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**REVIEW**

# Marine ecosystem perspectives on Chinook salmon recruitment: a synthesis of empirical and modeling studies from a California upwelling system

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ABSTRACT: We review the suite of biophysical factors in the Northeast Pacific Ocean basin and California Current shelf ecosystem that directly or indirectly relate to central California Chinook salmon *Oncorhynchus tshawytscha* growth and survival upon ocean entry, a critical life-history period for this population. Our synthesis provides a framework for integrating ecosystem process studies with empirical hypothesis testing to benefit fisheries management. Our hypothesis includes seasonality (phenology) as a key element of early salmon growth and survival. The strength and location of the North Pacific High (NPH) pressure system in winter influences salmon growth and survival via 'bottom-up' productivity and retention of key prey (euphausiid crustaceans and juvenile rockfishes *Sebastes* spp.) in nearshore habitats prior to and during salmon emigration to sea in spring. Prey retention, which is associated with increased consumption of krill and juvenile rockfishes, and is positively correlated with juvenile salmon body condition and ocean survival, appears to set cohort strength and return rates. We examined these mechanistic relationships by reviewing the results of a biophysical model coupled to an individual-based model for salmon. Our review results in a final hypothesis stating that early salmon growth and survival are positively related to intensity of early season upwelling, and associated (forage) nekton production and retention on the shelf during spring and summer.

KEY WORDS: Forage nekton · Krill · Upwelling phenology · Salmon survival · California Current Ecosystem · Numerical ecosystem modeling

## INTRODUCTION

Quantifying the effect of ecosystem drivers on the recruitment of fishes continues to be a vexing issue in fisheries science (Myers 1998, Begrano & Fowler 2011, Haltuch & Punt 2011, Punt et al. 2014). Empirical studies of ecosystem processes, such as the controls of primary and secondary productivity, can provide a basis for quantifying direct and indirect drivers of recruitment strength through variability in trophic

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relationships (Hunsicker et al. 2011). Numerical ecosystem models may facilitate the evaluation of expectant recruitment responses to ecosystem changes and management strategies that are not accessible using conventional empirical studies (Rose 2012, Rose et al. 2015). Moreover, integrating empirical and numerical ecosystem studies is likely to provide insight into recruitment processes (e.g. Houde 2008), but in few marine ecosystems have sufficient empirical and numerical ecosystem studies been conducted to conceptualize and test synthetic hypotheses (Cury et al. 2008). In particular, this approach may be used to quantify aspects of the production, retention, and concentration of prey resources (Lasker 1975, Cury & Roy 1989) to assess impacts on fish recruitment resulting from variable overlap between the fish and their prey temporally (Cushing 1981) and spatially (Sinclair 1988) during critical life stages.

Here, we synthesize ecosystem studies in the well-studied and modeled central California Current Ecosystem (CCE) to illustrate how these approaches can be integrated to better understand the recruitment variability of California Central Valley Chinook salmon *Oncorhynchus tshawytscha*, a recreationally, commercially, and culturally important species of North Pacific marine ecosystems. We focus on fall-run (determined by adults' return timing) Chinook salmon from the Sacramento River. Sacramento River fall-run Chinook salmon (SRFC) contribute the vast majority of Chinook salmon to the California Current Chinook salmon fishery (Lindley et al. 2009, Satterthwaite et al. 2015). The stock relies greatly on hatchery production due to river and estuary habitat loss and degradation, the impacts of water withdrawals for human uses, and a large number of dams and water diversions (Lindley et al. 2009). As a result, the relationships between ocean ecosystem variability and this hatchery-dependent stock's dynamics are quite apparent (Carlson & Satterthwaite 2011, Satterthwaite & Carlson 2015).

Our conceptual model of the interacting biophysical factors affecting salmon forage and salmon productivity is founded on the work of salmon ecologists (e.g. Pearcy 1992, Beamish & Mahnken 2001), fisheries oceanographers (e.g. Cury & Roy 1989, Bakun 1996), and physical oceanographers (e.g. Chelton et al. 1982, Bograd et al. 2009) (Fig. 1). We review the literature relevant to direct and indirect impacts of

