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Use of genetic stock identification data for comparison of the ocean spatial distribution, size-at-age, and fishery exposure of an untagged stock and its indicator: California Coastal versus Klamath River Chinook

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Abstract

Managing weak stocks in mixed-stock fisheries often relies on proxies derived from data-rich indicator stocks. For example, full cohort reconstruction of tagged Klamath River fall run Chinook salmon (*Oncorhynchus tshawytscha*) of northern California, USA, enables the use of detailed models to inform management. Information gained from this stock is also used in the management of the untagged, threatened California Coastal Chinook (CCC) salmon stock, by capping Klamath harvest rates. To evaluate use of this proxy, we used genetic stock identification (GSI) data to compare the two stocks' size-at-age and ocean distribution, two key factors influencing fishery exposure. We developed methods to account for both sampling and genetic assignment uncertainty in catch estimates. We found that, in 2010, the stocks were similar in size-at-age early in the year (age-3 and age-4), but CCC fish were larger later in the year. The stocks appeared similarly distributed early in the year (2010), but more concentrated near their respective source rivers later in the year (2010 and 2011). If these results are representative, relative fishery impacts on the two stocks might scale similarly early in the year but management changes later in the year might have differing impacts on the two stocks.

Introduction

Pacific salmon (genus *Oncorhynchus*) support fisheries of great economic and cultural importance, provide important food sources for marine (Ford et al. 1998) and terrestrial (Hilderbrand et al. 1999) predators, and provide key ecosystem services (Wilson and Halupka 1995; Levi et al. 2012). Balancing benefits to fisheries and ecosystems requires careful and informed management, particularly with many Pacific salmon stocks at reduced abundance and/or considered at risk of extinction (Good et al. 2005). Such management can prove particularly challenging because multiple stocks originating from different river systems co-occur in the same ocean area (Weitkamp and Neely 2002; Trudel et al. 2009; Weitkamp 2010), leading to mixed-stock fisheries in which salmon from multiple rivers and of multiple ecotypes are harvested simultaneously. This has led to "weak-stock management", where total harvest is constrained to keep impacts on all managed stocks within acceptable levels (Pacific Fishery Management Council 2012a,b). Often this is accomplished via time- and area-specific constraints on total harvest or fishing effort, attempting to maximize overall harvest opportunity without exceeding the acceptable level of impacts on weak stocks.

Information on stock-specific harvest is often limited. Coded-wire tags (CWT, Nandor et al. 2010) provide extensive information on tagged fish including their stock of origin and brood year, allowing cohort reconstructions (Hilborn and Walters 1992; Goldwasser et al. 2001; Mohr 2006) that estimate demographic parameters and exploitation rates. This information is, of course, only available for tagged stocks, so managers often use the information derived from tagged stocks as indicators of impacts on untagged stocks of concern (as well as the untagged portion of partially tagged stocks). The success of resulting management decisions depends on the appropriateness of the assumption that indicator stocks accurately reflect impacts on the stock of interest, which would require that the two stocks are similarly exposed to fisheries. Until recently there has been little opportunity to evaluate the concordance in exposure to fisheries between tagged, typically data-rich indicators and the untagged, typically data-poor stocks for which they are often proxies (but see Labelle et al. 1997, Weitkamp and Neely 2002, and Finding 5 of Hankin et al. 2005).

Genetic stock identification (GSI, Milner et al. 1985, Winans et al. 2001, Pacific Salmon Commission 2008), when combined with additional information, may allow tests for many aspects of assumed similarity between indicator and data-poor stocks. GSI can assign sampled fish to their most likely reporting group (stock or complex of stocks) of origin, typically with high confidence. The recent GSI sampling program for the California and Oregon commercial Chinook salmon (*Oncorhynchus tshawytscha*) fishery by the West Coast Salmon GSI Collaboration (`http://www.pcouncil.org/wp-content/uploads/INFO_SUP_RPT5_GSI_COLLABORATION_APR2012BB.pdf`) provides the first broad-scale, direct information on the ocean harvest of untagged stocks in salmon fisheries off of California and Oregon. Information obtained through this program can be combined with scale-derived ages, length measurements, and documentation of time- and area-specific fishing effort to estimate stock-specific spatial distribution and size-at-age, two significant factors influencing the degree to which individuals from a particular stock are vulnerable to fisheries. Direct estimation of fishery exploitation rates through cohort reconstruction is generally not possible for most untagged stocks, because the required suite of complete escapement, river harvest, and ocean harvest data for each age is not available. When direct comparisons of estimated harvest rates are not possible, comparisons between spatial distributions and size-at-age of tagged and untagged stocks can serve as useful indications of the likely relative impacts of ocean fisheries.

Our work is made possible by the ability of GSI to identify California Coastal Chinook salmon (hereafter CCC), defined as those populations spawning in coastal rivers from the Russian River in the south to Redwood Creek, Humboldt County, California in the north and making up the California Coastal Chinook Salmon Evolutionarily Significant Unit (ESU) (Williams et al. 2011), which is listed as threatened under the United States Endangered Species Act (ESA). No large-scale tagging of these fish occurs, and data on escapement are not sufficient to inform cohort reconstruction even if CCC were identified in the ocean catch (Williams et al. 2011; O'Farrell et al. 2012). As a result, the National Marine Fisheries Service (NMFS) implemented requirements for fishery compliance with the ESA based on a proxy determined for a well-studied indicator stock: fishery managers may target for an ocean harvest rate of age-4 Klamath River fall run Chinook (KRFC) salmon no greater than 16.0 percent (Pacific Fishery Management Council 2012c). O'Farrell et al. (2012) provides a summary of the development of this consultation standard. The fishing season is structured such that a model of KRFC ocean harvest (Prager and Mohr 2001; Mohr 2006) forecasts an ocean harvest rate that meets this standard. Harvest reflects the combined effects of area-specific fishing effort, how effort translates into site-specific catch, and retention of legal-sized catch. Thus harvest rates may vary among stocks for many reasons, such as their abundance, maturation and mortality schedules, distribution relative to fishing effort, and their size-at-age relative to legal minimum size limits.

Some of these metrics can only be estimated through a full cohort reconstruction, but GSI data on area- and time-specific harvest along with supplemental information on fish size and age allows estimation of spatial distribution and size-at-age for the CCC stock. If these factors are similar between the CCC and KRFC salmon stocks, it is reasonable to expect fishery exposure to covary among the two stocks - i.e. the proportions of the stocks that are vulnerable to fishing in a particular area or can be retained given a particular size limit should be similar. Conversely, differences in spatial distribution or size-at-age may reflect mechanisms whereby the two stocks could respond differently to changes in fishery management measures. Differences in spatial distribution may also result in differences in ocean environmental conditions experienced by the stocks and thus differences in natural mortality or maturation rates, which could affect the relative importance of harvest at different ages in driving the overall reduction in spawner numbers relative to unfished conditions.

Our objective was to compare fishery vulnerability between the CCC and Klamath River Chinook (KRC) stocks. We first estimated stock-specific size-at-age using length, scale-read age, and GSI data. We then compared ocean spatial distributions of CCC and KRC using a model developed to estimate local density using GSI and fishing effort data. We conclude with a discussion of the management relevance of fine-scale differences in vulnerability estimated for these two stocks.

Methods

Study system

The Klamath River basin supports both fall run and spring run Chinook salmon. The fall run is among the largest in the state of California, with pre-harvest ocean abundance estimates ranging between 6.8×10^4 and 1.4×10^7 during the period 1981-2011 (Pacific Fishery Management Council 2012b). The much less abundant and relatively data-poor spring run populations within the basin are genetically similar to the fall run populations and are not considered a distinct ESU (Williams et al. 2013). These stocks support commercial and recreational ocean fisheries as well as substantial in-river tribal and recreational fisheries. Fifty percent of the total KRFC harvestable surplus is allocated to river tribal fisheries; hence river fisheries (tribal and recreational) typically land more than half of the total realized harvest (Pacific Fishery Management Council 2012b). Salmon production in the basin is augmented by Iron Gate Hatchery on the Klamath River and the Trinity River Hatchery. Twenty-five percent of the Chinook salmon released from these hatcheries are marked with an adipose fin clip and tagged with a CWT.

