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Stock composition and ocean spatial distribution inference from California recreational Chinook salmon fisheries using Genetic Stock Identification

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Abstract

We apply genetic stock identification (GSI) data and models of the catch and sampling process to describe spatial and temporal patterns in the stock composition and stock-specific catch-per-unit-effort (CPUE) of both tagged and untagged stocks encountered in California recreational ocean Chinook salmon fisheries during the period 1998-2002. Spatial and temporal distributions inferred from GSI sampling of stocks with tagged hatchery components were broadly consistent with those previously inferred from studies of tag recoveries alone, while GSI provided additional insight into untagged stocks of conservation concern. The catch in all times and areas was dominated (typically ≥90%) by the "Central Valley Fall" genetic reporting group, which is comprised primarily of Sacramento River fall run Chinook. Other contributing stocks were more spread out in space and time with the exception of Central Valley winter run Chinook, which were rarely encountered by boats fishing in port areas north of Point Reyes. Localized stock-specific CPUE appeared to increase near a stock's respective natal river while decreasing in other port areas at the time of adult return to freshwater for spawning. We describe methods for quantifying uncertainty in stock proportions, stock-specific catch, and determining the statistical support for proposed management boundaries hypothesized to represent "break points" in the spatial distributions for stocks of concern, and find at most equivocal support for a proposed delineation line at Point Reyes in north-central California.

1. Introduction

Ocean salmon fisheries on the west coast of North America are generally mixed-stock fisheries, in that fish harvested in any given area usually come from multiple source rivers (Winans et al. 2001, Weitkamp and Neely 2002, Weitkamp 2010). While some stocks are usually relatively abundant and productive, their harvest is often constrained to protect less abundant or weaker stocks, including those managed under the U.S. Endangered Species Act (ESA) as "threatened" or "endangered" (Pacific Fishery Management Council [PFMC] 2012, 2013). The goal of "weak stock management," as practiced for these mixed-stock ocean salmon fisheries, is to maximize overall harvest opportunity while simultaneously meeting conservation benchmarks for all managed stocks. The primary tools used in California for implementing weak stock management are 1) allowing fishing only in specific times and areas (i.e., time-area fisheries) to minimize impacts on weak stocks and/or 2) establishing catch quotas. Currently, spatial management of salmon fisheries off the coast of California is accomplished primarily through seasonal openings of fisheries at relatively broad spatial scales, corresponding to the ocean areas delineated in Figure 1, based on an understanding of stock-specific spatial distributions informed by tag recoveries from stocks of interest or their proxies.

Until recently, managers have relied almost entirely on coded-wire tags (CWTs) recovered from harvested fish to obtain information on stock-specific harvest (Nandor et al. 2010). CWTs provide brood year, hatchery/stock of origin, and other pertinent information related to its respective release-group. In tandem with CWT recoveries from the escapement and in-river harvest, this allows cohort reconstructions (Hilborn and Walters 1992, Goldwasser et al. 2001, Mohr 2006) that are used to estimate demographic parameters and stock/age-specific ocean exploitation rates. These stock/age-specific exploitation rates serve as the basis for the management of almost all west coast ocean salmon fisheries (PFMC 2012), with some untagged natural or less abundant stocks managed on the basis of tagged "proxy" stocks. Since CWTs are almost exclusively deployed on hatchery-origin fish, the suitability of this approach relies on the assumption that tagged proxy stocks act similarly to the untagged stocks of interest, which can be comprised of natural-origin fish from nearby watersheds as well as the natural-origin component of stocks with hatchery supplementation. Thus, CWT-based management may not include direct information on the harvest of some stocks or stock components of interest.

Genetic stock identification (GSI) has the potential to identify any individual fish to its population of origin. Currently, genetic assignments are typically reported at the level of reliably distinguishable "reporting groups" in the genetic reference database (i.e., the baseline). Many genetic reporting groups, however, are composed of multiple genetically-similar populations (Seeb et al. 2007, Clemento et al. 2014), and reporting group boundaries do not always coincide with managed stocks, some of which may not themselves coincide with biological populations. Nevertheless, for convenience, we use the terms "stock" and "reporting group" interchangeably hereafter. Worldwide, GSI has been applied to multiple management problems in salmon fisheries, including monitoring and responding to stock composition in terminal fisheries or other geographically-restricted harvest situations (Beacham et al. 1987, Shaklee et al. 1999, Parken et al. 2008, Griffiths et al. 2010, Ensing et al. 2013), evaluating the suitability of proxies for untagged stocks (Bernard et al. 2014, Satterthwaite et al. 2014), estimating the stock composition of escapement (Hess et al. 2014), determining the composition of discarded bycatch (Wilmot et al. 1998), determining the source of introduced populations (Di Prinzio et al. in press), and determining the composition of mixed-stock Atlantic salmon fisheries (Koljonen et al. 2005, Koljonen et al. 2006, Gauthier-Ouellet et al. 2009). However, GSI has not been as widely applied in management as some have envisioned (Waples et al. 2008) and applications to open-ocean fisheries managed primarily with time-area regulations have been limited (Winans et al. 2001, Crozier et al. 2004, Satterthwaite et al. 2014). Nevertheless, GSI has the potential to inform time-area management, potentially at a finer scale than is currently practiced, especially when capture locations associated with individual fish are also recorded (Bellinger et al. in review). Even at the coarser spatial scale considered in current time-area management models, GSI has the potential to provide important information on the relative fishery exposure of untagged stocks for which direct distributional information is not available from CWT data.

To implement weak stock management using either time-area management or quotas, information regarding stock-specific spatial distributions is important. Understanding where and when certain stocks are more (less) prevalent and large (small) contributors to the fishery allows structuring of fisheries such that abundant stocks are targeted and impacts to weak stocks are limited.

We used GSI to analyze the stock composition of California recreational salmon fisheries between 1998 and 2002 and to define the contributions of individual Chinook salmon (*Oncorhynchus tshawytscha*) stocks to these fisheries. Because recreational fisheries tend to be confined to a relatively small geographic area near their respective home port of landing, harvest is likely to reflect the local area stock composition. We estimate the spatial and temporal distribution of multiple stocks, some of which already have distributional information available from CWT data and some of which are untagged. We present results as both stock proportions (e.g. Winans et al. 2001, Crozier et al. 2004, Tucker et al. 2009) and stock-specific CPUE (Sato et al. 2009, Satterthwaite et al. 2014, Bellinger et al. in review) to infer local stock mixtures and relative stock abundance, respectively. We then show how a model of stock-specific CPUE, accounting for the uncertainty introduced by genetic assignment, sampling, and process error, can be used to test for a hypothesized break point in stock distributions that might serve as a new delineation line between management areas. Finally, we evaluate the consistency of results obtained from GSI sampling with those previously obtained from CWT proxy stocks. These data offer a relatively unique opportunity to draw inference about the contribution of particular Chinook salmon stocks to these fisheries, as well as to define stock-specific ocean distribution on a relatively small scale.

2. Materials and Methods

2.1. Study System

Ocean salmon fisheries off the coast of California harvest a mix of Chinook salmon stocks (retention of coho [*O. kisutch*] is not currently permitted, and contacts with other salmonids in this area are minimal). Both commercial and recreational fisheries are substantial, with recreational fisheries generally contributing about a third of the total California ocean harvest, although they have made up as much as 58% of the catch in recent years (PFMC 2013). Since the mid-1990s, four "major port management areas" have been used by the Pacific Fishery Management Council (PFMC) when structuring ocean fisheries in California: 1) Klamath Management Zone (KC) area - Oregon/California border to Horse Mountain, 2) Fort Bragg (FB) area – Horse Mountain to Point Arena, 3) San Francisco (SF) area – Point Arena to Pigeon Point, and 4) Monterey (MO) area – Pigeon Point to U.S./Mexico border (Figure 1). Each major port area is comprised of several minor ports where fishery monitoring is conducted. Fisheries are predominantly managed on the basis of time-area closures and minimum legal size limits (typically 20 or 24 inches total length for recreational fisheries, larger for commercial fisheries), although quotas occasionally apply to the commercial catch in the two northern management areas.

