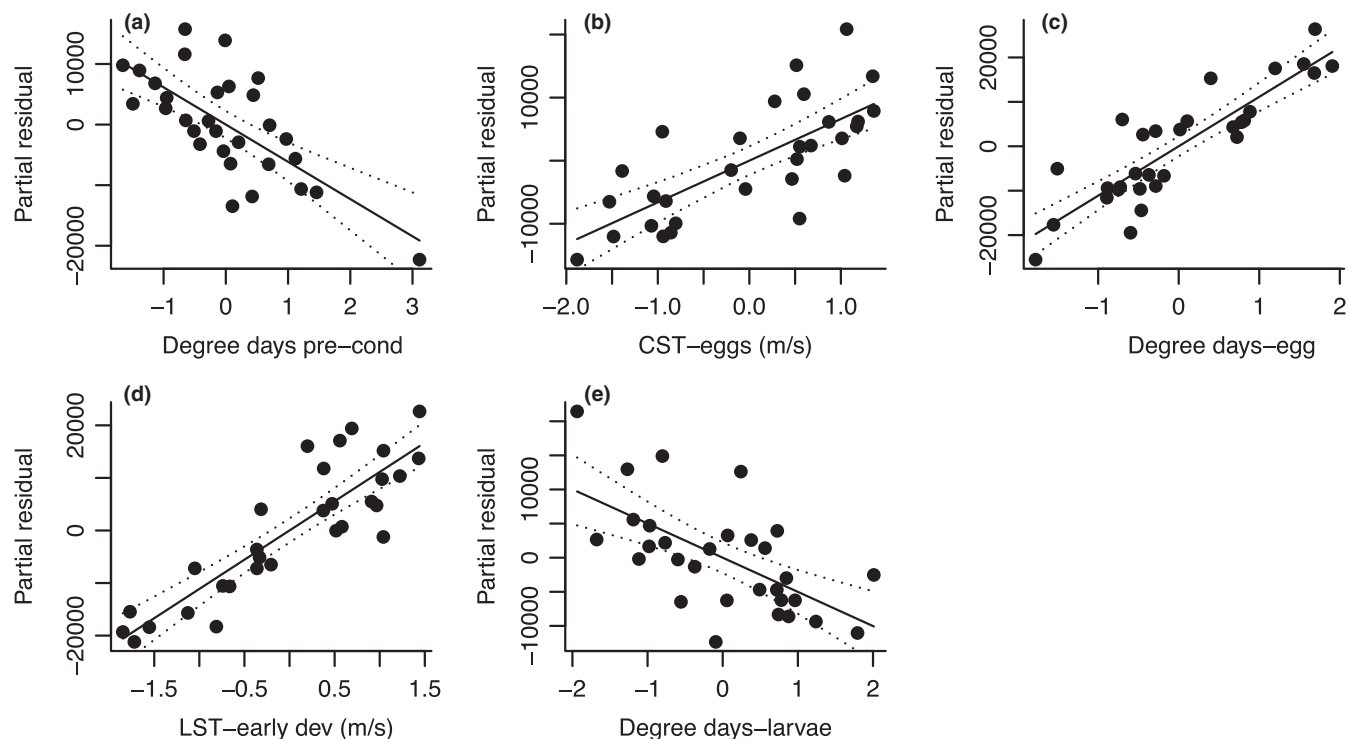
Using the jackknife resampling and re-running the entire model fitting process produced results that were largely consistent with the primary analysis. However, removing 1984, 1987, 1989 and 1991

did result in different best-fit models. Three of these models included  $Prey_{hake}$  as a predictor. Hake recruitment was above the 95% confidence intervals for estimated recruitment at unfished biomass in 1984 and 1987 but below it in 1989 and 1991 (see figure e and table c in Taylor et al., 2015). However, there were also other extreme years which did not alter the terms included in the model here. SSH was also selected in three models. Removal of any other year produced the same set of predictors as in the primary analysis (Table 5). Model predictions for the best-fit model closely followed observed model data for 1984, 1987 and 1989 but recruitment in 1991 was lower than predicted. Interestingly, there was no overlap between the three years that had the largest impact on the explanatory value of the best-fit model and those years that affected the re-fitting process.

Finally, the results from resampling the recruitment values (with error) and re-running the entire model fitting exercise one hundred times were also generally consistent with the best-fit model from the primary analysis. The predictors from the best-fit model also occurred in the majority of best-fit models from each iteration:  $DD_{pre}$  (72% of models),  $CST_{egg}$  (73%),  $DD_{egg}$  (89%),  $LST_{yolk}$  (83%), and  $DD_{larv}$  (70%). Additional predictors included  $Prey_{hake}$  (18%),  $LST_{pjuv}$  (18%) and  $SSH^2$  (21%).

### 3.2 | Northern copepod biomass anomaly

When refit to 1996–2010 data, the best-fit model explained 67% of the variation around the stock recruitment-relationship from the



**FIGURE 4** Partial residual plots for (a) degree days during female pre-conditioning, (b) net cross-shelf transport during the egg stage, (c) degree days during the yolk-sac stage, (d) long-shore transport during the yolk-sac stage, and (e) degree days during the larval stage

**TABLE 4** Correlations among variables included in the best-fit model

	DD <sub>pre</sub>	CST <sub>egg</sub>	DD <sub>egg</sub>	LST <sub>yolk</sub>	VIF
DD <sub>pre</sub>	—				2.17
CST <sub>egg</sub>	0.08	—			1.87
DD <sub>egg</sub>	0.62	−0.43	—		3.38
LST <sub>yolk</sub>	−0.17	0.23	−0.30	—	1.63
DD <sub>larvae</sub>	0.38	−0.14	0.55	−0.54	1.92

VIF, generalized variance inflation factor; DD, degree days; CST, cross-shelf transport; LST, long-shore transport; pre, preconditioning; egg, egg stage; yolk, yolk-sack larvae; larvae, larval stage.

