Winter ichthyoplankton biomass as a predictor of early summer prey fields and survival of juvenile salmon in the northern California Current

Elizabeth A. Daly[1],[*], Toby D. Auth[2], Richard D. Brodeur[3], William T. Peterson[3]

[1]Cooperative Institute for Marine Resources Studies, Oregon State University, Newport, Oregon 97365, USA
[2]Pacific States Marine Fisheries Commission, Hatfield Marine Science Center, Newport, Oregon 97365, USA
[3]NOAA Fisheries, Northwest Fisheries Science Center, Newport, Oregon 97365, USA

ABSTRACT: Diets of juvenile coho *Oncorhynchus kisutch* and Chinook *O. tshawytscha* salmon are made up primarily of winter-spawning fish taxa in the late-larval and early juvenile stages that are undersampled in plankton and larger trawl nets. Although we have no direct measure of the availability of fish prey important to juvenile salmon during early marine residence, we do have data on the larval stage of their prey that may be used as a surrogate for the later stages. Data on these prey items were obtained from ichthyoplankton samples collected along the Newport Oregon Hydrographic line (44.65° N) during January–March in 1998–2010. We explored winter biomass of prey fish larvae as a potential indicator of marine feeding conditions for young salmon the following spring. The proportion of total winter ichthyoplankton biomass considered to be common salmon fish prey fluctuated from 13.9 % in 2006 to 95.0 % in 2000. The relationship between biomass of fish larvae in winter and subsequent coho salmon survival was highly significant (r^2 = 50.0, p = 0.004). When the 2 outlier years of 1998 (El Niño) and 1999 (La Niña) were removed, this relationship was also highly significant for spring Chinook (r^2 = 70.7, p = 0.0002) and significant for fall Chinook salmon (r^2 = 34.0, p = 0.03) returns. Winter larval fish composition showed a high degree of overlap with juvenile salmon diets during May, but less overlap in June. Larval fishes appeared to be an early and cost-effective indicator of ocean ecosystem conditions and future juvenile salmon survival.

KEY WORDS: Ichthyoplankton · Juvenile salmon · Prey · Winter

INTRODUCTION

Each year from late spring to mid-summer, coho *Oncorhynchus kisutch* and Chinook *O. tshawytscha* salmon juveniles migrate to sea and enter the northern California Current (NCC) ecosystem. The conditions they encounter upon ocean entry are critical to early marine growth and the ultimate return to freshwater as adults (Pearcy 1992). A link between early marine survival of salmon and physical ocean conditions, such as temperature and upwelling, has been

well documented (Beamish et al. 1997, Logerwell et al. 2003, Sharma et al. 2013). However, few studies have examined the biological mechanisms underlying this connection (Tanasichuk & Routledge 2011).

Juvenile coho and Chinook salmon are among the most piscivorous fish in the marine nekton (Brodeur & Pearcy 1992, Miller & Brodeur 2007). Soon after ocean entry, the majority of the diets of juvenile salmon are made up of 0-age fish prey (Daly et al. 2009). In addition to the juvenile fishes eaten, juvenile salmon also eat modest amounts of crab mega-

lopae and adult euphausiids (Peterson et al. 1982, Brodeur 1991, Daly et al. 2009), and their diets exhibit substantial seasonal and interannual variability (Brodeur et al. 2007, Weitkamp & Sturdevant 2008).

Studies on the ocean ecology of juvenile salmon generally rely on samples of the physical environment, as well as of various biological components such as the zooplankton community. Due to their low trophic position, zooplankton are an important resource in the marine environment, and they respond rapidly to changes in the phytoplankton community and transfer this energy further up the food web. Significant correlations exist between copepods and survival of juvenile salmon (Peterson & Schwing 2003, Bi et al. 2011). However, because juvenile coho and Chinook salmon do not consume copepods directly, these correlations do not account for a trophic level between zooplankton and juvenile salmon, namely the age-0 fishes eaten by juvenile salmon that feed directly upon small zooplankton such as copepods, early stage euphausiids, and crab larvae (Emmett et al. 1991, Reilly et al. 1992).

Coastal zooplankton in the NCC are relatively well-studied in terms of their biological community, based primarily on a time series of data collected during sampling surveys along the Newport Hydrographic (NH) line off Newport, Oregon, USA (44.65° N) dating back to collections in the late 1960s (Hooff & Peterson 2006, Keister et al. 2011). Although larval fish have been examined throughout this time series, directed sampling programs of the juvenile stages of fish normally eaten by juvenile salmon in the NCC have been short in duration and difficult to accomplish due to sampling limitations (Brodeur et al. 2011a). While plankton samples collected along the NH line during May and June include species of fish larvae that are important prey for juvenile salmon during their early marine residence (Brodeur et al. 2008), juvenile salmon do not typically eat fish larvae but instead consume larger juvenile stage fishes (Daly et al. 2009). In the absence of direct sampling of the prey community important to juvenile salmon, we explored the ocean conditions and the larval fish community during winter and early spring, a time of peak larval fish abundance in the NCC (Brodeur et al. 2008), which may function as a surrogate for the early summer juvenile fish prey field of salmon.

Numerous biological correlations have suggested that coho and Chinook salmon production is limited by bottom-up production in the NCC (Peterson et al. 2012); however, a direct biological mechanism describing variability in salmon returns has yet to be tested. We hypothesized that our time series of winter ichthyoplankton data from the NH line could provide an index of the juvenile fish prey available to juvenile salmon during their first marine summer. Our null hypothesis was that survival to adulthood for juvenile coho and Chinook salmon in the NCC is not related significantly to marine ichthyoplankton biomass and species composition during the winter prior to ocean entry.

MATERIALS AND METHODS

Winter ichthyoplankton biomass

Ichthyoplankton samples were collected from 5 stations spaced ~9 km apart along the NH line, a single transect extending off the central Oregon coast (Fig. 1). Sampling was conducted approximately every 2 wk between January and March 1998–2010, and we collected 161 ichthyoplankton samples from 52 cruises. Our analysis included samples from only January–March, assuming that larvae collected during these months would have had sufficient time to grow to the average size of prey eaten by juvenile salmon in late spring and early summer (Daly et al. 2009). Additionally, we included for analysis only samples from stations that were 9–46 km from shore because of the consistency of sampling within this region. Due to inclement weather or equipment malfunctions, not all stations were sampled during all cruises.

Sampling was conducted primarily at night using either a 1 m diameter ring net with 333 µm mesh or a 60 cm diameter bongo net with 200 µm mesh (333 µm after 2005), as described in Brodeur et al. (2008). Each net was fished as a double oblique tow within the upper ~20 m of the water column at a retrieval rate of ~30 m min^{-1} and a ship speed of 1.0 to 1.5 m s^{-1}. A depth recorder and flowmeter were placed in the net during each tow to determine tow depth and volume of water filtered. Mean water volume filtered per tow was 88.1 m^3 (SE = 6.3 m^3).

