

Snake River Juvenile Salmon and Steelhead Transportation Synthesis Report

Gosselin JL, Van Holmes C, Iltis S, and Anderson JJ

Report by
Columbia Basin Research
School of Aquatic and Fishery Sciences
University of Washington

for

Division of Fish and Wildlife
Bonneville Power Administration
U.S. Department of Energy

Project No. 1989-108-00
Contract No. 74063 and 77308

3 April 2018

Highlights

- Changes were detectable in survival rates and transport-to-run-of-river survival ratios within and across life stages from before (1998-2005) to after (2006-2015¹) court order of increased spill. Although many changes in conditions have occurred in both the freshwater and marine environments across these two time periods, the trends identified can help support and generate hypotheses.
- Direct ocean and annual effects on survival can be very large, but freshwater-marine carryover and seasonal effects can still have significant effects on survival. The six factors (section 1.5) identified as moderate or high importance to transported and run-of-river survival in Anderson *et al.* (2012) are still relevant in the current literature review.
- Determining the direction and relative impact of factors on survival at each life stage – under various combinations of river and ocean conditions – would help clarify when and how the transportation program can be effectively improved.
- Non-linear models that test for positive effects, thresholds, and negative effects, along with estimates of certainty, will be important in identifying triggers. Some potential triggers include indices of river temperature, flow, total dissolved gas, migration timing, predators, and coastal and large-scale ocean conditions.
- New data collections with more contrast than that historically collected will help determine non-linear relationships with greater certainty. The environmental conditions in recent and upcoming years appear to provide such data. Transported fishes can continue to serve as a treatment group for comparison to run-of-river fishes.

¹ With PIT tag data available in these periods. Incomplete adult returns for smolt migration year 2015.

Executive Summary

Purpose and Scope: Review and synthesize research related to the Juvenile Fish Transportation Program and smolt-to-adult return (SAR) survival patterns of Snake River salmon and steelhead migrating through the Federal Columbia River Power System (FCRPS or hydrosystem), Snake and Columbia rivers, Washington and Oregon, USA.

Synthesis: The following sections summarize and discuss: 1) survival rates and ratios across life stages of transported and bypassed juvenile migrants (Box 1), 2) an updated literature review, 3) transport-related questions and 4) critical uncertainties.

1. Patterns of survival, D and $T:B$

Survival indices examined are juvenile hydrosystem survival, SARs, and adult hydrosystem conversion rates. SAR ratios were D (exclusive of hydrosystem) and $T:B$ (inclusive of hydrosystem) (Box 1). Values of D and $T:B$ greater than 1 indicate transportation is beneficial over run-of-river passage, exclusive and inclusive of the hydrosystem respectively. Patterns of survival indices are reported on annual and seasonal scales, and in context of before (1998-2005) and after (2006-2015¹) a court order of increased spill.

Annual patterns:

- Relative to the 1998-2005 period, in the 2006-2015¹ period, juvenile survival rates increased, while adult conversion rates decreased or were unchanged. These patterns occurred across species and rear-types.
- Some processes acting on transported vs. run-of-river fishes were different, as indicated by differing D and $T:B$ patterns across species and rear-types.
- Survival ratios and rates were most variable in fall² Chinook, followed by steelhead and then spring/summer Chinook salmon.
- Differential ratios of survival at each life stage (i.e., juvenile survival ratio, D , adult conversion rate ratio) and across life stages ($T:B$) showed how advantages and disadvantages from transport can change in particular years.

Seasonal patterns:

- Spring/summer Chinook and steelhead D and $T:B$ were more variable in the later period (2006-2015¹) than the early period (1998-2005).
- Fall Chinook D generally increased or was flat (i.e., advantageous or neutral effect of transportation), while the $T:B$ seasonal pattern was variable across years.
- Sockeye salmon D , based on available data beginning 2009, increased seasonally but decreased at the end of season in some years.

Life stages/species most negatively affected by juvenile fish transportation were:

- Marine life-stage: wild spring/summer Chinook, wild/hatchery fall Chinook, and possibly sockeye salmon were affected by negative carryover effects as evidenced by $D < 1$.

² Fall Chinook indicates subyearling fall Chinook, unless otherwise noted.

- Adult upstream life-stage: wild/hatchery steelhead, hatchery fall Chinook and sockeye salmon were affected by negative carryover effects as evidenced by lower conversion rates in transported fish.

In 2006-2015¹, SARs (inclusive of the hydrosystem) overall increased or were maintained, relative to 1998-2005. Determining whether and how the transportation program can help increase SARs and help meet recovery goals would require a closer examination of the life stages and species most affected by transportation, and under various river and ocean conditions.

2. Updated Literature Review

Ocean and annual effects on marine survival are generally larger than freshwater-marine carryover and seasonal effects (Boxes 2 and 3). Nonetheless, together freshwater-marine carryover and seasonal effects on marine survival can still significantly affect adult returns. In essence, the impacts of *freshwater carryover effects* are significant but mediated by *ocean conditions*:

- **Marine life stage:** Carryover hypotheses tested in recent literature included effects of smolt ocean arrival timing, migration rate, ocean entrance size, plume residence time and growth on survival and adult returns. The interrelatedness of factors makes it difficult to identify their individual contributions to SAR. Furthermore, seasonal and interannual changes in environmental conditions likely alter the ecological couplings of the factors.
- **Adult upstream life stage:** For certain species, juvenile transportation may interrupt imprinting during migration, cause adult straying and lower conversion rates of transported relative to run-of-river passage-types. In steelhead, the adult straying rate correlated with distance transported as juveniles. Fall Chinook can have high and variable rates of straying, depending on the population. In sockeye, lower adult conversion rates correlated with higher temperature and flow.

References are at the end of the report; abstracts and summaries are in the appendix.

3. Transport-related Questions

- **Fixed or flexible start date?** A fixed start date of transport is not optimal. For example, in 2016 the combination of early smolt migration and delayed Caspian tern breeding, relative to the fixed date of transportation, resulted in high avian predation of transported steelhead and sockeye in the estuary. Flexible transport start dates that optimize passage survival might be triggered from observed or forecasted river temperature, flow, total dissolved gas, smolt migration timing, and large-scale marine/climate indices.
- **Proportion of water spilled?** Determining the optimal level of spill is difficult and involves balancing the benefits of higher spill on smolts' lower travel times, predation risk and stress against the detriments of increased gas bubble trauma in smolts and delay in adult migration, among other constraints. To answer the present question of positive/negative effects of spill, determining critical thresholds and non-linear relationships across contrasting conditions are needed. New data collections under river and ocean conditions of greater contrast than that historically observed will help. Also, relative magnitudes of effect across life stages are important to quantify. Transported fishes can continue to serve as a treatment group for comparison to run-of-river fishes.

4. Critical Uncertainties

We provide a short list of critical uncertainties starting with the most comprehensive perspectives (first two bullet points) and narrow down to more specific uncertainties (last two bullet points).

- **Important factors and critical thresholds in context of direct and carryover effects.** Identifying which factors in the river, estuary, and ocean are most important to salmonid survival is challenging because both direct and carryover effects are occurring (Box 3). Determining *relative magnitudes of effect* (or effect statistics: mean difference, regression coefficients, odds ratio, etc.) associated with each factor would help identify the most important factors. For these factors, quantifying critical thresholds (or *triggers*) across large scales (e.g., ocean, annual, across species) and small scales (e.g., dam/site, seasonal, between passage-types) will help inform ways to effectively implement the transportation program. For example, the relative magnitudes of effect between direct effects from the ocean and carryover effects from the river will be informative on how much juvenile transportation can exert an effect or be swamped by ocean effects. Also, how the effects change under a wide range of river and ocean conditions will be important.
- **Survival differentials and tradeoffs across life stages.** The patterns of transport to run-of-river survival differentials can change across downstream (juvenile), ocean, and upstream (adult) life stages. Distinguishing among direct effects on juvenile survival, carryover effects at ocean entry and carryover effects during upstream migration will help elucidate relative magnitudes of effect from different factors and help quantify cross-life-stage tradeoffs. Cross-life-stage tradeoffs could be evaluated within a cohort across life stages; and/or, different tradeoffs across juvenile life stage and adult life stage of two cohorts in the hydrosystem environment could be evaluated. Furthermore, how cross-life-stage tradeoffs change annually and seasonally will help identify mechanistic processes.
- **Hydrosystem conditions and passage experience.** Among the hydrosystem-themed critical uncertainties listed in a recent report on critical uncertainties (ISAB/ISRP 2016), those of high criticality were in relation to flow and spill on juvenile and adult survival. These can be examined in context of relative magnitudes of effect compared to other factors, at annual and seasonal scales, and relative effects of direct and carryover effects across life stages, as listed in first two bullet points.
- **Adult upstream migration.** Continued and additional monitoring can help resolve this critical uncertainty. This includes examination of factors causing lower adult conversion rates in transported fishes than their run-of-river counterparts, particularly in steelhead, hatchery fall Chinook, and sockeye.

Long-term data sets are important for resolving these uncertainties, particularly when considering the inherent ecosystem complexity. As well, tradeoffs exist in context of data collection given the sample sizes necessary to observe patterns with reasonable certainty, logistical constraints, and economic and cultural necessities. Framing critical uncertainties and how reasonably they can be resolved in context of these tradeoffs, constraints and needs will help guide applied research related to the juvenile transportation program.

Acknowledgements

We thank Christine Peterson (Bonneville Power Administration, Department of Energy) for her continued support and feedback on all aspects of the report, Eric Buhle (Quantitative Consultants Inc., Biomark) for assistance with analysis, and Laurie Weitkamp and Rich Zabel (Northwest Fisheries Science Center, NOAA Fisheries) for comments on earlier versions of the report.

Funding was provided by the Bonneville Power Administration.

Acronyms and Concepts

BOA	Bonneville Dam, adult site
BON	Bonneville Dam, juvenile site
Carryover effects	Effect of a factor or experience in one life stage on traits or survival in a later stage (See Box 2 and Box 3)
CBR	Columbia Basin Research, University of Washington
CSSOC	Comparative Survival Study Oversight Committee
<i>D</i>	Differential delayed mortality; ratio of transported fish SAR to run-of-river fish SAR after Bonneville Dam and back to Bonneville Dam (See Box 1)
DART	Data Access in Real-Time; www.cbr.washington.edu/dart
DPS	Distinct Population Segment
ESA	Endangered Species Act
ESU	Evolutionary Significant Unit
FCRPS	Federal Columbia River Power System
LGA	Lower Granite Dam, adult site
LGR	Lower Granite Dam, juvenile site
NOAA	National Oceanic and Atmospheric Administration
NWFSC	Northwest Fisheries Science Center
PDO	Pacific Decadal Oscillation Index
PIT	passive integrated transponder
SAR	Smolt-to-adult survival rate
T:B	Ratio of transported fish SAR to run-of-river bypassed fish SAR from Lower Granite Dam as juveniles to Lower Granite Dam as adults (See Box 1)
TIR	Ratio of transported fish SAR to run-of-river (or in-river) fish SAR from Lower Granite Dam as juveniles to Lower Granite Dam as adults, sometimes differentiated from T:B with the use of never-detected or never-bypassed run-of-river fish at the dams (See Box 1)
USACE	U.S. Army Corps of Engineers

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1 Introduction

1.1 Background

The Juvenile Fish Transportation Program of the FCRPS (NOAA 2014; USACE 2015; USACE 2016) is a mitigation strategy to help increase survival and number of adult returns of Endangered Species Act (ESA)-listed salmon and steelhead (NWFSC 2015; Box 1). Although direct survival has been nearly 100% during barge transportation (McMichael *et al.* 2011), smolt-to-adult return (SAR) rates of transported fishes are sometimes lower than those of their run-of-river counterparts. Transportation can be beneficial or detrimental to SARs, depending on the environmental conditions, the time of year, species, rear-type, and biological and physical condition of the fish (Boxes 2 and 3). This leads to the question of: “How can transportation be most effective in increasing SARs and adult returns?”

Among the four transportation alternative strategies in the Configuration and Operational Plans of the USACE, Walla Walla District (USACE 2015), Alternative #4 of managed risk (seasonally manipulate collection proportion goals based on temporal data patterns and degree of confidence associated with the data) is recommended over Alternative #1 (50% of Snake River migrants transported), Alternative #2 (no transport), and Alternative #3 (emergency transport). Thus, information on real-time and forecasted conditions and scientific knowledge of the system are crucial for effective implementation of Alternative #4.

1.2 Sections of report and context

In this synthesis report, we first summarized trends of survival indices across years and seasons, and across life stages starting and ending at Lower Granite Dam (Section 2). We considered the patterns in context of before and after the 2005 court order of increased spill (or more broadly pre- [1998-2005] vs. post- [2006-2015¹] periods). These periods covered many changes in the freshwater and marine environments, but can still help to provide a broad overview. We then reviewed relevant literature (Section 3) published since the synthesis report of Anderson *et al.* (2012). We finish with a discussion on transport-related decisions (Section 4) and critical uncertainties (Section 5).

We present and discuss findings and literature in context of: 1) fish experiences in the freshwater habitat, 2) fish condition and behavior (Horodysky *et al.* 2015; Lennox *et al.* 2016),

and 3) selective forces in subsequent habitats or life stages (Box 2). This comprehensive view of ecological processes across habitats and life stages has been termed cumulative effects, freshwater-marine carryover effects, and delayed mortality in the literature. Interactions among factors across life stages can be involved in the effects of different passage-types on subsequent survival. For the applicability to transportation-related decisions, we focused on a small number of hypothesized mechanistic processes and recent publications that help answer the questions of when and how many fish to transport. Determining which ecological processes have biologically significant effects on survival will help identify which factors are most applicable to transport-related decisions.

1.3 Life history of Snake River Chinook salmon ESUs and steelhead DPS

In the current report, the Evolutionary Significant Units (ESUs) / Distinct Population Segment (DPS) (hereafter, termed species) considered in context of transport-related effects were: Snake River spring/summer Chinook salmon (*Oncorhynchus tshawytscha*) ESU, steelhead (*O. mykiss*) DPS, fall (subyearling) Chinook salmon ESU, and sockeye salmon (*O. nerka*) ESU, which are listed under the Endangered Species Act (NMFS 2016). These salmonid species exhibit different physical and biological traits (e.g., size, growth, age at smoltification) and behaviors (e.g., smolt and adult migration timing, migration depth, ocean distribution). These salmonid species were also summarized by hatchery and wild rear-types, and by run-of-river and transported passage-types because of potential differences (Beamish *et al.* 2012; Holsman *et al.* 2012; Weitkamp *et al.* 2015). It is thus important to consider their life history traits, their behaviors, the conditions they experienced and their responses when evaluating transportation-related effects.

The juvenile fishes begin to migrate out to the ocean the spring after emergence (i.e., subyearlings) or rear for a year and then outmigrate the following spring (i.e., yearlings) (Williams *et al.* 2006). The smolts of spring/summer runs of Chinook salmon migrate through the hydropower system of the Snake and Columbia rivers as yearlings between late March to early July, and mostly between mid-April and late May. Steelhead smolt yearlings have a similar timing of migration compared to the spring/summer Chinook smolts. The fall run of Chinook salmon, which can outmigrate as subyearlings or yearlings, have a much more extended season of downstream migration than the spring/summer Chinook runs. They pass Lower Granite Dam through all the seasons of the year, even in the winter (Tiffan *et al.* 2012). Although the subyearlings historically migrated out with an “ocean-type” life history in June and July, some

fall Chinook holdover in various locations and migrate out as “reservoir-types”. Wild sockeye yearlings migrate April through June, but their hatchery counterparts have a more condensed run occurring mid-May through early June.

The behaviors of the salmonid species in the estuary and coastal and early ocean environment also differ. The Snake River spring/summer Chinook salmon generally migrate out of the Columbia River and head north along the coast towards the Gulf of Alaska (McMichael *et al.* 2013; Rechisky *et al.* 2013b). The steelhead are generally thought to migrate relatively quickly and straight out west and south into the ocean (McMichael *et al.* 2013; Daly *et al.* 2014). Subyearling Chinook salmon rear in the estuary (Weitkamp *et al.* 2012) before entering the ocean. Snake River sockeye, similar to spring/summer Chinook salmon, exit the Columbia River and migrate northward along the coastal ocean to southeast Alaska (Tucker *et al.* 2015).

Many other differences in their physical traits and behaviors likely occur such as their physiological development, growth, tolerances of environmental conditions, diel migratory behaviors, water column depth at which they migrate, and upstream migratory behaviors. Identifying differences and even similarities among the Snake River salmon ESUs and steelhead DPS could illuminate ways of effectively implementing the juvenile fish transportation program.

1.4 A note on changes in river and ocean conditions and overall trends

The river and ocean conditions where the fishes occur have changed over the last few decades, with relatively drastic changes once again in the last few years (Peterson *et al.* 2014; Mann & Gleick 2015; Anderson *et al.* 2016). In addition to climate regime shifts that affect both marine and freshwater conditions, there has been the recent “Blob” of warm water off the Pacific Northwest coast caused by a “ridiculously resilient ridge” of atmosphere pressure (Mann & Gleick 2015; Swain 2015; Cavole *et al.* 2016). The salmon and steelhead have experienced warm conditions and very different ecological communities compared to the last few decades. As well, the hydropower system conditions have changed as efforts to mitigate negative hydrosystem effects continue, e.g., installing spillway weirs and surface bypass channels (U.S. Army Corps of Engineers, Northwestern Division), attaining regulatory survival compliance and other fish performance metrics (Skalski *et al.* 2014; Skalski *et al.* 2016), increasing water spilled to decrease fish passage through the turbines and decrease water transit times (Haeseker *et al.* 2012), and changes in predator removal or relocation programs (Roby *et al.* 2017; Williams *et al.* 2017).

The multiplicity of changes makes it challenging to determine the ecological processes affecting salmon and steelhead survival. In acknowledgement of the dynamic nature of natural and cultural ecosystems, we synthesize overall trends across years and seasons and delve into the details to the degree possible.

1.5 A continuation and expansion from Anderson et al. (2012) synthesis report

The previous synthesis report provided a database of over 200 scientific papers and reports related to *D*. From a review of this literature, Anderson *et al.* (2012) identified 12 potential factors affecting *D*:

- 1) pre-hydrosystem conditions,
- 2) arrival time to and through the hydrosystem,**
- 3) fish length and growth,**
- 4) fish physiology,
- 5) fish diseases,
- 6) dam operations,**
- 7) barge conditions,
- 8) Lower Columbia River conditions and predation,
- 9) estuarine conditions,**
- 10) oceanic conditions,**
- 11) straying,** and
- 12) estimation of survival and tags.

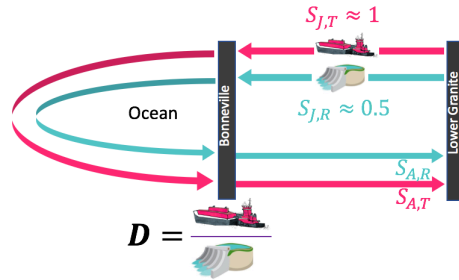
These factors were categorized into high, moderate, and low degrees of importance to *D* and two levels of data gaps and uncertainty (i.e., limited and extensive). The current report updates this database with approximately 200 paper and reports published since 2012. The report focuses on factors that were of high and moderate importance to *D* (bolded in list above). We synthesize the updated literature into hypotheses related to juvenile fish transportation and carryover effects on fish condition, behavior and survival. Wherever relevant, we synthesize how the marine and river conditions during post-smolt stages mediate the expression of carryover effects.

Two conceptual models were presented in the previous report (Anderson *et al.* 2012). First, the Multiple Regression Model captures how *D* depends on the difference of factors

experienced by barged and run-of-river fish. Second, the Culling Model incorporates a distribution of a survival capacity index that adjusts as the fish pass through the hydrosystem, estuary, and ocean. The survival capacity index relates to intrinsic processes within the fish, and extrinsic challenges that selectively cull individuals with low survival capacity. Again, the focus was on modeling concepts for *D*. In the current report, instead of presenting analytical approaches, we summarized patterns of survival based on PIT tag data across freshwater and marine life stages. Here the focus is on a more comprehensive view of transport-related carryover effects. This cross-life-stage approach helps present potential tradeoffs in the advantages/disadvantages of transportation in the juvenile, marine, and adult upstream life stages.

The previous report included a 2-day Workshop of presentations and discussions. Some of the transport-related decisions discussed were: 1) When to barge? 2) What proportion of fish to barge? 3) Which fish to barge? 4) Where to begin barging? 5) How to barge? 6) What environmental conditions increase barging success? In the current report we revisit these questions with the updated literature review, and consider the critical uncertainties in context of mechanistic factors and relative magnitudes of effect.

Box 1. Background on juvenile salmon and steelhead transportation effects on life-stage-specific survival and adult returns



The benefits of transportation are most evident in the nearly 100% direct juvenile survival (S_J) of transported (T) fishes, which can be double that of their run-of-river (R) counterparts.

Hydrosystem juvenile survival:

$$\begin{aligned} S_{J,T} &\approx 1 \\ S_{J,R} &\approx 0.5 \end{aligned}$$

However, because survival after downstream hydrosystem passage in the smolt-to-adult return life stage (i.e., SAR_{BON}) can be different between T and R fishes, transportation can have detrimental effects (i.e., $D < 1$) in the marine habitat.

Post-hydrosystem smolt-to-adult survival:

$$D = \frac{SAR_{BON,T}}{SAR_{BON,R}}$$

Differences among T and R fishes in their adult survival during upstream hydrosystem passage can also occur.

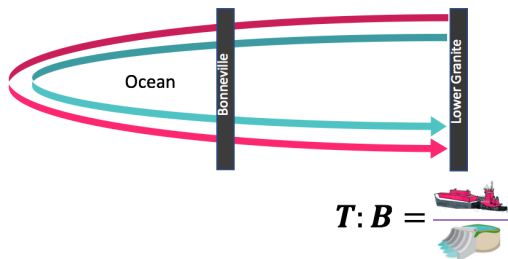
Hydrosystem adult conversion rate:

$$\frac{S_{A,T}}{S_{A,R}}$$

The overall relative effect of transportation on survival, including direct and delayed effects, can be assessed through the transport-to-in-river (TIR) or transport-to-bypassed (T:B) ratio.

Hydrosystem-inclusive smolt-to adult survival:

$$TIR \text{ or } T:B = \frac{SAR_{Hydro,T}}{SAR_{Hydro,R}} = \frac{S_{J,T} \cdot SAR_{BON,T} \cdot S_{A,T}}{S_{J,R} \cdot SAR_{BON,R} \cdot S_{A,R}}$$



Ultimately, the currency of interest is the number of adult returns (N_A).

Number of adult returns:

$$N_A = N_J \cdot SAR_{Hydro}$$

2 Patterns of survival rates and ratios

2.1 Background

Carryover effects from hydrosystem passage experiences can manifest in any subsequent life stage. Thus, differences and similarities in survival patterns in each life stage and across life stages can help identify processes underlying carryover effects. The benefits of nearly 100% survival during barge transportation may be outweighed by the disadvantages of lower survival in the marine and/or adult upstream life stages compared to run-of-river counterparts. Also, a comparison of patterns among species in context of their life history traits can also shed light on mechanistic processes. Such comparisons can be more robustly made with estimates of survival derived from the same type of data queries and same analytical model. Furthermore, one potential carryover effect common across species is the overall increased percentage of flow spilled, under the 2005 court order. We summarized survival patterns in two time periods of migration years 1998-2005 and 2006-2015¹. Although many changes in conditions have occurred in both the freshwater and marine environments across these two time periods, their comparison allows for a broad overview of patterns at first glance. The broad patterns can then help generate hypotheses to guide further detailed analyses of patterns and mechanisms.

2.2 Methods

2.2.1 Data

The data were passive integrated transponder (PIT) tag data for juvenile hydrosystem passage and adult return of spring/summer yearling Chinook salmon, steelhead, fall subyearling Chinook salmon, and sockeye salmon that originated upstream of Lower Granite Dam (ptagis.org; queried 2018/01/09 by C. Van Holmes and S. Iltis, Columbia Basin Research, School of Aquatic and Fishery Sciences, University of Washington). Thus, estimated survivals are based on a mix of fish tagged above and at Lower Granite Dam fish. Because jacks and mini-jacks exhibited anomalously high rates of return in select years, they were removed from the data sets for annual survival estimates of wild spring/summer Chinook salmon. These were not removed in the other species and rear-type combinations to take advantage of larger sample sizes, given that we found the general patterns were similar with and without jacks.

The data with juvenile detection sites included Lower Granite, Little Goose, Lower Monumental, Ice Harbor, McNary, John Day, and Bonneville dams, and the towed-array site

below Bonneville Dam. The data for adult detection sites included Bonneville, McNary, Ice Harbor, and Lower Granite dams, and any site upstream of Lower Granite Dam.

Because the objective of this analysis was to summarize descriptive patterns of survival, we only used the covariates of year of outmigration and the day-of-year of juvenile passage through Lower Granite Dam and Bonneville Dam. The data spanned migration years 1998-2015, with incomplete adult returns for migration year 2015. The fishes were grouped by their rear-type (hatchery/clipped; wild/unclipped) and passage-type (transported; run-of-river) for separate survival estimates.

2.2.2 Annual estimates

We applied a Bayesian analysis with Cormack-Jolly-Seber modeling (Cormack 1964; Jolly 1965; Seber 1965) to estimate probabilities of survival and detection. The process involves estimating apparent survival (ϕ) through the partially observed variable z for individual i at detection site d . This model assumes a Bernoulli process:

$$z_{id} \sim \text{Bernoulli}(z_{id-1}\phi_{id}) \quad \text{Eq. (1)}$$

Conditional on the survival model (Eq. 1), the observation process is also Bernoulli:

$$y_{id} \sim \text{Bernoulli}(z_{id}p_{id}) \quad \text{Eq. (2)}$$

We included random effects of year on survival and detection probabilities:

$$\text{logit}(\phi_{jd}) \sim N(\text{logit}(\mu_{\phi_d}), \sigma_{\phi}) \quad \text{Eq. (3)}$$

$$\text{logit}(p_{jd}) \sim N(\text{logit}(\mu_{p_d}), \sigma_p) \quad \text{Eq. (4)}$$

To estimate juvenile survival from LGR to BON, smolt-to-adult survival from BON to BOA, conversion rates from BOA to LGA, and smolt-to-adult survival from LGR to LGA, we determined the product of the relevant reach survivals. The patterns in periods 1998-2005 and 2006-2015 were summarized as the mean of annual medians, the interquartiles, and the 95% credible intervals across the respective years.

We conducted the analysis with the `stan` function in the `rstan` package version 2.16.2 in R© 2017 The R Foundation for Statistical Computing (version 3.4.1).

2.2.3 Seasonal estimates

We applied generalized linear mixed effects modeling (Zuur et al. 2009). Fixed effects were linear and quadratic terms of day-of-year of passage at Lower Granite Dam or Bonneville Dam. Random effects were year of outmigration and its interaction with the fixed effects. The binary outcome y_{ij} of whether or not individual i ($i = 1, \dots, n$) returns as an adult with probability p_{ij} in a Bernoulli distribution:

$$y_{ij} \sim \text{Bernoulli}(p_{ij}) \quad \text{Eq. (5)}$$

The probability is then defined by a mixed effects model:

$$\text{logit}(p_{ij}) = \beta_0 + b_{0j} + (\beta_1 + b_{1j})t_i + (\beta_2 + b_{2j})t_i^2 \quad \text{Eq. (6)}$$

$$b_{0j} \sim N(0, \sigma_0)$$

$$b_{1j} \sim N(0, \sigma_1)$$

$$b_{2j} \sim N(0, \sigma_2)$$

with a fixed effect intercept β_0 , a random effect intercept b_{0j} for year j , and fixed slopes β_1 and β_2 and random slopes b_{1j} and b_{2j} in year j for covariates t and t^2 , respectively. Random effects were assumed independent and normally distributed with zero means and constant respective variances σ . We conducted the analysis with the `glmer` function in the `lme4` package version 1.1-13. To plot the range of uncertainty in the model fits, we ran 1000 simulations based on the parameters from the sampling distributions of the maximum likelihood estimates from our generalized linear mixed effects models with the `sim` function from the `arm` package version 1.9-3 in R© 2017 The R Foundation for Statistical Computing (version 3.4.1).

2.3 Results and Interpretation

Interannual patterns of life-stage-specific survival rates and ratios were summarized by species, rear-type, and passage-type from PIT data in Table 1 and in the following figures:

Species	Rear-type	Passage-type	Pre- vs. post-period patterns of survivals and ratios	Annual patterns of survival	Annual patterns of survival ratios
Spring/summer Chinook	Wild	Run-of-river	Figure 1	Figure 2	Figure 4
		Transported		Figure 3	
	Hatchery	Run-of-river	Figure 5	Figure 6	Figure 8
		Transported		Figure 7	
Steelhead	Wild	Run-of-river	Figure 9	Figure 10	Figure 12
		Transported		Figure 11	
	Hatchery	Run-of-river	Figure 13	Figure 14	Figure 16
		Transported		Figure 15	
Fall Chinook salmon	Wild	Run-of-river	Figure 17	Figure 18	Figure 20
		Transported		Figure 19	
	Hatchery	Run-of-river	Figure 21	Figure 22	Figure 24
		Transported		Figure 23	
Sockeye salmon	Wild	Run-of-river	Figure 25	Figure 26	Figure 28
		Transported		Figure 27	
	Hatchery	Run-of-river	Figure 29	Figure 30	Figure 32
		Transported		Figure 31	

Seasonal patterns of *D* and T:B and were summarized (Tables 2 and 3, respectively) and plotted along with SARs for each migration year in the following figures:

Species	Rear-type	Passage-type	<i>D</i>	BON-BOA SAR	T:B	LGR-LGA SAR
Spring/summer Chinook	Wild	Run-of-river	Figure 33	Figure 34	Figure 35	Figure 36
		Transported				
	Hatchery	Run-of-river	Figure 37	Figure 38	Figure 39	Figure 40
		Transported				
Steelhead	Wild	Run-of-river	Figure 41	Figure 42	Figure 43	Figure 44
		Transported				
	Hatchery	Run-of-river	Figure 45	Figure 46	Figure 47	Figure 48
		Transported				
Fall Chinook salmon	Wild & Hatchery	Run-of-river	Figure 49	Figure 50	Figure 51	Figure 52
		Transported				
Sockeye salmon	Wild & Hatchery	Run-of-river	Figure 53	Figure 54	Figure 55	Figure 56
		Transported				

Overall, our life-stage-specific survival estimates for each species, rear-type and passage-type were comparable to those reported in other reports (Smith *et al.* 2013; DeHart *et al.* 2017; Faulkner *et al.* 2017) which provide more detailed estimates of survival and ratios of survivals (e.g., stock-specific, bypassed vs. never-detected estimates).

2.3.1 Annual survival rates and ratios

In the 2006-2015¹ period, juvenile survival rates tended to be higher compared to those in the 1998-2005 period (Table 1). In contrast, adult conversion rates tended to decrease or remain unchanged across these periods. Notably in hatchery spring/summer and fall Chinook, the conversion rates were lower for transported fish relative to bypassed fish, and were overall lower in the post-period relative to the pre-period (Figures 1 and 24). SARs from BON-BOA and LGR-LGA tended to increase or remain unchanged. The transport to run-of-river ratios of *D* and T:B for the most part tended to decrease across these periods. But some differences among species and rear-types occurred from the pre-period to the post-period (Table 1).

The annual estimates *D* and T:B at each life stage help provide a more in-depth understanding of the patterns across these periods. Please note that *D* and T:B are ratios, and are thus interpreted differently than absolute SAR estimates. LGR-LGA SARs were generally below 2% (further discussion on SARs in Section 2.3.3). Annual patterns of *D* and T:B across species and rear-types are described:

- **Wild spring/summer Chinook:** *D* and T:B ratios declined from the pre- to post-period (Figure 1). The high *D* and T:B ratios in the pre-period were in years 2001, 2003 and 2004 (Figure 4bd). Although T:B ratios were at or above 1 in the post-period, they were not as high as those select pre-period years (Figure 4d). The transportation advantage can be seen in the juvenile (Figure 4a) and ocean (Figure 4b) survival rates, particularly in those select years. There was some disadvantage from transportation with respect to conversion rates, but these were not particularly low in 2001, 2003 and 2004 relative to other years (Figure 4c).
- **Hatchery spring/summer Chinook:** In contrast to their wild counterparts, only 2001 showed very high *D* and T:B ratios (Figure 8). *D* and T:B were also moderately high in 2005. Overall, benefits and disadvantages from transportation fluctuated back and forth at each life stage. For example, transportation benefits at the juvenile stage (Figure 8a), with disadvantages to conversion rates (Figure 8c), can be seen in 2004 and 2011.

Nonetheless, D and T:B were approximately 1 in those years. In 2012, transported fish had higher survival than their run-of-river counterparts during downstream (Figure 8a) and upstream (Figure 8c) migration, but lower survival in the ocean (Figure 8b). In the end, T:B was about 1 in 2012 (Figure 8d).

- **Wild steelhead:** Similar to spring/summer Chinook, D and T:B were high and variable across the years in the pre-period compared to the post-period (Figure 12bd). D and T:B were particularly high in 2001 and 2004. The advantages of transportation appeared to be particularly important during the juvenile stage (Figure 12a), while affecting conversion rates at a relatively constant rate (Figure 12c).
- **Hatchery steelhead:** Patterns (Figure 16) were similar to those in wild steelhead, except that D and T:B were also high in 2005.
- **Wild fall Chinook:** D and T:B were variable in the pre-period, fluctuating from below 1 in 2000 to high values around 2 or more in 2001-2004 (Figure 20bd). Although D continued to fluctuate in the post-period (e.g. below 1 in 2006, 2011, 2012, and 2014; at or above 1 in 2009 and 2013), T:B remained at about 1 or higher. Generally, transportation was beneficial to juvenile survival (Figure 20a) with little detrimental effect to conversion rates (Figure 20c).
- **Hatchery fall Chinook:** SARs generally increased from the pre-period to the post-period, while D and T:B on the whole decreased (Figure 21). This was because D and T:B were particularly high in 2004. D and T:B continue to be variable in the post-period. T:B was moderately high in 2007, 2010 and preliminarily in 2015¹. The transport to run-of-river ratio of conversion rates (Figure 21; Figure 24) showed that hatchery fish were more affected than their wild counterparts (Figure 17; Figure 20).
- **Sockeye salmon:** There was much uncertainty in SAR rates and ratios (Figures 25 to 32), but increasing trends in SARs were possibly occurring (Figures 25 and 29).

Hypotheses for changes across the pre- to post-periods include:

- **Juvenile life stage:**
 - Survival increases and travel time decreases through hydrosystem because of *increased spill* and *decreased water travel time*.
 - The *percentage of fish transported* decreases because of increased spill and fewer fish passing through the bypass collection systems. Thus, greater number of fishes travel in-river and experience lower predation risk.

- *Structural improvements* such as the spillway weirs and surface bypass channels have helped guide the fish towards less stressful routes through the hydropower system, thus increasing their survival.
- **Estuary and Ocean life stage:**
 - Ocean survival is largely driven by *direct effects from ocean conditions*. In the pre-period, many years of ocean conditions were among the most unfavorable (1998, 2003, 2004, and 2005) but also included favorable ones (1999-2002). In the post-period, a mix of favorable (2008 and 2012) and unfavorable (2014 and 2015) years of ocean conditions also occurred. For examples of various indicators of ocean conditions, see NOAA's Ecosystem Indicator Stoplight Chart (Peterson *et al.* 2014).
 - Favorable experiences through hydrosystem passage positively affect the fish's physical and physiological condition and behavior. These positive effects carryover into the estuarine and ocean life stage.
- **Adult upstream life stage:**
 - Decreased conversion rates from Bonneville to Lower Granite dams can be caused by a combination of any number of factors including increased spill and flow, warm water conditions, straying, delay, and consequently increased mortality risk from natural causes and catch.
 - Greater straying by transported fish compared to in-river fish may be caused by factors related to disrupted imprinting. Some stocks are more genetically predisposed to straying than others.

