

Population dynamics of Chinook salmon *Oncorhynchus tshawytscha* relative to prey availability in the central California coastal region

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ABSTRACT: Mortality during the first period at sea is thought to be a primary determinant of salmon productivity and return rates. Here, we test this hypothesis by linking variation in prey resources during the initial phase at sea with measurements of central California Chinook salmon *Oncorhynchus tshawytscha* diet, condition, and later adult abundance. Specifically, we investigate linkages between the distribution and abundance of krill and other prey with juvenile Chinook salmon diet and body condition. Hydrographic features of the Gulf of the Farallones during May and June were related to the abundance and spatial organization of Chinook salmon prey. When upwelling was reduced, there were fewer krill on the inner Gulf of the Farallones shelf, thereby less available to outgoing juvenile Chinook salmon smolts. Notably, we found a 1 yr lag in the relationship between the abundance of adult *Thysanoessa spinifera* and the volume of krill in the diet of juvenile Chinook salmon. Body condition of juvenile Chinook salmon was positively related to the abundance of adult krill the year before and specifically to the proportion of *T. spinifera* in the diet. In turn, the condition of juvenile Chinook salmon was correlated to the abundance of mature Chinook salmon returning from the same cohort the next year. This information may be useful for fisheries management by improving sibling-based forecasting models as well as informing escapement goals.

KEY WORDS: California · Chinook salmon · Krill · Gulf of the Farallones · Condition · Survival

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INTRODUCTION

The population productivity of many marine fish is largely derived from survival during a critical period in their early life history, when it is essential that there be a match, temporally and spatially, between juvenile fish and their prey (Hjort 1914, Cushing 1990, Beaugrand et al. 2003). Specific to salmon, it is thought that growth and mortality during the first period at sea is a primary determinant of later adult salmon abundance from that cohort (Pearcy 1992, Beamish & Mahnken 2001, Beamish et al. 2004,

Quinn 2005). Indeed, previous research has suggested that the first few months in the ocean is the critical time for recruitment for central California Chinook salmon *Oncorhynchus tshawytscha* (MacFarlane 2010).

A dramatic example of this potential mechanism is represented by the population collapse of California's Sacramento River fall run Chinook salmon in 2007 to 2009. This population and fishery collapse is hypothesized to have been related to extremely poor survival of juvenile Chinook salmon entering the ocean in 2005 to 2007 (Lindley et al. 2009). In these

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years, weak and inconsistent upwelling led to poor primary productivity and reduced prey resources for local seabirds (Sydeman et al. 2006, Dorman et al. 2011), whose abundance is known to co-vary with Chinook salmon returns (Roth et al. 2007). However, to date, the mechanistic linkages between environmental forcing and salmon production have yet to be adequately investigated. Other than general effects of upwelling, no mechanistic understanding has been resolved quantifying the relationships between juvenile salmon, environmental variability, and the population abundance variability. Specifically, an ecosystem perspective in which predator–prey relationships are established may better elucidate the mechanisms acting to determine salmon population dynamics in the region. Such relationships have been established for seabirds (Wells et al. 2008a) and possibly could be developed for salmon (Thompson et al. 2012).

In late spring/early summer, the point of ocean entry for juvenile Chinook salmon is the inner-shelf of the Gulf of the Farallones, California, USA, located south of a major coastal headland, Point Reyes (38° N; Fig. 1). The predominant spring/summer wind stress

here is northwesterly causing an upwelling jet to form westward of Point Reyes. Overall, once the upwelling system is fully developed in early to mid-spring, 5 reasonably stable meso-scale features exist between Point Arena (38.3° N) and Monterey Bay (Graham & Largier 1997, Wing et al. 1998). These include the upwelling jet occurring at the prominence of Point Reyes, a back eddy forming in the Gulf of the Farallones, an oceanic ocean plume ingressing or freshwater outflow from San Francisco Bay, a second upwelling plume forming just north of Monterey Bay, and an upwelling shadow forming in Monterey Bay (Graham & Largier 1997, Wing et al. 1998). These local hydrographic features have the potential to work in concert with productivity to determine prey availability in the region. Specifically, the region south of Point Reyes and east of the Farallon Islands appears to be a retention zone where juvenile Chinook salmon and salmon prey aggregate during their initial time at sea (Wing et al. 1998, MacFarlane 2010).

Here, we test the hypothesis that linkages between physical and biological variables and juvenile Chinook salmon in the inner Gulf of the Farallones region is critical to the recruitment (return) dynamics of Chinook salmon. Specifically, our objectives are to (1) quantify the relationship between oceanographic and hydrographic parameters (i.e. upwelling wind) to aspects of the forage base for juvenile Chinook salmon in the region, (2) quantify the relationship between diet composition and prey resources to condition indices, and (3) examine the influence of condition and diet composition to return abundance 2 and 3 yr later.

MATERIALS AND METHODS

Study area and data collection

Our study area off central California spans from Point Reyes (38° N) to Monterey Bay (36.5° N; Fig. 1). In this region, long-term midwater-trawl surveys of juvenile rockfish, other forage fish, and krill (Sakuma et al. 2006) overlap with other, shorter term data sets on juvenile Chinook salmon *Oncorhynchus tshawytscha* distribution, abundance, food habits, and condition indices (MacFarlane 2010; Table 1). The midwater-trawl survey has operated annually from May to June, 1983 to the present. Forage fish samples were collected from a modified Cobb midwater trawl, with a head rope depth of 30 m (the average depth of the thermocline in the region) at a speed of ~2 knots

