

Contribution to the Theme Section 'Jellyfish blooms and ecological interactions'

Spatial overlap between forage fishes and the large medusa *Chrysaora fuscescens* in the northern California Current region

Richard D. Brodeur^{1,*}, Caren Barceló², Kelly L. Robinson³, Elizabeth A. Daly⁴,
James J. Ruzicka⁴

¹NOAA Northwest Fisheries Science Center, Hatfield Marine Science Center, Newport, OR 97365, USA

²College of Earth, Ocean and Atmospheric Sciences, Oregon State University, Corvallis, OR 97331, USA

³Department of Marine Science, The University of Southern Mississippi, Stennis Space Center, MS 39529, USA

⁴Cooperative Institute for Marine Resources Studies, Oregon State University, Newport, OR 97365, USA

ABSTRACT: As in many regions of the world, the shelf waters of the western United States have experienced large increases and high interannual variability in jellyfish populations in recent decades. The northern California Current (NCC) is a productive upwelling zone that is home to large populations of medusae, particularly during some years. Seasonal trawl surveys in the NCC over 13 yr have documented a substantial biomass of jellyfish consisting primarily of one species, the sea nettle *Chrysaora fuscescens*, with abundances generally peaking in late summer. Trophic overlap can be high in the NCC with planktivorous species such as Pacific sardines and herring that consume copepods and other zooplankton. In this study, we examine the spatial overlap and co-occurrence of *C. fuscescens* and Pacific herring *Clupea pallasii*, northern anchovy *Engraulis mordax* and Pacific sardine *Sardinops sagax* in the NCC using spatial analysis tools to determine the species that have the potential to be most affected by high jellyfish biomass and the geographic areas in which these interactions are likely to occur. Significant spatial overlap of *C. fuscescens* with these pelagic fishes occurred during certain months and years, although the results were highly variable. There was an overall negative relationship between the abundance of *C. fuscescens* and the catch of the 3 forage fishes for both June and September. End-to-end food web models show that jellyfish have a greater potential to affect production of pelagic forage fishes than the reverse.

KEY WORDS: Scyphomedusae · Planktivores · Spatial overlap · Seasonal variability · Interannual variability · Pelagic fishes

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INTRODUCTION

Evidence is accumulating that jellyfish populations are on the rise in many, if not most, coastal ecosystems of the world (Purcell et al. 2001, Richardson et al. 2009, Brotz et al. 2012, Condon et al. 2013). Although the proximate causes of these blooms are still being debated (Purcell et al. 2007, Richardson et al. 2009, Purcell 2012, Duarte et al. 2013, Gibbons &

Richardson 2013), their societal and economic impacts are well documented worldwide (Purcell et al. 2007, Quinones et al. 2013, Lucas et al. 2014, Graham et al. in press). In some productive pelagic ecosystems, overfishing of small pelagic fishes over the last few decades has been implicated as a cause of many of these massive blooms (Lynam et al. 2006, Uye 2011, Roux et al. 2013). It has been suggested that these jellyfish and pelagic fishes occupy a similar tro-

*Corresponding author: rick.brodeur@noaa.gov

phic niche and that depression of fish stocks through exploitation allows jellyfish populations to grow unabated (Richardson et al. 2009, Uye 2011).

As in many regions of the world, the shelf waters of the California Current have experienced large increases and high interannual variability in jellyfish populations (Brotz et al. 2012, Suchman et al. 2012). The northern California Current (NCC) is a productive upwelling zone that supports large populations of medusae, particularly during late summer. Pelagic trawl surveys in the region off Washington and northern Oregon every June and September since 1999 have documented a substantial biomass of jellyfish consisting primarily of one species, *Chrysaora fuscescens*, with the seasonal peak in biomass occurring of this species in late summer (Suchman et al. 2012). Spatial overlap of these jellyfish with pelagic fishes has been shown to occur (Brodeur et al. 2008) and there appear to be regions of intense spatial overlap where trophic interactions may be occurring. Seasonal and interannual variations in oceanographic conditions could impact the extent of spatial overlap, especially major changes related to climate (Eriksen et al. 2012).

The limited diet data available for *C. fuscescens* (Suchman et al. 2008) indicate that they are primarily planktivorous and have the potential to consume a high proportion of the available standing stocks of several key zooplankton prey. Both empirical (Brodeur et al. 2008) and modeling (Brodeur et al. 2011, Ruzicka et al. 2012) studies suggest that trophic overlap of jellyfish can be high with planktivorous species such as Pacific sardines *Sardinops sagax*, northern anchovies *Engraulis mordax* and Pacific herring *Clupea pallasii* that feed on similar prey and occupy approximately the same trophic level as jellyfish in the NCC.

In this study, we examine the extent of spatial overlap and co-occurrence of *C. fuscescens* and the aforementioned pelagic fish in the NCC to determine which pelagic forage species have the potential to be most affected by high jellyfish biomass and the geographic areas in which these interactions are likely to occur. Although many species have the potential to spatially overlap with *C. fuscescens*, we restrict our analysis to these 3 forage fish, which display the highest trophic overlap with this medusa during late summer (Brodeur et al. 2008). The spatial overlap between jellyfish and pelagic fishes in the NCC has been examined previously for one cruise by Brodeur et al. (2008), although that study did not look at seasonal or interannual variability in spatial overlap.

In this article, we evaluate differences in overlap between summer (June) and fall (September), as well as annual changes. We also determined covariation in catches of these forage fishes and *C. fuscescens* to examine whether high jellyfish biomass potentially affected the abundance patterns of these fishes on a seasonal or interannual scale. Finally, we use end-to-end ecosystem models to simulate the effects of increased jellyfish population biomass on these forage fishes and other food web compartments and compared outcomes with effects on this jellyfish species observed when forage fish are increased by a similar proportion.

MATERIALS AND METHODS

Pelagic fish and jellyfish were collected along up to 8 transect lines off the Washington and Oregon coast in June and September 1999 to 2011 (Suchman et al. 2012) (Fig. 1). We generally sampled 8 transects per

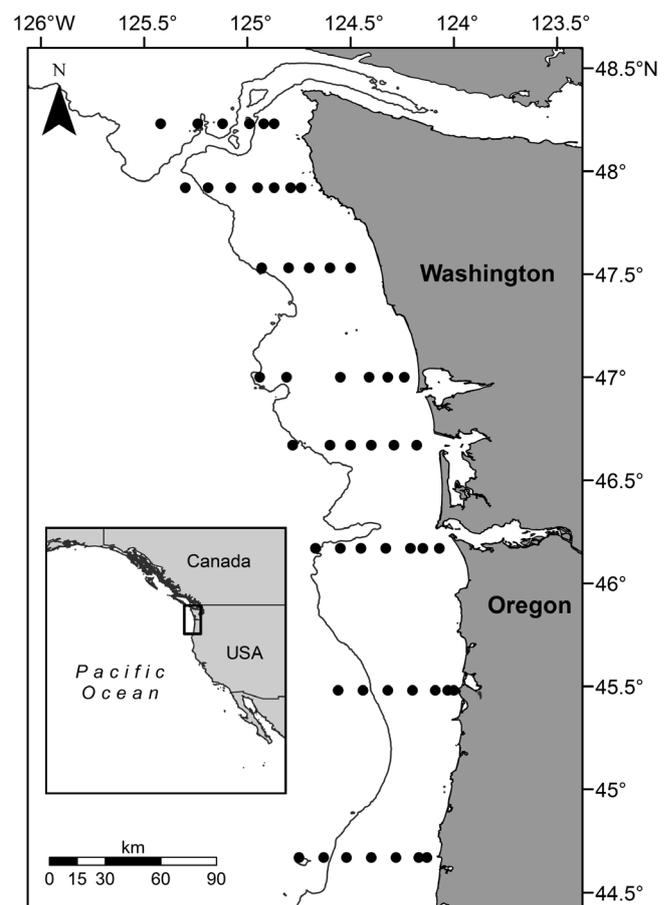


Fig. 1. Representative area sampled each June and September (1999–2011). Black circles are stations sampled during June 2011. The line is the 200 m isobath