Table 1. General trends of *D*, T:B, and life-stage-specific survival from pre- (1998-2005) to post- (2006-2015¹) periods for wild (W) and hatchery (H) Snake River spring/summer Chinook, steelhead, fall Chinook, and sockeye salmon.
Symbols: → = maintained, ↗ = increased, ↘ = decreased.

Survival ratio or rate	Sp/Sum Chinook		Steelhead		Fall Chinook		Sockeye salmon	
	W	H	W	H	W	H	W	H
D	↘	↘	↘	↘	↗	↘	uncertain	uncertain
T:B	↘	↘	↘	↘	→	↘	uncertain	uncertain
SAR (BON-BOA)	→	→	→	↗ROR →Transport	→	↗	↗	↗
SAR (LGR-LGA)	→	→	→	↗ROR →Transport	→	↗	↗	↗
Juvenile survival (LGR-BON)	↗	↗	↗	↗	↗	↗	uncertain	↗
Adult conversion rate (BOA-LGA)	↘	↘	→	→	→	↘	uncertain	uncertain

¹Incomplete adult returns for smolt migration year 2015.

2.3.2 Seasonal estimates of SARs, *D* and T:B

Seasonal patterns of survival were not always decreasing throughout the season as observed in some studies (Scheuerell *et al.* 2009; Gosselin & Anderson 2017), nor were they always increasing and then decreasing by end of the season as previously summarized (Anderson *et al.* 2012). A trend in the diversity of seasonal patterns appeared over the years (Tables 2 and 3):

- In the mid-to-late 2000s, *D* and T:B for spring/summer Chinook and steelhead switched from seasonal patterns of increasing only or increasing-then-decreasing to those that more often included flat and decreasing patterns.
- For fall Chinook, T:B was more variable in seasonal patterns across years, even though *D* generally increased or was flat. These patterns suggest transportation effects were neutral through the season in the marine environment, but seasonally variable in the hydrosystem environment.
- For sockeye, limited data resulted in much uncertainty. With more PIT tag data available since 2009, this wide range of uncertainty has been reduced. Since then, trends of *D* were seasonally increasing or increasing-then-decreasing.
- Overall, the differences in seasonal patterns between T:B and *D*, in a given year, suggests that different patterns of direct and carryover effects occur through the season. Note T:B includes the juvenile and adult stages in the hydrosystem, while *D* does not. Thus, if T:B and *D* had identical seasonal patterns in a given year, direct and carryover effects would likely be the same. Furthermore, different carryover effects can occur in the marine and the adult life stages.

Hypotheses for changes in seasonal patterns across the pre- to post-periods include:

- In the pre-period, the low *D* and T:B in the early season was hypothesized to be caused by transported fishes arriving to the ocean before the optimal window of ocean conditions. Low *D* and T:B in the late season was hypothesized to be caused by poor conditions of fishes in the warm river system.
- In the pre-period, the high proportion of fish transported left relatively few fish in-river compared to the post-period. This may have provided fewer and more straightforward types of seasonal patterns in pre-period years compared to post-period years.
- The higher levels of spill in the post-period, particularly late in the migration season, may provide more favorable river conditions for in-river smolts than in the pre-period. Thus,

the increased survival of in-river fish should lower D and T:B late in the season in the post-period compared to the pre-period.

- The lower proportion of fish being transported in the post-period relative to the pre-period resulted in higher numbers of fishes in-river, possibly reducing predation risk in the post-period relative to the pre-period. Such a reduction could in part reduce the high levels of D and T:B observed in late season. Observations support this hypothesis. In the pre-period D and T:B tended to increase in the post season while in the post-period both measures tended to decrease or flatten in the post-period.

Table 2. General seasonal patterns of *D* for wild (W) and hatchery (H) Snake River spring/summer Chinook, steelhead, fall Chinook, and sockeye salmon; see Figures 33, 37, 41, 45, 49, and 53, respectively, for seasonal fits to PIT data.

Symbols: → = constant, ↗ = increased, ↘ = decreased, ↻ = increased, then decreased, and ↷ = decreased, then increased.

Smolt migration year	W sp/sum Chinook	H sp/sum Chinook	W steelhead	H steelhead	W& H fall Chinook	W & H sockeye
2000	↷	↗	↗	↗	uncertain	uncertain
2001	↗	↗	↻	↗	↗	uncertain
2002	→	↗	↻	↗	↗	uncertain
2003	↗	→	↻	↗	↗	uncertain
2004	↗	↗	↻	↗	uncertain	uncertain
2005	↗	↗	↻	↗	↗	uncertain
2006	↻	↻	↻	↗	↗	uncertain
2007	↗	↻	↻	↗	↗	uncertain
2008	→	↻	↻	↘	↗	uncertain
2009	↗	↻	↻	↗	↗	↻
2010	→	↻	↘	↻	→	uncertain
2011	→	↗	→	↘	↗	↗
2012	→	↻	→	→	↗	↻
2013	↻	↻	↻	↗	→	↻
2014	↻	↻	↻	→	↗	↻

Table 3. General seasonal patterns of T:B for wild (W) and hatchery (H) Snake River spring/summer Chinook, steelhead, fall Chinook, and sockeye salmon; see Figures 35, 39, 43, 47, 51, and 55, respectively, for seasonal fits to PIT data.

Symbols: → = constant, **high** = relatively high through season, ↗ = increased, ↘ = decreased, ↻ = increased, then decreased, ↷ = decreased, then increased.

Migration year	W sp/sum Chinook	H sp/sum Chinook	W steelhead	H steelhead	W & H fall Chinook	W & H sockeye
2000	↗	↻	↗	↗	↘	uncertain
2001	↗	↻	↻	high	↘	uncertain
2002	↻	↻	→	↗	→	uncertain
2003	↗	↗	↻	high	→	uncertain
2004	↗	↗	↻	high	uncertain	uncertain
2005	↗	↗	↻	high	→	uncertain
2006	↻	↗	→	↗	↗	uncertain
2007	↗	↗	↗	↗	uncertain	uncertain
2008	↗	↗	↗	↗	↗	uncertain
2009	↗	→	↗	↗	→	uncertain
2010	↘	↻	↗	↗	↗	uncertain
2011	↷	→	↗	↗	↗	uncertain
2012	↗	→	↗	↗	→	uncertain
2013	→	↗	→	↗	→	uncertain
2014	↗	↗	↗	↗	uncertain	uncertain

2.3.3 Overall low SAR patterns and critical life stages related to transportation

Although the mean values of T:B in the 2006-2015¹ period generally showed neutral or beneficial transportation effects, LGR-LGA SARs on average still remained below the minimum goal of 2% (Northwest Power & Conservation Council (NPCC). 2014) for most stocks. Exceptions to this average were wild, transported Chinook salmon and wild, transported steelhead when jacks were included. Then again, species conservation does not depend exclusively on a minimum threshold of survival. Conservation also depends on other criteria such as abundance, productivity, spatial structure, and diversity, which are considered in the Viable Salmonid Population (VSP) concept (NMFS 2016). Furthermore, evolution can occur rapidly at temporal scales comparable to human disturbance and anthropogenic change (Ashley *et al.* 2003). The challenges in evolutionarily enlightened management are recognized, and efforts to align science and policy in this framework for conservation continue (Cook & Sgrò 2017).

Thus, for more effective use of the juvenile fish transportation program, it is important to determine mechanistic factors related to when and what conditions (i.e, fish, freshwater and marine conditions) are conducive for positive transport. The most affected life stages and species were:

- marine life stages of wild spring/summer Chinook salmon (without jacks), wild and hatchery fall Chinook salmon, and possibly sockeye salmon (as evidenced by $D < 1$)
- adult upstream life stage of hatchery spring/summer Chinook, wild/hatchery steelhead, hatchery fall Chinook and sockeye salmon (as evidenced by lower conversion rates in transported fish).

Targeting studies on these life stages and stocks may provide insights on the underlying mechanistic processes of carryover effects and result in more effective implementation of the juvenile fish transportation program across species, runs, and stocks. This section described annual and seasonal patterns of survival rates and ratios. The mechanistic hypotheses, synthesis of recent literature, and uncertainties are covered in the subsequent sections.

3 Literature Review and Synthesis: an update

Since the report of Anderson *et al.* (2012), approximately 200 reports and peer-reviewed papers related to factors identified as high and moderate importance to *D* have been published. Here, we synthesize new findings relevant to the potential effects of juvenile transportation on marine (Section 3.1) and adult upstream life stages (Section 3.2). We also synthesize the findings separately by salmonid species to account for potential differences stemming from their diverse life history traits such as migration timing and rate, body size, growth, and physiological development. Nonetheless, the hypotheses underlying these findings may be generally applicable across fishes and thus we also list studies by combinations of fish-related × environment-related factors (Table 1; Section 3.3).

These combinations of factors can be interpreted in context of carryover effects³ (O'Connor *et al.* 2014; O'Connor & Cooke 2015) (Box 2). Carryover effects are particularly important to consider in relation to the juvenile transportation program, given the disproportionately reduced survival sometimes experienced by transported fish in the marine and adult upstream life stages (Box 3).

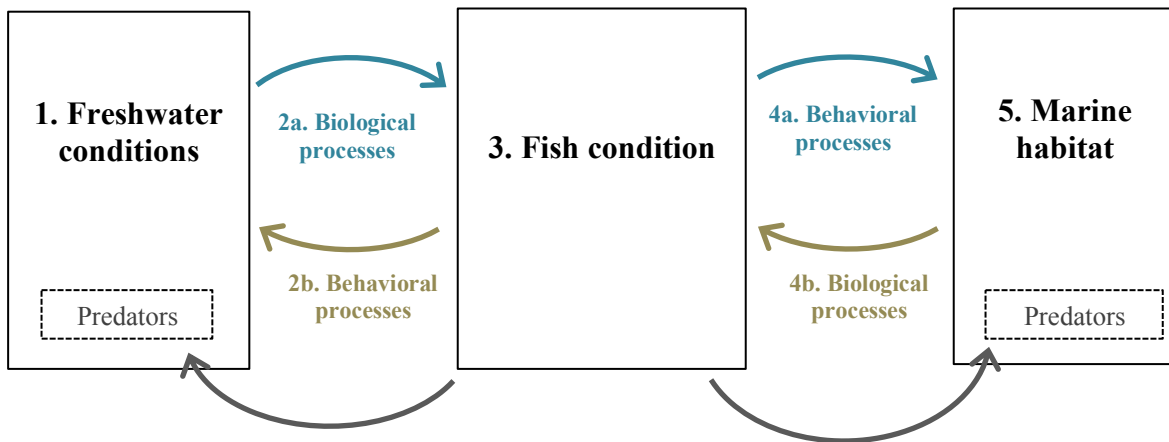
Overall, we highlighted a number of studies in the report and included many other references in the bibliography and abstracts/summaries in the appendix that the reader can use as a starting point for further study.

³ The term “carryover effects” is similar or equivalent to “delayed mortality”, “cumulative effects”, “latent mortality”, “extra mortality”, and “cross-life-stage effects” as termed in numerous other reports and peer-reviewed literature. We use the term “carryover effects” because of its concept generalizable across migratory species.

Box 2. General concept of carryover effects.

Carryover effects originating in the first habitat (i.e., freshwater habitat during the juvenile life stage) take place in the subsequent habitats and life stages (i.e., marine habitat and in freshwater habitat again during the adult stage). Fish condition links the carryover effects between habitats and life stages.

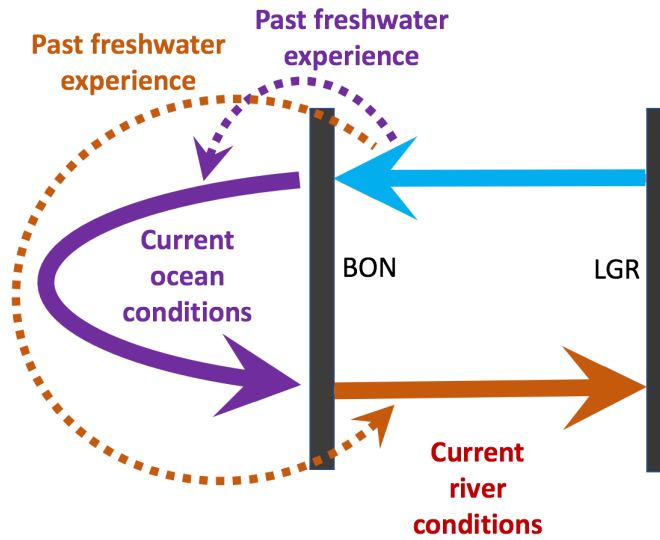
Considering indices of fish condition and how these are affected by their freshwater and marine experiences is important particularly because mortality is in part due to trait-mediated selective forces (see diagram below, arrows to predators). Thus, assessing the effectiveness of different scenarios of the transportation mitigation strategy requires these cross-life-stage considerations.



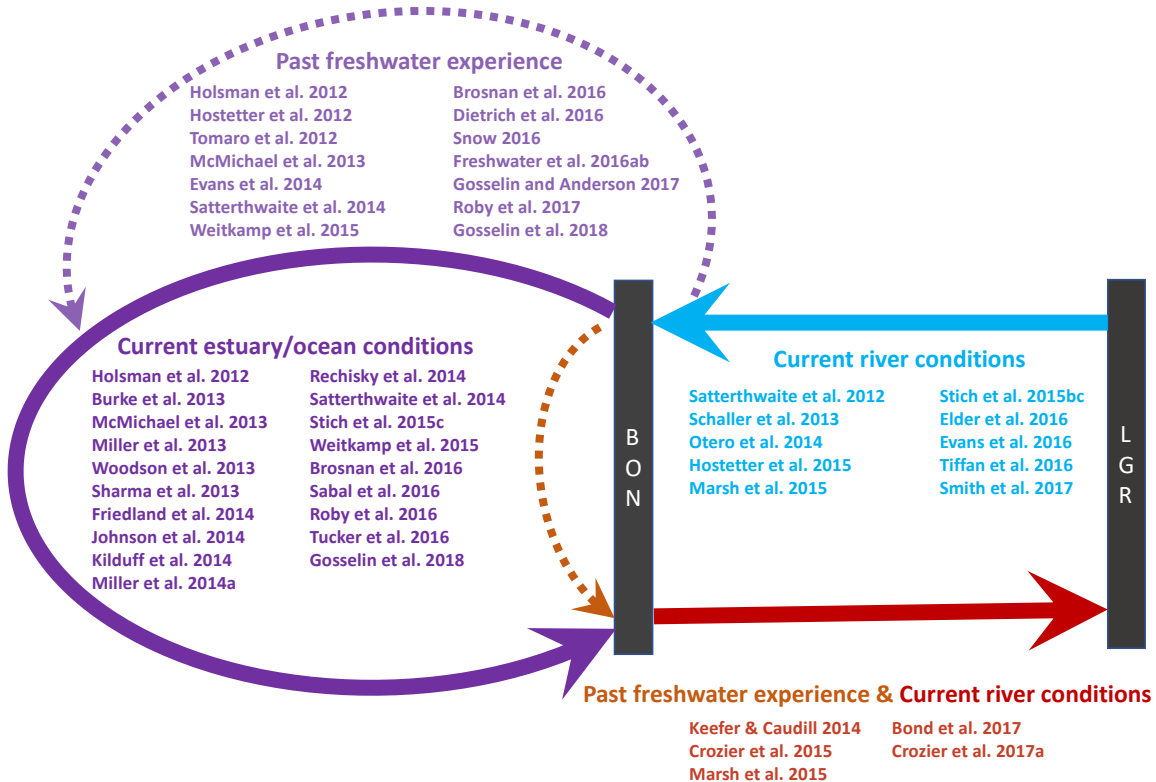
Conceptual diagram of carryover effects: (1) The freshwater conditions that the juvenile fishes experience include river temperature, flow, spill, total dissolved gas, transport or run-of-river passage, food availability, pathogens, competitors, and predators. (2a) These conditions can influence fish condition through biological processes related to physiology, disease, and development. (3) Changes in fish traits can occur in their migration timing, length, health and energetic reserves. (2b) As well, the fishes select the freshwater conditions they experience through their behaviors, which to some degree is by choice. (4a) Similarly, the fish decide when and where they migrate as they enter the (5) marine habitat, and (4b) the conditions they experience, such as sea surface temperature, upwelling, food resources, competitors, and predators, can again affect their condition, and ultimately their survival. This concept of carryover effects can be further extended to the adult upstream migration life stage.

Box 3. Direct effects within life stages, and carryover effects across life stages.

The hydrosystem experience of juveniles (blue arrow) can affect their current juvenile survival directly, and can also carryover (dotted arrows) to affect their survivals in the estuary/ocean (solid purple arrow) and adult upstream migration (solid orange arrow) life stages. The conditions they experience in the ocean and during upstream migration can be direct effects on survival, and can also mediate the expression of freshwater carryover effects.



Recent studies in context of direct river and ocean effects, and freshwater-marine carryover effects (see sections 3.1 to 3.3 for more details):



3.1 Marine life stage

3.1.1 Relative effects of freshwater and marine conditions

The ocean can exert strong, broad, direct effects on marine survival (Rupp *et al.* 2012; Sharma *et al.* 2013; Kilduff *et al.* 2014). For example, broad effects of the ocean as observed in Chinook salmon survival covaried on a spatial scale of 350-450 km (Sharma *et al.* 2013) in one study and about 700 km in another study (Kilduff *et al.* 2014). Because ocean effects are so large, interannual variability can also be expected to be large.

In contrast, the freshwater-marine carryover effects act on survival at both interannual and seasonal scales: interannually because the ocean influences the air temperature, precipitation, and consequently river flow conditions through climatic teleconnections; and seasonally because of freshet-associated conditions, and smolt migration timing and rate. These can also be viewed as basin or population effects at the annual scale, and as individual or trait-specific effects at the seasonal scale (Evans *et al.* 2014; Kilduff *et al.* 2014; Miller *et al.* 2014a).

Marine and interannual effects are generally larger than freshwater and seasonal effects. For example, Satterthwaite *et al.* (2014) observed a 19-fold difference in survival of Chinook across years, but 2.3-fold difference within seasons. Nonetheless, a 2-fold difference can equate to a sizeable increase of adult returns. Overall, providing knowledge of how much the ocean affects direct survival and how the estuary and ocean mediate the freshwater carryover effects can inform management decisions related to river conditions and fish passage experience. For example, Woodson *et al.* (2013) observed size- and growth-selective mortality during low-recruitment year of 2005 but not 2000 and 2001. Furthermore, in years of expected high marine survival, survival might further be improved by optimizing the fish freshwater experience as suggested by Evans *et al.* (2014).

Below, we list hypotheses under two **categories**:

- **Direct marine effects:** marine conditions affect behavior, survival and adult returns more than freshwater conditions
- **Carryover effects:** freshwater-marine carryover effects are mediated by estuary and ocean conditions (purple, dashed line in Box 3)

Each hypothesis listed within these categories is related to at least one of the *factors* identified as high/moderate importance to *D* in Anderson *et al.* (2012). The same factor can also occur in both categories, but as different processes (i.e., fish growth as direct marine and indirect freshwater-marine effects). We include literature in support for and against each hypothesis.

The interrelatedness among factors makes it difficult to determine whether their individual and combined effects are positive, negative, or neutral on SARs. For example, at ocean entrance, fish arrival timing, migration rate, size, and growth have been hypothesized to affect marine survival, but they also affect each other. It is thus important to keep in mind that the ecological processes underlying the hypotheses are not necessarily mutually exclusive. Also, the strength of particular ecological processes varies as environmental conditions and ecological dynamics change across climate phases/regimes and with extreme conditions.

3.1.2 Spring/summer Chinook

We begin with spring/summer Chinook salmon as they are the most studied among the Snake River salmon ESUs and steelhead DPS. Below, we list hypotheses related to their estuary/ocean survival and associated *factors* under the two categories:

- **Direct marine effects**
 - ***Ocean conditions***: Marine climate indices of PDO and NPGO had greater influence and direct effect on survival than Columbia river flow (Miller *et al.* 2014a). More specifically, marine variables (marine climate indices, northern copepod biomass, and ichthyoplankton species community index, etc.) were relatively more important predictors through their direct effects than indirect effects from river temperature and flow (Burke *et al.* 2013). Rechisky *et al.* (2014) also found little to no support for freshwater experience affecting subsequent ocean survival.
 - ***Estuary/plume conditions***: Faster migration through the estuary and plume reduces predation risk (Brosnan *et al.* 2014). Reduced plume residence time (and consequent predation risk) is negatively and more directly related to sea surface temperature than river discharge.
- **Freshwater-marine carryover effects**
 - ***Arrival timing and growth***: Earlier arrival timing provides more time to progressively increase early ocean growth (Weitkamp *et al.* 2015). Conversely, later migrating fish had higher growth and migration rates (Tomaro *et al.* 2012; Miller *et al.* 2014a). In the latter case, delayed migration can increase growth opportunities before ocean entry, and consequently reduce predation risk.

- **Arrival timing and coastal ocean conditions:** Although calendar date is a relatively good predictor of seasonal survival patterns, ecological indices such as time relative to spring transition date can be better predictors (Satterthwaite *et al.* 2014). Miller *et al.* (2014a) found a non-significant positive trend between SARs and Snake River spring/summer Chinook migrating later in the season relative to the spring transition date of upwelling.
- **Size and growth:** Early ocean growth is more important than migration timing and size for spring/summer Chinook salmon from the Snake, Upper and Mid-Columbia rivers (Miller *et al.* 2014a) and spring Chinook salmon from the Upper Columbia River (Tomaro *et al.* 2012). Possibly because in-river size-selective mortality results in more uniform size distributions at marine entry. Early marine growth then widens the variation upon which selection occurs during first overwinter mortality.
- **Fish health and condition:** Poor health or stressful experience from freshwater conditions (e.g., total dissolved gas > 120%) can result in increased mortality in the lower river, plume, and or ocean (Brosnan *et al.* 2016).
- **Passage-type and estuary conditions:** Chinook salmon barged 2006-2008 to Astoria experienced lower avian predation rates (0.95%) from East Sand Island than those barged to their usual Skamania release area below BON (5.11%) (Marsh *et al.* 2015). Although see straying effects in section 3.2.1.

3.1.3 Steelhead

Relative to Chinook salmon, steelhead migrate through the early ocean environment faster, but also closer to the water surface. Thus, they can experience different direct marine effects and freshwater-marine carryover effects than Chinook salmon, such as avian predation rates. We revisit some of the hypotheses:

- **Direct marine effects**
 - **Ocean conditions and growth:** Growth in the early marine environment is not as important as sustained growth conditions during summer and fall of the second marine year (Friedland *et al.* 2014).
- **Freshwater-marine carryover effects**

- **Arrival timing:** Earlier migrating steelhead generally exhibit higher SARs (Evans *et al.* 2014). Although, avian predation weekly estimates of the odds ratio between transported and run-of-river fishes are variable through the season (Roby *et al.* 2017). They are higher for transported steelhead earlier in the season in some years (e.g., 2007, 2008, 2010), but can also show no change (e.g., 2011), increases (e.g., 2012), and highly variable patterns (e.g., 2009) through the season.
- **Fish size:** Moderate-sized hatchery and wild juvenile steelhead (approx. 160 mm FL) experience higher avian predation risk than the largest and smallest juvenile steelhead (Osterback *et al.* 2014). Nonetheless, larger sized juvenile steelhead generally have higher SARs (Evans *et al.* 2014; Osterback *et al.* 2014). Thus, other sources of mortality such as those caused by fish predators are likely occurring. Still, decreasing avian predation occurring on moderate- and large-sized wild juveniles will help increase SARs.
- **Fish condition:** Poor condition from freshwater experience i.e., body injuries, fin damage, and external signs of disease) can decrease SARs (Evans *et al.* 2014).
- **Passage-type and estuary conditions:** Across salmonid species, transported Snake River steelhead experienced higher predation rates (11.3%; 95% CI = 8.9-16.2) by Caspian terns than transported Snake River spring/summer Chinook salmon (0.8%; 95% CI = 0.6-1.1), Snake River Fall Chinook salmon (1.1%; 95% CI = 0.8-1.6), and Snake River sockeye salmon (5.9%; 95% CI = 4.2-8.7) (Roby *et al.* 2017). In another study, steelhead barged 2006-2008 to Astoria experienced lower avian predation rates (3.51%) from East Sand Island than those barged to their usual Skamania release area below BON (20.35%) (Marsh *et al.* 2015). Although, see straying effects in section 3.2.2.

3.1.4 Fall Chinook

Some stocks of hatchery fall Chinook migrate later in the season relative to spring/summer Chinook salmon, steelhead and sockeye. Compared to the other salmon ESUs and steelhead DPS, fewer studies of marine survival have been conducted on fall Chinook in context of their survival in the ocean and upstream adult life stages. We highlight findings from one particularly relevant study (Smith *et al.* 2017) and synthesize other findings for fall Chinook salmon stocks in California relevant to hypotheses, under two **categories of hypotheses**.

- **Direct marine effects**

- ***Ocean conditions and prey:*** High productivity during cool ocean conditions can lead to increased survival and abundances, but result in fall Chinook salmon of smaller sizes or lower fish condition index in the coastal ocean (Miller *et al.* 2013; Dale *et al.* 2017). The plankton community assemblage (particularly proportion of invertebrates) during the first fall in the ocean and food competition may play an important role on survival and abundance of subyearling Chinook. The proportion of total winter ichthyoplankton biomass serves as an early indicator of ocean ecosystem conditions and future Chinook salmon survival and abundance (Daly *et al.* 2013).
- ***Ocean conditions and size-selective mortality:*** In a study on Upper Columbia River summer/fall Chinook salmon conducted in 2010 and 2011, size-selective mortality was not observed (Claiborne *et al.* 2014). But the authors did observe higher proportions of natural fish in the ocean than in the estuary, thus indicating higher mortality of hatchery fish in the ocean than in the estuary.

- **Freshwater-marine carryover effects**

- ***Arrival timing:*** Transportation, timing of passage, and rear-type (production vs. surrogate) affect their smolt-to-adult survival (Smith *et al.* 2017). Further details below:

A 6-year study (i.e., 2006, 2008-2012) was conducted to evaluate juvenile transportation effects (transported-with-spill [TSW] vs. bypassed-with-spill [BSW]) on SARs of “production” subyearlings, “production” yearlings, and “surrogate” (wild-resembling) subyearlings (Smith *et al.* 2017).

Preliminary results showed:

- Greater adult returns for transported “surrogate” subyearlings than bypassed counterparts (survival advantage of 8.5% for Snake River and 14.9% for Clearwater River releases), and
- Greater adult returns for bypassed “production” subyearlings (survival disadvantage of 6.3% for Snake River and 3.5% Clearwater River releases).
- Greater adult returns for transported than bypassed for both subyearling types (return rate for TWS fish greater than BWS fish by 2.1%; 90% bootstrap CI: -1.2%, 5.8%).

Seasonally, the survival advantage gained from transportation relative to bypassed counterparts was positively related to migration timing: lowest for Snake River production subyearlings, then Clearwater production subyearlings, Snake River surrogate subyearlings, and highest for Clearwater subyearlings.

Annually, survival advantages from transportation for surrogate subyearlings were 24% at Lower Granite, 28% at Little Goose, 25% at Lower Monumental, and 117% at McNary dams. In contrast, transportation effects for production subyearlings were disadvantaged: -24% at Lower Granite, -12% at Little Goose, and -6% at Lower Monumental dams. There may have been a strong transportation advantage (138%) for production subyearlings at McNary Dam, but with much uncertainty given the limited data available.

- ***Fish size***: Size-selective mortality and/or density-dependence may occur in Central Valley fall Chinook salmon (Sabal *et al.* 2016).
- ***Passage-type and estuary conditions***: Caspian terns and cormorants with colonies on East Sand Island exhibited greater predation on barged fish (0.7 and 3.3%, respectively) than run-of-river fish (0.5 and 1.3%, respectively) during migration year 2012 (Zamon *et al.* 2013).

3.1.5 Sockeye

Given the relatively low population sizes of sockeye salmon, fewer studies have been conducted relative to spring/summer Chinook salmon and steelhead. We revisit hypotheses under two **categories of hypotheses** with studies on sockeye salmon.

- **Direct marine effects**

- ***Ocean conditions*** indexed by the copepod biomass anomaly were important to sockeye returns (Tucker *et al.* 2015). Furthermore, high mortality occurs in juvenile sockeye in the early ocean environment because of predation (Clark *et al.* 2016). In contrast to this hypothesis, one study on Columbia River sockeye found freshwater conditions (Pacific Northwest Index) to be as important as marine conditions (April upwelling index) to MCN-BON SAR survival (Williams *et al.* 2014).

- **Freshwater-marine carryover effects**

- ***Arrival timing and fish size***: Ocean entry timing and fish size were strongly related to size at capture, migration rate and marine distributions, while early marine growth or size-selective mortality were not (Freshwater *et al.* 2016b; Freshwater *et al.* 2016a). Thus, freshwater effects that carryover into the ocean environment are important.
- ***Passage-type and ocean conditions***: The percentage of fish transported was negatively related to the number of adult returns to LGR (Tucker *et al.* 2015). In contrast, Clark *et al.* (2016) observed sockeye salmon from Chilko Lake, British Columbia experiencing higher early ocean survival when transported in trucks downstream.
- ***Arrival timing and estuary/ocean conditions***: The extent of the spatial and temporal overlap of predator and prey can be particularly important to survival in the estuary and early ocean (Roby *et al.* 2017). Caspian tern predation rates on Snake River sockeye salmon have generally been low (less than 2%), but were much greater for transported sockeye in 2016 (Roby *et al.* 2017). The authors remarked this likely occurred because transported sockeye salmon arrived at the estuary when most of in-river migrants had already passed and Caspian terns had protracted nesting chronology. Thus, passage of transported sockeye salmon coincided with the peak breeding season of Caspian terns.

3.2 Adult upstream life stage

Juvenile transportation can increase rates of straying⁴ and fallback in Snake River salmon ESUs and steelhead DPS (Crozier *et al.* 2016; Crozier *et al.* 2017a). Straying in transported fishes likely occur through interruptions of and negative effects on sequential olfactory imprinting (Keefer & Caudill 2012; Keefer & Caudill 2014). Specific hypotheses of straying mechanisms listed by the authors were:

- transport speed: insufficient time for juvenile imprinting, or biased perception of river distance

⁴ Straying from the population (i.e., donors) and not straying to the population (i.e., recipients).

- transport timing: asynchrony between diel or seasonal timing of transport and juvenile physiological development related to imprinting
- spatial experience: lack of sampling habitats
- in-barge experience: stress, disease, physiology, toxins, water circulation, etc.
- hatchery stock: predisposition for straying increased by barging
- population/stock: predisposition for straying increased by barging
- adult timing: return migration date through maturation status and consequent river conditions that may elicit thermoregulatory behaviors
- a combination of above mechanistic factors.

Manipulative studies have shown a positive relationship between distance barged and straying rates (Solazzi *et al.* 1991; reviewed in Keefer and Caudill 2014; Marsh *et al.* 2012; Marsh *et al.* 2015). A number of other studies reviewed in Keefer and Caudill (2014) showed differences in physiological and stress indices among passage-types, rear-types and across the juvenile migration season that imply complex tradeoffs between advantages and disadvantages of juvenile transportation.

Controlled experiments, needed to differentiate the above hypotheses, would require large sample sizes for sufficient adult returns among treatment groups, and manipulations of barging schedules and/or routes (Keefer & Caudill 2012). Such experiments would help determine how to balance advantages (e.g., reduced juvenile mortality) and disadvantages (e.g., increased straying rates) of transportation. As well, the studies would need to consider the effects of interannual differences in environmental conditions. Overall, strategies to help decrease straying of transported fishes are needed (Keefer *et al.* 2016). Below we synthesize findings from recent studies related to straying, fallback, delay, and overall conversion rates.

We revisit each species/run and list hypotheses and findings from recent literature that fall under the category of **downstream, juvenile—upstream, adult carryover effects** (orange, dashed line in Box 3).

3.2.1 Spring/summer Chinook

- Upstream survival was slightly lower for transported juvenile fish (0.79) than run-of-river fish (0.81) (Crozier *et al.* 2016). Overall, negative effects from temperature, spill and catch were most important to upstream hydrosystem survival (Crozier *et al.* 2017a). Rear-

type, age, and transport vs. run-of-river passage-type were also important but not consistently across stocks and models.

- Lower conversion rates (lower by 10%) were associated with increased barging distance when Chinook salmon were released at Astoria instead of Skamania Landing (Marsh *et al.* 2015). There were low rates of straying observed for Chinook salmon barged to Astoria (2.6%) and to Skamania Landing (2.0%).

3.2.2 Steelhead

- Juvenile transportation has a negative effect on adult survival from BON to MCN (Crozier *et al.* *In progress-a*).
- Lower conversion rates (lower by 20-22%) were associated with increased barging distance when steelhead were released at Astoria instead of Skamania Landing (Marsh *et al.* 2015). This is a 50% increase in transportation distance of Snake River juvenile steelhead from approximately 400 km (Lower Granite Dam to below Bonneville Dam) to 600 km (Lower Granite Dam to near the Columbia River Estuary). There were higher rates of straying in steelhead barged to Astoria than Skamania Landing (28% for wild, 47% for hatchery). Straying rates to John Day and Deschutes rivers were higher for steelhead barged to Astoria than Skamania Landing (52% for wild, 54% for hatchery). Similar Astoria to Skamania patterns of comparisons also occurred for permanent straying (64% for wild, 51% for hatchery).

3.2.3 Fall Chinook

Overall, donor straying rates of fall subyearling (i.e., ocean-type) Chinook salmon can be high (mean of 34.9% across Snake and Columbia river stocks) and variable ranging from a median of 1% to over 50% across a number of transplant studies reviewed in Keefer and Caudill (2014). More specifically, straying of subyearling and yearling fall Chinook salmon barged from Snake River dams was 10-19 times more likely than their run-of-river migrants or those transported from MCN (Bond *et al.* 2017). The odds ratio of temporary or permanent straying into the lower Columbia River were 15.3 (95% CL 10.5–22.3), 10.4 (95% CL 7.0–15.2), and 19.4 (95% CL 12.8–29.2) for fall Chinook salmon barged from Lower Granite, Little Goose, and Lower Monumental dams, respectively, compared to run-of-river migrants. In another model that also included temperature at BON, these odds ratios were 3.10 (95% CL 2.15–4.47), 2.15 (95%

CL 1.08–3.15), and 1.85 (95% CL 1.08–3.15), respectively. Greater rates of straying were associated with increased temperature on day of BON passage (odds ratio = 2.2 per °C). This is likely because adults were seeking thermal refuge. Barged fish were also migrating upstream at a slower rate than their run-of-river counterparts. The slower migration may increase their susceptibility to harvest and natural mortality. Overall, improvements on imprinting may help to reduce straying and increase successful return of adults.

3.2.4 Sockeye

In a study by Crozier *et al.* (2014), adult sockeye salmon in 2008-2013, that were transported as juveniles, have greater rates of fallback than their run-of-river counterparts. Their rates were greater than that reported for spring/summer Chinook and steelhead as well. In 2013, fallback rates were particularly higher for transported than run-of-river sockeye. Temperature and/or flow correlated strongly with probability of fallback; dissolved gas and fish history were also influential, but to a lesser degree. Adult sockeye survival was most influenced by thermal exposure and travel time, particularly in 2013. Across all years, there appears to be an upper critical threshold temperature of 18°C. Furthermore, survival in the Columbia River was also influenced by juvenile transportation and fishery catch. Overall, data were only available in a small number of years, with unbalanced representation and narrow ranges of predictive factors. Even though temperature was a driving factor, because of limited data, forecasting 2013 from previous years was underestimated, especially for survival from Ice Harbor Dam to the Sawtooth Valley. An updated analysis for 2014 showed that juvenile transportation and fishery catch were important factors of adult survival and fallback at Columbia River dams, while temperature was most important to fallback at Snake River dams (Crozier *et al.* 2015). Also, transported juveniles were 2.9 times more likely to fallback than their run-of-river counterparts. Preliminary results for years 2015-2017 show that juvenile transportation, river temperature, and fallback continue to be important factors on adult upstream migration and survival (Crozier *et al.* *In progress-b*).

