

## Evidence that summer jellyfish blooms impact Pacific Northwest salmon production

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**Abstract.** Interannual variability in salmon (*Oncorhynchus* spp.) production in the northeast Pacific is understood to be driven by oceanographic variability and bottom-up processes affecting prey availability to juvenile salmon. Scyphozoan jellyfish have an important role in shaping the pathways of energy flow through pelagic food webs. While jellyfish obtain high production rates and biomasses as major consumers of zooplankton production, they have few predators and may divert plankton production away from higher trophic levels. Although jellyfish are planktivorous and juvenile coho (*O. kisutch*) and Chinook (*O. tshawytscha*) salmon are mainly piscivorous, they may be indirect competitors for plankton production. Ecosystem model simulations suggested that among all trophic interactions within the Pacific Northwest coastal food web, juvenile salmon are particularly sensitive to jellyfish blooms, and that salmon production will be suppressed in years of high summer jellyfish biomass. Pelagic surveys off Oregon and Washington (1999–2012) were used to examine the interannual relationship between salmon production and the dominant jellyfish species, the sea nettle *Chrysaora fuscescens*, off the Pacific Northwest coast. There was a significant, negative correlation between sea nettle biomass and the strength of adult coho and Chinook salmon returns to the Columbia River. Examination of spatial distributions across years showed a positive association between sea nettles and salmon. Within individual years, significant differences between the distribution of sea nettles and yearling coho and Chinook salmon generally occurred during cooler ocean summers, perhaps due to the greater expanse of optimal salmon habitat resulting from more upwelling. Whether the association is behavioral or a product of oceanographic processes, association enhances the opportunity for indirect competition. Examination of feeding incidence in September showed that salmon stomachs were less full at locations with higher sea nettle biomass.

**Key words:** Chinook salmon; *Chrysaora fuscescens*; coho salmon; Columbia River; competition; ecosystem model; food web; jellyfish; Northern California Current; *Oncorhynchus kisutch*; *Oncorhynchus tshawytscha*; sea nettles.

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### INTRODUCTION

With relatively stable numbers of hatchery salmon produced in the Pacific Northwest every year (Daly et al. 2012), fluctuations in the year-class strengths of coho (*Oncorhynchus kisutch*) and Chinook salmon (*O. tshawytscha*) are believed to be driven by ocean conditions and ecological

processes acting during the year of smolt entry to the ocean (Pearcy 1992, Beamish et al. 2004). Top-down predation and bottom-up resource limitation have both been recognized as pressures regulating juvenile salmon survival off the coasts of Oregon and Washington (Peterson and Schwing 2003, Emmett et al. 2006). Most of our understanding of salmon recruitment dynamics

has come from correlative studies of climatic and oceanographic proxies for ecosystem productivity and prey availability (e.g., Pearcy 1992, Mantua et al. 1997, Logerwell et al. 2003). However, complex and difficult to observe the factors affecting the efficiency of energy transfer through the food web may also be important for regulating juvenile salmon growth and survival. The efficiency of energy transfer from primary producers to juvenile salmon is a function of community composition, and the diets and physiological rates of the different living groups within the ecosystem.

By preying on fish eggs and larvae, jellyfish can directly reduce recruitment into fish populations (e.g., Purcell and Grover 1990, Kideys et al. 2005). Jellyfish also have several characteristics that place them in an influential position to restructure energy flow through pelagic food webs: high rates of growth and reproduction, broad planktivorous diets, and apparently few predators as adults (Condon et al. 2012, Robinson et al. 2014). When abundant, large scyphozoan jellyfish and small gelatinous zooplankton (e.g., ctenophores, salps, and larvaceans) are major consumers of zooplankton (Schneider and Behrends 1998, Brodeur et al. 2002, Suchman et al. 2008) and can divert a substantial portion of zooplankton production away from trophic pathways supporting fish production (Aydin et al. 2005, Lynam et al. 2006, Ruzicka et al. 2012). Consistent with this hypothesis (but also with possible anthropogenic forcing) is the observed inverse latitudinal relationship between the abundance of planktivorous fishes and gelatinous zooplankton within Puget Sound, Washington (Rice et al. 2012), and an inverse trend of increasing gelatinous zooplankton but decreasing planktivorous fish abundance over the past 40 yr (Greene et al. 2015).

The dominant jellyfish off the Pacific Northwest coast is the sea nettle, *Chrysaora fuscescens*. Sea nettle biomass is highly variable between years, but summer sea nettle blooms often represent a major portion of the pelagic biomass (Shenker 1984, Suchman et al. 2012) and are major consumers of zooplankton production (Ruzicka et al. 2007). Sea nettles and juvenile salmon overlap temporally and spatially (Brodeur et al. 2008, Reese and Brodeur 2015); there is an opportunity for trophic interaction. However, there is very little overlap in juvenile salmon and sea nettle diets. Juvenile coho and Chinook salmon are

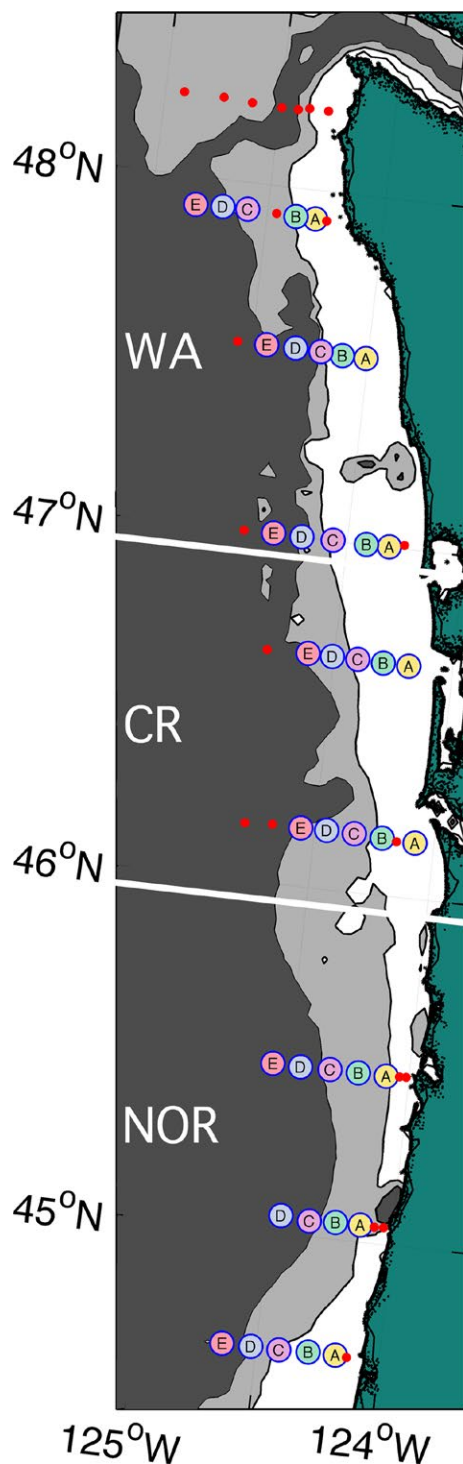
primarily piscivorous (Daly et al. 2009), whereas sea nettles are highly planktivorous, occupying a full trophic level below the juvenile salmon (Brodeur et al. 2008, Suchman et al. 2008). Our goal was to see how sea nettles could impact salmon production, despite low diet overlap, via direct and indirect interactions within the food web.

We expected jellyfish to be an important food web structuring agent in the Pacific Northwest coastal ecosystem given their potential to exert heavy predation pressure upon the zooplankton community. Using a combination of pelagic survey and salmon production time-series observations, observations of juvenile salmon feeding incidence, and ecosystem model simulations, we studied the potential and the realized impact of jellyfish blooms on Pacific Northwest salmon. We evaluated the temporal and spatial co-occurrence of sea nettles, yearling coho, sub-yearling Chinook, and yearling Chinook salmon using pelagic survey observations along the Oregon and Washington coasts. We analyzed stomach contents for evidence of reduced feeding intensity among juvenile salmon in locations where sea nettle biomass was high. We used ecosystem model simulations to estimate the effects of sea nettle blooms on energy flow patterns throughout the shelf food web and upon juvenile salmon in particular. Finally, we used pelagic survey time series and observed adult freshwater returns to evaluate the relation between sea nettle biomass during the season when salmon smolts enter the ocean and subsequent salmon production.

## MATERIALS AND METHODS

### *Ocean time-series observations of sea nettles and juvenile salmon*

Seasonal sea nettle (*Chrysaora fuscescens*) and juvenile salmon abundances off Washington and northern Oregon were obtained from pelagic trawl surveys conducted by NOAA and Oregon State University (OSU). Daytime surveys sampled the upper 20 m of the water column using an 30 m wide Nordic 264 Rope Trawl at predetermined stations along eight cross-shelf transects between 44.6 ° and 48.3 °N during May, June, and September each year from 1999 to 2012 (Brodeur et al. 2005, Suchman et al. 2012)



(Fig. 1). Jellyfish were identified to species and counted in small catches or systematically subsampled and expanded to total catch using methods described in Suchman et al. (2012). Live

Fig. 1. Eight transects sampled by the Bonneville Power Administration salmon surveys 1999–2012. Stations are labeled according to distance from coastline and latitude zone: “A” (7–11 km from coastline), “B” (17–18 km), “C” (26–31 km), “D” (35–41 km), “E” (43–50 km), “WA” (Washington 47°–48°N), “CR” (Columbia River 46°–47°N), and “NOR” (northern Oregon 44.5°–45.5°N). Red dots represent stations not consistently visited between years and seasons and not used in spatial analyses.

weights of individual jellyfish were estimated from bell diameters ( $BD$ ) using Shenker’s (1985) empirical relation for *C. fuscescens* off Oregon: wet weight (mg) =  $0.06844 \cdot BD \text{ (mm)}^{2.9702}$ . Regional mean sea nettle biomasses and juvenile salmon population densities were estimated using the method of Pennington (1996) for log-normally distributed survey data that includes zero-catch trawls.

