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Short communication

Inferred ocean distributions of genetically similar Chinook salmon stocks compared across run timing and river/hatchery of origin

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ABSTRACT

Klamath River Fall Chinook (KRFC) salmon from the Klamath-Trinity Basin are central to management of the ocean salmon fishery off the coasts of northern California and southern Oregon, with tagged KRFC serving as proxies for other stocks including spring run (KRSC). There has been no formal comparison of fall versus spring run ocean distributions, and published studies using genetic stock identification do not distinguish the runs. We modeled the spatial distribution of hatchery-origin fall versus spring run, inferred from coded-wire tag recoveries in the ocean commercial (troll) fishery while explicitly accounting for fishing effort, sampling rate, and release of sublegal-sized fish before sampling. Distributions for all stocks were confined to a similar core range, but varied seasonally, and with higher relative density of KRSC in the north. Only equivocal evidence was found for differences by age or within-basin source hatchery. The potential for such differences should be considered for analyses of coarser groupings in these and other stocks. Sensitivity analyses revealed differences in distributions inferred from recreational versus commercial fishery data, emphasizing the importance of recognizing the limitations of fishery-dependent data in representing the underlying spatial distribution of fish populations rather than spatial patterns in their interactions with specific fisheries.

1. Introduction

Ocean fisheries for Chinook salmon (*Oncorhynchus tshawytscha*) off the coast of North America are inherently mixed stock fisheries, managed to promote fishing opportunity on strong stocks while constraining impacts on weaker stocks to acceptable levels (PFMC, 2016; PSC, 2017). Managers use harvest models parameterized for select data-rich indicator stocks, which typically have a hatchery origin component that is tagged with coded-wire tags (CWT) on the assumption that fishery impacts on other stocks of interest will be similar to carefully selected indicators, but the suitability of such indicator stocks is rarely tested rigorously. There have been increasing calls for the use of genetic stock identification (GSI) in management, in part because GSI would allow directly quantifying the catch of untagged fish and GSI information could be used to test the suitability of some hatchery indicators (PSC, 2008). At the same time, it is important to realize that substantial heterogeneity may exist among the individual stocks or stock components that are combined into a single genetic reporting group, a possibility that we explore using a case study of Klamath River Chinook, a stock complex of high management and conservation interest.

The Klamath-Trinity River basin in northern California and southern Oregon supports the second-largest Chinook salmon stock complex in California. Klamath River Fall Chinook (KRFC) salmon play a central role in management of the ocean salmon fishery off the coasts of northern California and southern Oregon. KRFC is an actively managed stock under the Pacific Fishery Management Council's salmon fishery management plan (PFMC, 2016) with conservation objectives defined based on exploitation rate limits and escapement goals. KRFC experienced low 2015–2016 escapements and a very low escapement was forecast for 2017. This resulted in the declaration that the KRFC stock was approaching an overfished condition (PFMC, 2017). KRFC also serves as the indicator stock for the Southern Oregon Northern California Chinook stock complex, and the current Endangered Species Act consultation standard for the threatened and data-poor California Coastal Chinook stock is based on limiting the anticipated harvest rate on KRFC (NMFS, 2000; O'Farrell et al., 2012, 2015).

Although fall run Chinook salmon are numerically dominant in the Klamath-Trinity River basin (Williams et al., 2013), spring run (KRSC) salmon are present as well. From the perspective of ocean fisheries management, KRSC are considered part of the larger stock complex and are not presently managed with stock-specific measures.

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Phenotypically, fall versus spring run fish within the Klamath-Trinity Basin display distinctive life histories, but there is less genetic differentiation between fall versus spring run fish from the Trinity River than there is between fall run fish from the Trinity versus Klamath Rivers (Kinziger et al., 2013). A petition to list KRSC under the United States Endangered Species Act was denied (NOAA, 2012), but KRSC was identified as a stock of critical concern by Moyle et al. (2017).

The suitability of KRFC as an indicator for KRSC, particularly with respect to interactions with the ocean fishery, depends on the similarity between the two run timings in their ocean spatial distribution. Differences in the ocean spatial distribution between fall and spring run fish from the same basin have been observed for other Chinook salmon populations (Weitkamp, 2010), but we are not aware of any published analyses of KRSC ocean distribution.