Ichthyoplankton samples were preserved at sea in a 10% buffered-formalin seawater solution. In the laboratory, fish larvae from each sample were sorted, counted, and identified to the lowest taxonomic level possible using a dissecting microscope. For each taxon within a sample, length of each individual was measured if fewer than 30 individuals were present; otherwise, a random subsample of 30 was measured. Larvae were measured to the nearest 0.1 mm using Image Tool (Wilcox et al. 2002), with measurement
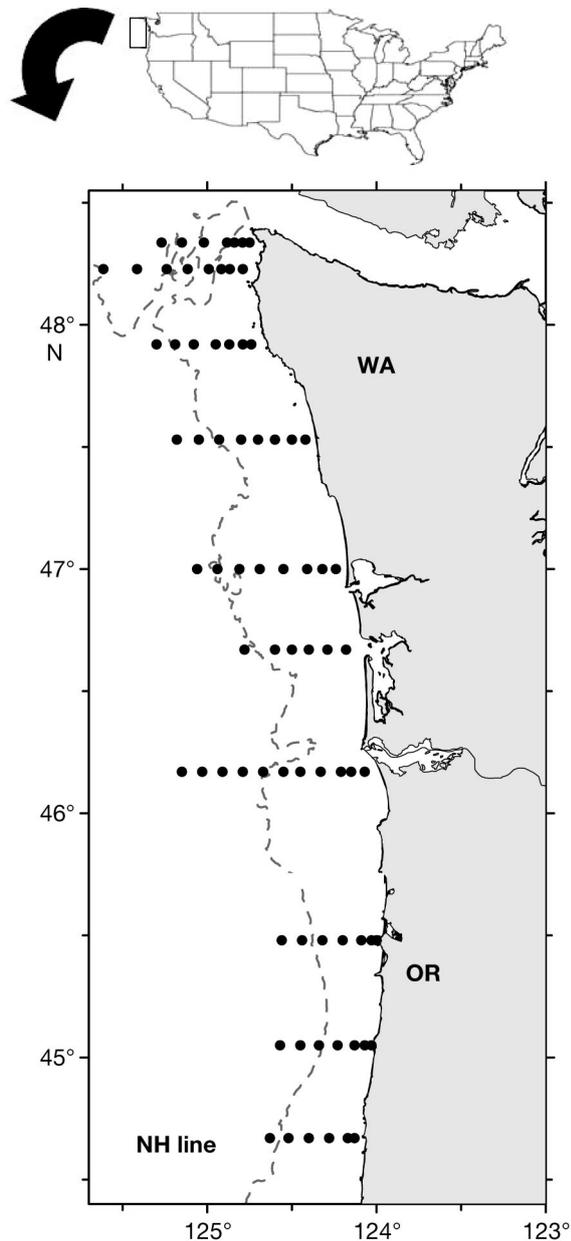
Fig. 1. Location of stations sampled during winter (January–March) in 1998–2010 along the Newport Hydrographic (NH) line, and location of stations sampled for juvenile salmon. The 200-m isobath is shown as a dashed line. WA: Washington; OR: Oregon, USA

expressed as standard length (SL) or notochord length (NL) for preflexon larvae.

From the ichthyoplankton data set, we calculated the winter biomass of important salmon prey as a potential indicator of feeding conditions that would be available to juvenile salmon the following spring and early summer. The following 5 larval fish taxa were included in the indicator, based on importance

as salmon prey: Pacific sand lance *Ammodytes hexapterus*, rockfishes *Sebastes* spp., smelts (Osmeridae), sculpins (Cottidae), and northern anchovy *Engraulis mordax* (Daly et al. 2009). Clupeids such as Pacific herring and sardine can at times be important fish prey for juvenile salmon, but they were not included for analysis due to their complete absence in our larval fish collections.

Ichthyoplankton taxa were grouped largely at the family level due to the low degree of identification possible in the diet samples, where digestion made species-level identification difficult (see subsequent salmon diet description). We estimated ichthyoplankton carbon content based on literature values from regression equations that relate body morphology to carbon weight of individuals (Lasker et al. 1970, Pepin 1985, Norton et al. 2001). We used 22 equations to calculate the carbon content, including multiple equations for some taxa based on their larval size range if values were available. Some taxa did not have species-specific equations available; we then used equations from fish taxa in their same family. At stations where greater than 30 fish were sampled, the remaining unmeasured fish carbon content was calculated from the station average. Total biomass of each taxonomic grouping was calculated for each sampling station as the sum of the carbon weights of individuals per m^3 and expressed as mg C 1000 m^{-3}. We tested for significant differences in winter ichthyoplankton biomass among years using ANOVA and a Tukey's multiple range test which were applied to the $\log_e(n + 0.1)$-transformed biomass totals. All ANOVA tests were performed using JMP statistical software (SAS Institute 2007) and statistical significance was set at $p < 0.05$.

Physical environment and winter larvae

We conducted stepwise multiple regressions to assess potential relationships of winter larval biomass and environmental conditions. Models were run separately for each of the 5 important salmon prey larval fish, total larvae, prey larvae and non-prey larvae biomass. Environmental metrics (MEI, PDO, UPI and SST; see description below) were included as potential independent variables. All regressions were run as backward stepwise procedures. We explored several time lags in environmental data relative to larval biomass and found that the highest relationships occurred 3 mo prior to the larval stage (October–December); therefore, we only

report the multiple regressions with October–December mean environmental variables. Environmental variables included were (1) Multivariate El Niño-Southern Oscillation Index (MEI; www.esrl. noaa.gov/psd/enso/mei/), (2) Pacific Decadal Oscillation (PDO; www.jisao.washington.edu/data/pdo/), (3) Upwelling Index (UPI) from 45.00° N, 125.00° W (www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/upwelling.html), and (4) sea-surface temperature (SST) from the National Oceanic and Atmospheric Administration's (NOAA) Stonewall Banks buoy located 20 nautical miles west of Newport, Oregon (www.ndbc.noaa.gov/station_page.php? station=46050). The UPI values during October–December were negative, indicating downwelling conditions. Prior to analyses, larval biomass data were $\log_e(n + 0.1)$-transformed to normalize the data and homogenize residual variances. We used STATGRAPHICS Centurion XV software for the multiple regression analyses and statistical significance for retaining variables was $p < 0.05$.

Changes in the composition of the winter larval community were explored using a non-parametric multi-response permutation procedure (MRPP) to test for significant changes in the composition of winter larval biomass between years and between cold/warm regimes (defined below). The MRPP generates an A-statistic ranging from 0 to 1, with the maximum value indicating complete agreement between groups (McCune & Mefford 1999). Factors for MRPP were regime (cold or warm), and groups within those factors were years (1998–2010). Regimes defined as warm included the years 1998, 2003–2005, 2007, 2010; those defined as cold included 1999–2002, 2006, 2008, 2009. These designations followed upon those outlined in Brodeur et al. (2008) and as indicated by positive (warm) and negative (cold) phases in the MEI and PDO.