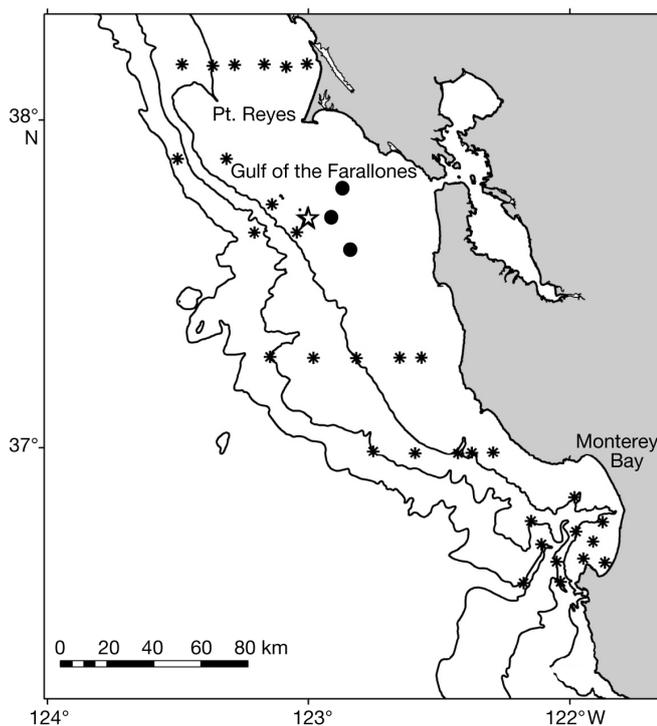


Fig. 1. Central California region sampled during the midwater trawl survey (Sakuma et al. 2006). Asterisks and closed circles: stations sampled from 1990 to 2010. Closed circles: locations used to estimate abundance of overall krill in the Gulf of the Farallones. Star: Farallon Islands

shelf relative to *T. spinifera* (Santora et al. 2011a), and an average 91% (SD = 0.16) of the krill captured in the Gulf of the Farallones was *T. spinifera*.

Sampling of *Thysanoessa spinifera* was carried out using traditional zooplankton nets in 2008 to 2010, to better quantify population dynamics. In 2008 and 2010, 0.7 m diameter bongo nets equipped with 505 μm nets and codends were used, while in 2009 a 1 m² Tucker trawl equipped with 333 μm net and codend was utilized. For both years, tows were conducted immediately before the first midwater trawl of the evening in an identical manner (15 min duration at 30 m depth or 10 m depth if needed to match the midwater trawl). *T. spinifera* were only found in the inner-shelf stations.

Environmental data

We averaged upwelling indices from 39°N in May and June to represent the intensity of northerly/alongshore winds (www.pfeg.noaa.gov/products/pfel/modeled/indices/). While upwelling winds are critical for nutrient introduction and development of meso-scale structure (e.g. upwelling plumes, eddies, fronts), wind also results in turbulence, advection, and more diffuse aggregations of prey (Lasker 1981, Cury & Roy 1989, Santora et al. 2011b). We used QuikSCAT satellite data (<http://coastwatch.pfeg.noaa.gov/erddap/>) to represent the climatological local mesoscale structuring (e.g. retention areas, plumes, etc.) and meridional Ekman transport for the region.

Chinook salmon data

Catches of juvenile Chinook salmon from the midwater-trawl survey were too infrequent to discern temporal trends; however, they were adequate to characterize the spatial distribution of juvenile Chinook salmon during May and June. From mid-May to August, 1995 to 2005, juvenile Chinook salmon were also collected from the surface. For each of these surface-trawl fish captured (N = 1541) we determined a Fulton's *K* index of body condition [Fulton 1904; $K = (\text{weight}/\text{length}^3 \times 10^5)$] and calculated an average for each year. We collected Chinook salmon stomach contents and quantified their diet during 1995 and 1997 to 2003 (N = 321, yearly averages were used in analyses), using the methods described in MacFarlane & Norton (2002). During 1995 and 1997 to 2003 we quantified the average lengths of whole *Thysanoessa spinifera* in juvenile

Chinook salmon diets. We restricted our analysis to juvenile salmon <200 mm to best target those Chinook salmon that emigrated to the sea in the current year and had not spent a full year rearing in freshwater; these are the salmon that ultimately make up the majority of the fishery and for which a later abundance is explicitly calculated. From May to August, fish >200 mm are more likely to represent those fish that migrated the year before or had spent a full year in freshwater before migrating (MacFarlane & Norton 2002).

We examined variability in the average percent volume of 4 prey species/groups in the diets of juvenile Chinook salmon: crab (primarily megalopa and zoea of Dungeness crab *Cancer magister*), fish, and the krill species *Thysanoessa spinifera* and *Euphausia pacifica*. Importantly, soft-bodied prey, such as krill, tend to be digested more rapidly in predator stomachs, the significance of krill in these results could, therefore, be underestimated (Tanasichuk 1999). Relationships were quantified between krill abundance in the Gulf of the Farallones and the volume percent of fish, crab, and krill in the diets; krill abundance does not directly represent fish and crab abundance in the environment but may provide a surrogate for productivity and passive retention in the Gulf of the Farallones. We related average Fulton *K* values to diets. Average Fulton *K* values and day of the year of capture were not related ($p = 0.2926$, $R^2 = 0.1219$); furthermore, in regressive approaches day of the year of capture was insignificant and was removed from the analysis.

The juvenile salmon used in the present study were overwhelmingly Sacramento River Chinook salmon that had been spawned in the winter and reared in the river (or hatchery) for only a few months, as determined by emigration timing and size. Abundances of returning Chinook salmon that had spent only a single winter in the ocean and then matured (commonly referred to as 'jack' salmon), and the abundances of those that had spent at least 2 winters at sea were obtained from the Pacific Fisheries Management Council (PFMC 2011). The abundance of the single-winter ocean fish returning to spawn represents a confounded estimate of the number of emigrants from the cohort, first-year survival, and maturation rate (PFMC 2011). However, they relate to the abundance of adults a year later (PFMC 2011). We used values for the Sacramento Index, a measure of adult abundances of Sacramento River Chinook salmon based on harvest and the number of returning spawners (PFMC 2011), as the final measure of Chinook salmon productivity. Specifically, the Sacra-

mento Index represents adult abundance of Chinook salmon that originated from the Sacramento River system and migrated to sea in early spring after having spent little time rearing in the freshwater; these are the fish we attempted to isolate in our juvenile analysis. While the Sacramento Index represents largely the number of fish that had spent 2 winters at sea, it is not age specific and also includes a smaller fraction of older fish (PFMC 2011).