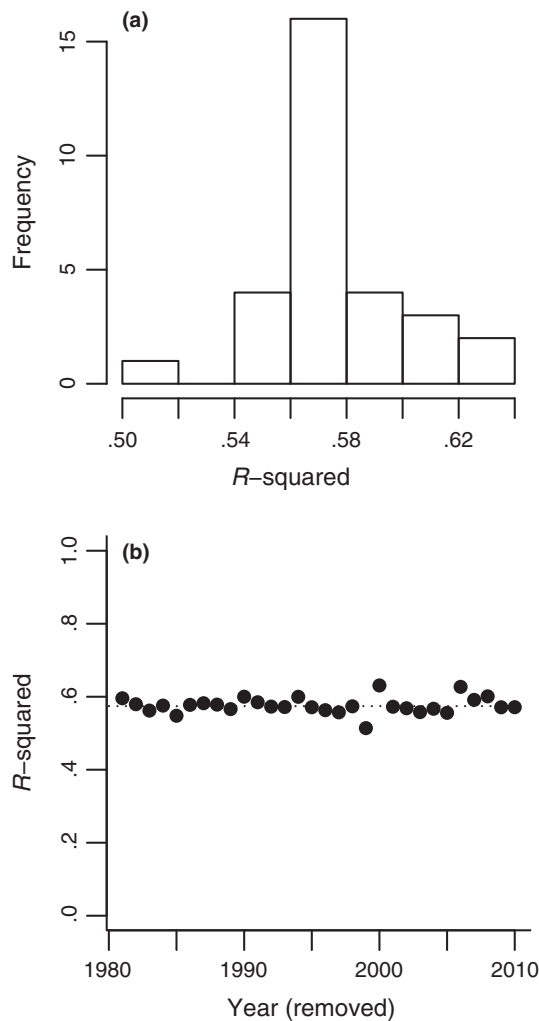
stock assessment. Alone the copepod index explained 24% of the variation in recruitment over the 1996–2010 period. However, adding the northern copepod biomass anomaly did not increase the variation explained (also 67%). The anomaly was moderately correlated with most other predictors in the best-fit model with the exception of CST<sub>egg</sub>: DD<sub>pre</sub> ( $r = -.46$ ), CST<sub>egg</sub> ( $r = -.01$ ), DD<sub>egg</sub> ( $r = .56$ ), LST<sub>yolk</sub> ( $r = .48$ ), and DD<sub>larv</sub> ( $r = -.57$ ). Thus, while food supply is likely important, the other physical parameters may act as sufficient proxies in the absence of a full time series of copepod data.

## 4 | DISCUSSION

Our results suggest that multiple mechanisms acting at different stages in the life history of sablefish drive recruitment (Figure 6).

The best-fit model explained approximately 57% of the variation around the stock-recruitment curve and fit the recruitment data well (specifically residuals from the stock-recruitment relationship in the assessment in Figure 3). Nevertheless, it is not unreasonable to consider this work as an effort to formalize potential hypotheses that should be investigated further.

Colder conditions during the spawner pre-conditioning period led to higher recruitment. Given sufficient food, warmer temperatures allow for faster growth and larger female size, which results in higher fecundity (Harvey, 2009). However, colder water temperatures may lower metabolic costs allowing female sablefish to divert more energy to egg production. However, the variability in the ROMS output for this parameter is likely driven primarily by temperature variation at shallower depths, and may not represent female exposure in deeper regions. More likely, colder conditions may be linked to stronger upwelling, which leads to productivity and food availability (Chavez et al., 2003; Harvey, 2005; Peterson, 2009; Sydeman et al., 2011). While we are unaware of data connecting female condition to egg production in sablefish, individuals may skip spawn (Rodgveller et al., 2016) given limited energy reserves and degraded body condition as seen in other species like Atlantic cod *Gadus morhua* (Skjæraasen et al., 2009, 2012) and Pacific ocean perch (Hannah & Parker, 2007). The results from the jackknife refitting of the entire selection process support the hypothesis that food resources are likely important for females during the period leading up to spawning. For three of the 4 years that when omitted produced different best-fit models, Prey<sub>hake</sub> (positive correlation with recruitment) replaced DD<sub>pre</sub> as a



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

**TABLE 5** Best-fit models from jackknife refits of the entire model-fitting process

	Year removed			
Main model	1984	1987	1989	1991
DD <sub>pre</sub>	Prey <sub>hake</sub>	DD <sub>spawn</sub>	Prey <sub>hake</sub>	Prey <sub>hake</sub>
CST <sub>egg</sub>	CST <sub>larv</sub>	LST <sub>yolk</sub>	DD <sub>egg</sub>	DD <sub>egg</sub>
DD <sub>egg</sub>	LST <sub>pjuv</sub>	CST <sub>pjuv</sub>	LST <sub>pjuv</sub>	LST <sub>yolk</sub>
LST <sub>yolk</sub>	SSH <sup>2</sup>	LST <sub>bjuv</sub>	DD <sub>bjuv</sub>	LST <sub>pjuv</sub>
DD <sub>larv</sub>		FWI <sub>bjuv</sub>	SSH	SSH

Removing the years 1984, 1987, 1989 and 1991 changed the best-fit model in those iterations. All other years produced models with the same covariates as in the main model.

predictor suggesting that a large hake prey base may also lead to better female condition and recruitment.