The largest populations in the CCC ESU are likely in the Eel and Russian Rivers. Historically this ESU contained both fall and spring run populations (Bjorkstedt et al. 2005), but only the fall run remains, and at a significantly reduced abundance (Good et al. 2005). There is no current hatchery production within the ESU, only minor hatchery production in the last several decades, and no consistent, large-scale tagging. Details about data availability and the history of protective measures for CCC are summarized by O'Farrell et al. (2012).

Data sources

We analyzed data collected by the commercial fishery and partners in the West Coast Salmon Genetic Stock Identification Collaboration during 2010 and 2011. Effort data for both California and Oregon were tracked using hand-held global positioning system (GPS) units set to record vessel location at five-minute intervals. In 2010, the California fishery was constrained due to low abundance of Sacramento River fall run Chinook salmon (Pacific Fishery Management Council 2011), resulting in closures during much of the normal fishing season. The only commercial fisheries in 2010 in California waters were in the FB management area (areas are defined in Figure 1) for all of July and August, and for a few days (July 1-4 and 8-11) in areas south of FB. However, collection of GSI samples via non-retention fishing was allowed in many area-month combinations closed to commercial retention fisheries. These contracted fishing trips in California were constrained to remain within a single management zone in the ocean, allowing tracking of effort out of each port city as shown in Figure 1. Contracted fishing trips in Oregon were not constrained to management zones except during the months of June (KO only) and September.

For Oregon in 2010, and both states in 2011, there was a more extended commercial fishing season. Trips sometimes crossed multiple management zones, so area-specific effort was tracked in terms of hours spent in ocean areas as defined in Figure 1, with every 8 hours of effort counted as one day. Thus in Oregon, and for California in 2011, the data were analyzed at a coarser spatial scale than the 2010 California data. Note that we refer to ocean areas (Oregon, and California in 2011) using capitalized abbreviations while referring to individual ports (California in 2010) by their full names. Total fishing effort by expended by fishers while collecting GSI samples is summarized in Table 1. The total number of fish harvested by samplers on active sampling days in each area/port-month combination was also tracked. The number of fish successfully genotyped for each area/port-month combination is reported in Table 2. As described below, the uncertainty in stock-specific CPUE for a particular area/port-month combination is a function of effort, number of fish genotyped, and confidence in individual fish assignments.

Fish length and location of catch (GPS coordinates) were recorded for each sampled fish, with scales and fin clip samples collected for aging and genetic analysis. The most likely stock assignment, and an estimate of associated posterior probability, was determined using the program gsi_sim (Anderson et al. 2008), which uses well-established methods for genetic stock identification (Smouse et al. 1990; Paetkau et al. 1994; Rannala and Mountain 1997). In Oregon, genetic stock assignments were based on genotypes from a panel of 13 microsatellites, and compared to a baseline of 28,545 fish from 238 populations comprising 43 reporting units (Seeb et al. 2007). The Microsatellite Toolkit (Park 2001) was used to screen for cross-contamination of samples, which can occur during field or laboratory handling. Values of 90% matching alleles or greater were used to identify and exclude samples with identical or nearly identical genotypes (presumed to be multiple tissue samples from the same fish). Fish with data from fewer than 7 of 13 loci were excluded from further analysis. In California, the basis for assignment was a panel of 95 single nucleotide polymorphisms (SNPs) with reference to a baseline of 8,031 fish from 68 populations in 38 reporting units (Clemento et al. in review). An additional locus was employed that discriminates coho and Chinook salmon, to identify and eliminate miscategorized coho erroneously sampled as Chinook.

Details of the SNP baseline and assessments of its accuracy for GSI are reported fully in Clemento et al. (in review). The microsatellite baseline used in Oregon is a revised version of that reported in Seeb et al. (2007). We undertook a self-assignment analysis to assess the accuracy of each of these baselines for distinguishing fish from the CCC ESU and the Klamath River. Briefly, every fish, in turn, was left out of the baseline, the population allele frequencies were recalculated, and then, assuming a uniform prior over populations, the posterior probability that the fish originated from each of the populations in the baseline was calculated. Such calculations were performed using `gsi_sim` (Anderson et al. 2008) using the unit information prior on allele frequencies. These posteriors were summed over populations within each reporting unit to calculate the posterior probability that each fish originated from each of the different reporting units represented in the baseline. Fish were assigned to the reporting unit with highest posterior probability and we summarized these results in a table of counts of correct and incorrect assignments to and from the CCC, Klamath, and other reporting units. We considered the results from all assignments, and also only those assignments for which the maximum posterior probability for reporting unit exceeded 70%.

Stock proportions were estimated and individual stock assignments were conducted separately for each month and fishery management zone, based on all genotyped fish from a sampling stratum. Most sampled fish were genotyped, but some fish were not analyzed due to the stratum sample size target being less than the number of fish sampled, occasional sample loss, poor tissue sample preservation, or uninterpretable results from an analyzed sample. For fish collected in Oregon, aging was performed by the Oregon Department of Fish and Wildlife, while in California aging was performed by the California Department of Fish and Game (Kormos et al. 2011) for 2010 collections only. No measures of aging uncertainty were reported, as only three KRC fish that were aged contained CWT for validation (all were aged correctly). However, in 2010 scale-read ages of fish with CWT from any California fall run stock matched ages determined from CWT 73 of 75 times in California and 18 of 18 times in Oregon. We report ages following the convention used in KRFC management (O'Farrell et al. 2010), with ages advancing on September 1 of each year.

Note that current GSI techniques do not reliably resolve all fish to individual rivers within the CCC ESU, or separate fall run and spring run stocks within the Klamath River basin (thus KRFC are a subset of KRC). Fall run typically considerably outnumber spring run salmon in the Klamath River basin (Williams et al. 2013), so metrics derived for KRC should be largely representative of KRFC.

Size-at-age model

For the purpose of estimating size-at-age, we assumed scale-read ages were correct and included in our analysis all aged fish assigning to either KRC or CCC with a posterior probability of at least 0.8 (this required discarding 60 out of 997 fish which had most likely assignment to one of these two stocks, but a posterior assignment probability below the threshold). We then used maximum likelihood estimation to fit the mean and standard deviation in fish length for each stock-age-month combination, assuming lengths were normally distributed for samples collected in non-retention fisheries and assuming a truncated normal distribution for fish collected in retention fisheries with a minimum size limit (Goldwasser et al. 2001; Satterthwaite et al. 2012).

Spatial distribution model

We made independent monthly distribution estimates for each stock each year, as well as for non-retention and retention fisheries, as applicable. For 2010 only, we also estimated age-specific distributions. We estimated local density on the basis of area-specific catch per unit effort (CPUE), including an accounting for genetic assignment uncertainty. We did not make adjustments to account for varying minimum size limits for retention among areas (c.f. Satterthwaite et al. 2013) since we lacked age information for many fish and it was not always possible to estimate stock-specific size-at-age, age-specific catch, or proportion of age-specific catch that was of legal size. Minimum size limits were 27 inches total length for California retention fisheries and 28 inches total length for Oregon fisheries, so (assuming similar age structures) a slightly smaller proportion of fish contacted would be of legal size to retain in Oregon.

We assume the rate of catch per unit effort λ with fish from stock r in area x during month m of year y is given by the product of local density D (total fish in the fished area over which effort is spread) and catchability of individual fish q (a list of variables is provided in Table 3). In the absence of information on catchability, we assume q is independent of D and constant across areas x, and use λ as a proxy for relative density. We estimate local density separately for each age, month, year, and area, suppressing subscripts for m, y, and x in later notation. Estimates of distribution may be confounded by a nonlinear relationship between local abundance and contacts per unit effort (Harley et al. 2001), but our analysis assumes a linear relationship. Given this assumption, the number of fish from a particular stock caught in a single unit of effort (c_r) is predicted to follow a Poisson distribution with mean λ_r.