3.3 Fish-related × environment-related factors

Table 4. Interactions between Snake River Basin fish condition/behavior and environment. Number of dots represent semi-quantitatively the potential magnitude of effect on *D* and T:B. This table is an update of Table 4.2 in Anderson *et al.* (2012), with a particular focus on factors of high/moderate importance to *D*.

Fish Condition/ Behavior	Environment				
	Prehydrosystem conditions	Hydrosystem conditions	Barging collections, schedule & location	Estuary conditions (BON–river mouth)	Ocean conditions
Arrival timing and rate	●● (Satterthwaite <i>et al.</i> 2012; Otero <i>et al.</i> 2014)	●● (Schaller <i>et al.</i> 2013; Stich <i>et al.</i> 2015b; Stich <i>et al.</i> 2015c; Gosselin & Anderson 2017)	●● (Marsh <i>et al.</i> 2015; Smith <i>et al.</i> 2017)	●●● (Morris <i>et al.</i> 2014; Dietrich <i>et al.</i> 2016; Roby <i>et al.</i> 2017)	●●● (Holsman <i>et al.</i> 2012; McMichael <i>et al.</i> 2013; Satterthwaite <i>et al.</i> 2014; Freshwater <i>et al.</i> 2016b; Freshwater <i>et al.</i> 2016a; Snow 2016; Gosselin <i>et al.</i> 2018b)
Size and growth	● (Satterthwaite <i>et al.</i> 2012; Thompson & Beauchamp 2014; Thompson & Beauchamp 2016; Beckman <i>et al.</i> 2017)		●● (Hostetter <i>et al.</i> 2015b)	●● (Hostetter <i>et al.</i> 2012; Satterthwaite <i>et al.</i> 2012; Evans <i>et al.</i> 2014; Osterback <i>et al.</i> 2014; Goertler <i>et al.</i> 2016b)	●● (Tomaro <i>et al.</i> 2012; Miller <i>et al.</i> 2013; Woodson <i>et al.</i> 2013; Friedland <i>et al.</i> 2014; Johnson <i>et al.</i> 2014; Miller <i>et al.</i> 2014a; Weitkamp <i>et al.</i> 2015; Freshwater <i>et al.</i> 2016a; Freshwater <i>et al.</i> 2016b; Sabal <i>et al.</i> 2016; Tucker <i>et al.</i> 2016)
Physiological and physical condition	● (Beckman <i>et al.</i> 2017)	●● (Hostetter <i>et al.</i> 2015b; Brosnan <i>et al.</i> 2016; Elder <i>et al.</i> 2016)	●● (Hostetter <i>et al.</i> 2015b; Gosselin & Anderson 2017)	●● (Hostetter <i>et al.</i> 2012; Stich <i>et al.</i> 2015c)	●● (Evans <i>et al.</i> 2014; Stich <i>et al.</i> 2015c)
Straying, fallback and delay		●●● (Crozier <i>et al.</i> 2015; Bond <i>et al.</i> 2017; Crozier <i>et al.</i> 2017a)	●●● (Keefer & Caudill 2014; Marsh <i>et al.</i> 2015; Bond <i>et al.</i> 2017)		

4 Transport-related Decisions

The questions from Anderson *et al.* (2012) of when, where, under what conditions, how many fish, and which fish to barge for increased effectiveness of the juvenile fish transportation can be distilled to two main questions:

- 1) Fixed or flexible start dates of barging?
- 2) Proportion of water spilled and proportion of fish transported?

Flexible start dates imply that the initiation of barging is triggered by environmental and fish conditions that are ever-changing (i.e., when, where, under what conditions, and which fish). Proportion of water spilled affects the river conditions experienced by fish, and also the proportion of fish available for transport (i.e., how many fish pass through the bypass system and thus how many can be collected at the juvenile fish facilities). Below, we consider these two main questions in more detail.

4.1 Fixed or flexible start date of transportation?

Seasonal environmental conditions can affect SARs, and thus the juvenile transportation program could be started given “triggers” in environmental conditions such as a river temperature of 9.3°C (Anderson *et al.* 2005). However, there is uncertainty in determining an optimal start date across salmonid species, river and ocean conditions, and other operational decisions.

The start date at Lower Granite Dam has generally been May 1. The 2014 Supplemental FCRPS Biological Opinion states that: the transport start date will be decided annually upon reviewing transportation study results and annual recommendations to achieve the goal of transporting about 50% of juvenile steelhead; and that planning dates to start juvenile transport at Lower Granite Dam will be April 21 to April 25, unless the USACE adopts TMT recommendation to start later but no later than May 1.

If the recent trend of the prolonged extreme environmental conditions continues a fixed start date for transportation will likely not be advantageous in some years. In 2016, for example, given relatively warm and high flow conditions, the smolt migration season was early by a few weeks (Faulkner *et al.* 2017). An estimate of 74% of the yearling Chinook and 58% of the steelhead populations had already passed Lower Granite Dam by the time transportation began on May 2. In contrast, the peak of the Caspian tern breeding season was delayed (Roby *et al.* 2017).

These factors may explain the higher predation rates on transported sockeye and steelhead observed in 2016 relative to other years (Roby *et al.* 2017).

Possible “triggers” for initiating transportation include:

- critical thresholds of river temperature and/or river discharge
- critical threshold of total dissolved gas that help reduce delayed mortality (Brosnan *et al.* 2016)
- a date, forecasted from river temperature, flow and/or observed from PIT data, when x percentile of spring/summer Chinook and steelhead pass Lower Granite Dam,
- a date when y (low) percentile of production subyearling Chinook and z (high) percentile of surrogate subyearling Chinook pass Lower Granite Dam, which is generally early-mid-July (Smith *et al.* 2017)
- an annual baseline of ocean conditions that interacts with river “triggers”; e.g., increased survival of transported wild Snake River Chinook relative to their run-of-river counterparts, during a cool PDO phase (Gosselin *et al.* 2018b)
- annual and seasonal indices of estuary and coastal ocean predation and alternative prey (Wells *et al.* 2017)

4.2 Proportion of water spilled and subsequently proportion transported?

The proportion of water spilled at the dams affects fish travel time, the proportion of fish passing through the bypass collection system, and consequently the proportion of fish available for transport (Schaller *et al.* 2013; McCann *et al.* 2016; Faulkner *et al.* 2017). The benefits of increased spill are faster migration rate through the hydropower system and earlier arrival to the ocean, both of which have been associated with increased freshwater and marine survival. The proportion of water spilled at dams are set at levels to limit total dissolved gas supersaturation, to prevent gas bubble trauma to fishes and other organisms in the rivers, and for other logistical constraints (USACE 2016).

Even when exposure to gas supersaturation below the dams is non-lethal, it may reduce their fitness and increase their susceptibility to predation (Mesa & Warren 1997). Run-of-river Chinook salmon that experienced greater than 120% total dissolved gas experienced higher daily mortality rates in the lower river and in the plume than fish that experienced less than 120% (Brosnan *et al.* 2016). In contrast, transported fish collected and transported across total dissolved gas levels below and above 120% did not experience significantly different daily mortality rates.

In addition, the effects of barometric pressure can play an important role on survival influenced by acute and chronic stresses from dissolved gas concentrations (Elder *et al.* 2016).

These studies together suggest that the benefits of increased spill occur during low river flows (e.g., 2001), while the disadvantages occur at high rates of spill during high river flows (e.g., high percentages of total dissolved gas [TDG] in 2011). A non-linear relationship between percent spill and survival likely occurs, but determining the threshold at which spill changes from being a positive to a negative effect on survival has yet to be determined. Although methods to quantify such ecological thresholds for resource management exist (Foley *et al.* 2015; Samhoury *et al.* 2017), limited data available encumber actually determining such thresholds. Replication of various treatments across different combinations of river and ocean conditions would require many years of study. Also, there are risks in what types of data can be collected (e.g., repeating treatments of very low spill under different river and ocean conditions that could significantly impact salmon stocks). Designing experimental treatments to better understand the impacts of spill and percentage of fish transported on future survival — especially under changing climate and environmental conditions — is complex.

A current proposal to increase spill levels (CSSOC 2017) evaluated four scenarios: Biological Opinion levels, 115% forebay / 120% tailrace TDG, 120% tailrace TDG, and 125% tailrace TDG. Metrics analyzed were juvenile fish travel rates, juvenile survival, SARs, ocean survival, and TIR; and predictors included various river and ocean condition indices. The spill experiment could be implemented with an annual or seasonal (e.g., bi-weekly cohorts) scale of spill level treatments. Whether it is conducted at an annual scale or finer temporal resolution, transported fishes can serve as another treatment group for comparison to run-of-river fishes. The proposed increased spill presents an opportunity to collect data under a combination of river and ocean conditions not yet observed. Such data would help better understand hypothesized non-linear relationships between spill on survival.

Overall, the decisions related to juvenile transport can depend heavily on ocean conditions. In Chinook salmon, the change in survival from annual effects (likely from the ocean) can be much larger than the change in survival from seasonal effects (likely from freshwater-marine carryover effects) (Satterthwaite *et al.* 2014; Gosselin *et al.* 2018a). Estimates of the relative magnitude of effect for each hypothesized factor under various freshwater and marine conditions would help elucidate the potential ramifications, if any in some years, of various transport decisions on survival. For example, when are the effects from the ocean swamping the carryover effects from the river? Are the freshwater-marine carryover effects stronger under certain ocean

conditions than others? As well, what is the degree of certainty in these effects? We address critical uncertainties further in the next section.

5 Critical Uncertainties

Studying salmon and their survival is challenging because it involves natural and cultural ecosystem-based approaches (Williams *et al.* 2006). Presently, the topic at hand entails assessing the effectiveness of the juvenile fish transportation program, and essentially whether the program can replace certain ecosystem functions lost as a result of the hydropower system. In the last decade, progress in research related to juvenile fish transportation has provided some insights on direct and carryover effects (Section 3). These include seasonal patterns of travel rates, size-selective avian predation, individual-trait-related mortality, straying, and differences in various biological responses among salmon ESUs and steelhead DPS. Nonetheless, many critical uncertainties remain. A discussion of critical uncertainties related to salmon survival can quickly evolve to consider many ecosystem-based approaches and the ecological and cultural factors therein. We therefore focus our discussion on the juvenile fish transportation program as a mitigation strategy in context of direct and carryover ecological effects across juvenile to adult life stages (Box 3).

We present two general frameworks under which current data and continued data collection can be analyzed (first two bullet points). The last two bullet points are more specific to hydrosystem conditions, and can be examined in context of the two frameworks presented.

- **Direct and carryover effects: Important factors and critical thresholds.** A general uncertainty is which factors in the river, estuary, and ocean are most important in context of direct and carryover effects on survival (Box 3). These effects can manifest across different temporal, spatial and biological scales:
 - At a **large scale**, the factors involve annual and ocean processes and the effects can occur across species and stocks.
 - At a **small scale**, the factors can involve natural and disrupted phenological processes (or seasonal processes) and specific areas in the river and coastal ocean. The effects can differ among species and between run-of-river and transported passage-types.

Determining the relative magnitudes of influence on survival from different factors at large and small spatial and temporal scales is important. In particular, quantifying the *relative magnitude of effect* from large-scale factors at an annual scale (e.g. ENSO, PDO, NPGO and PNI indices, winter ichthyoplankton index, and a snow water equivalent index) and fine-scale factors at a seasonal scale (e.g., hydrosystem passage timing, river temperature, and timing of avian breeding season) is particularly important. Also, determining *similarities and discriminatory effects* among different hypothesized factors will help ascertain the limitations of particular hypothesized factors as predictors of survival. For example, many environmental and biological covariates can be correlated with each other during an El Niño coupled with a warm PDO index. Which among these covariates have the same effect on survival? If differential effects exist among some covariates, which are they and why? Similarities and differences in mechanisms across species can help identify *cross-species and species-specific* triggers.

- **Survival differentials and tradeoffs across life stages.** The patterns of transport to run-of-river survival differentials can change across the downstream (juvenile), ocean, and upstream (adult) life stages. In wild spring/summer Chinook for example, the effect of transport on survival in the juvenile, ocean, and adult life stages were respectively very beneficial, neutral and neutral in 2001, but were respectively beneficial, disadvantageous and neutral in 2011 (Figure 4). In the end, T:B was high in 2001 but neutral in 2011. The survival benefits of transportation during the juvenile life stage may be counteracted by negative carryover effects in the ocean and during upstream migration. To what degree these tradeoffs change can depend on annual and seasonal changes in freshwater and ocean conditions. Understanding these life-stage-specific differential estimates would require identifying *trait-mediated* direct and carryover effects. For example, river conditions that are most optimal for juveniles can differ from those most favorable for adults. Transportation can increase juvenile survival but increase adult straying. Furthermore, spillway weirs and surface bypass channels designed to improve juvenile dam passage can result in moving warm surface waters that increase the probability of adult straying, particularly for some transported fish. Distinguishing among the direct effects on juvenile survival, carryover effects at ocean entry and carryover effects during upstream migration will help elucidate relative magnitudes of effect from different traits (or covariates) and help quantify cross-life-stage tradeoffs.

- **Hydrosystem conditions and passage experience.** Among the hydrosystem-themed critical uncertainties listed in a recent report on critical uncertainties (ISAB/ISRP 2016), those of high criticality were in relation to flow and spill on juvenile and adult survival. In particular, criticality was deemed high for examining the effects of *flow and spill* on *smolt travel time and survival and water quality*. It was also high for determining the effects of *multiple dam passages, transportation and spill* operations on SARs (blue and purple arrows, Box 3). These critical uncertainties can be examined in context of the framework outlined in our first two bullet points. For example, the *relative impacts* of percent spill and an ocean productivity index on SARs will likely differ across years of different river and ocean conditions: low flow and warm river conditions, coupled with productive ocean conditions in migration year 2001; high flow and cool river conditions, coupled with unproductive ocean conditions in migration year 2017; and all other combinations. Most importantly, under what conditions are the effects from increased spill beneficial to salmon survival and why are they beneficial? When are freshwater-marine carryover effects swamped by ocean conditions? Understanding the patterns and underlying mechanisms can help determine ways of capitalizing on triggers when the opportunities arise. As well, knowing how much *certainty* there is in their effects across a *range of values for each factor* will be important. Recent river and ocean conditions (e.g. high river flow, and lingering effects from the Blob in the ocean) provide more contrast within datasets for which to examine effects on survival across life stages. Furthermore, the proposed increased levels of spill will provide important data that can add more contrast to these data sets. These data can be particularly important if there are non-linear relationships between spill and survival.
- **Adult upstream migration.** Many recent studies have made progress in examining transportation-related effects on adult upstream migratory behaviors such as straying, delay and fallback (Section 3.2). Continued and additional monitoring can help resolve this critical uncertainty. This includes examination of factors causing lower *adult conversion rates* in transported fishes than their run-of-river counterparts, particularly in *steelhead, hatchery fall Chinook, and sockeye* (blue and orange arrows, Box 3). Elucidating the mechanistic processes would help generate support for or against certain triggers (e.g., species- and site-specific temperature thresholds that significantly increase the probability of straying).

The relationships among factors and salmon survival are numerous in context of freshwater and marine ecosystems. Including other factors such as density-dependent effects and food web dynamics drive home the real but daunting existence of *ecosystem complexity* wherein lie salmon. But particularly, because of the inherent ecosystem complexity, collecting *long-term data sets* will be important. Given the large variation in river and ocean conditions in the recent past and the plausibility of continued variability, opportunities to address these critical uncertainties arise. The long and continuing observation time series are becoming amenable to more robust and complex analyses (e.g., rich data sets of capture histories in the PIT tag information system and coded-wire tag data sets from the Regional Mark Processing Center, physical condition of fishes from the Smolt Monitoring Program run by the Fish Passage Center, various biological data sets from the NOAA juvenile salmon offshore sampling surveys). *Tradeoffs* also exist in data collections when considering the relative biological impacts on salmon, the sample sizes necessary to observe patterns with reasonable certainty, *logistical constraints*, and *economic and cultural necessities*. Framing critical uncertainties and how reasonably they can be resolved in context of these tradeoffs, constraints and needs will help guide applied research related to the juvenile transportation program.

6 Figures

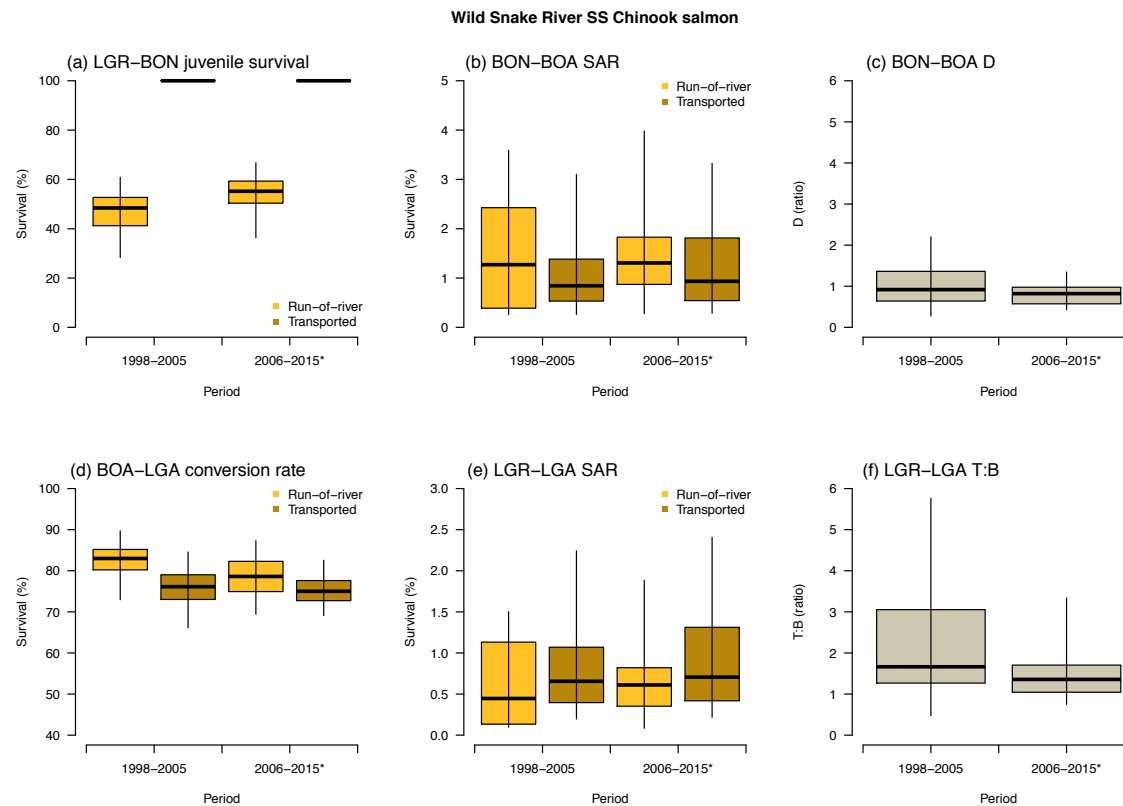


Figure 1. Survival rates and ratios of wild, run-of-river and transported, Snake River spring/summer Chinook salmon: a) juvenile survival, b) BON-BOA SARs, c) D, d) BOA-LGA conversion rates, e) LGR-LGR SARs, and f) T:B in the pre- and post-periods. Thick black lines represent medians, boxes represent the interquartiles, and vertical lines represent the 95% credible intervals. * Incomplete adult returns for smolt migration year 2015.

Wild run-of-river Snake River SS Chinook salmon

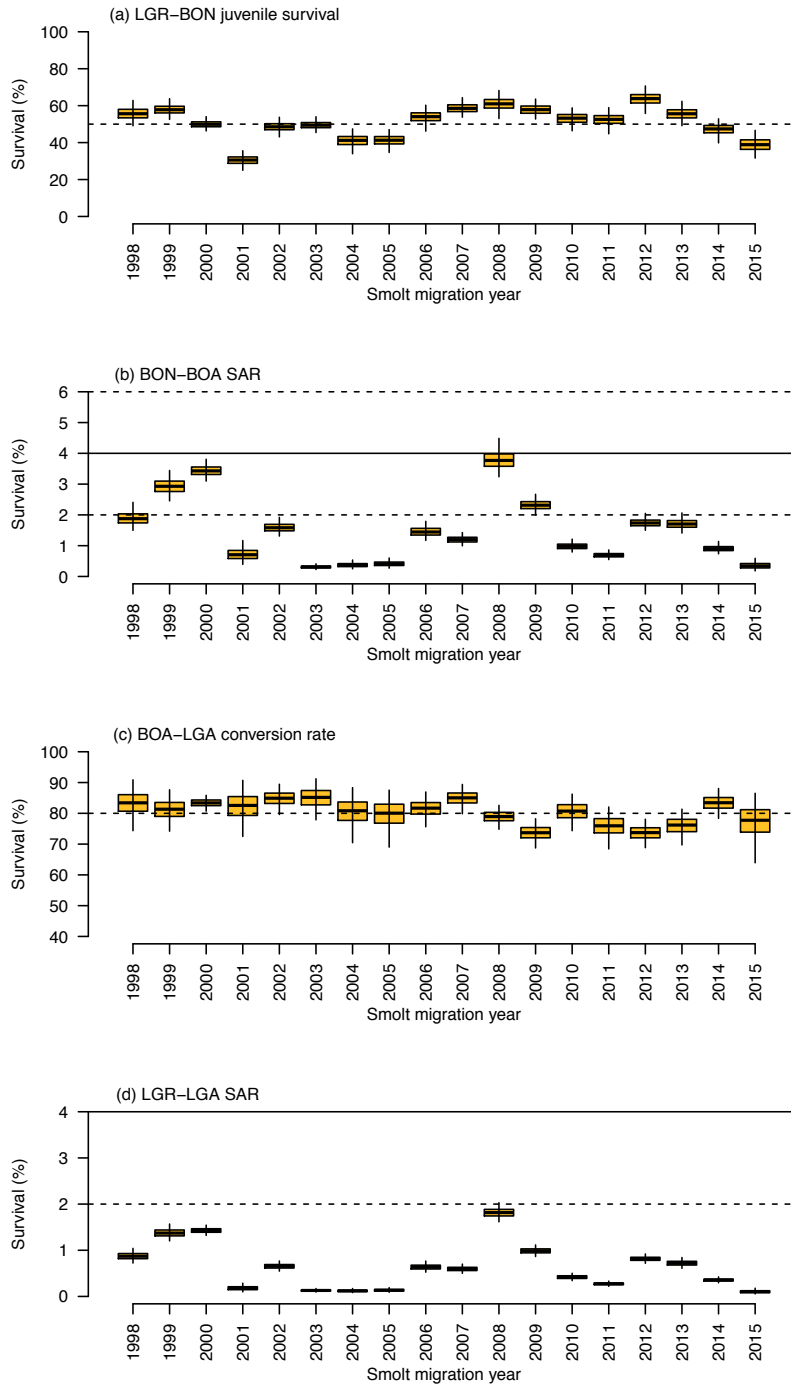


Figure 2. Yearly survival rates of wild, run-of-river, Snake River spring/summer Chinook salmon: a) juvenile survival, b) BON-BOA SARs, c) BOA-LGA conversion rates, and d) LGR-LGR SARs. Thick black lines represent medians, boxes represent the interquartiles, and vertical lines represent the 95% credible intervals. N.B. incomplete returns for migration year 2015.

Wild transported Snake River SS Chinook salmon

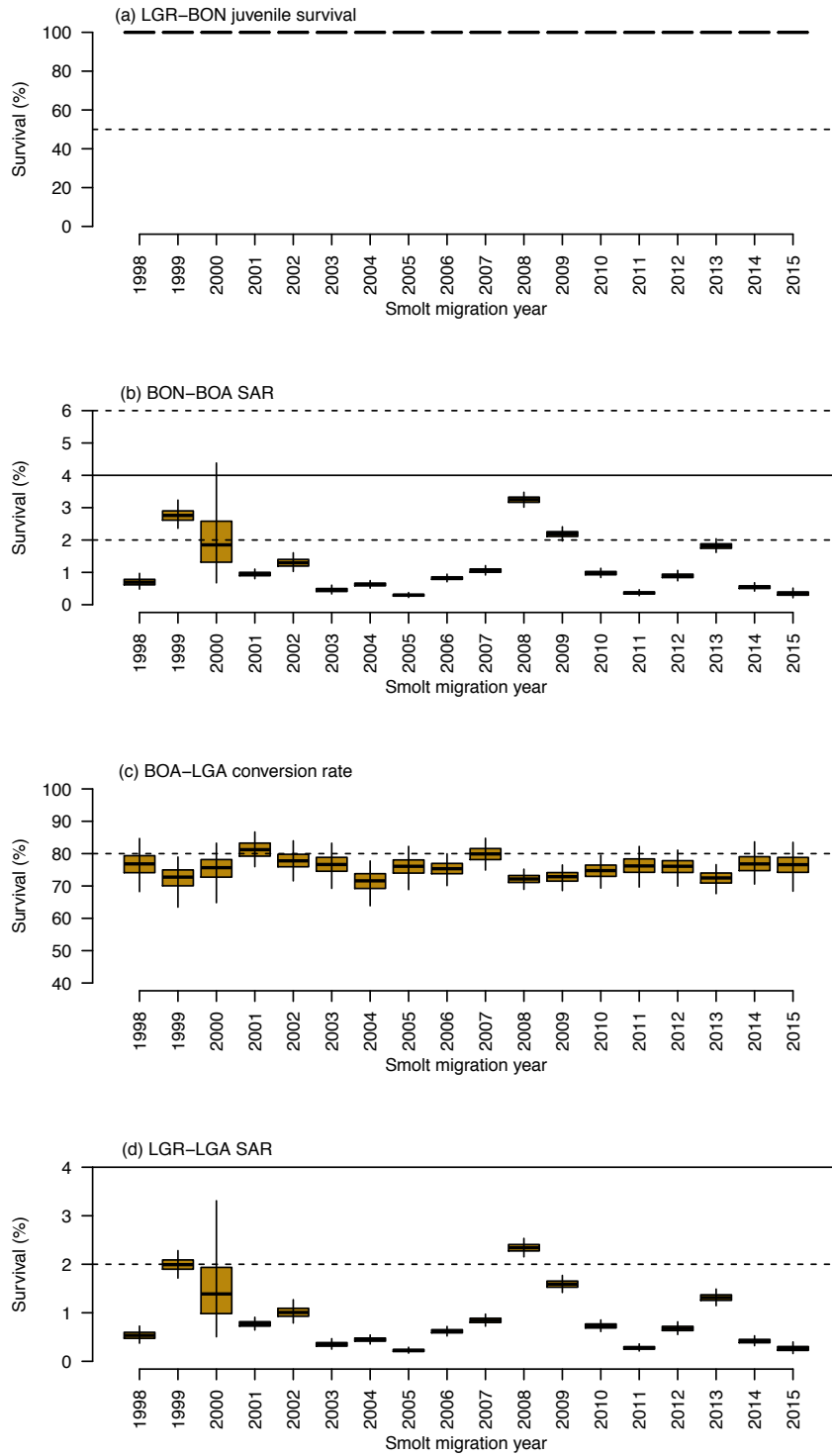


Figure 3. As Figure 2, with wild, transported, Snake River spring/summer Chinook salmon.

Wild Snake River SS Chinook salmon

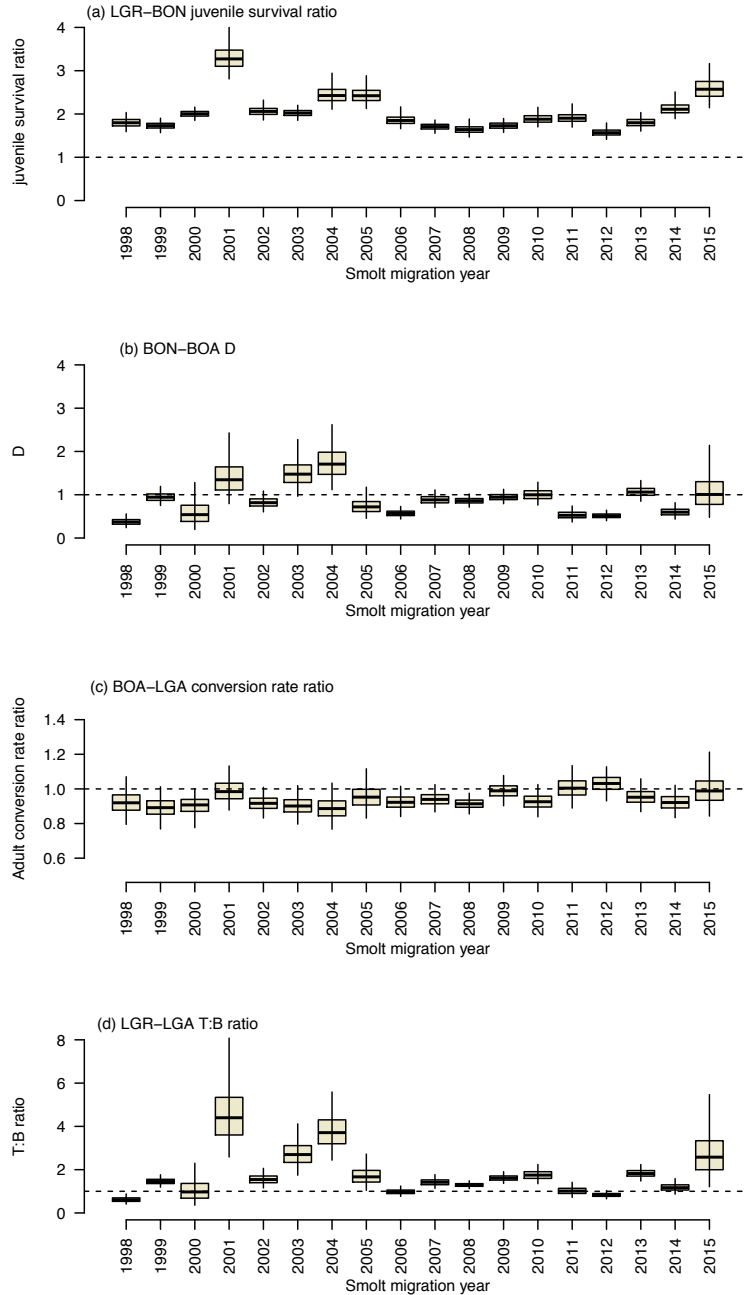


Figure 4. Ratios of transported to run-of-river survival indices for wild Snake River spring/summer Chinook salmon. Thick black lines represent medians, boxes represent the interquartiles, and vertical lines represent the 95% credible intervals. N.B. incomplete returns for migration year 2015.

Hatchery Snake River SS Chinook salmon

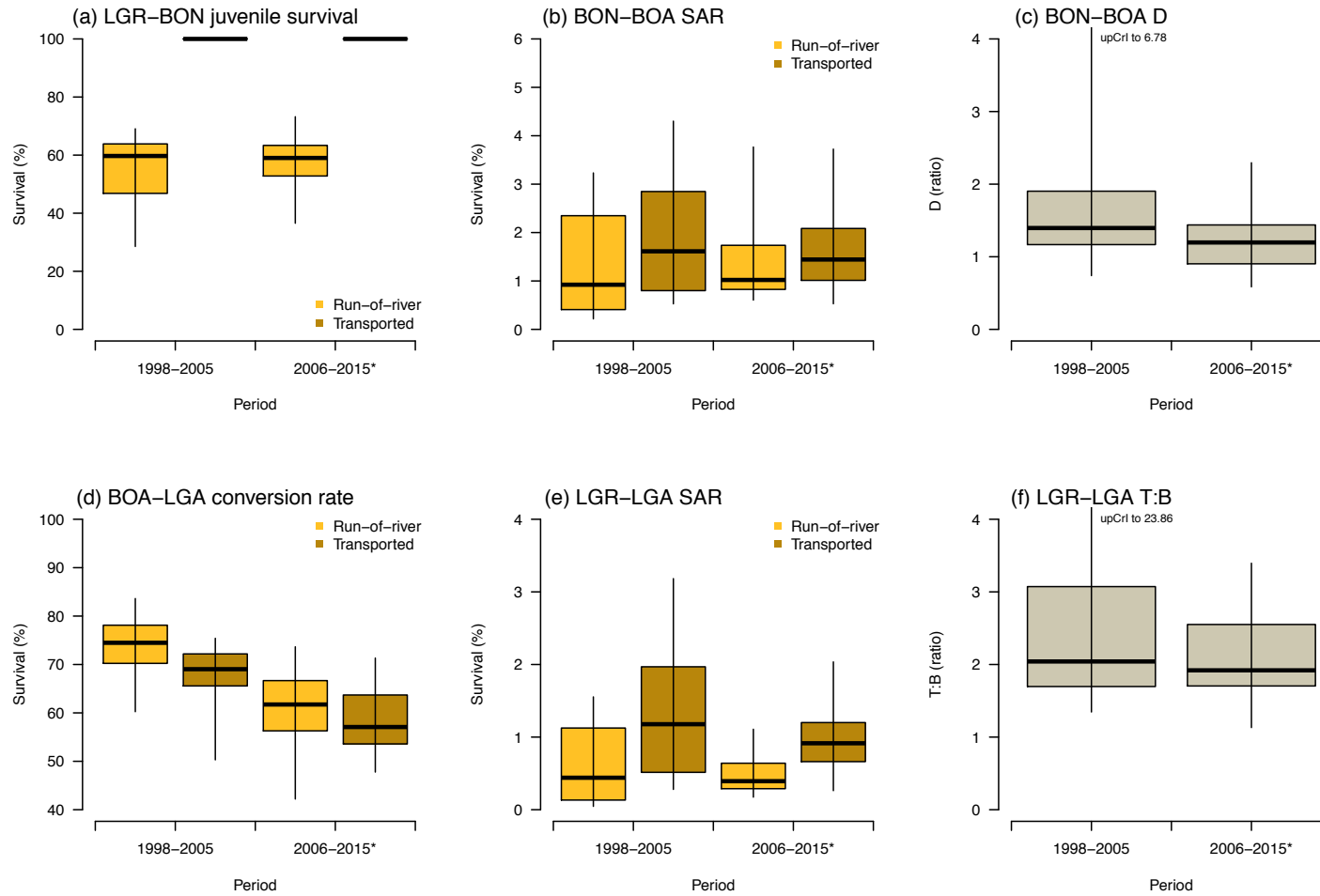


Figure 5. As Figure 1, with hatchery, run-of-river and transported, Snake River spring/summer Chinook salmon.