Juvenile salmon caught during each survey were identified to species and classified by life history, specifically, their size and age when they enter the ocean from freshwater. Yearling juveniles have spent one winter in freshwater before entering the ocean. Subyearling juveniles have not overwintered in freshwater and are smaller than yearlings at ocean entry. Juvenile Chinook salmon from survey trawls were classified as subyearling or yearling according to their fork length at the time of capture: subyearling (May: <120 mm, June: <140 mm, September: <250 mm); yearling (May: 120–250 mm, June: 140–280 mm, September: 250–400 mm). Chinook salmon life history classifications were based on Percy and Fisher (1990). All juvenile coho salmon (*O. kisutch*), a mix of Columbia River Basin and coastal river stocks (Teel et al. 2003), were assumed to be yearlings based on scale-aging analyses of adults returning to the Columbia River (e.g., CRITFC 2004, 2013).

Abundance (salmon) and biomass (sea nettles) within individual pelagic trawls were represented as the CPUE, the count or biomass live weight (t) caught per kilometer trawled. Spatial distributions were characterized north-to-south by the fraction of the cruise total abundance and biomass observed along each of eight latitudinal transects. Cruise totals were the sums of the CPUEs of all hauls within a particular

season (June or September) and year. Spatial distributions across the shelf (east-to-west) were characterized by the fraction of the cruise total abundance and biomass observed within each of five cross-shelf bands from the coastline to the upper continental slope: A (2–11 km from coastline), B (13–22 km), C (26–35 km), D (37–48 km), and E (>48 km) (Fig. 1). Latitudinal distributions were characterized by the fraction of the cruise total abundance and biomass observed within each of three north-south zones: Washington (three transects between 47 ° and 48 °N), Columbia River mouth (two transects between 46 ° and 47 °N), and northern Oregon (three transects between 44.5 ° and 45.5 °N). This trawl-distribution strategy provided nearly complete sampling of the inner and mid shelf bands (A, B, and C) in June and September of each year from 1999 to 2012. Only band A within the Columbia River mouth zone was missed in September 2000. Outer shelf band D was not sampled off northern Oregon, only 1 yr in June (2000) and 3 yr in September (2007, 2010, 2011). Outermost band E was less well surveyed. In the Washington and Columbia River mouth zones, band E was surveyed in June of every year except 2005. In September, band E was surveyed 8 yr off Washington and 6 yr in Columbia River mouth zone. Off northern Oregon, outermost band E was surveyed only twice in June and never surveyed in September.

#### *Association between juvenile salmon and sea nettles*

We performed three investigations of the spatial relationships between sea nettles and juvenile salmon. First, the spatial overlap between sea nettles and juvenile salmon was estimated as the proportion of stations surveyed each year along the eight cross-shelf transects off Washington and Oregon where both sea nettles and juvenile salmon were present together. We used a Fisher's exact test (Fisher 1954) to determine the significance of each overlap metric. The null hypothesis that sea nettles and juvenile salmon were independently distributed among stations was tested against the alternate hypothesis that salmon and sea nettles co-occurred at more stations than expected by chance (left-tailed probability).

A Syrjala test (Syrjala 1996) was used to test null hypothesis that the spatial distributions of

juvenile salmon and sea nettles were independent. The Syrjala test is nonparametric. Unlike the Fisher exact test, it accounts for spatial differences in population densities, but it is independent of the relative size of the two populations. The test statistic,  $\Psi$ , is calculated as the square of the difference between the cumulative distributions of two populations, summed over all sampled stations. Cumulative distributions are calculated relative to each of the four geographic corners of the survey region, and the mean value of  $\Psi$  is used as the test statistic. The significance of the observed  $\Psi$  is defined relative to the distribution of 9999 random permutations of both populations redistributed independently across survey stations. For this analysis, we used the *Syrjala* function in the *ecspa* package (De la Cruz 2008) of the R programming language (R Development Core Team 2013, <http://cran.r-project.org/web/packages/ecspa/index.html>).

Finally, to determine whether the cross-shelf distributions of juvenile salmon and sea nettles were related, we calculated interannual correlations between the fraction of the sea nettle biomass observed inshore of 11 km of the coastline (cross-shelf band A) and the fraction of juvenile salmon observed over the inner-to-mid shelf zone within 22 km from the coastline (cross-shelf bands A+B). The significance of each time-series correlation was calculated correcting for autocorrelation (Pyper and Peterman 1998).

#### *Relation between juvenile salmon feeding intensity and local sea nettle biomass*

A subsample of up to 30 juveniles representing both salmon species and life history strategies were analyzed from each haul for stomach fullness. An Index of Feeding Intensity (IFI) was calculated for each individual as described by Daly et al. (2009):

$$\text{IFI} = \frac{(\text{stomach content weight})}{(\text{total fish weight} - \text{stomach content weight})} \quad (1)$$

The relationship between juvenile salmon feeding intensity and sea nettle biomass was examined by comparing the IFI values among stations grouped within sea nettle biomass quartiles. Sea nettle biomasses within individual trawls (CPUE, tons wet weight per km trawled)



were grouped by quartile within each season but all years were pooled (June: 25% quartile  $<0.03$  t/km<sup>2</sup>, 50% quartile 0.03–0.25 t/km<sup>2</sup>, median and greater  $>0.25$  t/km<sup>2</sup>. September: 25% quartile  $<0.06$  t/km<sup>2</sup>, 50% quartile 0.06–0.55 t/km<sup>2</sup>, median and greater  $>0.55$  t/km<sup>2</sup>). Statistical differences between salmon IFI and jellyfish biomass quartiles were evaluated using the nonparametric Kruskal–Wallis test for each salmon species and life history and each summer survey (June and September). Significance was set at  $P < 0.05$ .

#### *Ecosystem model metrics and simulations*

We used the Northern California Current end-to-end ecosystem model and ECOTRAN analysis methods described by Steele and Ruzicka (2011) and Ruzicka et al. (2012) to investigate the role of sea nettle blooms in the coastal ecosystem in terms of energy flow and their impact upon juvenile salmon. The model describes the trophic connections between phytoplankton (two size classes), zooplankton (10 functional groups), gelatinous zooplankton (three groups), pelagic fishes and squids (30 groups), benthic invertebrates (11 groups), demersal fishes (seven groups), seabirds (eight groups), marine mammals (seven groups), fisheries (17 gear groups), eggs (two pools), detritus (three pools), and nutrients (three pools). There are 1663 defined trophic linkages. The currency of production and “energy” flow across trophic linkages is the rate of live weight biomass gain or loss (t·km<sup>-2</sup>·yr<sup>-1</sup>). The primary data set used to derive the summer composition of the pelagic zooplankton, fish, and seabird communities were the series of NOAA and Oregon State University pelagic surveys. Jellyfish diets were obtained from Suchman et al. (2008), and juvenile salmon diets were obtained from Daly et al. (2009). Jellyfish biomass was rescaled by a factor of 0.13 so that a unit of jellyfish biomass had approximately the same water content as that of fish: dry weight:wet weight of fish = 0.3 and dry weight:wet weight of large jellyfish = 0.04 (derived from tables in Shenker 1985). Further details about the data sets and literature used to construct the model are described in Ruzicka et al. (2007, 2012). Parameter definitions and values are provided as Supplement S1.

In this study, we performed three types of model analyses. First, we estimated the demands of jellyfishes (sea nettles), juvenile salmon, and other key pelagic groups upon total ecosystem production (the “footprint”) and the contribution of these groups to total consumer production in the ecosystem (the “reach”) (Ruzicka et al. 2012). Second, we conducted a systematic sensitivity analysis to identify the living groups and the trophic linkages having the greatest effect on energy availability to juvenile salmon. Finally, we estimated the consequent changes in jellyfish biomass, simulating high sea nettle biomass years (i.e., “blooms”), had upon the entire ecosystem and upon juvenile salmon in particular.

Sensitivities to changes in food web structure and the effects of the jellyfish bloom simulation are expressed as the percent change in a group’s production ( $\Delta P$ ) in the bloom-scenario model ( $P_{\text{scen}}$ ) relative to the group’s production in the base model ( $P_{\text{base}}$ ):

$$\Delta P = 100 \cdot (P_{\text{scen}} - P_{\text{base}}) / P_{\text{base}} \quad (2)$$

Both analyses were constructed in similar ways, using similar assumptions. For the food web structure sensitivity analysis, the rate of energy flow through each trophic linkage was sequentially and individually increased by 25%. For the jellyfish bloom simulation, sea nettle biomass and consumption rate was increased by 1 standard deviation (SD) over the 1999–2012 summer mean biomass from the NOAA - OSU pelagic surveys used to define the base model. One standard deviation over the mean observed summer biomass represents a 1.97-fold increase. For both sensitivity and bloom simulation analyses, changes in the predation pressure upon any prey group caused by a forced change in the energy demand of a particular consumer group was offset by an opposite change in predation pressure by all other groups competing for that prey (i.e., total grazing or predation pressure upon the prey group was unchanged). Change in energy flow to each competing consumer was proportional to its original relative importance as a consumer. Also, food webs modified during each analysis remained mass-balanced; total predation pressure upon any group was not allowed to exceed its production rate. A forced increase in the predation of any

prey group by the modified consumer group(s) was limited to the total consumer demand upon that group (although a large increase in the modified consumer group could completely exclude competitors for a particular prey group). Responses in the sensitivity and bloom simulation analyses were expressed as changes to group production rates relative to production rates in the original base model.