Recruitment was positively correlated with water temperature during the egg stage (DD<sub>egg</sub>). In marine fishes, increased temperature results in faster development, shorter stage duration, earlier hatch

#### Female preconditioning (50–1,200 m)

$$(-) DD_{pre}$$

Cold water is associated with higher system productivity and lower metabolic costs making more energy available for reproduction

#### Eggs (300–825 m)

$$(+) CST_{egg}$$

Onshore transport maintains larvae near settlement habitat

$$(+) DD_{egg}$$

Faster development in warm water

#### Yolk-sack (1000–1200 m)

$$(+) LST_{yolk}$$

Transport to the north results in better feeding later on northern zooplankton

#### Pelagic larvae (surface waters)

$$(-) DD_{larv}$$

Cold water is associated with higher system productivity and lower chance of starvation

**FIGURE 6** Conceptual model for sablefish 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 sablefish stock-recruitment relationship. See Figure 4 for plots of these relationships

date and increased hatching rates, up to a species-specific temperature maxima after which developmental abnormalities occur (Llopiz et al., 2014; Peck, Huebert, & Llopiz, 2012; Pepin, 1991; Tsoukali, Visser, & MacKenzie, 2016). Growth in sablefish is strongly related to temperature (Sogard, 2011; Sogard & Olla, 2001) suggesting that a similar physiological response would be likely for development. Moving more quickly through the egg state may reduce susceptibility to egg predators and reduce dispersal, the latter potentially important for match-mismatch dynamics with prey resources (Peck et al., 2012). Offshore transport due to upwelling occurs primarily in surface waters. Since eggs are buoyant but yolk-sac larvae found at depth (1,000–1,200 m), entering deep water sooner may help to avoid advection offshore.

Cross-shelf transport was important from January to April corresponding to life-history stages for which sablefish are non- or only

minimally motile: eggs and yolk-sac larvae. The positive correlation with  $CST_{egg}$  is fairly straightforward: being transported to near-shore nursery environments leads to higher recruitment. At first glance this result may seem at odds with Schirripa and Colbert (2006) who found a negative correlation between recruitment strength and on-shore cross-shelf transport during June. However, the time periods (January to April versus June) and the depths (300–825 m versus approximately 0–150 m) differ suggesting that the two predictors relate to different processes: (i) transport of eggs onshore following spawning (our analysis), and (ii) and upwelling leading to higher productivity and food resources later in the season.

Recruitment was also positively correlated with transport to the north during the yolk-sac stage ( $LST_{yolk}$ : February to May at 1,000–1,200 m). Again this result may initially appear to contradict Schirripa and Colbert (2006) who found that stronger southerly transport of surface waters (50–100 m) in February correlated with higher recruitment. However, the depths differ, and these two results may tell different parts of the same story. Southerly transport of surface waters brings boreal copepods into the Northern California Current Ecosystem. These copepods are larger, higher in fatty acids, and a better food source than southern copepods (McFarlane & Beamish, 1992; Peterson, 2009; Peterson & Keister, 2002). Yolk-sac larvae, however, are found at much deeper depths (1,000–1,200 m). Northern transport at these depths likely brings these larvae to the north where they are more likely encounter these energy-rich copepods once the larvae rise to the surface, start feeding, and eventually grow large enough to feed on the copepods. Access to this food resource might then result in high recruitment through any number of mechanisms including faster growth rates (size-related predation avoidance) and reduced starvation risk.

Temperature during the larval stage ( $DD_{larv}$ , February–May, surface waters) was negatively correlated with recruitment. Sogard (2011) found increased growth at warmer temperatures and higher recruitment in years with good growth, the latter after adjusting for fish size and temperature. However, Schirripa and Colbert (2006) found higher recruitment with offshore transport of surface waters, which coincides with colder upwelled water. Combined, these results suggest a trade-off between better food resources under colder conditions but faster growth for metabolic reasons in warm water. Colder temperatures may index two different mechanisms that result in higher prey availability or quality: enhanced upwelling and higher primary production, and the southerly transport of northern copepods. At the same time, larvae may be more susceptible to starvation under warm conditions due to increased metabolism and lack of prey. Both daily growth and daily mortality are positively correlated with temperature in marine fish larvae in general, although stage-duration decreases (Houde, 2008). Growth of early juvenile sablefish increases with increasing water temperature, but this effect requires sufficient food resources (Sogard, 2011; Sogard & Olla, 2001). Since sablefish have limited capacity or compensatory growth (Sogard & Olla, 2002), they appear to have a risk-prone strategy growing as quickly as possible (Sogard, 2011; Sogard & Olla, 2002) and may be susceptible to starvation under warm conditions. In the lab larvae

will move to colder water as rations are decreased, indicating an energy-conservation strategy when food is limited (Sogard & Olla, 1998, 2001). Adjusting for water temperature and fish size, Sogard (2011) found higher than expected growth under cold conditions in some years suggesting better food resources under cold conditions.

Rapid growth may help individuals avoid predation through a number of mechanisms (e.g., “bigger-is-better”, stage-duration) that cannot be untangled in this study. However, Sogard (2011) did not find evidence for size-selective mortality, possibly because the higher temperatures also lead to increased predator activity and consumption (e.g., Akimova, Hufnagl, Kreis, & Peck, 2016). One might also expect the offshore transport associated with cold, upwelled waters to advect sablefish larvae away from suitable settlement habitat. Sablefish larvae are found in these surface waters where most of this offshore transport occurs. However, sablefish larvae develop large pectoral fins suggesting that they may have evolved to control their position in the water column (Kendall & Matarese, 1987; Shotwell et al., 2014), and many fish larvae are strong swimmers, especially prior to settlement (Montgomery et al., 2001). Thus, rapid development earlier in the season (warm waters during  $DD_{egg}$ ) may allow sablefish larvae to develop the swimming capacity to utilize high quality food resources later in the year ( $DD_{larv}$ , indexed by cold water) while maintaining position in the water column and staying closer to appropriate settlement habitat.

Many of the years that either affected the model fit in the jack-knife exercises or in which observed recruitment fell outside the 95% confidence intervals for the best-fit model appear to be associated with El Niño or La Niña events in some way. For example, recruitment was higher than predicted in 2000 and 2008 coincident with La Niña conditions as measured by the ONI (Oceanic Niño Index (ONI) [http://www.cpc.ncep.noaa.gov/products/analysis\\_monitoring/ensostuff/ensoyears.shtml](http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml)) from the summer of 1998 through spring of 2001 and late summer 2007 through late spring of 2008. Observed recruitment was lower than predicted 2005–2007, with variable El Niño conditions between late summer of 2005 and early 2007. However, in other El Niño or La Niña years the observed recruitment was within the 95% confidence limits for the model predictions. We did try adding both the tri-monthly ONI and bi-monthly MEI (Multivariate ENSO Index (MEI) <https://www.esrl.noaa.gov/psd/enso/mei/>) indices to the best-fit model to determine if El Niño/La Niña information would improve the model fit, but all such models had higher AICc values than the best-fit model. This result does not necessarily mean that El Niño/La Niña events do not affect sablefish recruitment as the effects on food availability, temperature, and transport are likely already caught in the ROMS parameters.