Hatchery run-of-river Snake River SS Chinook salmon

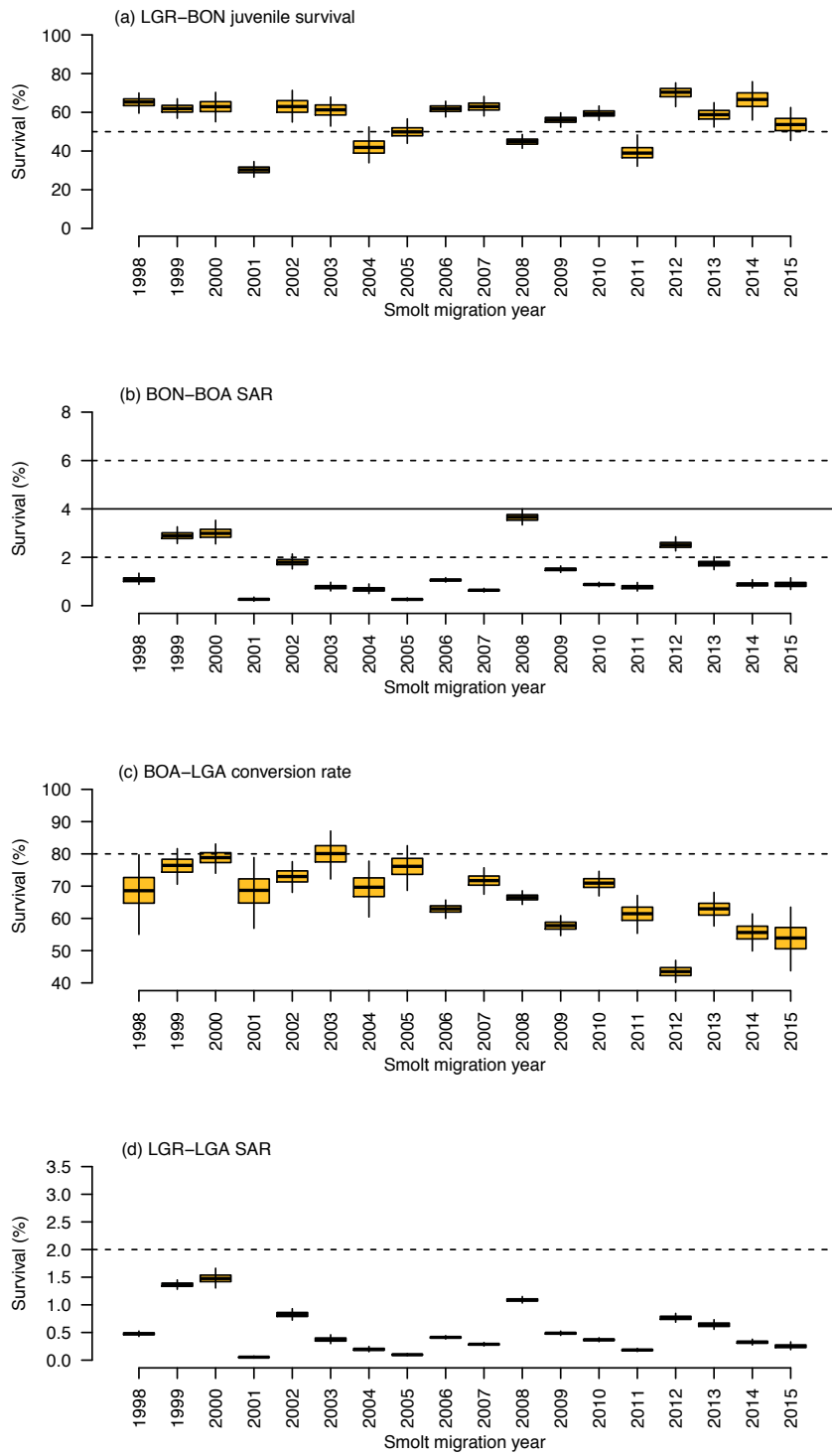


Figure 6. As Figure 2, with hatchery, run-of-river, Snake River spring/summer Chinook salmon.

Hatchery transported Snake River SS Chinook salmon

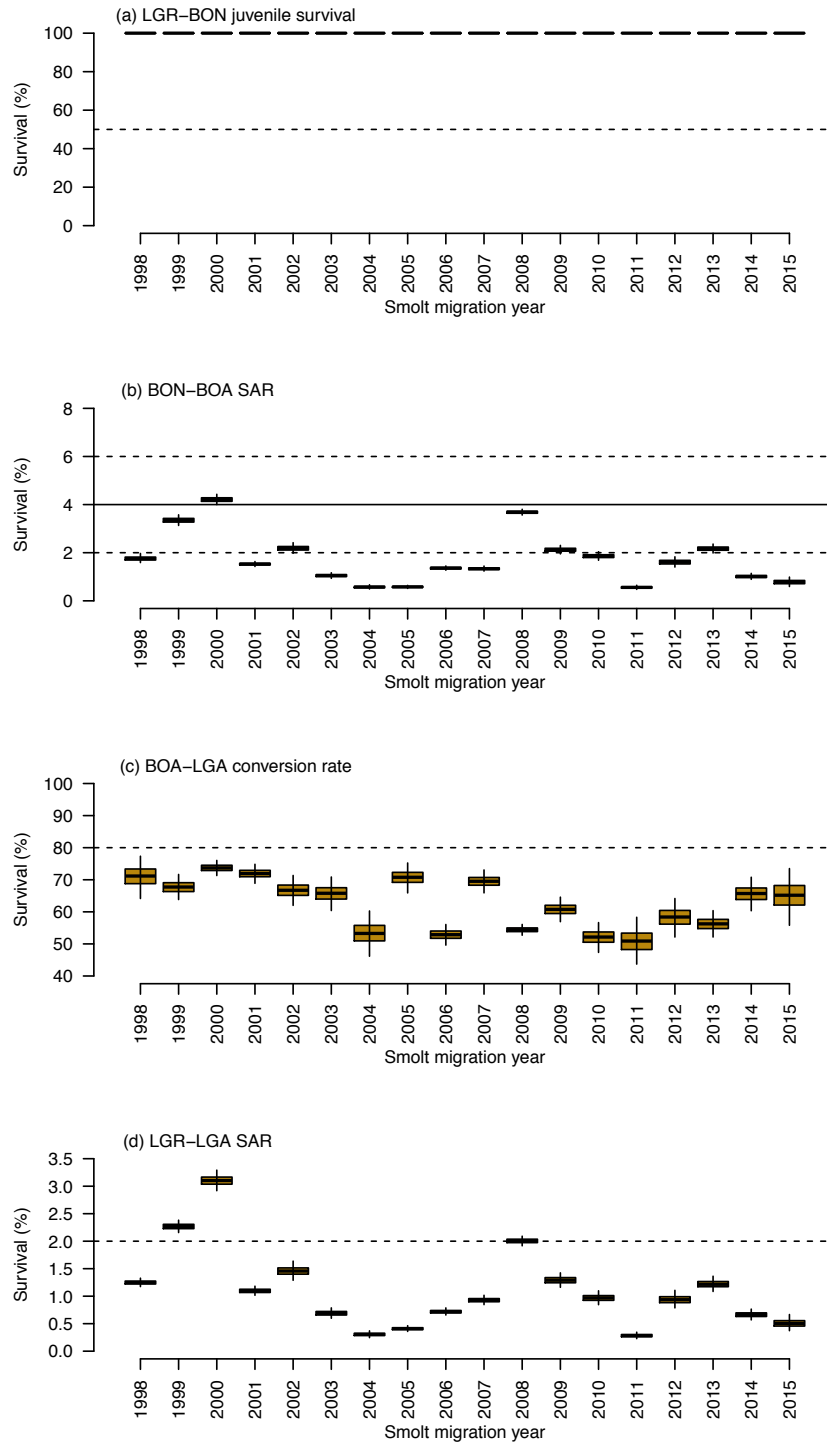


Figure 7. As Figure 2, with hatchery, transported, Snake River spring/summer Chinook salmon.

Hatchery Snake River SS Chinook salmon

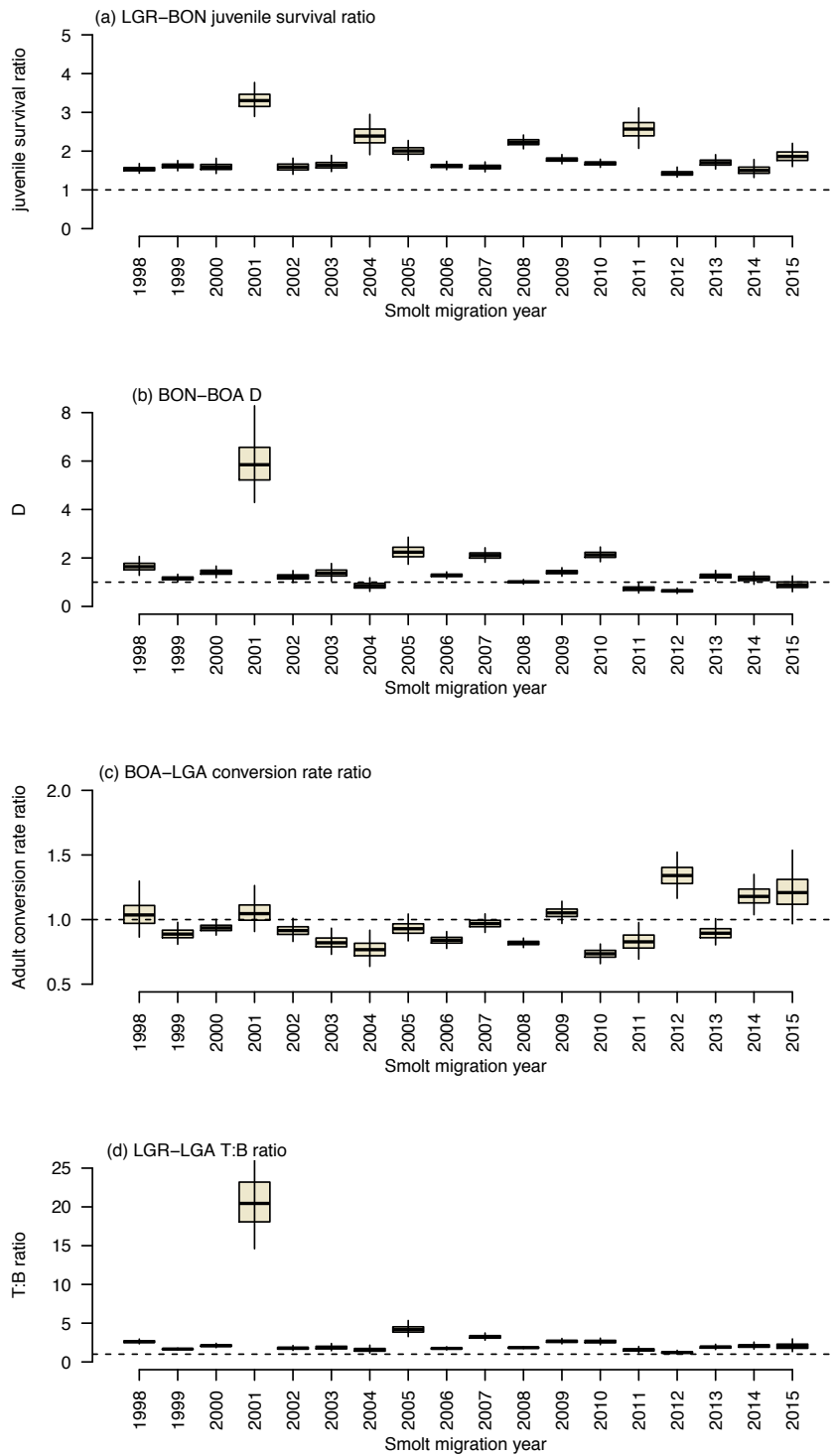


Figure 8. As Figure 4, for hatchery Snake River spring/summer Chinook salmon.

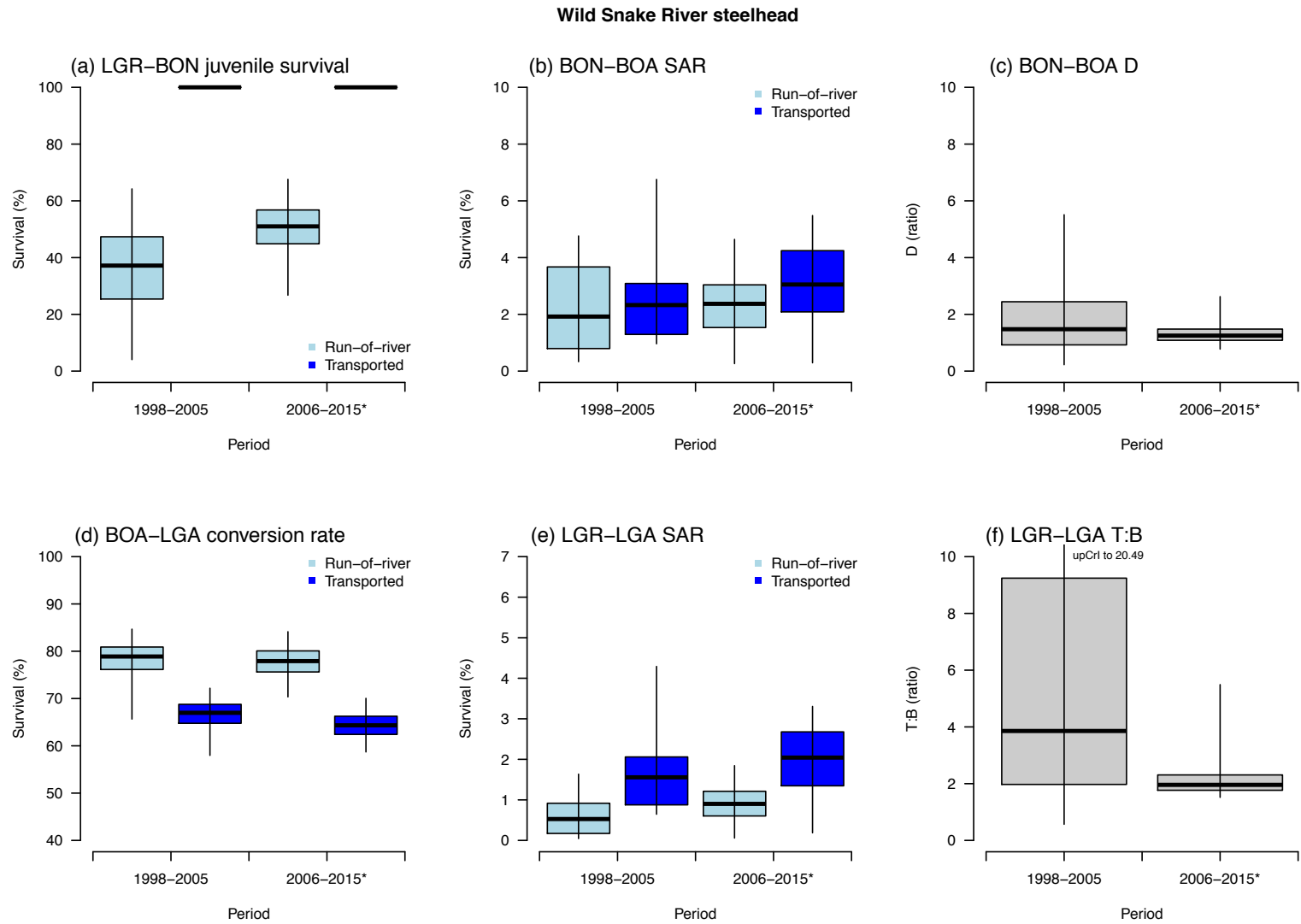


Figure 9. As Figure 1, with wild, run-of-river and transported Snake River steelhead.

Wild run-of-river Snake River steelhead

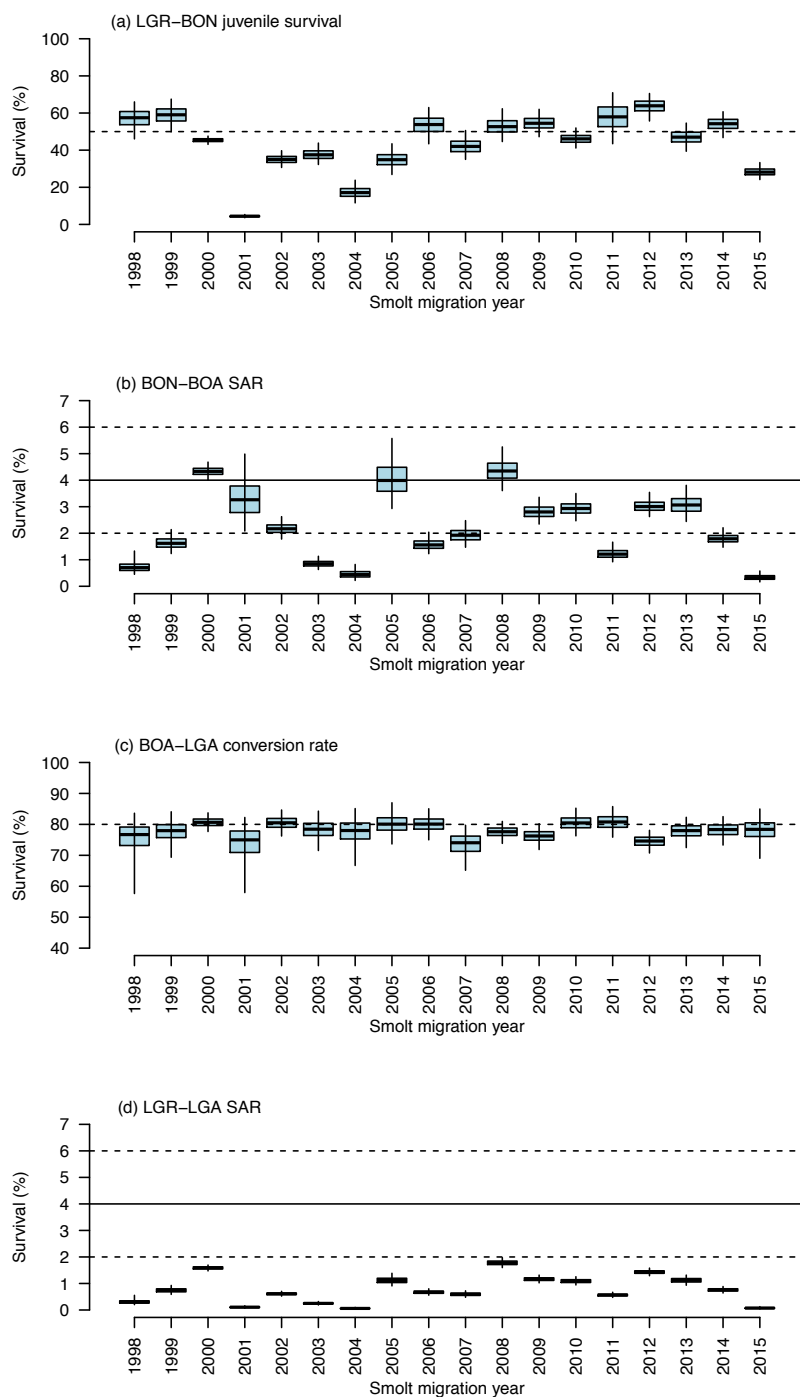


Figure 10. As Figure 2, with wild, run-of-river, Snake River steelhead.

Wild transported Snake River steelhead

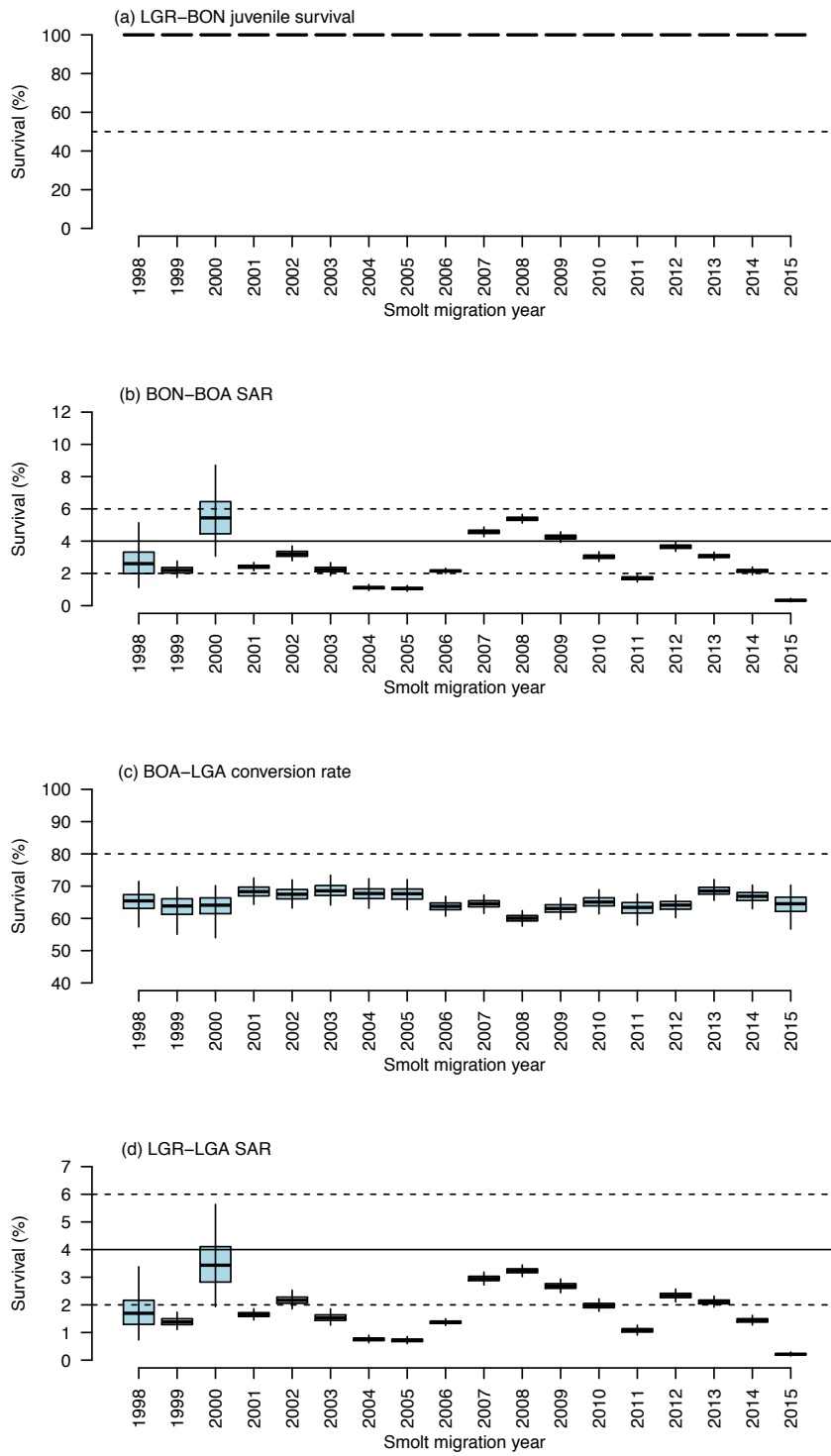


Figure 11. As Figure 2, with wild, transported, Snake River steelhead.

Wild Snake River steelhead

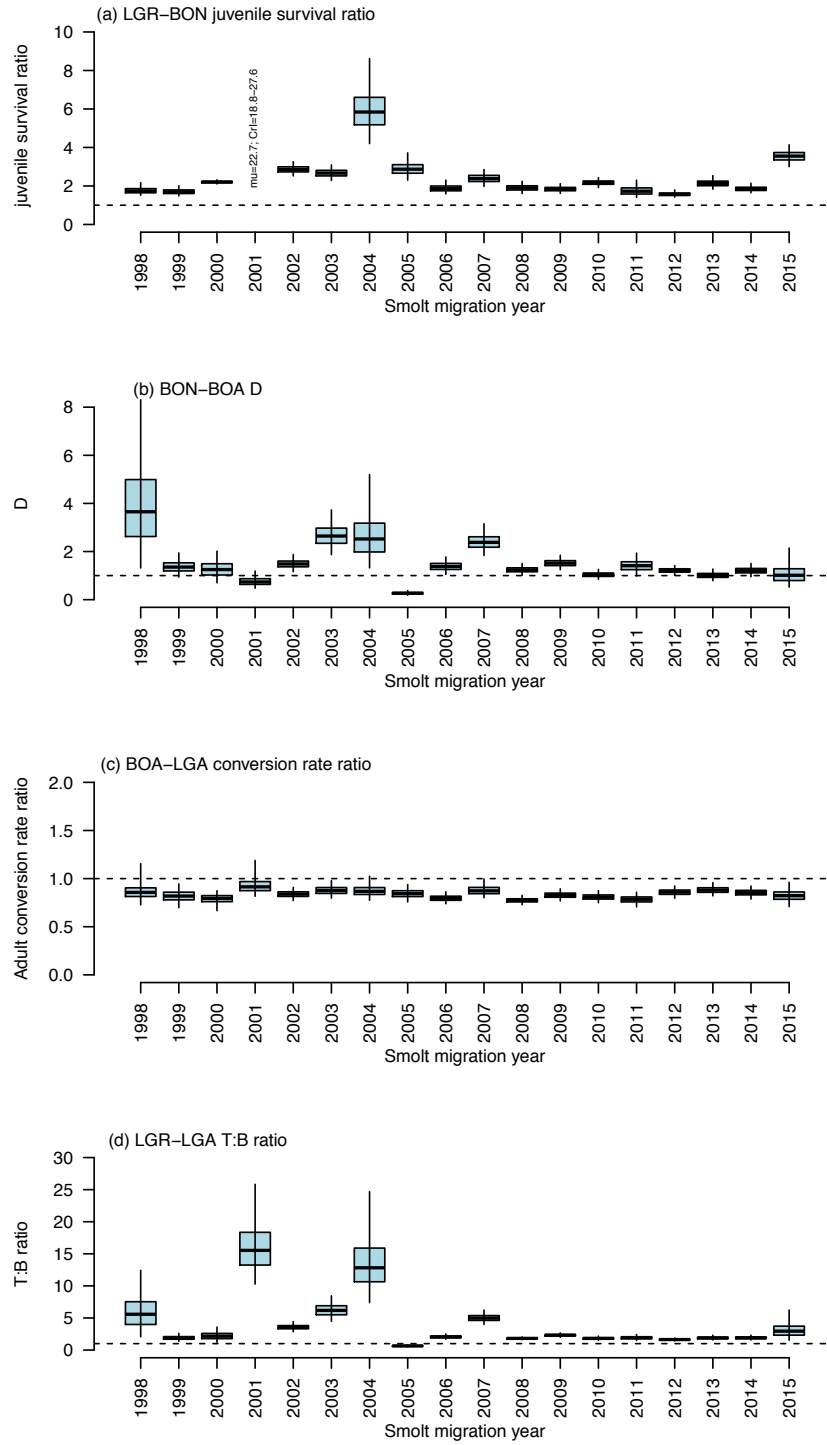


Figure 12. As Figure 4, with wild Snake River steelhead.

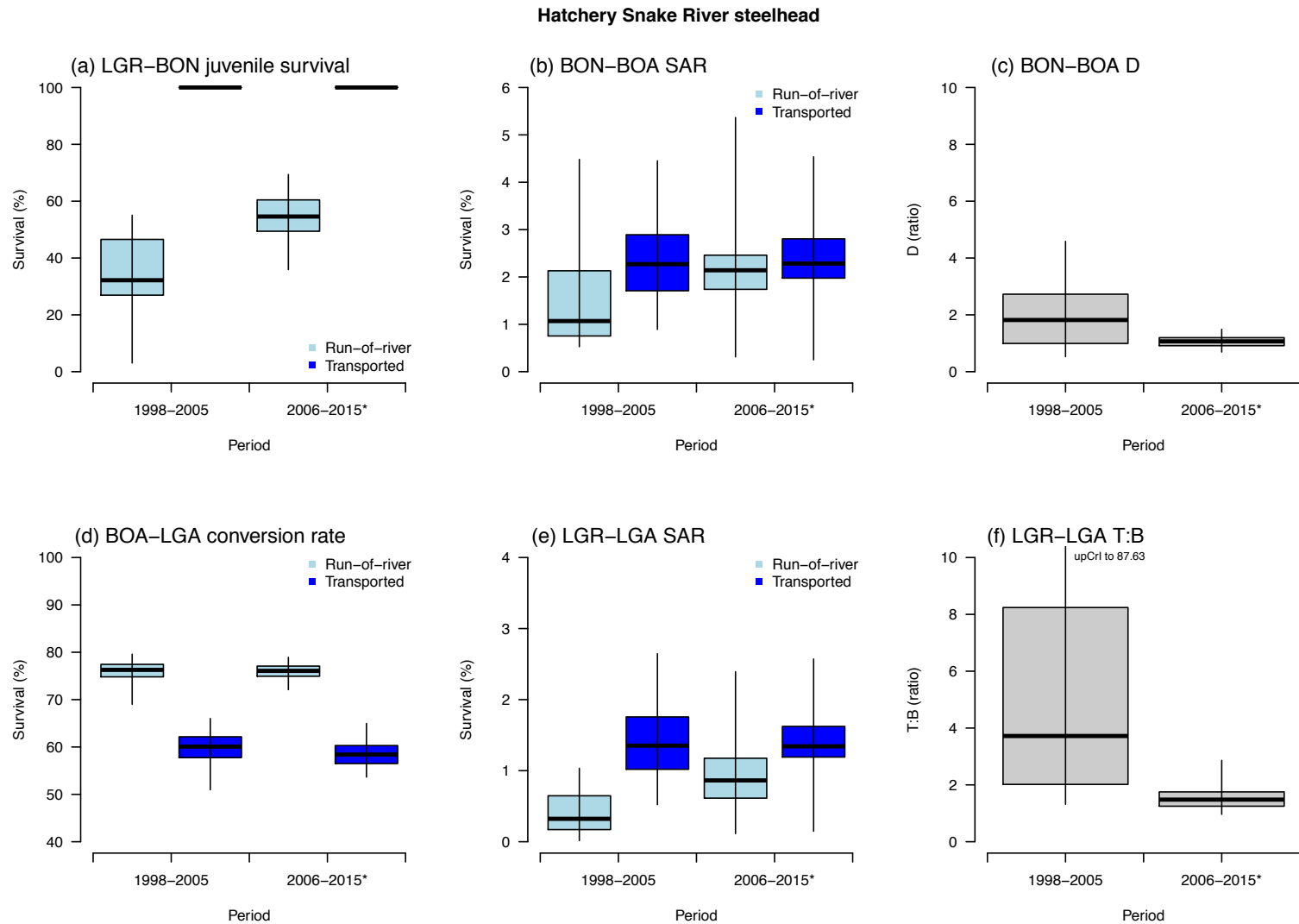


Figure 13. As Figure 1, with hatchery, run-of-river and transported Snake River steelhead.

Hatchery run-of-river Snake River steelhead

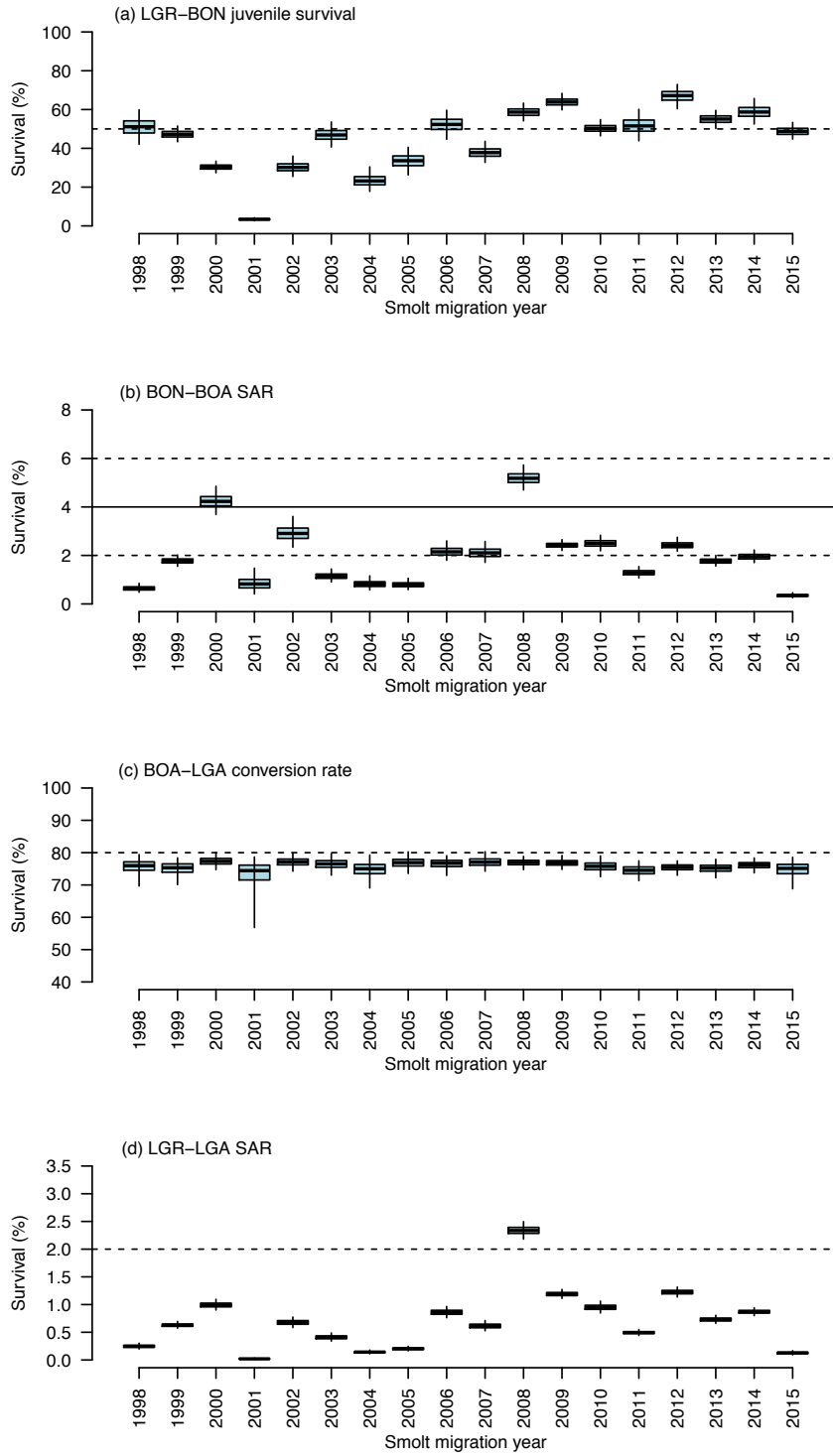


Figure 14. As Figure 2, with hatchery, run-of-river, Snake River steelhead.

Hatchery transported Snake River steelhead

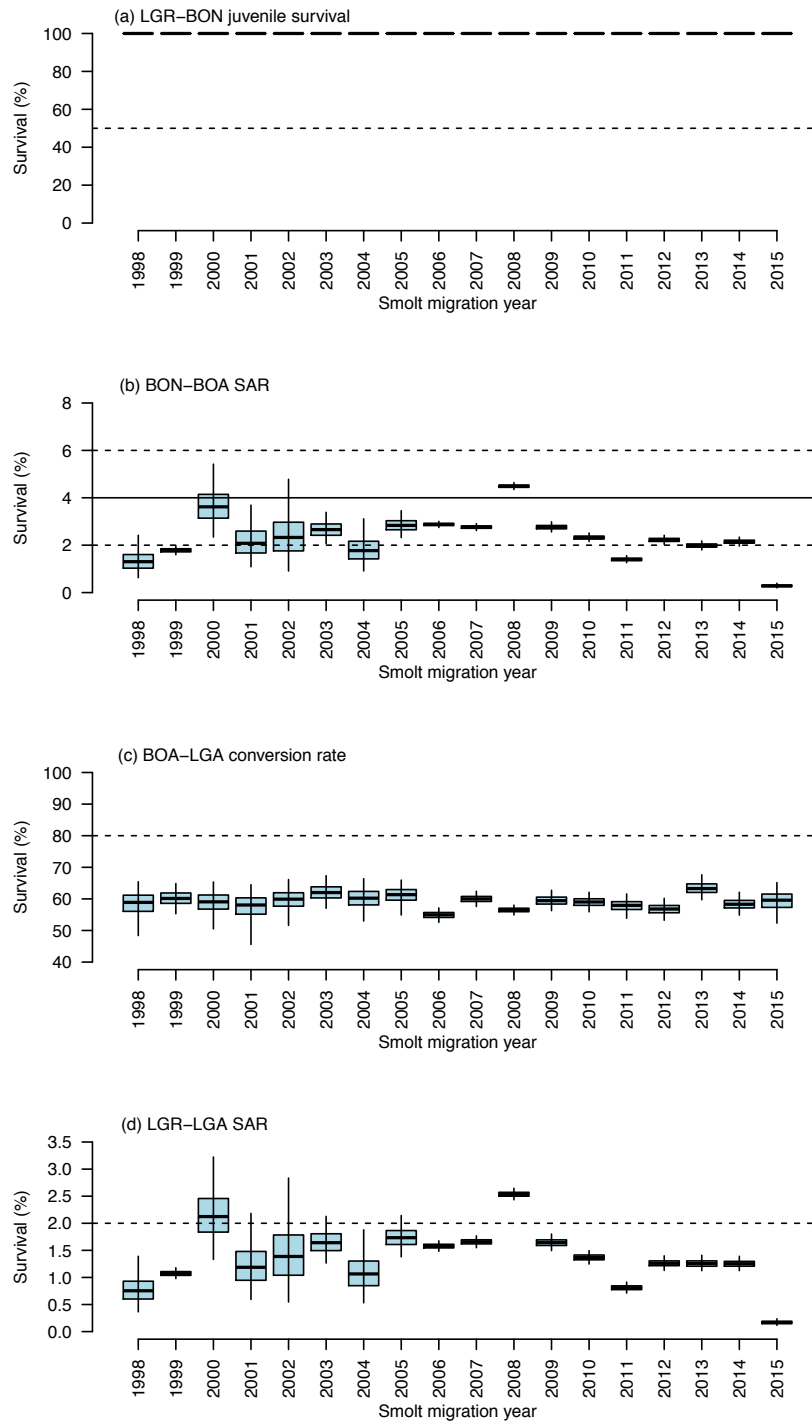


Figure 15. As Figure 2, with hatchery, transported, Snake River steelhead.