RESULTS

Krill distribution and abundance

During May and June, Ekman transport in the lee of Point Reyes was weak relative to the waters north and west of the headland (Fig. 2A). There were concentrations of krill associated with this relaxed area within the inner-shelf of the Gulf of the Farallones (Fig. 2B). Coinciding with this time period, juvenile Chinook salmon *Oncorhynchus tshawytscha* emigrate from San Francisco Bay into the Gulf of the Farallones and display spatial overlap with this high concentration of krill (Fig. 2C).

Species composition data from 2002 to 2010 indicate that the inner-shelf of the Gulf of the Farallones had a greater abundance of *Thysanoessa spinifera* than in Monterey Bay, the outer-shelf, and offshore (ANOVA, $p = 0.0017$). By contrast, *Euphausia pacifica* were chiefly distributed in deeper offshore waters along the shelf break and overlapping with the deep submarine canyon system of Monterey Bay ($p = 0.0358$; for further details see Santora et al. 2011a,b). Therefore, krill availability to juvenile Chinook salmon is chiefly related to the inner-shelf of the Gulf of the Farallones, and specifically attributed to the abundance of *T. spinifera* (Fig. 2B). Moreover, the interannual variability of krill abundance within the gulf is positively related to upwelling magnitude (log-linear regression, $p = 0.0047$, $N = 21$; Fig. 3).

Comparison of bongo net, Tucker, and midwater trawls from 2008 ($N = 6$), 2009 ($N = 11$), and 2010 ($N = 7$) indicated the midwater trawl (larger mesh size compared to zooplankton nets) was not capturing small *Thysanoessa spinifera* (less than ~ 16 mm; Fig. 4). An examination of 2008 krill length-frequency data (Fig. 4A) indicated that there were no small *T. spinifera*, but, in 2009, a much smaller cohort of krill lengths was present (Fig. 4B). In 2010, there was a bimodal pattern of krill lengths balanced fairly equally between the 2 krill cohorts (Fig. 4C).

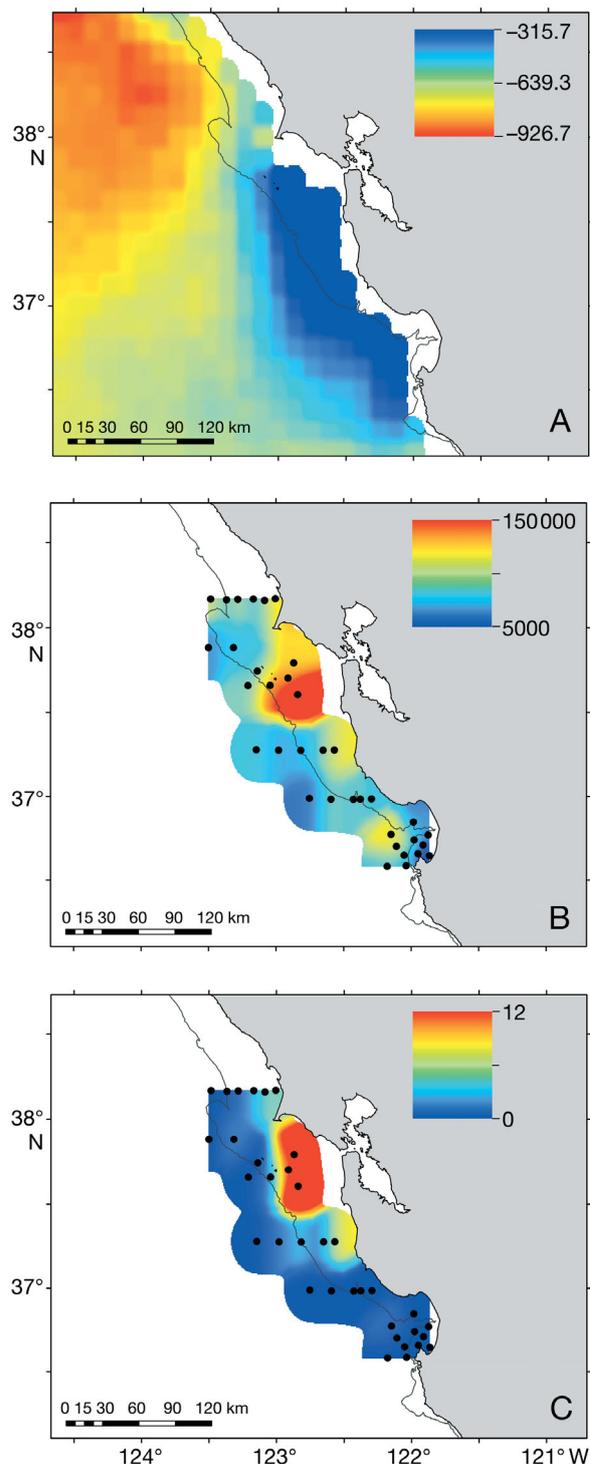


Fig. 2. Spatial patterns of (A) Ekman offshore transport (kg ms^{-1}) (metrics), (B) overall krill, and (C) juvenile Chinook salmon *Oncorhynchus tshawytscha* in coastal central California during May and June. (A) The Ekman transport climatology from 2000 to 2009 was estimated from the QuikSCAT satellite. (B) Abundance of euphausiids is the long-term mean number of individuals collected per net haul (black dots) from 1990 to 2010. (C) Abundance of salmon is total number of individuals collected per station during 1990 to 2010