The propagation of variability and parameter uncertainty through the model was estimated using Monte Carlo analysis (Ruzicka et al. 2012). Alternate models were generated by randomly drawing new parameter sets from predefined normal error distributions about each model parameter (biomass, physiological parameters, fishery landing and discards, and diet; see Supplement S1). Jellyfish bloom simulations were simultaneously performed on 1000 alternate mass-balanced descriptions of the food web, and all model metrics and simulations are presented with associated uncertainty ( $\pm 1$  SD of all alternate food webs).

#### *Relation between salmon production and sea nettle biomass*

The relation between salmon production and sea nettle biomass was examined by calculating the interannual correlation between metrics of salmon production and the regional mean sea nettle biomass during the year of smolt entry to the ocean. Two classes of salmon production metrics were used: adult returns to freshwater and estimates of juvenile survival in the ocean (details below). As most jellyfish and juvenile salmon were observed along transects from the Columbia River mouth and northward (see Fig. 2), the analyses of relationships between sea nettle biomass and salmon production were based upon sea nettle biomass estimates off the Washington coast and excluded trawls off northern Oregon (see Fig. 4). Sea nettle biomasses were natural log transformed for these analyses, and each season (May, June, and September) was considered separately. The significance of each time-series correlation was calculated correcting for autocorrelation

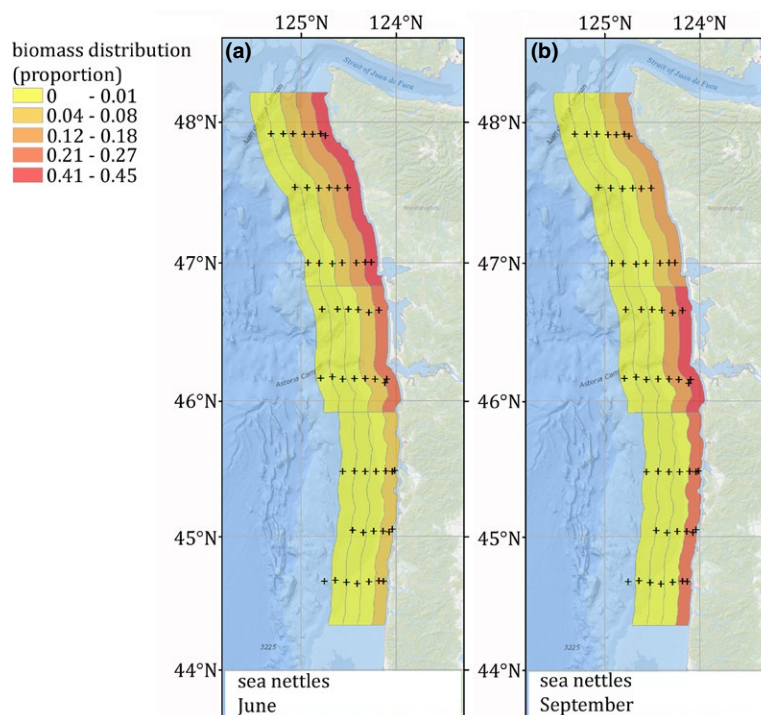


Fig. 2. The mean interannual distribution of sea nettle biomass in (a) June and (b) September as the proportion of total biomass observed during each survey.

following the recommendations of Pyper and Peterman (1998).

The indices of salmon production used included censuses of adult returns to Bonneville dam, adult coho salmon returns to public hatcheries (Oregon Production Index Hatchery, OPIH), adult wild coho salmon returns to coastal freshwater systems (Oregon Coast Natural, OCN), and annual numbers of adult coho and Chinook salmon returning to the Columbia River at Bonneville Dam (river km 235) available from the Columbia River DART data server, [www.cbr.washington.edu/dart/adult\\_annual.html](http://www.cbr.washington.edu/dart/adult_annual.html). Chinook salmon were classified into three stocks defined by their arrival date at Bonneville dam: spring Chinook salmon (March 15–May 31), summer Chinook salmon (June 1–July 31), and fall Chinook salmon (August 1–November 15) (Fish Passage Center, [http://www.fpc.org/documents/metadata/FPC\\_Adult\\_Metadata.html](http://www.fpc.org/documents/metadata/FPC_Adult_Metadata.html)). Chinook salmon returns to Bonneville dam were further classified by smolt life history (subyearling or yearling) and the number of winters spent at sea before returning to the Columbia River. These classifications were extrapolated from annual retrospective scale-aging observations made by the Columbia River Inter-Tribal Fish Commission of the returning adults (e.g., CRITFC 2004, 2013). The majority of spring Chinook salmon uses the yearling life history strategy and the majority of fall Chinook salmon produces subyearling offspring (see Table 6).

Oregon Production Index Hatchery coho salmon stocks are produced predominantly by public hatcheries along the Columbia River, but also include a smaller number of adults produced by public hatcheries along Oregon coastal rivers and within the Klamath River Basin which empties off Northern California. Annual adult OPIH coho salmon returns are reported by the Pacific Fisheries Management Council (PFMC 2013). OCN coho salmon stocks are wild salmon produced in Oregon coastal rivers and lakes north of Cape Blanco. Annual adult OCN coho salmon returns are reported by the Oregon Department of Fish and Wildlife (ODFW 2013).

Indices of juvenile salmon survival were available for OPIH coho salmon and for Snake River wild spring and summer Chinook salmon and wild steelhead. Survival of juvenile OPIH coho salmon was estimated as the ratio of hatchery

smolt release numbers to hatchery adult freshwater returns in the year following smolt entry into the ocean. Smolt production numbers and adult terminal run size are reported by the PFMC (2013). Estimated ocean survival of juvenile Snake River wild spring and summer Chinook salmon and wild steelhead were obtained from a survival study of PIT-tagged smolts (Fish Passage Center 2013).

## RESULTS

### *Ocean time-series observations and spatial associations of sea nettles and juvenile salmon*

*Spatial associations of sea nettles and juvenile salmon.*—The mean June and September interannual spatial distributions of sea nettle biomass and juvenile salmon abundance densities are shown in Figs. 2 and 3. In June and September of most years, >75% of the sea nettle biomass was found from the Columbia River mouth (46°N) and north. The apparent September concentration of sea nettles in northern Oregon can be attributed to 2 yr, 2000 and 2008, both of which had low overall sea nettle biomass throughout the entire survey region. In June and September, yearling coho and yearling Chinook salmon were most abundant off the northern Washington coast (north of 47°N). Subyearling Chinook salmon were also most abundant off northern Washington in June but were more evenly distributed along the entire Washington and northern Oregon coast in September. The spatial overlap metrics (Table 1) and Syrjala tests (Table 2) show that yearling coho salmon were usually distributed independently from sea nettles with little co-occurrence at individual stations and little spatial overlap. Sea nettles were concentrated within 22 km of the coastline in June and September of all survey years, while yearling coho salmon were more broadly distributed across the shelf (Figs. 2 and 3). As with sea nettles, subyearling and yearling Chinook salmon were most abundant inshore in June and in September. Both yearling and subyearling Chinook salmon significantly overlapped with sea nettles during more survey years than did yearling coho. Subyearling Chinook salmon had the higher number of years with significant overlap in June and September using both spatial analyses (Tables 1 and 2).