Hatchery Snake River steelhead

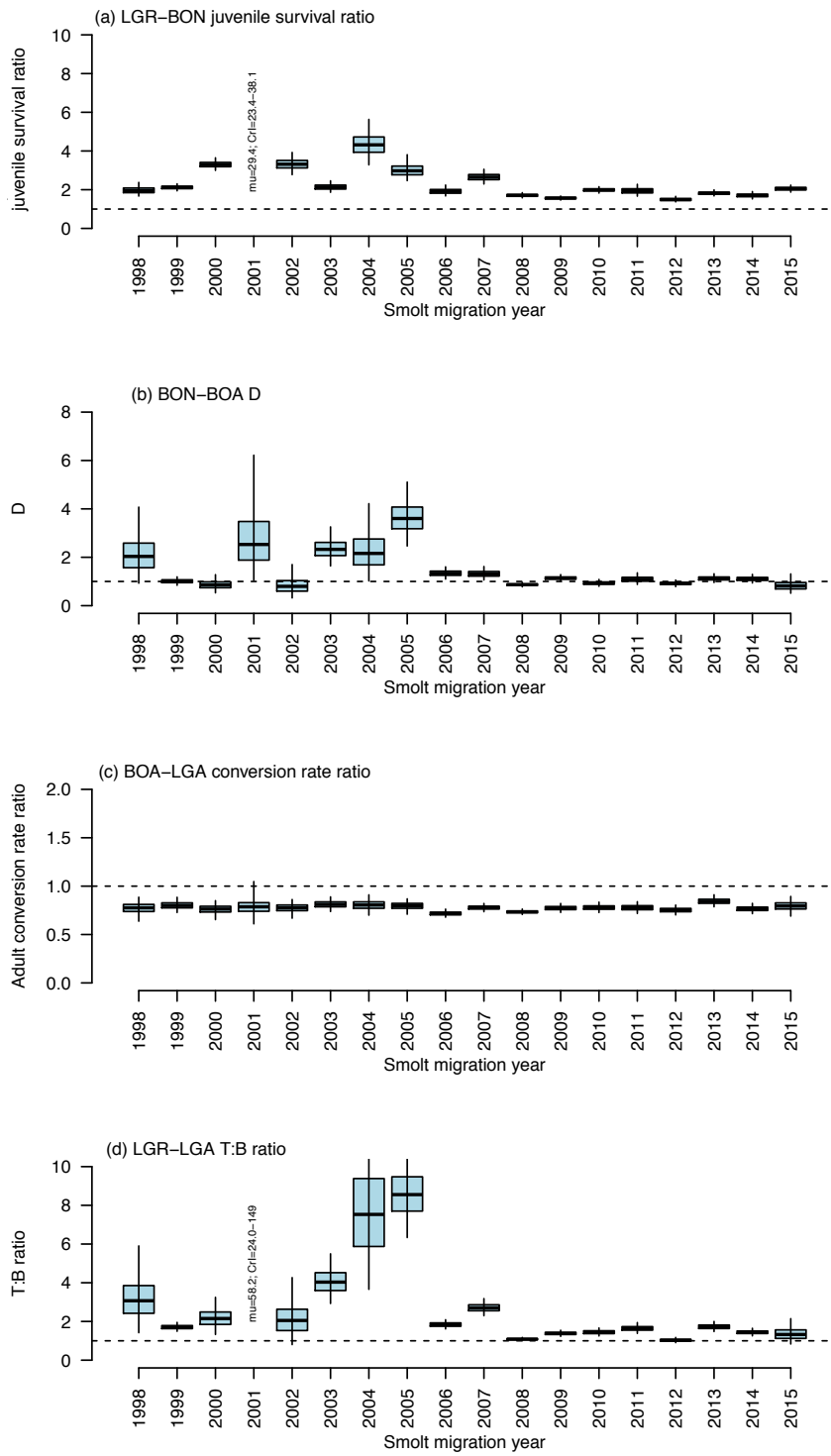


Figure 16. As Figure 4, with hatchery Snake River steelhead.

Wild Snake River Fall subyearling Chinook salmon

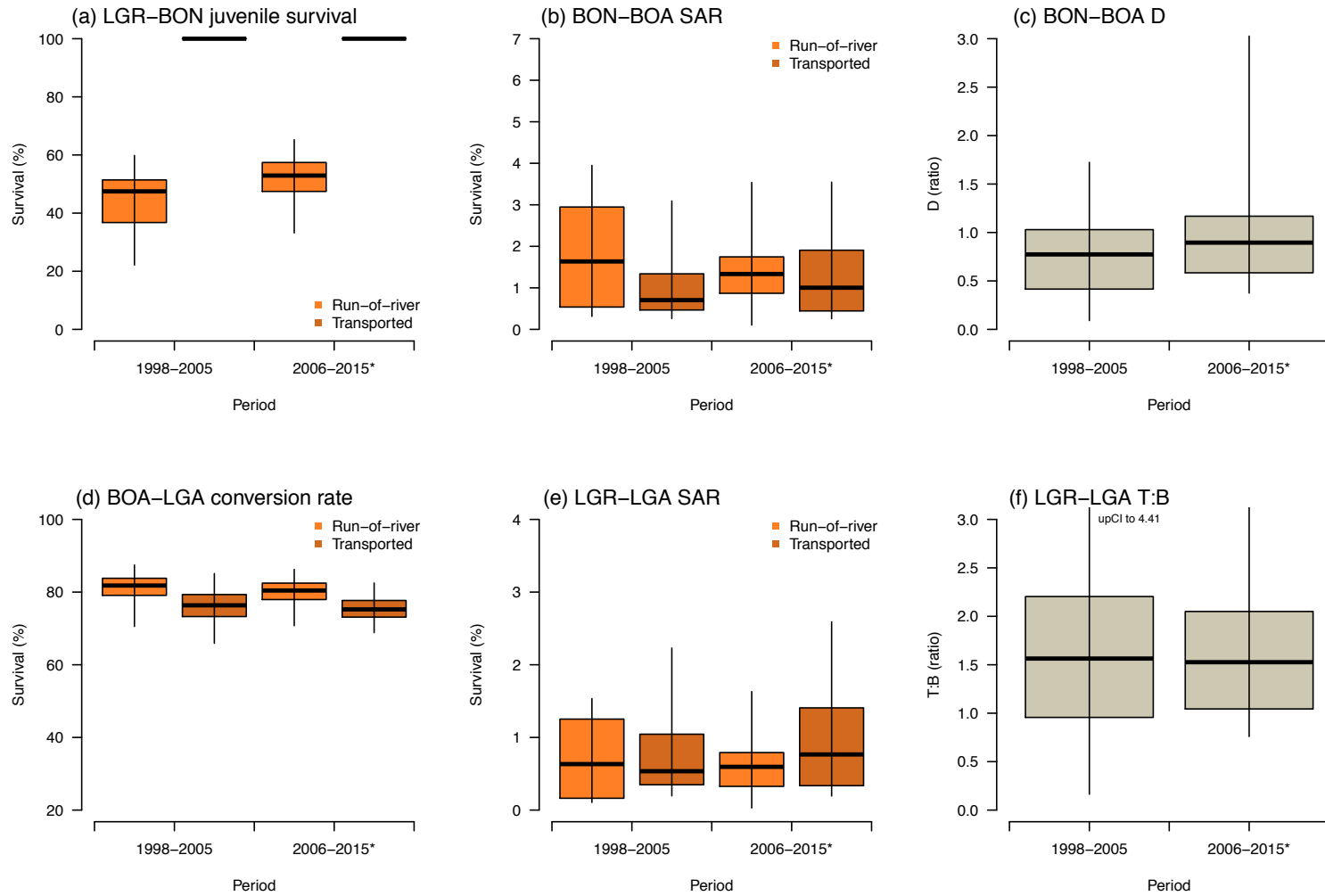


Figure 17. As Figure 1, with wild, run-of-river and transported Snake River fall Chinook salmon.

Wild run-of-river Snake River Fall subyearling Chinook salmon

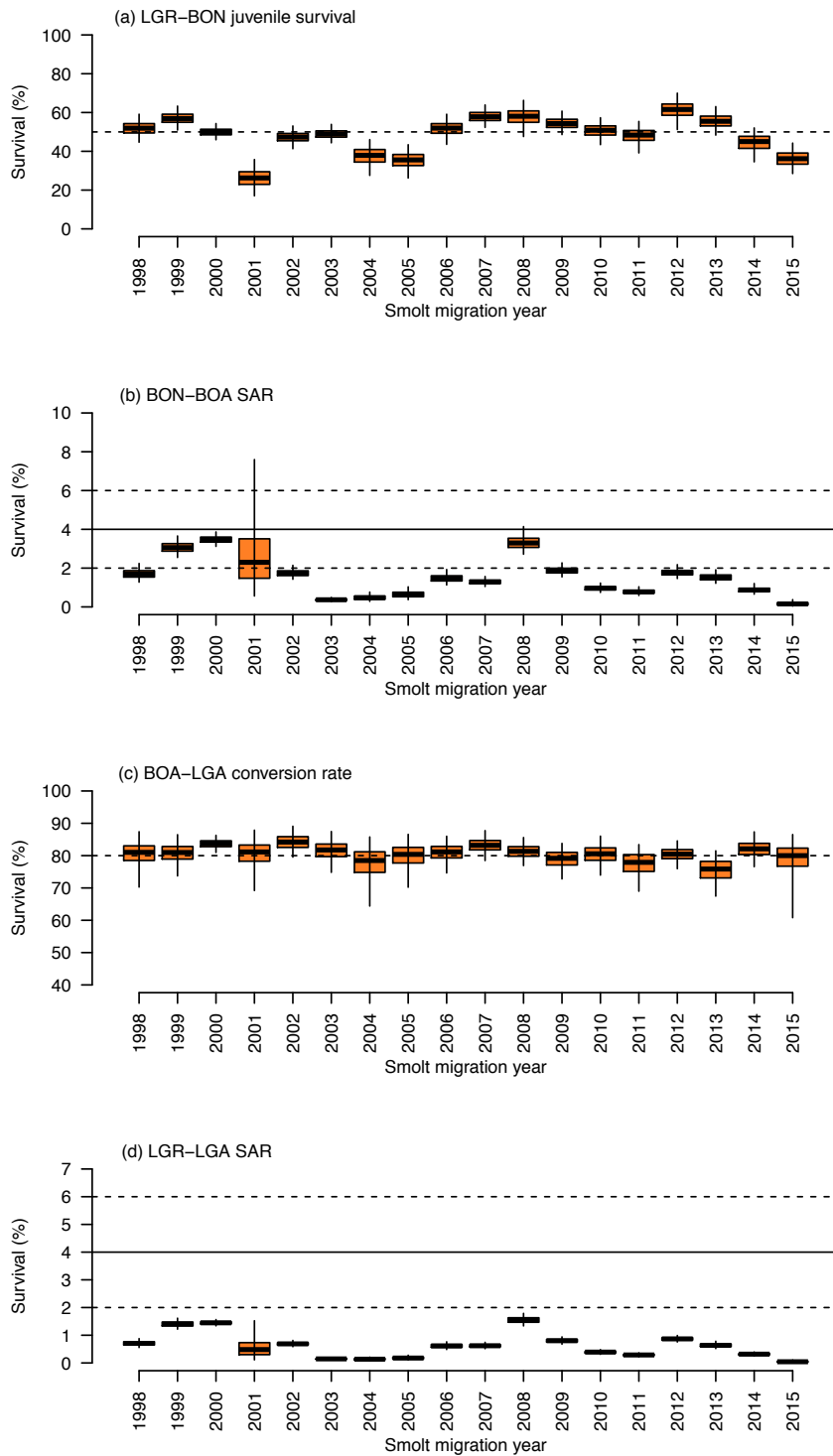


Figure 18. As Figure 2, with wild, run-of-river, Snake River fall Chinook salmon.

Wild transported Snake River Fall subyearling Chinook salmon

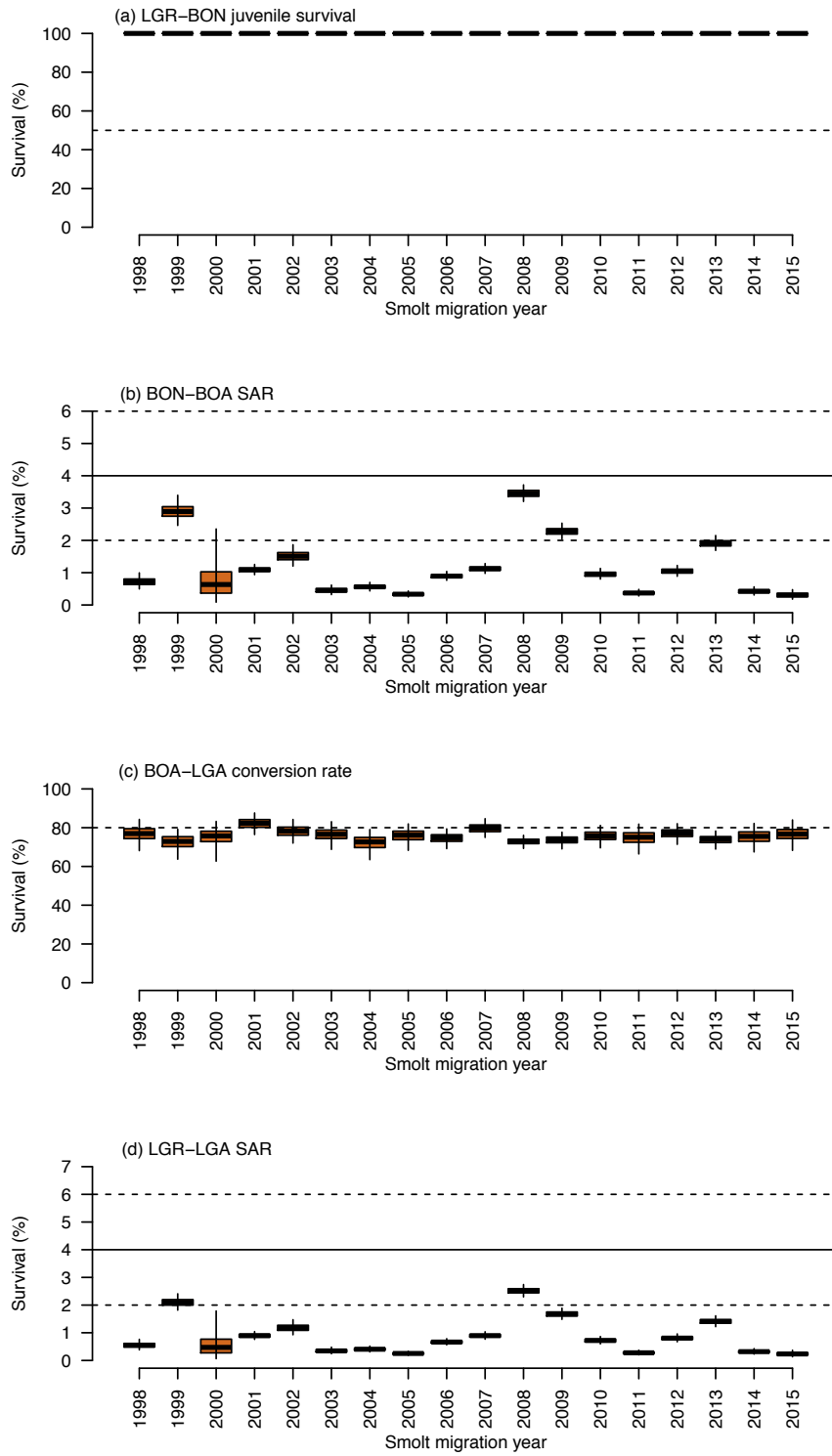


Figure 19. As Figure 2, with wild, transported, Snake River fall Chinook salmon.

Wild Snake River Fall subyearling Chinook salmon

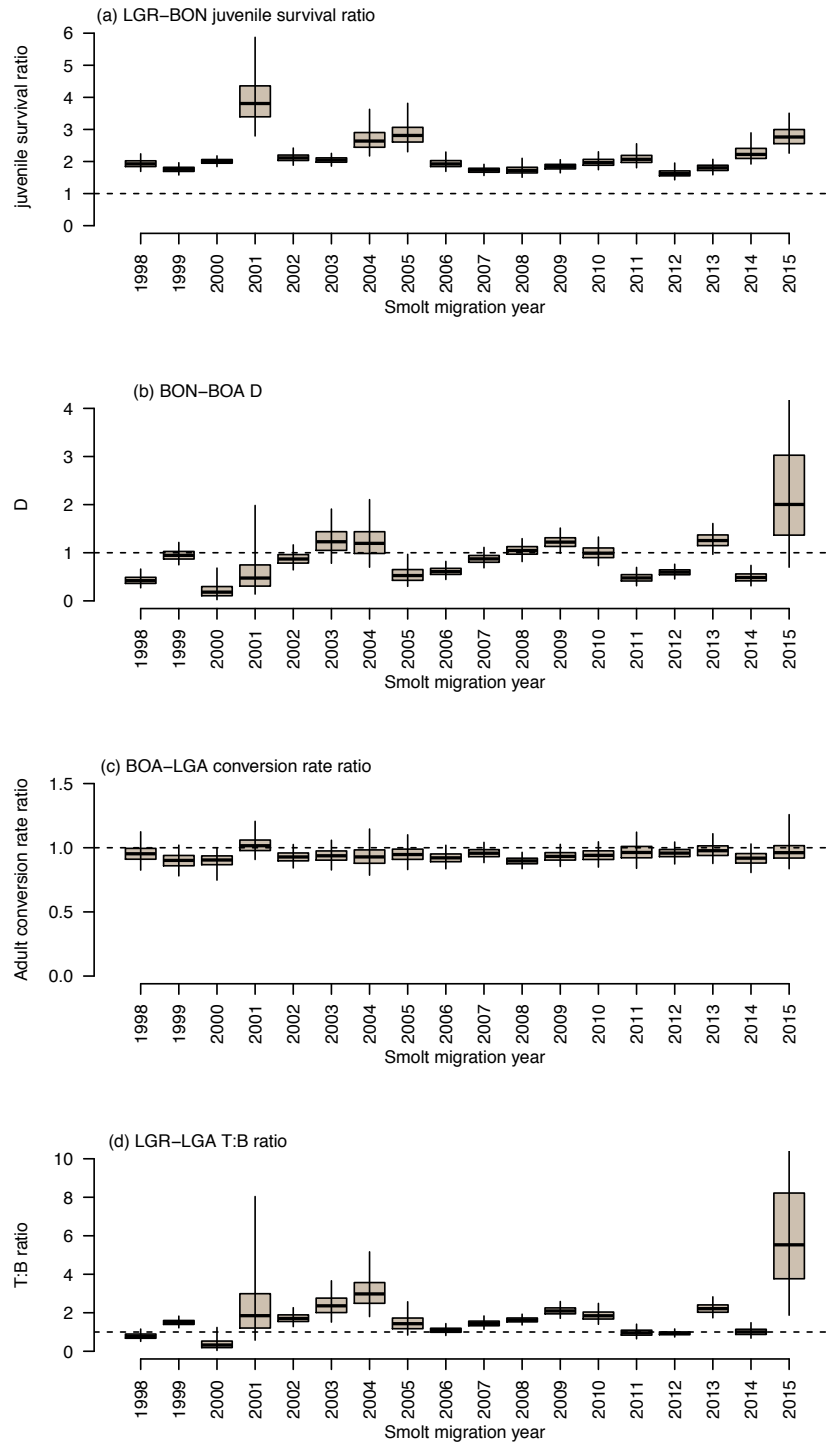


Figure 20. As Figure 4, with wild Snake River fall Chinook salmon.

Hatchery Snake River Fall subyearling Chinook salmon

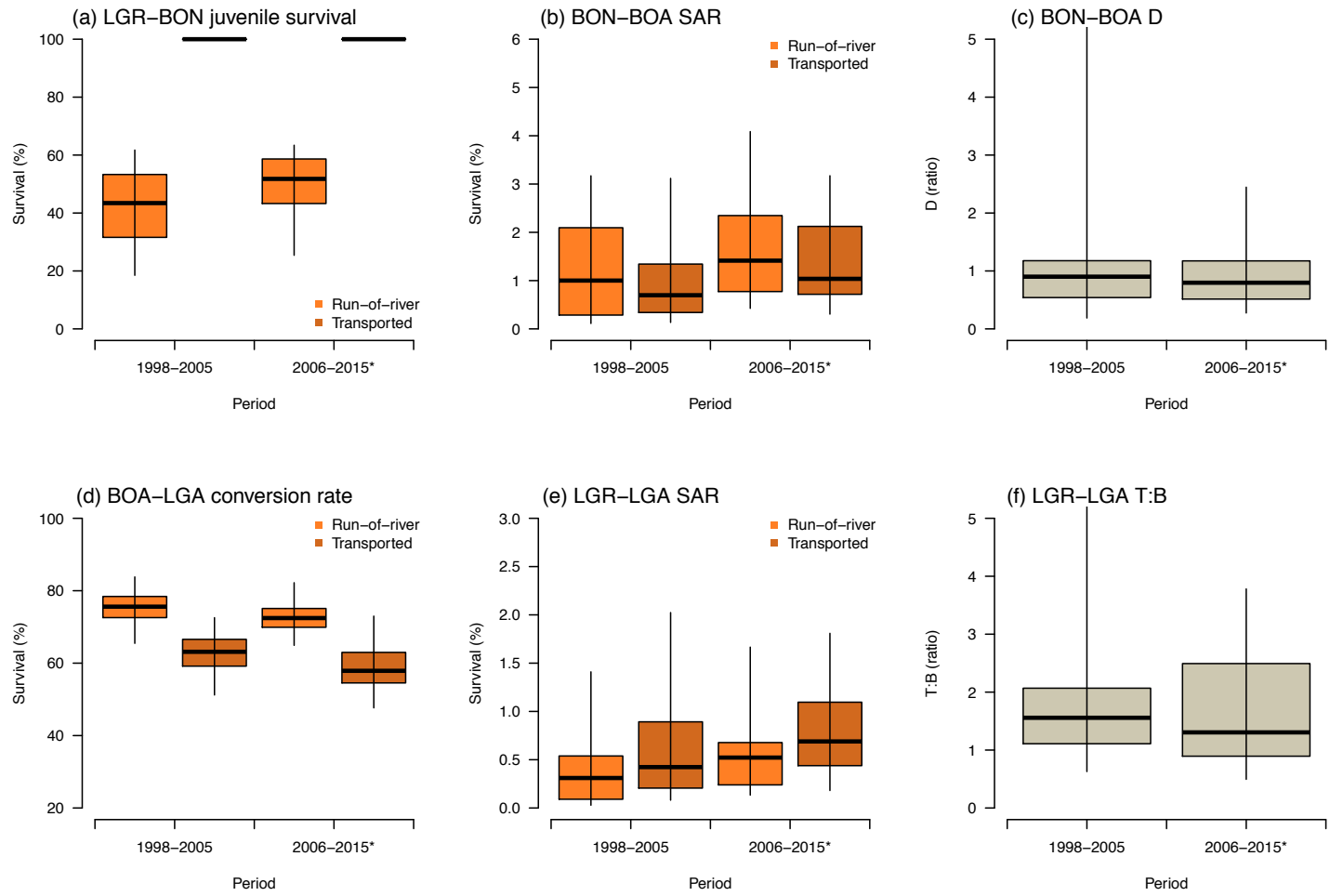


Figure 21. As Figure 1, with hatchery, run-of-river and transported Snake River fall Chinook salmon.

Hatchery run-of-river Snake River Fall subyearling Chinook salmon

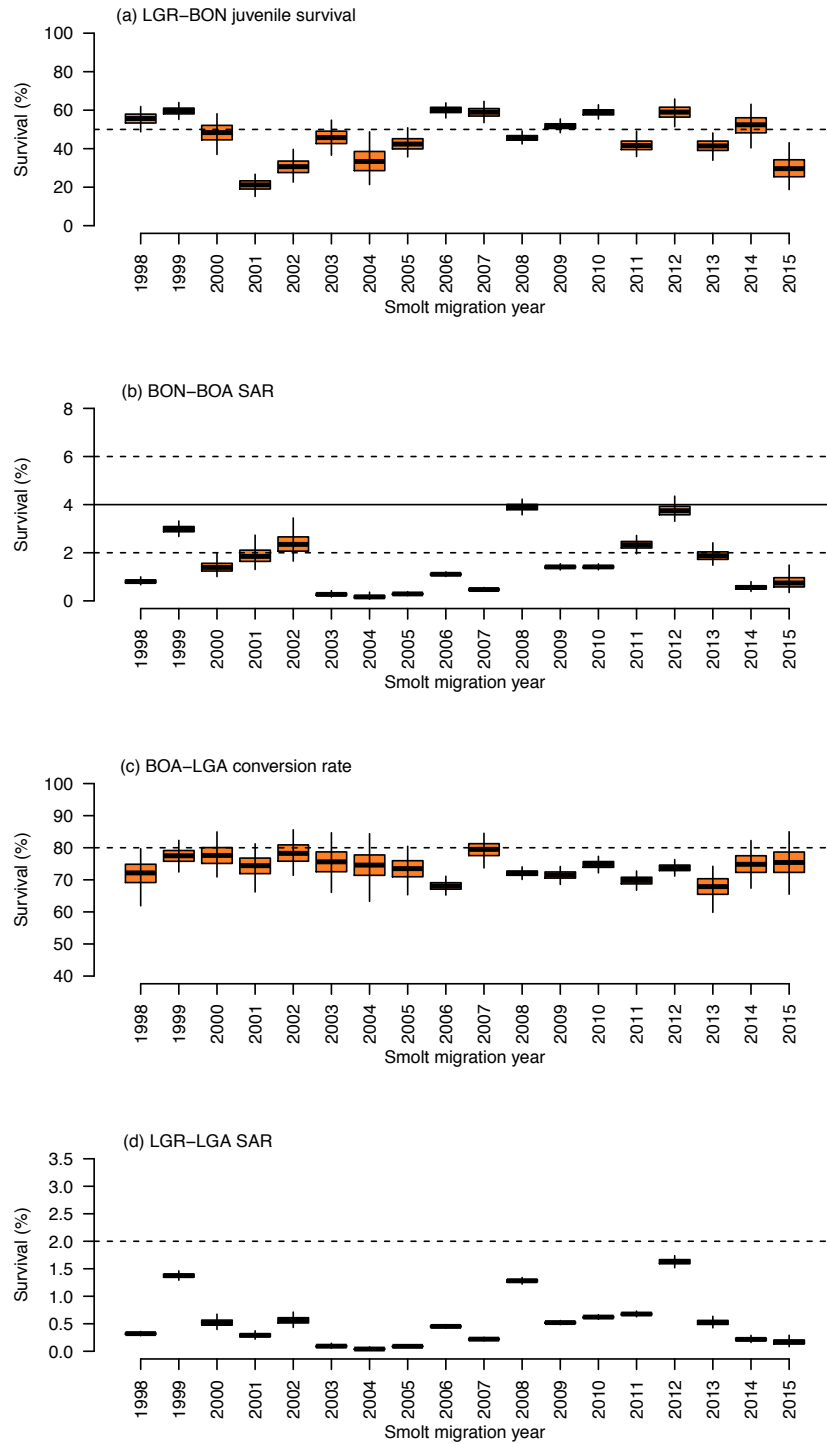


Figure 22. As Figure 2, with hatchery, run-of-river, Snake River fall Chinook salmon.

Hatchery transported Snake River Fall subyearling Chinook salmon

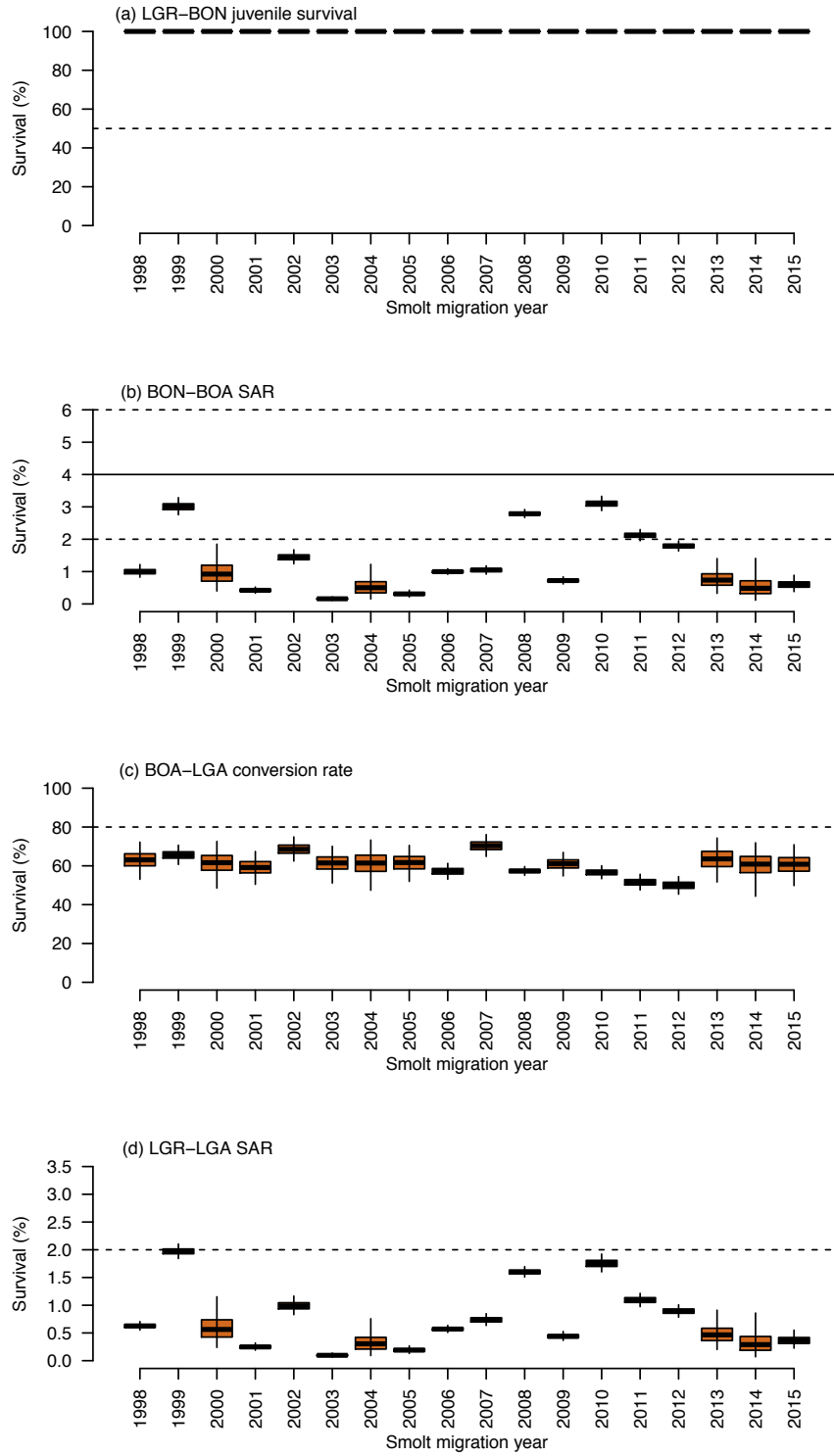


Figure 23. As Figure 2, with hatchery, transported, Snake River fall Chinook salmon.

Hatchery Snake River Fall subyearling Chinook salmon

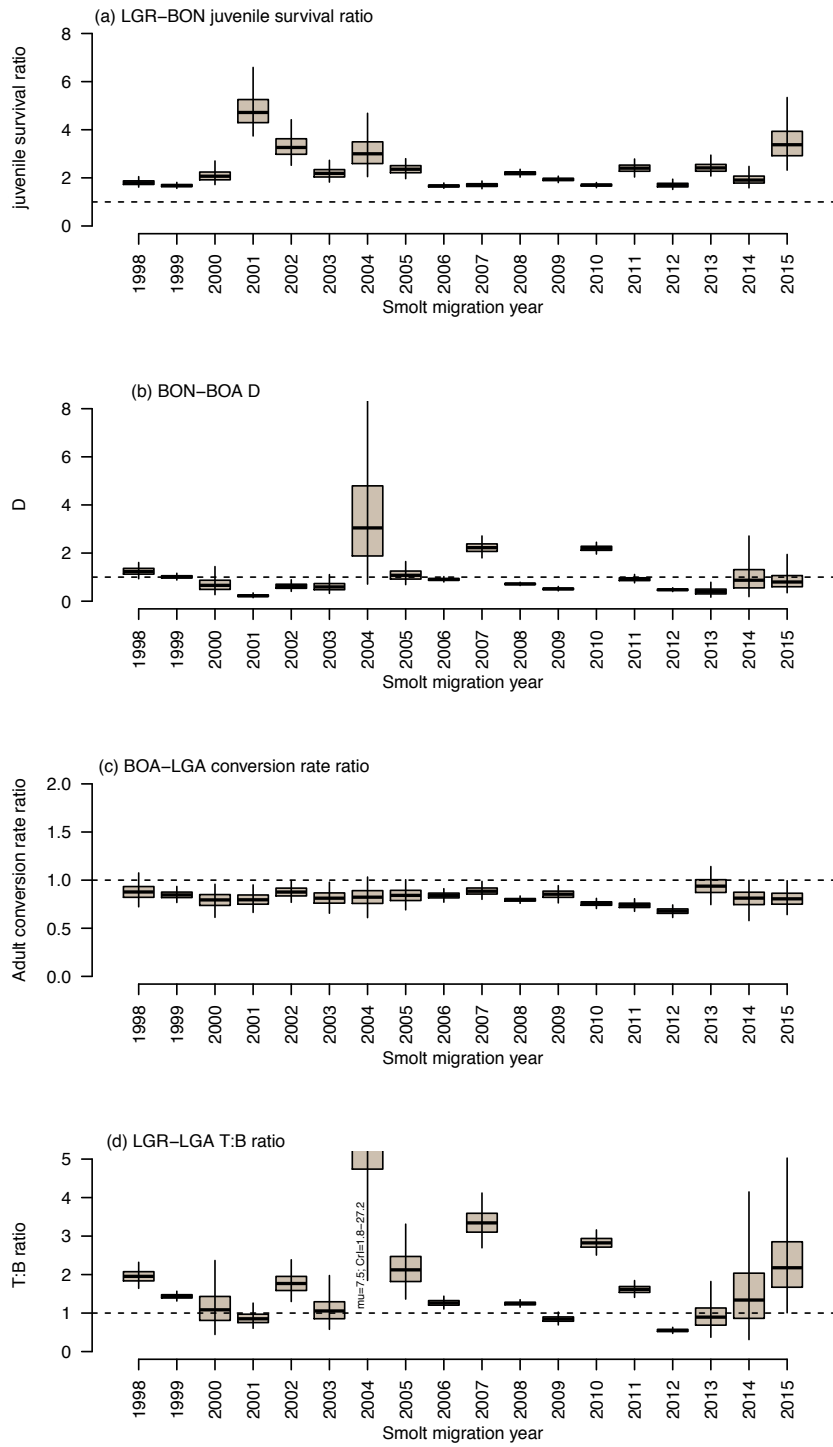


Figure 24. As Figure 4, with hatchery Snake River fall Chinook salmon.