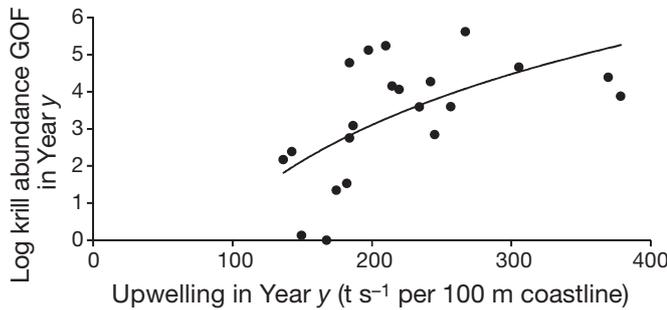


Fig. 3. Relationship between upwelling intensity for May and June at 39°N and the abundance (geometric mean per station) of overall krill sampled by the midwater trawl in the Gulf of the Farallones (GOF)

Chinook salmon diet and condition

The 4 greatest contributors to the average percent volume of diet were juvenile fish (27%), crab (20%), and the krill species *Euphausia pacifica* (11%), and *Thysanoessa spinifera* (7%). These percentages represent the average Chinook salmon (with and without the prey item); however, when present in the diet of the individual salmon, fish prey represented an average 67% of the diet volume, crab represented 48%, *T. spinifera* represented 41%, and *E. pacifica* represented only 21%. This suggests the juvenile Chinook salmon feed on a patchy prey field.

Abundance of krill in the Gulf of the Farallones during May and June did not relate to the volume percent of krill nor fish in the diet of juvenile Chinook salmon collected from June to August. However, there was a positive relationship between abundance of krill in the Gulf of the Farallones and crab volume in juvenile Chinook salmon diet (logistic regression; $p = 0.0001$, $N = 8$; Fig. 5B).

There was a 1 yr lag in the proportion of *Thysanoessa spinifera* in juvenile Chinook salmon diet and the abundance of krill in the Gulf of the Farallones (logistic regression, $p = 0.0001$, $N = 8$; Fig. 5C). This positive relationship was represented dramatically between years 1998 and 1999. In 1998 anomalously low abundance of krill were encountered in the midwater-trawl survey, yet krill were observed in juvenile Chinook salmon diet. By contrast, 1999 represented greater (albeit, still below the long-term mean) krill abundance on the shelf, yet there were no krill found in juvenile Chinook salmon diets, which were numerically dominated by juvenile fishes. There was no significant relationship between the abundance of adult *T. spinifera* in the Gulf of the Farallones in one year to the abundance of adult *T. spinifera* the next (linear regression, $p = 0.7751$,

$N = 8$), indicating the adult populations are not statistically related to the production of the larger cohort the next year. Proportional contributions of *Euphausia pacifica* (Fig. 5C), fish, and crab to the diet of juvenile Chinook salmon did not show a pattern with year lags.

The frequency plots for all juvenile Chinook salmon for which *Thysanoessa spinifera* in the diets were measured indicated juvenile Chinook salmon feed on the entire krill length-frequency distribution (Fig. 5D, $N = 68$). However, the midwater-trawl samples tend to catch only larger *T. spinifera* relative to those found in the diet (Fig. 4).

There was no relationship between condition (Fulton's K) of juvenile Chinook salmon and the abundance of krill in the Gulf of the Farallones in the same year ($p = 0.300$). However, the condition of juvenile Chinook salmon was related to the abundance of krill

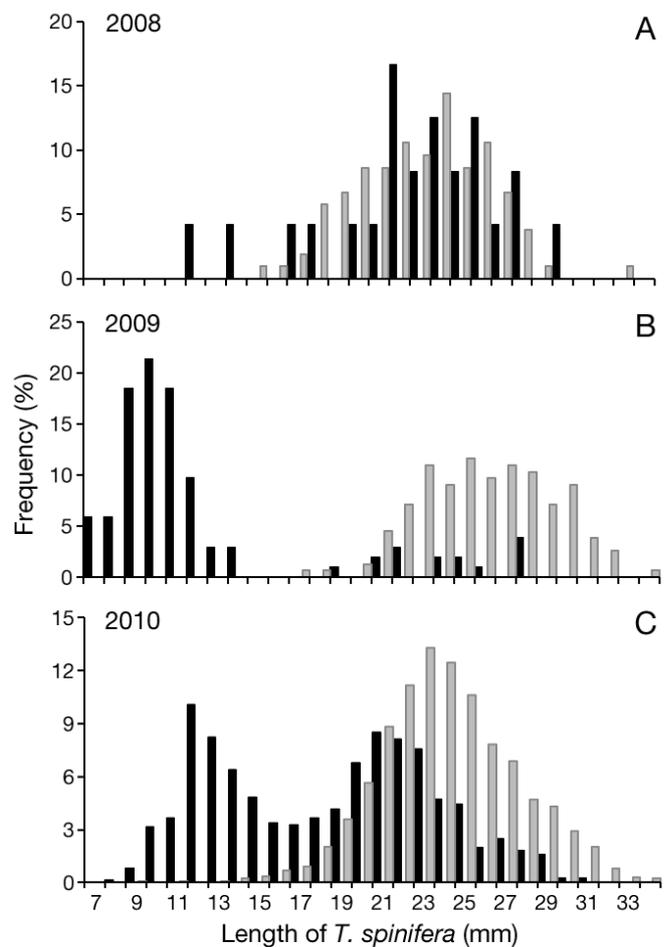


Fig. 4. *Thysanoessa spinifera*. Size distributions captured in (A) bongo nets (black) and midwater trawls (gray) in 2008, (B) Tucker trawls (black) and midwater trawls (gray) in 2009, and (C) in bongo nets (black) and midwater trawls (gray) in 2010