For f units of fishing effort expended, the expected total catch of fish from a particular stock, C_r, is the sum of the catch corresponding to each unit of effort, which assuming independence is

$$C_r = \sum_{k=1}^{f} c_{rk} \sim \text{Poisson}(\sum_{k=1}^{f} \lambda_r) = \text{Poisson}(f\lambda_r), \tag{1}$$

and thus (for integer values of $C_r \geq 0$):

$$p(C_r | f, \lambda_r) = e^{-f\lambda} \frac{(f\lambda)^{C_r}}{C_r!}. \tag{2}$$

Applying Bayes theorem,

$$p(\lambda_r|C_r, f) = \frac{p(\lambda_r)p(C_r|\lambda_r, f)}{p(C_r, f)}, \tag{3}$$

where $p(C_r, f)$ is a constant with respect to λ_r and thus can be neglected in sampling the posterior distribution of λ_r via Markov Chain Monte Carlo (MCMC, Gelman et al. 2004) sampling methods. For $p(\lambda_r)$ we assumed a uniform prior distribution with minimum 0 and maximum greater than the highest observed CPUE for all stocks combined.

We accounted for two sources of uncertainty in C_r by drawing new values for C_r in each iteration of the MCMC chain when determining the distribution of λ_r (via equation 3). The first corresponds to genetic assignment uncertainty for those fish that were genotyped. We accounted for this uncertainty by probabilistically assigning each fish in the applicable area-month-year dataset to a stock based on its posterior assignment probabilities produced by gsi_sim. Assuming that the entire sample consisting of n total fish is successfully genotyped, the vector $\boldsymbol{n}$ of the number of fish from each stock r (n_r) is the sum of multinomial random vectors, each of a single trial with cell probabilities given by $\boldsymbol{g_i}$, the vector of posterior probabilities that fish i originated from each of the possible source stocks (g_{ri}):

$$\{n_1, n_2, ...n_R\} \sim \sum_{i=1}^{n_{total}} \text{Multinomial}(trials = 1, p = \{g_{1i}, g_{2i}, ...g_{Ri}\}). \tag{4}$$

The second uncertainty arises only in situations where not all sampled fish in a particular area-month-year combination were successfully genotyped. We assume that the probability of missing or uninterpretable genetic results is independent of stock of origin. Let N_r represent the total number of fish caught from stock r given N total fish are sampled, of which n are successfully genotyped and u are not genotyped. N_r is the sum of n_r genotyped fish from that stock and u_r ungenotyped fish from that stock. The composition of u, of course, depends on the unknown proportion of the sample consisting of each stock π_r. In the course of the MCMC we simulate realized values of the vector of stock proportions $\boldsymbol{\pi}$ from their posterior distribution given the currently drawn values of n_r (from equation 4) and a unit information Dirichlet prior:

$$\{\pi_1, \pi_2, ...\pi_R\} \sim \text{Dirichlet}(n_1 + 1/R, n_2 + 1/R, ..., n_R + 1/R), \tag{5}$$

where R is the total number of distinguishable stocks in the baseline. We then draw u_r from a multinomial distribution with values for $\boldsymbol{\pi}$ drawn via equation 5:

$$\{u_1, u_2, ...u_R\} \sim \text{Multinomial}(trials = u; p = \{\pi_1, \pi_2, ...\pi_R\}), \tag{6}$$

and calculate C_r as the sum of n_r and u_r, which we use to update λ_r via MCMC with equation 3 giving the target density.

For descriptive plots, we determined posterior medians and 68% credible intervals, inspired by typical error bars of one standard error in frequentist plots. When assessing how distributions vary across particular spatial or temporal divisions, we calculated posterior distributions on ratios of the CPUE between sampling strata and determined 95% credible intervals on these ratios. λ is difficult to estimate when both catch and effort are low. In addition, equation 1 implies that zero catch is plausible whenever $f\lambda$ is small, and does not allow for negative values of λ. Thus the posterior median and credible interval boundaries for λ will always be greater than zero. We manually adjust such points when plotting so that the lower bound and posterior median are plotted at zero whenever there was no catch with most likely assignment to a specific run, while leaving the upper bound of the credible interval as calculated.

Age-specific distribution

We estimated age-specific distributions for 2010 only, since this was the only year with age data in California waters. Estimation was as before, with $C_{r,a}$, the catch of age-a fish from stock r, substituted for C_r. Since aging via scale reading was done conditional on stock assignment, without reports of error, and not all scales were analyzed (overall, scale-read ages were assigned to 91% of California samples and 63% of Oregon samples), we could not fully account for the uncertainty in joint stock and age assignment. To approximate uncertainty resulting from uncertain age structure of the catch, we assumed that the probability that a fish in a particular sampling stratum from a particular stock was age a could be approximated by the proportion of aged fish in the stratum with most likely assignment to that stock which were of age a. We then simulated $C_{r,a}$ by drawing from a binomial with C_r trials and a probability of age a estimated as described.

Results

Performance of genetic baselines

Table 4 reports the results of our self-assignment test. Assigning fish using the SNP baseline, with no restriction on the posterior probability, only 6 of 189 CCC fish (3.2%) were missasigned to the wrong reporting unit; four of these were to the Northern California / Southern Oregon reporting unit (not shown). Of the 1,526 Klamath fish in the baseline, only 42 (2.8%) were misassigned; most of these misassignments were to Rogue River and other Oregon reporting units. Misassignments to CCC and Klamath using SNPs were also infrequent, occurring in only 6 fish for CCC and 8 for Klamath out of over 6,000 fish. The microsatellite baseline is somewhat less accurate at assigning fish from CCC and Klamath: 28 of 278 (10.1%) of CCC fish and 25 of 407 (6.1%) of Klamath fish were misassigned. Misassignments to the CCC and the Klamath with microsatellites were relatively infrequent. Out of over 28,000 fish in the baseline, only 9 and 36 were misassigned to CCC and Klamath, respectively. For both microsatellites and SNPs most of the fish misassigned to the CCC were from stocks that do not appear in great abundance in California fisheries, and so it is unlikely that fish identifed as from CCC in our samples will not be from CCC. Finally, misassignments between CCC and Klamath are very infrequent—we observed none with SNPs and only one with microsatellites.

Table 4 also presents the misassignment table for fish assigned to reporting unit with a posterior probability greater than 70%. The accuracies are improved by using such a cutoff. This demonstrates that the posterior probability does reflect the certainty with which assignments can be made and it indicates that our MCMC analysis will correctly propagate the uncertainty of genetic assignments (via the influence of posterior probabilities for assignments on the posterior for the mixing proportions).

Size-at-age

Estimates from California and Oregon 2010 GSI data indicated that, early in the year, both age-3 and age-4 KRC fish were similar in size to CCC fish of the same age (Figure 2). Later in the year, mean size-at-age of age-3 fish seemed to start decreasing sooner and/or more rapidly for KRC than for CCC. Estimated standard deviations in individual fish lengths (not shown) were usually similar with overlapping confidence intervals, except that, in September, CCC fish had larger standard deviations for fish transitioning from age-2 to age-3 and for fish transitioning from age-3 to age-4.

Distribution

In 2010, the two stocks appeared similarly distributed early in the year (Figure 3). Later in the year (i.e., by August) the highest CPUE for the KRC occurred in the KC-n area while the highest CPUE for CCC was in the FB area (note however the KC-s area was not sampled), although the CPUE for CCC fish in August was similar in KC-n and FB. In 2011, there were limited data early in the year, but by August, CPUE for the CCC stock was once again highest in FB while CPUE for KRC was highest in KCn (although comparable to FB,

Figure 4). Both stocks had low CPUE south of Point Reyes.

As Figure 5 demonstrates, there was a distinct northward shift in CPUE of KRC but not CCC in August of both years. In June of 2010, both stocks had their highest CPUE in Fort Bragg, with the 95% posterior credible intervals for the ratio between CPUE in Eureka and Fort Bragg never including values greater than 0.45 for either stock. For CCC, a slight shift to the north in relative CPUE was evident later in the year as the ratio between Eureka and Fort Bragg CPUE increased, but CPUE likely remained at least as high in Fort Bragg throughout the year (posterior median on ratio always <1). In contrast, KRC CPUE was comparable between Eureka and Fort Bragg in July 2010 (posterior 95% credible interval 0.50-1.37) and considerably higher in Eureka (95% credible intervals on the CPUE ratio between ports entirely above 2.6) for August and September of 2010.