Wild Snake River Sockeye salmon

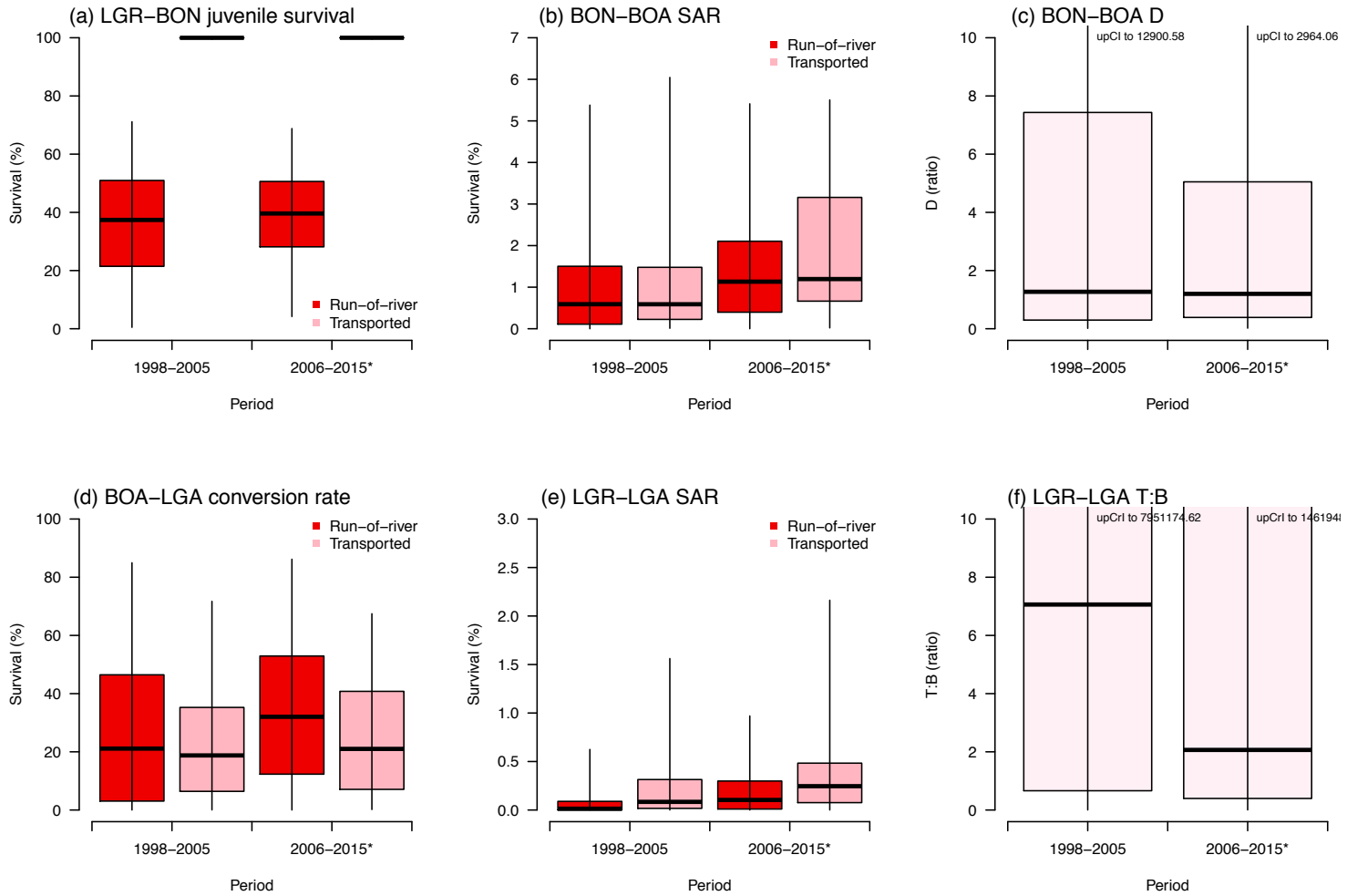


Figure 25. As Figure 1, with wild, run-of-river and transported Snake River sockeye salmon.

Wild run-of-river Snake River Sockeye salmon

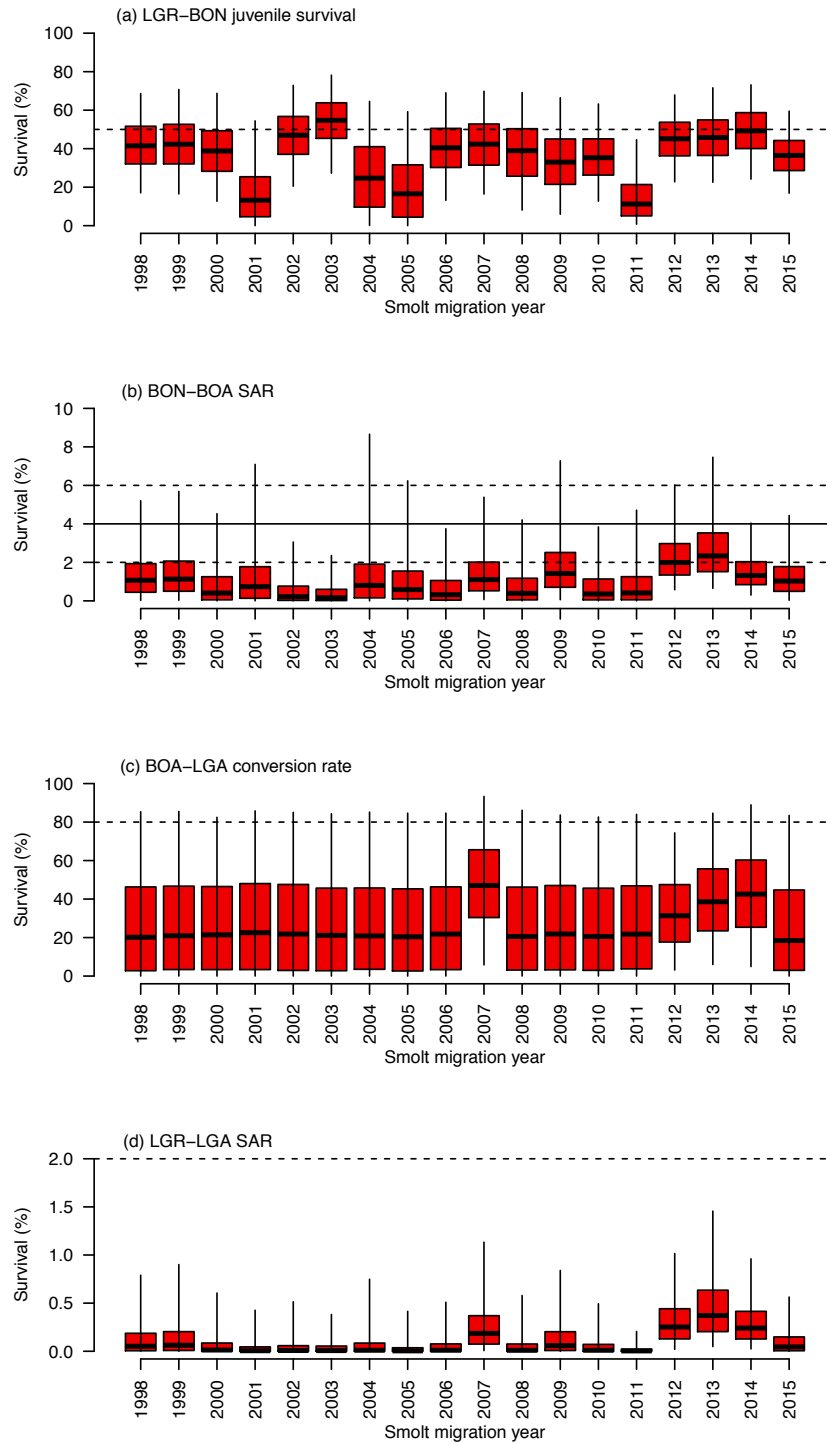


Figure 26. As Figure 2, with wild, run-of-river, Snake River sockeye salmon.

Wild transported Snake River Sockeye salmon

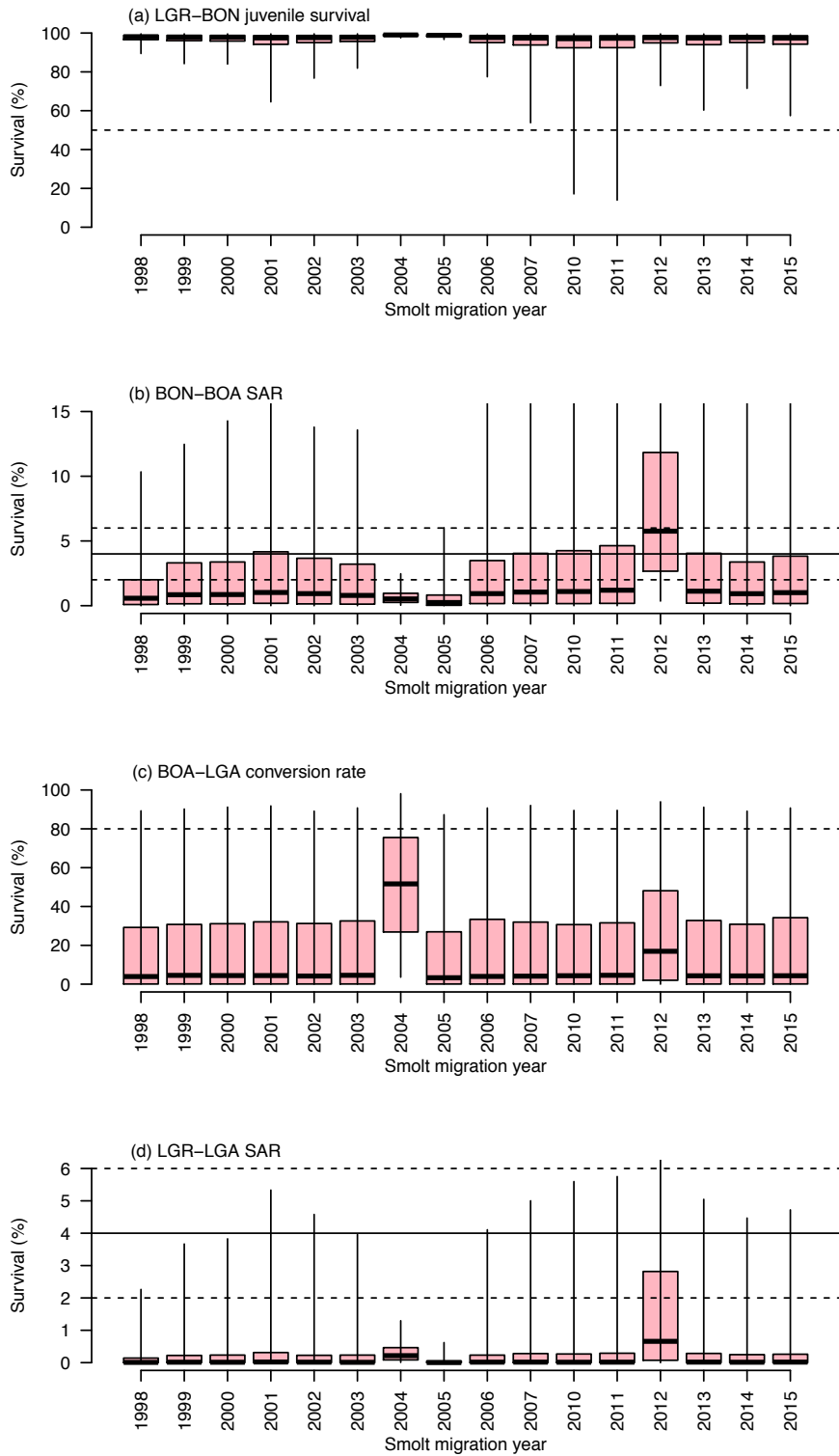


Figure 27. As Figure 2, with wild, transported, Snake River sockeye salmon.

Wild Snake River Sockeye salmon

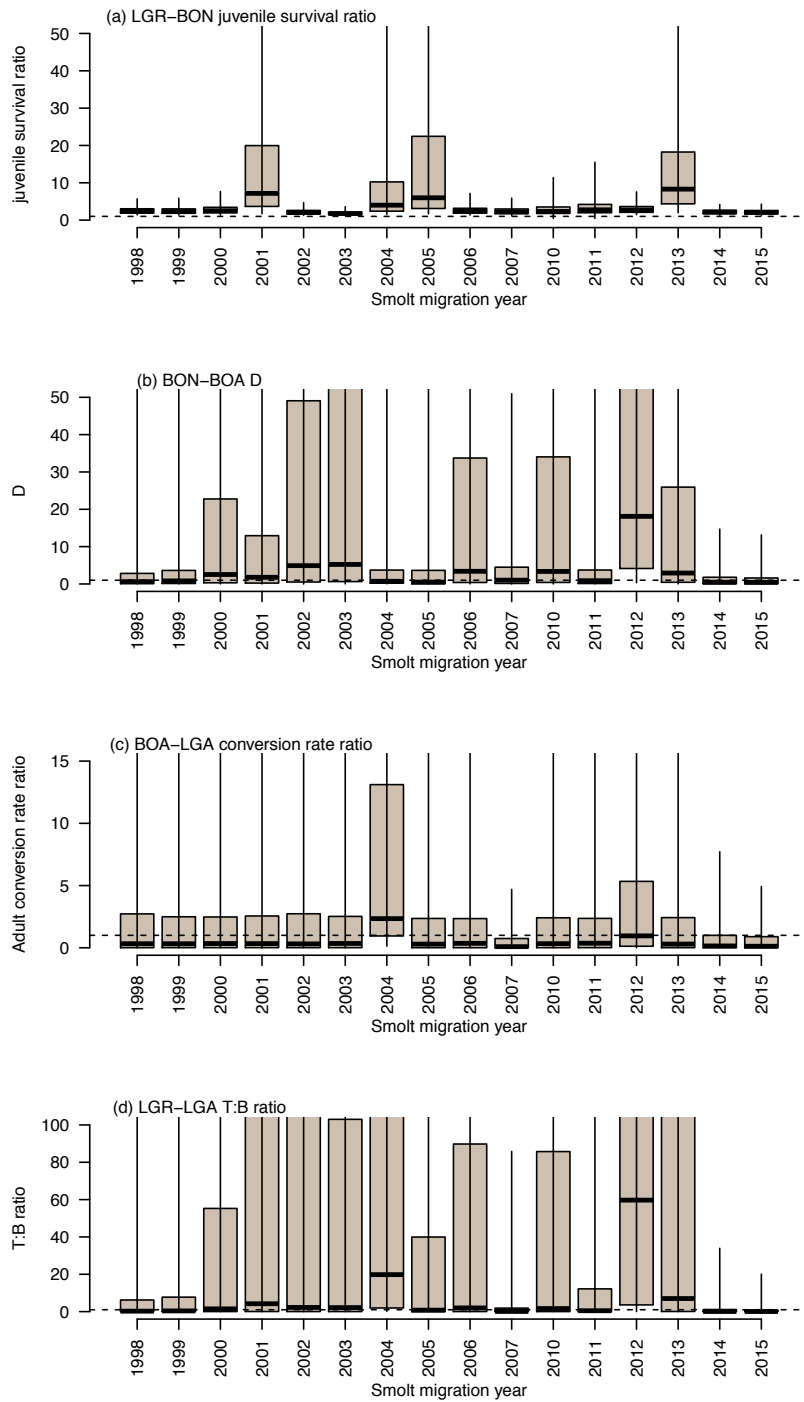


Figure 28. As Figure 4, with wild Snake River sockeye salmon.

Hatchery Snake River Sockeye salmon

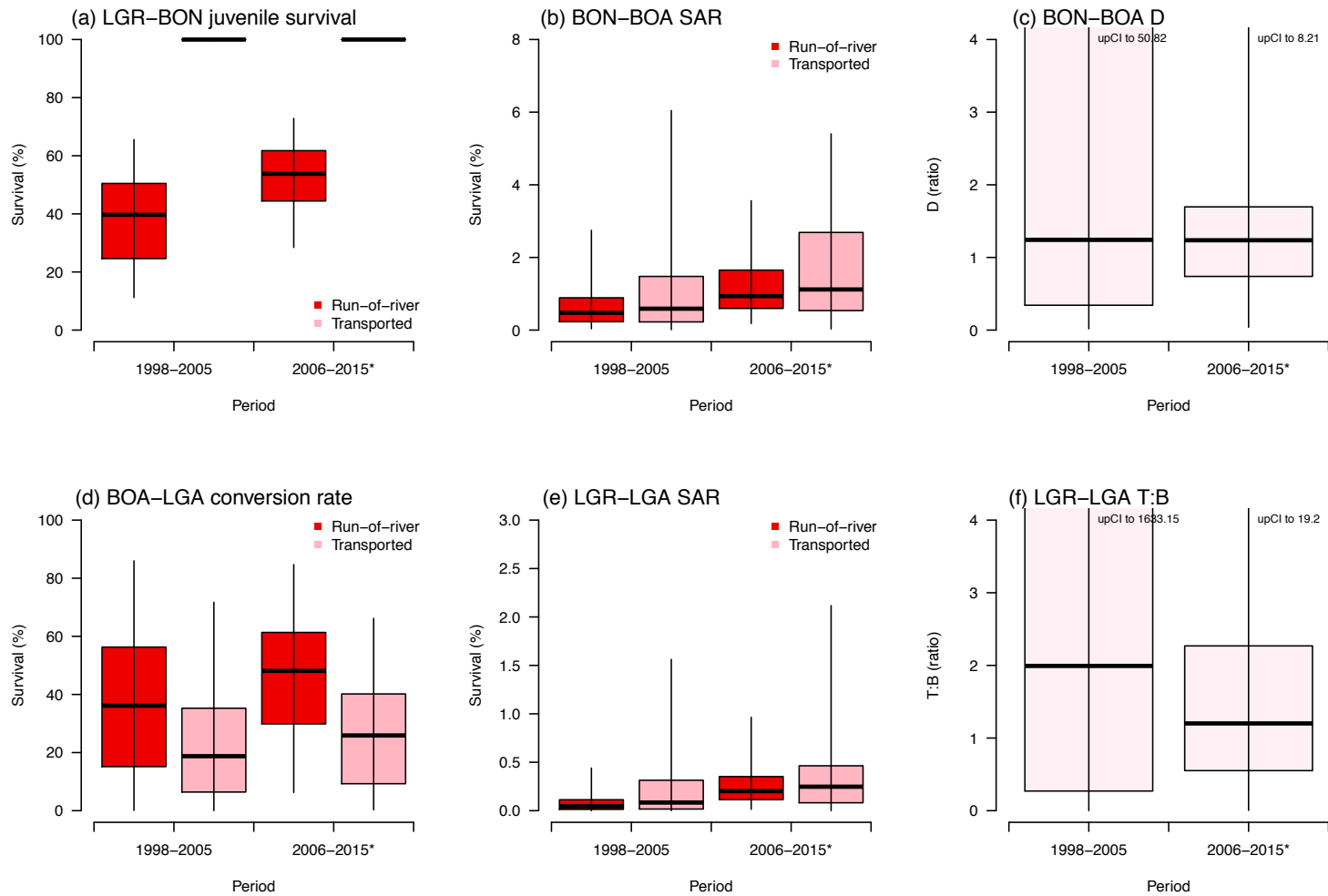


Figure 29. As Figure 1, with hatchery, run-of-river and transported Snake River sockeye salmon.

Hatchery run-of-river Snake River Sockeye salmon

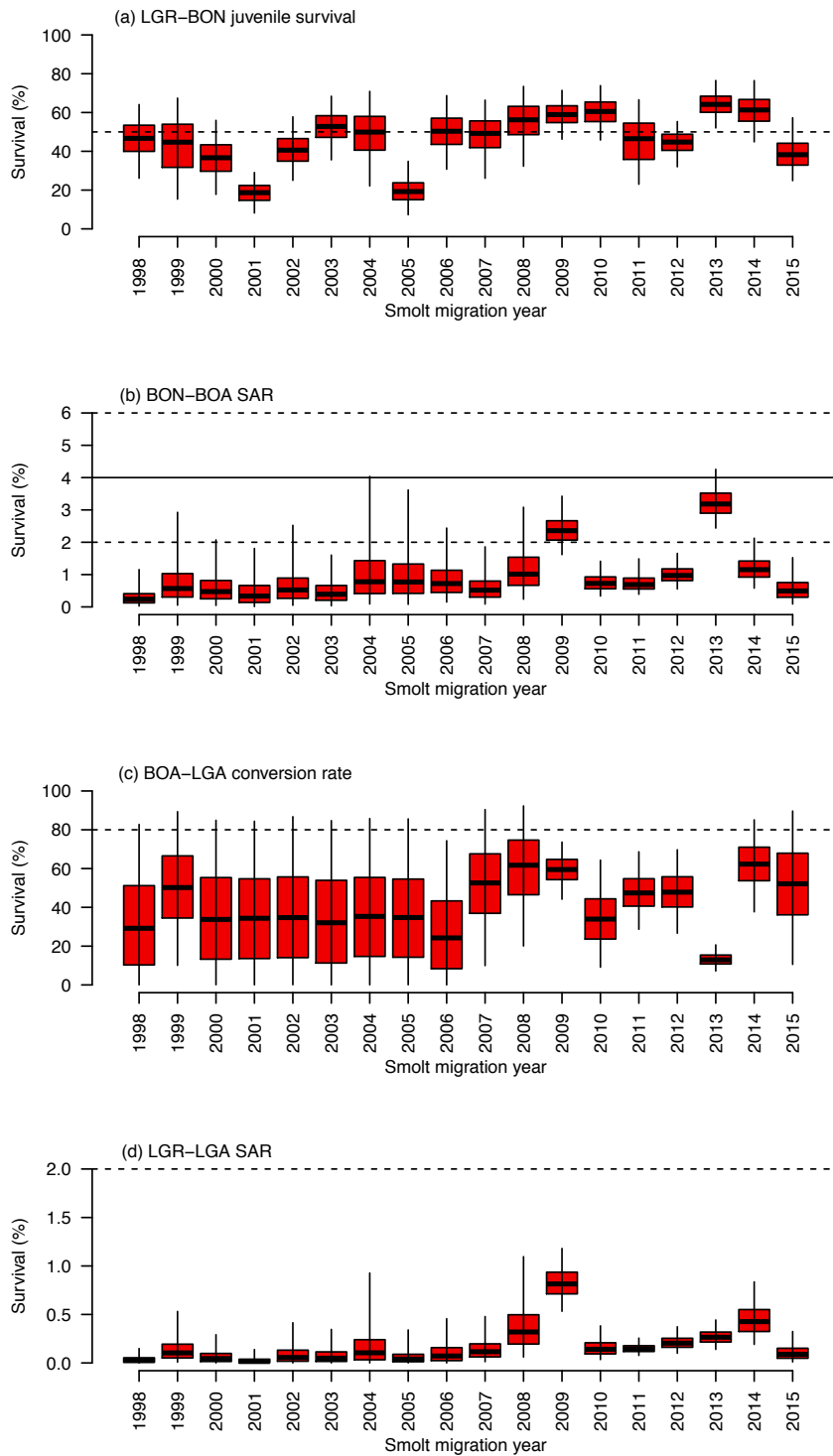


Figure 30. As Figure 2, with hatchery, run-of-river, Snake River sockeye salmon.

Hatchery transported Snake River Sockeye salmon

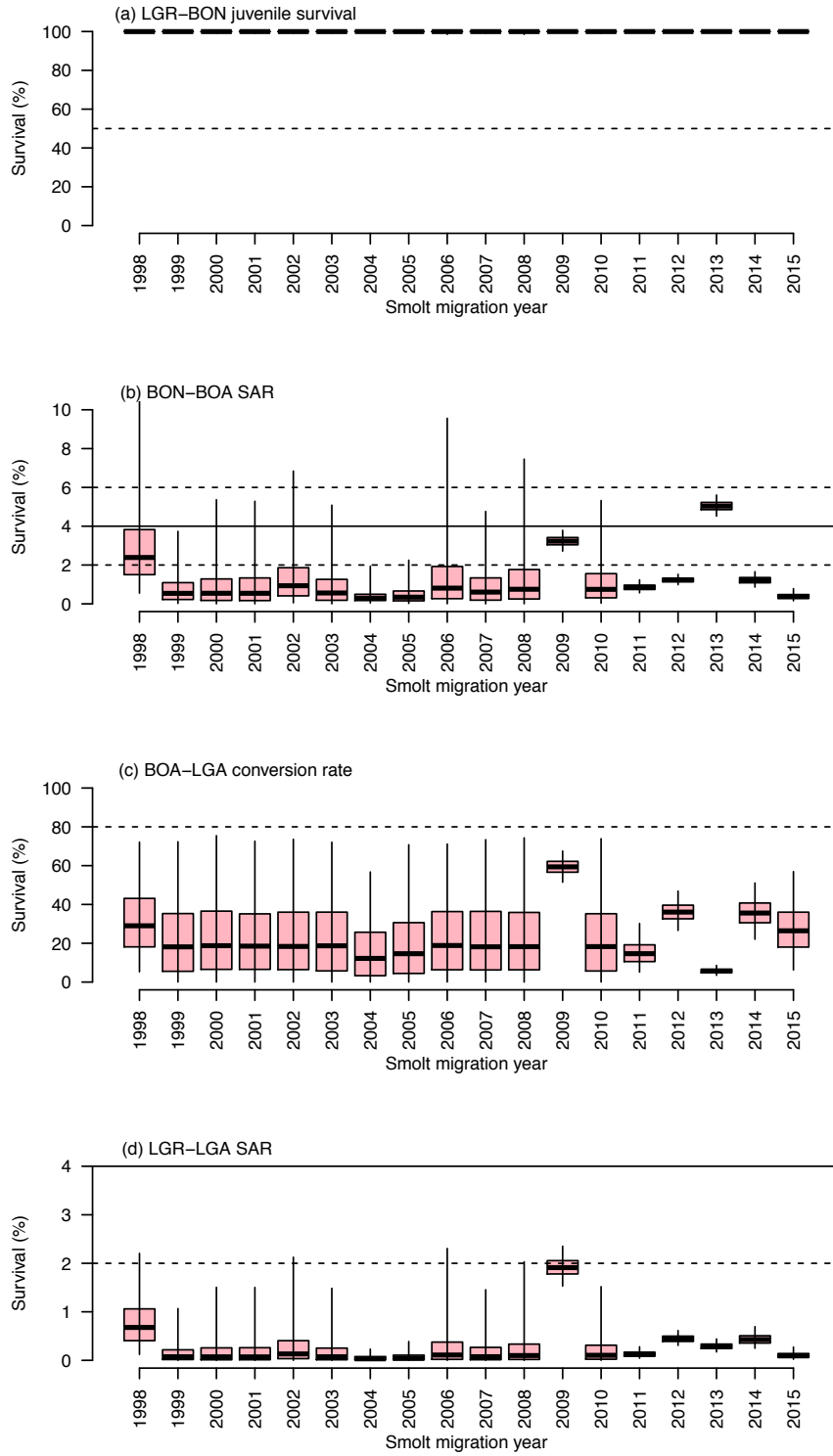


Figure 31. As Figure 2, with hatchery, transported, Snake River sockeye salmon.

Hatchery Snake River Sockeye salmon

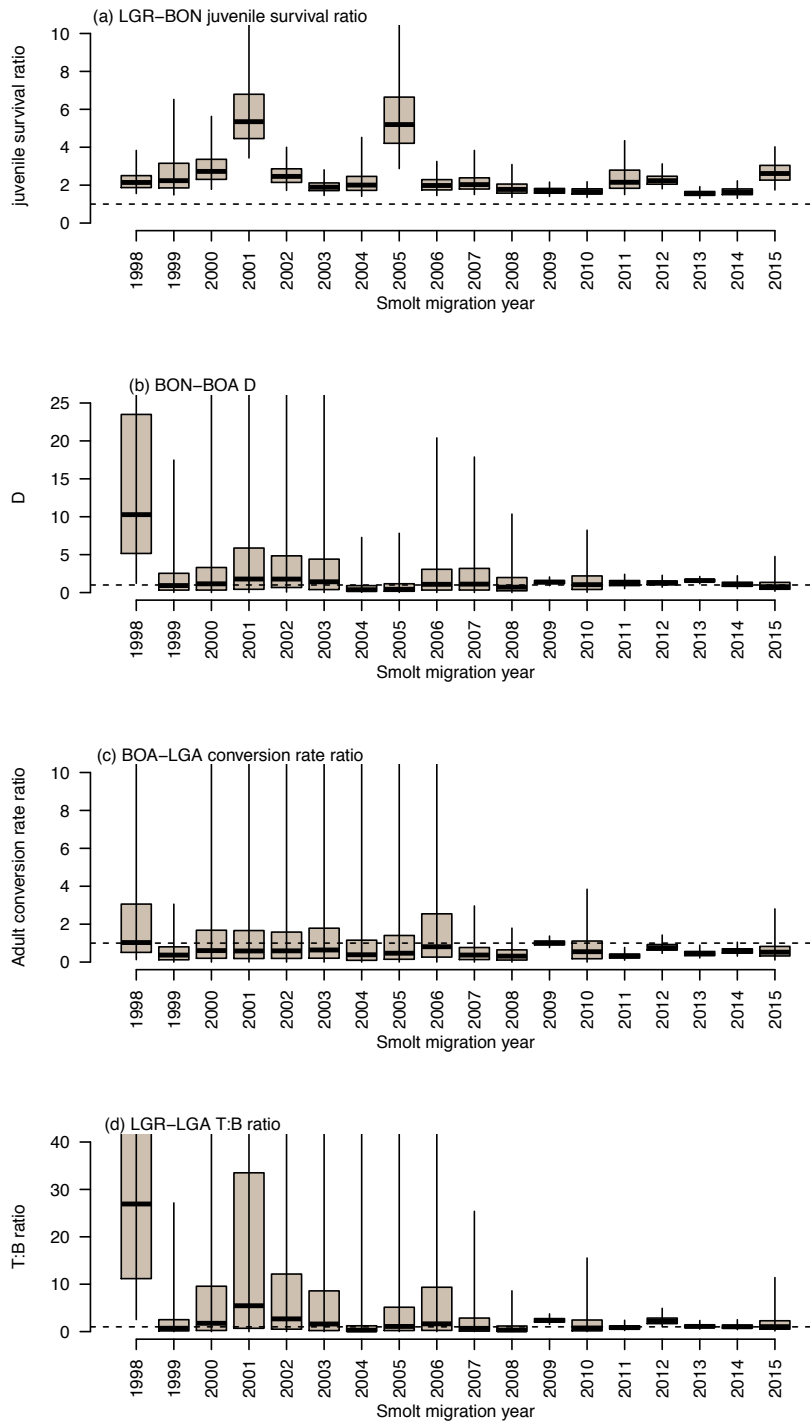


Figure 32. As Figure 4, with hatchery Snake River sockeye salmon.

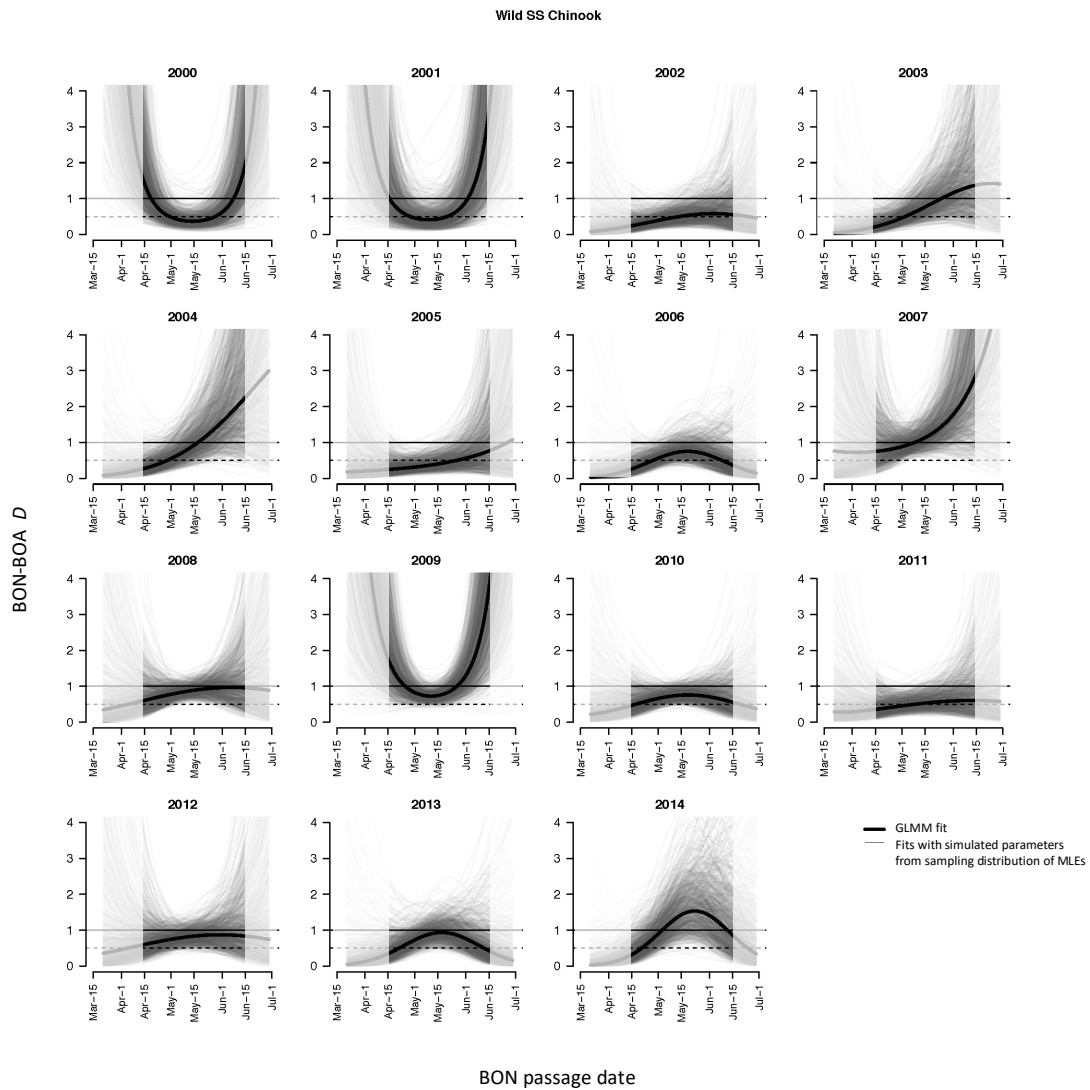


Figure 33. Wild spring/summer Chinook D by BON passage date. Thick black lines represent year-specific generalized linear mixed effect model (GLMM) fits with parameter estimates by maximum likelihood. The thin gray lines represent fits with simulated parameters from sampling distribution of maximum likelihood estimates. Transparent panels help to visually focus on patterns within the migration season, while providing information on uncertainty at earlier and later dates. See Figure 34 for associated SARs and relative sample sizes.