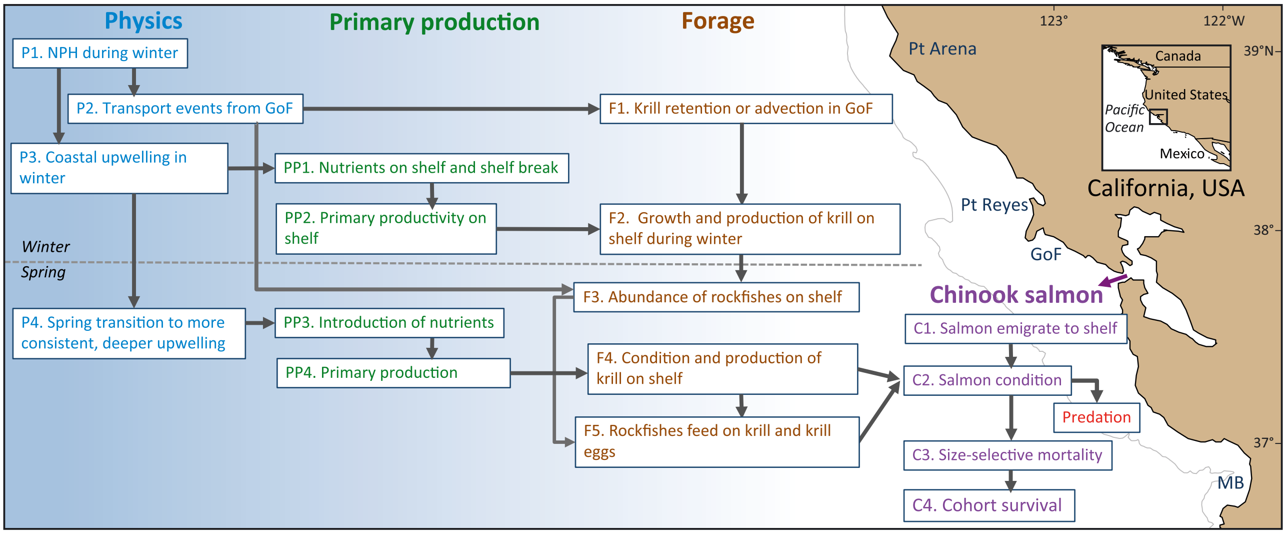

Fig. 1. A conceptual model of interacting spatial and temporal aspects related to juvenile Chinook salmon prey availability, and salmon growth and survival. Factors are arranged relative to the physics (blue), primary production (green), forage (brown), and Chinook salmon (purple) responses. Upper and lower portions represent factors related to winter and spring conditions, respectively. This is not a complete list of proposed ecosystem factors determining salmon growth and survival, nor is it meant as a predetermined model for salmon growth and survival, but it allows for a broad examination of the system to identify the direct and indirect effects of factors on salmon and forage dynamics. NPH: North Pacific High pressure; MB: Monterey Bay; GoF: Gulf of the Farallones. The relationships between the factors within the ecosystem model are supported by the literature. Factor P1: Schroeder et al. (2009), Black et al. (2011), Schroeder et al. (2013); P2: Dorman et al. (2011); P3: Black et al. (2011), Schroeder et al. (2011); P4: Bograd et al. (2009), Schroeder et al. (2013); PP1: Garcia-Reyes et al. (2014), Schroeder et al. (2014); PP2: Kahru et al. (2009), Dorman et al. (2011); PP3: Garcia-Reyes et al. (2014); PP4: Kahru et al. (2009); F1: Dorman et al. (2011); F2: Feinberg & Peterson (2003), Garcia-Reyes et al. (2014), Dorman et al. (2015); F3: Ralston et al. (2013), Schroeder et al. (2014); F4: Wells et al. (2008), Dorman et al. (2011), Garcia-Reyes et al. (2014); F5: Reilly et al. (1992); C1: Satterthwaite et al. (2014); C2: MacFarlane (2010), Woodson et al. (2013b); C3: Woodson et al. (2013b); C4: Lindley et al. (2009), Kilduff et al. (2014), Satterthwaite et al. (2014); Predation: LaCroix et al. (2009), Tucker et al. (2016)

biophysical factors on the productivity of the shelf ecosystem and resulting salmon survival. We acknowledge that this synthesis is not a complete accounting of the ecosystem factors, nor does it represent a prescribed chain of events that predetermine salmon productivity. What the synthesis does provide is a conceptual model of biophysical factors that current research has demonstrably linked to shelf ecosystem dynamics and Chinook salmon dynamics in the CCE. Our examination of the conceptual model also provides an understanding of the consequences to the shelf ecosystem resulting from variability at different spatial and temporal scales. Therefore, we focus our review on the spatiotemporal dynamics at meso- (10 to 100 km), regional (100 to 1000 km), and basin scales in order to assess the interactive effects of these scales on the central California shelf ecosystem during the period leading up to the emigration of juvenile salmon. We complete our synthesis by reviewing the results of a numerical ecosystem model to examine the effect of ecosystem variability on the growth of juvenile Chinook salmon during contrasting survival years. The results of the mechanistic ecosystem model are useful to evaluate the appropriateness of the conceptual model and provide a tool to assess the effect of ecosystem variability on salmon productivity.

We organize this synthesis with 3 overarching questions relevant to quantifying dynamics of salmon forage and salmon growth and survival early after emigration to the ocean each year, with a specific focus on seasonality (phenology) of ocean–climate conditions:

(1) How does variability in forage availability (abundance, distribution, and species composition) affect juvenile Chinook salmon growth and survival?

(2) How do regional transport and upwelling characteristics interact to retain and sustain forage on the shelf through the initial time of salmon emigration in spring?

(3) How does basin-scale atmosphere/ocean variability influence the development of neritic food webs upon which juvenile salmon depend?

## EFFECT OF VARIABILITY IN FORAGE AVAILABILITY ON JUVENILE CHINOOK SALMON GROWTH AND SURVIVAL

The central California region of the CCE between Point Arena (39° N) and Monterey Bay (36° N), including the Gulf of the Farallones, is a highly productive coastal ecosystem (Fig. 1). The wide shelf located south of Point Reyes provides essential habitat for krill (Santora et al. 2011) and other forage nekton (Wing et al. 1998, Largier et al. 2006, Vander Woude et al. 2006) (Figs. 1 & 2), and hosts major populations of marine birds (Ainley & Lewis 1974, Santora et al. 2012). Spring and summer in the central California region of the CCE is considered a critical period in the life history of SRFC during which the impacts of mortality can vary greatly between cohorts (Wells et al. 2012, Kilduff et al. 2014). Estimates of first-year survival from Kilduff et al. (2014) indicate a nearly 20-fold difference between the minimum of 0.16% and maximum of 3.04% for the cohorts emigrating from 1980 to 2006. The result is that cohort strength and return rate appear to be set shortly after emigration to sea (Wells et al. 2012, Woodson & Litvin 2015). In support, an examination of the results reported in Kilduff et al. (2014) demonstrates the covariation between first-year Chinook salmon survival and later adult abundance (Fig. 3F). Suspected agents of mortality on salmon emigrating to the region include starvation, disease, and, perhaps, increased relative predation on slower growing juveniles (Emmett & Krutzikowsky 2008, Tucker et al. 2016).

Evolution of productivity on this shelf ecosystem depends on a suite of physical and biological processes occurring at the appropriate magnitude, spatial scale, and temporal window to ensure prey availability to newly arrived Chinook salmon smolts (Fig. 1) (Cushing 1981, Satterthwaite et al. 2014). The condition of the forage community on the shelf that juvenile salmon experience on emigration is correlated to later adult abundance (Thompson et al. 2012, Wells et al. 2012). The relatively few natural origin SRFC smolts (as opposed to hatchery) enter the Gulf of the Farallones generally between March and July, with the bulk arriving to sea during April through May (Lindley et al. 2009); presumably this timing matches the peak of prey availability in spring (Quinn 2005). Spreading the time over which salmon emigrate to sea is a bet-hedging approach to increase the probability that a portion of the population will intersect an appropriate forage base and exhibit improved survival (Scheuerell et al. 2009, Satterthwaite et al. 2014). There are a number of potential forage species in the Gulf of the Farallones for juvenile salmon. The 4 prey that dominate juvenile salmon diet (by volume) off central California are *Euphausia pacifica*, *Thysanoessa spinifera*, fish (predominantly juvenile rockfishes, *Sebastes* spp.), and crab megalopia (MacFarlane & Norton 2002, Wells et al. 2012). Growth and recruitment of juvenile Chinook salmon are related to the abundance and distribution of these forage species at