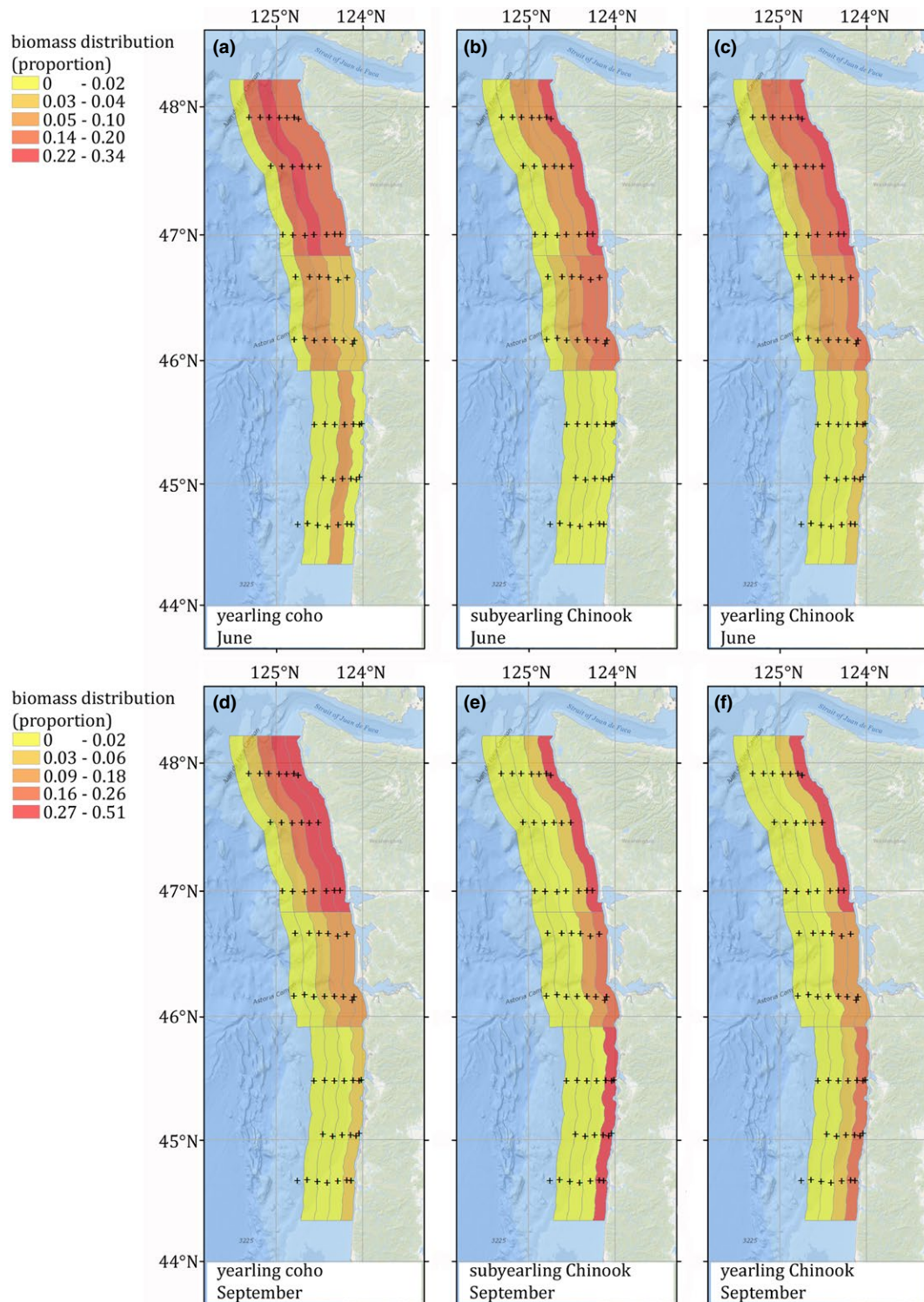


Fig. 3. The mean interannual distributions of juvenile salmon in June: (a) yearling coho, (b) subyearling Chinook, and (c) yearling Chinook; and the mean interannual distributions of juvenile salmon in September: (d) yearling coho, (e) subyearling Chinook, and (f) yearling Chinook as the proportion of total population observed during each survey.



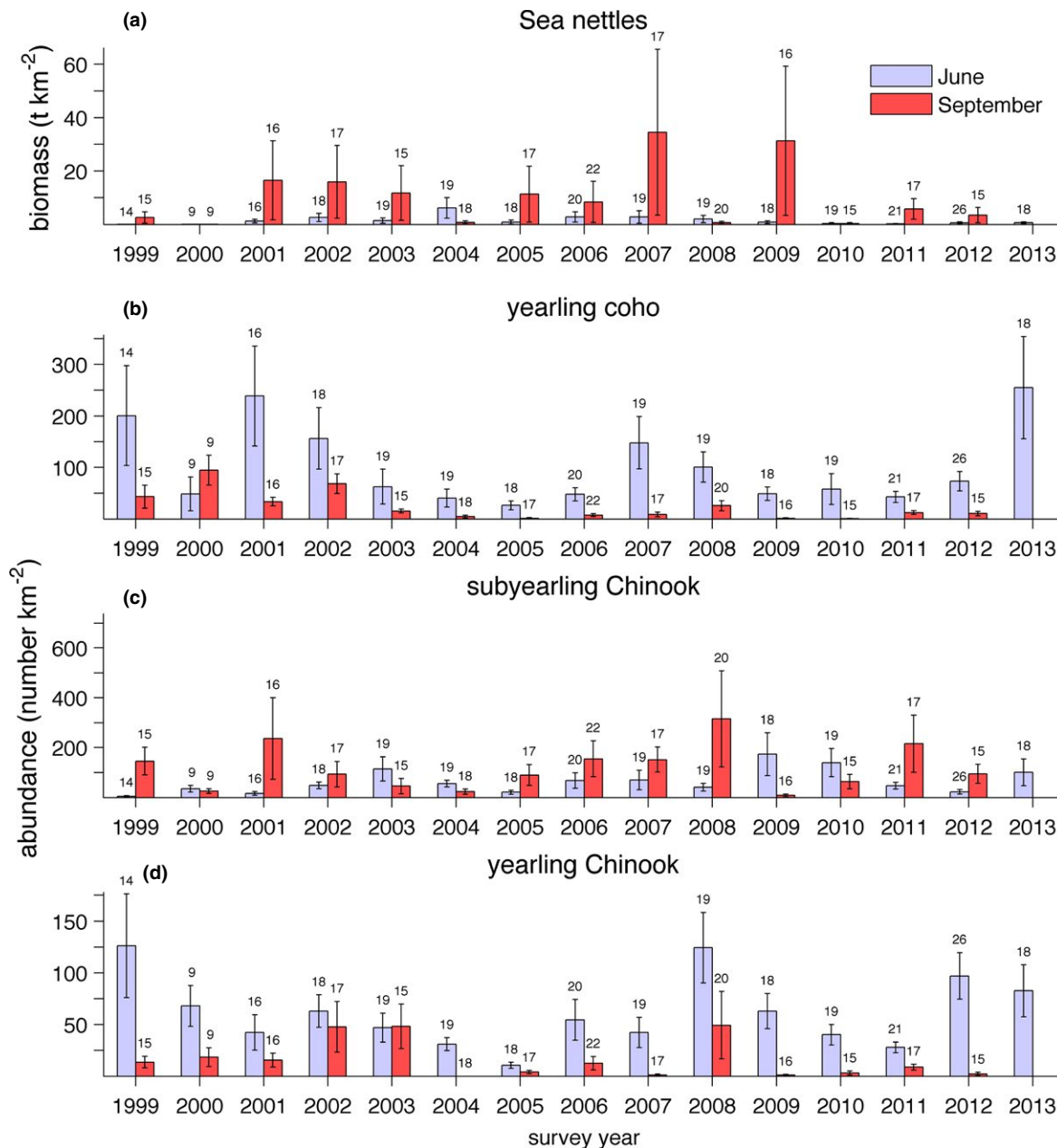


Fig. 4. Time series of the mean observed June and September sea nettle biomass (a) and juvenile salmon abundances (b, c, and d) along the Washington coast, from the mouth of the Columbia River northward (46°–48°N) and within the 100 m isobath. Error bars represent  $\pm 1$  SD about the mean. Numbers above the bars are the number of trawls. There were no observations made in September 2013.

Interannual changes in the cross-shelf distribution of subyearling Chinook salmon offshore (>26 km) were correlated with the fraction of the sea nettle biomass concentrated inshore (<11 km, Table 3). In years when sea nettles were

concentrated inshore, subyearling Chinook were also concentrated inshore. The cross-shelf distributions of neither yearling coho nor yearling Chinook salmon were related to the cross-shelf distribution of sea nettles.

Table 1. Spatial overlap between sea nettles and juvenile salmon as fraction of stations where juvenile salmon and sea nettles co-occur.

Year	June				September			
	Yearling coho	Subyearling Chinook	Yearling Chinook	n	Yearling coho	Subyearling Chinook	Yearling Chinook	n
1999	0.22	0.04	<b>0.27*</b>	45	0.07	<b>0.19**</b>	0.09	43
2000	0.18	0.21	0.29	28	0.11	0.11	<b>0.14*</b>	28
2001	0.31	0.08	0.17	48	<b>0.32**</b>	<b>0.30***</b>	<b>0.18**</b>	44
2002	<b>0.53***</b>	<b>0.38***</b>	<b>0.51***</b>	53	0.21	<b>0.33**</b>	0.23	48
2003	0.25	0.20	0.27	59	0.24	0.16	0.24	38
2004	0.30	<b>0.32**</b>	<b>0.45***</b>	56	0.10	<b>0.24**</b>	0.04	49
2005	0.21	0.12	0.17	42	0.00	<b>0.19**</b>	0.07	43
2006	0.23	<b>0.30***</b>	<b>0.23*</b>	60	0.06	<b>0.23**</b>	0.06	52
2007	0.20	0.11	0.22	45	0.05	<b>0.19*</b>	0.05	37
2008	0.24	0.24	0.36	45	<b>0.15*</b>	<b>0.25**</b>	<b>0.17**</b>	48
2009	0.26	<b>0.28**</b>	0.26	43	0.02	<b>0.13*</b>	0.04	47
2010	0.21	<b>0.29*</b>	0.35	48	0.05	<b>0.29***</b>	<b>0.10*</b>	42
2011	0.28	<b>0.26*</b>	<b>0.32**</b>	47	0.20	<b>0.35***</b>	0.28	40
2012	0.23	0.14	0.28	43	0.14	<b>0.28***</b>	0.05	43
2013	0.35	<b>0.28***</b>	<b>0.35**</b>	43	...	...	...	0
Percent of years where salmon significantly overlap with sea nettles	7%	47%	40%	15	14%	86%	29%	14

Notes: Probability values are from left-tailed Fisher's exact tests that the observed overlap was greater than expected by chance. Significant values are bold. Ellipses represent periods with no observations (i.e., September 2013).

\*  $P < 0.05$ .

\*\*  $P < 0.01$ .

\*\*\*  $P < 0.001$ .

*Sea nettle and juvenile salmon biomass time-series.*—The June and September sea nettle biomass time-series along the Washington coast, from the mouth of the Columbia River northward ( $46^{\circ}$ – $48^{\circ}$  N) and within the 100 m isobath, are shown in Fig. 4 (top panel). The sea nettle biomass was usually an order of magnitude higher in September than in June and varied substantially between years. Sea nettle biomasses in September 2007 and 2009 were particularly large. The June and September juvenile salmon abundance time series within the same region are shown in Fig. 4 (lower three panels). All three juvenile salmon groups were encountered in June and September. Yearling coho and Chinook salmon were most abundant in June, while subyearling Chinook were most abundant in September, in most years. All time-series data are shown with station standard deviations (SD) for each seasonal survey.