To determine which larvae contributed to significant differences between years or regimes, we performed an indicator species analysis (ISA) on the $\log_e(n + 1)$-transformed larval fish biomass data. For ISA, we used 5000 random restarts for each Monte Carlo simulation to test taxonomic fidelity within each group (Dufrêne & Legendre 1997). All MRPP and ISA analyses were performed using PC-Ord statistical software (McCune & Mefford 2006).

Juvenile and adult salmon data

Juvenile salmonids were collected as part of a multi-year survey conducted off coastal Oregon and Washington during May and June 1999–2010 and June 1998. Salmon were collected using a pelagic rope trawl (264 Nordic) with a mouth opening of 20 by 30 m, which was towed at the surface. Surveys followed along 5–10 transect lines running perpendicular to shore, with sampling stations along each transect extending 3 to 50 km offshore (Fig. 1). Captured salmon were immediately frozen. In the laboratory, stomachs were removed and placed in a 10% formaldehyde solution for approximately 2 wk, then rinsed with fresh water for 24 h before being transferred into 70% ethanol. We analyzed up to 30 stomachs of each species and life history stage from each haul. Stomach contents were identified to the lowest possible taxonomic category using a dissecting microscope. Prey were enumerated, measured, and weighed to the nearest 0.001 g. We calculated the salmon diet composition (by weight of prey consumed) on a subset of the salmon prey community; using the top 5 most important fish prey consumed for comparisons with the environmental ichthyoplankton community; Pacific sand lance *Ammodytes hexapterus*, rockfishes *Sebastes* spp., smelts (Osmeridae), sculpins (Cottidae), and northern anchovy *Engraulis mordax.* We reallocated unidentifiable fish remains to identifiable fish categories at the smallest spatial scale possible (sampling station) as the diets of juvenile salmon have been shown to be most similar to the salmon caught with them (Weitkamp & Sturdevant 2008). When all fish prey at a station were unidentifiable, these diets were omitted from the analysis.

Winter ichthyoplankton prey community and the salmon diets were visually compared using nonmetric multidimensional scaling ordination (MDS). An averaged diet composition of the top 5 salmon prey was calculated for each May and June for coho and yearling Chinook salmon and June subyearling Chinook salmon for all years possible (n = 63 salmon/month/year diet combinations). Too few coho salmon were caught in May 2005, and analyses of subyearling Chinook diets included only averages for June, as too few subyearlings are caught in May. These were compared to the annual average composition of winter ichthyoplankton based on proportion of biomass (n = 13). Data were arcsine square root-transformed prior to analysis to achieve normality of proportional data. The MDS to compare the diet and prey community was based on a matrix constructed from pairwise Bray-Curtis similarity indices. We tested for significant community differences using MRPP, and when significant differences were identified, we used ISA to detect which spe-

cies contributed significantly to the differences between the salmon diets and the ichthyoplankton community.

The relationship between marine survival of salmon and the index of ichthyoplankton biomass available during early marine residence of juvenile salmon was explored using regression analysis. Marine survival was compared to the $\log_e$-transformed annual average winter biomass of the 5 important salmon prey taxa. For marine survival estimates of hatchery coho salmon, we used the Oregon Production Index, which is an estimate of total freshwater escapement adjusted for ocean and freshwater hatchery catch (OPIH; Pacific Fishery Management Council 1998–2010). For Chinook salmon, our survival estimates were based on the counts of adult returning to the Columbia River. With the stable hatchery production of Chinook salmon in the Columbia River, the variability in return counts of adult salmon was used as a proxy for marine survival (Columbia River Data Access in Real Time www.cbr.washington.edu/dart/adult_rpt.html). We used counts of spring Chinook taken during 15 March to 31 May each year, and count data were lagged by 2 yr to reflect year of ocean entry for these adults. For spring Chinook, the years 1998 and 1999 were excluded from analysis because the studentized residuals from the regression model were greater than 4 standard deviations above the mean. Survival of adult fall Chinook salmon was based on adult counts at Bonneville Dam between 1 August and 15 November, and these data were also lagged by 2 yr to reflect the year of ocean entry.

In addition to exploring prey biomass, we investigated if changes in ichthyoplankton composition or the prey community was related to salmon marine survival. The ichthyoplankton community for each year was the averaged composition of the proportional biomass of the 5 important salmon prey fish larvae. To create a univariate measure for each year of the ichthyoplankton community, we took the multivariate compositional data and created a MDS ordination plot using a Bray-Curtis distance matrix. The resulting 2-dimensional ordination was rotated such that the maximum variance explained was along Axis 1 (59.0% of the variance explained). The ordination scores for Axis 1 thusly represented the separation of the annual prey composition oriented along one axis and represented a univariate value of the separation of the ichthyoplankton composition. These annual community scores were used to explore relationships with overall salmon returns.

RESULTS

Larval fish community

A total of 5802 fish larvae representing 20 taxa were collected throughout the study (Table 1). Eight taxa accounted for 90% of the total standardized larval biomass, which was composed of 36.7% flatfishes, 18.9% Pacific sand lance, 10.2% rockfishes, 9.2% pricklebacks, 6.3% smelts, 5.1% sculpins, 3.0% greenlings, and 0.1% northern anchovy. Larval barracudinas (Paralepididea) comprised 4.0% of the total standardized larval biomass but were only found at one station (28 km from shore) during one cruise in March 2010. Of the Pleuronectiformes, English sole *Parophrys vetulus* was consistently dominant across all years of the study. Life history information for the 5 important salmon prey taxa (i.e. Pacific sand lance, rockfish, smelts, sculpins, and northern anchovy) are presented in Table 2 along with the average size of the prey eaten by juvenile salmon.

The biomass of larval fish taxa varied among years for each of the 5 important salmon prey, although the annual differences were not significant for larval sculpins or northern anchovy (Table 3, Fig. 2). Total biomass of salmon prey taxa was highest in 2000 and 2008, while total larval biomass (both prey and non-prey taxa) was highest in 2001, 2008 and 2010. The highest proportion of salmon prey biomass relative to total larval fish biomass was observed in 2000, and the lowest observed in 2001, when biomass of non-salmon prey taxa was unusually high (Fig. 2). Larval northern anchovy were collected only in 1998 and 2003, both warm El Niño years.

Winter ichthyoplankton biomass (total and salmon-prey taxa), *Ammodytes hexapterus,* and cottids were significantly related to only one of the environmental metrics: PDO (Table 4). Increases in total biomass and the biomass of fish larvae important to juvenile salmon occurred when negative PDO (cool) conditions took place in late fall and early winter. Results of MRPP analyses revealed significant differences in larval biomass between groups within each year (A-statistic 0.066, p < 0.001) and regime factor (A-statistic 0.015, p = 0.004). Smelts and rockfishes were identified as significant indicator taxa for 2010. There were significant prey taxa identified as indicator species for both the warm and cold regime years. Two prey taxa were indicators of warm ocean conditions (northern anchovy and rockfishes), while one (Pacific sand lance) was an indicator of cold conditions.