Our analysis focuses on six genetic "reporting groups" (Seeb et al. 2007, Clemento et al. 2014) of management or conservation relevance in this region: 1) "Central Valley Fall" consists of Sacramento River fall run, San Joaquin River fall run, Sacramento River late fall run, and Feather River Hatchery spring run. Sacramento River fall run is far more abundant than other stocks in this reporting group, is typically dominated by hatchery-produced fish (Barnett-Johnson et al. 2007, Kormos et al. 2012, Palmer-Zwahlen and Kormos 2013), and makes up a large proportion of the catch in California and Southern Oregon in most years (PFMC 2013). Late fall run fish also have a hatchery component and may have a more southerly ocean distribution than fall run fish (Satterthwaite et al. 2013). San Joaquin River fall run fish are much less abundant than Sacramento River fall run (Carlson and Satterthwaite 2011; Kormos et al. 2012; Palmer-Zwahlen and Kormos 2013) and are also supplemented by hatchery production. Feather River Hatchery spring run are highly introgressed with Feather River Hatchery fall run and thus cannot be distinguished with GSI (Clemento et al. 2014). All of these components are supplemented by hatcheries with marking and tagging programs. 2) “Central Valley Spring” consists of naturally produced spring run fish primarily from Deer, Mill, Butte, Battle and Clear creeks. Feather River Hatchery spring run (marked and tagged) are excluded from the genetic reporting group but included in the Central Valley spring run evolutionarily significant unit (ESU), which is listed under the United States Endangered Species Act (ESA) as threatened (Lindley et al. 2004). There is no hatchery production in the Central Valley Spring reporting group, although there have been brief and relatively small-scale efforts to tag natural-origin smolts. 3) “Central Valley Winter” consists of a mix of naturally spawned and conservation hatchery produced winter run fish from the upper Sacramento River basin and this ESU is ESA-listed as endangered (Lindley et al. 2004). Winter run fish have also been inferred to have a more southerly distribution than fall run fish on the basis of ocean fishery recoveries of CWT deployed by an ongoing hatchery program (O’Farrell et al. 2012a, Satterthwaite et al. 2013). 4) “Klamath River” consists of predominantly

Klamath-Trinity Basin fall run Chinook but includes the genetically similar spring run as well (Williams et al. 2013). Both the fall and spring runs from this reporting group are supplemented by hatchery production with marking and tagging programs, with the fall run typically much more abundant than spring run and a substantial contributor to ocean and river fisheries (PFMC 2013). 5) "California Coast" corresponds to California Coastal Chinook ESU, which is ESA-listed as threatened and consists of coastal fall run stocks between the Klamath River (exclusive) and the Russian River (inclusive). Some of these watersheds formerly contained spring run stocks as well, but they have been extirpated (Bjorkstedt et al. 2005, Spence et al. 2008). Since there is currently no hatchery production or tagging of fish from this ESU (a small number of tags were released by a since-discontinued hatchery program), the ocean harvest rate of age-4 Klamath River fall run Chinook is used as a management proxy (O'Farrell et al. 2012b). Using GSI data collected by the commercial fishery, Satterthwaite et al. (2014) found generally similar spatial patterns in CPUE of Klamath River and California Coast fish in spring and early summer with some divergence apparent in the late summer and fall. 6) "Rogue River" consists of a composite of natural-origin fall run fish and hatchery-origin spring run fish with a tagging program (Seeb et al. 2007).

2.2. Data collection and genotyping

During 1998-2002, the California Department of Fish and Wildlife (CDFW) collected approximately 23,000 fin clips during the routine dockside sampling of private skiffs and charterboats in the California recreational Chinook ocean salmon fishery. Sampling occurred at approximately 20 fishing ports located between the Oregon-California border and Point Conception (Figure 1) and fin clips were stored in ethanol and frozen prior to DNA extraction.

The amount of fishing effort (angler-days) and catch (retained Chinook salmon from any stock) corresponding to the number of sampled recreational trips from which genetic samples were taken was tracked and compiled separately for each month/major port area/year combination (stratum), except that Bodega Bay (BB) was analyzed separately from the rest of the SF management area, which we termed Golden Gate (GG), due to a hypothesized change in stock-specific local density occurring at Point Reyes. In addition, data from the Klamath Management Zone was separated into Crescent City (CR) and Eureka (EU), since these subareas are sampled and reported separately in PFMC salmon documents. Since the CDFW samples approximately 20% of all salmon landings, and thus only a subset of fishing trips was sampled for genetic analyses, these catch and effort values are less than those reported in PFMC documents (e.g., PFMC 2013) for the recreational fishery as a whole. The smaller values used here allow for direct calculation of CPUE from catch estimates made using our dataset since effort and total catch are measured for the same subset of the fishery.

Budgetary and staffing constraints only allowed the genotyping of approximately one half of the samples. Selection of tissues for genotyping was done using stratified random sampling, with complete sampling of small strata. If less than 111 tissue samples were collected within a stratum, all tissue samples from that stratum were genotyped. For strata with larger collections, 110 tissue samples were selected at random for genotyping. For this subsampling, FB, BB, GG, and MO (Figure 1; Table 1) were each treated as distinct areas, while CR and EU were treated as a single area.

Genomic DNA was extracted from each fin clip with DNeasy 96 extraction kits using a BioRobot 3000 (Qiagen Inc.). DNA extractions were diluted 1:2 and 1.25 μl of this dilution was added to a pre-amplification PCR containing 2.5 μl PCR master mix (Qiagen) and unlabeled primer pairs from each of the 96 SNP loci used in Clemento et al. (2014), each with a final concentration of 0.05 μM. Reaction products were diluted ~6:1 and added to 2.5 μl of PCR master mix and 0.25U AmpliTaq Gold DNA polymerase (Applied Biosystems) following the manufacturer's protocols. These were then mixed with 96 TaqMan assays (Applied Biosystems), on 96.96 Dynamic Arrays (Fluidigm Corporation) using the Fluidigm IFC Controllers to create 9,216 individual PCR reactions that were thermal cycled on a Fluidigm FC1™ thermal cycler, with products imaged on an EP1 Reader. Genotypes were called and the data compiled using the Fluidigm SNP Genotyping Analysis software. During this scoring process, the relative fluorescence of alternate assays at each locus was visualized as a scatterplot for 96 individuals. Individual points that fell outside of clusters diagnostic of either the heterozygote or alternate homozygote genotypes were considered to have poor data quality (due to poor sample condition or laboratory error) and left uncalled for that locus (Clemento et al. 2011). Individual genotypes with more than 5 uncalled loci were excluded from later analyses as described below.

2.3. Genetic Stock Identification

The resultant 96-locus genotypes were used to determine the most probable reporting group of origin using the software gsi_sim (Anderson et al. 2008). This program uses established genetic stock identification (GSI) methods (Smouse 1990, Rannala and Mountain 1997) to compare each genotype to allele frequencies estimated for previously-sampled, distinct populations included in the "reference baseline" (Clemento et al. 2014). In our case the baseline consists of 68 North American Chinook salmon populations plus California coho (which are occasionally mistaken for Chinook salmon). Because some populations cannot be reliably discriminated on the basis of these 96 loci, the populations are grouped into 38 reporting groups

(37 Chinook groups, plus coho) that can be reliably differentiated. This baseline is focused on California and Oregon stocks but includes populations from as far north as Alaska and is expected to include representatives of every stock likely to be encountered in fisheries off the coast of California.