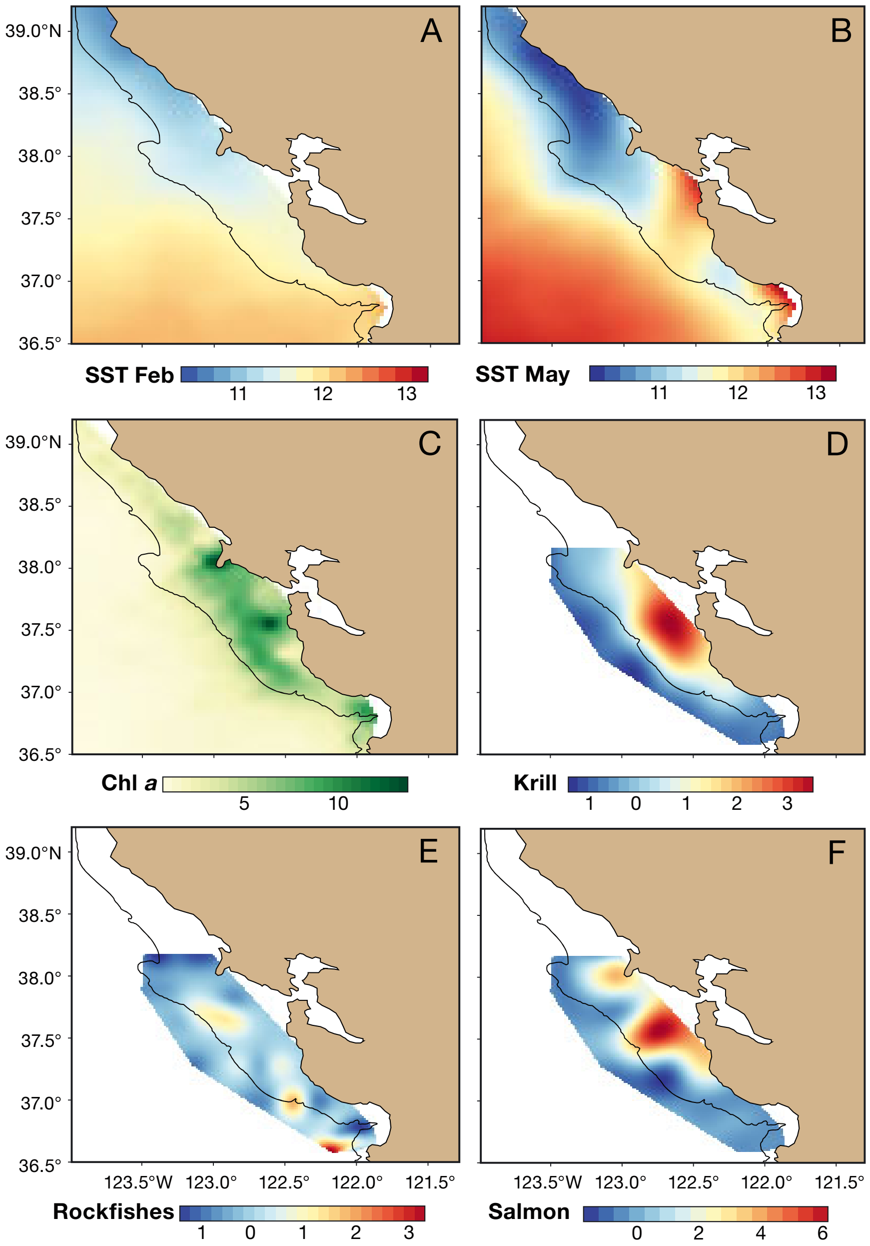

Fig. 2. Distributions of environmental and biological values from central California. (A) Average sea surface temperature (SST; °C) in February 2002–2013 (http://coastwatch.pfeg.noaa.gov/erddap/griddap/erdBAsstamday.html). (B) Average SST (°C) in May (same source as A). (C) Average chl *a* concentration (mg m$^{-3}$) from SeaWiFS, May 1997–2006 (http://coastwatch.pfeg.noaa.gov/erddap/griddap/erdSAchlamday.html). Biological distribution data are derived from Santora et al. (2012) and represent the standardized distribution patterns for (D) krill, (E) juvenile rockfishes, and (F) juvenile Chinook salmon in May 1990–2010

the time of juvenile salmon entry into the Gulf of the Farallones from San Francisco Bay (MacFarlane & Norton 2002, Wells et al. 2012) (Fig. 1, Factor C1).

Generally, krill are the primary salmon prey in early spring, followed by a shift to forage fishes in later summer as the salmon grow (MacFarlane & Norton 2002, Wells et al. 2012). Salmon body condition is significantly related to the consumption of the euphausiid *T. spinifera* (Wells et al. 2012) and juvenile fishes (MacFarlane & Norton 2002) (Fig. 1, Factor C2). *T. spinifera*, a neritic species, is abundant on the shelf and is rarely observed in substantial numbers off the shelf (Fig. 2D) (Santora et al. 2012). Juvenile rockfishes feed on krill and krill eggs (Reilly et al. 1992), so may be related to the abundance of *T. spinifera* as well. As a result, the abundance and distribution of juvenile rockfishes on the shelf are positively associated with that of krill (Wells et al. 2008, Santora et al. 2014). Path analysis suggests that the role of krill in juvenile salmon recruitment is both direct and indirect through rockfish prey (Thompson et al. 2012, Sydeman et al. 2013) (Fig. 1, Factors F4 and F5). Therefore, it is apparent that krill availability during the spring, at the time of first ocean entry, and that of the forage fishes that prey on krill, are critical to salmon survival and recruitment to the spawning population (Wells et al. 2012) (Fig. 1, Factor C4).

Body condition and growth dynamics of salmon may determine mortality (Woodson et al. 2013) (Fig. 1, Factors C2 and C3) and recruitment to the adult population (Wells et al. 2012). Woodson et al. (2013) demonstrated that during years characterized by poor upwelling and limited prey resources, such as early spring of 2005 (Fig. 3), smaller, slower growing Chinook salmon were subjected to significantly more mortality than their larger, faster growing counterparts. As noted in Fig. 3F, the survival of Chinook salmon emigrating to sea during 2005 was exceptionally low, as was later adult abundance. Although untested in central California, the smaller juvenile salmon may have experienced relatively more predation (Pearcy 1992, Tucker et al. 2016) (Fig. 1, Factor C3).