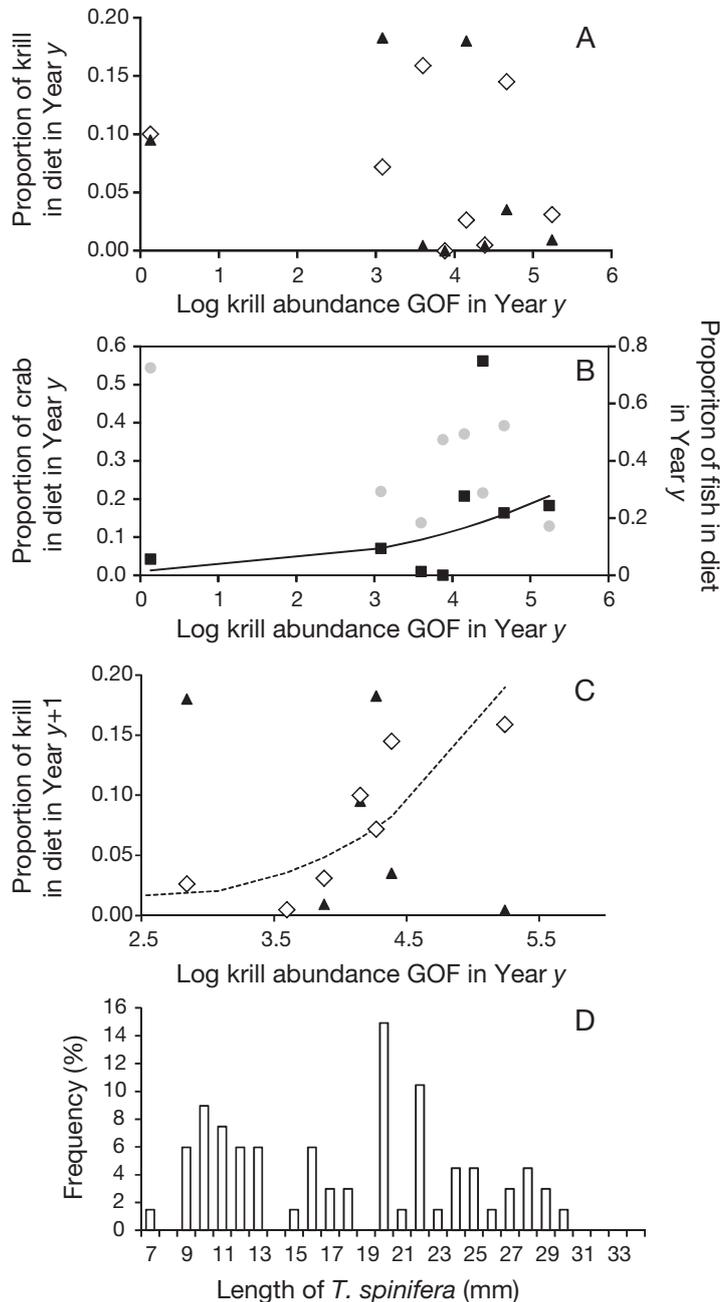


Fig. 5. *Oncorhynchus tshawytscha*. (A) Insignificant relationships between *Thysanoessa spinifera* (◇) and *Euphausia pacifica* (▲) volume proportions in the diet of juvenile salmon and the abundance (geometric mean per station) of overall krill in the Gulf of the Farallones (GOF). (B) Relationships between volume proportions of crab (■; significant logistic trend is in black) and fish (●; insignificant) in the diets of juvenile salmon and the abundance of overall krill in the GOF. (C) Significant relationship between the abundance of krill in the GOF and the volume proportion of *T. spinifera* in the juvenile salmon diet the next year (◇; significant logistic trend is shown by the dashed line; for better visualization datum x -axis = 0.12969, y -axis = 0 is offscale but was used in the regression analysis), while the relationship for *E. pacifica* is not significant (▲, datum x -axis = 0.12969, y -axis = 0 is offscale). (D) Size distribution of *T. spinifera* measured in the juvenile salmon diets

from the previous year (minus the extreme outlier datum for 1999; linear regression, $p = 0.0190$, $R^2 = 0.51$, $N = 10$; Fig. 6A). When abundance of krill was greater the year before juvenile Chinook salmon ocean entry, juvenile Chinook salmon diet had proportionally more *Thysanoessa spinifera* (Fig. 5C). The condition of juvenile Chinook salmon was log-linearly related to the amount of *T. spinifera* in juvenile Chinook salmon diet when present (log-linear regression, $p = 0.025$, $R^2 = 0.67$, $N = 7$, with 1999 removed as the fraction of *T. spinifera* in the diet was 0%; Fig. 6B). The percent volume of *Euphausia pacifica*, crab, and fish in the diet was not related to fish condition (Fig. 6B,C).

Projecting Chinook salmon abundance

The number of Chinook salmon returning to spawn after 1 winter at sea covaried with the condition of juvenile salmon the year before when they first entered the ocean system (power regression, $p = 0.057$, $R^2 = 0.35$, $N = 11$; Fig. 7A). These abundances of juvenile Chinook salmon that only spent a year at sea are significantly related to the cumulative number of adults (Sacramento Index) harvested or returned to the river the next year (linear regression, intercept = 0, $p = 0.0001$, $R^2 = 0.55$, $N = 22$; Fig. 7B; sensu PFMC 2011).

DISCUSSION

We tested the hypothesis that physical and biological environmental and juvenile Chinook salmon *Oncorhynchus tshawytscha* conditions during the first period at sea account for a significant amount of variability in later abundance of the adult population. We demonstrated a probable connection between wind, habitat, prey resources, and Chinook salmon productivity. Specifically, increased northerly winds, and hence upwelling, led to an increase in the abundance of adult *Thysanoessa spinifera* in the relatively relaxed Gulf of the Farallones. These krill co-occurred with the emigrating juvenile Chinook salmon and largely determined the condition of juvenile salmon and the abundance of adult salmon 3 yr later. Interestingly, we show that the overall abundance and distribution of larger krill in one