The gsi_sim program jointly estimates the mixing proportions---the unknown proportions of fish from each population or reporting group in the baseline present in the stratum being analyzed---and each individual's posterior probabilities of group membership. These individual posterior probabilities are influenced by the mixing proportions estimated from the sample in which the fish was analyzed, and thus the level at which data are stratified or aggregated could influence the individual fish assignments. We therefore evaluated the effect of aggregating our data over different temporal and spatial strata, by comparing individual assignments in the 1998 season under five different levels of aggregation against CWT data that were available for 121 fish from that season. Going from coarsest to finest, the five levels of aggregation were: (1) a single stratum of all fish from all times and locations, (2) calendar month by area/subarea (Figure 1), (3) calendar month by sampling port, (4) 3-week sliding window by area and (5) 3-week sliding window by sampling port. The results showed very little difference among these five levels of aggregation (concordance between GSI and CWT in 119 of 121 fish for all 5 levels of aggregation) so we used a 3-week sliding window and management area prior because it was the finest resolution that still yielded sample sizes greater than 20 for most strata.

The baseline includes genotypes from coho salmon, which are fixed for a single allele at nearly all 96 of the loci, allowing us to identify and remove from analysis a relatively small number of mis-identified salmon that had been retained by fishermen. The exclusion probability for the multilocus SNP genotypes was $p < 10^{-20}$ for unrelated individuals, and identical genotypes therefore represent the same fish which was inadvertently sampled more than once. All but the first instance of an identical genotype was removed from the analysis. Finally, we removed genotypes with low-confidence assignments from the analysis. Low confidence was due to poor data quality (individual heterozygosity [iHZ] < 0.16 or > 0.56, indicating allelic dropout or sample contamination, respectively) or high uncertainty in reporting group assignment as indicated by the log of a fish's genotype probability falling more than three standard-deviations from the log-genotype probability expected in the population to which the fish was assigned and posterior probability of reporting group membership (see below) < 0.9 or data missing from more than 5 loci (see Clemento et al. 2014 for further details about these criteria). Following removal of these genotypes, we plotted stock-specific catch for each year-month-area combination both proportionally and scaled as catch per unit effort.

2.4. Stock-specific catch and distribution model

We assumed that stock-specific CPUE served as a proxy of local density. Estimates were made separately each month to encompass the effects of seasonal fish movements, but we combined information across years, assuming additive effects of area and year on log-CPUE (constant multiplicative effects on CPUE) as in Satterthwaite et al. (2013). That is, for each reporting group *r* in each month *m*, the mean catch rate (λ) for an assumed negative binomial process was modeled as

$$\lambda_{rmyx} = e^{\beta_{rm}+\gamma_{rmy}+\rho_{rmx}} \qquad (1)$$

where *y* indexes years, *x* indexes fishing areas, β_{rm} is the (stock- and month-specific) intercept, γ is the year effect, and ρ is the area effect. Thus year effects were assumed to scale monthly stock-specific CPUE up or down uniformly through space (i.e., an effect of cohort strength), with the scaling of relative CPUE across space constant through time. For identifiability, $e^{\beta_{rm}}$is the estimate for stock *r* in month *m* in GG in 1998, with $\rho_{GG} = \gamma_{1998} = 0$.

We accounted for stochasticity in the catch and sampling process, as well as genetic assignment uncertainty, as in Satterthwaite et al. (2014), except that, since we had multiple years of data for a particular month/area combination, we modeled overdispersion relative to a Poisson catch process by using a negative binomial distribution (Mangel 2006, Satterthwaite et al. 2013). Briefly, given *f* units of fishing effort expended in a given area and month/year (subscripts suppressed), the expected mean for the total catch of fish from a particular stock, C_r, is the product of effort and stock-specific mean catch rate, λ_r:

$$C_r \sim \text{NegativeBinomial}(mean = f\lambda_r, dispersion = k) \tag{2}$$

and thus p(C_r,|λ_r,*k*,*f*) is given by the probability density function of a negative binomial distribution. By Bayes' theorem,

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

and since p(C_r,*f*) is a constant with respect to λ_r and *k* it can be neglected in sampling the posterior distributions of β, γ, and ρ (the constituents of λ_r, see equation 1) and *k* via Markov Chain Monte Carlo (MCMC; Gelman et al. 2004) sampling methods. For the constituents of λ_r, we assumed independent log-uniform prior distributions allowing for lambda values as low as 10^{-87} and as high as 100 (which is well beyond the bounds of the data), while our uniform prior on *k* allowed values as low as 0.2 (highly overdispersed, even lower values were excluded because they led to convergence problems) and as high as 1000 (essentially equivalent to a Poisson).

Since only a subset of the catch corresponding to trips from which samples were collected was genotyped, and assignments to reporting groups are uncertain, C_r is not known with certainty. Given *n* fish successfully genotyped, the vector $\boldsymbol{n}$ of the number of such fish assigning to each reporting group n_r is the sum of multinomial random vectors, each of a single trial with cell probabilities given by $\boldsymbol{g}_\mathrm{i}$, the vector of posterior probabilities that fish *i* originated from each of the *R* total possible reporting groups (g_{ri}), expressed as:

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

Given *C* total fish caught over all of the sampled trips (of which *n* were genotyped and *u* were not, $C=n+u$), the total number of fish from each reporting group C_r is the sum of n_r genotyped fish from that stock and u_r un-genotyped fish from that stock, with the composition of $\boldsymbol{u}$ depending on the unknown proportion of the sample consisting of each stock π_r. In the course of the MCMC, we simulated 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, expressed as

$$\{\pi_1, \pi_2, \ldots, \pi_R\} \sim \text{Dirichlet}\left(n_1 + \frac{1}{R}, n_2 + \frac{1}{R}, \ldots, n_R + + \frac{1}{R}\right). \qquad (5)$$

We then drew u_r from a multinomial distribution with values for $\boldsymbol{\pi}$ drawn via equation (5), expressed as

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

and calculated C_r as the sum of n_r and u_r, which we used to update k and the components of λ_r via MCMC with equation (3) giving the target density.

We thus have several options for quantifying uncertainty in metrics of stock-specific catch. We can quantify uncertainty in the composition of the genotyped sample by examining the posterior distribution of n_r/n, we can quantify uncertainty in the catch composition (including ungenotyped catch) using the posterior distribution of C_r/C, we can describe uncertainty in the stock composition of the source population being sampled using the posterior distribution for π_r, and we can quantify uncertainty in stock-specific catch using the posterior distribution of C_r. Similarly, we can quantify uncertainty in stock-specific CPUE using the posterior distribution for λ_r. See the Discussion (sections 4.1 and 4.2) for guidance on quantifying uncertainty when no fish assigning to the stock of interest are recovered from the genotyped sample. We examined the importance of accounting for assignment error by comparing our posterior credible intervals of catch proportions to confidence intervals calculated assuming hypergeometric sampling with known stock identities in a set of illustrative examples varying in sample size and stock proportion.

2.5. Hypothesis testing

We evaluated the strength of evidence for a delineation in stock-specific local density at Point Reyes by comparing estimates of stock-specific CPUE for sampled recreational trips out of GG (San Francisco, Sausalito, Berkeley, Emeryville, and Princeton/Half Moon Bay, corresponding primarily to fishing south of Point Reyes) against trips out of BB (Bodega Bay, corresponding primarily to fishing north of Point Reyes). For each stock/month, we used the MCMC chains generated as described above to establish the posterior distribution of the ratio between stock specific catch rates in the southern (GG) versus northern (BB) portions of the SF management area:

$$D_{rm} = \frac{\exp\left(\rho_{r,m,x=GG}\right)}{\exp\left(\rho_{r,m,x=BB}\right)} \tag{7}$$

We used the quantiles of this chain to determine whether credible intervals on this ratio were entirely above or below 1.0 and used the posterior median as a point estimate of how much the distribution of a particular stock within the current SF management area (our GG and BB areas combined) was skewed south of Point Reyes ($D > 1$) or north of it ($D < 1$).