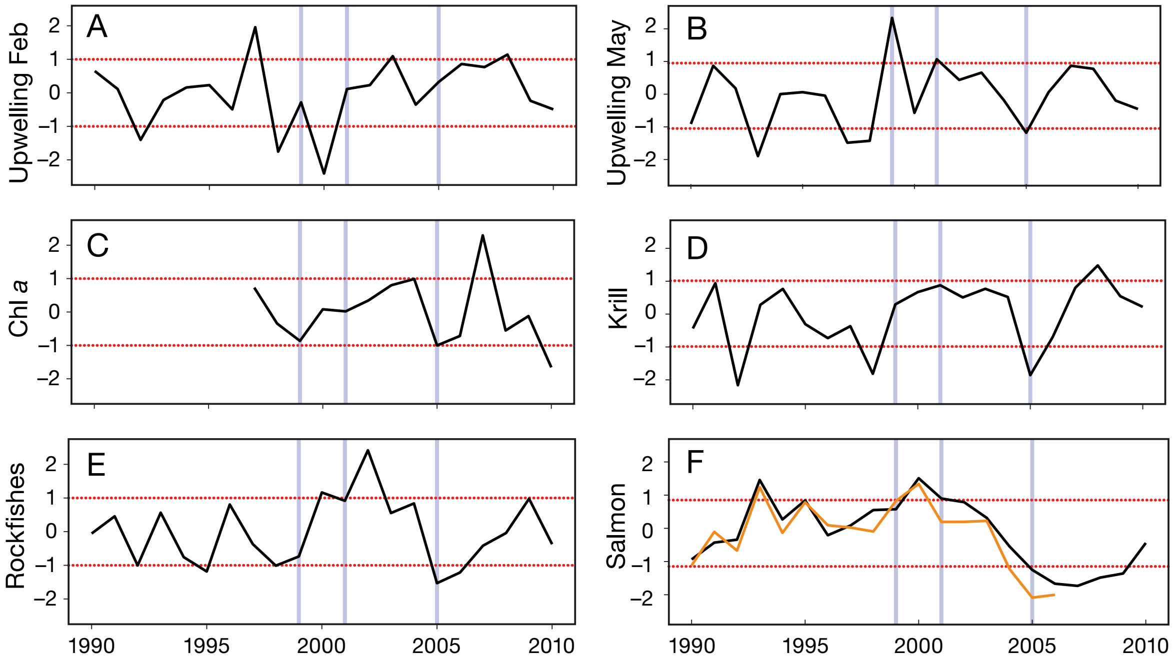

Fig. 3. Environmental and biological time series from central California. We focus on 1990–2010 to allow comparisons between standardized time series. Red horizontal lines represent ±1 SD. Blue vertical lines represent 1999, 2001, and 2005. (A) Time series of upwelling in February at 39° N (http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/upwelling.html). (B) Time series of upwelling in May at 39° N (same source as A). (C) Time series of chl *a* concentrations averaged over depths 6 to 22 m from *in situ* collections during May in central California (see Santora et al. 2012 for details). Biological time series of (D) krill and (E) juvenile rockfishes are from Santora et al (2014). (F) Black line shows the adult abundance of Chinook salmon as represented by an index of adult abundance with a 2 yr lag to match the timing of emigration to sea (O'Farrell et al. 2013). Orange line shows the standardized log-transformed survival estimates of cohorts 1990–2006 from Kilduff et al. (2014)

## INTERACTION OF REGIONAL TRANSPORT AND UPWELLING CHARACTERISTICS TO RETAIN AND SUSTAIN FORAGE ON THE SHELF THROUGH THE INITIAL TIME OF SALMON EMIGRATION IN SPRING

The spatial structure of the spring community of krill and forage fishes (as well as ecologically dependent seabirds) off central California is typically defined by a suite of habitat factors including bathymetry, geographic prominences, freshwater plumes, and upwelling intensity (Santora et al. 2012) (Fig. 2). Point Reyes marks the northern boundary of the Gulf of the Farallones (Fig. 1) and this promontory is associated with upwelling of cool waters (Fig. 2B). Concomitant with the southwestern flow from Point Reyes is a cyclonic eddy that creates a retentive area of typically warmed water (Fig. 2B), which retains primary productivity (Fig. 2C) and a number of shelf-dependent species, such as juvenile rockfishes (Fig. 2E), krill (Fig. 2D), sanddabs, and squid; all significant forage for salmon (Wells et al. 2012, Thayer et al. 2014) on the shelf (Fig. 2F). At much smaller scales (<10 km), Woodson & Litvin (2015) demonstrated that the presence of fronts on the shelf, concentrating nutrients and secondary production, are significantly correlated to forage dynamics and later salmon abundance.

Upwelling during spring and summer is largely determined by regional scale wind patterns (Schwing et al. 2002b). Off central California, coastal winds are upwelling-favorable throughout the year, but become more intense in late winter and early spring (Bograd et al. 2009). The transition of the CCE to an intense upwelling system is related to the North Pacific High (NPH) atmospheric pressure cell gaining strength and size as well as moving more northward (Schroeder et al. 2013) (Fig. 1, Factor P4; Fig. 4). As the NPH gains strength and moves northward, the gradient between low pressure on land and higher pressure over the ocean increases, which results in the strengthening of northerly coastal winds.

While increased northerly winds in the spring relate to the overall productivity of the CCE, the balance between nutrient input and advection of primary and secondary production associated with

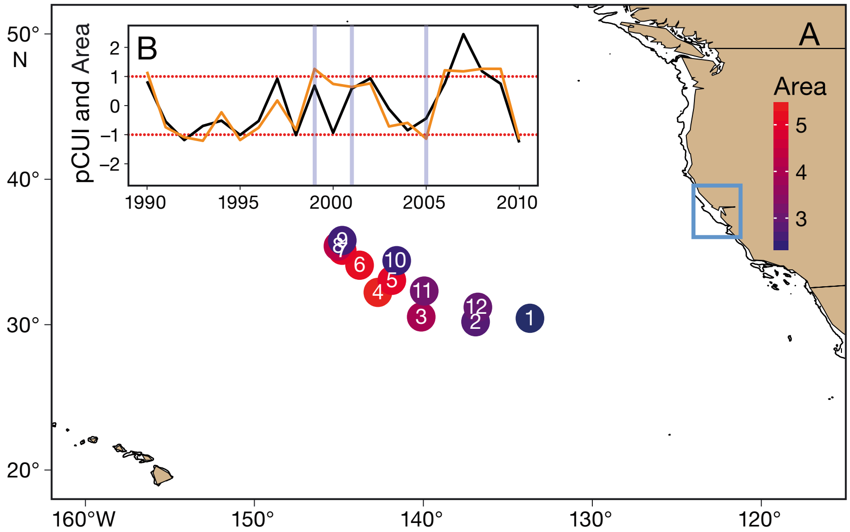

Fig. 4. Location and size of the North Pacific High (NPH) pressure cell during winter relates to productivity on the shelf in the spring. (A) Average monthly location and size (area encompassing the 1200 hPa isobar; km$^2$ × 10$^6$) of the NPH, 1967–2010 (Schroeder et al. 2013). (B) Standardized time series 1990–2010 of the area of the NPH (orange) and the preconditioning upwelling index (pCUI; black) for central California (Schroeder et al. 2013). Red horizontal lines represent ±1 SD. Location represented by the pCUI is shown as the blue inset box on plot A. Blue vertical lines represent the years 1999, 2001, and 2005

upwelling is not temporally and spatially consistent along the entire California coast. Santora et al. (2011) demonstrated that the distribution of krill abundance hotspots (determined from acoustics surveys) along the California coast is negatively related to the magnitude of northerly winds (Ekman transport) and is disassociated with strong upwelling centers. Santora et al. (2011) ascribed this relationship to the optimal environmental window theory (Cury & Roy 1989), whereby enough wind to provide upwelled nutrients is essential, but as the wind increases (especially near upwelling centers; Dorman et al. 2015), offshore Ekman transport causes advection of phytoplankton and zooplankton away from the coast (Fig. 1, Factors P2 and F1).