In 2011, both stocks had lower CPUE in KC-n than FB in July (95% posterior credible intervals on this ratio of 0.16-0.34 for CCC and 0.37-0.58 for KRC), but by August a shift of KRC into KC-n and CCC into FB was apparent as in August CPUE of CCC was much lower in KC-n than FB (95% posterior credible interval 0.004-0.06 for the ratio of KC-n to FB CPUE) while KRC CPUE was comparable between zones (95% credible interval 0.56-1.25).

Comparison across age-classes was possible in 2010 (Figures 6 & 7). Generally speaking, both age-classes appeared similarly distributed within each stock. In most cases, estimated CPUE for both stocks in retention vs. non-retention fisheries operating in the same month-port combination also had overlapping credible intervals, although CPUE was considerably higher for the retention fishery in Bodega Bay during July 2010.

Discussion

GSI methods provided the novel ability to estimate size-at-age and ocean spatial distributions for an untagged stock of conservation concern and compare these metrics to a tagged indicator stock. Our results suggest similar patterns in size-at-age and spatial distributions for CCC and KRC in the spring and early summer, with differences becoming apparent in late summer and early fall. These results are relevant to fisheries management because a cap on the preseason-predicted KRFC age-4 ocean harvest rate is currently used to limit ocean fisheries that contact CCC. The efficacy of this fishery management constraint for protection of the CCC ESU in part depends on the degree of concordance in the vulnerability of CCC and KRFC to ocean fisheries. This demonstrates the utility of GSI methods for evaluating the suitability of indicator stocks when untagged stocks or portions of stocks are of concern.

Size-at-age

The similar size distributions of CCC and KRC fish in May through July suggests that similar proportions of each stock are above legal size limits early in the fishing season. However, the earlier/faster decrease in mean size at age for KRC fish suggests that size limits later in the year could have different effects on the two stocks. Ecologically, the earlier decrease in mean size-at-age in KRC, along with similar mean sizes of age-4 fish early in the year, suggests that the KRC and CCC stocks have similar annual maturation and mortality schedules, but that CCC fish may return to their natal rivers later in the year than do KRC. Indeed, Shebley (1922) (in Yoshiyama and Moyle 2010) noted that early entrants to the Eel River needed to hold near its mouth until the river rose in the fall, and Bjorkstedt et al. (2005) pointed out that anadromous fish may not gain access to smaller coastal rivers until the arrival of winter storms, especially in watersheds closed by sandbars during the summer. Thus, harvest later in the fishery season (from August until the fishery closes) may have higher relative impacts on the CCC than on the KRFC indicator stock, both because maturing fish remain vulnerable to the fishery for a longer period in the later-returning stock, and because a greater proportion of fish contacted will be of legal size for retention.

Distribution

Relative fishery impacts on the two stocks may also be sensitive to differences in their spatial distribution relative to fishing effort. In both 2010 and 2011, the stocks appeared to diverge in their spatial distributions late in the fishing season. Results from 2010 suggested that the stocks may be similar in their distribution early in the year, but there were not adequate data from early in 2011 to determine if this pattern held the next year. The lack of samples from the KC-s area presents a challenge in interpreting and comparing the distributions of the two stocks, since there is no information from a central part of the distributional range. In addition, CCC salmon originate from multiple rivers spread along $2^{\circ}50'$ of latitude, and individual populations within this ESU may be distributed differently and thus differentially impacted by the fishery.

The patterns in relative CPUE for the two stocks clearly differed by August, with highest CPUE of KRC shifted toward the KC-n area near the mouth of the Klamath River while

CPUE for CCC was shifted toward FB. Although a broadly similar pattern of shifting CPUE held in both years, there were notable differences. In August of 2010, CPUE of CCC was similar in both FB and KC-n, whereas KRC CPUE was much higher in KCn. Yet, in August of 2011, CCC CPUE was much higher in FB than KC-n whereas KRC CPUE was comparable between both areas. Thus, while stocks seem to be moving toward their source rivers in both years, the magnitude of the shift in CPUE is also affected by other sources of variation in local density and/or catchability, which may be due to underlying distribution shifts, effects of local conditions on catchability, or other aspects of the fishery-fish interaction. Still, the general pattern of increasing CPUE toward the south for CCC fish later in the season is not unexpected, as the source rivers are all south of the Klamath.

Caveats

We are limited in this analysis to two years' data, and more complicated patterns would likely emerge over time. We might expect a high concentration of CCC fish in the KC-s area as spawners return from the north to the Eel River, but we cannot test this hypothesis directly with the current data. Non-retention sampling in closed areas, as well as expanded seasonal coverage, could provide additional insights into distributions and migration patterns. Sampling programs maintained over several years would be needed to gain confidence in the consistency of patterns observed.

As with all fishery-dependent surveys, nonrepresentative sampling is a concern when interpreting the results of this study. Fishermen target their effort where they expect to catch fish, so the areas they sample are not necessarily representative of ocean areas in their entirety. In addition, not all fish collected during retention fisheries were sampled (i.e., had fin clips collected for later genotyping) and sampling rates tended to be much lower when catch rates were high. Thus, assuming similar stock compositions for sampled and unsampled fish caught within a particular area-month combination may not be appropriate, especially if high catch rates and reduced sampling results from encountering a high density cluster of fish from a particular stock. However, the most abundant stock subject to this fishery is the Central Valley fall Chinook stock, suggesting it would most likely be the stock responsible for “hot bites”, if indeed such bites are even necessarily dominated by a single stock. Thus relative patterns in CPUE of CCC versus KRC should not be affected. Given all of the factors that can influence CPUE regardless of stock (e.g. weather conditions, nonrandom spatial sampling), we suggest caution against over-interpreting patterns in CPUE as reflective of absolute spatial distributions, suggesting focusing instead on differences between stocks in how their CPUE varies across space.

Management relevance

Our results suggest that, if 2010 conditions are typical, the harvest rate on the KRFC stock early in the season may provide a good indicator of the harvest rate on the CCC stock early in the season. Thus, management actions which change early-season KRFC harvest rate will likely cause a similar proportional change in CCC harvest rate, but by July or August, the CCC harvest rate will likely be more sensitive to changes in FB (and KC-

s) management, while the KRFC harvest rate will be more sensitive to changes in KC-n management. However, we note that the original development of this proxy did not assume that harvest rates on the two stocks were perfectly correlated (O'Farrell et al. 2012).

Since 1991, effort in the FB and KC management areas has been concentrated later in the year, largely due to conservation constraints for both KRFC and CCC fish. Between 1991 and 2011, commercial effort in both the FB and KC areas has always been greater in August-October than earlier in the year (Pacific Fishery Management Council 2012c), with no fishing effort prior to August in 10 of 18 years open to fishing in FB for at least part of the year during this period and 10 of 13 years open to fishing in KC. Thus, in recent years the majority of effort has been expended when the apparent spatial mismatch between the KRFC and CCC stocks is likely to be most important. ~~High harvest rates late in the season in the FB ocean area may therefore result in a CCC harvest rate that is not well reflected by the age-4 KRFC harvest rate proxy. Total commercial Chinook salmon harvest in August and September in the FB area has been greater than in the KC area in 29 of the last 36 years, and in every year with open fisheries since 2000 (Pacific Fishery Management Council 2012c). The ratio in total harvest has been highly variable, with a geometric mean of 4.3x as much harvest in FB and a maximum of 72x during the period 1991-2011 (excluding five years during this period with no commercial harvest in KC and three years with no commercial harvest in either KC or FB).~~

We note that the indicator employed in the ESA compliance standard for the CCC ESU is the harvest rate on age-4 KRFC. Thus, strictly speaking, a comparison of likely fishery exposure should focus on age-4 KRFC as the indicator. However, we observed little difference in the distributions inferred in 2010 for the different ages. In addition, KRFC age-3 and age-4 harvest rate estimates have been highly correlated historically ($r = 0.93$, calculated from Table II-2 in Pacific Fishery Management Council 2012b), so age-4 harvest rates are likely proportional to overall harvest rates. An additional complication is the inclusion of spring run fish in the genetically-identified KRC stock. However, recoveries of CWT'd Klamath fall run fish greatly outnumbered recoveries of spring run CWTs in samples of the California and Oregon commercial troll fishery in 2011 (308 fall run to 28 spring run). Since nearly 100% of spring run hatchery production is tagged compared to approximately 25% of fall run production, and there is substantially more fall run spawning habitat than spring run habitat in the system, the overall ocean catch is likely even more skewed toward the fall run.