Published information on the ocean spatial distribution of Klamath River Chinook (KRC, encompassing both run timings) is limited. Inferences of spatial distribution from patterns in catch per unit effort (CPUE) based on recoveries of CWTs from KRFC fish recovered in the commercial and recreational ocean fisheries are implicit in the Klamath Ocean Harvest Model used in fishery management (Mohr, 2006), but estimates of spatial distribution are not directly provided. Three papers describe spatial patterns in CPUE of Klamath River Chinook (KRC, not distinguishing fall from spring run) based on GSI applied to 5 years of recreational fishery data in California (Satterthwaite et al., 2015b), 2 years of commercial fishery data in California and Oregon (Satterthwaite et al., 2014), or 1 year of commercial fishery data in California and Oregon (Bellinger et al., 2015).

Because the current GSI baseline cannot reliably distinguish KRFC from KRSC (Clemento et al., 2014), these GSI-based studies are not informative about KRSC distribution and may offer an inaccurate picture of KRFC distribution to the extent that results are confounded by unknown differences between KRFC and KRSC. Additionally, in almost all cases (one year of analysis in Satterthwaite et al., 2014 being the exception), these GSI-based studies have not considered fish age. Because the CCC consultation standard is based specifically on the harvest rate of age-4 KRFC (NMFS, 2000), it is important to understand whether and how spatial distribution of KRC varies with age. Since CWT data reveal the hatchery, release type, run timing, and brood year (BY) of origin for each sampled fish, analysis of archived data derived from comprehensive sampling of fisheries for CWT over the last several decades has the potential to address current knowledge gaps regarding age-specific spatial distribution of KRFC and KRSC. Analysis of CWT data also allows for a comparison between fall run fish sourced from the Trinity River Hatchery (TRH) and those released from Iron Gate Hatchery (IGH) on the Klamath River, to compare the magnitude of differences across run timings within the Trinity to the magnitude of differences across rivers within the fall run. Age-specific CWT data also allow adjusting CPUE to account for the effects of (spatially and temporally variable) minimum size limits on the proportion of fish contacted which are retained and available for sampling (Satterthwaite et al., 2013), facilitating more accurate comparisons of contact rates, and thus implied densities, across areas.

2. Methods

2.1. Data sources

Our analyses of spatial patterns in CWT recoveries were based on records from the Regional Mark Processing Center (RMPC, http://www.rmpc.org/). To obtain the relevant harvest data, we queried "Standard Reporting, All Recoveries" for all recoveries of Chinook salmon originating from the Klamath-Trinity Basin occurring in the recreational (fishery code = 40, 41, or 42) or troll (fishery code = 10) ocean salmon fishery (additional codes for commercial and recreational fisheries exist in RMIS, but are not used in the areas covered by this analysis). This yielded records of individual fish recoveries including their CWT tag code (allowing determination of source location, run timing, and age), fish length, date and port of landing, and the sampling rate associated with those landings. Due to the potential for confusion resulting from different "birthdays" for spring versus fall run fish, we define fish age as the number of calendar years elapsed since the brood year.

2.2. Choice of fisheries, years, and release types for analysis

We performed the bulk of our analyses on data from the commercial troll fishery due to substantially higher KRC tag recoveries compared to the recreational fishery (Supplementary Appendix A). We obtained data on fishing effort and minimum size limits from Pacific Fishery Management Council (PFMC) archives available at http://www.pcouncil.org/salmon/background/document-library/historical-data-of-ocean-salmon-fisheries/, extended back to 1983 using personal archives (Satterthwaite et al., 2013). Our analysis used recovery data from 1983 to 1989. Data on recoveries prior to 1983 were excluded due to a lack of effort and size-limit data, whereas data after 1989 was excluded due to substantial reductions in catch and effort, along with extended closures, that greatly reduced tag recovery rates and increased uncertainty in more recent years. We excluded fish landed north of Cape Falcon (45°46′N) due to low recoveries of KRC tags and current management practices focused on KRC impacts south of Cape Falcon, and sorted the remaining landings into seven ocean management areas as defined by the PFMC (PFMC, 2016, see Fig. B.1 in Supplementary Appendix B, the "MO" area was dropped from this analysis due to low tag recoveries and consequent problems with mixing of the Bayesian model used to estimate distributions).