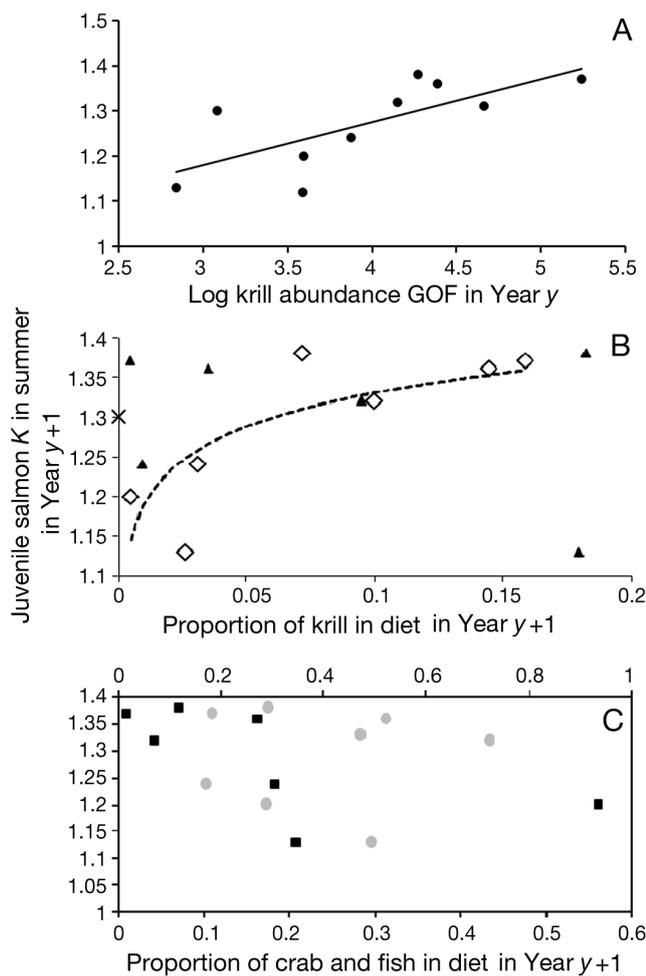


Fig. 6. *Oncorhynchus tshawytscha*. (A) Distribution of krill from midwater-trawl samples relates to the condition of juvenile salmon the next year (an outlier was removed from regression and is not shown to better visualize the significant relationship remaining; Year $y = 1999$, x -axis = 0.129692, y -axis = 1.33). Abundance is the geometric mean per station. (B) Proportion of *Thysanoessa spinifera* (\diamond) in the diet is positively related to the condition of juvenile salmon, but *Euphausia pacifica* (\blacktriangle) is not, while 'x' represents 1999 during which no krill were present in the juvenile salmon diets. (C) Neither the proportion of crab in the diet (\blacksquare , lower x -axis) nor fish (\bullet , upper x -axis) were related to the condition of the juvenile Chinook salmon. K : Fulton's index of body condition

year, that which we could estimate with our midwater trawl, is correlated to the production of juvenile Chinook salmon emigrating the next year. This indicates a multi-year accumulation of krill on the inner-shelf that produces an appropriate biomass for a productive ecosystem (Dorman et al. 2005, Shaw et al. 2010). This relationship was reliable enough that the dynamics of Chinook salmon juveniles were correlated with overall krill abundance and distribution the year before juveniles had even emigrated to sea.

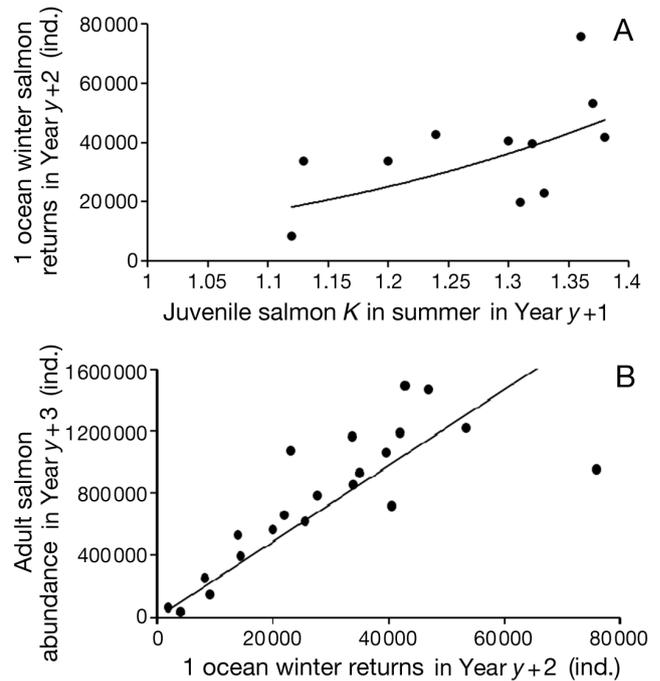


Fig. 7. *Oncorhynchus tshawytscha*. (A) The condition of juvenile Chinook salmon in the summer is positively related to the number of Chinook salmon from the same cohort returning to spawn the next year. K : Fulton's index of body condition. (B) The number of Chinook salmon returning after only a single winter at sea (1 ocean winter returns) relates positively to the abundance of adult fish predominantly from the same cohort (Sacramento Index), returning the following year

Importantly, given an ecosystem approach as taken here, process error can accumulate and result in weakly significant relationships or completely obscure biologically but not statistically significant relationships, suggesting our statistically significant results are conservative.

Inner-shelf ecosystem and early condition of Chinook salmon

The Gulf of the Farallones is a shallow region in the lee of the Point Reyes upwelling plume and receives nutrients from the plume water by means of eddies (Wing et al. 1998). These eddies in the slow relaxed region of the Gulf of the Farallones provide proper conditions for primary productivity and retention of krill (Santora et al. 2011a,b) and pelagic larval fish (Wing et al. 1998). If there are optimal winds (Cury & Roy 1989) and hence increased upwelling, nutrient influx, mesoscale structuring, and limited advection, krill biomass is accumulated over at least 2 yr (Dorman et al. 2005, Shaw et al. 2010). This accumulated

krill is then spatially coherent with juvenile Chinook salmon. The relationships between the consumption of 4 prey items to Chinook salmon condition and productivity shows that only *Thysanoessa spinifera* was significantly related. Therefore, Chinook salmon dynamics are related to the abundance and distribution of krill, whereby increased availability of *T. spinifera* relates to better condition and productivity. Specifically, in the present study it is important to focus on the climatological match between environment, prey, and juvenile Chinook salmon (Fig. 2) and the positive effect of greater krill abundance on juvenile condition (Fig. 6A) and the ultimate positive effect on the later abundance of Chinook salmon as adults: an indication of the effect of early survival and condition on population dynamics.