cruise (June 2000 was an exception, with only 5 transects sampled) extending from northern Washington (48.3° N) to central Oregon (44.7° N), with stations starting 5–8 km offshore at dawn and continuing to just beyond the shelf break near or shortly after sunset (see Fig. 1 for typical sampling scheme). Fish were collected using a 30 × 20 × 100 m (width × height × length) Nordic 264 pelagic rope trawl (NorEastern Trawl Systems). Mesh size in the trawl varied from 162.6 cm near the headrope down to 8.9 cm in the cod end, in which a liner of 0.8 cm stretch mesh was sewn. Following Suchman & Brodeur (2005), we used a smaller, effective mouth area of 123 m² to calculate the densities of *Chrysaora fuscescens*. For each sample, the trawl was towed over the upper 20 m of the water column at a speed of ~6 km h⁻¹ for 30 min except on a few occasions, such as when the trawl became filled with jellyfish, resulting in shortened tows. Trawling was generally along an isobath, either towards the north or south depending upon wind direction and sea state. Trawling was initiated several kilometers north (or south) of each station such that the midpoint of a trawl was at the geographical location of each designated station.

To determine whether the potential for competition exists between the dominant jellyfish present (*C. fuscescens*) and forage fishes, we estimated their spatial overlap for each year using several measures operating at different scales. At the cruise level of variability, we first determined the center of gravity (CG) and the inertia (*I*) of the distributions of *C. fuscescens* and each of the forage species. Specifically, following Woillez et al. (2007), the CG was defined as follows:

$$CG = \frac{\sum_{i=1}^N x_i z_i}{\sum_{i=1}^N z_i} \quad (1)$$

with sampled population abundances (z_i) at locations (x_i , short for 2-dimension notation [x, y]). CG is interpreted as the mean spatial location of the surveyed population. Next, we calculated the inertia of the location of individuals in the population:

$$I = \frac{\sum_{i=1}^N (x_i - CG)^2 z_i}{\sum_{i=1}^N z_i} \quad (2)$$

defined as the mean square distance between a positive catch location and the CG of the population. Then, from CG and *I* calculations we compared the geographic overlap of different species using the Global Index of Collocation (GIC; Woillez et al. 2007).

The GIC was calculated by taking the distance between the CGs of both species (ΔCG) and their respective inertias (I_1 and I_2):

$$GIC = 1 - \frac{\Delta CG^2}{\Delta CG^2 + I_1 + I_2} \quad (3)$$

This index calculates the extent to which 2 populations are geographically distinct, by comparing the distance between their CGs and their respective inertias (Bez & Rivoirard 2000, Woillez et al. 2009). The index ranges between 0, in the extreme case, when no individuals of either of the 2 species co-occur at any sample location, and 1, where the 2 CGs coincide.

Next, we compared overlap at the station level using the empirical station-by-station catches subjected to a Cramér-von Mises randomization test (Syrjala 1996). The population densities are sampled at random, and a spatial distribution function is fit across the study area. In this analysis, a single test statistic Ψ was calculated for each pairing of *C. fuscescens* and a forage fish for each survey (month/year) using the function Syrjala in the *ecspa* package in the R programming language (<http://cran.r-project.org/web/packages/ecspa/index.html>; last accessed 2 November 2012). Significance of the spatial overlap was calculated based on 9999 random permutations of the data. This test is sensitive to differences in the way the populations are distributed across the study area but insensitive to differences in abundance between the 2 populations.

Finally, we examined the degree of spatial overlap of all 3 forage fish species combined with *C. fuscescens* using geostatistical methods similar to those described in Brodeur et al. (2008). As some cruises had extreme outliers, we first removed those values and replaced them with the next highest value, as suggested by Chiles & Delfiner (2012). Kriging estimators are sensitive to the presence of a few unusually large (or sometimes small) values in the data (i.e. outliers). Chiles & Delfiner (2012) suggest reducing the largest outliers to the value of the upper limit of the range of values not including the outlier, leaving all others unchanged, as a reasonable compromise to handle such outliers. The data were explored in the geostatistical analyst extension of ArcGIS (ESRI, v10) to determine whether the data approached a normal distribution and whether there were directional trends needing to be incorporated when fitting the predictive model (Johnston et al. 2001). Data were $\log_{10}(x + 1)$ transformed to reduce skewness and kurtosis. The data were then tested for overall spatial autocorrelation using Moran's *I* test in ArcMap Spatial Analyst with Euclidean distance method and a minimum distance threshold of 20 km². Data were determined to be significantly autocorrelated at p -values ≤ 0.05 .

Continuous coverage layers of *C. fuscescens* and combined forage fish distributions were produced

using Geostatistical Analyst in ArcGIS. Observed values at stations were used to interpolate predicted values at all other locations within the shelf area surveyed each summer and fall. Given the distance between stations, maps are intended to elucidate broad-scale patterns in the spatial distribution of forage fish and jellyfish rather than represent small-scale processes (Brodeur et al. 2008). Ordinary kriging models were fit for each \log_{10} -transformed data set, removing any first- or higher-order trends when observed. In instances in which spatial autocorrelation (overall or directional) was not detected, inverse distance weighting was used to produce continuous coverage layers. Geostatistical results were evaluated using cross-validation. Multiple models of each \log_{10} -transformed jellyfish and combined forage fish data set were evaluated and compared. Models whose mean error, root-mean-square error, average standard error, and root-mean-square standardized error values were closest to target values described by Johnston et al. (2001) were selected to create the continuous coverage layer. Predicted values were then aggregated into 3 classes to illustrate areas where *C. fuscescens* or summed forage fish were absent (biomass = 0), present (biomass > 0), and highly abundant (biomass \geq 75th quantile). We then produced polygon features that estimated where *C. fuscescens* and the summed fish overlapped at any level (both values >0) and where they had the highest overlap (greater than the 75th percentile for both) in the USA Contiguous Albers Equal Area Conic USGS projection coordinate system. The area within each polygon feature was then expressed in square kilometers. Percent overlap area was then calculated by dividing the area of the polygon feature where distributions of *C. fuscescens* and combined forage fish overlapped by the total area surveyed (km^2) \times 100. Percent spatial overlap was also calculated by sample stations as follows: (number of stations with *C. fuscescens* and a forage fish species \times 100 / (number of stations with a forage fish species)).

To examine whether years with high *C. fuscescens* abundance have the potential to negatively affect the abundance of any of the forage fishes, we estimated the mean standardized densities (number per km^2) for the entire shelf region sampled for each year and fit linear correlations between the densities of *C. fuscescens* and each of the forage fish species without temporal lags for each sampling month and year. Due to potential sampling biases for small pelagic forage fishes known to have patchy distributions, we adjusted our yearly abundance values in our sampling with scaling factors based on resource assess-

ments of the proportion of the total population that is within the NCC (see Ruzicka et al. 2012 for more information).