Juvenile salmon diets

Juvenile salmon were highly piscivorous during their first few months in the marine environment (May and June), and although they were eating a broad range of fish prey, the major proportion of their diets was derived from a small number of fish species. Mean values of piscivory during the May and June diet were 73.9% (±18.5%) for coho, 85.6% (±12.1%) for yearling Chinook, and 71.1% (±22.6%)

Table 1. Taxonomic composition, number of species of each taxon found in study area, frequency of occurrence, mean biomass (mg C 1000 m^{-3}), and percent of total mean biomass for all larval fish collected for this study during winter (January–March) in 1998–2010 along the Newport Hydrographic (NH) line. Asterisks indicate important salmon prey taxon

Taxon	Common name	No. of species	Frequency of occurrence	Mean biomass	Total biomass (%)
Clupeidae	Pacific herring, Pacific sardine	2	<0.01	0.003	<0.01
Engraulidae					
Engraulis mordax[*]	Northern anchovy	1	0.04	0.06	0.14
Osmeridae[*]	Smelts	7	0.16	2.51	6.35
Paralepididae	Barracudinas	3	<0.01	1.57	3.98
Myctophidae	Lanternfishes	20	0.28	0.64	1.63
Gadidae	Cods, tomcods	5	0.09	0.89	2.26
Scorpaenidae					
Sebastes spp.[*]	Rockfishes	65	0.52	4.01	10.15
Sebastolobus spp.	Thornyheads	3	0.04	0.008	0.02
Anoplopomatidae	Sablefish	1	<0.01	0.01	0.04
Hexagrammidae	Greenlings	9	0.16	1.17	2.95
Cottidae[*]	Sculpins	>100	0.36	2.02	5.11
Liparidae	Snailfishes	17	0.08	0.61	1.54
Bathymasteridae	Ronquils	4	0.07	0.14	0.35
Stichaeidae	Pricklebacks	26	0.04	3.63	9.2
Cryptacanthodidae	Wrymouths	2	0.02	0.21	0.54
Pholidae	Gunnels	9	<0.01	0.002	<0.01
Icosteidae	Ragfish	1	<0.01	0.003	<0.01
Ammodytidae					
Ammodytes hexapterus[*]	Pacific sand lance	1	0.24	7.48	18.94
Gobiidae	Gobies	3	0.01	0.002	<0.01
Pleuronectiformes	Flatfishes	31	0.58	14.5	36.72
Unidentified			0.06	0.02	0.05
Total prey taxa[*]			0.76	16.06	40.69
Total non-prey taxa			0.75	23.42	59.31
Total larvae			0.9	39.48	100

Table 2. Life history information for the 5 important salmon prey larval fish taxa collected during this study: (Richardson 1973, Stein 1973, Fukuhara 1983, Houde 1989, Matarese et al. 1989, Laidig et al. 2004, Auth & Brodeur 2006, Auth 2009, Doyle et al. 2009). ? = no data or incomplete information. Average total length of salmon prey eaten by juvenile salmon during May and June (±SD)

Taxon	Peak larval abundance (season)	Spawning location	Larval habitat	Length at hatching (mm)	Larval stage duration (d)	Avg. total length (mm) in in salmon diets
Ammodytes hexapterus	Nov–May	Intertidal	Coastal/Shelf	6–7	102–131[a]	41.9 ± 11.7
Sebastes spp.	Year round (?)	Upper slope (?)	Coastal/Shelf/Offshore	3.8–7.5[b]	~80[c]	36.2 ± 6.7
Osmeridae	Jan–Jun	Gravel beaches	Coastal/Shelf	3–7	~150	40.1 ± 24.5
Cottidae	Nov–May	Intertidal	Coastal/Shelf	2.9–7	42–49[d]	20.5 ± 15.1
Engraulis mordax	May–Aug	Plume	Coastal/Shelf/Offshore	2.5–3	24–51[e]	59.7 ± 15.5

[a]Larval stage duration reported for *A. americanus.* [b]Length at which *Sebastes* spp. larvae are extruded. [c]Larval stage duration reported for *S. wilsoni.* [d]Larval stage duration reported for *Oligocottus maculosus.* [e]Larval length at transformation reported for *E. japonica*

Table 3. Annual mean winter biomass (mg C 1000 m^{-3}) for the 5 important salmon prey larval fish taxa, total prey taxa, total non-prey taxa, and total larvae collected during this study ±1 SE. For between-year comparisons of each taxon, different superscript letters indicate significant differences (ANOVA p < 0.05)

Taxon	1998	1999	2000	2001	2002	2003	2004
Ammodytes hexapterus	0.5 ± 0.4^{abc}	1.3 ± 0.6^{abc}	60.4 ± 39.6^{a}	13.1 ± 6.5^{ab}	8.8 ± 5.7^{abc}	0.2 ± 0.1^{bc}	0 ± 0^{c}
Sebastes spp.	0.3 ± 0.1^{b}	1.4 ± 1.3^{ab}	0.8 ± 0.6^{b}	1.1 ± 0.4^{b}	0.1 ± 0.1^{b}	0.4 ± 0.1^{b}	3.4 ± 2.9^{b}
Osmeridae	0.2 ± 0.2^{bc}	0 ± 0^{bc}	0.5 ± 0.4^{abc}	0 ± 0^{c}	0.1 ± 0.1^{bc}	1.9 ± 1.8^{bc}	0.1 ± 0.1^{c}
Cottidae	0.3 ± 0.1	5.2 ± 3.0	1.4 ± 0.8	3.5 ± 2.1	2.2 ± 1.1	0.5 ± 0.4	0.4 ± 0.2
Engraulis mordax	0.1 ± 0.02	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.5 ± 0.5	0 ± 0
Total prey taxa	1.3 ± 0.6^{bc}	7.9 ± 3.7^{abc}	63.1 ± 41.1^{ab}	17.6 ± 6.7^{abc}	11.2 ± 5.6^{abc}	3.4 ± 2.4^{bc}	3.8 ± 2.9^{c}
Total non-prey taxa	3.8 ± 1.6^{ab}	11.0 ± 4.2^{ab}	3.3 ± 1.9^{ab}	77.2 ± 33.8^{ab}	30.0 ± 14.9^{ab}	3.7 ± 2.2^{b}	15.5 ± 7.5^{ab}
Total larvae	5.1 ± 1.6^{bc}	18.9 ± 3.9^{abc}	66.4 ± 42.6^{abc}	94.9 ± 34.4^{ab}	41.2 ± 18.8^{abc}	7.1 ± 3.0^{c}	19.3 ± 10.0^{bc}