In summary, multiple mechanisms likely drive recruitment of sablefish (Figure 6). Cold conditions during the pre-conditioning period for spawners may allow females to divert more energy to egg production due to lower metabolic costs, or these colder temperatures may be indicative of upwelling or southerly transport of boreal copepods and better food resources also allowing for more egg production. Warmer temperatures during the egg stage likely allow for higher growth rates and predation avoidance through bigger-is-

better mechanisms. On shore transport during the egg and yolk-sac stages retains individuals on shore near settlement habitat and reduces losses due to advection. Northern long-shore transport appears to bring larvae to regions where they are more likely to encounter food resources as they rise to surface waters to start feeding. The mechanism behind the negative correlation between recruitment and water temperature (degree days) during the larval stage is less clear. However, colder water may index better or alternate food resources due to upwelling or the southerly transport of boreal copepods, and may also reduce basal metabolism and reduce the risk of starvation.

#### 4.1 | Implications for stock assessment

This study provides the underlying process-orientated hypotheses to address three issues in the stock assessment and management of U.S. west coast sablefish: (i) the reconstruction of what historical recruitment could have been in the absence of length- and age-composition data to inform recruitment during the period when the fishery was operating, (ii) sub-annual to 1 year ahead forecasting of recruitment based on both observed oceanographic conditions and potentially sub-annual forecasts of environmental conditions, and (iii) long-term projections of potential future stock productivity and the evaluation of the robustness of harvest control rules (HCRs) to changes in stock productivity evaluation via Management Strategy Evaluation (MSE).

The five oceanographic indicators identified as important drivers of sablefish recruitment in this study can inform recruitments for historical periods that lack fishery age- and length-composition data and for near-term forecasts. These historical and near-term forecasts generally rely upon average recruitment from the stock recruitment curve. However, recruitment is often far above or below the average, with large annual deviations around the stock-recruitment curve. Furthermore, the most uncertain periods in the stock assessment model are those that either lack age and length composition data, or have sparse data. Hind-casting recruitments during periods of high fishery removals without good age and length composition data should result in a reduction in uncertainty during early model years. The oceanographic indices identified during this study could be used as a survey index of recruitment in the stock assessment during the historical time period. Using the five oceanographic indicators from this study to estimate what recruitment deviations could have been, or may be into the near-term future, can provide both better estimates of historical recruitment, and therefore the un-fished spawning biomass reference point used for managing the fishery, as well as the incoming recruitment 1 year ahead, providing better catch advice based on what recruitment is likely to be entering the fishery in the near term (Kaplan, Williams, Bond, Hermann, & Siedlecki, 2016; Siedlecki et al., 2016). Finally, if long-term forecasts of these five oceanographic drivers of sablefish recruitment are available from either Global or downscaled regional Climate Models (GCMs), they could be used to provide long-term strategic projections for fishery management planning that could include not only the fishing industry

and managers (PFMC) but those groups interested in the identification of potential climate-adaptation strategies given the long-term outlook for the sablefish fishery. This could include societal adaptations that build community resilience to climate driven changes in the sablefish resource such as: (i) market development for a higher quality and priced product, (ii) evaluation of the resilience of the sablefish supply chain to projected changes in catch, and (iii) aquaculture research and development (Norman-López et al., 2013; Norman-López et al., 2014).

A number of issues with respect to the oceanographic modeling and data availability will need continuing work. First, the easily available ROMS outputs that were used for this study span the period from 1980 to 2010. However, the current recruitment estimates from the sablefish stock assessment model continue through 2014, and will continue into the future. There is currently a discontinuity in the ROMS model outputs between 2010 and 2011 because drivers for the surface forcing (heat flux, wind) come from different products for 2011–2015, as does the input for the ocean boundary conditions. This discontinuity prevents the use of the most recent recruitment estimates in evaluating the hypotheses posed in this study. Continuous ROMS model outputs for both the pre-1980 and the post-2010 periods are necessary for fully using the results of this study in sablefish stock assessment and management. Future oceanographic modeling work should investigate the ability of ROMS models to provide informative, short-term seasonal to annual forecasts of relevant oceanographic covariates. Skillful ROMS forecasts could better inform recruitments entering the fishery prior to the availability of survey data.

It is important that the oceanographic drivers of sablefish recruitment identified in this study continue to be periodically re-evaluated as the fundamental relationships could change through time, particularly if the impacts of global climate change cause variability in the California Current to exceed recent historical levels (Cheung et al., 2016). This continued re-evaluation depends upon both maintaining current oceanographic and biological monitoring programs that will allow for tracking of potential non-stationarity. Finally, best methods for integrating these relationships into the stock assessment model should be investigated. The current stock assessment (Johnson et al., 2016) uses the environmental data as a survey index of recruitment, but new tools to incorporate environmental drivers in the population dynamics with uncertainty are becoming available (Methot & Wetzel, 2013).