We analyzed the potential impact that increasing *C. fuscescens* abundances would have on forage fishes and other pelagic planktivores within the NCC using a modified version of the NCC end-to-end model described in Ruzicka et al. (2012, 2013). The NCC end-to-end model describes the flow of energy through the ecosystem starting with the input of nutrients, through the production of phytoplankton, zooplankton grazers, fish, seabirds, mammals, and fisheries, to detritus and back to recycled nutrients, accounting for production losses physically exported from the system (Steele & Ruzicka 2011). The model domain covers the continental shelf off the coasts of Oregon and Washington. In terms of functional groups, the model has 3 nutrient pools (nitrate, surface ammonium, and sub-surface ammonium), 78 living groups representing both the pelagic and benthic communities, and the invertebrate and vertebrate egg pools, 3 detritus groups, and 17 fisheries and gear types. The model was informed by a combination of contemporaneous bottom-trawl surveys (e.g. Keller et al. 2012); pelagic community surveys of plankton, fish, and seabirds (Brodeur et al. 2005, Morgan et al. 2005, Emmett et al. 2006, Zamon et al. 2013); fish and mammal stock assessments (e.g. Kaplan & Helser 2007, Carretta et al. 2009); and fishery harvest and discard statistics (PacFIN, pacfin.psmfc.org; RecFIN, recfin.org) from the past 15 yr.

To examine the impact that changes in jellyfish and forage fish abundances have on each other, we conducted a short series of structural scenarios. Structural scenarios estimate the immediate implications of imposed changes to trophic network structure, i.e. changes to energy flow along one or several trophic pathways or to the abundance of any group or fishery harvest rate. Structural scenarios show the cumulative change in energy transfer to each functional group via all direct and indirect trophic paths (Steele 2009).

We first simulated the impact of a 50% increase in *C. fuscescens* abundance over their mean summer (1999–2011) abundances. In separate scenarios, we increased the abundances of the 3 forage fishes by similar proportions (+50%) and estimated their individual effects on *C. fuscescens* and other components of the ecosystem. In this set of scenarios, functional relationships between predator and prey were linear, and the total predation pressure upon each prey group was held constant. A forced increase in the consumption rate of the modified group, jellyfish or

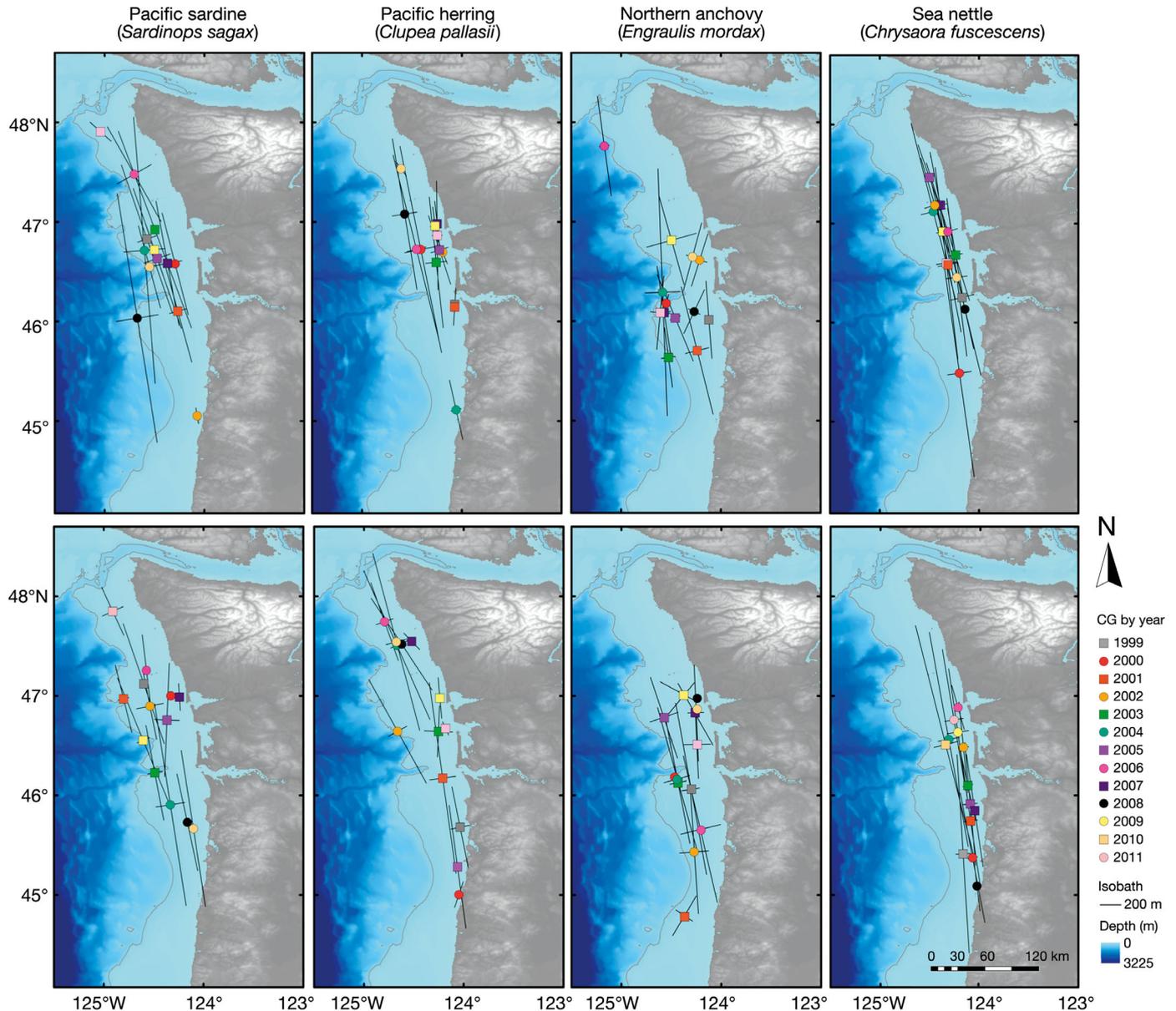


Fig. 2. Distribution of the center of gravity (CG) and axes of inertia for *Chrysaora fuscescens* and the dominant 3 forage fishes in June (top panels) and September (bottom panels) for 1999–2011

forage fish was offset by reducing the consumption rates of its direct competitors in proportion to their relative importance as consumers in the un-modified model. In all scenarios, diets and physiological parameters were held constant for all trophic groups. Scenario effects are expressed in terms of change to group production rates. As an index of our level of confidence in the scenario estimates, each scenario was run on 125 thermodynamically balanced Monte Carlo models randomly sampled from pre-defined uncertainty distributions about each biomass, diet, and physiological parameter (see Ruzicka et al. 2013 supplementary material).

RESULTS

Spatial overlap between *Chrysaora fuscescens* and forage fishes

The distributions of *Chrysaora fuscescens* and forage fish as measured by their CGs showed both monthly and annual shifts in location. While the CGs of *C. fuscescens* varied substantially along the shelf between years, they showed relatively little variation across the shelf and were found within a narrow band 30–40 km off the coast during all June cruises (Fig. 2). In contrast, the forage fishes demonstrated

much more cross-shelf variability in addition to latitudinal variability in CG. Pacific herring were found the furthest inshore of the 3 species and northern anchovy further offshore, with their CGs often situated near the shelf break (Fig. 2). Similar results were found in the September cruises, although the CGs were found further south than in June, especially for *C. fuscescens* and northern anchovy (Fig. 2). Pacific sardine and northern anchovy were generally found further offshore than *C. fuscescens*.