In our primary analysis, we considered all release groups of a given run timing from a given hatchery together, in part to maximize sample sizes and aid model convergence. However, important differences have been documented in the maturation and exploitation rates of typical "fingerling" releases of young fall run fish in spring or early summer compared to "yearlings" held for extended rearing periods and released in the following fall (Hankin 1990; Hankin and Logan 2010). Although adequate sample sizes were not available to reliably estimate separate distributions for each release type each month, we present selected comparisons across release types as a sensitivity analysis (see Supplementary Appendix C). Similarly, because fisheries act as a filter in sampling the underlying ocean abundance of fish (e.g., commercial vessels often fish in deeper waters and farther from port), we performed similar analyses on CWT recoveries from the recreational fishery, with select comparisons presented in Supplementary Appendix D. These comparisons were all carried out for recoveries in July, the month with the most tag recoveries.

2.3. Models

We used contact rate as a proxy for fish density in a particular time and area, where "contacts" are defined to include all fish caught on a hook, whether retained in the harvest or not. We modeled the fishery/stock/age/time/area-specific contact rate using a Bayesian hierarchical model developed and described in Satterthwaite et al. (2013). In brief, we assumed that contact rate λ for a particular stock is a function of its density D and catchability q. We further assumed that q was constant across space for a given fishery, time, and stock, and therefore we only estimate λ rather than q and D, and assume that differences in relative λ reflect distributional differences. Under this assumption, the stock-specific contacts resulting from a single unit (angler-day) of fishing effort follows a Poisson distribution with mean λ, and the total stock-specific contacts C resulting from f angler-days of effort follow a Poisson distribution with mean $f\lambda$. In model elaborations with sufficient data to estimate more parameters, we account for overdispersion by using a negative binomial distribution in place of the Poisson, corresponding to drawing a value of λ from a shared gamma distribution before making a draw of C from the Poisson (see below). Given stock-specific total contacts C, the stock-specific number of fish of legal size to retain in the harvest H was assumed to follow a binomial distribution driven by the proportion of fish that are legal-sized, π. The value of π was determined based on the size limit in effect at the time and place each harvested fish was sampled along with estimates of the mean and standard deviation of fish size-at-age obtained by fitting truncated normal distributions as described by Satterthwaite et al. (2012) to stock-specific CWT recovery data. Given the stock-specific number of harvested fish H, the stock-specific number of fish sampled S was assumed to follow a binomial distribution driven by the time/area-specific sampling rate ζ.

For each fishery/stock/area/month stratum, we combined information across years assuming multiplicative effects (additive on the log scale) of year and area, essentially assuming a similar proportional distribution of the stock through space, with density scaled up or down equally in each area based on abundance that year. Specifically, for a particular stock– age–month-fishery combination (therefore subscripts for stock, age, month, and fishery are suppressed), we modeled $\log(\lambda)$ in calendar year y and area x as the sum of a baseline density β, a fixed year effect γ_y, and a fixed area effect ρ_x, so that $\log(\lambda_{yx}) = \beta + \gamma_y + \rho_x$.

Because factors such as aggregations of fish, bag limits in recreational fisheries, and variation in local density on temporal or spatial scales smaller than the sampling unit can lead to overdispersed contacts (Cormack and Skalski, 1992), we assumed that contacts C in a particular year/area followed a negative binomial distribution with mean $f\lambda_{yx}$ and an area-specific dispersion parameter. We used vague priors on all parameters as in Satterthwaite et al. (2013).

For statistical comparisons of the distributions implied for different stocks or at different times, we calculated an index D of the proportion of cumulative contacts per unit effort occurring in either a single management area (SF, the southernmost area) or all management areas in California (SF through KC), similar to the distribution index calculated by Satterthwaite et al. (2013):

$$D_{SF} = \frac{\exp(\rho_{SF})}{\sum_{x\in(SF:NO)} \exp(\rho_x)},\quad D_{CA} = \frac{\sum_{x\in(SF:KC)} \exp(\rho_x)}{\sum_{x\in(SF:NO)} \exp(\rho_x)}. \tag{1}$$

In the summation notation used in Eq. (1), a:b denotes all areas moving south to north from a to b, inclusive. This metric provides a simple numeric summary of the cumulative distribution that can be compared across stocks, ages, fisheries, or time periods.

3. Results

3.1. Monthly patterns in contacts per unit effort

The degree of concordance among the stocks in their spatial patterns of tag recoveries varied across months (Fig. 1). Tag recoveries prior to May or after September were inadequate to estimate distribution for any stock (Supplementary Appendix A). No stock ever had its highest contacts per unit effort at the northernmost or southernmost management areas analyzed, suggesting that this study successfully captured the core of all stocks' distributions and that these core distributions were not radically different.