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## REFERENCES

- Akimova, A., Hufnagl, M., Kreuz, M., & Peck, M. A. (2016). Modeling the effects of temperature on the survival and growth of North Sea cod (*Gadus morhua*) through the first year of life. *Fisheries Oceanography*, 25, 193–209. <https://doi.org/10.1111/fog.12145>
- Alderdice, D. F., Jensen, J. O. T., & Velsen, F. P. J. (1988). Preliminary trials on incubation of sablefish eggs (*Anoplopoma fimbria*). *Aquaculture*, 69, 271–290.
- Allen, M. J., & Smith, G. B. (1988). *Atlas and zoogeography of common fishes in the Bering Sea and northeastern Pacific*. Seattle, WA, NOAA Tech Rep 66, National Marine Fisheries Service, 151 pp.
- Bailey, K. M. (1981). Larval transport and recruitment of Pacific hake *Merluccius productus*. *Marine Ecology Progress Series*, 6, 1–9. <https://doi.org/10.3354/meps006001>
- Basson, M. (1999). The importance of environmental factors in the design of management procedures. *ICES Journal of Marine Science*, 56, 933–942. <https://doi.org/10.1006/jmsc.1999.0541>
- Boehlert, G. W., & Yoklavich, M. M. (1985). Larval and juvenile growth of sablefish, *Anoplopoma fimbria*, as determined from otolith increments. *Fisheries Bulletin*, 83, 475–481.
- Brock, V. E. (1940). Note on the young of the sablefish, *Anoplopoma fimbria*. *Copeia*, 1940, 268–270. <https://doi.org/10.2307/1438590>
- Burnham, K. P., & Anderson, D. R. (1998). *Model selection and inference: A practical information-theoretic approach*. New York, NY: Springer-Verlag. <https://doi.org/10.1007/978-1-4757-2917-7>
- Chavez, F. P., Ryan, J., Lluch-Cota, S. E., & Niquen, C. M. (2003). From anchovies to sardines and back: Multidecadal change in the Pacific Ocean. *Science*, 299, 217–221. <https://doi.org/10.1126/science.1075880>
- Cheung, W. W. L., Frolicher, T. L., Asch, R. G., Jones, M. C., Pinsky, M. L., Reygondeau, G., ... Watson, J. R. (2016). Building confidence in projections of the responses of living marine resources to climate change. *ICES Journal of Marine Science*, 73, 1283–1296. <https://doi.org/10.1093/icesjms/fsv250>
- Chezik, K. A., Lester, N. P., & Venturelli, P. A. (2014). Fish growth and degree-days I: Selecting a base temperature for a within-population study. *Canadian Journal of Fisheries and Aquatic Sciences*, 71, 47–55. <https://doi.org/10.1139/cjfas-2013-0295>
- Coffin, B., & Mueter, F. (2015). Environmental covariates of sablefish (*Anoplopoma fimbria*) and Pacific ocean perch (*Sebastes alutus*) recruitment in the Gulf of Alaska. *Deep-Sea Research II*, 132, 194–209.
- Di Lorenzo, E., Mountain, D., Batchelder, H. P., Bond, N., & Hofmann, E. E. (2013). Advances in marine ecosystem dynamics from US GLOBEC: The horizontal-advection bottom-up forcing paradigm. *Oceanography*, 26, 22–33. <https://doi.org/10.5670/oceanog>
- Field, J. C., Francis, R. C., & Aydin, K. (2006). Top-down modeling and bottom-up dynamics: Linking a fisheries-based ecosystem model with climate. *Progress in Oceanography*, 68, 238–270. <https://doi.org/10.1016/j.pocean.2006.02.010>
- Frank, K. T., Petrie, B., & Shackell, N. L. (2007). The ups and downs of trophic control in continental shelf ecosystems. *Trends in Ecology & Evolution*, 22, 236–242. <https://doi.org/10.1016/j.tree.2007.03.002>
- Grover, J. J., & Olla, B. L. (1987). Effects of an El Niño event on the food habits of larval sablefish, *Anoplopoma fimbria*, off Oregon and Washington. *Fishery Bulletin*, 85, 71–79.
- Hamel, O. S., Sethi, S. A., & Wadsworth, T. F. (2009). *Status and future prospects for lingcod in waters off Washington, Oregon, and California as assessed in 2009*. Portland, OR: Pacific Fishery Management Council. 458 pp.
- Hannah, R. W., & Parker, S. J. (2007). Age-modulated variation in reproductive development of female Pacific ocean perch (*Sebastes alutus*) in waters off Oregon. In J. Heifetz, J. DiCosimo, A. J. Gharrett, M. S. Love, V. M. O'Connell, & R. D. Stanley (Eds.), *Biology, assessment, and management of North Pacific rockfishes* (pp. 1–20). Fairbanks, AK: Alaska Sea Grant.
- Hart, J. L. (1973). *Pacific fishes of Canada*. St. Andrews, New Brunswick, Canada: Fisheries Research Board of Canada, Bulletin 180. 740 pp.
- Harvey, C. J. (2005). Effects of El Niño events on energy demand and egg production of rockfish (Scorpaenidae: *Sebastes*): A bioenergetics approach. *Fishery Bulletin*, 103, 71–83.
- Harvey, C. J. (2009). Effects of temperature change on demersal fishes in the California Current: A bioenergetics approach. *Canadian Journal of Fisheries and Aquatic Sciences*, 66, 1449–1461. <https://doi.org/10.1139/F09-087>
- He, X., Pearson, D. E., Dick, E. J., Field, J. C., Ralston, S., & MacCall, A. D. (2011). *Status of the widow rockfish resource in 2011*. Santa Cruz, CA: National Marine Fisheries Service, Southwest Fisheries Science Center, Fisheries Ecology Division.
- Head, M. A., Keller, A. A., & Bradburn, M. (2014). Maturity and growth of sablefish, *Anoplopoma fimbria*, along the US West Coast. *Fisheries Research*, 159, 56–67. <https://doi.org/10.1016/j.fishres.2014.05.007>
- Hixon, M. A., & Jones, G. P. (2005). Competition, predation, and density-dependent mortality in demersal marine fishes. *Ecology*, 86, 2847–2859. <https://doi.org/10.1890/04-1455>
- Hjort, J. (1914). Fluctuations in the great fisheries of Northern Europe. *Rapports et Procès-verbaux des Réunions, Conseil International pour l'Exploration de la Mer*, 20, 1–13.
- Holmes, E. E., Ward, E. J., & Scheuerell, M. D. (2014). *Analysis of multivariate time-series using the MARSS package*. Seattle, WA: NOAA Fisheries, Northwest Fisheries Science Center. 238 pp.
- Holmes, E. E., Ward, E. J., & Wills, K. (2012). MARSS: Multivariate autoregressive state-space models for analyzing time-series data. *The R Journal*, 4, 11–19.
- Houde, E. D. (1987). Fish early life dynamics and recruitment variability. *American Fisheries Society Symposium*, 2, 17–29.
- Houde, E. D. (1997). Patterns and trends in larval-stage growth and mortality of teleost fish. *Journal of Fish Biology*, 51, 52–83. <https://doi.org/10.1111/j.1095-8649.1997.tb06093.x>
- Houde, E. (2008). Emerging from Hjort's shadow. *Journal of Northwest Atlantic Fishery Science*, 41, 53–70. <https://doi.org/10.2960/J.v41.m634>
- Hunt, G. L. Jr, & McKinnell, S. (2006). Interplay between top-down, bottom-up, and wasp-waist control in marine ecosystems. *Progress in Oceanography*, 68, 115–124. <https://doi.org/10.1016/j.pocean.2006.02.008>
- Hunter, J. R., Macewicz, B. J., & Kimbrell, C. A. (1989). Fecundity and other aspects of the reproduction of sablefish, *Anoplopoma fimbria*, in central California waters. *California Cooperative Oceanic Fisheries Investigations Reports*, 30, 61–72.
- Jacox, M. G., Bograd, S. J., Hazen, E. L., & Fiechter, J. (2015). Sensitivity of the California Current nutrient supply to wind, heat, and remote ocean forcing. *Geophysical Research Letters*, 42, 5950–5957. <https://doi.org/10.1002/2015GL065147>
- Jacox, M. G., Fiechter, J., Moore, A. M., & Edwards, C. A. (2015). ENSO and the California Current coastal upwelling response. *Journal of Geophysical Research: Oceans*, 120, 1691–1702.
- Jacox, M. G., Hazen, E. L., & Bograd, S. J. (2016). Optimal environmental conditions and anomalous ecosystem responses: Constraining bottom-