The critical period

The tenet is that the first period at sea for Chinook salmon accounts for a great amount of mortality across the life history and, therefore, is a significant period of time at which the abundance of spawners and fish available to the fishery is established (Beamish et al. 2004). There has been limited direct evidence of this relationship. For instance, given the size selectivity of the fishery and limited mark recovery, the youngest age for which a reliable estimate of mortality can be obtained is over a year after ocean emigration. Here we show that the condition of Chinook salmon captured during the summer of ocean entry is correlated to the number of Chinook salmon to return to spawn a year later. The relationship was relatively weak and based on only a few points; however, the abundance of the single-winter ocean fish returning to spawn represents a confounded estimate of the number of emigrants from the cohort, first-year survival, and maturation rate (PFMC 2011). This implies, then, that the relationship we uncovered may be a conservative estimate. The abundance of fish returning after a single winter correlates to their early condition and also to the number of fish remaining after 2 winters at sea. This indicates that recruitment is indeed set at the period of ocean entry, and dynamics occurring later in life are relatively stable.

Salmon are migratory fish living in a dynamic environment related to the climate at different spatial and temporal scales. Large-scale events and conditions such as El Niño or Pacific Decadal Oscillation phase shifts can affect the entirety of the California Current ecosystem. However, when salmon first enter the

ocean they may be most strongly affected by local and mesoscale features, with greater sensitivity to larger scale features and conditions as they age and migrate. Wells et al. (2006, 2007, 2008b) demonstrated that the size at maturity, growth rate, and maturation rates can be affected by conditions at large (1000s of km) and regional scales (100s of km). Here, we show the relationship of juvenile Chinook salmon condition to local structure (10s of km).

Krill as an ecosystem indicator of Chinook salmon condition and survival

Krill, specifically *Thysanoessa spinifera*, make up, on average, only 7% of the volume of the diet but clearly have a positive log-linear relationship on the condition of juvenile Chinook salmon (Fig. 6B). The same was not true for other prey items. This suggests that, while *T. spinifera* does not represent the greatest fraction of the prey observed in stomachs, it is essential as a trophic component of the shelf ecosystem. Fig. 3A shows that the region of the Gulf of the Farallones typically has a much higher abundance of krill (specifically *T. spinifera*) than the other locations sampled in the present study. *Euphausia pacifica* is broadly distributed but generally more abundant in waters at or beyond the shelf-break (200 to 1000 m) and over submarine canyons such as Monterey Bay, whereas *T. spinifera* populates coastal habitats on the inner-shelf (Brinton 1962, Tanasichuk 1998a,b, Marinovic et al. 2002, Feinberg & Peterson 2003, Dorman et al. 2005, Gómez-Gutiérrez et al. 2005). The reproductive ecology of both *E. pacifica* and *T. spinifera* involves multiple spawning attempts throughout the year, the timing of which appears to be synchronized to increased wind events (Brinton 1962, 1976, Tanasichuk 1998a,b, Feinberg & Peterson 2003, Shaw et al. 2010). *T. spinifera* are larger than *E. pacifica* and more lipid rich (Daly et al. 2010). In total, the presence of multiple cohorts of *T. spinifera* on the shelf offers a potential nutrient-rich and abundant prey resource for juvenile Chinook salmon using that environment.

The relationship between Chinook salmon productivity and *Thysanoessa spinifera* presence on the inner-shelf may relate less to *T. spinifera* and more to the conditions that covary with *T. spinifera* and/or that *T. spinifera* may be improving the quality of fish prey on which salmon feed—imparting better condition to the prey. Firstly, we demonstrate that adult *T. spinifera* abundance in the Gulf of the Farallones is related to upwelling intensity. Had *T. spinifera* not been the only prey item related to juvenile Chinook

salmon condition we could have relied on the environmental covariate wind and assumed the significance of *T. spinifera* was only the result of many improved ecosystem conditions. It is likely, however, that *T. spinifera* itself not only provides improved nutrition to juvenile Chinook salmon but also to forage fish on which juvenile Chinook salmon prey (Reilly et al. 1992). We do not have any data on the condition/quality of fish prey to test this hypothesis, although we note that juvenile rockfish, sanddab, and krill abundance from the trawl survey tend to covary over time (Bjorkstedt et al. 2010). Regardless, we have made a reliable connection between wind, overall krill distribution, abundance of *T. spinifera*, and ultimate productivity of Chinook salmon.

Our data suggest a positive relationship between crab volume in the diet and adult krill abundance in the Gulf of the Farallones in the same year. It is likely that crab become entrained on the shelf much like krill. Unlike krill, which appear to remain regionally for at least 2 yr, crab would not be expected to show a lag in pattern between diet and trawl survey results; the planktonic period is completed in the first year. Interestingly, the increased crab in the diet did not lead to better condition. This suggests the juvenile Chinook salmon may not be selecting crab, but rather, feeding on them because they are within the size range of their diet (mean size of crab = 3.5 mm, minimum = 1 mm, maximum = 6 mm), while the smaller cohort of *Thysanoessa spinifera* was not present. As such, we demonstrate that during years with increased abundance of only the larger cohort of *T. spinifera*, the fish have a higher proportion of crab in their diet.