However, differences between fall and spring run frequently occurred at the scale of management area. Overall, TRH spring run appeared distributed somewhat to the north relative to both TRH and IGH fall run, and this was especially apparent for age-4 fish in May and June (Fig. 2). TRH spring very rarely had more than negligible contacts per unit effort in the southernmost SF and FB areas (and when it did, lower bounds on credible intervals were still quite low), whereas peak or near-peak contacts per unit effort occurred for some month/age combinations in FB for both IGH and TRH fall run (Fig. 1).

There did not appear to be consistent differences across ages within stocks, or between IGH versus TRH fall run. In most cases of apparent differences, the different posterior median estimates were within the respective credible interval bounds, and the two largest age-specific differences were observed for only one of the two source hatcheries. Age-3 TRH fall fish appeared nearly absent from the KC management area in May, even though the peak contacts per unit effort for age-4 TRH fall fish occurred in that same area that month. The peak in contacts per unit effort for age-3 IGH fall in September was in the CO management area, but age-4 IGH fall fish were rarely recovered there and had peak recovery rates in KO.

3.2. Sensitivity analyses

Restricting analyses to just fingerlings or yearlings (only possible within fall run) necessarily decreased sample sizes and thus increased uncertainty (Supplementary Appendix C). While it is difficult to draw firm conclusions based on these sample sizes, there was some indication that yearling releases of fall run Chinook from both Iron Gate and Trinity River Hatcheries had a more northerly distribution (Supplementary Appendix C, Fig. C.1).

Spatial patterns in contact rates showed some differences between commercial and recreational fisheries (Supplementary Appendix D). Peak contact rates for recreational fisheries in July always occurred in the KC management area (Supplementary Appendix D, Fig. D.1). However peak contact rates for the commercial fishery usually occurred in the adjacent FB or KO management areas, and relative contact rates in the SF and CO management areas were usually higher for commercial fisheries as well (see Fig. D.1 in Supplementary Appendix D).

4. Discussion

All three stocks were similarly distributed on a coastwide scale, with low contacts per unit effort in SF or NO and peak contacts per unit effort most often in KC or KO. Age-4 fish tended to be concentrated in the KO area near the time of adult return (May/June for spring run and September for fall run), suggesting the aggregation of returning adults near the natal river mouth. Although the mouth of the Klamath River is within the KC management area, it is closer to Brookings, Oregon (in KO) than it is to Eureka, CA (in KC), which are the two largest fishing ports in the respective management areas.

However, while the observed differences were small compared to the species range of Chinook salmon as a whole (ranging from Central California to Alaska along the eastern Pacific, and covering similar latitudes off Asia), there did appear to be consistent differences between KRFC and KRSC with KRSC distributed slightly more to the north. A more northerly distribution, and/or a distribution further from the source river for spring run has been observed in other stocks (Healey 1991; Weitkamp, 2010; Satterthwaite et al., 2013). This may have implications on realized fishery impact rates on KRFC versus KRSC since fisheries are structured based on time/area-specific limits (days open to fishing or catch quotas), and a more detailed understanding of KRSC distribution would be required if more active management of that stock was desired.

This also means that GSI-based estimates of KRC distribution (e.g., Satterthwaite et al., 2014, 2015b; Bellinger et al., 2015; Otto et al., 2016) might not fully reflect KRFC distributions. This could complicate evaluations of tagged KRFC as a suitable proxy for other stocks (e.g. Satterthwaite et al., 2014) and could be particularly problematic in more northern areas where the relative density of KRSC seems higher (Otto et al., 2016). The significance of this dilution of course would depend on the relative number of spring versus fall run KRC in the ocean. While reconstructed ocean abundances of spring run fish are not available, there is substantially more fall than spring run spawning habitat in the Klamath-Trinity basin. For years 2006–2010 (2007–2011 for South Fork Trinity Spring), the geometric mean escapement of spawning fall run fish to the upper Klamath-Trinity Basin was approximately nine times the spawning escapement of spring run (Williams et al., 2013), although spring run escapement is highly