#### *Relation between juvenile salmon feeding intensity and local sea nettle biomass*

The relation between juvenile salmon feeding intensity (IFI) and sea nettle biomass was

examined by comparing IFI values among stations grouped by sea nettle biomass quartiles, all years pooled. In September, yearling coho, subyearling Chinook, and yearling Chinook salmon stomachs were all significantly more full at stations with low sea nettle biomass (Fig. 5; Kruskal–Wallis test,  $P < 0.05$ ). At stations where sea nettles were absent or rare (the lower 25% biomass quartile), juvenile salmon had the highest IFI values. However, juvenile salmon caught at stations where the sea nettle biomass was above the median did not necessarily show the lowest IFI values. The relationship between sea nettle biomass and feeding intensity in June, when sea nettle biomass was much lower, was not as clear as that in September. Among yearling coho salmon, IFI values were lower at stations with higher June sea nettle biomasses, but there was no relationship for subyearling or yearling Chinook salmon. IFI data are shown with standard errors (SE) associated with each quartile grouping.

In order to consider the possibility that differences in IFI may be due to differences in cross-shelf distribution between juvenile salmon and

Table 2. Probability values from Syrjala tests (Syrjala 1996) of the null hypothesis that spatial distributions of juvenile salmon and sea nettles in individual trawls were independent.

Year	June				September			
	Yearling coho	Subyearling Chinook	Yearling Chinook	n	Yearling coho	Subyearling Chinook	Yearling Chinook	n
1999	0.490	<b>0.005**</b>	<b>0.032*</b>	45	0.157	<b>0.005**</b>	0.125	43
2000	<b>0.001**</b>	0.072	<b>0.001**</b>	28	<b>0.013*</b>	0.694	0.258	28
2001	<b>0.046*</b>	0.844	<b>0.028*</b>	48	<b>0.006**</b>	<b>0.004**</b>	<b>0.007**</b>	44
2002	<b>0.041*</b>	0.687	0.093	53	<b>0.001**</b>	0.362	<b>0.006**</b>	48
2003	<b>0.001**</b>	0.217	<b>0.001**</b>	59	<b>0.001**</b>	0.519	<b>0.008**</b>	38
2004	0.110	0.693	0.191	56	0.586	0.448	<b>0.020*</b>	49
2005	0.131	0.235	0.280	42	...	0.176	0.430	43
2006	0.080	0.204	0.101	60	<b>0.018*</b>	0.111	0.110	52
2007	<b>0.002**</b>	0.169	0.083	45	0.220	0.326	0.346	37
2008	<b>0.006**</b>	<b>0.001**</b>	<b>0.001**</b>	45	<b>0.025*</b>	0.292	0.109	48
2009	<b>0.001**</b>	0.369	<b>0.011*</b>	43	0.268	0.289	0.942	47
2010	<b>0.003**</b>	<b>0.006**</b>	<b>0.002**</b>	48	0.529	0.482	0.326	42
2011	<b>0.002**</b>	0.435	0.074	47	<b>0.001**</b>	0.077	<b>0.043*</b>	40
2012	<b>0.043*</b>	0.413	0.065	43	0.217	0.527	0.461	43
2013	<b>0.036*</b>	0.172	<b>0.034*</b>	43	...	...	...	0
Percent of years where salmon overlap sea nettles (spatial distributions NOT significantly different)	27%	80%	47%	15	46%	86%	64%	14

Notes: Significant values are bold. Ellipses represent years with no observations (i.e., September 2013) or periods where the Syrjala test was not run because a target group was not encountered during the survey (i.e., no yearling coho salmon were encountered in September 2005).

\*  $P < 0.05$ .

\*\*  $P < 0.01$ .

\*\*\*  $P < 0.001$ .

sea nettles, we repeated the IFI analysis for trawls restricted to the inshore cross-shelf bands A, B, and A+B (see Fig. 1). In September, the subyearling Chinook salmon IFI remained significantly higher at low sea nettle biomass stations (25% quartile) when data was restricted to band A ( $P < 0.0001$ ), band B ( $P = 0.002$ ), or to bands A+B ( $P < 0.0001$ ). The yearling Chinook salmon IFI in September remained significantly related to sea nettle biomass when the data were restricted to bands A+B ( $P = 0.025$ ), but was not significant when the data were further restricted to band

A ( $P = 0.7$ ) or to band B ( $P = 0.06$ ). In June, the subyearling and yearling Chinook salmon IFI remained unrelated to sea nettle biomass when the data were subdivided into cross-shelf bands. For yearling coho salmon, there was no significant relationship in June or in September when the data were subdivided by cross-shelf band.

#### Ecosystem model metrics and simulations

*Large-scale pattern of energy flow through the food web.*—Figure 6 shows the percentage of total ecosystem production required to support sea

Table 3. Interannual correlations (r-values) between the fraction of the sea nettle biomass observed inshore of 11 km off the coastline (cross-shelf band A) and the fraction of juvenile salmon observed over the inner-to-mid shelf zone within 22 from the coastline (cross-shelf bands A+B).

Salmon distribution	June				September			
	Yearling coho	Subyearling Chinook	Yearling Chinook	n	Yearling coho	Subyearling Chinook	Yearling Chinook	n
Bands A+B	0.22	0.46	0.25	15	0.08	<b>0.78**</b>	0.17	14

Notes: Probability values are two-tailed and corrected for autocorrelation following Pyper and Peterman (1998). Significant values are bold.

\*\* $P < 0.01$ .



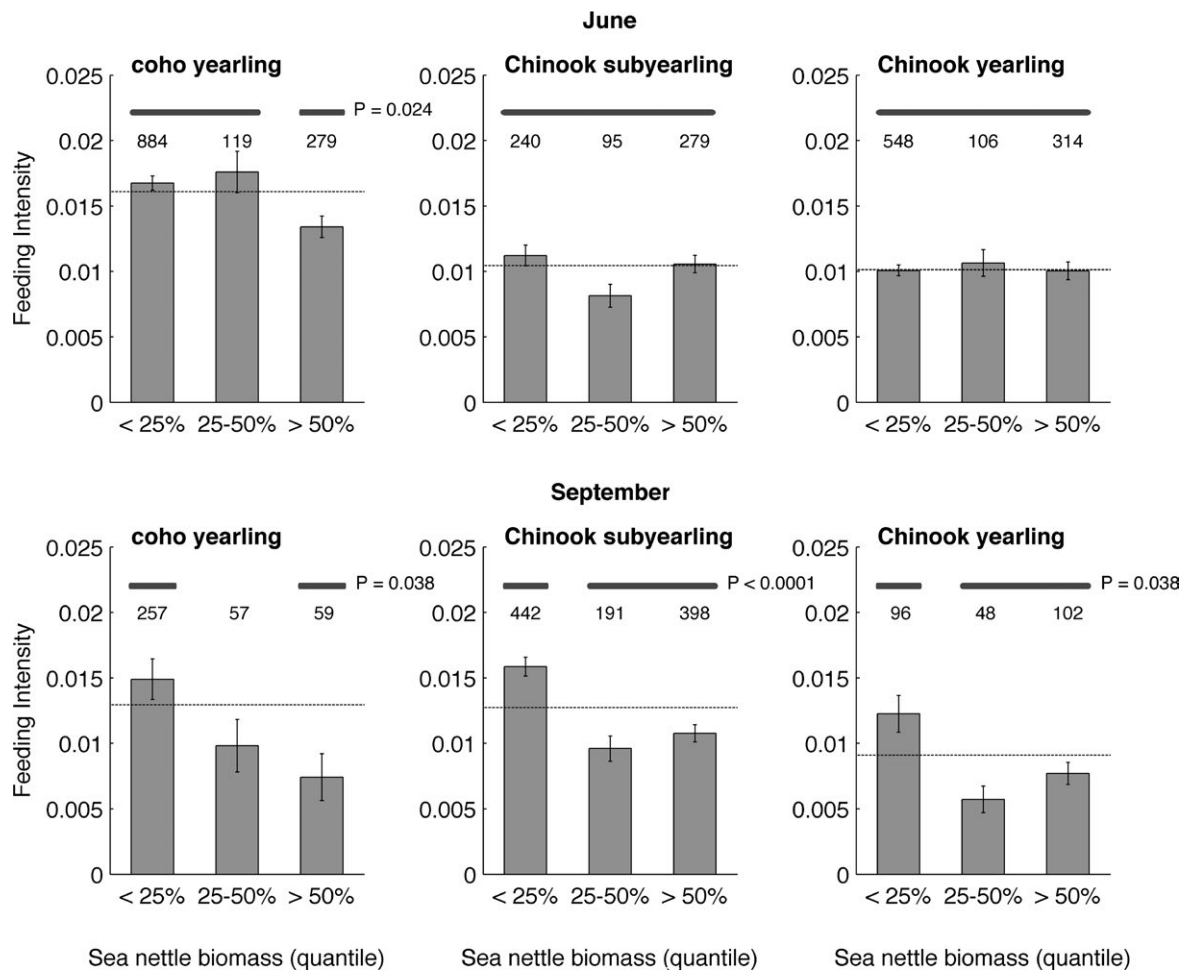


Fig. 5. Indices of Feeding Intensity (IFI, Eq. 3) for juvenile salmon captured in June and September from the mouth of the Columbia River and northward ( $46^{\circ}$ – $48^{\circ}$  N) within the 100 m isobath. Trawls were pooled across years and grouped by sea nettle biomass quartile and season. Heavy black lines above bars indicate quartile groups that are significantly different with corresponding  $P$ -values (Kruskal–Wallis test). Numbers above bars are the number of stomachs analyzed. Light dashed line represents the median feeding intensity each season. Error bars represent  $\pm 1$  SE.

nettles, juvenile salmon, and other key mid-trophic level groups (footprint) and the percentage of total consumer production supported by these groups (reach) off the Pacific Northwest coast. Juvenile salmon are such a relatively small group that they are barely visible when plotted on the same scale as the other groups (footprint =  $0.012\% \pm 0.0007\%$ ; reach =  $0.0007\% \pm 0.00005\%$ ). While jellyfish and forage fish (sardine, anchovy, herring, and smelts) are supported by roughly similar fractions of total ecosystem production, forage fish return more of that energy to the food web than do jellyfish. Jellyfish are supported by  $2.6\% (\pm 0.5)$  and forage

fishes by  $1.4\% (\pm 0.05)$  of the total ecosystem production. In contrast, forage fish support 20 times more of the total consumer production in the NCC ecosystem,  $0.11\% (\pm 0.003)$ , than do the large jellyfish,  $0.005\% (\pm 0.0005)$ . Note that the reported footprint and reach values ( $\pm 1$  SD) exclude the costs of metabolism and production lost to feces production.