Monthly values of the GIC for northern anchovy and *C. fuscescens* were coherent from year to year, such that in a year when there was overlap in June, there was also overlap in September, or when they did not overlap in June, they also did not overlap in September. The exceptions were in 2003 and 2008, when there was substantial discrepancy between the 2 months (Fig. 3). For Pacific herring, the GIC with *C.*

fuscescens showed the same pattern for June and September until 2002, but then these species were inversely related until 2008, when they became synchronous again. Pacific sardine showed similar trends between months, but the magnitude of overlap was often different, with the exception of 2003, 2009, and 2011 (Fig. 4). Examination within the same

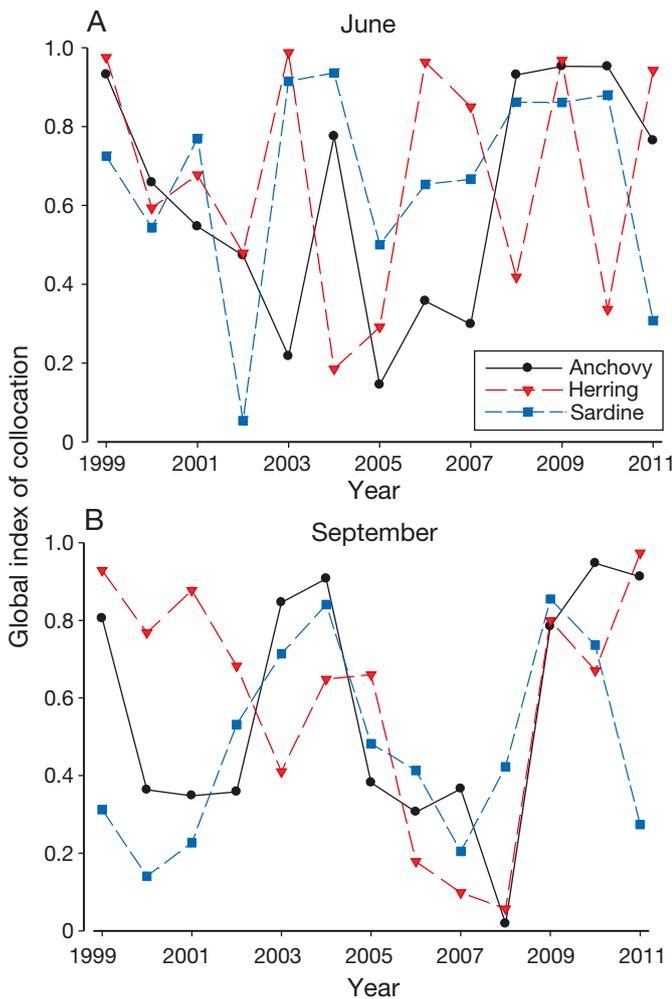


Fig. 3. Interannual variability of the global index of collocation with *Chrysaora fuscescens* for the dominant 3 forage fishes for June (A) and September (B)

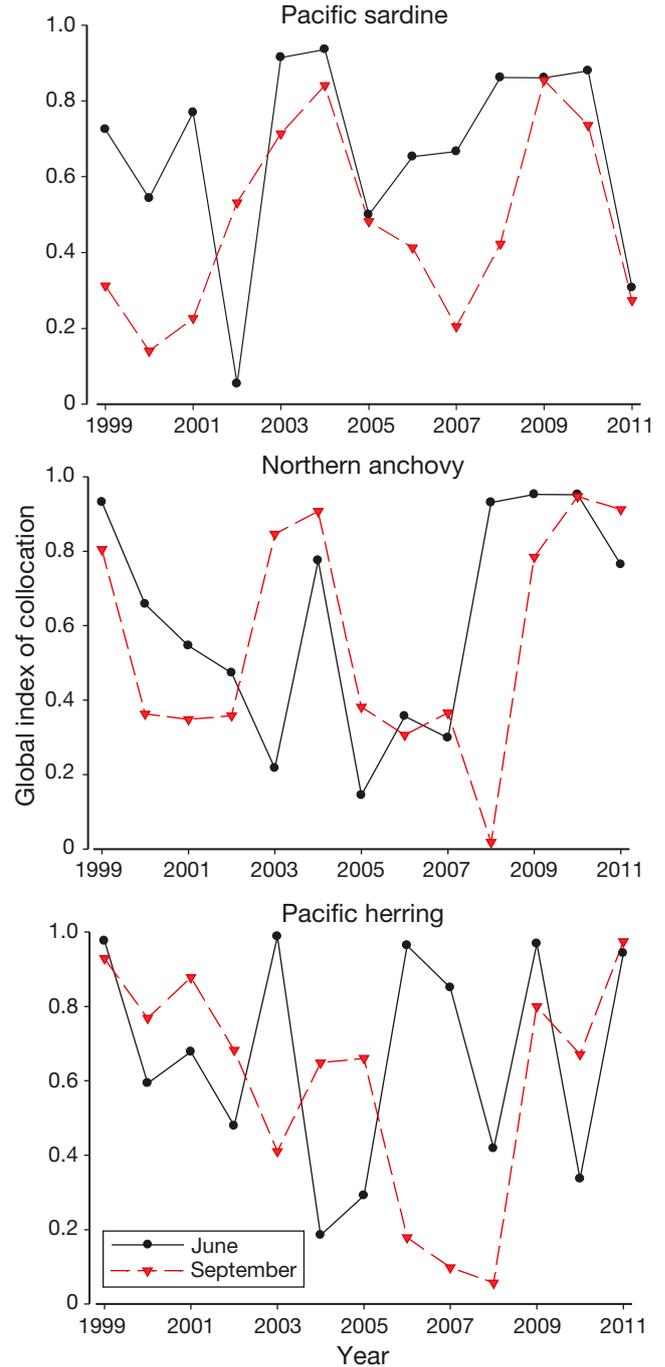


Fig. 4. Monthly variability of the global index of collocation with *Chrysaora fuscescens* for the dominant 3 forage fishes by year

Table 1. Cramér-von Mises p-values for the difference between the spatial distributions of *Chrysaora fuscescens* and forage fishes in June and September. ns: p > 0.05

Year	June			September		
	Herring	Sardine	Anchovy	Herring	Sardine	Anchovy
1999	ns	ns	ns	ns	ns	ns
2000	ns	ns	ns	ns	ns	ns
2001	ns	ns	ns	ns	0.001	0.003
2002	<0.001	<0.001	0.011	ns	0.001	0.025
2003	ns	ns	<0.001	ns	0.024	ns
2004	<0.006	ns	0.038	ns	0.001	0.003
2005	ns	ns	0.031	ns	0.038	ns
2006	ns	ns	ns	0.004	ns	0.006
2007	ns	ns	0.018	0.044	ns	ns
2008	<0.001	<0.001	ns	0.009	ns	ns
2009	ns	ns	ns	ns	ns	ns
2010	0.005	0.020	ns	ns	ns	ns
2011	ns	<0.001	0.002	0.033	0.003	ns