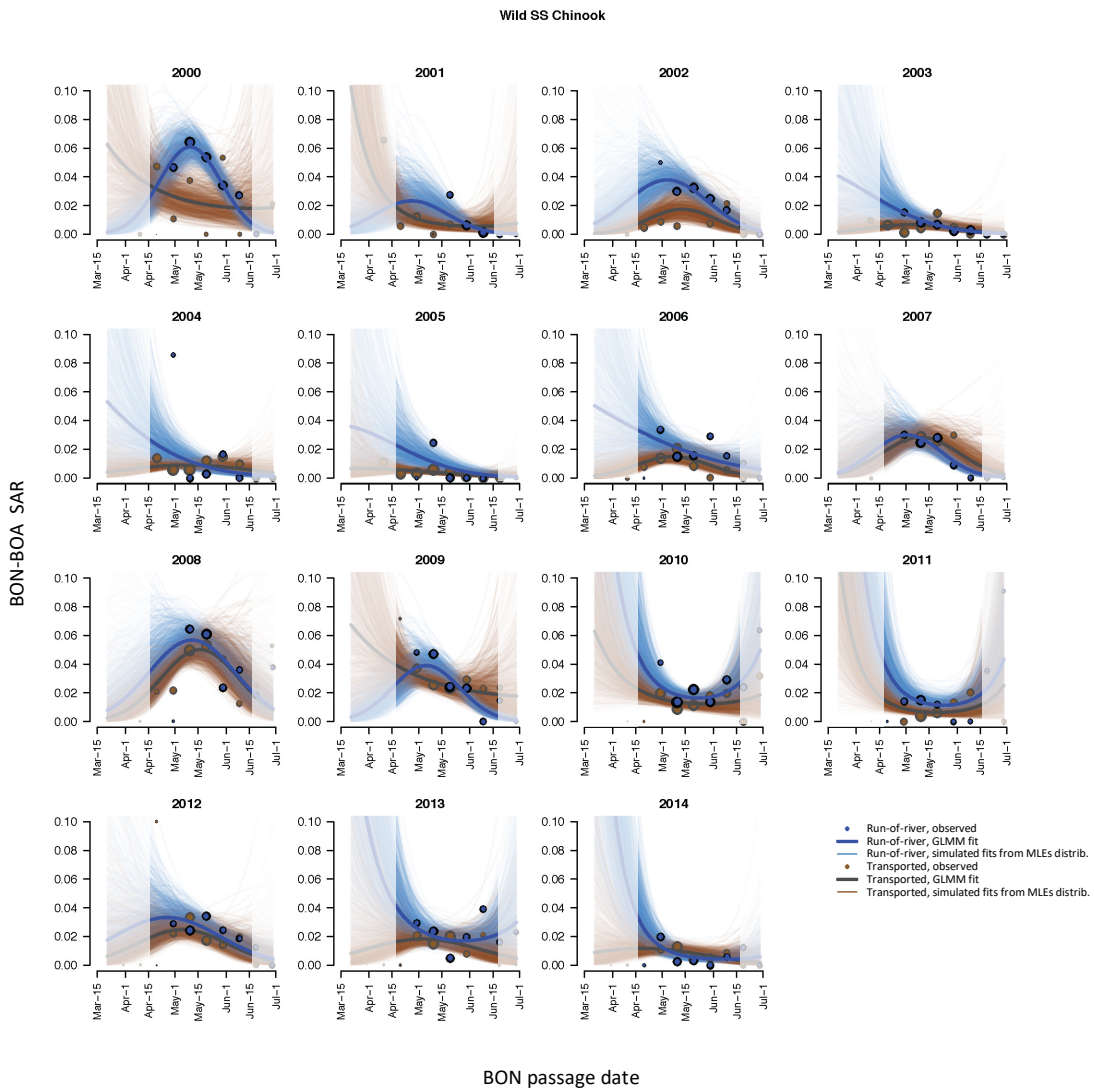


Figure 34. Wild spring/summer Chinook BON-BOA SAR by BON passage date. Thick lines represent year-specific generalized linear mixed effect model (GLMM) fits with parameter estimates by maximum likelihood. The thin lines represent fits with simulated parameters from sampling distribution of maximum likelihood estimates. Size of points reflect relative sample sizes in 10-day bins. Transparent panels help to visually focus on patterns within the migration season, while providing information on uncertainty at earlier and later dates.

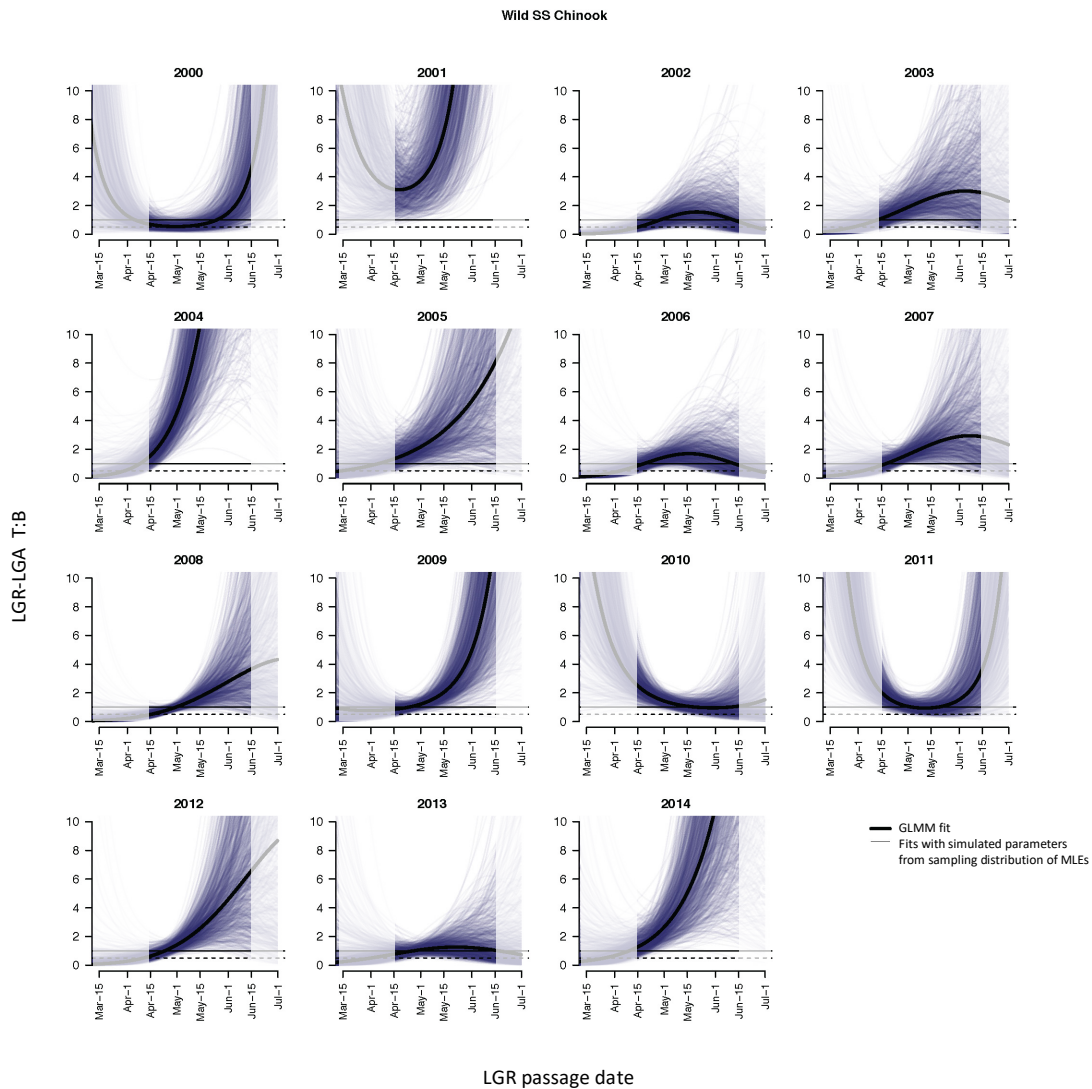


Figure 35. Wild spring/summer Chinook T:B by LGR passage date. Thick black lines represent year-specific generalized linear mixed effect model (GLMM) fits with parameter estimates by maximum likelihood. The thin navy lines represent fits with simulated parameters from sampling distribution of maximum likelihood estimates. Transparent panels help to visually focus on patterns within the migration season, while providing information on uncertainty at earlier and later dates. See Figure 36 for associated SARs and relative sample sizes.

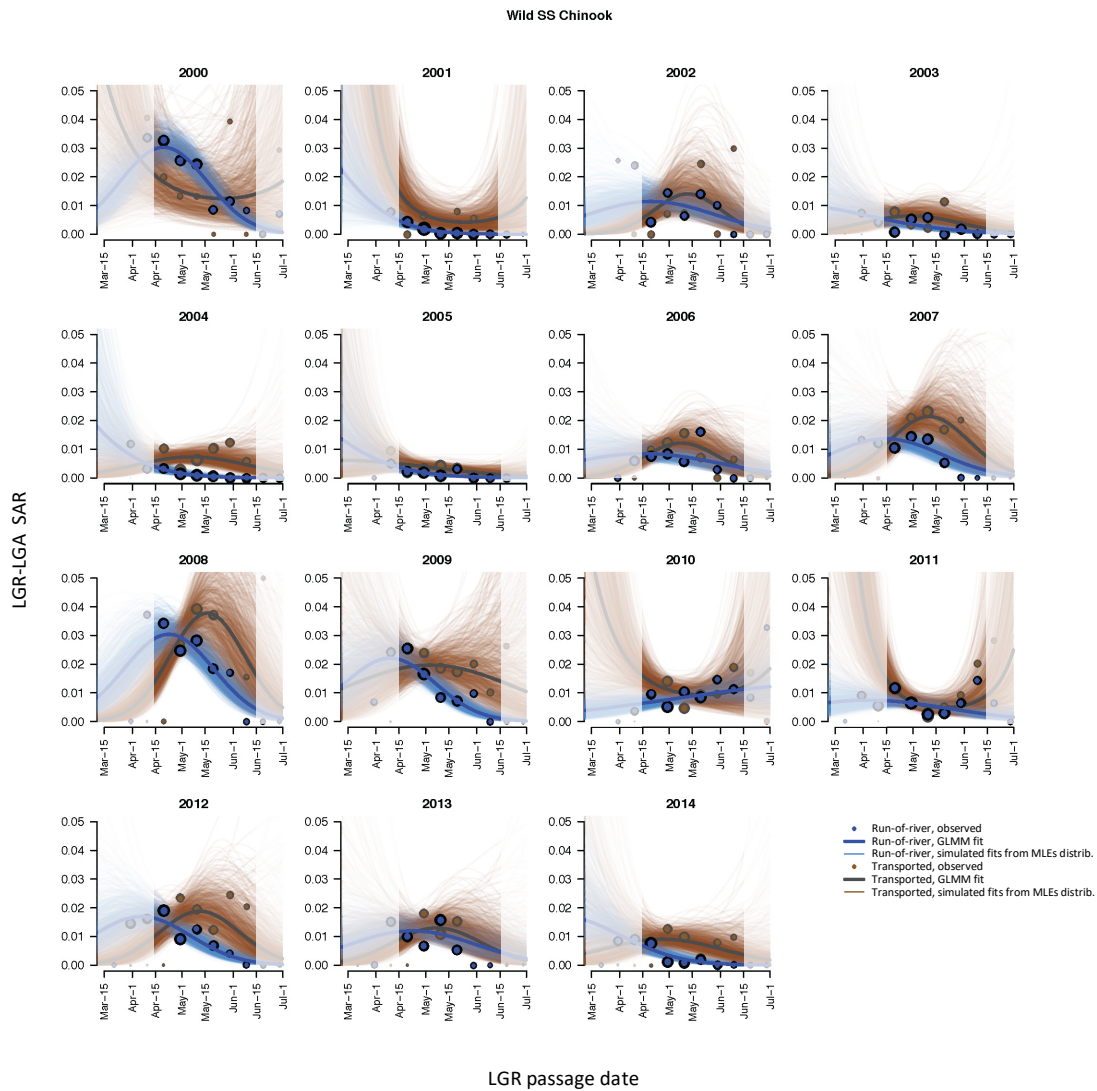


Figure 36. Wild spring/summer Chinook LGR-LGA SAR by LGR passage date. Thick lines represent year-specific generalized linear mixed effect model (GLMM) fits with parameter estimates by maximum likelihood. The thin lines represent fits with simulated parameters from sampling distribution of maximum likelihood estimates. Size of points reflect relative sample sizes in 10-day bins. Transparent panels help to visually focus on patterns within the migration season, while providing information on uncertainty at earlier and later dates.

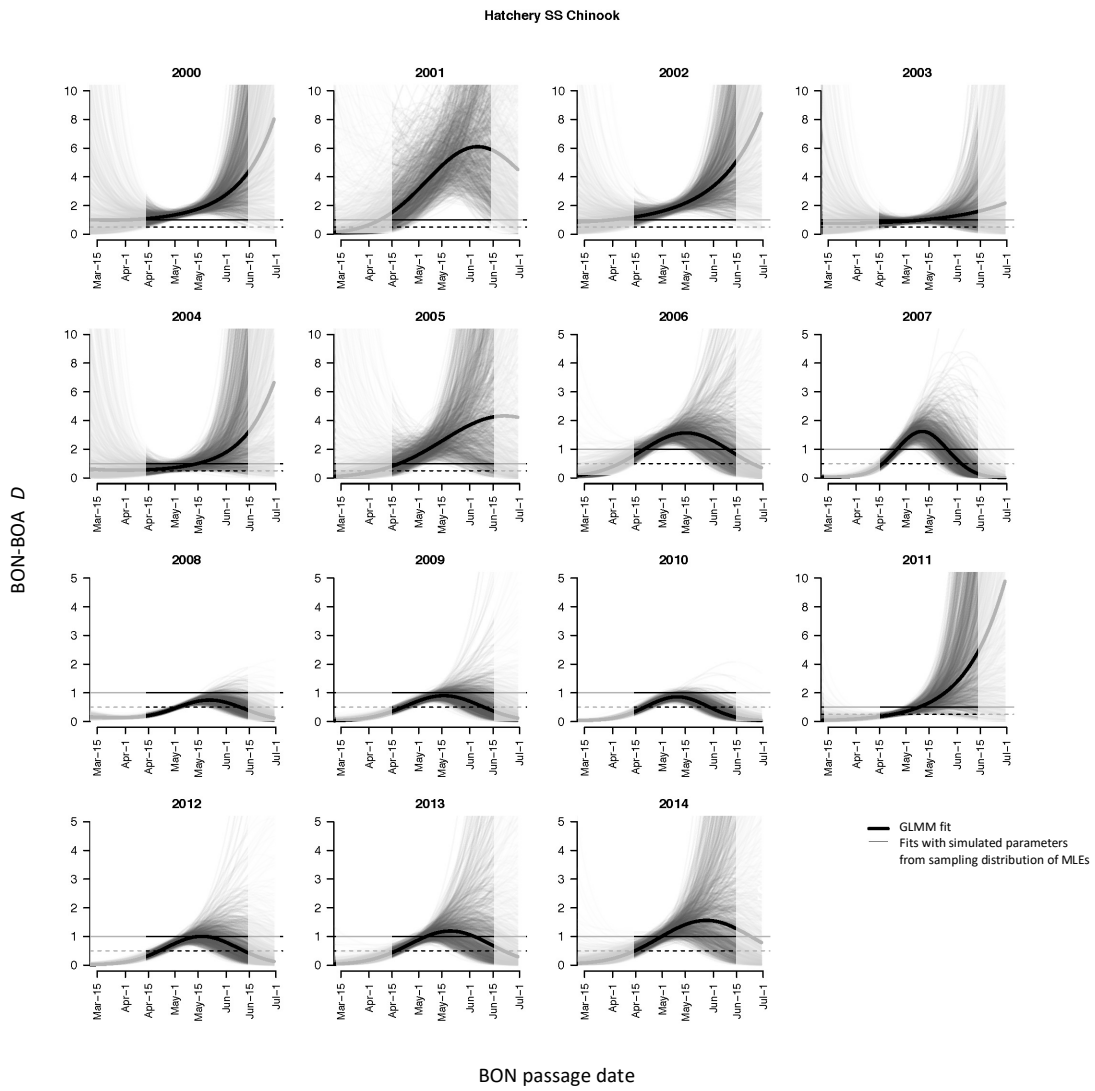


Figure 37. As Figure 33, except for hatchery spring/summer Chinook D and associated SARs in Figure 38.

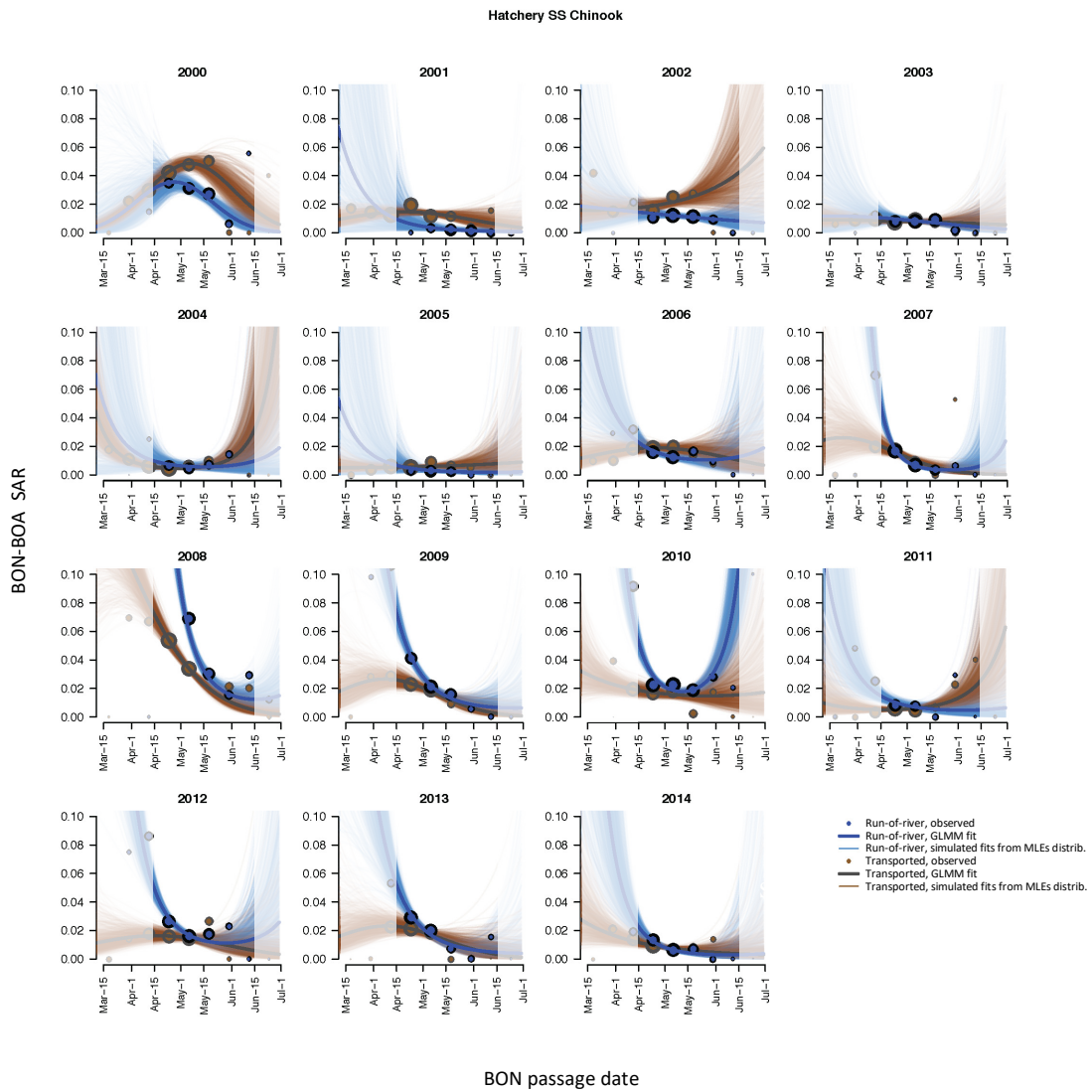


Figure 38. As Figure 34, except for hatchery spring/summer Chinook BON-BOA SAR.

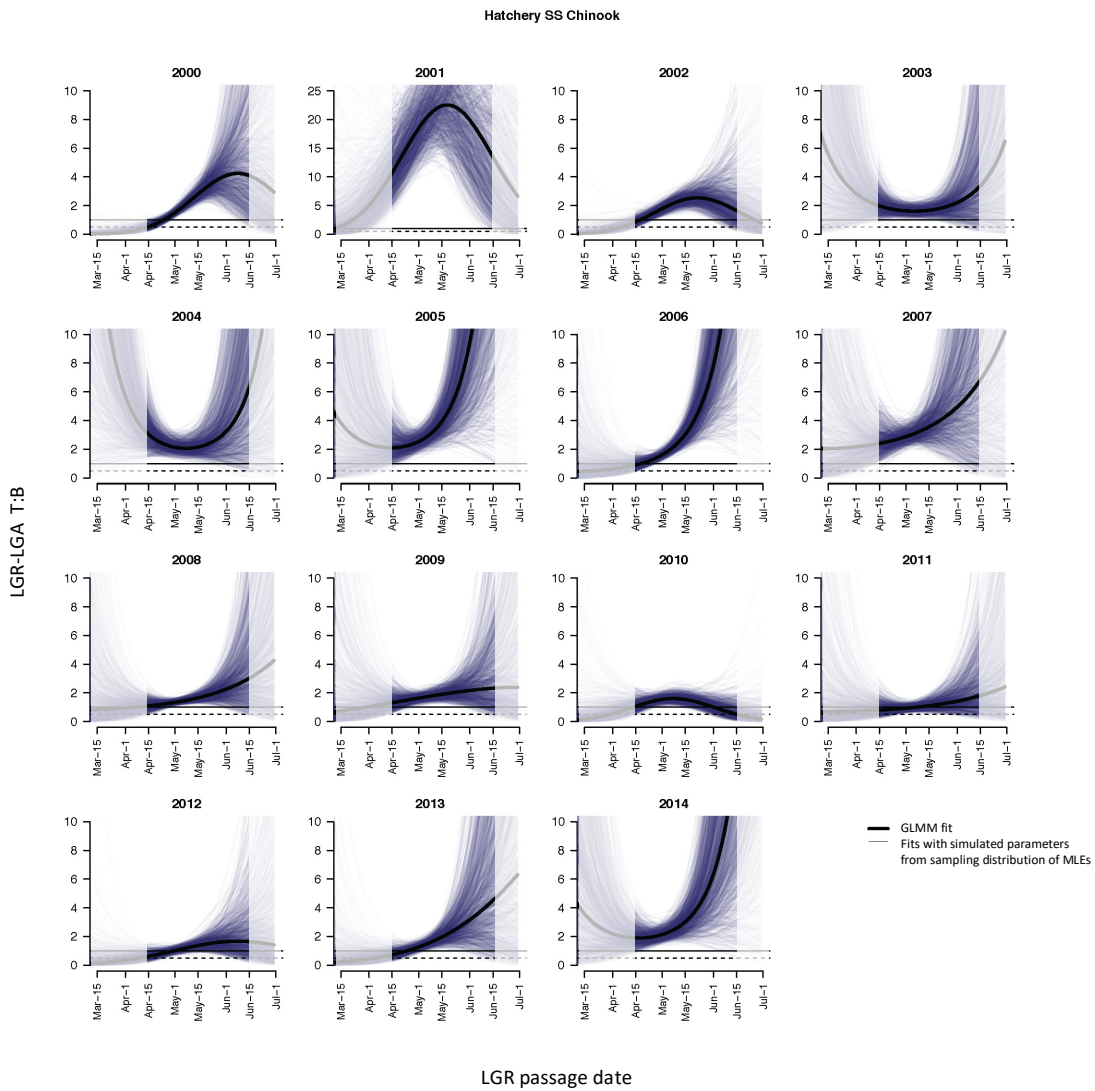


Figure 39. As Figure 35, except for hatchery spring/summer Chinook T:B, and associated SARs in Figure 40.

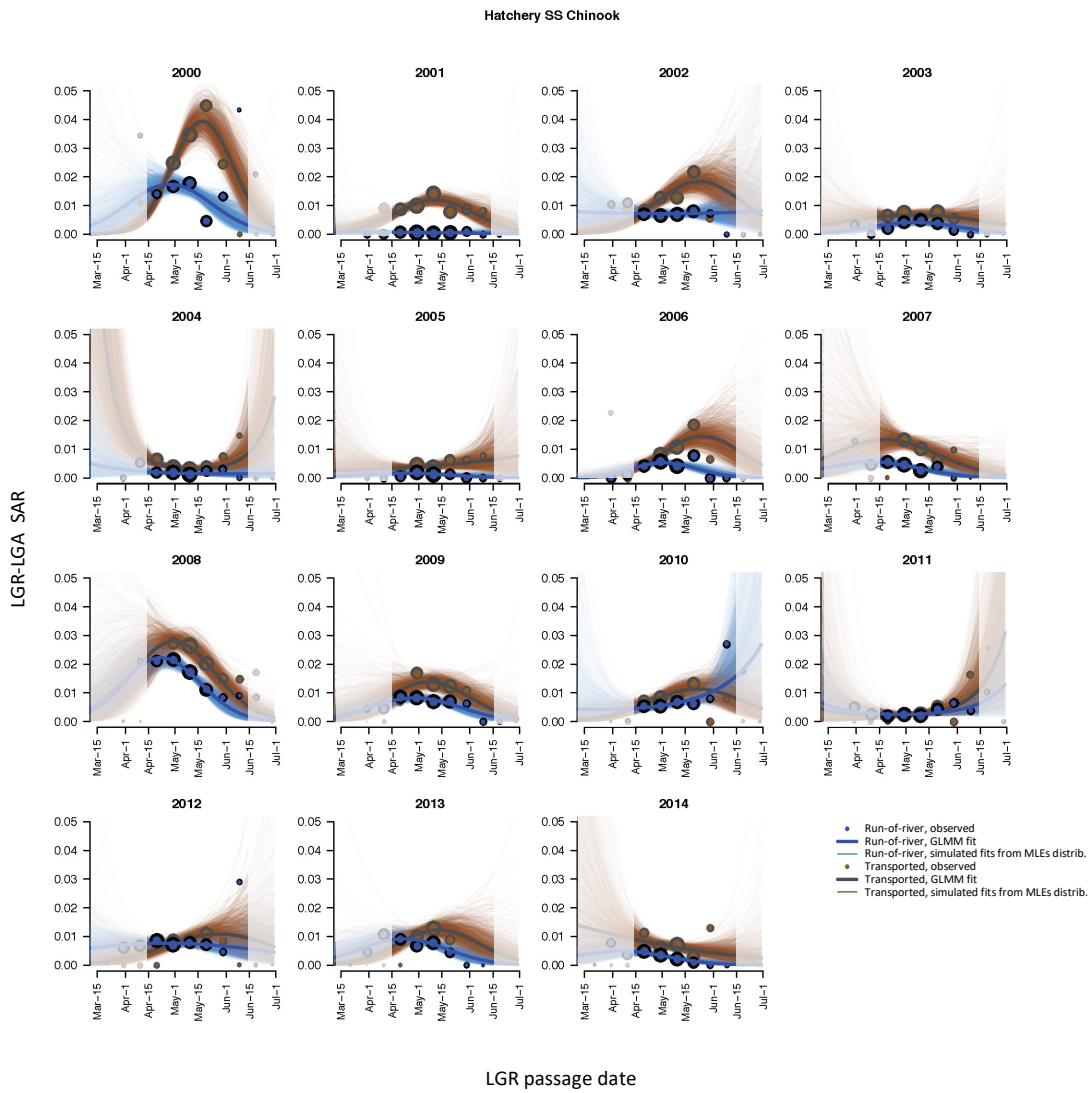


Figure 40. As Figure 36, except for hatchery spring/summer Chinook LGR-LGA SAR.

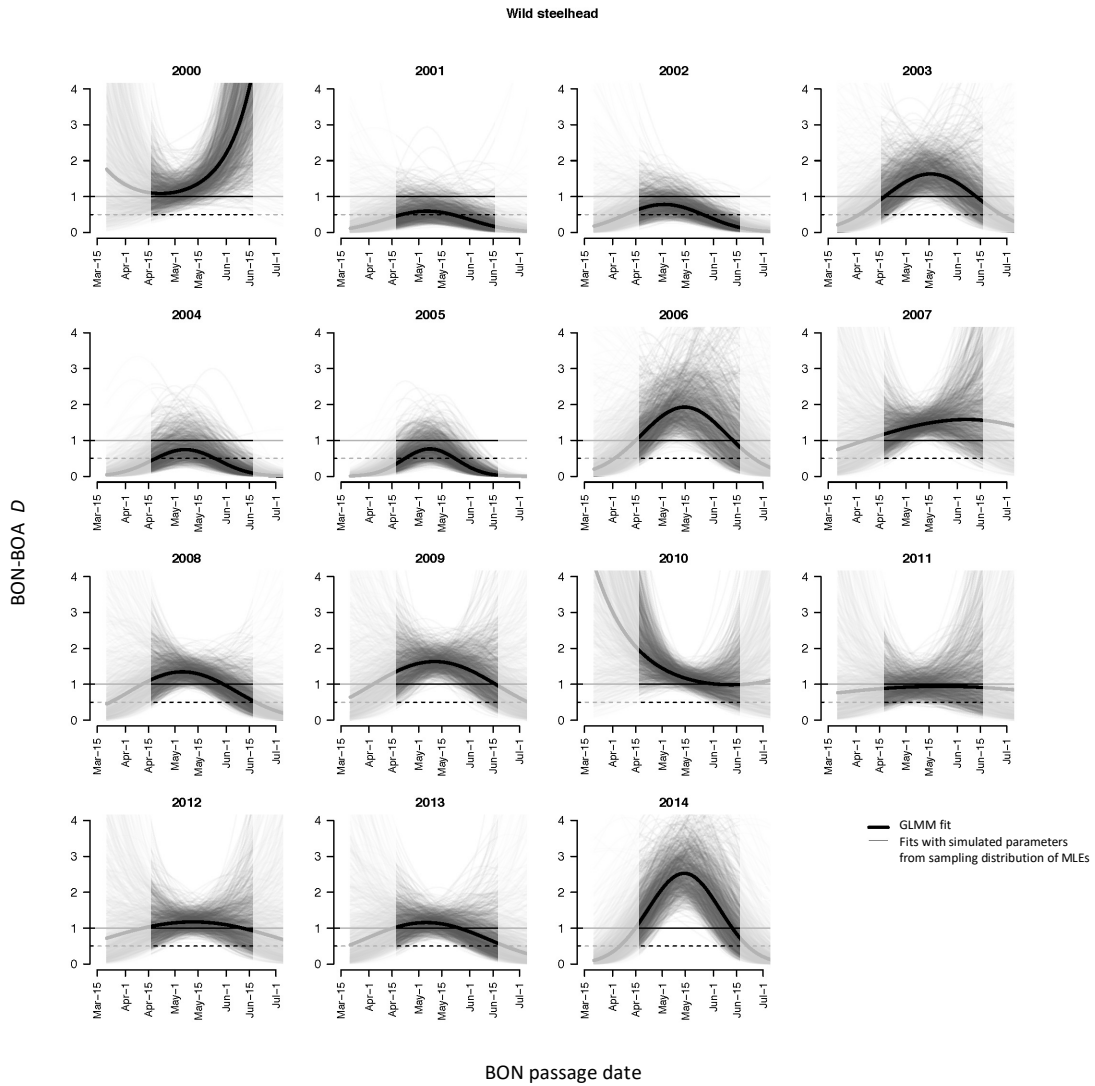


Figure 41. As Figure 33, except for wild steelhead D , and associated SARs in Figure 42.

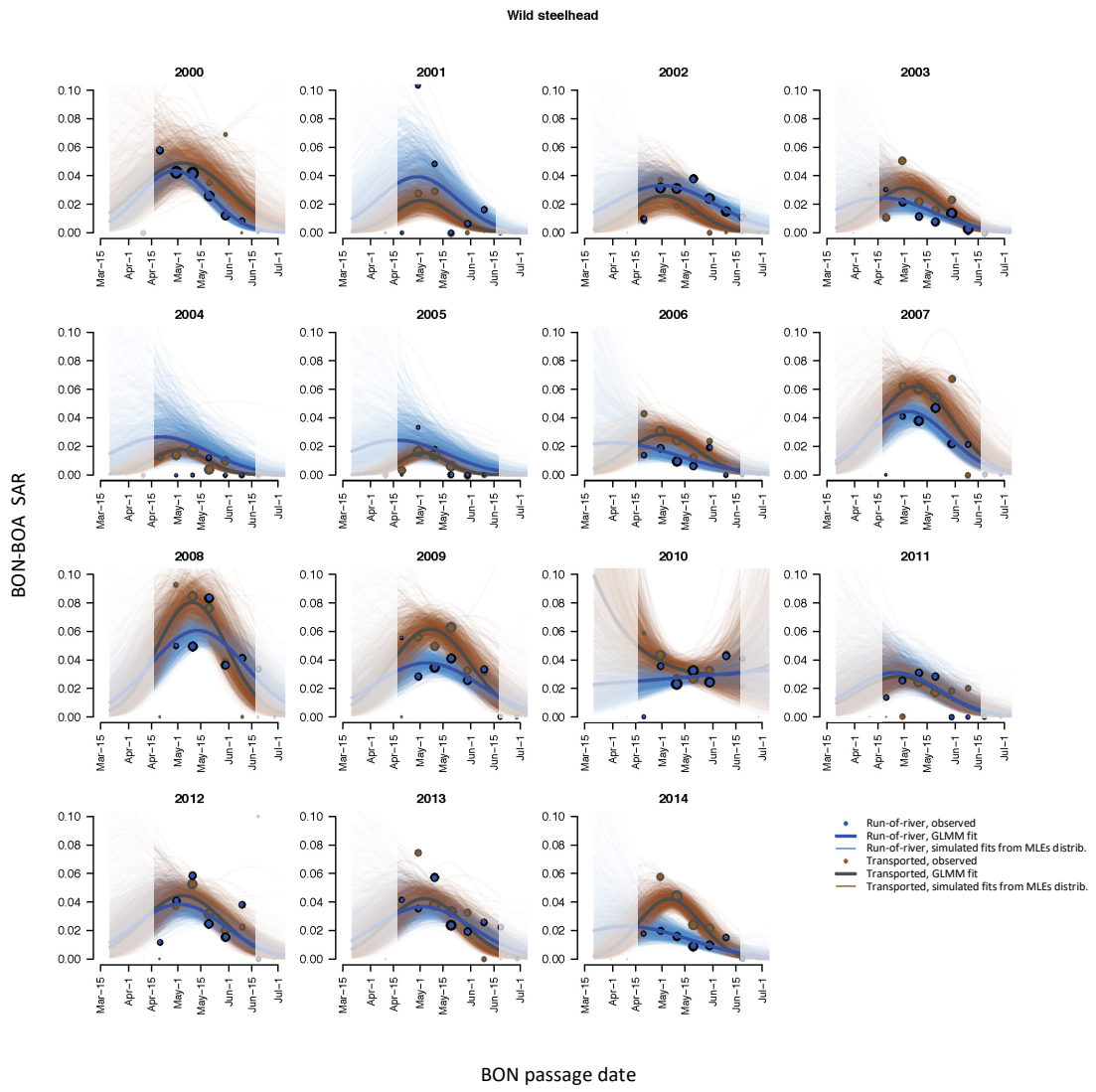


Figure 42. As Figure 34, except for wild steelhead BON-BOA SAR.

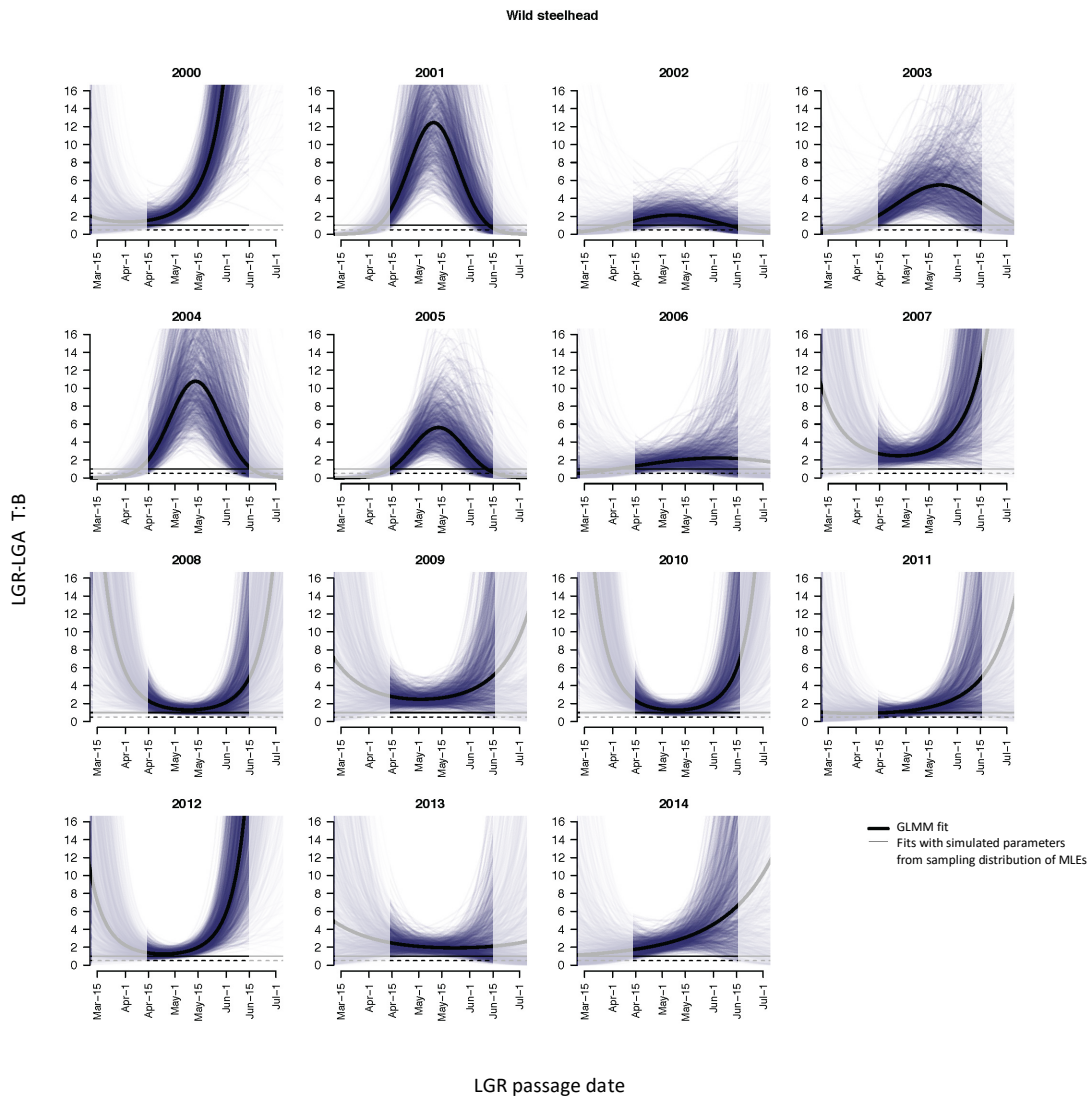


Figure 43. As Figure 35, except for wild steelhead T:B, and associated SARs in Figure 44.