Taxon	2005	2006	2007	2008	2009	2010
Ammodytes hexapterus	0.02 ± 0.02^{bc}	3.0 ± 3.0^{abc}	0.2 ± 0.2^{bc}	40.9 ± 39.1^{abc}	0.9 ± 0.4^{bc}	7.4 ± 5.6^{abc}
Sebastes spp.	4.9 ± 2.4^{ab}	0.1 ± 0.1^{b}	0.2 ± 0.1^{b}	0.7 ± 0.3^{b}	2.2 ± 0.9^{b}	27.3 ± 10.7^{a}
Osmeridae	0.02 ± 0.02^{c}	0.4 ± 0.4^{abc}	0 ± 0^{c}	26.2 ± 22.1^{ab}	1.3 ± 1.2^{c}	8.1 ± 3.6^{a}
Cottidae	1.8 ± 0.9	0.5 ± 0.3	3.5 ± 1.9	1.4 ± 0.7	3.4 ± 1.3	1.7 ± 1.0
Engraulis mordax	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Total prey taxa	6.7 ± 2.4^{abc}	3.9 ± 3.5^{abc}	4.0 ± 1.9^{bc}	69.3 ± 61.6^{abc}	7.7 ± 2.3^{abc}	44.5 ± 11.8^{a}
Total non-prey taxa	8.2 ± 3.4^{ab}	24.1 ± 17.6^{ab}	12.0 ± 4.5^{ab}	30.2 ± 12.5^{ab}	8.5 ± 4.2^{b}	79.8 ± 27.6^{a}
Total larvae	15.0 ± 4.0^{abc}	28.0 ± 21.1^{abc}	16.0 ± 4.5^{bc}	99.5 ± 66.8^{abc}	16.2 ± 6.0^{c}	124.3 ± 32.3^{a}

for subyearling Chinook salmon (Fig. 3). Approximately 60 % of the juvenile salmon piscivorous diets were derived from 5 fish prey: Pacific sand lance, rockfishes, smelts, sculpins, and northern anchovy (Fig. 3).

When comparing the larval composition of common salmon prey in the winter ichthyoplankton to that of juvenile salmon diets during early marine residence in the MDS plot (Fig. 4), there was a high degree spatial overlap with diets in May, but less in June. This was accounted for by the higher proportions of juvenile rockfishes in June diets than in the winter prey composition, particularly for coho salmon (Fig. 4).

In the MDS plot shown in Fig. 4, positive scores on Axis 1 represent May salmon diets, the community of winter larvae, and June salmon diets from cold regime years within our sampling period. Negative or neutral values on Axis 1 represent May diets during the warm regimes and almost all June diets, along with the winter ichthyoplankton community during the warm regime years of 2003–2005 and 2010 (Fig. 4). Overall, the differ-

ence between community of winter larvae and juvenile salmon diet was not statistically significant in May (MRPP, p = 0.64), but it was significant in June (MRPP, p = 0.0004). Rockfishes were identified as the taxon most responsible for significant differences
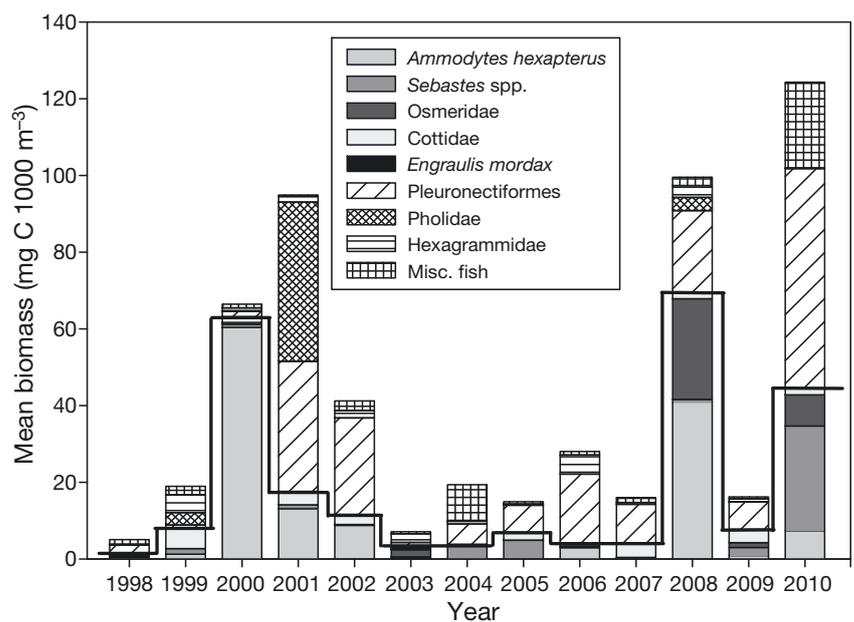

Fig. 2. Annual mean biomass (mg C 1000 m^{-3}) of the 5 important salmon prey taxa (below solid black line) and 4 other dominant larval fish taxa (above solid black line) collected during winter (January–March) in 1998–2010 along the Newport Hydrographic (NH) line
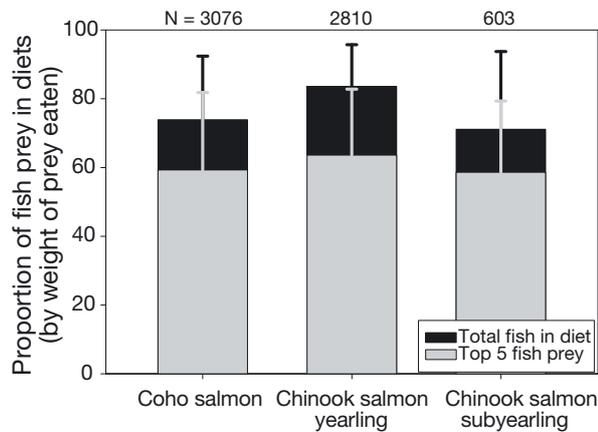
Fig. 3. Proportion of total prey eaten that were fish (black) and proportion of the top 5 most important prey taxa (grey) for coho, and Chinook salmon (yearling and subyearling). Number of salmon diets analyzed at top of bar plots

Table 4. Significant multiple regression models for the annually averaged (n = 13) biomass (mg C 1000 m^{-3}) of 5 important salmon prey larval fish taxa, total prey taxa, total non-prey taxa, and total larvae collected during this study in relation to the Year-1 annually averaged October–December basin-scale environmental variables: Multivariate El Niño-Southern Oscillation Index (MEI), Pacific Decadal Oscillation (PDO), Upwelling Index (UPI) (45° N, 125° W), and sea-surface temperature (SST) recorded from the National Oceanic and Atmospheric Administration's (NOAA) Stonewall Banks buoy located 20 nm west of Newport, Oregon (44.64° N, 124.50° W). Models with Osmeridae, *Sebastes* spp. and total non-prey taxa were not significant, and there was insufficient data to do an analysis for *Engraulis mordax*

Model	Adj. r^2	p
Ammodytes hexapterus = 0.10 − 1.48 × PDO	0.40	0.01
Cottidae = 0.24 − 0.51 × PDO	0.26	0.04
Total prey = 1.95 − 8.80 × PDO	0.36	0.02
Total larvae = 3.08 − 0.61 × PDO	0.29	0.03

between winter larvae and June diets (ISA, p = 0.0002), and was maximized in coho salmon. Pacific sand lance was also a significant June indicator species (p = 0.048) due its high values in the winter larval community relative to that in salmon diets.