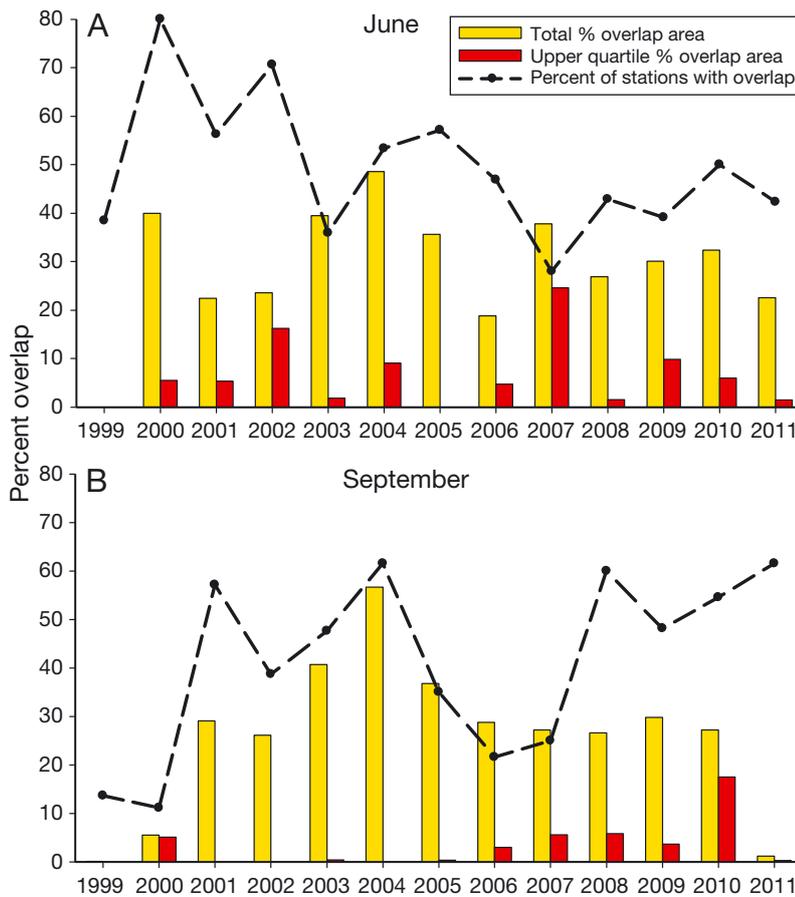


Fig. 5. Interannual variability of the spatial overlap of the biomass of *Chrysaora fuscescens* and the combined biomass of dominant 3 dominant forage fishes for the (A) June and (B) September cruises by year based on GIS interpolated maps. Shown are the total overlap area as a percent of the total area sampled, the area of overlap of the pixels containing >75% of the biomass of both *Chrysaora fuscescens* and the forage fishes, and the total percentage of stations where overlap occurred (points and dashed lines) for each June cruise

month but across years shows high variability. However, a high (>0.8) level of collocation was observed for at least 2 of the fish species in June 1999, 2003, 2008, and 2010, and for all 3 species in 2009. September overlap values overall were generally lower than June and were high among at least 2 species only in 1999, 2004, 2009, and 2011 (Fig. 4).

The Cramér-von Mises tests indicated there was high spatial overlap between *C. fuscescens* and dominant forage fishes during summer and fall most years (Table 1). More than half of the comparisons for the June cruises showed no significant differences in the distribution of jellyfish and the individual forage fishes, and all 3 had distributions similar to that of *C. fuscescens* in 1999 through 2001, 2006, and 2009. Only June 2002 showed all 3 forage fishes having different distributions than *C. fuscescens*. Pacific herring and Pacific sardine showed the highest overlap with *C. fuscescens* distributions in June, with both showing 9 of 13 comparisons that were not significantly different (Table 1). For September, the same pattern held true—high spatial overlaps by year, with 1999, 2000, 2004, 2009, and 2010 showing no significant difference in the distribution for all 3 forage fishes with *C. fuscescens* (Table 1). However, in this comparison it was northern anchovy showing the highest overlap, with 77% of tests (10 of 13) not significantly different, followed by Pacific herring 69% (9/13) and Pacific sardine 62% (8/13).

Based on the geostatistical analysis for the June cruises, the spatial overlap between the biomass of *C. fuscescens* and the combined biomass of the 3 forage fish species of the total sampling area varied between 18.8% (2006) and 48.6% (2004), with an overall average of 31.53% (Fig. 5A). When limited to the area circumscribed by the 75th percentile biomass of both groups, the overlap

decreased to a mean of 7.2% of the sampled area, ranging from 0% in 2005 to a maximum of 24.6% in 2007 (Figs. 6A & 7). These interpolated values of overlap were not related to the percentage of stations within each cruise that showed overlap of *C. fuscescens* and any forage fish presence (data points and dashed line in Fig. 5). For the September cruises, although the spatial overlap areas were generally comparable to June, the areas with the highest overlap of biomass (75th quartile) were comparatively low (Fig. 5B). The 2001 to 2005 period was particularly striking in this regard, with high spatial overlap by overall area and number of stations, but almost no overlap at the highest biomass levels of the 2 groups.

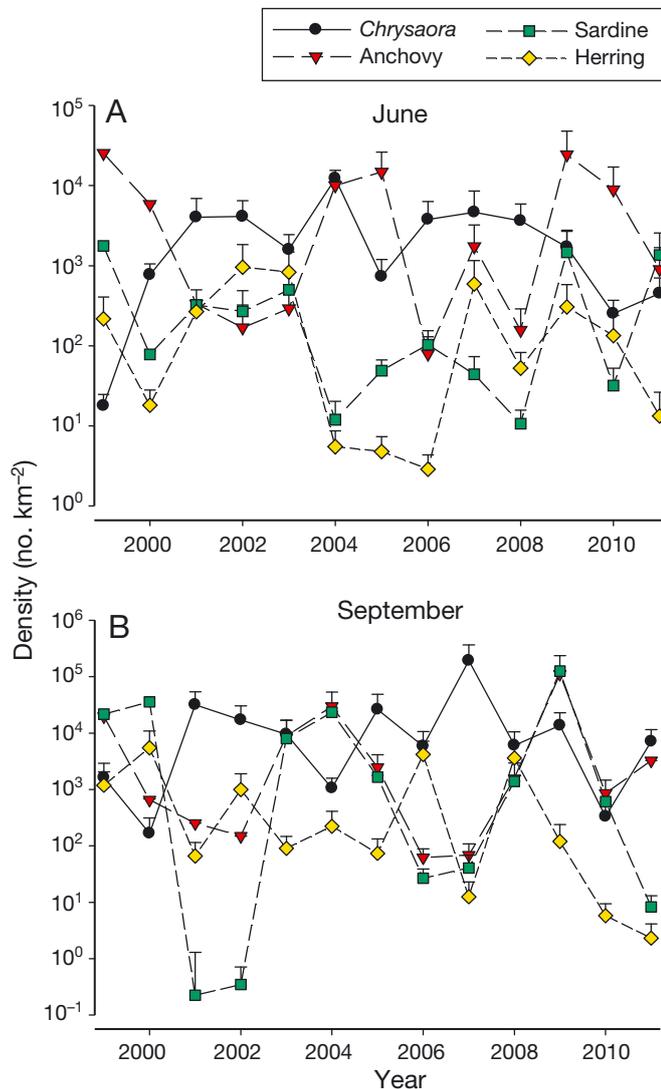


Fig. 6. Mean (± 1 SE) standardized densities of *Chrysaora fuscescens* and the dominant 3 forage fish species by year for June (A) and September (B) cruises

Covariation in medusa and forage fish abundance

With the exception of the low density in June 1999 and high density in September 2007, the density of *C. fuscescens* tended to fluctuate by an order or 2 of magnitude between years, whereas the forage species show more dramatic interannual changes in density (e.g. 2 to 3 orders of magnitude; Fig. 6). The density trajectory of the jellyfish was generally inversely related to the forage species. The correlation bi-plots of all species pairs for both months indicated a negative correlation between jellyfish density and fish density in all cases, although neither the June nor September relationships for Pacific herring were significant (Fig. 8).

Modeled competitive impacts

Model estimates of the net direct and indirect competitive impacts of a 50% increase in *C. fuscescens* abundance on the production rates of other major components of the NCC food web are shown in Fig. 9A. All trophic groups were negatively affected, with the exception of small copepods (as consumers of phytoplankton and micro-grazers, small copepods are not competitors of *C. fuscescens*). The production rates of all 3 forage species decreased, but anchovies were the most strongly affected. In contrast, when the abundances of the 3 forage fish species were increased, they individually had a negative effect on the other forage fish and other species that feed at a similar trophic level (small squid, shad, and smelt), but increased forage fish abundance had positive effects on higher trophic level taxa such as pinnipeds and sooty shearwaters (Fig. 9B–D). Pacific sardines had the greatest impact on other species and Pacific herring the least. In all cases, *C. fuscescens* had a larger impact on the forage fish than the individual forage fish had on *C. fuscescens*, although the differences were not pronounced (1–4% greater negative impact; Fig. 9).