Conclusions and further applications

Through use of GSI data and supplemental information, we have demonstrated general concordance between ocean spatial distribution and size-at-age of the CCC and KRC salmon stocks early in the fishing season, and differences late in the fishing season that may affect relative exposure to fisheries and thus the extent to which harvest rates will covary between the untagged CCC and the indicator KRFC stocks. This sort of evaluation of correspondence between indicator and untagged stocks was made possible by taking advantage of inborn genetic information present in all fish, regardless of source. We did not attempt to estimate total harvest of the CCC stock, since there are not sufficient escapement data to provide context. However, in principle, stock-specific catch estimates for the entire fishery could be generated by estimating proportions from a genotyped subsample of the catch and then expanding them to total catch in a management stratum via an approach analogous to that described in equations 5 and 6, substituting total harvest in the management stratum for N when calculating u. This would require the genotyped subsample to be representative of catch from the fishery management stratum as a whole, and thus that the fishers who participate in GSI sampling are a representative sample of the entire fishery. Alternatively, a representative sample could be obtained via comprehensive dock-side sampling of harvest, as is currently done for CWTs. Stock-specific harvest for the CCC ESU, or other reporting groups distinguishable via GSI, could then be estimated along with a measure of uncertainty.

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Tables

Table 1. Summary of sampling effort (angler-days) in each area-month combination. Italics denote non-retention sampling. When a single area in California contains multiple ports, the 2010 effort is reported for each port individually while the 2011 effort is for the entire area. Effort in Oregon was always tracked by area rather than individual ports.

		May		June		July		Aug.		Sept.	
Area	Port	2010	2011	2010	2011	2010	2011	2010	2011	2010	2011
MO-s	Santa Barbara Morro Bay	*4* *3*	18	*6* *6*	16	*4* *6*, 10	10	*8* *12*	2	*4* *6*	0
MO-n	Santa Cruz	*37*	86	*42*	23	*20*, 64	28	*40*	7	*26*	2
SF-s	Princeton San Francisco	*26* *27*	114	*30* *29*	5	*25*, 34 *15*, 17	8	*26* *30*	51	*36* *30*	87
SF-n	Bodega Bay	*24*	82	*58*	50	*32*, 61	156	*60*	99	*60*	32
FB	Fort Bragg	*9*	0	*46*	18	117	223	117	214	*68*	77
KC-s		0	0	0	0	0	0	0	0	0	0
KC-n	Eureka Crescent City	0 0	0	*27* *11*	0	*39* *8*	141	*40* *18*	40	*40* *20*	0
KO	Brookings	0	0	*32*	2	9	4	24	71	*30*	0
CO	Coos Bay	116	48	164	154	29	43	185	78	*36*	0
NO	Tillamook, Newport	85	41	231	101	88	14	186	59	*38*	0

Table 2. Number of fish successfully genotyped in each area-month combination (note that this may be less than the total sampled harvest for a stratum). When a single area in California contains multiple ports, the 2010 numbers are reported for each port individually while the 2011 numbers are for the entire area. Numbers in Oregon were always tracked by area rather than individual ports. For California in 2010, non-retention numbers are reported in italics while numbers from retention fisheries are reported in plain text.

Area	Port	May 2010	2011	June 2010	2011	July 2010	2011	Aug. 2010	2011	Sept. 2010	2011
MO-s	Santa Barbara Morro Bay	*0* *2*	16	*1* *4*	23	*0* *5*, 7	3	*2* *7*	0	*2* *14*	0
MO-n	Santa Cruz	*17*	160	*21*	81	*154*, 239	30	*148*	25	*92*	1
SF-s	Princeton San Francisco	*45* *69*	509	*163* *123*	1	*27*, 46 *36*, 9	11	*9* *110*	196	*24* *58*	525
SF-n	Bodega Bay	*47*	322	*112*	576	*55*, 342	845	*160*	131	*50*	53
FB	Fort Bragg	*100*	0	*173*	0	489	2110	540	1462	*490*	207
KC-s		0	0	0	0	0	0	0	0	0	0
KC-n	Eureka Crescent City	0 0	0	*54* *17*	0	*124* *10*	398	*421* *55*	48	*339* *29*	0
KO	Brookings	0	0	*42*	12	9	2	66	62	*131*	0
CO	Coos Bay	426	103	550	905	67	149	570	155	*88*	0
NO	Tillamook, Newport	383	200	790	488	369	21	438	235	*29*	0

Table 3. Variable names and definitions.

Variable name	Definition
r	Stock
a	Age
m	Month
y	Year
x	Location (ocean area or port)
λ	Fishery catch rate (fish per vessel-day)
q	Catchability of individual fish
D	Density of fish
c	Number of fish caught in single unit of effort
f	Fishing effort (vessel-days)
k	Index for individual days of fishing effort
C	Total catch
N	Number of fish harvested in a sampling stratum
i	Index for individual fish
g_{ri}	Genetic assignment probability for fish i belonging to stock r
n	Number of fish sampled and successfully genotyped
u	Number of fish not successfully genotyped
R	Total number of stocks in baseline
π	Stock proportion

Table 4. Results of self-assignment analyses with SNP and microsatellite baselines. The Origin column gives the true origin of individuals. The numbers assigned to different reporting units are given in the columns. The left collection of three columns are results for the SNP baseline. The right collection of three columns are results for the microsatellite baseline used in Oregon. "All" refers to the results with no cutoff in posterior probability. "PP>70%" denotes results when restricting attention only to those fish assigned to a reporting unit with posterior probability exceeding 70%.

		Assignment. SNPs			Assignment. Microsatellites		
	Origin	CCC	Klamath	Other	CCC	Klamath	Other
All							
	CCC	183	0	6	250	1	27
	Klamath	0	1,484	42	0	382	25
	Other	6	8	6,302	9	36	27,815
PP>70%							
	CCC	180	0	4	247	1	12
	Klamath	0	1,463	16	0	377	11
	Other	3	7	5,501	6	26	23,374

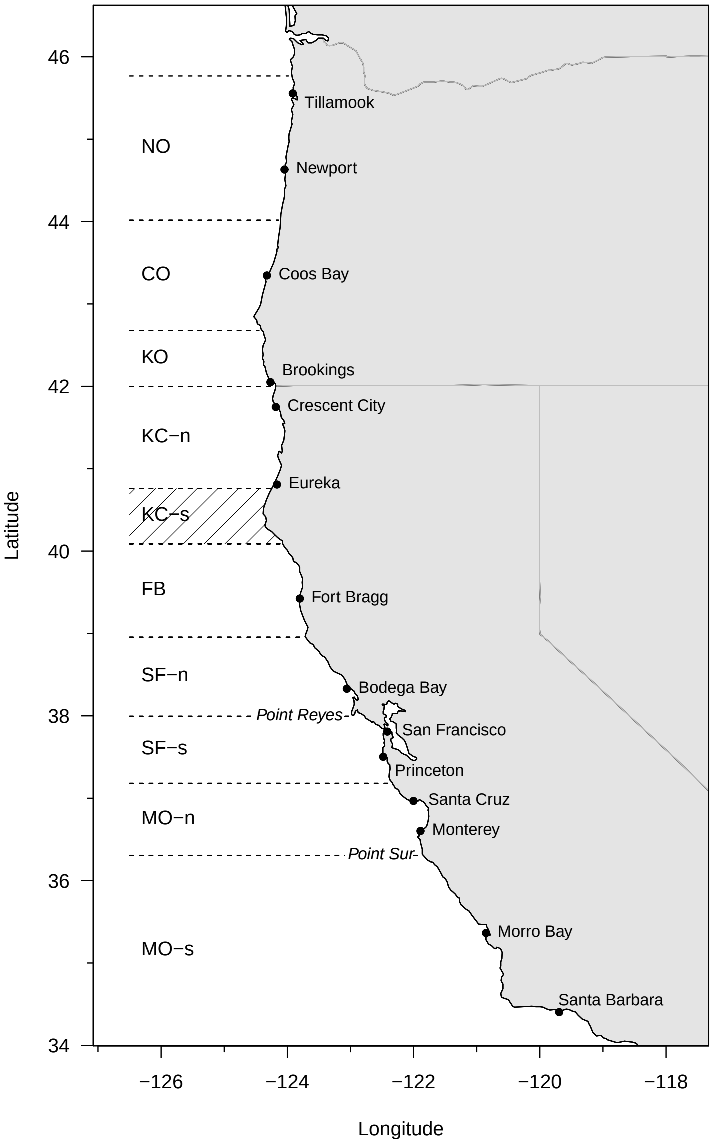

Figure 1: Ports (circles) and ocean areas (dotted lines) evaluated in this analysis, along with key landmarks. Ocean areas are those commonly used by the Pacific Fishery Management Council (Pacific Fishery Management Council 2012a), with the following exceptions. We split the KC area into the KC-n and KC-s subareas since the KC-s area was closed to all sampling and fisheries, we split the SF area into subareas SF-n and SF-s because of anecdotal reports of different stock compositions north versus south of Point Reyes, and we split the MO area into areas north versus south of Point Sur, CA.

