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Summer Jellyfish Blooms in an Upwelling Ecosystem: Modeling Impacts upon Fish Production and Evaluating Evidence

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Summary
What are the consequences should jellyfish consume an increasingly greater share of plankton production? Jellyfish may play a role shaping energy flow through pelagic food webs by diverting plankton production away from higher trophic levels. In the Northern California Current, scyphozoan jellyfish attain high biomasses during summer months, but their abundance is variable from year to year. Do large jellyfish blooms have an observable impact on the rest of the ecosystem? Sensitivity analyses with an end-to-end ecosystem model of the Northern California Current were used to examine the potential effects of increased jellyfish production upon higher trophic levels. These analyses suggest that salmon are particularly sensitive to jellyfish blooms. Although jellyfish and young salmon feed at different trophic levels, they may be indirect competitors for plankton production. Pelagic surveys off Oregon and Washington were used to examine the relationship between the dominant jellyfish (*Chrysaora fuscescens*) and salmon production. There was a significant, negative correlation between *C. fuscescens* abundance and the strength of salmon returns to the Columbia River in subsequent years. Further examination showed that juvenile salmon stomachs were less full at locations with higher *C. fuscescens* biomass.

Materials and Methods
Using both ecosystem model sensitivity analyses and statistical analyses of time-series ocean observations, we analyzed three relationships between salmon and sea nettles (*Chrysaora fuscescens*): (1) the theoretical (modeled), indirect competition between jellyfish and juvenile salmon for plankton resources, (2) the relation between salmon production indices (adult returns to the Columbia River system) and summer sea nettle biomass during the year of smolt entry to the ocean, and (3) the relation between juvenile salmon feeding intensity and sea nettle biomass observed during pelagic surveys.

Model analyses of the effects of changes in sea nettle biomass on other groups in the pelagic community were made with an ECOTRAN food web model of the Northern California Current representing the period of 1999 – 2010 (Steele & Ruzicka 2011, Ruzicka *et al*. 2012). Analyses were conducted to estimate changes in salmon productivity following a doubling in jellyfish abundance due to increased jellyfish consumption of zooplankton production and decreased energy available along trophic pathways (direct and indirect) supporting fish production. Seasonal sea nettle and juvenile salmon abundances off Washington and northern Oregon were obtained from pelagic trawl surveys along cross-shelf transects between 44.6°N and 48.3°N during May, June, and September each year from 1999 - 2013 (Brodeur et al., 2005; Emmett et al., 2006). Salmon productivity was estimated from adult salmon returns to the upper Columbia River system at Bonneville Dam (www.cbr.washington.edu/dart/adult_annual.html). Smolt life-history and number of winters spent at sea before returning to the Columbia River were extrapolated from annual retrospective scale-aging observations made by the Columbia River Inter-Tribal Fish Commission of returning adults (e.g., Kelsey *et al*. 2011). The relationship between juvenile salmon feeding success and sea nettle biomass was examined by comparing Indices of Feeding Intensity (Daly *et al*. 2009) and local jellyfish biomass at survey individual stations.

Results and Discussion

Model sensitivity analyses show that energy flow to juvenile salmonids in the Northern California Current off the Washington and Oregon coasts were sensitive to competition from sea nettles. A doubling of jellyfish biomass (roughly a 1 standard deviation increase over the mean 1999 – 2010 September biomass) resulted in an 18 – 20% decrease in energy flow to juvenile salmon.

The relationships between adult salmon returns and September jellyfish biomasses of smolt ocean entry years were significantly negative or several Columbia River salmon runs (Figure 1). This could be the apparent effect of young salmon and jellyfish both responding to shared ocean conditions, but in the opposite manner. However, juvenile salmon feeding success was also significantly lower at stations where sea nettle biomasses were elevated (Figure 2).

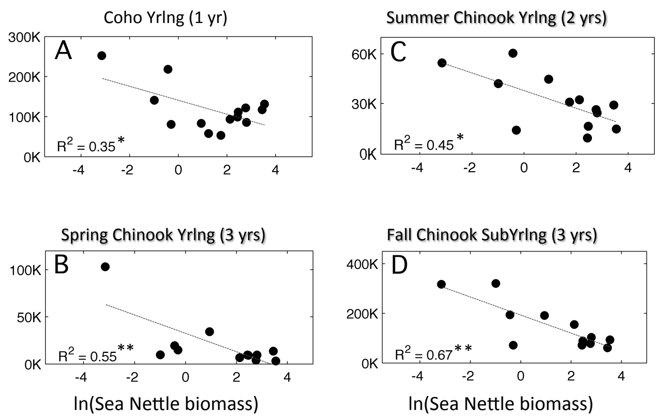

Figure 1. Relationships between sea nettle biomass off the Washington coast during September of the year of salmon smolt entry to the ocean and subsequent adult salmon returns to the upper Columbia River system. Years in parentheses are the number of years (winters at sea) between smolt ocean entry and adult salmon returns.

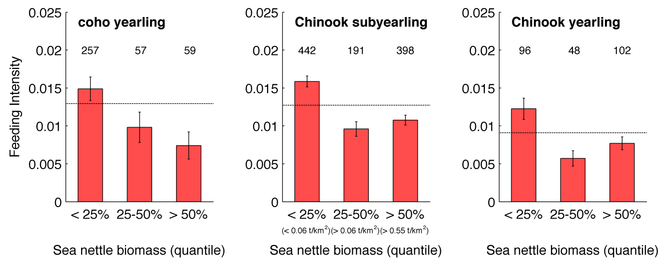

Figure 2. Indices of Feeding Intensity at individual pelagic survey stations binned by local sea nettle biomass. IFI = (stomach content weight)/((total fish weight-stomach content weight)).

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