Note that if catch of fish assigning to a particular stock was zero or very low in the southern portion of the SF area (GG), this ratio will be near 0 and the MCMC sampler will typically converge. However, if assigned catch is near zero in the northern portion, the ratio will approach infinity and cause convergence problems. It is thus informative to inspect cases of poor convergence to determine whether assigned catch was near zero in both areas or only the northern portion of the SF management area (BB).

We considered there to be strong support for a change in stock distributions around the Point Reyes boundary if the median GG/BB ratio was > 2 (for GG) or < 0.5 (for BB), AND the lower/upper bound of the 95% credible interval was 0.1 more/less than 1. We considered there to be moderate support for such a difference if the lower/upper bound of the credible interval was 0.1 more/less than 1. We considered there to be weak support for a difference if the lower/upper bound of the credible interval was 0.01 more/less than 1, or if zero fish plausibly assigning to the applicable stock were sampled in one of the two areas (GG or BB).

All MCMC chains were "burned in" for at least 5,000 iterations and run for at least 25,000 iterations in the retained chain. Additional burn-in iterations were performed if a Geweke (1992) diagnostic on the posterior chain for the ratio returned a $|z|>2.0$ when comparing the first 10% to the last 50% of the retained chain, and additional iterations were performed if a Raftery and Lewis (1995) diagnostic indicated that the retained chain was not sufficient to identify the 0.025 quantiles to an accuracy of ±0.02 with probability of at least 0.95, with diagnostics implemented using the R (R Core Team 2013) package "coda" (Plummer et al. 2006).

3. Results

We successfully genotyped 10,278 fish that were sampled during the five-year 1998-2002 period, representing between 1 – 12% of the total recreational landings in these areas each month (Table 1; month/area strata with landings < 15 are excluded from this range). Of these fish, 189 were genetically identified as coho salmon and removed from further analysis. An additional 406 genotypes were removed from the dataset for poor data quality and 41 were removed due to high uncertainty in group assignment, leaving a total of 9,642 genotypes for further analysis. To assess whether the fish removed due to low-confidence assignments were not representative of all the fish genotyped, we compared the maximum a-posteriori assignments of the 41 fish removed due to high uncertainty in reporting group assignments to those of all 9,642 fish that were not removed. There was no significant difference in the distribution of assigned reporting units amongst the two groups (χ^2 test, $p > 0.25$, by simulation). For all years combined, our genetic assignments were concordant with coded-wire tag data for 292 out of 298 cases (Table 2), indicating a discordance rate of 2.0% between GSI and CWT.

3.1. Stock Proportions and Stock-Specific Total Catch

Stock proportions were dominated by fish from the Central Valley Fall reporting group for nearly all times and areas for which data were available, with the exception of CR during August and September, which, in some years, showed a high proportion of Klamath River fish (Figure 2). However, it should be noted that the sample size for CR during these exceptional years was small (<35 fish per stratum). In the interest of legibility, Figure 2 does not reflect uncertainty in the individual stock proportion estimates, but uncertainty in both proportions and catch are addressed in section 4.1 of the Discussion.

3.2. Spatial and Temporal Variability in Stock-Specific CPUE

Other than the Central Valley Fall group, all stocks were caught at less than 0.5 fish per angler-day in all time-area combinations, and catch rates above 1.0 fish per angler-day were rare even for Central Valley Fall (Figure 3). These fisheries had a bag limit of two fish per angler day, which may cause the relationship between local abundance and CPUE to be concave down at high density. At the same time, the relationship may be concave up at low density if higher abundances make it easier for fishermen to cue in on dense aggregations. As a result it is unclear whether we are likely to be overestimating or underestimating differences in fish densities among management areas.

The location of highest CPUE for Central Valley Fall fish tended to vary across months: it was typically highest in southern areas in April and May, with a more even north-south distribution in June and July, and with relatively low CPUE in the north in August and September. Similarly, CPUE of Klamath River fish was highest near EU and CR (located just south and north of the Klamath River mouth, respectively), and was often zero or near zero in southern ports during August and September. Instances of nonzero CPUE were also more spread out earlier in the year.

There was no consistent time-area combination for the highest within-year CPUE of Central Valley Fall fish. While the highest CPUE was observed in July for all years except 2002, the location of highest CPUE varied among GG, BB, and FB. In 2002, CPUE of Central Valley Fall fish was highest in GG for all months except April (FB) and September (CR). In the interest of legibility, Figure 3 does not reflect uncertainty in the individual stock-specific CPUEs, but factors contributing to uncertainty in CPUE are addressed in section 4.2 of the Discussion, and section 3.3 describes inference about statistical support for differences in CPUE.

3.3. Changes in Stock-Specific CPUE Across Point Reyes

Fish assigned to the Central Valley Winter reporting group were never sampled north of FB and very rarely sampled north of Point Reyes. Thus in most months there appeared to be support for a hypothesized difference in local density of winter run fish north (i.e., BB) and south (i.e., GG) of Point Reyes (Table 3), although the small number of winter run fish sampled limit the strength of conclusions that we can draw. There appeared to be strong support for higher CPUE of Central Valley Spring fish in BB during June but higher CPUE in GG during September. There was strong support for higher Central Valley Fall CPUE in GG during May but not in other months. There was strong support for higher CPUE of California Coast fish in BB during April, contrasted with weak support for higher CPUE of California Coast fish in GG during May. There was weak support for higher CPUE of Klamath River fish in GG in May, but strong support for higher CPUE in BB during July and weak support for higher CPUE in BB during September. There was moderate support for higher CPUE of Rogue River fish in GG during April, and weak support for the same pattern in June and September.

4. Discussion

Genetic stock identification methods provided the ability to estimate spatial and temporal variation in stock proportions and stock-specific CPUE for a suite of untagged and partially tagged stocks of conservation concern, including untagged California Coast and Central Valley Spring stocks (both listed as threatened) and the partially tagged Central Valley Winter stock, and to evaluate the consistency of observed patterns with previous assumptions or inferences made from tagged proxy stocks. It also allowed analysis of partially tagged stocks (Central Valley Fall, Klamath River, Central Valley Winter, Rogue River) and comparison of these observed patterns to those determined in previous studies utilizing just the tagged components of these stocks. These results allowed for a relatively comprehensive characterization of the stocks that contributed to the California recreational ocean salmon fishery during the five year study period.

The 298 fish with known stock of origin provided via CWT suggested a discordance rate of 2.0% (6/298), similar to the 1.05% rate reported by Clemento et al. (2014, 11/1052, $\chi^2 = 1.75$, $p > 0.18$) for a fishery sample that allowed substantially more comparisons due to a large increase in the Central Valley Fall CWT tagging rate starting in brood year 2007 (Buttars 2012).

Discordant assignments were too rare to identify particularly problematic stocks with high confidence, although apparent misassignments either to or from the Rogue River stock made up 33% of discordant results in this study despite the overall small proportion of Rogue River fish. Similarly, Clemento et al. (2014) reported only a 45% GSI~CWT agreement rate for Rogue River, noting that Rogue River fish are genetically similar to fish from the Klamath River and North California / South Oregon Coast reporting groups.

4.1. Stock Proportions

Stock proportions did not vary in any consistent way across years, with the proportion of Central Valley Fall fish consistently high relative to all other reporting groups including Klamath River. While Klamath River and other non-Central Valley Fall stocks often contribute to fisheries in the northern areas of California, even constituting the majority of the catch on occasion, the same was not observed for the southern areas. In all years, months, and areas considered here, areas south of FB rarely had substantial contributions from stocks originating outside of the Central Valley. However, a separate study showed that in 2007, a year of unusually low Sacramento River fall Chinook abundance, fish assigning to the Central Valley Fall reporting group made up only 71% of a sample of 340 fish collected from the MO recreational fishery (Lindley et al. 2009). During this study, the average proportion of Central Valley Fall fish in the MO fishery was 92% among all months and years.