Along the entire California coast, relevant to krill, Santora et al. (2011) demonstrated clear evidence of the descending (right) side of Cury and Roy's hypothetical dome-shaped relationship (declining localized abundance with high levels of transport), but did not provide evidence for the ascending (left) side of the dome (see Fig. 7 in Santora et al. 2011). The limited demonstration of the ascending portion of the dome likely resulted from examination of krill in exposed regions along the California coast. Within the Gulf of the Farallones, in the lee of Point Reyes, Wells et al. (2012) demonstrated that the interannual variability of krill abundance (derived from nets) during spring was positively related (exhibiting an asymptotic response) to the intensity of coastal upwelling winds; demonstrating the ascending side of the Cury and Roy's parabolic relationship. These findings are complementary, as they elucidate the different scale-dependent relationships that coastal forage communities have with wind conditions at regional and local scales. Similar results from an individual-based model of krill aggregations indicate that in the more exposed area north of Point Reyes (Fig. 1), the intensity of krill hotspots is reduced with increased upwelling; however, in the protected region in the Gulf of the Farallones, the relationship is inverse (Dorman et al. 2015).

Garcia-Reyes et al. (2014) provided additional insight into relationships among upwelling intensity, primary productivity and krill abundance on the central California shelf (Fig. 2A–D). In agreement with Wells et al. (2012), Garcia-Reyes et al. (2014) did not show a dramatic descending side in the relationship between krill abundance and regional upwelling intensity (see Fig. 6 in Garcia-Reyes et al. 2014), suggesting more intense upwelling results in more krill on the shelf in areas protected from the direct effect of wind (Fig. 2D). However, the relationship between upwelling intensity and chl *a* concentration indicates a clear parabolic relationship, where too much upwelling may lead to increased advection of primary production away from the shelf ecosystem (see Fig. 6 in Garcia-Reyes et al. 2014). As a demonstration here through an examination of 1999, a strong La Niña year, intense upwelling (Fig. 3B) and advection in the spring is associated with reduced chl *a* concentration on the shelf (Fig. 3C), yet not reduced krill (Fig. 3D). In all, upwelling intensity, when great, can have a negative impact on the retention of primary production, but not necessarily krill production, on a protected shelf.

There are 10 numerically dominant juvenile rockfish species that comprise a significant proportion of the forage assemblage on the shelf in spring following winter parturition (i.e. release of larval rockfish) (Ralston et al. 2013). The abundance of juvenile rockfishes on the shelf depends largely on the balance between transport and production resulting from upwelling dynamics (Fig. 1, Factors F3 and F5; Fig. 2E). Off central northern California, Ralston et al. (2013)

demonstrated that high juvenile rockfish abundance in late spring is associated with strong southward (equatorward) transport in winter months (as evaluated with regional relative sea level height), while years of very low abundance correspond with stronger northward (poleward) transport in winter months. Schroeder et al. (2014) provided additional insight into the interannual variability of juvenile rockfish abundance through examination of the 26.0 isopycnal depth over the rockfish spawning grounds during winter parturition. The 26.0 isopycnal depth in central California represents a region of high nutrients (Palacios et al. 2013). Shoaling of the 26.0 isopycnal occurs during upwelling events and associated southward transport (Collins et al. 2003, Lynn et al. 2003). Schroeder et al. (2014) concluded that high juvenile rockfish abundance in spring is associated with a shallower 26.0 isopycnal depth over the spawning ground (i.e. shelf break) in winter as a result of transport dynamics and/or better feeding conditions immediately following the release of larval rockfishes (parturition).

There is evidence that the increased spring upwelling during the La Niña of 1999 — an example of an extreme event — resulted in relatively low abundance of rockfishes in the Gulf of the Farallones, despite average krill abundance, likely due to the intensity of advection and upwelling during the timing of the rockfish survey that year (Fig. 3B) (Schwing et al. 2000, Ralston et al. 2013, Ralston et al. 2015). In 1999, the abundance of rockfishes caught in small mesh trawl surveys in the region was below mean values (Fig. 3E), perhaps due to high offshore Ekman transport; yet, this cohort is now recognized as one of the strongest recruitment events on record for most central California coast rockfishes (Ralston et al. 2013, Thorson et al. 2013). Therefore, it is important to consider not simply the production of rockfishes as a measure of potential prey to salmon, but also the degree to which that production may be advected out of the Gulf of the Farallones at the critical period for juvenile salmon growth and survival.

## INFLUENCE OF BASIN-SCALE ATMOSPHERE/OCEAN VARIABILITY ON DEVELOPMENT OF NERITIC FOOD WEBS UPON WHICH JUVENILE SALMON DEPEND

The strength of the California Current relates positively to the transport of nutrients and biotic material (plankton) from subarctic northern waters to southward coastal communities, which increases the transport of nutrients and prey between neighboring neritic communities (Chelton et al. 1982, Roesler & Chelton 1987, Sydeman et al. 2011). A demonstrated benefit of a stronger California Current is the introduction of lipid-rich copepods from the Gulf of Alaska into the northern California Current. These species are associated with increased production of northern California Current Chinook and coho salmon *Oncorhynchus kisutch* through direct and indirect effects on salmon prey (Peterson & Keister 2003, Peterson & Schwing 2003, Peterson 2009, Carretta et al. 2011, Keister et al. 2011). In addition, the increased production associated with lipid-rich copepods may reduce the impact of competition and predation on salmon (Pearcy 1992, Emmett et al. 2006).