Two other important groups are shown for comparison. Pacific hake (*Merluccius productus*) have seasonally high biomasses, support the largest fishery off the Pacific Northwest coast, and are a major energy transfer node (footprint =  $0.78\% \pm 0.05\%$ ;

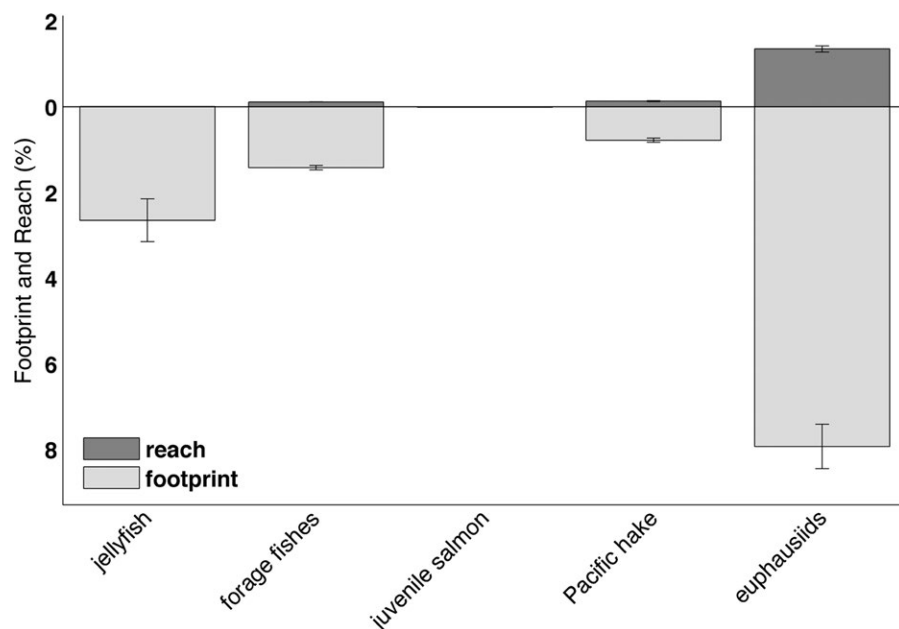


Fig. 6. Footprint and reach metrics showing the relative importance of jellyfish, juvenile salmon, and other important mid-trophic level groups as consumers and producers. Lightly shaded bars are the footprints, the fraction of total ecosystem production consumed by each group. Darkly shaded bars are the reach, the fraction of total ecosystem consumer production supported by each group.

reach =  $0.13\% \pm 0.001\%$ ). Euphausiids (*Euphausia pacifica* and *Thysanoessa spinifera*) are a major consumer and are very important in the diets of many groups off the Pacific Northwest coast. The euphausiids are a dominant energy transfer node between lower and upper trophic levels as shown by their very large footprint and reach values (footprint =  $7.9\% \pm 0.52\%$ ; reach =  $1.4\% \pm 0.071\%$ ).

*Sensitivity analysis: juvenile salmon response to changes in trophic relationships.*—The food web sensitivity analysis was used to estimate how net energy flow to juvenile coho and Chinook salmon would change following an increase (+25%) in energy flow through an individual producer → consumer trophic linkage. Table 4 shows the trophic linkages that had the greatest positive and greatest negative impacts upon each juvenile salmon group from among the 1663 systematically investigated links. Juvenile salmon benefited directly from increased prey availability, particularly the availability of juvenile fishes. Young salmon benefited indirectly from increased zooplankton consumption by juvenile fish, which led in turn, to greater energy flow to

young salmon preying upon juvenile fishes (Table 4, left). Juvenile coho and Chinook salmon were particularly sensitive to increased competition with Pacific hake and with large jellyfish (Table 4, right). Hake act as direct trophic competitors with young salmon for small fish as prey. Increased consumption of juvenile fishes by hake had the largest negative effect on juvenile salmon of all modeled food web linkages. Large jellyfish, predominately sea nettles, act as indirect trophic competitors with juvenile salmon. Jellyfish consume the zooplankton prey that support juvenile fishes that, in turn, support young salmon.

*Bloom simulation: effects of jellyfish blooms on the ecosystem and juvenile salmon.*—The simulated increase in jellyfish biomass and energy demands resulted in reduced productivity for most pelagic groups (Fig. 7; Table 5). Having the greatest similarity in diet with sea nettles, the small carnivorous jellyfishes (*Mitrocoma celluaria*, *Eutonina indicans*) were the most strongly impacted of all groups. The more planktivorous vertebrate groups, the smelts, the juvenile fishes,

Table 4. The most influential trophic linkages in the food web affecting juvenile coho and Chinook salmon production in the Northern California Current.

Response group	Strengthened trophic linkages lead to INCREASED energy flow to juvenile salmon		Strengthened trophic linkages lead to DECREASED energy flow to juvenile salmon	
	Producer → consumer	(%)	Producer → consumer	(%)
Yearling coho	Juv. fish → Yearling coho	10	Juv. rockfish → Hake	-7
	Juv. rockfish → Yearling coho	9	Juv. fish → Hake	-7
	Macrozooplank. → Yearling coho	4	Small copepods → Large jellyfish	-2
	Small copepods → juv. fish	4	Macrozooplank. → Large jellyfish	-1
	Invert. larvae → juv. fish	3	Juv. fish → Small benth. fish	-1
SubYrln Chinook	Juv. fish → SubYrln Chinook	14	Juv. fish → Hake	-10
	Small copepods → juv. fish	4	Small copepods → Large jellyfish	-2
	Invert. larvae → juv. fish	4	Juv. fish → Small benth. fish	-2
	Macrozooplank → SubYrln Chinook	3	Juv. fish → Caridean shrimp	-1
	E. pacifica → SubYrln Chinook	2	Juv. rockfish → Hake	-1
Yearling Chinook	Juv. rockfish → Yearling Chinook	10	Juv. rockfish → Hake	-8
	Juv. fish → Yearling Chinook	7	Juv. fish → Hake	-5
	Macrozooplank. → yearling Chinook	3	small copepods → Large jellyfish	-2
	Small copepods → juv. rockfish	3	Macrozooplank. → Large jellyfish	-1
	Invert. larvae → juv. fish	3	Juv. rockfish → Small benth. fish	-1

Note: Trophic linkages shown are the five that lead to the greatest net increase and the five that lead to the greatest net decrease in energy flow to juvenile salmon following a 25% increase in energy flow through that individual trophic linkage from producer to consumer. Values shown are the percent change in energy flow to yearling coho, subyearling Chinook, and yearling Chinook salmon.

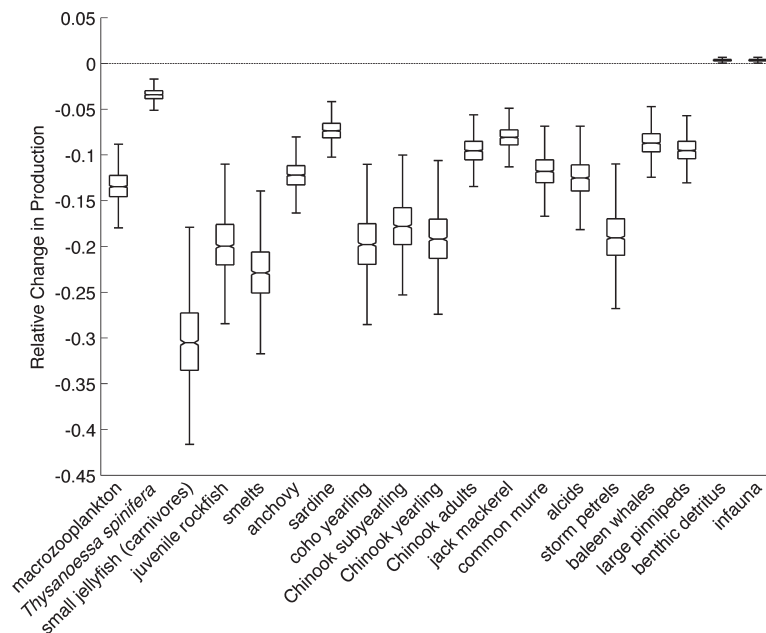


Fig. 7. Relative change in group production ( $\Delta P$ , Eq. 2) following an increase ( $\times 1.97$ ) in the biomass and consumption of large jellyfish (predominately *Chrysaora fuscescens*) in the Northern California Current ecosystem. Boxplots represent distributions of 1000 randomly generated models. Center of notch represents the median and shaded area represents the interquartile range between the 1st and 3rd quartiles. Whiskers represent highest and lowest observations within 150% of the interquartile range. Median values are significantly different at the 5% level when notch intervals do not overlap.