Uncertainty in stock proportion estimates depends primarily on the sample size and the magnitude of stock proportions, with smaller relative error as sample sizes increase or stock proportions increase (Allen-Moran et al. 2013). Additionally, if the interest is in composition of the catch per se (sampled without replacement) as opposed to the source population from which the catch was sampled (generally large enough to consider as sampled with replacement), uncertainty decreases for a given sample size when that sample size makes up an increasing fraction of the total catch. Thus for illustrative purposes we present uncertainty calculations for two sampling strata: MO in July 1999 which had a relatively large sample size that constituted approximately 20% of the total harvest (the target sampling rate for the current CWT program), and CR in September 2001 which had a small sample size but nevertheless genotyped approximately 40% of the total harvest for that stratum.

For CR in September of 2001, 29 total fish were harvested by sampled trips, of which 12 fish were successfully genotyped. Of these 12 fish, 7 assigned with high probability to Central Valley Fall, 4 assigned with high probability to Klamath River, and 1 indeterminate fish assigned with moderate probability to either Klamath River or Rogue River (but almost certainly one of those two). Resultant 95% credible intervals on the proportion of catch from each reporting group were 0.34-0.76 Central Valley Fall, 0.21-0.59 Klamath River, and 0.0-0.10 Rogue River. Assuming all assignments were certain and that the indeterminate fish assigned to Rogue River, the methods described in Allen-Moran et al. (2013) applying a normal approximation to a hypergeometric sampling model yield approximate 95% confidence intervals of 0.37-0.80 for Central Valley Fall, 0.20-0.63 for Klamath River (assuming the indeterminate fish was Klamath River, otherwise the bounds drop to 0.13-0.54), and 0-0.20 for Rogue River. These differences appear to result largely from propagating the uncertainty associated with assignment error, but in part because the normal approximation employed by Allen-Moran et al. (2013) breaks down with small numbers of fish, and because our method explicitly accounts for the simultaneous estimation of multiple proportions. An exact solution implemented via the "Sprop" function in R package "samplingbook" (Manitz et al. 2013) yields confidence intervals of 0.31-0.83 for Central

Valley Fall, 0.17-0.69 for Klamath River (or 0.14-0.62 if the indeterminate fish is of Rogue River origin), and 0.03-0.34 for Rogue River (assuming the indeterminate fish is of Rogue River origin).

For MO in July 1999, 574 total fish were harvested by sampled trips, of which 108 were successfully genotyped. 102 assigned with high probability to Central Valley Fall, 4 assigned with essential certainty to Central Valley Winter, and 2 fish assigned to Rogue River with high probability. Resultant 95% credible intervals on the proportion of catch from each reporting group were 0.88-0.97 Central Valley Fall, 0.01-0.07 Central Valley Winter, and 0.0-0.05 Rogue River. Assuming all assignments were certain, the methods described in Allen-Moran et al. (2013) applying a normal approximation to a hypergeometric sampling model yield approximate 95% confidence intervals of 0.91-0.98 Central Valley Fall (0.89-0.98 using exact method), 0.01-0.07 Central Valley Winter (0.01-0.09 using exact method), and 0-0.04 Rogue River (0.004-0.06 using exact method). Thus in this case accounting for assignment error causes relatively little change in the estimated uncertainty.

These results suggest that future GSI sampling programs should employ larger sample sizes (and/or sample a large fraction of the catch) if confident inference about rare stocks is desired. In general, the sample size required scales inversely with the target proportion (i.e. a proportion half as small requires twice the sample size) and with the square of the desired precision (i.e. halving the standard error requires quadrupling the sample size, Allen-Moran et al. 2013).

Uncertainty in stock-specific catch is similar to uncertainty in catch stock proportions when total catch is assumed known, as was the case in this study. The MCMC sampler we developed could be readily expanded to account for uncertainty in total catch by integrating over the plausible range of variability in the number of ungenotyped fish u.

A related concern is the detection of rare stocks. For detection of stocks present in the sampled ocean area, the sampled fish can be treated as taken with replacement and modeled using a binomial, such that the probability of sampling at least one fish (Q_1) with a sample of size n given stock proportion p is:

$$Q_1 = 1 - (1 - p)^n \tag{8}$$

And the required sample size to achieve a specified probability of detection is:

$$n = \frac{\log(1 - Q_1)}{\log(1 - p)} \tag{9}$$

When determining the presence of a stock in the catch catch (totaling C), sampling is without replacement and modeled as a hypergeometric process:

$$Q_1 = 1 - \frac{\binom{C(1-p)}{n}}{\binom{C}{n}} \tag{10}$$

And the required sample size is approximately (see Allen-Moran et al. 2013 for an exact solution):

$$n = \left(1 - \left(1 - Q_1\right)^{\frac{1}{Cp}}\right)\left(C - \frac{Cp - 1}{2}\right) \qquad (11)$$

Equations 8 and 10 suggest a way of quantifying uncertainty about rare stock presence, given no recoveries of that stock in a sample. Subtracting the relevant equation from 1.0 yields the probability of obtaining 0 recoveries from a stock, given it is present at proportion p; and this can serve as a likelihood function for determining the probability of any value of p, given 0 observed recoveries and some prior on p, in a Bayesian framework. The prior merits careful consideration and one might want to consider an approach that shares information across space and/or time, such that an observation of 0 recoveries for a particular stock is considered stronger evidence for absence if the same stock has been consistently undetected in adjacent areas and/or the same area at different times.

4.2. Spatial and Temporal Variability in Stock-Specific CPUE

Consistent with earlier studies of CWT recoveries, Central Valley Winter fish appear most concentrated in the south (O'Farrell et al. 2012a, Satterthwaite et al. 2013) and are almost never recovered from samples north of the SF management area. Central Valley Fall fish appear to concentrate in the Gulf of the Farallones, near the mouth of the Central Valley river network in the fall, with CPUE in northern areas dropping at the time adult spawners return to the Central Valley, as previously inferred from CWT (Satterthwaite et al. 2013). These results suggest that inferences based on tagged hatchery fish from these stocks are representative of the hatchery plus natural origin composite, at least in terms of coarse scale spatial distribution (see also Weitkamp and Neely 2002, Weitkamp 2010). However, since Central Valley Fall appears dominated by hatchery-origin fish (Barnett Johnson et al. 2007, Kormos et al. 2012, Palmer-Zwahlen and Kormos 2013), little difference between hatchery-origin fish and the composite would be expected even if natural-origin fish differed in their distribution. Still, the Central Valley Winter composite is primarily natural-origin (Winship et al. 2014), suggesting that the tagged hatchery fish are similar in distribution to their natural-origin counterparts. Despite considerable variation in the reconstructed abundance of Sacramento fall run Chinook salmon over these years (O'Farrell et al. 2013), peak CPUE of Central Valley Fall fish was between 1.0 and 1.5 fish per angler day in all years, with limited predictability in when and where the peak CPUE occurred.

In August and September of most years, CPUE of the untagged California Coast stock was highest in Fort Bragg while CPUE of Klamath River fish was highest in Eureka and Crescent City, similar to the pattern found by Satterthwaite et al. (2014) using commercial data collected in 2011 and 2012 and consistent with the results in NMFS (2000) derived from CWT recovery data from a since-discontinued hatchery program. Thus the potential for these stocks to diverge in their spatial distribution, likely to the mouths of their natal rivers in the fall, appears to be supported for an extended time period and across fishery sectors. The reinforcement of this result supplied by this study is particularly relevant because an upper limit to the expected age-4 Klamath River fall run harvest rate is used to constrain the ocean fisheries for the purpose of protecting the California Coast stock (O’Farrell et al. 2012b).