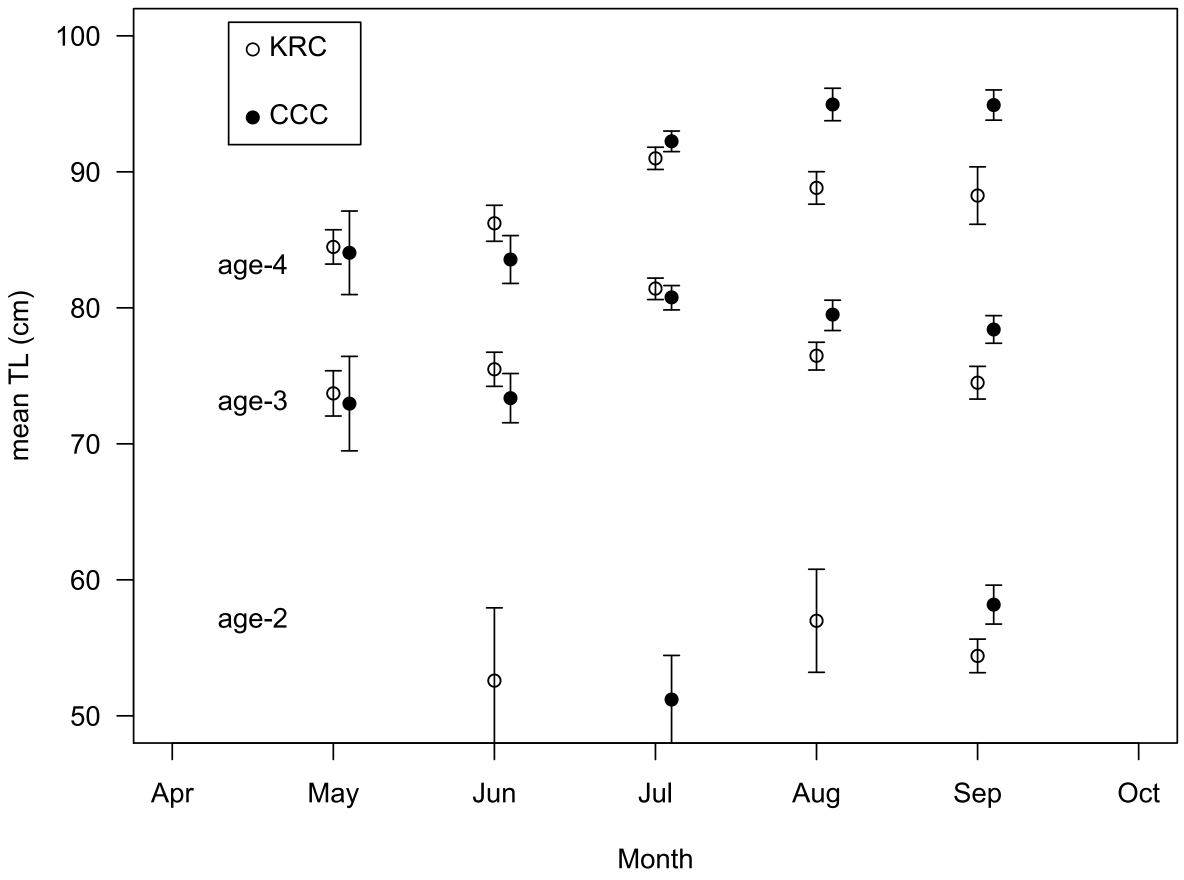

Figure 2: Monthly mean size-at-age estimated from 2010 GSI data for Klamath River (KRC) and California Coastal Chinook (CCC) salmon. Error bars are 68% confidence intervals. Estimates are not available for age-2 fish in some months due to low or zero catch, especially in retention fisheries. Note that under the management convention of ages advancing on September 1, fish are considered one year older than the graph labels imply in September.

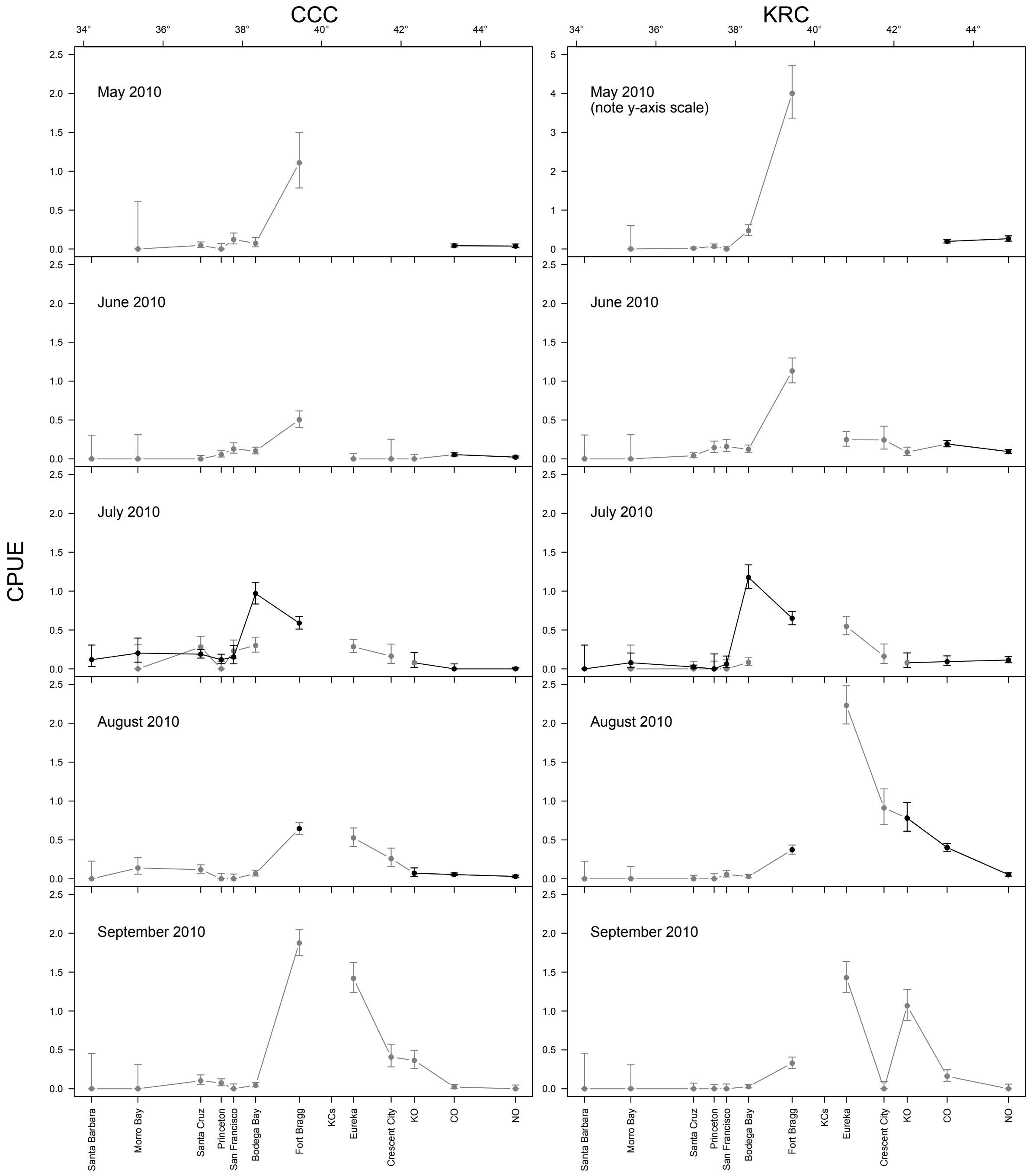

Figure 3: Monthly ocean distributions estimated from GSI data for Klamath (KRC) and California Coastal Chinook (CCC) salmon in 2010, for all ages combined. Black circles represent retention fisheries while grey circles represent samples collected in non-retention fisheries. Note that in port-month combinations with both retention and non-retention samples, the two fishery types operated at different times within the month, not concurrently. In July and August, the KO fishery had a 30 fish/day limit. Points are posterior medians and error bars are 68% credible intervals.