Table 5. Responses of select pelagic groups to a simulated jellyfish bloom as percent change in production ( $\Delta P$ ).

Group category	Response group	Percent change in production ( $\Delta P$ )
Zooplankton groups	Macrozooplankton	$-13.3 \pm 1.78$
	Thysanoessa spinifera	$-3.41 \pm 0.66$
	Small jellyfish (salps, larvaceans)	$-1.80 \pm 0.35$
	Small jellyfish (ctenophores)	$-30.2 \pm 4.71$
	Large jellyfish	$79.8 \pm 4.77$
Planktivorous fish groups	Juvenile rockfish	$-19.8 \pm 3.37$
	Smelts	$-22.8 \pm 3.40$
	Sardine	$-7.31 \pm 1.22$
	Herring	$-7.07 \pm 1.27$
	Anchovy	$-12.12 \pm 1.70$
Juvenile salmon groups	Coho yearling	$-19.7 \pm 3.36$
	Chinook subyearling	$-17.7 \pm 3.04$
	Chinook yearling	$-19.1 \pm 3.24$
Piscivorous fish groups	Coho salmon (adults)	$-11.9 \pm 1.82$
	Chinook salmon (adults)	$-9.46 \pm 1.52$
	Jack mackerel	$-8.02 \pm 1.26$
	Piscivorous rockfishes	$-9.27 \pm 1.53$
	Dogfish	$-9.57 \pm 1.46$
Seabird groups	Common murre	$-11.7 \pm 1.90$
	Gulls & terns	$-9.72 \pm 1.40$
	Coastal divers	$-10.1 \pm 1.55$
	Alcids	$-12.4 \pm 2.14$
	Storm petrels	$-18.9 \pm 3.12$
Marine mammal groups	Gray whales	$-15.1 \pm 2.76$
	Baleen whales	$-8.59 \pm 1.55$
	Sea lions	$-9.41 \pm 1.43$
	Small odontocetes	$-1.86 \pm 2.08$
	Orcas	$-10.4 \pm 1.70$

*Note:* A jellyfish bloom was simulated by raising jellyfish biomass by 1 SD ( $\times 1.97$ ) over the 1999–2012 summer mean biomass used to infer energy flow rates through the ecosystem. Jellyfish bloom effects are expressed as the percent change in production in the bloom model relative to the base model ( $\Delta P$ , Eq. 2). Uncertainty values are  $\pm 1$  SD of 1000 random, mass-balanced models.

and the storm petrels were also strongly impacted. All juvenile salmon groups, their diets depending heavily upon juvenile fishes, were more strongly impacted by jellyfish blooms than were most forage fishes. A twofold increase ( $\times 1.97$ ) in sea nettle biomass resulted in 20% reductions in energy flow to juvenile salmon. In comparison, anchovy, sardine, and herring production was reduced by 7–12%.

We assumed that senescent jellyfish sink directly to the benthos, but the twofold increase in jellyfish production resulted in an only moderate relative increase in energy flow to the benthic food web given the large input of detritus to the benthos from all other pelagic sources. The flow to the benthic detritus pool increased by only 0.3%, as did detritivore production (infauna, benthic crustacean, and echinoderms).

#### *Relation between salmon production and summer sea nettle biomass*

The relationship between sea nettle biomass and salmon production was examined by calculating the interannual correlations between the mean regional sea nettle biomass observed each season (May, June, and September) and annual salmon production metrics: adult returns and adult return-to-smolt production (SAR) (Fig. 8; Table 6). Because sea nettles and juvenile salmon were concentrated off the Columbia River and northward, we examined the relationships between salmon production and jellyfish biomass off the Washington coast estimated from the five transects from the Columbia River and northward.

The significant correlations were negative in all cases. In years of high sea nettle biomass, subsequent adult coho and Chinook salmon

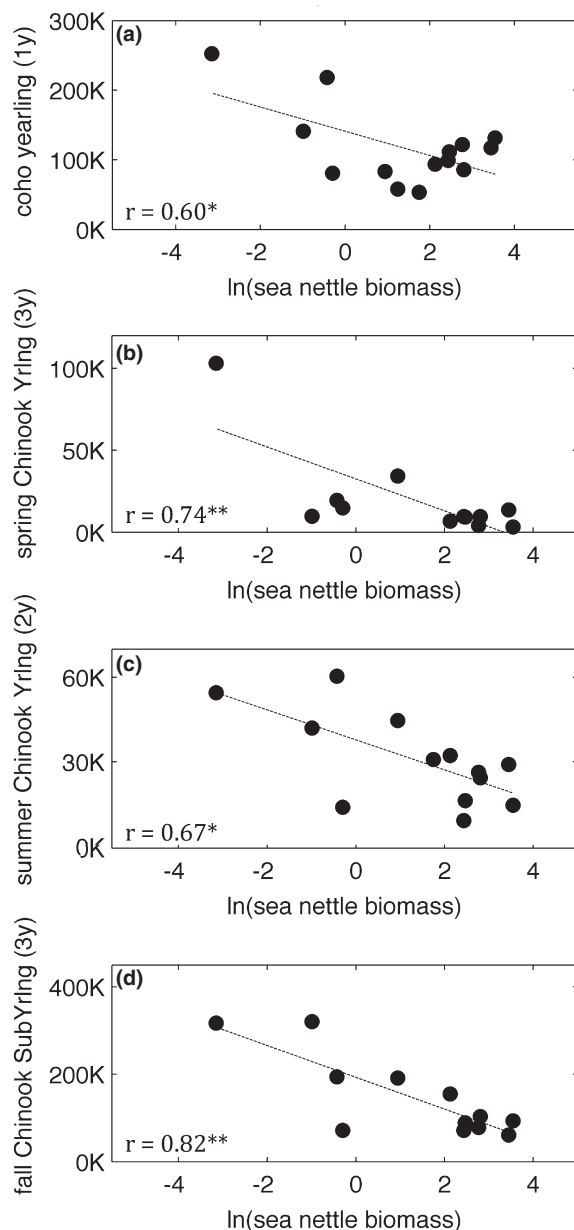


Fig. 8. Adult salmon returns to Bonneville dam plotted against the September sea nettle biomass off the mouth of the Columbia River and north ( $46^{\circ}$ – $48^{\circ}$ N) within the 100 m isobath. (a) Coho returns vs. sea nettles lagged 1 yr from yearling smolt ocean entry, (b) Spring Chinook returns vs. sea nettles lagged 3 yr from yearling smolt ocean entry, (c) Summer Chinook returns vs. sea nettles lagged 2 yr from yearling smolt ocean entry, (d) Fall Chinook returns vs. sea nettles lagged 3 yr from subyearling smolt ocean entry. (See Table 6 for correlation analyses).

returns to Bonneville Dam were lower. Some distinctions can be observed among the different Chinook salmon runs and juvenile life histories. Columbia River spring and summer Chinook are predominately yearlings as ocean juveniles. Spring Chinook returns to Bonneville Dam were correlated with the sea nettle biomass off the Columbia River and Washington in June and September of 2 and 3 yr previous. Summer Chinook returns were correlated with the sea nettle biomass in September of 2 yr previous and with the sea nettle biomass in May and June of 3 yr previous. Columbia River fall Chinook salmon runs are predominately subyearlings as ocean juveniles. Fall Chinook returns to Bonneville Dam were significantly correlated with the sea nettle biomass in June and September of 3 yr previous.

Non-Columbia River coho salmon were not significantly correlated with sea nettle biomass. Non-Columbia River coho include wild coho from Oregon coastal rivers (OCN coho) and the total hatchery production from the Columbia, the Klamath, and Oregon coastal rivers (OPIH coho). Survival of OPIH coho, as estimated by the smolt production to adult return ratio (SAR), was also not correlated with sea nettle biomass. Finally, while survival of Snake River wild spring and summer Chinook salmon was significantly correlated with sea nettle biomass, the survival of wild Snake River steelhead was not.

## DISCUSSION

The year-class strengths of salmon populations in the Pacific Northwest are set during their early marine residence (Percy 1992, Beamish et al. 2004). Variability in survival has been attributed to changes in bottom-up processes controlling prey and quality (Logerwell et al. 2003, Peterson and Schwing 2003, Trudel et al. 2005, Tomaro et al. 2012). However, survival is not always clearly related to indices of overall ecosystem productivity (Lawson 1997, Miller et al. 2013). Food web structure, competition, and the efficiency of energy transfer through the food web may be as important for limiting energy flow to young salmon as are physical processes regulating plankton production. We

Table 6. Correlation (r-values) between annual adult salmon returns (or SAR, adult-to-smolt ratio) and the natural log of the May, June, and September sea nettle biomass during the year of smolt entry to the ocean.