The apparent, but weak, tendency for higher CPUE of Rogue River fish in GG than BB was unexpected since the Rogue River is the northernmost source river among the stocks analyzed. Given all of the factors besides stock that can influence CPUE (e.g. weather conditions, nonrandom spatial sampling by fishermen), these patterns in CPUE should not be over-interpreted as reflective of absolute spatial distributions, but they are reflective of spatial patterns of overlap with fisheries, which may be more relevant from a management perspective than absolute spatial distribution.

Uncertainty in CPUE is affected by the same considerations as stock proportions and catch (described in section 4.1) and also by the amount of fishing effort, with uncertainty decreasing as fishing effort increases (Satterthwaite et al. 2013). Because Equation 3 has a nonzero value for positive λ_r even when C_r=0, the posterior distribution for λ_r calculated using our methods will always account for the possibility that a stock was present (had some nonzero probability of being caught) even if it was not sampled, becoming more confident at ruling out all but very low probability of presence as fishing effort increases. As with stock proportions, careful consideration should be given to prior specification and/or sharing information across space or time when making inference about rarely sampled stocks.

An additional challenge in interpreting either stock proportions or stock-specific CPUE results from this study are the effects of minimum size limits in the fishery. Since fish sampled in this study were not aged, and there is not detailed information on size-at-age available for all of the stocks studied here, we were unable to adjust catch on the basis of stock-specific expected proportions of fish that are legal size (Satterthwaite et al. 2013) and thus underestimating contacts with stocks of fish with smaller body size such as Central Valley Winter, for which age-3 fish (those most commonly encountered in the fishery) have mean total lengths growing from approximately 21 to 28 inches over the course of the fishing season with a standard deviation of about 2 inches (O'Farrell et al. 2012a). In addition, the minimum size limit in effect varied both spatially and temporally throughout the study period, ranging from 20 to 24 inches total length. It was also common for the minimum size limit in the KC to be less than the limit in effect for the southern areas, especially during the spring fisheries.

4.3. Suitability of Point Reyes as a Management Delineation Line

This study yielded limited support for using Point Reyes as an additional management delineation line. Although marginal statistical support was found for changes in local CPUE for some stocks, these differences were not found consistently for all months. The most consistent pattern was found for Central Valley Winter fish, which were almost never sampled north of Point Reyes, but contact rates with Central Valley Winter fish tend to be low in GG as well, and without more intensive sampling it is difficult to quantify how much lower CPUE of Central Valley Winter fish might be in BB versus GG. A general decrease in CPUE moving north would be expected based on previous results (O'Farrell et al. 2012a, Satterthwaite et al. 2013), but these studies also reported occasional winter run fish even further north than BB. Only 1% of all Central Valley Winter CWTs recovered in California ocean recreational fisheries have been taken north of BB.

4.4. Fishery Implications

The consistently high proportions of Central Valley Fall fish in all times and areas demonstrate how vitally important this stock is to California recreational fisheries. Central Valley Fall abundance was relatively high during the study period, yet a rapid decline a few years after the end of the study period culminated in the lowest recorded abundance of this stock (Lindley et al. 2009) and the closure of nearly all ocean salmon fisheries in California and Oregon during 2008 and 2009. While other stocks, such as the Klamath River and Central Valley Winter, have more frequently constrained California ocean salmon fishing opportunity, the much lower relative CPUE of other contributing stocks demonstrates that the abundance of the Central Valley Fall stock is the primary driver of the recreational fishery in terms of catch per angler day and suggests that fishery success would not be buffered by these stocks during times of low Central Valley Fall abundance.

4.5. Utility of Approach

The ability of GSI to produce stock proportion estimates could be useful in forecasting impacts of quota fisheries, which are currently rare in California but are more frequently employed in other areas. However, because the observed proportions of the stocks of greatest conservation concern (e.g., Central Valley Winter, California Coastal) were quite small, large sample sizes would be required to estimate these proportions with precision or to be confident that a sample not containing any fish from the stock of interest equates to a very low proportion of that stock existing in the ocean fishery being sampled (Allen-Moran et al. 2013). Understanding the full impacts of the ocean fisheries would also require increased spatial coverage since many of these stocks are also harvested in appreciable numbers in fisheries off the coast of Oregon (Satterthwaite et al. 2013). Representative sampling of both commercial and recreational fisheries would need to occur simultaneously to get a complete picture of tagged and untagged stock distribution by time and area; however, because the current management framework does not directly limit impacts on untagged stocks, it is not immediately clear how such information could be used.

The documentation of spatio-temporal variation in stock-specific CPUE is largely consistent with previous inferences from CWT recoveries. This suggests that the common practice of extrapolating from tagged proxy stocks to untagged surrogates can be appropriate in at least some cases, although the total number of comparisons made to test this assumption is still limited, and the Central Valley Fall case may not be very informative given the predominance of hatchery-origin fish in the aggregate stock. New insights into the spatial distribution of untagged stocks is somewhat limited by their rarity. The CPUE of Central Valley Spring fish was so consistently low that differences between strata with low CPUE and strata with zero catch are generally statistically indistinguishable (Satterthwaite et al. 2013). This is a general problem with inference about rare stocks, regardless of the type of tag employed, and reiterates the need for large sample sizes (Allen-Moran et al. 2013) when rare stocks are of interest. An additional complication in interpreting our estimates of stock proportions or CPUE is that these estimates are not age-specific. Thus, the collection and analysis of supplemental age data (e.g., scale aging, Kormos et al. 2010) is necessary to gain information on the strength of specific cohorts and to conform with the current age-specific harvest management goals in place for many of these stocks (PFMC 2012).

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Figure Captions

Figure 1. Map of California salmon fishery management areas (KC, FB, SF, MO), sub-areas defined in this paper (CR, EU, BB, GG), sampled ports, and natal rivers of major Chinook salmon populations.

Figure 2. Chinook salmon stock proportions by year, month, and area. Numbers below bars indicate the number of Chinook salmon successfully genotyped. Blank bars indicate no data (due either to fishery closure or lack of samples collected). (color required)

Figure 3. Stock-specific CPUE (fish per angler-day) for sampled fish. Blank bars indicate no data (due either to fishery closure or lack of samples collected). (color required)

Table 1

Table 1. California ocean recreational fishery Chinook salmon landings: total fish landed for the period 1998-2002 compared to the number of Chinook salmon analyzed. Landing data provided by CDFW. Blank cells indicate fishery closures.

		Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
CR	Genotyped				86	105	106	136	49		
	Landed				4,458	13,113	6,177	14,712	3,852		
	Prop. Genotyped				0.02	0.01	0.02	0.01	0.01		
EU	Genotyped				199	405	229	321	87		
	Landed				4,458	13,113	6,177	14,712	3,852		
	Prop. Genotyped				0.04	0.03	0.04	0.02	0.02		
FB	Genotyped	2	82	252	363	410	373	375	172	2	1
	Landed	14	664	3,712	9,923	21,441	32,684	21,599	2,621	6	2
	Prop. Genotyped	0.14	0.12	0.07	0.04	0.02	0.01	0.02	0.07	0.33	0.50
BB	Genotyped		9	87	80	152	176	106	100	32	3
	Landed		9	3,955	5,312	13,042	49,639	11,347	7,287	569	14
	Prop. Genotyped		1.00	0.02	0.02	0.01	0.004	0.01	0.01	0.06	0.21
SF	Genotyped		7	434	362	371	346	398	350	298	123
	Landed		779	20,232	32,170	48,162	66,104	46,101	21,311	14,001	3,184
	Prop. Genotyped		0.01	0.02	0.01	0.01	0.005	0.01	0.02	0.02	0.04
MO	Genotyped		234	443	436	423	468	327	122		
	Landed		7,371	86,439	36,806	30,186	28,693	5,100	1,847		
	Prop. Genotyped		0.03	0.01	0.01	0.01	0.02	0.06	0.07		

Table 2. Concordance between CWT and GSI assignments to stock of origin. The "Concordant CWT" column gives the number of CWT'd fish for which the GSI stock assignment matched the reporting group corresponding to the CWT release code, while the "Discordant CWT" column lists the other stocks from which CWT were recovered, and how often, for fish assigning to a given reporting group.