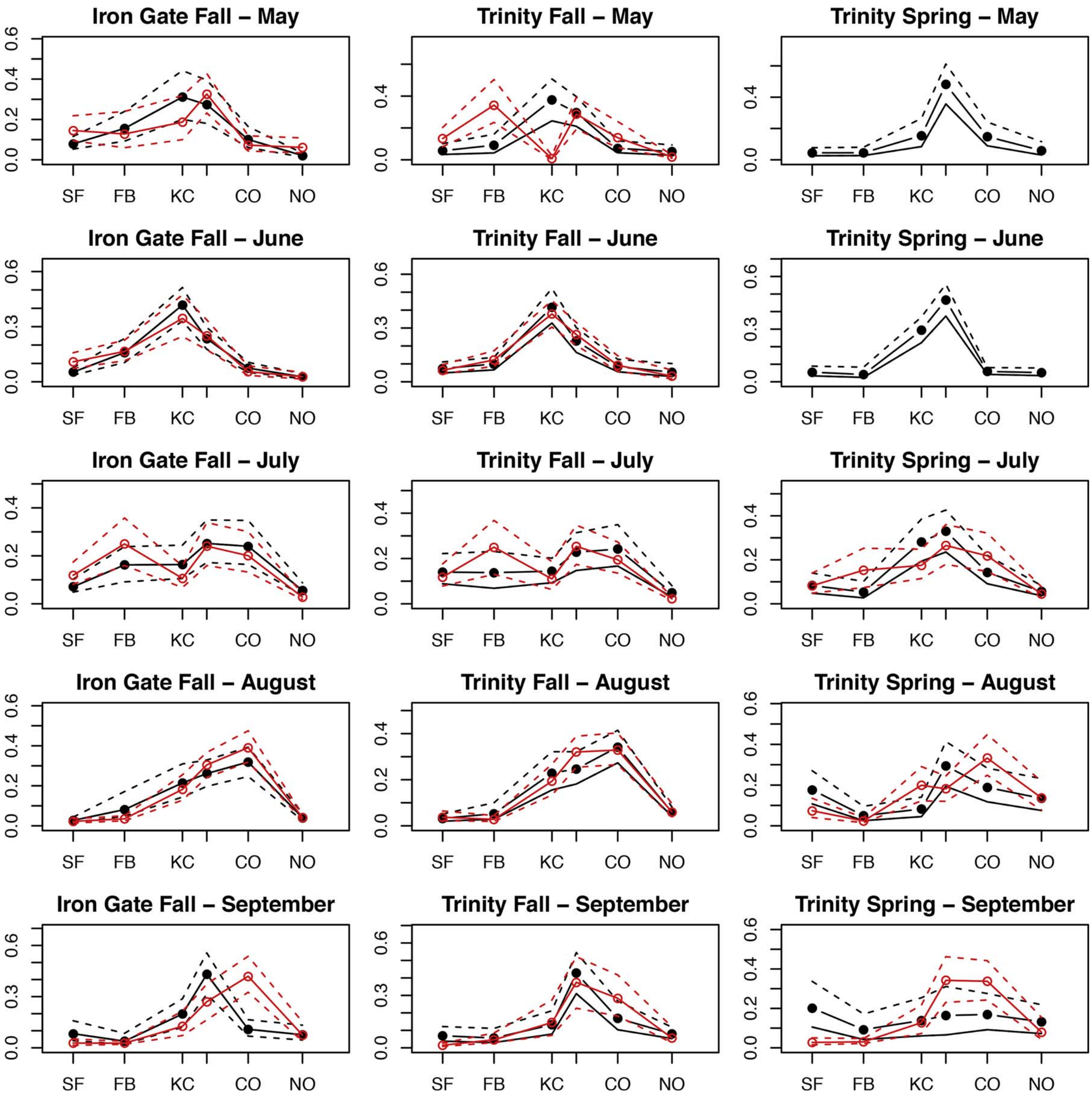

Fig. 1. Monthly spatial patterns in relative contacts per unit effort for the three stocks (Iron Gate Hatchery Fall, Trinity River Hatchery Fall, and Trinity River Hatchery Spring) in the ocean troll fishery. Management areas are ordered from south on the left to north on the right, with position along the x-axis reflecting the latitudinal midpoint of each area (the KO label is omitted for legibility). Black lines and filled circles indicate fish recovered four years after the brood year, red (online)/grey (print) lines and open circles indicate fish recovered three years after the brood year. Solid lines are posterior medians while dashed lines indicate central 68% credible intervals. Sometimes estimates for a particular stock-month-brood year did not converge, and such results are not plotted.

variable and appears to have made up nearly 33% of Klamath-Trinity escapement in 1988 (Williams et al., 2013, their Fig. 8).