- up controls of phytoplankton biomass in the California current system. *Scientific Reports*, 6, 27612. <https://doi.org/10.1038/srep27612>
- Jacox, M. G., Moore, A. M., Edwards, C. A., & Fiechter, J. (2014). Spatially resolved upwelling in the California Current System and its connections to climate variability. *Geophysical Research Letters*, 41, 3189–3196. <https://doi.org/10.1002/2014GL059589>
- Johnson, K. F., Rudd, M. B., Pons, M., Akselrud, C. A., Lee, Q., Hurtado-Ferro, F., ... Hamel, O. S. (2016). *Status of the U.S. sablefish resource in 2015*. Portland, OR: Pacific Fisheries Management Council. 377 pp.
- Kaplan, I. C., & Helser, T. E. (2007). *Stock assessment of the arrowtooth flounder (Atheresthes stomias) population off of the west coast of the United states in 2007*. Seattle, WA: NOAA National Marine Fisheries Service, Northwest Fisheries Science Center, Fishery Resource Analysis and Monitoring.
- Kaplan, I. C., Williams, G. D., Bond, N. A., Hermann, A. J., & Siedlecki, S. A. (2016). Cloudy with a chance of sardines: Forecasting sardine distributions using regional climate models. *Fisheries Oceanography*, 25, 15–27. <https://doi.org/10.1111/fog.12131>
- Keller, A. A., Horness, B. H., Fruh, E. L., Simon, V. H., Tuttle, V. J., Bosley, K. L., ... Wallace, J. R. (2008). *The 2005 U.S. West Coast bottom trawl survey of groundfish resources off Washington, Oregon, and California: Estimates of distribution, abundance, and length composition*. U.S. Department of Commerce, NOAA Technical Memorandum. NMFS-NWFSC-93. 136 pp.
- Kendall, A. W., & Matarese, A. C. (1987). Biology of eggs, larvae, and epipelagic juveniles of sablefish, *Anoplopoma fimbria*, in relation to their potential use in management. *Marine Fisheries Review*, 49, 1–13.
- Laidig, T. E., Adams, P. B., & Samiere, W. M. (1997). Feeding habits of sablefish, *Anoplopoma fimbria*, off the coast of Oregon and California (Technical Report No. 130). National Marine Fisheries Service: Seattle, WA.
- Leggett, W. C., & DeBlois, E. (1994). Recruitment in marine fishes: Is it regulated by starvation and predation in the egg and larval stages? *Netherlands Journal of Sea Research*, 32, 119–134. [https://doi.org/10.1016/0077-7579\(94\)90036-1](https://doi.org/10.1016/0077-7579(94)90036-1)
- Litvak, M. K., & Leggett, W. C. (1992). Age and size-selective predation on larval fishes: The bigger-is-better hypothesis revisited. *Marine Ecology Progress Series*, 81, 13–24. <https://doi.org/10.3354/meps081013>
- Llopiz, J. K., Cowen, R. K., Hauff, M. J., Ji, R. B., Munday, P. L., Muhling, B. A., ... Sponaugle, S. (2014). Early life history and fisheries oceanography new questions in a changing world. *Oceanography*, 27, 26–41. <https://doi.org/10.5670/oceanog>
- Mason, J. C., Beamish, R. J., & McFarlane, G. A. (1983). Sexual maturity, fecundity, spawning, and early life history of sablefish (*Anoplopoma fimbria*) off the Pacific coast of Canada. *Canadian Journal of Fisheries and Aquatic Science*, 40, 2126–2134. <https://doi.org/10.1139/f83-247>
- Maunder, M. N., & Watters, G. M. (2003). A general framework for integrating environmental time series into stock assessment models: Model description, simulation testing, and example. *Fishery Bulletin*, 101, 89–99.
- McFarlane, G. A., & Beamish, R. J. (1992). Climatic influence linking copepod production with strong year-classes in sablefish, *Anoplopoma fimbria*. *Canadian Journal of Fisheries and Aquatic Sciences*, 49, 743–753. <https://doi.org/10.1139/f92-083>
- Methot, R. D. Jr, & Wetzel, C. R. (2013). Stock synthesis: A biological and statistical framework for fish stock assessment and fishery management. *Fisheries Research*, 142, 86–99. <https://doi.org/10.1016/j.fishres.2012.10.012>
- Mitchell, C. T., & Hunter, J. R. (1970). Fishes associated with drifting kelp, *Macrocystis pyrifera*, off the coast of southern California and northern Baja California. *California Fish and Game*, 56, 288–297.
- Montgomery, J. C., Tolimieri, N., & Haine, O. S. (2001). Active habitat selection by pre-settlement reef fishes. *Fish and Fisheries*, 2, 261–277. <https://doi.org/10.1046/j.1467-2960.2001.00053.x>