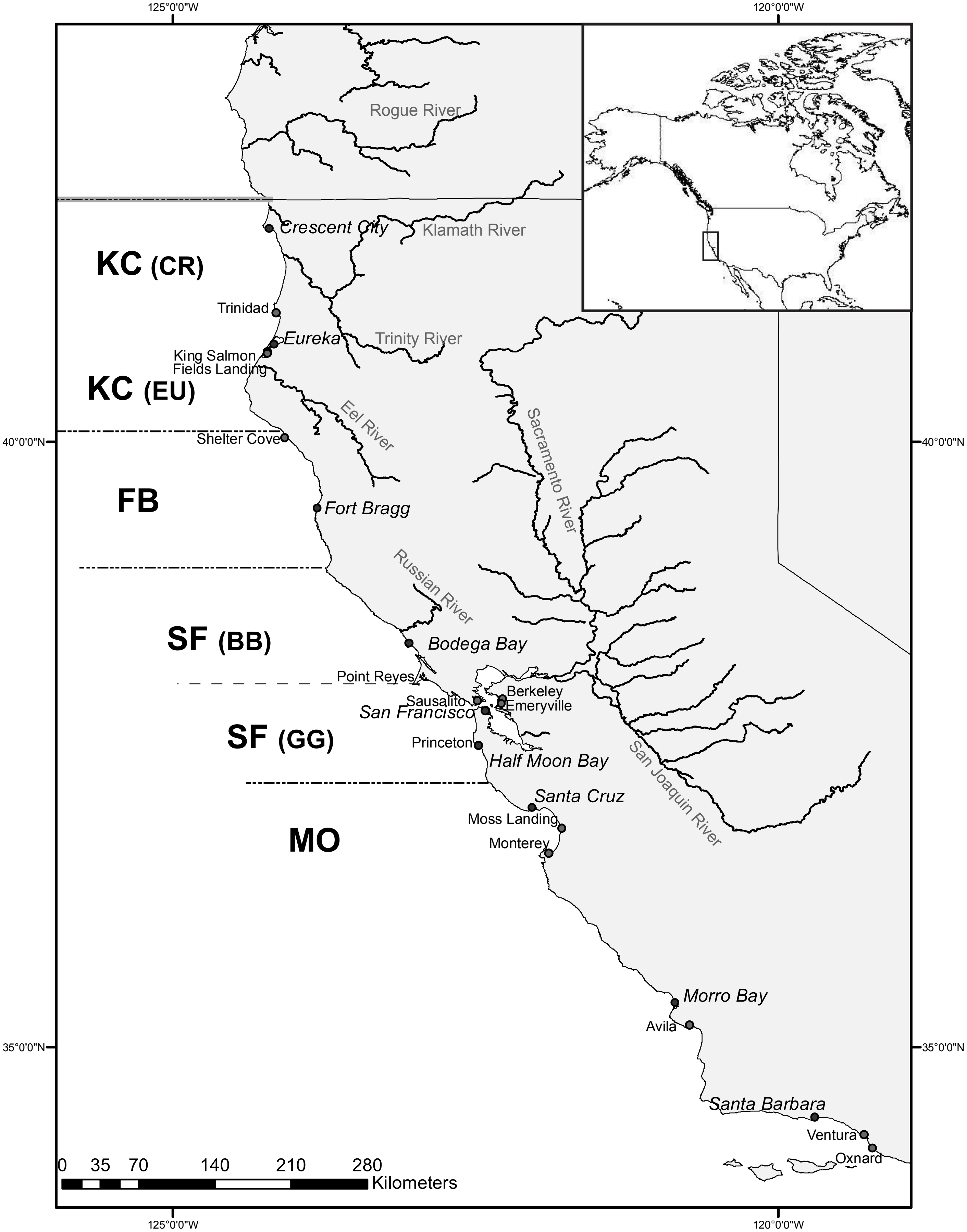
Reporting group	**Concordant CWT**	**Discordant CWT**
Central Valley Spring	1	none
Central Valley Fall	281	Klamath River (1), Upper Columbia Summer/Fall (1)
Klamath River	4	Rogue River (1), Central Valley Fall (2)
Rogue River	3	Central Valley Fall (1)
Mid Oregon Coast	1	none
Mid Columbia River Tule	1	none
Snake River Fall	1	none

Table 3

Table 3. Stocks with significantly greater CPUE south of Pt. Reyes (GG) or north of Pt. Reyes (BB). ++ indicates that the median GG/BB ratio is > 2 (for GG) or < 0.5 (for BB), AND the lower/upper bound of the 95% credible interval is 0.1 more/less than 1. A + indicates that the lower/upper bound of the credible interval is 0.1 more/less than 1. If there is no additional mark, but an area is reported, the lower/upper bound of the credible interval is 0.01 above/below 1, or zero fish plausibly assigning to the applicable stock were genotyped in either GG or BB. Blank cells showed little or no evidence of a difference.

	April	May	June	July	August	September
Rogue R.	GG+		GG			GG
Klamath R.		GG		BB++		BB
CA Coast	BB++	GG				
CV Fall		GG++				
CV Spring			BB++			GG++
CV Winter	GG	GG	GG		GG	GG

Figure 1



125°0'0"W
120°0'0"W
Rogue River
Crescent City
Klamath River
KC (CR)
Trinidad
Eureka
Trinity River
King Salmon
Fields Landing
KC (EU)
Eel River
Sacramento River
40°0'0"N
Shelter Cove
FB
Fort Bragg
Russian River
SF (BB)
Bodega Bay
Point Reyes
Berkeley
Sausalito
Emeryville
San Francisco
SF (GG)
Princeton
Half Moon Bay
San Joaquin River
Santa Cruz
MO
Moss Landing
Monterey
Morro Bay
Avila
35°0'0"N
Santa Barbara
Ventura
Oxnard
0 35 70 140 210 280
Kilometers