Conditions in the North Pacific basin during winter have dramatic effects on the primary and secondary productivity of the California Current coastal ecosystem (Fig. 1, Factors P1, PP1 and PP2). The area (size) of the NPH and its centroid, in part, determine the coastal ecosystem state in winter and productivity of the shelf ecosystem into spring (Schroeder et al. 2013); nearer the coast, a larger NPH in winter is associated with increased primary and secondary production in the following spring (Fig. 4). For example, variability of forage species composition and seabird reproduction during spring and summer is related to NPH area and location during January and February. Schroeder et al. (2013) calculated a preconditioning upwelling index (pCUI; Fig. 4B) from the sum of positive upwelling events in January and February. Winter upwelling is significantly positively related to juvenile rockfish abundance and the reproductive success of seabirds off central California and, therefore, is indicative of a productive shelf ecosystem in the spring (Schroeder et al. 2013, 2014) (Fig. 3E).

Winter upwelling may 'precondition' (Logerwell et al. 2003) or jump-start ecosystem productivity by providing nutrients for an early pulse of primary production (Fig. 1, Factors P3, PP1 and PP2), which may in turn sustain secondary and tertiary productivity (Fig. 1, Factor F2) (Feinberg & Peterson 2003, Kahru et al. 2009, Garcia-Reyes et al. 2014) on which predators depend (Schroeder et al. 2009, 2013, 2014, Black et al. 2010, 2011). While coastal upwelling winds are less frequent and intense in winter than spring (as indicated in Fig. 2A,B by sea surface temperatures that are greater at Point Reyes in winter than spring), they occur over a less-stratified water column along the coast (Palacios et al. 2004), allowing for easier introduction of nutrients to the shelf. In addition, increased NPH area during the winter and the southward winds it produces along the CCE (Schroeder et al. 2013) could reduce the likelihood of northward transport of plankton from the Gulf of the Farallones (Fig. 1), which can be substantial during periods with frequent northward winds and associated alongshore currents (Dorman et al. 2011) (Fig. 1, Factors P2 and F1).

Schroeder et al. (2014) demonstrated that krill abundance on the shelf in spring relates to shoaling of the 26.0 potential density isopycnal depth during winter, an indication of enhanced winter upwelling and southward transport. In support, Dorman et al. (2011) demonstrated that advection of krill northward out of the Gulf of the Farallones in winter determines, in part, the abundance of krill on the shelf in spring (Fig. 1, Factors P2 and F1). The northward advection of krill from the central California shelf during the winter of 2005 was associated with reproductive failure and mortality of krill-dependent predators such as salmon (Fig. 3F) (Kilduff et al. 2014) and seabirds (Sydeman et al. 2006, Wells et al. 2008). Specifically, as spring approaches, forage species for juvenile salmon are dependent on the nearshore supply of plankton resulting from the upwelling of a nutrient-rich water mass characterized by the 26.0 isopycnal depth (Fig. 1, Factors P4, PP3, PP4 and F4; Fig. 3B–D). Schroeder et al (2014) also demonstrated that for juvenile rockfishes, their abundance on the shelf (Figs. 2E & 3E) is tied to a shoaling of the 26.0 isopycnal depth at the shelf break during winter (Fig. 1, Factors PP1, F3 and F5). Once krill abundance increases on the shelf, production of a number of forage species, including juvenile rockfishes, relates to krill abundance and distribution (Wells et al. 2008, Santora et al. 2014) (Figs. 2D,E & 3D,E).

SRFC hatchery-origin smolts have an increased likelihood of survival to maturity when released approximately 3 to 4 mo following the timing of the spring transition to a dominantly upwelling system (Satterthwaite et al. 2014). Presumably, following on the findings of Croll et al. (2005) and Garcia-Reyes et al. (2014), this is the time needed from initial nutrient introduction to the ocean's mixed layer to result in sustained krill density on the shelf. Furthermore, juvenile rockfishes are transported from the shelf break onto the shelf during spring, where parturition occurred 3 mo earlier (Ralston & Howard 1995, Schroeder et al. 2014). Once on the shelf, juvenile rockfishes rely on krill and krill eggs as prey (Fig. 1, Factor F5; Fig. 2D,E) (Reilly et al. 1992). Ultimately, a robust forage base of krill (Fig. 2D) and juvenile rockfishes (Fig. 2E) may be available on the shelf for juvenile salmon (Fig. 2F) after winter seasons with an anomalously strong NPH that leads to stronger-than-average winter upwelling on the central CCE coast. This is provided that winter and spring upwelling are strong enough to maintain a supply of nutrients to promote primary productivity (Fig. 2C) on the shelf, reduce northward advection of krill from the shelf, and facilitate transport and retention of juvenile rockfishes on the shelf.

We provide time series to compare the difference in ecosystem indicators between contrasting years (Figs. 3 & 4). The years 2001 and 2005 are highlighted here to represent a good (2001) and poor (2005) year of primary, secondary, and tertiary production on the shelf (Schwing et al. 2002a, Peterson et al. 2006, Ralston et al. 2015). During 2001, the area of the NPH during winter was near the highest values of the time series (1990 to 2010), and pCUI was equally high (Fig. 4B). Fig. 3 shows that winter and spring upwelling at 39° N, and production of chl *a*, krill, rockfishes, and salmon were also increased. Conversely, in 2005, when the area of the NPH and the pCUI were low (Fig. 4B), the conditions and forage production on the shelf were below average (Fig. 3), resulting in exceptionally low survival and recruitment of Chinook salmon (Fig. 3F).

## NUMERICAL ECOSYSTEM MODELING

Numerical ecosystem models provide a framework, often including a number of sub-models (Rose et al. 2010), that integrates biochemical ocean processes and the response of lower and higher trophic level functional groups (Travers et al. 2007).

When ecosystem modeling is linked to observations, it necessitates the incorporation of measured environmental data and evaluation of model output at each biophysical sublevel. Schroeder et al. (2014) demonstrated that a data-assimilative oceanographic model tuned to the California Current system (Moore et al. 2011) provided a reasonably accurate representation of the spatial and temporal oceanographic characteristics at a resolution sufficient for examining dynamics of juvenile forage fishes and krill. Santora et al. (2013) demonstrated that a coupled physical–biochemical model (CoSiNE; Chai et al. 2002) captured the spatial variability of krill hotspots along the California coast, and temporal variability of *Thysanoessa spinifera* within the central California shelf, and its connection to seabird reproduction and spatial distribution. Fig. 5 (modified from Santora et al. 2013) shows that ROMS-CoSiNE successfully captured interannual variability of observed krill abun-