There was a log-linear relationship between upwelling and the abundance of krill in the Gulf of the Farallones, yet krill did not show a correlation with the diets of juvenile Chinook salmon until the next year. This is curious and, at first, counter-intuitive. However, the explanation may lie in the biology of *Thysanoessa spinifera*. Interestingly, *T. spinifera* has multiple cohorts in a given year (Fig. 4). Data from the bongo-net and Tucker trawl samples collected between 2008 and 2010 suggest that the large spawning stock of *T. spinifera* in 2008 produced strong juvenile recruitment in 2009 as a consequence of winter/early spring spawning. Further, the juvenile stock produced in 2009 aged and produced an additional cohort for 2010. We also demonstrated that the smaller cohort of *T. spinifera* was represented in the diets of juvenile Chinook salmon. Specifically, the juvenile Chinook salmon diet was made up of the juveniles resulting from the previous year's spawn-

ing stock. Yet, the midwater trawl, the data for which we have longest and most reliable series, fails to capture the smaller cohort of the *T. spinifera* from the current year.

We have not captured all the mechanisms forcing salmon dynamics, and the system is more complex than that presented here. For instance, we removed 1999 from our analysis of the effect of *Thysanoessa spinifera* in the diet on the condition of juvenile Chinook salmon, because during a year when no krill were present in juvenile Chinook salmon diets (following 1998 at which time no adult population of krill was detected) fish maintained reasonably good condition (Fig. 6B). In fact, the responses that foragers have to a dynamic prey field are not linear, with opportunities to switch prey. Also, the possibility exists that poor prey conditions occurring before the salmon survey began could have already resulted in strong size-selective mortality, leading to non-intuitive relationships; we may have sampled a select group of survivors from 1999. It is worth noting that 1999 also represented one of the largest recruitment events on record for many species of rockfish, as indexed in adult populations (Wallace & Lai 2006, Field 2008, Stewart 2008, Field et al. 2010), as well as the recruitment of other groundfish such as Pacific hake (Stewart & Forrest 2010) and sablefish (Stewart et al. 2011). However, the midwater-trawl survey, designed specifically for the enumeration of juvenile rockfishes, observed below-average recruitment in 1999. The year was anomalous with respect to the intensity of upwelling in central and northern California, which led to an offshore distribution of chlorophyll, coastal pelagic species, and juvenile rockfish (Schwing et al. 2000). This suggests that unusual conditions occurred that may have altered the distribution or catchability of typical prey, but that the year itself was productive across virtually all trophic levels, and indeed a greater appreciation for the spatial scales of the dynamics of these stocks led to a decision to expand the spatial scale of the juvenile rockfish survey in 2003 (Sakuma et al. 2006).

Environmental conditions in the ocean have been implicated as a factor in forcing salmon dynamics. However, few studies have drawn the direct link between atmospheric conditions and prey and the recruitment of salmon to the spawning population (Peterson & Schwing 2003). Here, we have demonstrated a likely path between wind, adult krill distribution and abundance, and early salmon condition and production; if wind slows during the upwelling season or the upwelling season begins late, the nutrient introduction to the inner-shelf is likely reduced.

This, in turn, alters the production and distribution of krill and the abundance of a critical prey item, *Thysanoessa spinifera*. As we demonstrated a 1 yr lag in the relationships between adult krill abundance and salmon condition, it is also important, in a yet to be determined manner, that conditions in the winter and/or early spring be conducive for production of a juvenile cohort of krill the next year. Interestingly, *T. spinifera* do not have any inter-annual autocorrelation. Therefore, this is likely a biannual system of production, whereby, if there is a dominant larger krill cohort in one year and appropriate environmental conditions over the winter and into spring, a smaller krill cohort will occur and the juvenile salmon, which feed on these smaller prey, as well as the larger krill that may be present, will have improved condition (sensu Schroeder et al. 2009).

Application to management

We have demonstrated significant relationships between juvenile Chinook salmon diet, condition, and later recruitment by simply including a 1 yr lag in the data between midwater-trawl samples and the juvenile Chinook salmon that enter the ocean system a year later. While this lag is derived, in part, from sampling biases, there remains value in the data. Firstly, we have an understanding of the mechanism and, therefore, can remove the primary concerns of the bias from our analysis. Secondly, we have the opportunity to use the midwater-trawl survey to inform our estimates of the condition and survival of juvenile Chinook salmon a year before they even reside in the ocean. Future efforts will allow us to confirm (or refute) this hypothesis, as krill are now routinely identified to the species level in the surveys described here, and ongoing efforts are being undertaken to compare catch rates and size selectivity among multiple types of gear.

As part of the present study we inherently included a forecasting model for the number of fish available to fishery and spawning (Fig. 7B). Specifically, the Sacramento Index was forecasted using a regression on the number of younger fish to return the year prior (sensu PFMC 2011). This model assumes that most of the variability in mortality occurs in the first year. Here we show that this is likely the case. In addition, we show that there is potential to improve the forecast model by including information from the earliest period at sea or even the year before the cohort emigrates to the sea, the year in which the previous cohort returned to spawn.

A goal of salmon management is to make certain that a given number of spawners is allowed to enter the river to spawn and assure the viability of the stock. Currently, managers make no adjustments to the escapement goals they set forward; a static escapement goal is used between years. Yet, there may be interest in adjusting this value if, in a given year when spawners are returning, the midwater trawl indicates there are very few adult *Thysanoessa spinifera*. Following, there would be fewer of the next cohort of *T. spinifera* available to juveniles entering the ocean the next year. If managers act cautiously, they may mitigate the deleterious effects on the juveniles the next year, whether that be by promoting the production of more juveniles to counteract greater mortality or by promoting the production of fewer juveniles with consideration of increased density dependence during a period of limited resources. More likely, if there is an indication of poor production resulting in reduced adult abundance 3 yr later, managers could consider feathering harvest mortality across all the available cohorts as opposed to making all harvest decisions in the final year on predominantly 1 cohort. This may provide the opportunity for the first application of ecosystem information and mechanisms to improve fishery management.

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