Adult salmon return variability and winter ichthyoplankton biomass and community

Ichthyoplankton biomass and community composition of prey taxa during the winter before juvenile salmon entered the ocean was significantly and positively related with their ocean survival or adult returns of coho salmon 1 yr later and Chinook salmon 2 yr later (Fig. 5). Adult returns of spring Chinook salmon showed the strongest relationship with winter larval biomass (r^2 = 70.7, p = 0.0007; Fig. 5b) and community composition of prey (r^2 = 61.3, p = 0.003; Fig. 5e). There were 2 outlier years when more spring Chinook salmon returned than predicted (1998, 1999). When we included these outliers in the regression, the relationship between community type and diet was positive but not significant. When we excluded only 1999, the relationship was significant, but less variance was explained (biomass r^2 = 41.8, p = 0.01) or the relationship was not changed (community r^2 = 61.1, p = 0.002). Regressions between coho salmon survival rate and winter larval prey biomass and
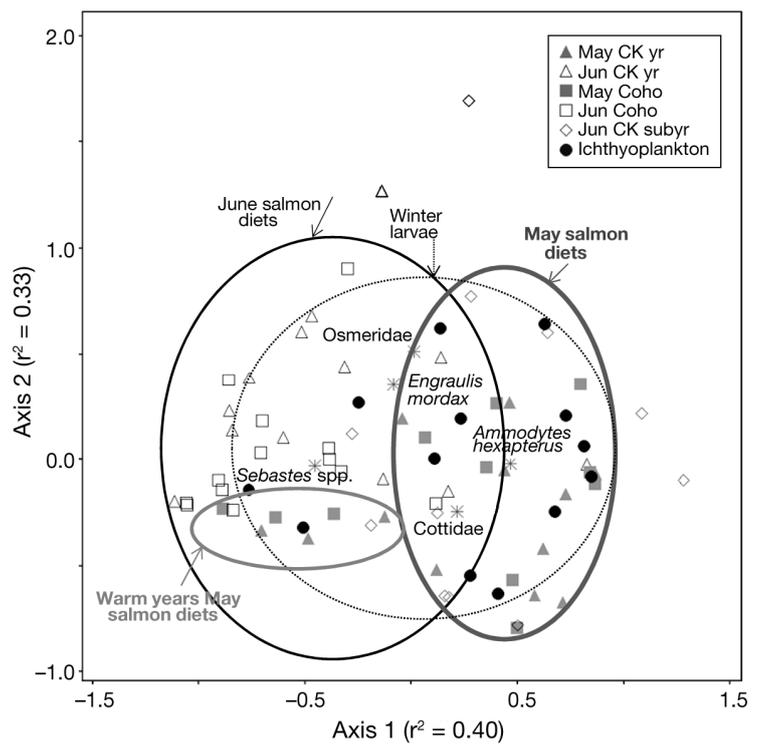

Fig. 4. Non-metric multidimensional scaling ordination (MDS) plot of the juvenile salmon diet community (proportion of the prey weight) and ichthyoplankton prey biomass (proportion of biomass). Salmon diet symbols (triangle, square and diamond) represent average monthly salmon diets (May or June) and salmon species. Winter larvae are represented by filled black circles which represent the average composition January–March for each year. Centroids of individual larval fish taxa are indicated with asterisks. Coho = coho salmon; CK yr = Chinook salmon yearling; CK subyr = Chinook salmon subyearling. Ellipses represent the spatial area of the winter larvae (dotted circle), May salmon diets (dark grey ellipse) and warm years May diets (grey ellipse), and June salmon diet (black ellipse). There are 2 outlier winter ichthyoplankton years, and 4 outlier years of June salmon diets that are not represented in the ellipses
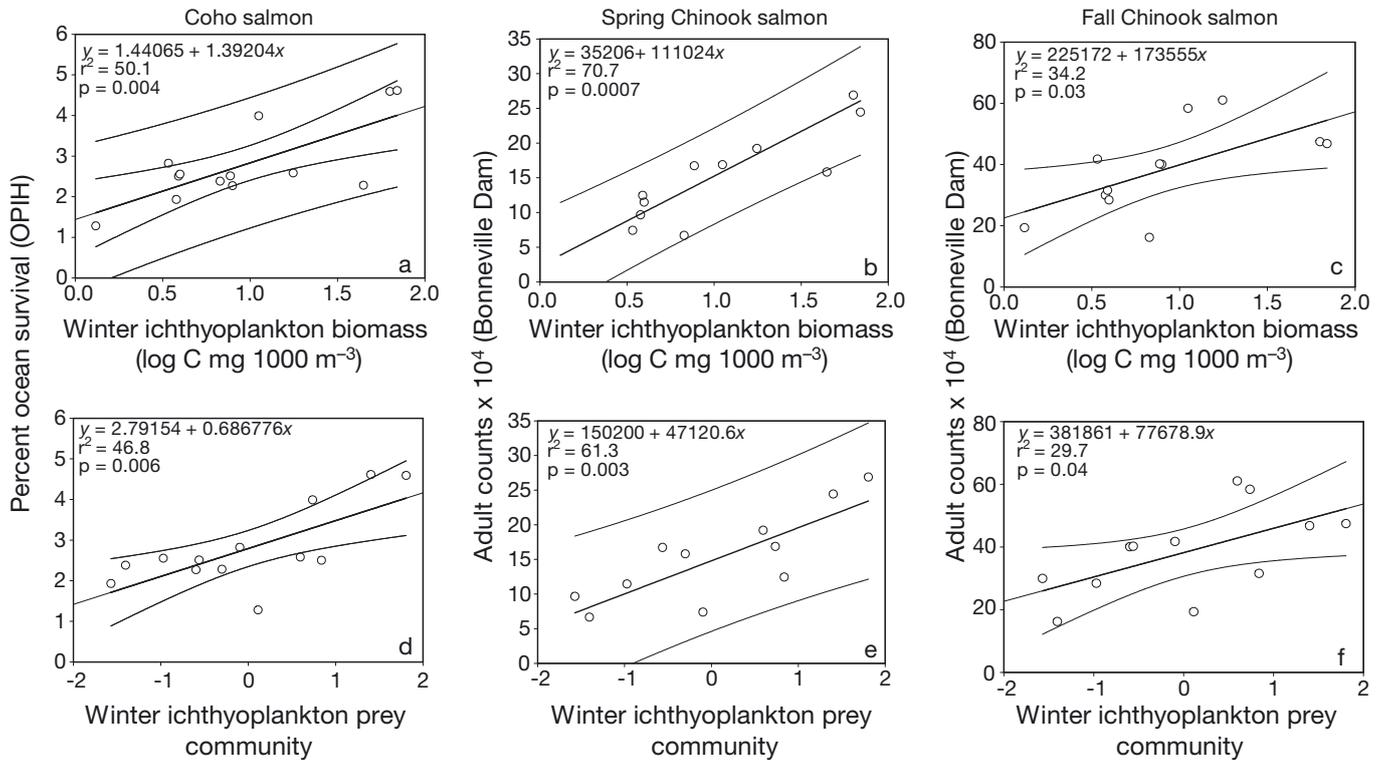
Fig. 5. Linear regressions of salmon ocean survival rate and biomass of winter ichthyoplankton prey taxa (top) and community of winter ichthyoplankton prey taxa Axis 1 multi-dimentional scaling (MDS) scores (bottom) for (a,d) coho (b,e) spring Chinook, and (c,f) and fall Chinook salmon. Each panel shows the regression line (inner line) and 95% confidence interval (outer 2 lines)