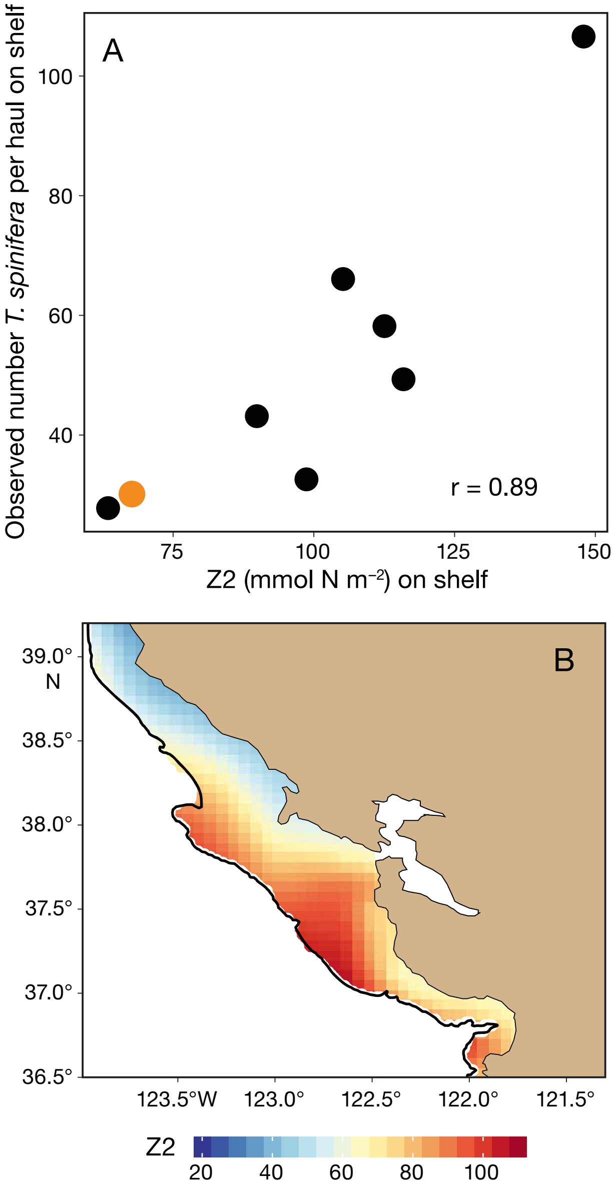

Fig. 5. (A) Evaluation of the coherence between modeled mesozooplankton (Z2), within depths of 0 to 100 m, and observed krill abundance (net hauls of *Thysanoessa spinifera*) off central California (derived from Santora et al. 2013). 2006, the only overlapping year between the analyses of Santora et al. (2013) and Fiechter et al (2015a), is shown (●). The data identified 2006 as a poor year of salmon survival and growth. (B) Averaged (May 2002–2009) spatial distribution of Z2 (mmol N m$^{-2}$) from the ocean–ecosystem model (CoSiNE) is coherent with observed krill distribution shown in Fig. 2D

dance and distribution on the shelf. Going up a trophic level, Fiechter et al. (2015b) used a linked biophysical modeling system to realistically hindcast population dynamics and abundance cycles of the forage fishes sardine *Sardinops sagax* and northern anchovy *Engraulis mordax* in the CCE from 1959 to 2008.

Fiechter et al. (2015a) applied a numerical ecosystem model that combines a regional ocean circulation model (Shchepetkin & McWilliams 2005, Haidvogel et al. 2008), a nutrient–phytoplankton–zooplankton model (NEMURO; Kishi et al. 2007), and an individual-based model for juvenile salmon. Model simulations examined factors that affect juvenile Chinook salmon growth during early marine residence. Specifically, Fiechter et al. (2015a) tested the hypothesis (Fig. 1) that the phenology and intensity of upwelling, and resultant primary and secondary productivity, affect salmon growth differentially between years of good and poor survival. Model results indicated that the early onset of intense upwelling is associated with increased growth of salmon. During years of improved survival (1984, 1986, and 2000) (Kilduff et al. 2014), early upwelling was more intense than in years of poor survival (1989, 1990, and 2006), as indirectly demonstrated by lower modeled temperatures in late March through September (Fig. 6A). Associated with increased upwelling was greater primary productivity in March, which was sustained through September (Fig. 6B). By May, modeled zooplankton was significantly greater during good years of salmon survival relative to poor years (Fig. 6C). Salmon growth associated with the modeled years of good survival was significantly greater than during years of poor survival. While Fiechter et al. (2015a) focus on the relative results, it is also worth noting that the results from the simulation are similar to observed values of salmon body condition and growth observed in juvenile Chinook salmon collected at sea (MacFarlane 2010).

## SUMMARY

Based on our review and synthesis, we developed a conceptual model for the key biophysical processes operating at basin to mesoscales that together influence the year-to-year variations in hatchery-origin SRFC marine survival (Fig. 1). A growing body of evidence suggests that variations in early marine growth and survival rates are strongly linked, and that the first few weeks at sea represents a critical period for this and many other Pacific salmon stocks. Moreover, early marine survival appears to be highly correlated with total marine survival, as is apparent through examination of the covariation of early marine survival rates and later adult abundance estimates shown in Fig. 3F.