- Moore, A. M., Jacox, M. G., Crawford, W. J., Laughlin, B., Edwards, C. A., & Fiechter, J. (2017). The impact of the ocean observing system on estimates of the California Current circulation spanning three decades. *Progress in Oceanography*, 156, 41–60. <https://doi.org/10.1016/j.pocean.2017.05.009>
- Moser, H. G., Charter, R. L., Smith, P. E., Lo, N. C. H., Ambrose, D. A., Meyer, C. A., ... Watson, W. (1994). Early life-history of sablefish, *Anoplopoma fimbria*, off Oregon and California, with application to biomass estimation. *California Cooperative Oceanic Fisheries Investigations Reports*, 35, 144–159.
- Myers, R. A. (1998). When do environment-recruitment correlations work? *Reviews in Fish Biology and Fisheries*, 8, 285–305. <https://doi.org/10.1023/A:1008828730759>
- Neveu, E., Moore, A. M., Edwards, C. A., Fiechter, J., Drake, P., Crawford, W. J., ... Nuss, E. (2016). An historical analysis of the California Current circulation using ROMS 4D-Var: System configuration and diagnostics. *Ocean Modelling*, 99, 133–151. <https://doi.org/10.1016/j.ocemod.2015.11.012>
- Norman-López, A., Plagányi, B., Skewes, T., Poloczanska, E., Dennis, D., Gibbs, M., & Bayliss, P. (2013). Linking physiological, population and socio-economic assessments of climate-change impacts on fisheries. *Fisheries Research*, 148, 18–26. <https://doi.org/10.1016/j.fishres.2012.02.026>
- Norman-López, A., Pascoe, S., Thébaud, O., van Putten, I., Innes, J., Jennings, S., ... Plagányi, E. (2014). Price integration in the Australian rock lobster industry: Implications for management and climate change adaptation. *Australian Journal of Agricultural Resource Economics*, 58, 43–59. <https://doi.org/10.1111/1467-8489.12020>
- Peck, M. A., Huebert, K. B., & Llopiz, J. K. (2012). Intrinsic and extrinsic factors driving match-mismatch dynamics during the early life history of marine shes. *Advances in Ecological Research*, 47, 177–302. <https://doi.org/10.1016/B978-0-12-398315-2.00003-X>
- Pepin, P. (1991). Effect of temperature and size on development, mortality, and survival rates of the pelagic early life-history stages of marine fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 48, 503–518. <https://doi.org/10.1139/f91-065>
- Peterson, W. T. (2009). Copepod species richness as an indicator of long-term changes in the coastal ecosystem of the northern California Current. *California Cooperative Oceanic Fisheries Investigations Reports*, 50, 73–81.
- Peterson, W. T., & Keister, J. E. (2002). The effect of a large cape on distribution patterns of coastal and oceanic copepods off Oregon and northern California during the 1998-1999 El Nino-La Nina. *Progress in Oceanography*, 53, 389–411. [https://doi.org/10.1016/S0079-6611\(02\)00038-1](https://doi.org/10.1016/S0079-6611(02)00038-1)
- Rodgveller, C. J., Stark, J. W., Echave, K. B., & Hulson, P. F. (2016). Age at maturity, skipped spawning and female sablefish (*Anoplopoma fimbria*) during the spawning season. *Fishery Bulletin*, 114, 89–102. <https://doi.org/10.7755/FB>
- Schirripa, M. J. (2002). Status of the sablefish resource off the U.S. Pacific coast in 2002. In: *Pacific Fishery Management Council 2002. Appendix: Status of the Pacific coast groundfish fishery and recommended biological catches for 2003: stock assessment and fishery evaluation*. Portland, OR: Pacific Fishery Management Council.
- Schirripa, M. J. (2007). *Status of the sablefish resource off the Continental U.S. Pacific coast in 2007*. Newport, OR: NOAA Fisheries, Northwest Fisheries Science Center. 104 pp.
- Schirripa, M. J., & Colbert, J. J. (2006). Interannual changes in sablefish (*Anoplopoma fimbria*) recruitment in relation to oceanographic conditions within the California Current System. *Fisheries Oceanography*, 15, 25–36. <https://doi.org/10.1111/j.1365-2419.2005.00352.x>
- Schirripa, M. J., Goodyear, C. P., & Methot, R. M. (2009). Testing different methods of incorporating climate data into the assessment of US West Coast sablefish. *ICES Journal of Marine Science: Journal du Conseil*, 66, 1605–1613. <https://doi.org/10.1093/icesjms/fsp043>
- Schirripa, M. J., & Methot, R. D. (2001). Status of the sablefish resource off the U.S. Pacific coast in 2001. *Appendix B in Pacific Fishery Management Council. Status of the Pacific coast groundfish fishery through*