DISCUSSION

Our study is the first attempt to examine seasonal and interannual spatial overlap between a dominant scyphomedusan species and several important forage fish species in the California Current. Our use of fisheries-independent data collected in a consistent manner over more than a decade allowed us to examine interannual changes in spatial resource use.

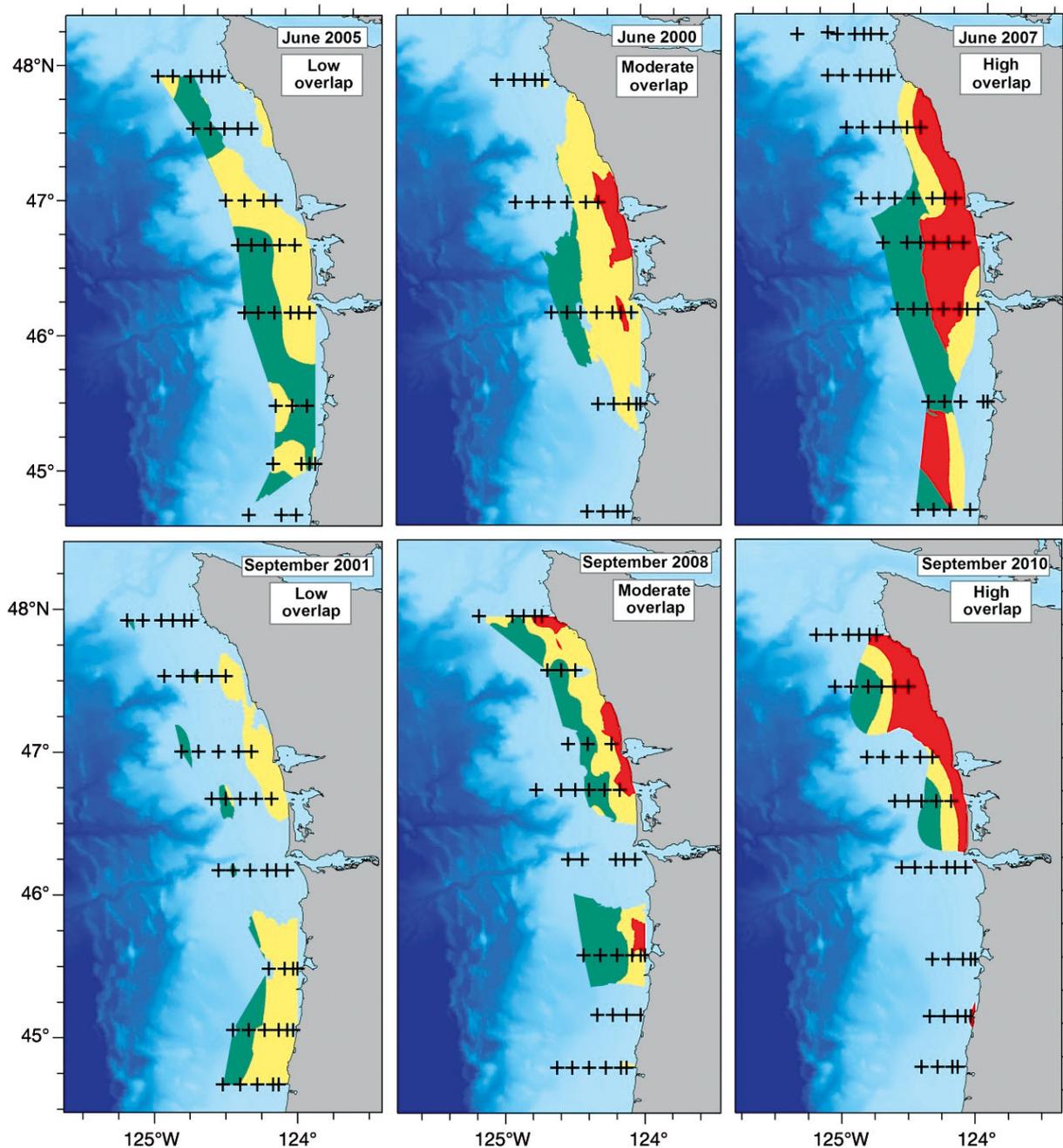


Fig. 7. GIS spatial maps for selected cruises showing low, medium and high overlap for June (top panels) and September (bottom panels) cruises. Shown are the sampling stations (crosses) and the occurrence of forage fish (green area), overlap between forage fishes and jellyfish (yellow area) and region of maximum overlap (>75th percentile of biomass of both combined forage fish and jellyfish; red area)

We also examined these interactions at several different scales, although potential limitations exist based on sampling design and gear selectivity at the different scales. The trawls we used to quantify catch, although relatively short in duration, sampled a kilometer or more in the horizontal direction, thus potentially integrating several water masses with different

jellyfish and fish densities. Both groups are likely to be aggregated on smaller spatial scales (e.g. swarms and schools, respectively), which may inflate the variance between stations. Clearly, such interactions are best examined at relatively fine scales (at a particular sampling site) with detailed resolution on the horizontal and vertical spatial overlap as well as site-

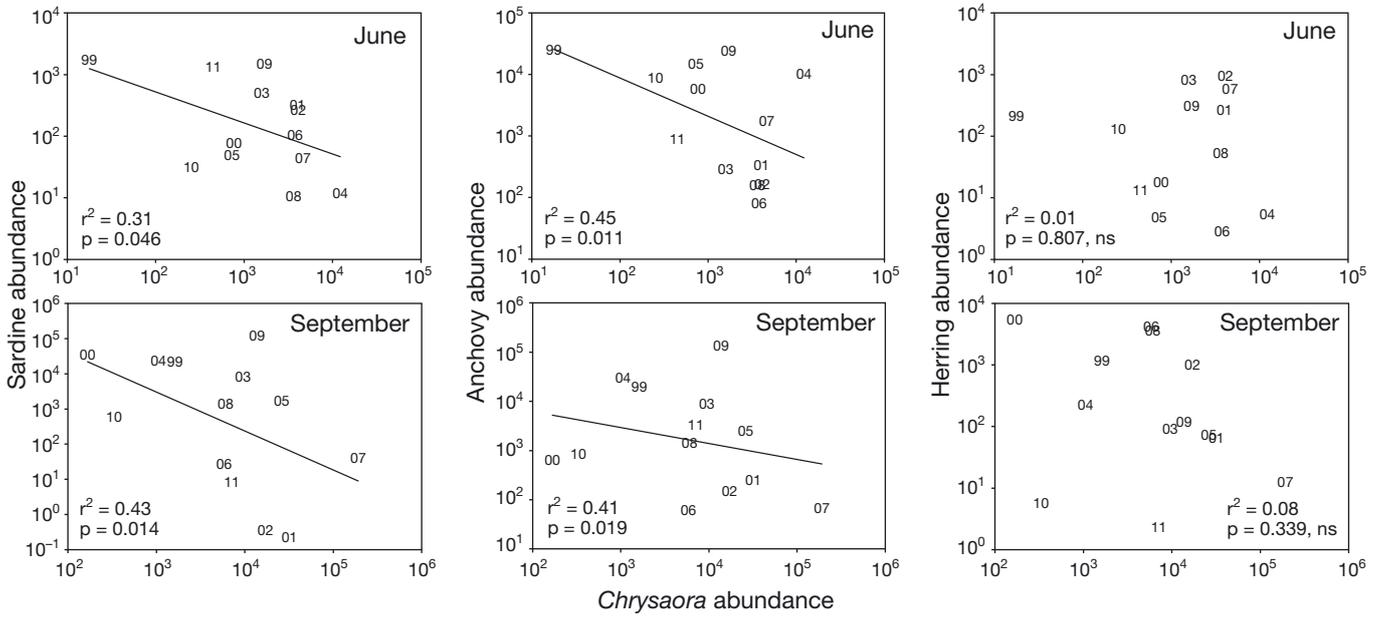


Fig. 8. Relationship between log abundances of *Chrysaora fuscescens* and the 3 forage fishes for June (top panels) and September (bottom panels). Also shown are the coefficients of determination (r^2) and significance of the relationship (p-value). ns: $p > 0.05$