Production metric	Species and adult run type	Population and life history	May	June	September	Chinook run composition (%)
Adult returns	Coho	OPIH (all)	-0.43	-0.30	-0.51	...
		OPIH (Bonneville dam)	0.03	-0.19	<b>-0.60*</b>	...
		OCN	0.29	0.25	-0.09	...
	Spring Chinook	Bonneville dam (lag 2 yr)	-0.16	<b>-0.70*</b>	<b>-0.52*</b>	...
		Subyearling	0.26	-0.03	-0.41	0.1
		Yearling	-0.16	<b>-0.70*</b>	<b>-0.52*</b>	74.0
		Bonneville dam (lag 3 yr)	-0.46	<b>-0.73**</b>	<b>-0.74**</b>	...
		Subyearling	0.17	0.11	0.24	0.2
		Yearling	-0.46	<b>-0.73**</b>	<b>-0.74**</b>	11.7
	Summer Chinook	Bonneville dam (lag 2 yr)	0.03	-0.51	<b>-0.65*</b>	...
		Subyearling	0.05	0.12	-0.02	3.3
		Yearling	0.03	-0.54	<b>-0.67*</b>	33.0
		Bonneville dam (lag 3 yr)	<b>-0.59*</b>	<b>-0.76*</b>	-0.35	...
		Subyearling	-0.44	-0.03	0.13	11.6
		Yearling	-0.48	<b>-0.88**</b>	-0.48	23.1
	Fall Chinook	Bonneville dam (lag 2 yr)	0.14	-0.31	-0.28	...
		Subyearling	0.17	-0.24	-0.28	26.5
		Yearling	0.00	-0.44	-0.21	7.1
		Bonneville dam (lag 3 yr)	-0.01	<b>-0.62*</b>	<b>-0.80**</b>	...
		Subyearling	-0.09	-0.62	<b>-0.82**</b>	33.7
		Yearling	-0.16	-0.36	-0.27	2.9
SAR (survival)	Coho	OPIH (all)	-0.28	-0.04	-0.39	...
	Spring/summer Chinook	Wild Snake River	-0.01	-0.52	<b>-0.56*</b>	...
	Steelhead	Wild Snake River	0.11	-0.38	-0.45	...

Notes: Sea nettle biomasses were estimated from trawls off the Washington coast and the Columbia River within the 100 m isobath. Chinook run composition represents fraction of the run population in terms of juvenile life history (subyearling or yearling) and number of winters spent in the ocean (lag 2 yr or lag 3 yr) before being observed as adults at Bonneville dam, as estimated from CRITFC age studies. Probability values are two-tailed and corrected for autocorrelation following Pypers and Peterman (1998). Significant values are bold.

\*  $P < 0.05$ .

\*\*  $P < 0.01$ .

expected large scyphozoan jellyfish to be an important food web structuring agent given their capacity for rapid population growth, seasonally high biomass, and ability to exert heavy predation pressure upon the zooplankton community. Inverse correlations between annual abundances of jellyfish and forage fish have been taken as evidence of competitive interactions within coastal ecosystems in general (Robinson et al. 2014) and within the Northern California Current (NCC) in particular (Brodeur et al. 2014). We propose that during periods of high consumption of zooplankton by jellyfish, less energy flows along the trophic pathways between the plankton and young salmon, leading to slower juvenile salmon growth and thus lower survival to adulthood.

The most abundant scyphozoan jellyfish along the Oregon and Washington coast is the sea nettle, *Chrysaora fuscescens* (Suchman et al. 2012). Three investigative tracks show that summer sea nettle blooms can have a substantial impact on salmon production. There is temporal and spatial co-occurrence between sea nettles and yearling coho, subyearling Chinook, and yearling Chinook salmon, with evidence of locally reduced feeding intensity among juvenile salmon where sea nettle biomass is highest. Ecosystem model simulations demonstrated that jellyfish blooms cause substantial changes to energy flow patterns throughout the food web and reductions in prey availability to juvenile salmon. Finally, there was found an inverse relationship between the size of sea nettle blooms



in the summer of smolt entry to the ocean and subsequent adult returns of Columbia River basin stocks.

There is little overlap in the diets of sea nettles and juvenile salmon. Sea nettles are planktivorous (Suchman et al. 2008, Zeman 2015), while even the smallest juvenile salmon are predominately piscivorous. The small fish that make up the prey of young salmon (juveniles of rockfish, anchovy, smelt, herring, cottids, and Pacific sand lance, Daly et al. 2009) themselves have diets similar to *C. fuscescens* (Miller and Brodeur 2007, Bosley et al. 2014). In areas of high sea nettle biomass, zooplankton could be sufficiently reduced to negatively impact the availability of young planktivorous fish for juvenile salmon to forage upon at the next trophic step. The results of the feeding incidence study are consistent with such a mechanism of indirect exploitative competition. Feeding success of juvenile salmon was significantly higher at survey stations where jellyfish biomass was low. This pattern was most pronounced in September. Alternatively, some form of interference competition may operate, leading to avoidance of otherwise productive foraging areas with high jellyfish densities by small pelagic fish and/or changes in forage effectiveness by juvenile salmon due to jellyfish presence. At present, there are insufficient data for these juvenile pelagic fish to determine whether their numbers, distribution, or somatic condition change when jellyfish are abundant.

Model simulations of resource competition by jellyfish showed that even in summers of moderately large blooms (1 SD over 1999–2012 mean biomass), the demands of jellyfish for zooplankton had broadly distributed, negative effects throughout the food web. Indirect, trophic competition from jellyfish reduced energy flow to juvenile salmon by almost 20% relative to average conditions (i.e., the mean 1999–2012 community composition from which food web structure was inferred). This is a substantial impact. For some context on the scale of the model response relative to variability in survival, the mean annual smolt-to-adult survival ratio of Oregon coho from the Columbia, Klamath, and coastal rivers over the 1999–2012 period is 0.027 with a coefficient of variation of 39% (PFMC 2015). The model simulation estimates changes in resource availability rather than of survival, but it does

suggest that competition with jellyfish accounts for a nontrivial portion of observed variability in juvenile salmon survival. Note that the simulation presupposed that prey were limiting and was constructed so that increased predation by jellyfish was offset by a net reduction in predation from competing planktivores. If we were to assume that jellyfish blooms were supported in part by “surplus” plankton production that would otherwise be lost to the detritus or exported from the shelf via Ekman transport, then the effects of jellyfish blooms would be lower than estimated here. Ruzicka et al. (2007) hypothesized that availability of otherwise unconsumed surplus plankton production may limit the impact that jellyfish blooms have on small pelagic fishes. However, the negative correlations between sea nettle biomass and salmon production and between local sea nettle biomass and juvenile salmon feeding incidence are both consistent with energy resource competition between jellyfish and young salmon.

Most salmon stocks and runs that we examined showed negative correlations between sea nettle biomass in the summer of smolt ocean entry and subsequent adult returns to freshwater. Differences in the strength of the correlation can be related to juvenile life histories. Life histories with greater spatial and temporal overlap with sea nettles had stronger negative correlations. Adult returns of Chinook salmon with subyearling juvenile life histories showed the strongest negative correlation of the salmon groups resolved in our analysis. Subyearling Chinook salmon migrating down the Columbia River are most abundant in the lower estuary in mid-to-late June (Weitkamp et al. 2012). In the ocean, they were most abundant during the September ocean surveys and concentrated inshore of 11 km; their spatial distributions differed significantly from sea nettles in only 14% of the surveys. In addition, subyearling Chinook salmon enter the ocean younger and smaller than either coho or Chinook yearlings. We hypothesize that lower energy reserves and less skillful foraging associated with small size contributes to subyearling salmon sensitivity to local resource limitation and competition.

Yearling salmon enter the ocean earlier in the season than subyearling salmon. Columbia River yearling coho and Chinook salmon are most

abundant in the lower estuary in late May, just prior to ocean entry (Weitkamp et al. 2012). Yearling Chinook salmon spend on an average only ~30 d off Oregon and Washington (Tomaro et al. 2012), limiting the opportunity for competition and allowing ocean foraging and growth before the peak jellyfish biomass in September. Among Chinook salmon with yearling juveniles, spring and summer Columbia River runs were significantly correlated with sea nettle biomass in both June and September of the year of smolt ocean entry. In contrast, yearling coho salmon were distributed broadly across the shelf in June and September and had the lowest spatial overlap with sea nettles (see also Bi et al. 2008). Coho returns to the Columbia River were only modestly correlated with sea nettle biomass off the Washington coast during the September of smolt ocean entry. The salmon population that showed the weakest correlation with sea nettle biomass was the naturally produced Oregon coast coho salmon (OCN coho). OCN yearling migrate long distances north shortly after ocean entry relative to other coho salmon populations (Morris et al. 2007), and may have one of the lowest temporal and spatial overlaps with sea nettles off Oregon and Washington.

## CONCLUSION

Jellyfish consumption rates in the Northern California Current can exceed that of other pelagic fish groups by the end of the summer (Ruzicka et al. 2007). Their importance in the food web and the effects they have on other species should not be ignored in the NCC or in other ecosystems with large jellyfish populations (Robinson et al. 2014). Our model simulations reveal a mechanism by which sea nettle blooms can redirect energy flow through the food web and contribute substantially to interannual variability in salmon production in the Pacific Northwest. Negative correlations between the size of summer jellyfish blooms and subsequent adult salmon returns are consistent with this mechanism. Alternatively, sea nettles and juvenile salmon may covary with the same underlying set of environmental conditions, though with opposite responses, and not affect each other. However, observations of significantly reduced feeding incidence

among juvenile salmon at locations where sea nettle biomass is high provide support for indirect exploitative competition. Competitive interactions, in general, may be a more important factor affecting ocean survival of young salmon than is usually considered within the “top-down” vs. “bottom-up” paradigm. The model sensitivity analysis suggests that competition with Pacific hake (*Merluccius productus*) for small pelagic fish also deserves closer investigation.

There is evidence that jellyfish populations in coastal ecosystems throughout the world may be on the rise (Brotz et al. 2012, Purcell 2012) or undergo periodic blooms that cycle over years to decades (Condon et al. 2013). Regardless of the underlying causes, both long-term and periodic increases in jellyfish populations have serious and generally negative implications for coastal ecosystem services on which humans depend (Pauly et al. 2009, Richardson et al. 2009, Purcell 2012, Graham et al. 2014, Conley and Sutherland 2015). The key to developing appropriate management responses to both chronic and episodic jellyfish blooms is to have an understanding the role of jellyfish within the context of food web structure as well as the direct and the indirect effects jellyfish have on the larger ecosystem.

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