- 2001 and recommended acceptable biological catches for 2002. Portland, OR: Pacific Fishery Management Council.
- Shotwell, S. K., Hanselman, D. H., & Belkin, I. M. (2014). Toward biophysical synergy: Investigating advection along the Polar Front to identify factors influencing Alaska sablefish recruitment. *Deep-Sea Research II*, 107, 40–53. <https://doi.org/10.1016/j.dsr2.2012.08.024>
- Siedlecki, S. A., Kaplan, I. C., Hermann, A. J., Nguyen, T. T., Bond, N. A., Newton, J. A., ... Feely, R. A. (2016). Experiments with seasonal forecasts of ocean conditions for the northern region of the California Current upwelling system. *Scientific Reports*, 6, 27203. <https://doi.org/10.1038/srep27203>
- Skjæraasen, J. E., Kennedy, J., Thorsen, A., Fonn, M., Strand, B. N., Mayer, I., & Kjesbu, O. S. (2009). Mechanisms regulating oocyte recruitment and skipped spawning in Northeast Arctic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Science*, 66, 1582–1596. <https://doi.org/10.1139/F09-102>
- Skjæraasen, J. E., Nash, R. D. M., Korsbrekke, K., Fonn, M., Nilsen, T., Kennedy, J., ... Kjesbu, O. S. (2012). Frequent skipped spawning in the world's largest cod population. *Proceedings of the National Academy of Science*, 109, 8995–8999. <https://doi.org/10.1073/pnas.1200223109>
- Sogard, S. M. (2011). Interannual variability in growth rates of early juvenile sablefish and the role of environmental factors. *Bulletin of Marine Science*, 87, 857–872. <https://doi.org/10.5343/bms.2010.1045>
- Sogard, S. M., Berkeley, S. A., & Fisher, R. (2008). Maternal effects in rockfishes *Sebastes* spp.: A comparison among species. *Marine Ecology Progress Series*, 360, 227–236. <https://doi.org/10.3354/meps07468>
- Sogard, S. M., & Olla, B. L. (1998). Contrasting behavioral responses to cold temperatures by two marine fish species during their pelagic juvenile interval. *Environmental Biology of Fishes*, 53, 405–412. <https://doi.org/10.1023/A:1007485417486>
- Sogard, S. M., & Olla, B. L. (2001). Growth and behavioral responses to elevated temperatures by juvenile sablefish *Anoplopoma fimbria* and the interactive role of food availability. *Marine Ecology Progress Series*, 217, 121–134. <https://doi.org/10.3354/meps217121>
- Sogard, S. M., & Olla, B. L. (2002). Contrasts in the capacity and underlying mechanisms for compensatory growth in two pelagic marine fishes. *Marine Ecology Progress Series*, 243, 165–177. <https://doi.org/10.3354/meps243165>
- Sogard, S. M., & Spencer, M. L. (2004). Energy allocation in juvenile sablefish: Effects of temperature, ration and body size. *Journal of Fish Biology*, 64, 726–738. <https://doi.org/10.1111/j.1095-8649.2004.00342.x>
- Stephens, A., & Taylor, I. (2014). *Stock assessment and status of longspine thornyhead (Sebastes altivelis) off California, Oregon and Washington in 2013*. Newport, OR: Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, U.S. Department of Commerce.
- Stewart, I. J., & Forrest, R. E. (2011). *Status of the Pacific hake (whiting) stock in U.S. and Canadian waters in 2011*. Joint U.S. and Canadian Hake Technical Working Group. 217 pp.
- Stewart, I. J., Monnahan, C. C., & Martel, S. (2015). *Assessment of the Pacific halibut stock at the end of 2015*. International Pacific Halibut Commission: Report of assessment and research activities.
- Stewart, I. J., Thorson, J. T., & Wetzel, C. (2011). *Status of the U.S. sablefish resource in 2011*. Portland, OR: Pacific Fisheries Management Council.
- Sydeman, W. J., Thompson, S. A., Field, J. C., Peterson, W. T., Tanasichuk, R. W., Freeland, H., & Rykaczewski, R. R. (2011). Does positioning of the North Pacific Current affect downstream ecosystem productivity? *Geophysical Research Letters*, 38, L12606. <https://doi.org/10.1029/2011GL047212>
- Taylor, I., Grandin, C., Hicks, A. C., Teylor, N., & Cox, S. (2015). *Status of the Pacific Hake (whiting) stock in U.S. and Canadian waters in 2015*. Joint Technical Committee of the U.S. and Canadian Pacific Hake/Whiting Agreement, National Marine Fishery Service and Canada Department of Fisheries and Oceans. 159 pp.
- Taylor, I. G., & Wetzel, C. (2011). *Status of the U.S. yelloweye rockfish resource in 2011 (Update of the 2009 assessment model)*. Seattle, WA: National Marine Fisheries Service, Northwest Fisheries Science Center.
- Tolimieri, N. (2015). Density dependence and independence and the population dynamics of coral reef fishes. In C. Mora (Ed.), *Ecology of fishes on coral reefs* (pp. 227–231). Cambridge, UK: Cambridge University Press. <https://doi.org/10.1017/CBO9781316105412>
- Tolimieri, N., Holmes, E. E., Williams, G., Pacunski, R., & Lowry, D. (2017). Population assessment using multivariate time-series analysis: A case study of rockfishes in Puget Sound. *Ecology and Evolution*, 7, 2846–2860. <https://doi.org/10.1002/ece3.2901>
- Tsoukali, S., Visser, A. W., & MacKenzie, B. R. (2016). Functional responses of North Atlantic fish eggs to increasing temperature. *Marine Ecology Progress Series*, 555, 151–165. <https://doi.org/10.3354/meps11758>
- Veneziani, M., Edwards, C. A., Doyle, J. D., & Foley, D. (2009). A central California coastal ocean modeling study: 1. Forward model and the influence of realistic versus climatological forcing. *Journal of Geophysical Research*, 114, C04015.
- Wallace, R., Cheng, Y. W., & Tsou, T. S. (2008). *Status of the black rockfish resource north of Cape Falcon, Oregon to the U.S.-Canadian border in 2006*. Olympia, WA: Washington Department of Fish and Wildlife.

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