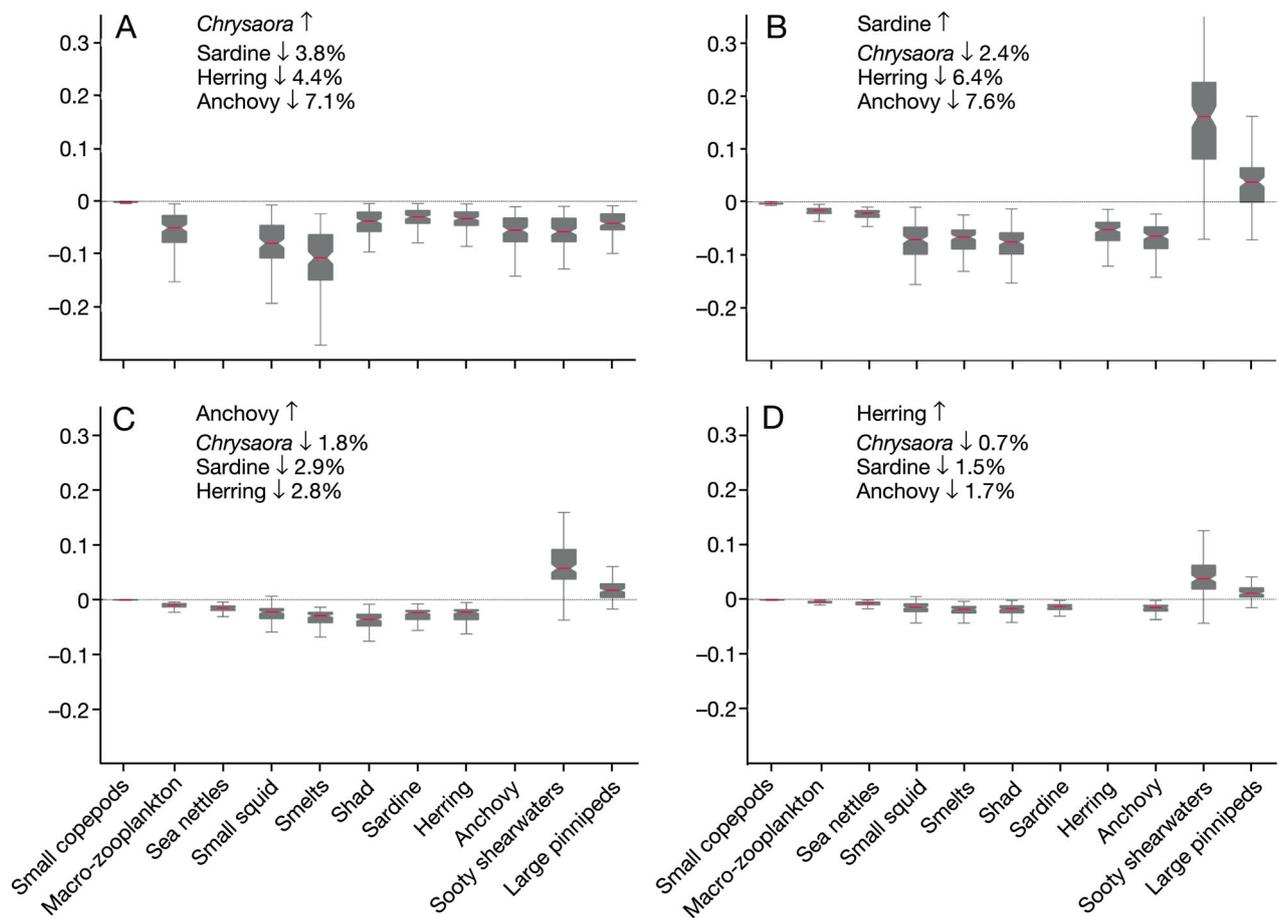


Fig. 9. Scenarios examining the effect of increasing the abundance of (A) *Chrysaora fuscescens* by 1.5-fold on the dominant 3 dominant forage fishes and other key food web representatives and (B) the opposite effect of increasing sardine, (C) anchovy and (D) herring on *C. fuscescens* (shown in x-axis labels as sea nettles) production. For each box, the red line is the median, the notch marks the 5% range, the top and bottom of the boxes are 25% and 75% percentiles, and the whiskers cover all observations within 150% of the inter-quartile range

specific diet data. Although we presently have diet data for the forage fishes over multiple years (Hill et al. unpubl. data), obtaining trophic habits of jellyfish is more problematic requiring less damaging sampling techniques than trawling (Suchman et al. 2008).

We do not adjust for day-night differences in abundance of the forage fishes (Krutzikowsky & Emmett 2005, C. Barceló unpubl. data) and our overall densities (and overlap values) for these species are only reflective of daytime densities in the upper 20 m of the water column. Our sampling occurred during the daytime, and given the diel migrations of some forage fish species, we speculate that spatial overlap may increase at night when some forage species occur in the shallower layers that the jellyfish occupy throughout the diel period (Emmett et al. 2004, Krutzikowsky & Emmett 2005, Suchman et al. 2012). Suchman & Brodeur (2005) did not find day/night differences in the catches of *Chrysaora fuscescens* at 2 diel stations at the southern end of our sampling area. Further studies are necessary to examine these differences, and they require spatially explicit sampling of the same region during the day and night in order to determine the overlap of forage fish with *C. fuscescens* throughout a full diel cycle.

The extent of spatial overlap between planktivorous fishes and large siphonomedusae varied annually and to a lesser degree over the summer period. A detailed analysis of the local and regional environmental factors that may lead to high overlap in some years and not others is beyond the scope of the present study, but some generalities can be gleaned from our data. For example, years with high interspecific spatial overlap (1999, 2008, and 2009) tended to be cooler and more productive La Niña years with strong upwelling, whereas the warm, low productivity period showing delayed or low cumulative upwelling from 2005–2007 and 2011 had generally lower overlap (see NOAA Ocean Indicator Web Page, www.nwfsc.noaa.gov/research/divisions/fe/estuarine/oeip/g-forecast.cfm#Table2). It was not surprising that all 3 forage species did not show the same annual or seasonal trends in abundance or spatial overlap with *C. fuscescens*. Previous studies of the community structure of these forage species indicated that they do not show synchronous population trends and often show different responses to the same environmental variable (Brodeur et al. 2005, Emmett et al. 2006, Litz et al. 2014). Indeed, Litz et al. (2014) found that these forage fishes showed a strong association with different axes in multivariate space and Brodeur et al. (2005) found that they were indicator species for different cluster groups. Pacific her-

ring and, to a lesser extent, northern anchovy are associated with cooler, low-salinity water, whereas Pacific sardine are found in warmer, more saline waters (Brodeur et al. 2005, Litz et al. 2014). *C. fuscescens*, in contrast, generally are in highest abundance in cool but highly saline nearshore waters that are likely to be recently upwelled (Suchman et al. 2012).