community were also significant, with about 50% of the variability in rate of return explained (Fig. 5a,d). Fall Chinook salmon also had a significant relationship with larval prey biomass and community, but with only about 30% of variability in returns explained (Fig. 5c,f). In contrast, regressing salmon ocean survival against the entire biomass of winter larvae, rather than just common prey fish, resulted in non-significant correlations or a reduction in variance explained.

DISCUSSION

Late fall–early winter oceanographic conditions in the NCC were related to the availability of winter food resources important to the marine survival of coho and Chinook salmon. Lower biomass of winter ichthyoplankton occurred during warmer ocean conditions. Lower salmon survival coincided with depressed larval biomass, also when the larval community in winter was increasingly composed of rockfish larvae. Conversely, high ichthyoplankton biomass and a larval fish community that was dominated by Pacific sand lance and sculpins were highly posi-

tively related with salmon marine survival which occurred under cooler ocean conditions. This relationship was reflected in the diets of juvenile salmon, such that winter-spawned rockfishes were increasingly consumed in May particularly during warmer years, and greater consumption of Pacific sand lance was observed in May and June diets during cooler years.

Previous studies have found enhanced growth or reproductive success of piscivores was related to ocean conditions during winter. In the California Current, Schroeder et al. (2009) indicated that productivity was enhanced even with modest upwelling in early winter and was followed by increased abundance of prey resources and earlier nesting phenology in seabirds. Additionally, rockfish growth and seabird reproductive success has been related to winter ocean conditions, particularly during February (Black et al. 2010). Logerwell et al. (2003) and Burke et al. (2013) observed significant relationships between juvenile salmon marine survival and ocean conditions during the winter prior to ocean entry. The link between biological performance measures and winter ocean conditions has not been limited to predators; winter ocean conditions have also been associ-

ated with the early life history stages of other fishes. Wilson et al. (2008) demonstrated that in winter-spawned fish, such as rockfishes and the sculpin *Scorpaenichthys marmoratus*, year-class strength is established early in the larval stage during winter and spring. There are several studies suggesting that winter oceanographic conditions during the larval stage of *Sebastes* spp. have the strongest relationships with recruitment (Larson et al. 1994, Ralston & Howard 1995, Laidig et al. 2007). The present study suggests a further connection between winter ichthyoplankton biomass, including core future food resources for juvenile salmon, and late fall/early winter ocean conditions.

The diets of May-caught juvenile salmon reflected winter larval taxa and their associations with cooler and warmer ocean conditions, but this relationship was reduced in the June salmon diets, especially for coho salmon. Diets of coho salmon in June had higher proportions of juvenile rockfishes in quantities not reflected in the winter larval community, where increases in rockfishes were seen specifically during warmer ocean conditions. June coho salmon consumed juvenile rockfishes during both cold and warm regime years, but coho salmon also had more offshore distribution patterns than Chinook salmon (Peterson et al. 2010), where catches of early stage rockfishes are generally found (Auth 2009). Chinook salmon consumed lower amounts of rockfish in general (Daly et al. 2012), with the amount they consumed increasing during warm regime years, a pattern that reflected the higher proportions of larval rockfishes in the winter larval community during these years.

Such a disparity for coho salmon could be the result of the large number of different species of *Sebastes* found in the NCC (n = ~40) (Love et al. 2002). Presently, most larval rockfishes cannot be distinguished to species based on meristic or pigmentation patterns. Variability among rockfish species may result from differences in spawn timing, location, and conditions, with peak larval abundance for each species occurring at different times of year. Thus, the species of *Sebastes* found in June coho salmon diets could be different from those found in the May diets, and these fishes may not have been adequately sampled during January–March surveys.

The prey community available to juvenile salmon in June may be more reflective of the transition from winter to summer upwelling conditions than of physical conditions that occurred months earlier. A low biomass of winter fish larvae during a warm regime year may be increased considerably by strong

upwelling in spring of larvae such as *Sebastes* spp., which are transported through passive advection enhanced by diel vertical migration to take advantage of selective Ekman transport (Auth et. al 2007). During spring and summer, these larvae tend to move from sub-surface waters in offshore rearing areas to more nearshore environments (Norcross & Shaw 1984, Auth et al. 2007, Auth 2009). Francis et al. (2012) found that zooplankton community structure and biotic interactions along the Newport Line were strongly affected by upwelling, especially during warm periods, and by advection during cooler periods. Advection of larvae and juveniles from offshore sub-surface areas would transport prey resources inshore via Eckman transport after the onset of spring upwelling, and this transport would also be dependent on whether the ocean conditions were warmer or cooler than average (Auth et al. 2007, Keister et al. 2011).

Using winter larval fish biomass as an indicator of the juvenile prey fish available the following spring may be problematic in some years for several reasons. There is the possibility of recruitment failure between the larval and juvenile stage, which can result from anomalous oceanographic conditions between these periods. This may have been the case in 2005, when large numbers of larval rockfishes were collected during winter surveys but juvenile rockfishes were found in below average abundances during the following summer (Brodeur et al. 2011b). Unusual atmospheric circulation patterns in 2005 may have led to a delayed spring transition, occurring in late July rather than in March or April, resulting in low productivity and anomalously high water temperatures during spring and early summer (Brodeur et al. 2006, Schwing et al. 2006, Barth et al. 2007). This may have led to fewer larvae surviving or a shift in their distribution off the shelf, potentially rendering them unavailable to juvenile salmon as prey. This delayed upwelling negatively affected larval fish growth and survival as well as seabird breeding success (Sydeman et al. 2006, Auth 2008, Takahashi et al. 2012). El Niño years may also be characterized by reduced or ineffective upwelling that has been shown to result in dramatic changes in the ichthyoplankton communities in the NCC (Brodeur et al. 1985, Doyle 1995, Lenarz et al. 1995).

The temporal mis-match in fish larval sampling and salmon prey fields the following summer may affect the degree to which the interannual survival of salmon relate to winter larval biomass. The most significant relationships between salmon survival and winter biomass were with the 2 salmon populations

that are typically in entering the ocean by May (coho and yearling Chinook salmon). Subyearling Chinook salmon are later migrants into the NCC (Weitkamp et al. 2012), and an index of larval prey biomass available later in the spring may improve the relationship between their ultimate survival and food resources.