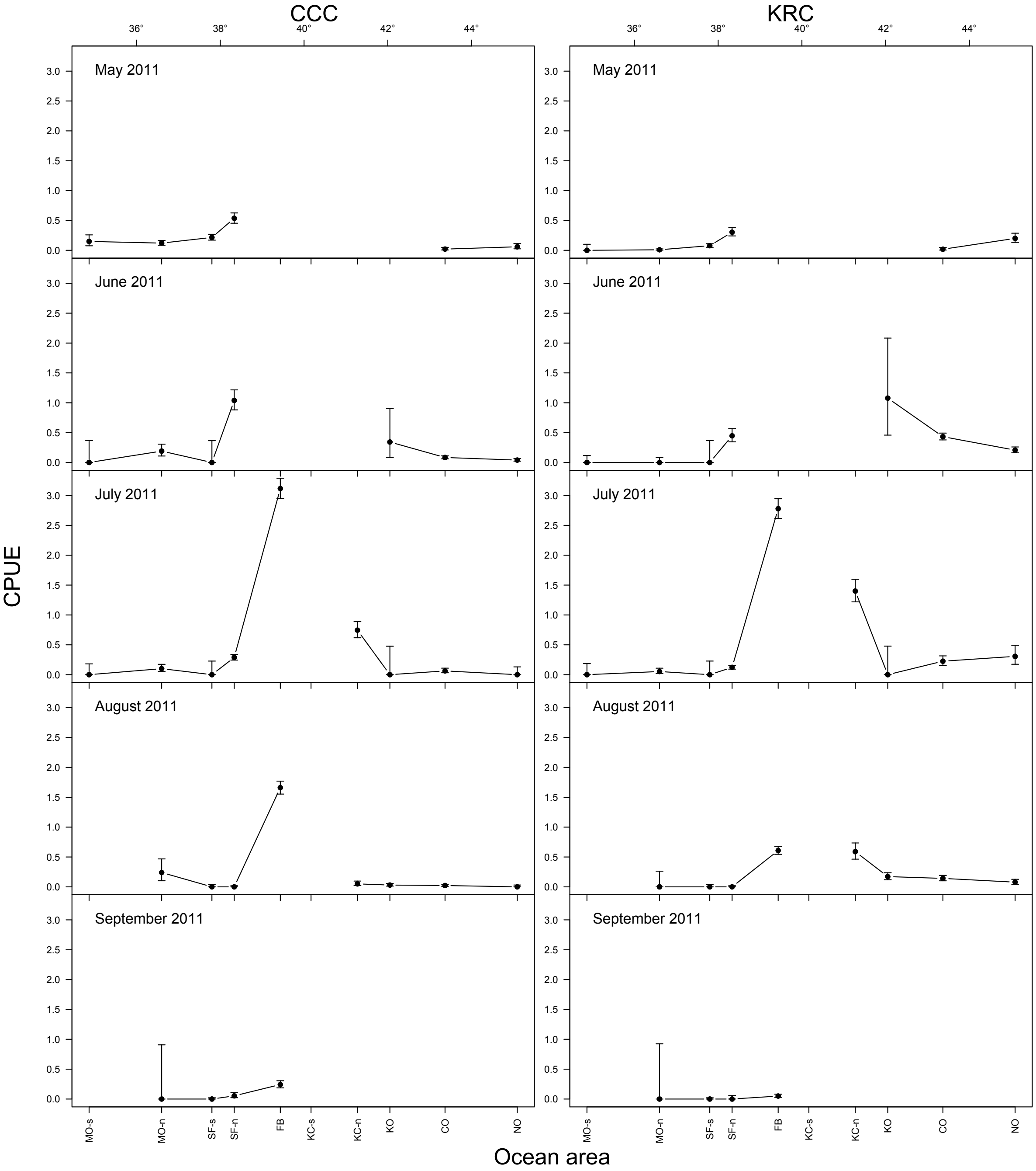

Figure 4: Monthly ocean distributions estimated from GSI data for Klamath (KRC) and California Coastal Chinook (CCC) salmon in 2011. All 2011 fisheries were retention, but in KC-n there was a 15 fish landing/possession limit per vessel and in Oregon (KO, CO, and NO) the limit was 30-50 fish. Points are posterior medians and error bars are 68% credible intervals.

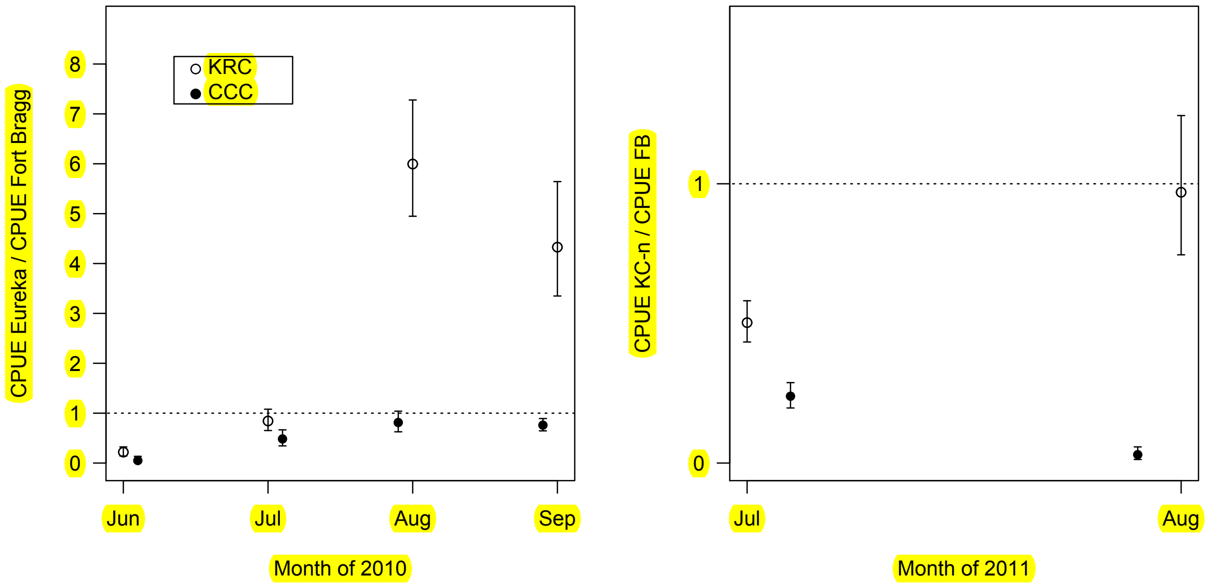

Figure 5: Monthly CPUE ratios for areas immediately north of (the Eureka port in 2010, the KC-n management area in 2011) versus immediately south of (the Fort Bragg port in 2010, the FB management area in 2011) the KC-s closed area. Circles are posterior medians, error bars are 68% credible intervals (95% credible intervals on key ratios are provided in the text).