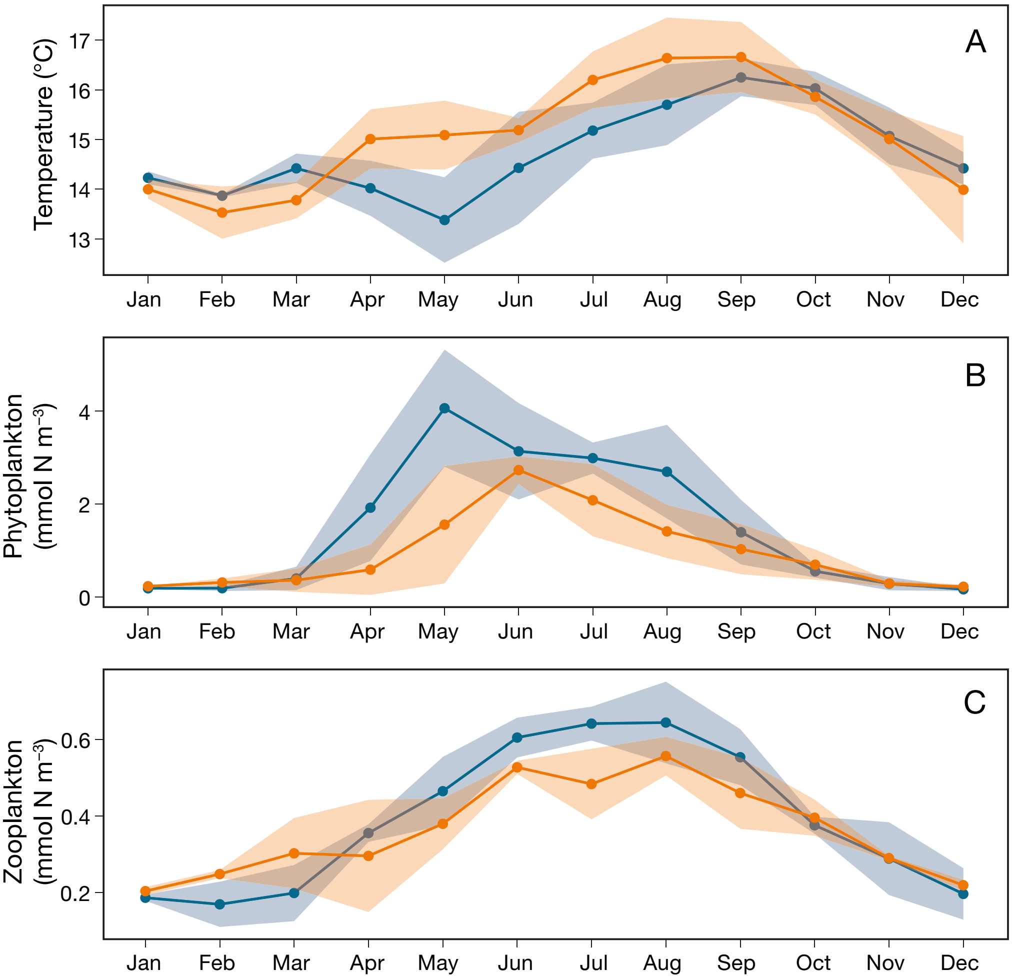

Fig. 6. Monthly biophysical model results from Fiechter et al. (2015a) representing years of good (blue) and poor (orange) Chinook salmon survival (mean ± 1 SD). The results demonstrate that during years of known good survival for Chinook salmon, (A) cooler temperatures occurred earlier (representing upwelling), (B) phytoplankton production occurred earlier, and (C) zooplankton was more productive and sustained than during years of poor survival (compare results to orange circle in Fig. 5A)

At the basin scale, the strength and location of the NPH during winter preconditions the coastal ecosystem for the amount of productivity it will have during spring and summer (Schroeder et al. 2009, 2013, Black et al. 2011, Thompson et al. 2012). Preconditioning promotes the continued supply of nutrients and production of a robust forage assemblage on the shelf during winter (Wells et al. 2012, Thayer et al. 2014). As spring approaches and the transition to intense upwelling occurs, the strength and duration of the upwelling season will depend, in part, on the date of that transition, as moderated by the regional winds determined by the location and strength of the NPH. Namely, if the ecosystem experiences more intense and consistent early upwelling (Bograd et al. 2009, Sydeman & Bograd 2009, Fiechter et al. 2015a), early and continued nutrient introduction enables the development and maintenance of populations of krill, forage fishes and higher-trophic-level predators in the Gulf of the Farallones. Otherwise, there can be a mismatch between the timing of the predators' requirements and the development of a forage base on the shelf (e.g. Sydeman et al. 2006, Ainley et al. 2009, Satterthwaite et al. 2014). Relevant to salmon, the appropriate forage must be available immediately upon ocean entry in the Gulf of the Farallones (Fig. 2D–F), otherwise anomalously high mortality may occur (Lindley et al. 2009, Woodson et al. 2013).

The general model of interactions acting on salmon dynamics we reviewed is subject to vary as climate change impacts shelf ecosystems. Several studies showed that northerly alongshore winds that force coastal upwelling intensified (from the early 1980s to early 2000s) along the California Current (Bakun &

Parrish 1990, Schwing & Mendelssohn 1997, Garcia-Reyes & Largier 2010, Sydeman et al. 2014). However, any benefits to the ecosystem owing to the increased upwelling from the intensified winds may be mitigated by increased stratification, changes in the upper ocean thermal structure, and/or changes in source water nutrient concentrations, all of which influence the biological efficacy of upwelling (Bakun et al. 2015). Further, owing to basin-scale forcing, variability in coastal winds has increased (Macias et al. 2012), contributing to a recent increase in the variability of production of salmon and seabirds in the region (Sydeman et al. 2013).

This work has applications to management of the SRFC. A recent collapse in the SRFC stock resulted in the closure of the fishery in 2008 and 2009, with limited opening in 2010. The collapse and subsequent disaster declaration resulted in an exhaustive search for the causes of the run failures (Lindley et al. 2009). Although a firm conclusion was elusive, there were indications that late and/or weak upwelling in the coastal ocean was the proximate cause for increased early marine mortality of juvenile salmon (Lindley et al. 2009). Our synthesis of the literature provides a detailed conceptual model for the likely causes of the collapse. In addition, there is demonstrated value in using the numerical ecosystem model to anticipate future collapses under varying environmental conditions.

We largely focused on bottom-up factors related to early marine salmon growth and recruitment. A substantial amount of mortality of juvenile salmon may be due to increased predation of the slower growing, smaller members of a cohort (Cowan et al. 1996, Tucker et al. 2016). In essence, we expect top-down impacts caused by predation to be related to bottom-up determinants of juvenile salmon growth dynamics (Fig. 1). The effect of these top-down impacts likely increases as alternative prey becomes more limited (LaCroix et al. 2009). Furthermore, interactions between juvenile salmon and predators can vary with changes in their distributions associated with variability in ocean conditions (Pearcy 1992, Emmett et al. 2006).

Our synthesis is appropriate to a general functional understanding of the central California shelf ecosystem. The life history of many species within the greater Gulf of the Farallones region has evolved in response to winter and spring conditions that support krill and juvenile rockfishes being present on the shelf in spring and summer as a prey resource. For instance, planktivorous and piscivorous seabird species (e.g. Cassin's auklet *Ptychoramphus aleuticus* and common murre *Uria aalge*) that nest on the Farallon Islands during the spring have lay dates that are correlated with February sea surface temperatures and northerly winds, which correspond to increased May to June forage abundance on which the nestlings can feed (Schroeder et al. 2009).

## FUTURE RESEARCH DIRECTIONS

There are a number of important issues yet to be addressed for central California Chinook salmon: (1) the impact of freshwater and estuarine conditions on condition and mortality in the ocean; (2) the impact that predators have on salmon; and (3) an evaluation of ecosystem factors contributing to mortality and maturation dynamics after the first winter at sea. Further, upon addressing these issues, we could also ask questions about the impact of salmon on the ecosystem. Such objectives should include quantifying salmon predator response to variability in salmon distribution, growth, and mortality. Furthermore, there should be an analysis of how all of the interacting factors (e.g. environment, forage, salmon production, and predatory responses) impact fisheries, food security, and cultures, and how we may mitigate the influences of competing interests. In short, the present work is a piece of the overall requirements for defining and implementing inclusive ecosystem management objectives.

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