There is also the potential for a spatial mis-match, as our ichthyoplankton samples were taken only from the NH line, which represents a small subset of the wider NCC region where most juvenile salmon are found (Peterson et al. 2010). However, a study comparing the copepod community from the NH line relative to the broader region of the NCC where we collected our juvenile salmon suggests that the copepod community was relatively homogenous over the region where our salmon sampling occurred (Lamb 2011). Winter ocean conditions in the NCC are typically downwelling with south–north water mass transport near-shore, yet we believe that the ichthyoplankton from the NH line represents the near-shore region along the entire NCC ecosystem. Larvae that are advected from the coastal areas in winter are replaced with a similar community, concentrations, and biomass from coastal waters south of the NH line. Doyle et al. (2002) examined the spring and early summer ichthyoplankton assemblages in the NCC from Washington to northern California and found substantial latitudinal coherence in the species assemblages, with most of the spatial variability related to cross-shelf differences. Additionally, Auth (2008) found that the ichthyoplankton community between southern Oregon and central Washington (43.00–47.00° N) in May 2004–2006 was similar in terms of concentration, distribution, and community structure, while Auth (2011) also found no significant north–south concentration pattern for total larvae collected in May–October 2004–2009 between south-central Oregon and southern Washington (44.00–46.67° N). Finally, the relationship between the larval community in this region and broad NCC basin-scale indices such as MEI, NOI, and PDO has been documented in several recent studies (Auth 2008, 2011, Brodeur et al. 2008, Auth et al. 2011).

A secondary spatial issue is that the method of net sampling the top 20 m at nighttime along the NH line was established for the collection of zooplankton and not for sampling ichthyoplankton. While there are fish larvae found at depths below 20 m, previous studies indicate that the larvae are primarily found in the upper 20 m of the water column (Auth & Brodeur 2006, Auth et al. 2007). Lastly, as fish larvae develop, their ability to detect nets and avoid capture increases (Shenker 1988, McGurk 1992, Brodeur et al. 2011a).

In cold regime years, 2008 for example, fish larvae were longer, and while the overall abundance of fish larvae was relatively low, the average size of larvae was larger than in warm regime years. Therefore, estimates of biomass based on plankton samples collected during cooler ocean conditions, when early larval growth was enhanced, may have been biased low.

Juvenile salmon are not entirely piscivorous, and consumption of invertebrate prey may be important to their growth and survival as well. Tanasichuk & Routledge (2011) found significant and strong correlations between the marine survival of sockeye salmon *Oncorhynchus nerka* and the biomass of specific invertebrate prey. In some years, significant proportions of juvenile coho and Chinook salmon diets are made up of adult euphausiids *Thyansoessa spinifera* and crab *Cancer* spp. megalopae (Brodeur et al. 2007, Daly et al. 2009). Earlier spring transition and the start of the summer upwelling season has been tied to increases in the coastal presence of euphausiids (Gómez-Gutiérrez et al. 2005) and crab and fish larvae (Miller & Shanks 2004) transported from offshore waters in the NCC. Transport of Dungeness crab *Cancer magister* megalopae into coastal waters is closely tied to timing of the NCC transition to spring conditions (Shanks & Roegner 2007). Earlier timing of the spring transition to upwelling conditions may hasten the transport of post-winter prey resources that would constitute the summer prey community available for juvenile salmon.

Several studies have also correlated higher salmon survival with an earlier spring transition (Logerwell et al. 2003, Scheuerell & Williams 2005). Conversely, a delayed spring transition to upwelling conditions has been associated with warmer ocean conditions (Barth et al. 2007), which may create a mismatch in timing between the presence of a summer prey community and juvenile salmon marine entry, as well as for later migrants into the NCC. For juvenile salmon, early marine growth is critical to avoiding size-selective mortality (Cross et al. 2009), and salmon that migrate to sea in early summer may depend on prey resources that originate during winter. This critical early growth may be limited during warm ocean conditions, not only by the lack of food resources associated with reduced biomass of important winter prey, but also by a delayed arrival of the summer prey community. Delays in the arrival timing of this summer prey resource, or in the transition from a winter to summer prey community, may result in a deficit in the food available to higher trophic levels, including salmon. A metric that combined measurement of

annual winter prey biomass with biomass available after the spring transition could potentially improve the predictive ability of prey biomass as an index of salmon marine survival.

In warmer ocean conditions, juvenile salmon were significantly smaller and in lower abundance than during colder ocean conditions (Daly et al. 2012), suggesting lower growth and recruitment success. During warmer ocean conditions, the food resources important to marine survival of juvenile salmon are not only reduced in abundance, but the quality of these resources may be diminished as well. Copepod samples taken along the NH line over many years (concurrent with our ichthyoplankton sampling) have identified distinct communities and biomass levels that vary in relation to cool vs. warm ocean regime years (Peterson 2009). Copepod communities present during cool ocean conditions are dominated by lipid-rich species and are characterized by high biomass. Thus, these communities represent higher quality in the food available to larval fish and other salmon prey (Hooff & Peterson 2006). The essential fatty acid composition of copepods also varies according to ocean conditions, with poor copepod feeding conditions leading to reduction in species that contain the essential fatty acids important to upper trophic levels (El-Sabaawi et al. 2009). In describing the lipid and fatty-acid quality of juvenile fish and invertebrate prey available to juvenile salmon, Daly et al. (2010) observed an apparent preference for prey with higher levels of essential fatty acids. However, the study was not able to address interannual variability of juvenile salmon prey quality, which can fluctuate substantially between cooler and warmer ocean conditions (Litzow et al. 2006, Litz et al. 2010).

Predictive models forecasting salmon adult returns are important to fishery and hatchery managers. Hatcheries release similar numbers of salmon juveniles each year, but these fish enter the ocean under variable food conditions. For juvenile salmon, ichthyoplankton biomass during the winter prior to ocean entry explains 34 to 85% of the variability in marine survival or adult returns. Burke et al. (2013) used a multivariate model with 31 environmental and biological processes to predict spring Chinook salmon stock specific adult return and the most important indicators were bottom-up processes including the winter ichthyoplankton data set. Most of the indicators used in the Burke et al. (2013) model relied on environmental or biological factors that are typically available or measured in late spring or summer after the hatchery salmon juveniles have been released.

However, the winter ichthyoplankton index is based on data collected only until the end of March and therefore can be calculated earlier in the year, potentially offering hatchery managers the ability to adjust their salmon release schedules. As such, managers could utilize winter ichthyoplankton data as a tool for timing the release of the hatchery salmon to coincide with ocean entry during optimal feeding conditions, i.e. early release when winter larvae production is high and after upwelling onset when winter ichthyoplankton production is low. Moreover, our results suggest that the restoration of endangered and threatened Pacific salmon stocks may depend to a surprising degree on non-commercially important salmon prey, such as smelts, sculpins, and particularly Pacific sand lance, for which little information on their early life stages is available.

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