Years of increased spatial overlap, high abundances of large jellyfish, or both can substantially affect the production of pelagic fishes and the fisheries that depend on them in several ways. The most direct impacts are the loss of fisheries catch or opportunities due to the clogging or fouling of nets or spoiling of catch in commercial fisheries operations (Graham et al. 2003, in press, Purcell et al. 2007, Kim et al. 2012, Quiñones et al. 2013). Another direct, but somewhat less quantifiable, impact is through predation by jellyfish on the earlier life history stages of fish, thereby reducing the realized adult population (Möller 1984, Purcell & Grover 1990, Purcell & Arai 2001). Finally, a more subtle and much more difficult to quantify impact stems from the spatial and dietary overlap of many jellyfish and planktivorous fishes (Purcell & Sturdevant 2001, Brodeur et al. 2008, Shoji et al. 2009). Studies suggest that an increase in the jellyfish to fish ratio, either through increases in jellyfish or decreases (possibly due to fishing) in fish populations is highly detrimental to the sustainability of fish populations (Daskalov 2002, Lynam et al. 2006, Uye 2011, Roux et al. 2013). The nonvisual feeding mechanism of jellyfish allows them to outcompete many planktivorous fishes under highly eutrophic conditions (Haraldsson et al. 2012), and recent studies have indicated that jellyfish food searching and capture abilities are equivalent to, or in some cases exceed, those of planktivorous fishes (Acuña et al. 2011, Hays et al. 2012, Gemmell et al. 2013). Therefore, although most upwelling systems show a propensity to be dominated by small planktivorous fishes, recent evidence suggests that disturbed systems may favor gelatinous forms over fish through exploitative competition, thereby preventing recovery of depressed fisheries stocks, as observed in the Benguela Current off Namibia (Flynn et al. 2012, Roux et al. 2013).

Competition is well known to occur in marine systems, especially among closely related species or in sessile organisms (Branch 1984). Our ability to detect competition in highly mobile or even somewhat sedentary marine fishes is hindered by the inherent difficulty in performing controlled experimentation with fish (Hixon & Jones 2005, Hixon 2006). Link &

Auster (2013) reviewed the challenges in documenting competition at the scales relevant to marine fishes, and recommended that 4 criteria should be met to infer competition: (1) opposing population trajectories, (2) spatio-temporal overlap, (3) high dietary overlap, and (4) some indication of resource limitation. Brodeur et al. (2008) examined both dietary and spatial overlap between *C. fuscescens* and the next most abundant large scyphomedusae (*Aurelia labiata*) with 9 species of pelagic fishes collected during a single cruise in August 2002, in a dynamic region just south of the present study (Newport, OR, to Crescent City, CA). They found the highest trophic overlaps (all ~60% or higher) with *C. fuscescens* for the 3 species examined here as well as Pacific saury *Cololabis saira*, although the latter was generally collected at offshore stations and had no spatial overlap with this jellyfish species. Although the 3 forage fishes showed somewhat moderate spatial overlap with *C. fuscescens* (21.6–33.5%) due to their low abundance in this region, they showed the highest potential niche overlap (a combination of spatial and temporal overlap indices) among all the species examined (Brodeur et al. 2008). These authors suggested that the low spatial overlap between the jellyfish and forage fish on an individual station level may be due to indirect or 'interference' competition (Case & Gilpin 1974), whereby dense aggregations of *C. fuscescens* with their long tentacles extending many meters below the bell may exclude planktivorous fishes from feeding in the same area, thus limiting their available habitat. Another explanation is that environmental conditions affecting the food webs that are beneficial to jellyfish may be detrimental to planktivorous fishes, leading to some spatial segregation, as hypothesized for the disjunct spatial patterns between the 2 groups seen in the nearby Puget Sound (Rice et al. 2012).

We do not have a sufficiently long time series to robustly test the first of Link & Auster's (2013) criteria based on opposing population trajectories, but evidence presented here indicates that cruises that showed high *C. fuscescens* abundance generally corresponded to low abundance of the 3 forage species, and vice versa. It is not possible to ascertain whether this pattern was the result of direct competition or even interference competition as describe above, since this inverse pattern could also arise from differences in environmental preferences. It could also be the result of top-down predation on the early stages of these forage fish, but such effects would require lagged relationships with age-structured data, which we lack. Large forage fish populations could also

keep *C. fuscescens* in check by consuming the early pelagic stages (ephyra) of the jellyfish that are present in surface waters during early spring, but unfortunately we have no sampling at that time of the year. Thus the underlying mechanisms leading to the inverse relationships between *C. fuscescens* and the forage fishes are unknown and are likely to be due to several complex ecological relationships, of which competition is only one hypothesis.

Finally, even the highest degree of spatial and temporal overlap could be tolerated with little effect on either competitor if the quantity of shared resources exceeds the needs of both competitors. As affirmed by Link & Auster (2013), proving that resources are limiting in open marine systems is likely infeasible at the scales of interest. They suggest instead that food web simulation models may be the only way to 'test' this hypothesis, although there are limitations to this approach. In our modeling exercises, we used a taxonomically detailed end-to-end model (Ruzicka et al. 2012) based on an earlier ECOPATH mass balance model developed for the NCC (Ruzicka et al. 2007). The results included herein suggest some support for the food limitation hypothesis in that running the model with *C. fuscescens* abundances increased by half again their long-term mean values led to decreased production of all 3 forage fishes and of several higher trophic levels (pinnipeds and seabirds). Similar increases in each of the other forage fishes negatively impacted jellyfish abundance, but to a smaller degree, while actually benefitting the same higher trophic levels. The latter effect is due to comparatively high pass-through of energy via forage fishes to higher trophic levels in the NCC food web, compared with jellyfish, termed the 'trophic reach' (Brodeur et al. 2011, Ruzicka et al. 2012). This discrepancy is in part due to the deemed unimportance of these large medusae to higher trophic levels (i.e. trophic dead end). There may be biases in the estimates of gelatinous prey in many predator stomachs (Pauly et al. 2009), which may underestimate the importance of jellyfish to the upper food web. However, most fish species in this region consume their prey as whole items and (with few exceptions such as the ocean sunfish *Mola mola*) do not have a sufficiently large gape to consume the larger medusae that are present in the summer, although many smaller gelatinous zooplankton present (ctenophores and salps) may be eaten by some fish species (Mianzan et al. 1996, 2001, Purcell & Arai 2001, Arkhipkin & Laptikhovskiy 2013, R. D. Brodeur unpubl. data).

The results presented herein have important prospects for ongoing ecosystem-based management

efforts in the California Current (Field & Francis 2006, Levin et al. 2009). In a study of 7 food webs around the globe, Samhuri et al. (2009) found that overall jellyfish biomass and the forage fish to jellyfish ratio were among the strongest indicators of ecosystem health in most systems. Data on jellyfish abundance also have been shown to exhibit utility in detecting ecosystem thresholds (Samhuri et al. 2010). At the present time, we do not know whether human activities (e.g. greenhouse gas emissions, fishing, pollution, and eutrophication) have modified the balance between these forage fishes and jellyfish, or in some way affected their spatial structure (Ciannelli et al. 2013), although our data may provide important baselines that can be used to gauge the effects of any future changes in these stressors. As the California Current becomes increasingly hypoxic (Pierce et al. 2012), gelatinous predators that appear to be little affected by low oxygen levels (e.g. Breitburg et al. 1994, Shoji et al. 2009) may be at a competitive advantage relative to most fishes, particularly if the habitat that these fishes can occupy becomes spatially compressed (Prince & Goodyear 2006). Once the balance is tipped towards gelatinous zooplankton in coastal systems, it may be challenging to return the ecosystem to a fish-dominated state (Richardson et al. 2009, Uye 2011).

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