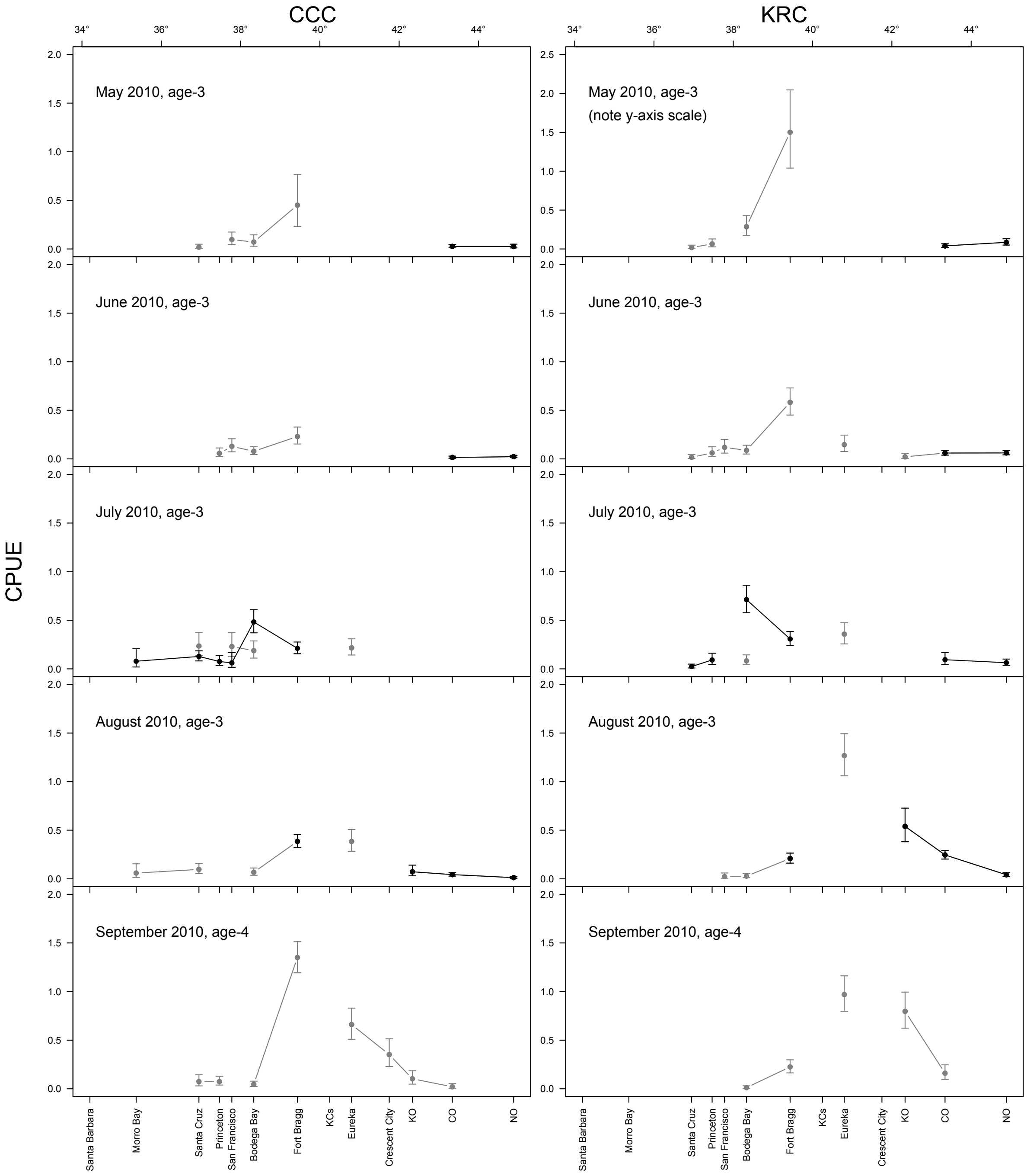

Figure 6: Monthly ocean distributions estimated from GSI data for Klamath and California Coastal Chinook salmon in 2010, for all age-3 fish (turning age-4 in September). Black circles represent retention fisheries while grey circles represent samples collected in non-retention fisheries. Note that in port-month combinations with both retention and non-retention samples, the two fishery types operated at different times within the month, not concurrently. In July and August, the KO fishery had a 30 fish/day limit. Points are posterior medians and error bars are 68% credible intervals.

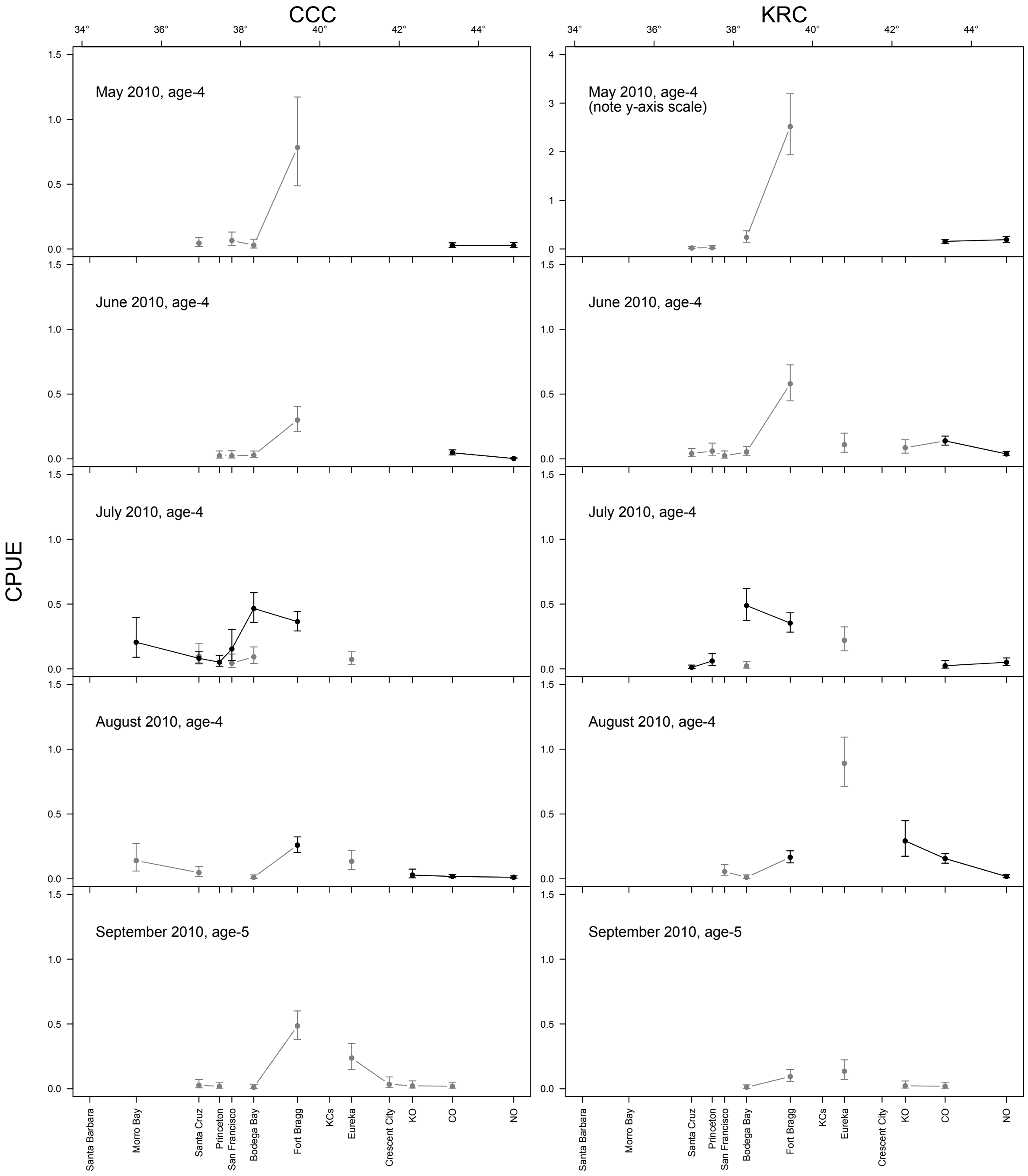

Figure 7: Monthly ocean distributions estimated from GSI data for Klamath (KRC) and California Coast Chinook (CCC) salmon in 2010, for all age-4 (turning age-5 in September) fish. Black circles represent retention fisheries while grey circles represent samples collected in non-retention fisheries. Note that in port-month combinations with both retention and non-retention samples, the two fishery types operated at different times within the month, not concurrently. In July and August, the KO fishery had a 30 fish/day limit. Points are posterior medians and error bars are 68% credible intervals.