Although evidence for age-specific distributions was equivocal, there was some indication of more northerly distributions for yearling compared to fingerling releases of fall run Chinook. Relative contact rates outside the centers of the stocks' ranges appeared higher in commercial versus recreational fisheries, indicating that fishery-dependent data reflects underlying distribution of the population as filtered by fishery-specific factors.

Future GSI studies should be cognizant of the potential for seasonal differences in fall versus spring run distribution. The extent to which this limits GSI-based inference on KRFC will depend on year-specific ratios in fall versus spring run abundance, which should be assessed for the specific years relevant to GSI studies. This problem might be resolved by extracting and analyzing otoliths from fish genetically identified as KRC and distinguishing fall from spring run based on inferred juvenile life history (Barnett-Johnson 2010 et al., 2010; Johnson et al., 2016), or by screening fish identified as KRC at additional genetic loci that may allow distinguishing populations of interest within broader genetic reporting groups (Meek et al., 2016). GSI studies should also prioritize aging of scales collected to date (and/or otoliths collected in the future) and consider the potential for age-specific distributional differences. GSI sampling programs used to inform ocean fisheries management might also be combined with parentage-based tagging (PBT, Anderson and Garza 2006), with screening at the same loci ideally serving both to identify all fish to their genetic reporting group of origin, and to identify the parents of specific fish if their parents were genotyped prior to spawning. With properly designed hatchery programs, this would allow identifying hatchery-origin fish back to their specific release group of origin (Satterthwaite et al., 2015a) and thus determining ages and distinguishing fall from spring run for those fish. PBT can in theory be applied to natural-origin fish as well, but this is much more expensive and logistically challenging than applying PBT in a hatchery setting (Satterthwaite et al., 2015a).

Similar considerations likely apply for other stocks and should be kept in mind when responding to calls for increased use of genetic

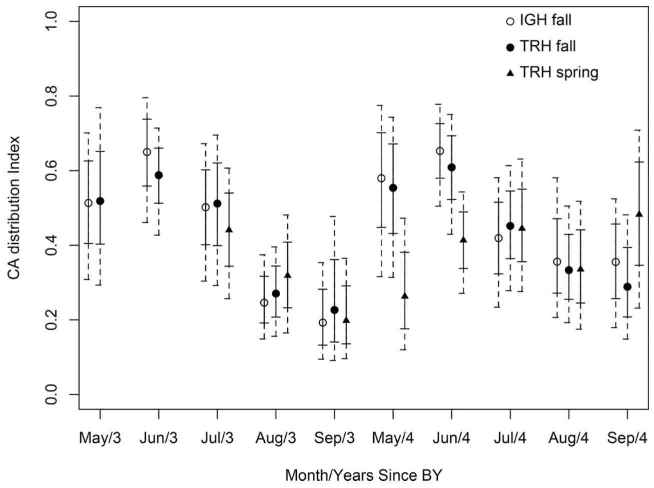

Fig. 2. Monthly spatial patterns in cumulative proportion of contacts per unit effort for the three stocks (Iron Gate Hatchery Fall, Trinity River Hatchery Fall, and Trinity River Hatchery Spring) in the ocean troll fishery that occurred within California management areas (D_{CA}). Lower values indicate more northerly distributions. Points are posterior medians while heavily and lightly dashed error bars indicate central 68% and 95% credible intervals, respectively. Sometimes estimates for a particular stock-month-brood year did not converge, and such results are not plotted.

information in ocean fisheries management (e.g., PSC, 2008; Otto et al., 2016). While our results are specific to KRC, we expect that similar issues will need to be considered in other areas. Because ocean harvest of Chinook salmon occurs over a wide area, and stocks in any one area may come from disparate geographic locations, the genetic baselines used in GSI studies must be able to distinguish among a multitude of stock complexes based on a modest number of genetic loci and so are tuned mainly to discriminate among rather than within regions. Thus while it is possible to develop higher resolution baselines for specific regions (e.g., Meek et al., 2016), to our knowledge all published applications of GSI to ocean-harvested Chinook salmon have used coarser baselines developed to cover broader regions (e.g. Beacham et al., 2006; Seeb et al., 2007; Clemento et al., 2014). The use of such baselines seems appropriate for the first pass of data analysis in a broad-scale GSI sampling program, but our results suggest significant value in following this up with additional analyses (whether based on additional loci, pedigree analyses, or otolith work) of fish from genetic reporting groups containing substocks with significant management or conservation concern.

Conflicts of interest

None.

Acknowledgments

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fishres.2017.11.006.

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