Figure 2

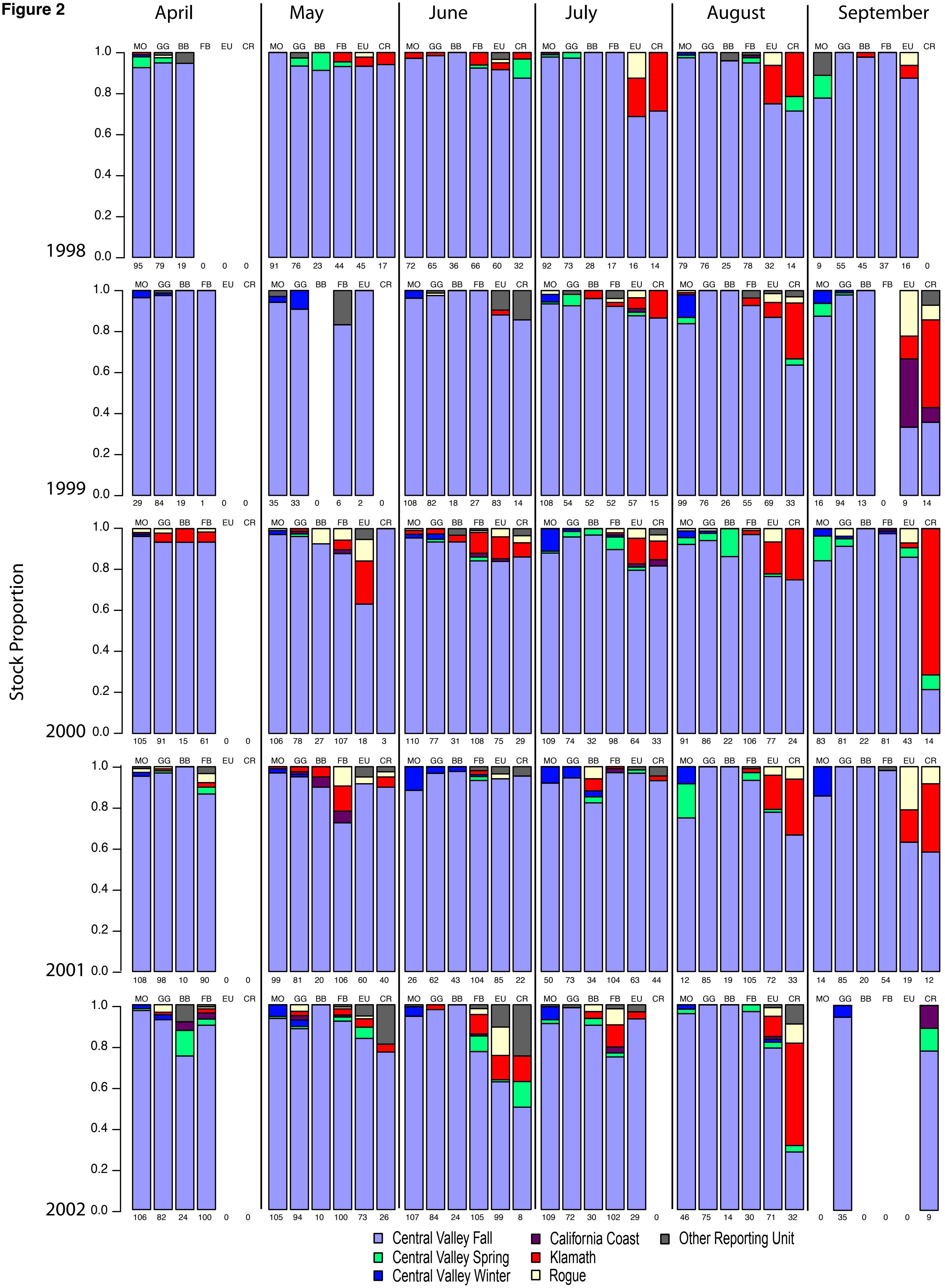
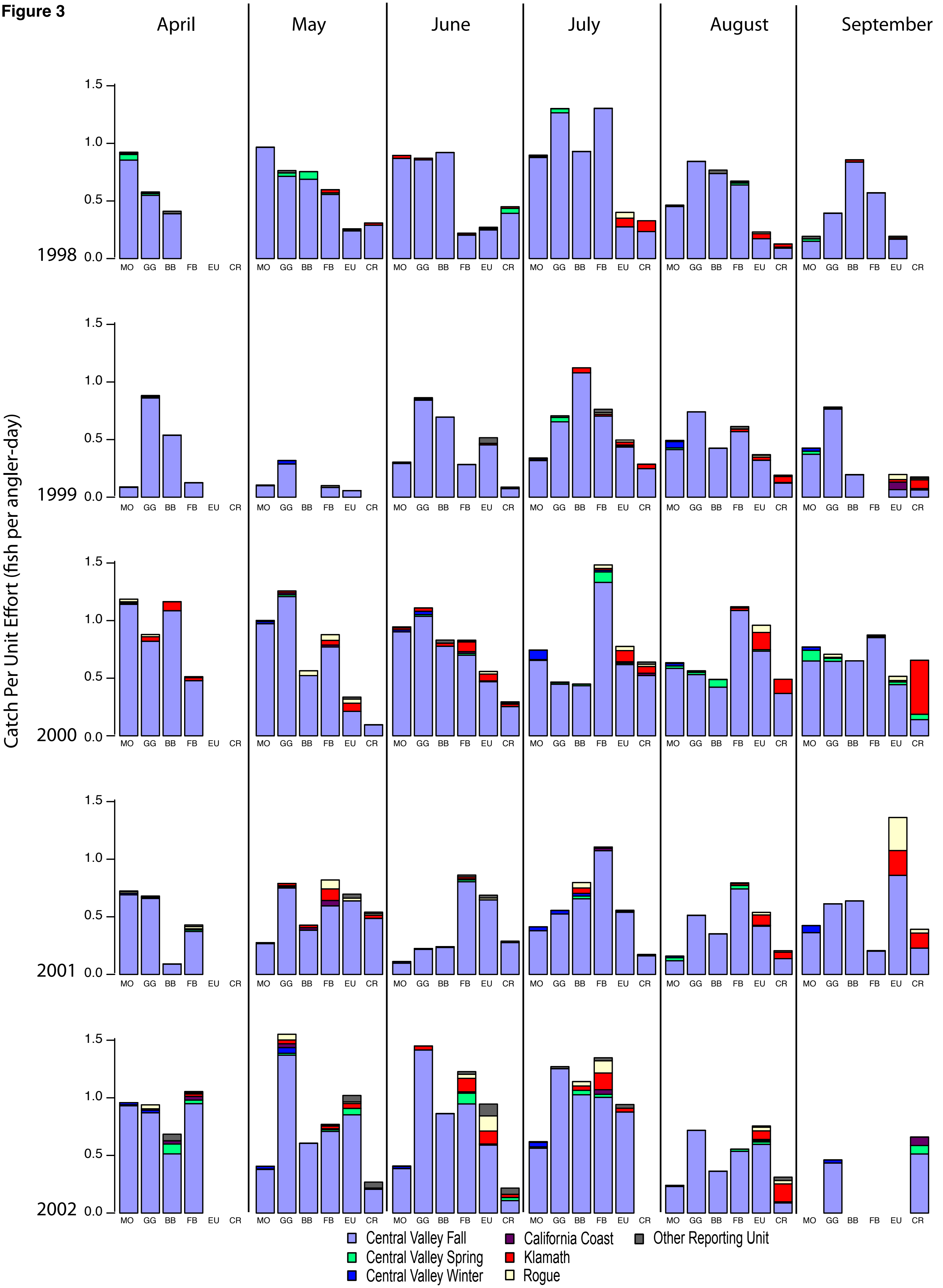

April
May
June
July
August
September
Stock Proportion
1998
1999
2000
2001
2002
0.0
0.2
0.4
0.6
0.8
1.0
MO GG BB FB EU CR
1998: 95 79 19 0 0 0 | 91 76 23 44 45 17 | 72 65 36 66 60 32 | 92 73 28 17 16 14 | 79 76 25 78 32 14 | 9 55 45 37 16 0
1999: 29 84 19 1 0 0 | 35 33 0 6 2 0 | 108 82 18 27 83 14 | 108 54 52 52 57 15 | 99 76 26 55 69 33 | 16 94 13 0 9 14
2000: 105 91 15 61 0 0 | 106 78 27 107 18 3 | 110 77 31 108 75 29 | 109 74 32 98 64 33 | 91 86 22 106 77 24 | 83 81 22 81 43 14
2001: 108 98 10 90 0 0 | 99 81 20 106 60 40 | 26 62 43 104 85 22 | 50 73 34 104 63 44 | 12 85 19 105 72 33 | 14 85 20 54 19 12
2002: 106 82 24 100 0 0 | 105 94 10 100 73 26 | 107 84 24 105 99 8 | 109 72 30 102 29 0 | 46 75 14 30 71 32 | 0 35 0 0 0 9
Central Valley Fall
Central Valley Spring
Central Valley Winter
California Coast
Klamath
Rogue
Other Reporting Unit

Figure 3


April
May
June
July
August
September
Catch Per Unit Effort (fish per angler-day)
1998
1999
2000
2001
2002
0.0
0.5
1.0
1.5
MO
GG
BB
FB
EU
CR
Central Valley Fall
Central Valley Spring
Central Valley Winter
California Coast
Klamath
Rogue
Other Reporting Unit