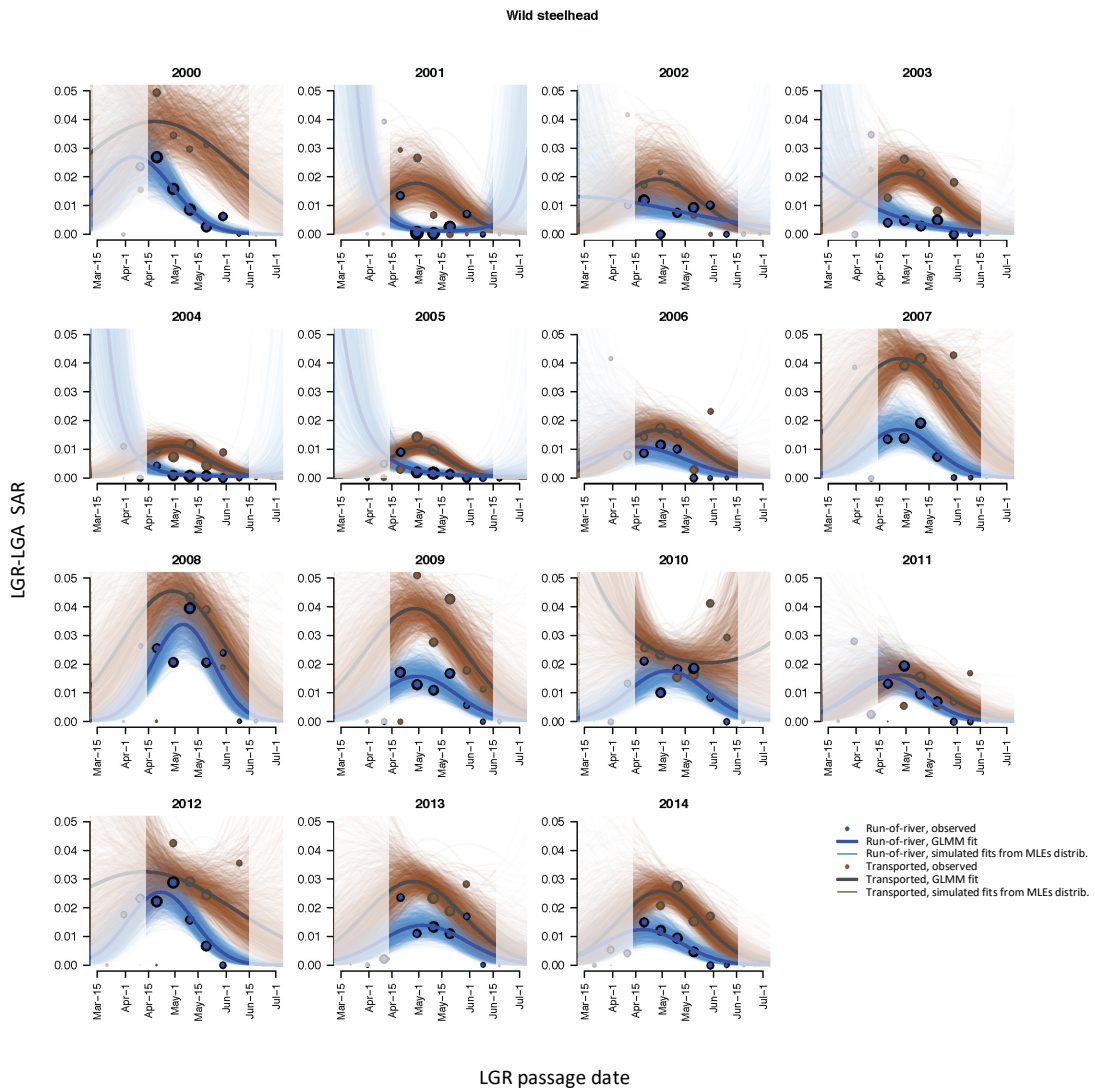


Figure 44. As Figure 36, except for wild steelhead LGR-LGA SAR.

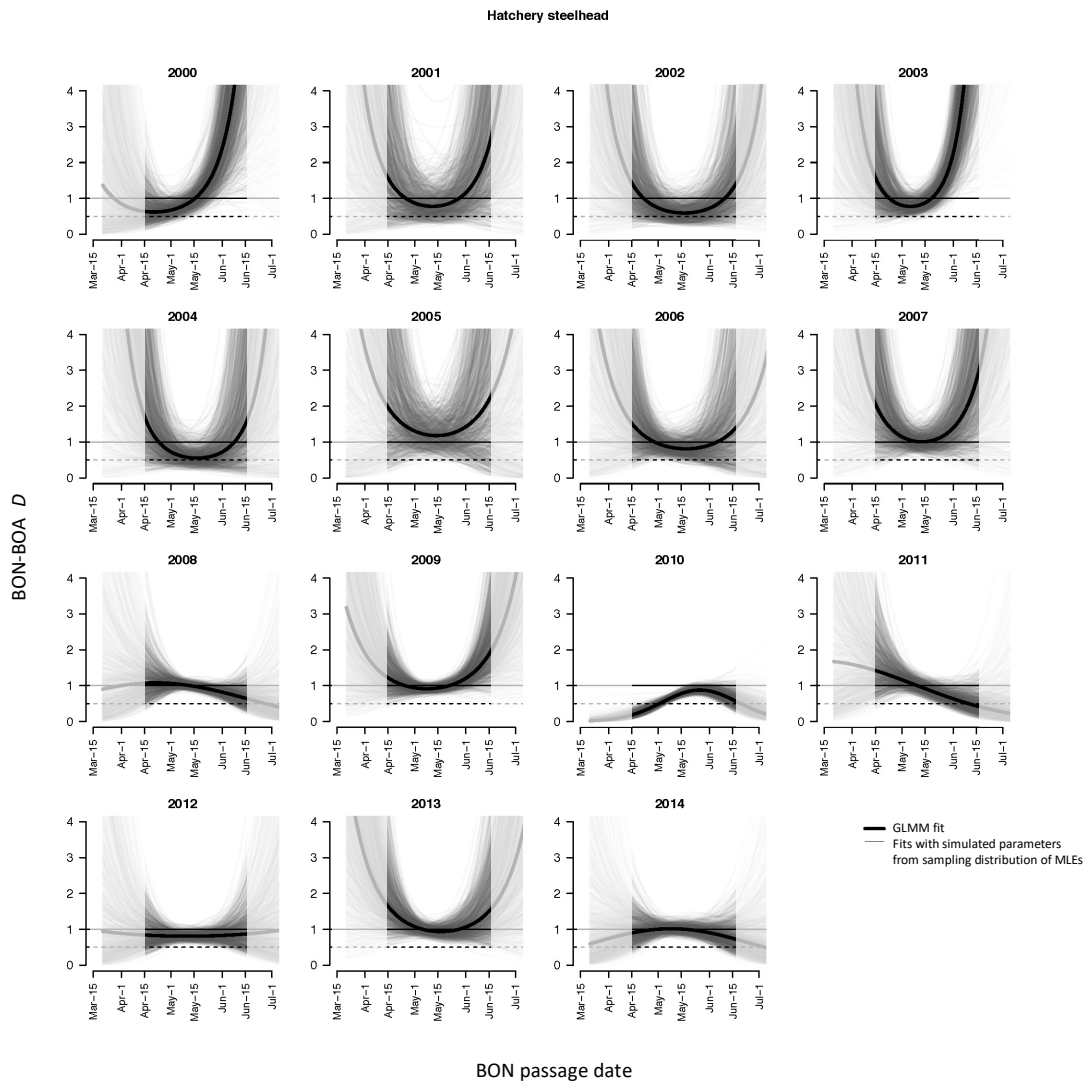


Figure 45. As Figure 33, except for hatchery steelhead D , and associated SARs in Figure 46.

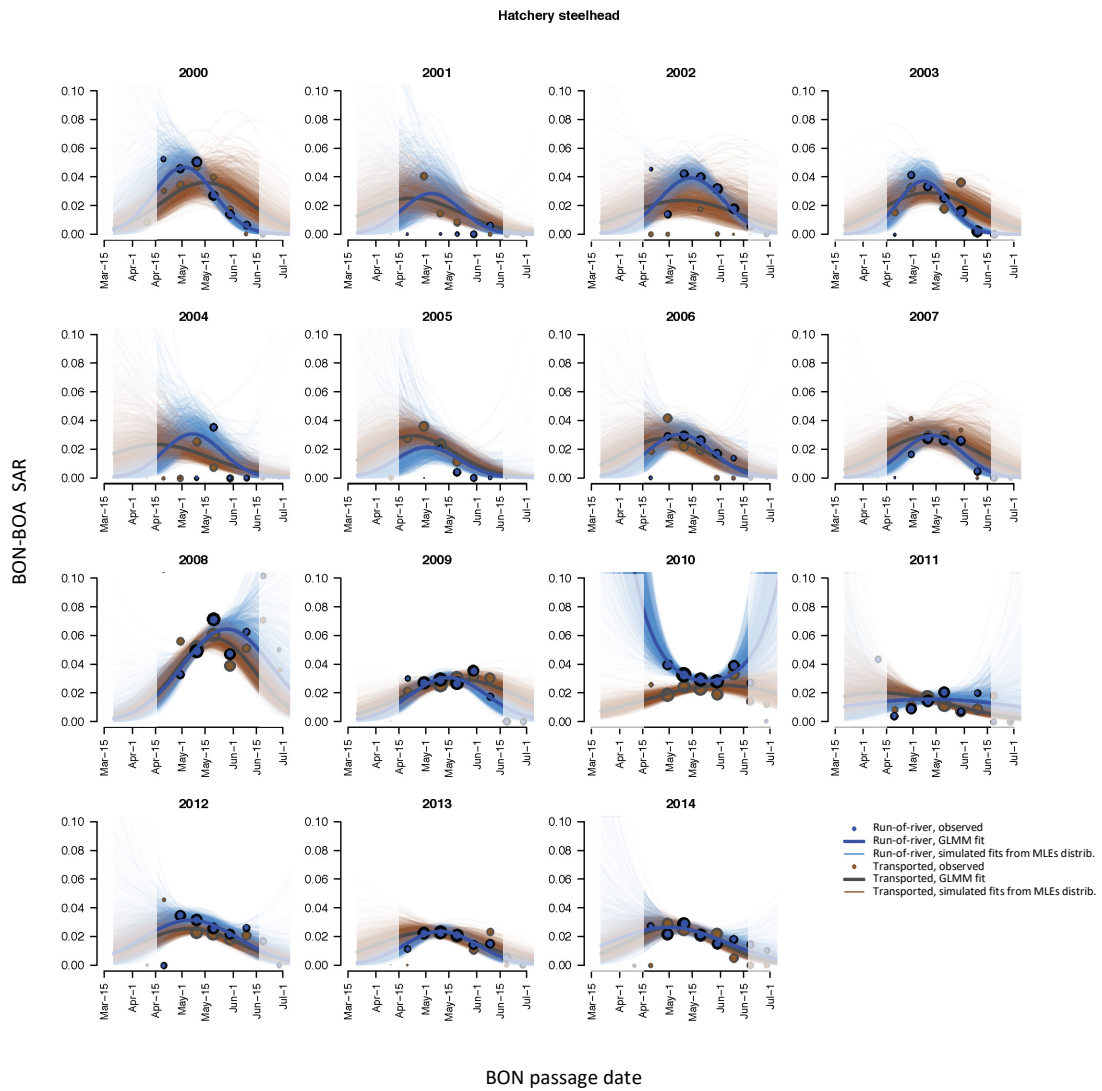


Figure 46. As Figure 34, except for hatchery steelhead BON-BOA SAR.

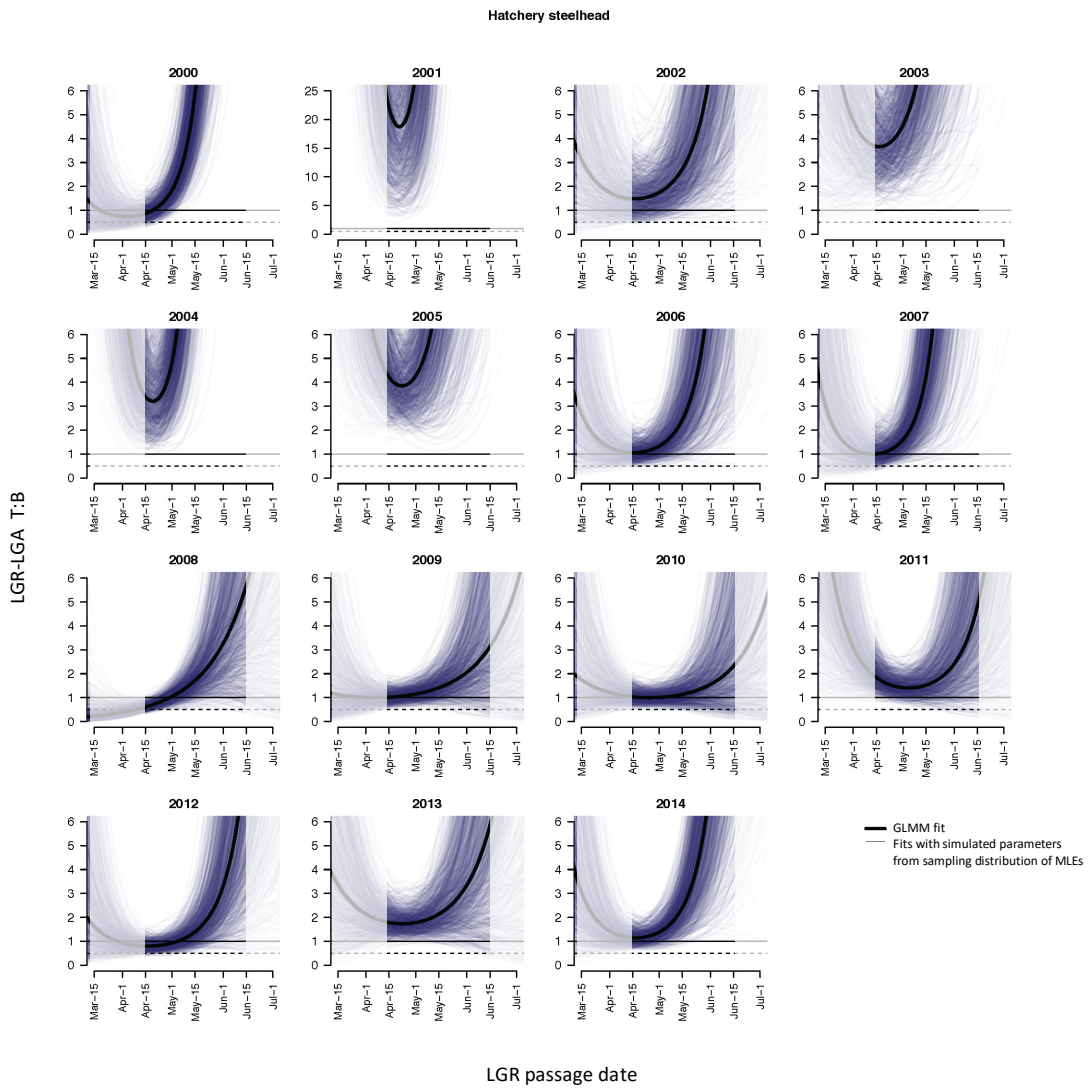


Figure 47. As Figure 35, except for hatchery steelhead T:B, and associated SARs in Figure 48.

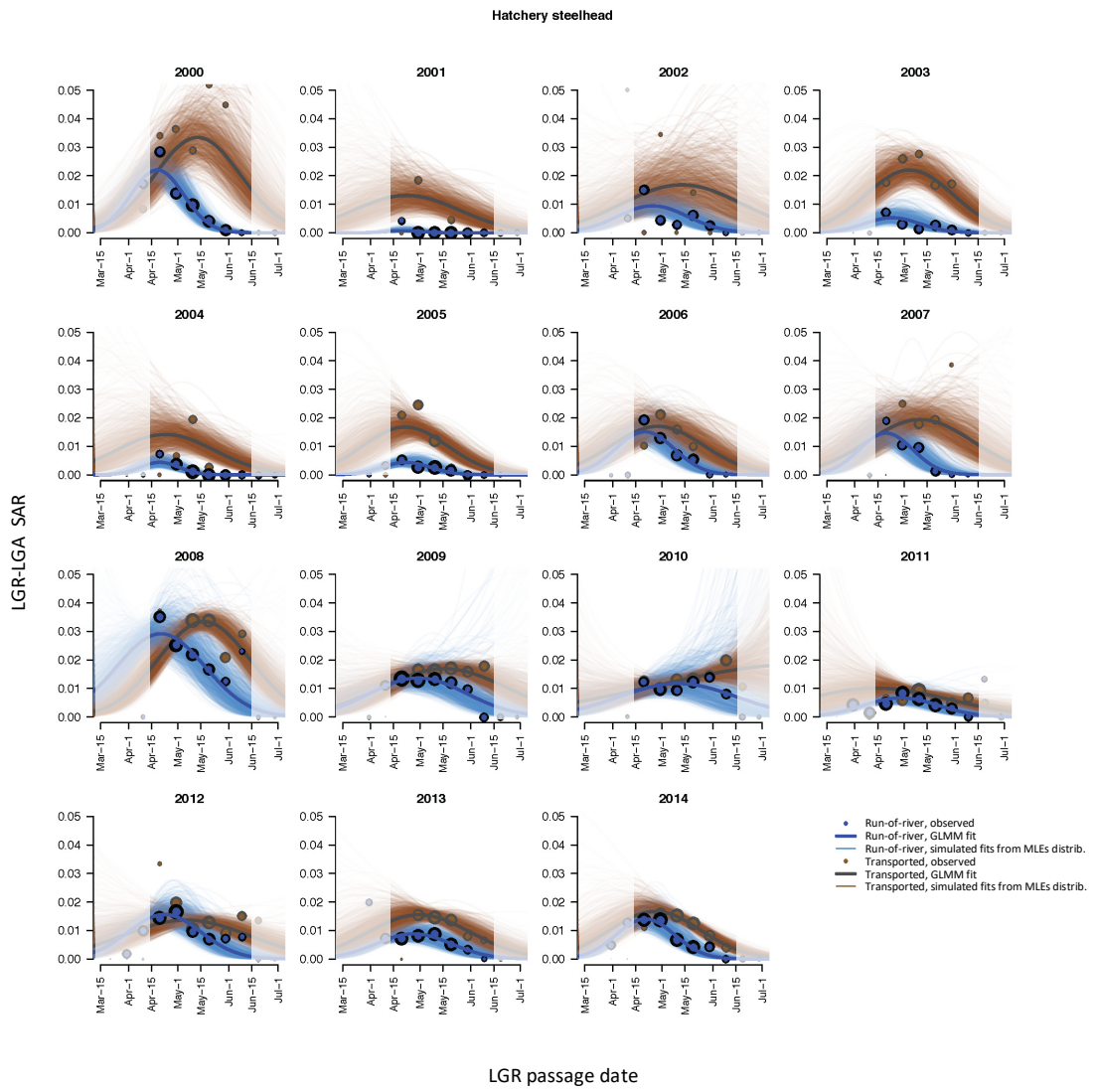


Figure 48. As Figure 36, except for hatchery steelhead LGR-LGA SAR.

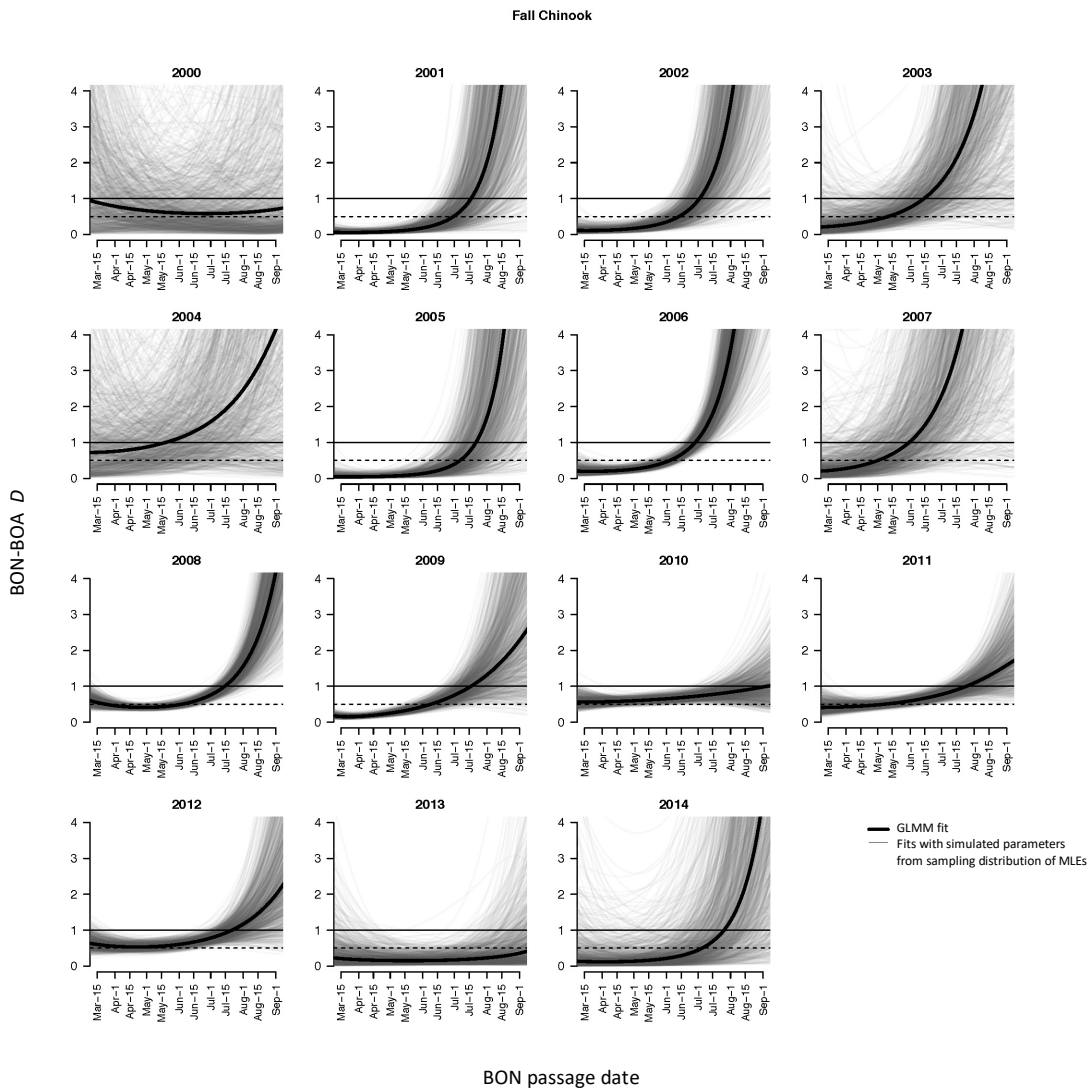


Figure 49. As Figure 33, except for wild and hatchery fall Chinook D , and associated SARs in Figure 50.

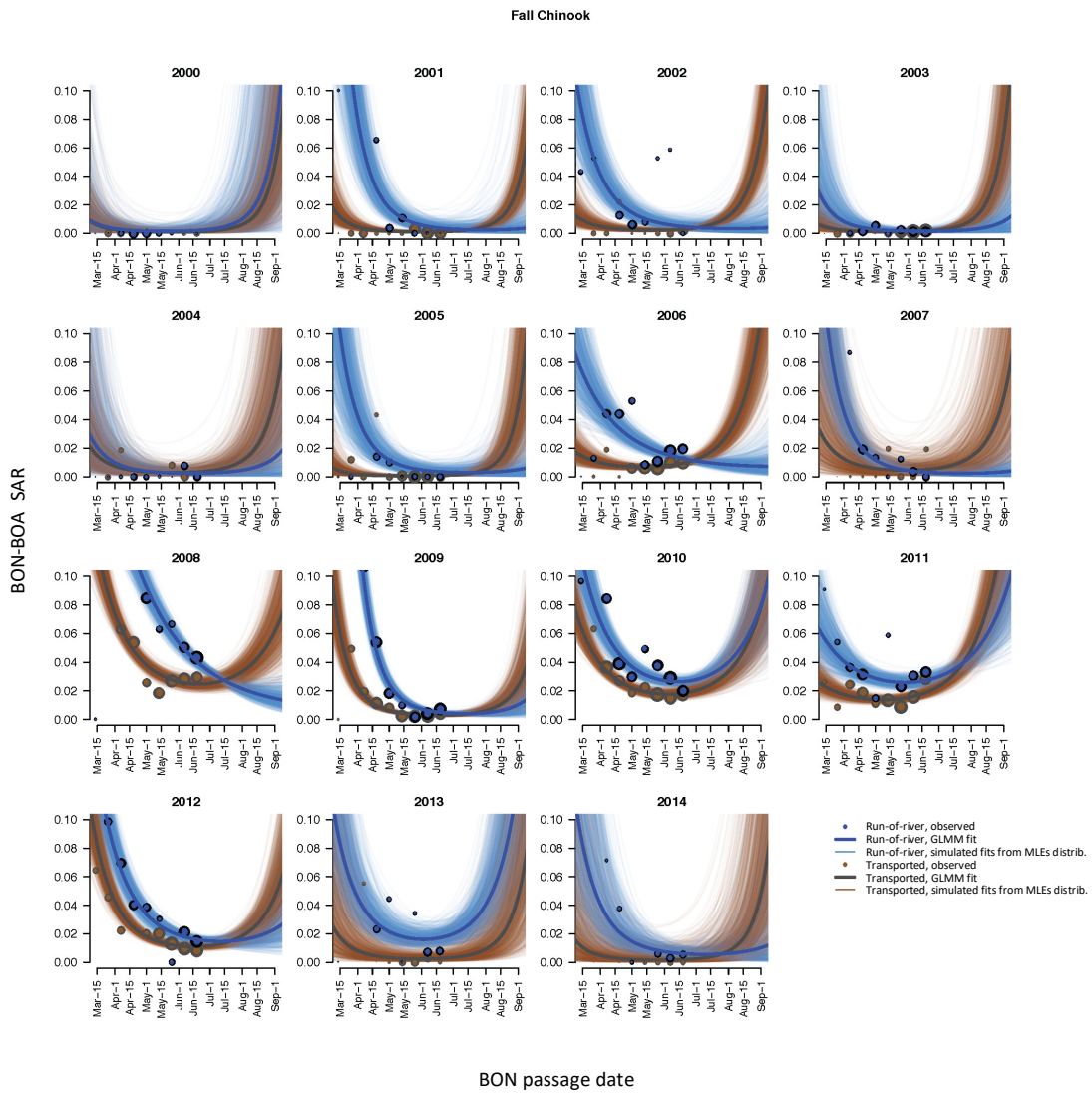


Figure 50. As Figure 34, except for wild and hatchery fall Chinook BON-BOA SAR.

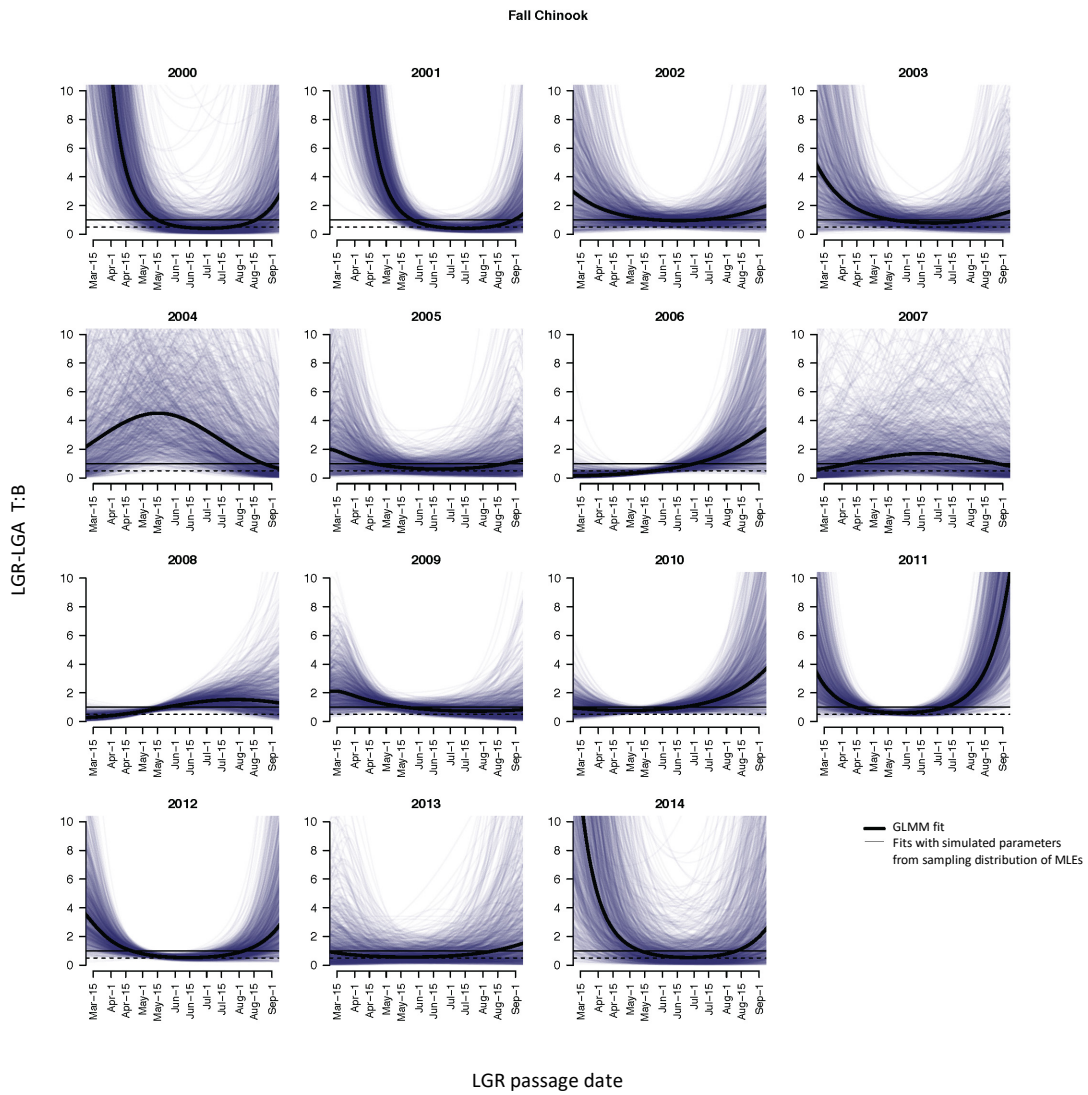


Figure 51. As Figure 35, except for wild and hatchery fall Chinook T:B, and associated SARs in Figure 52.

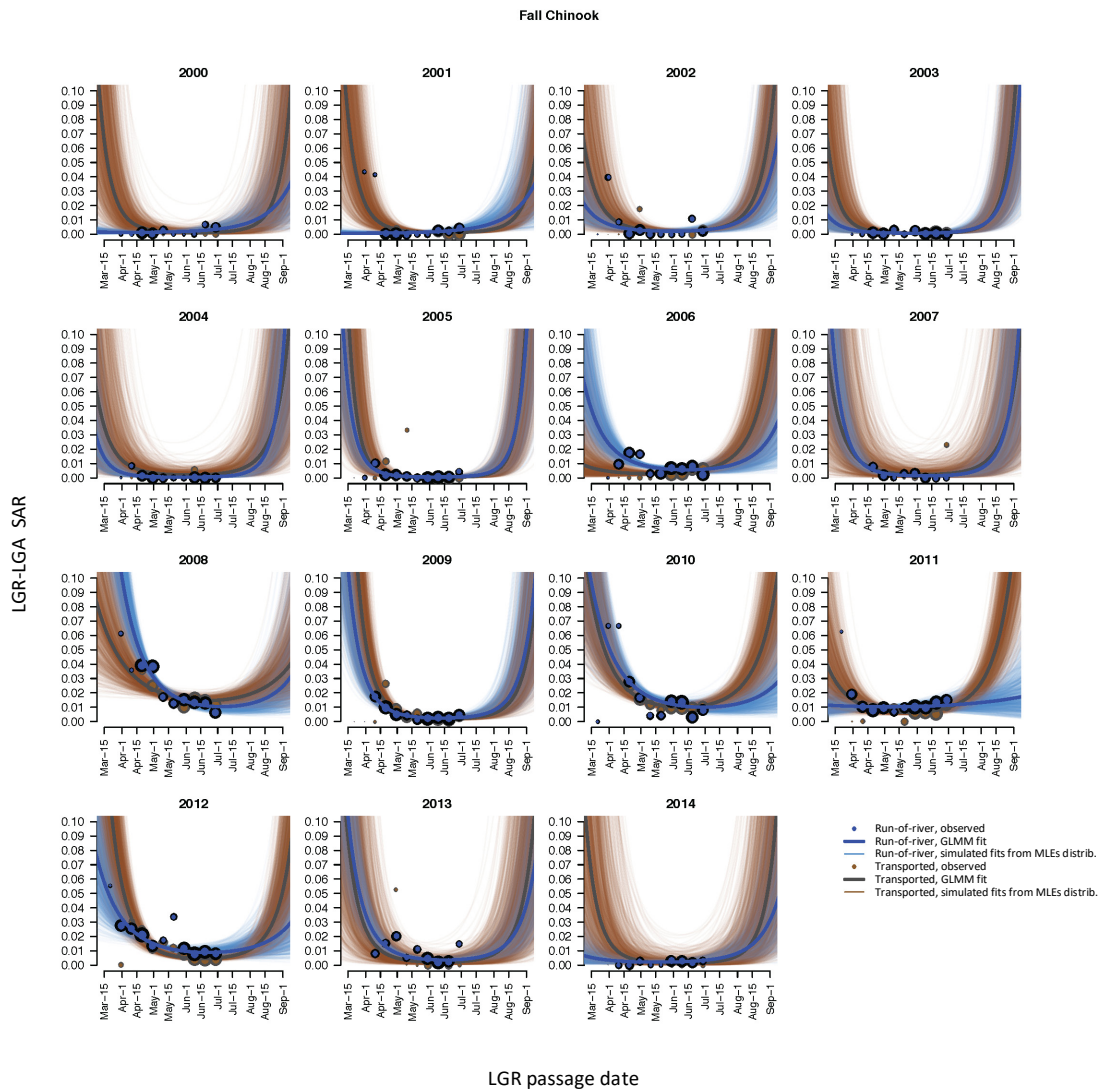


Figure 52. As Figure 36, except for wild and hatchery fall Chinook LGR-LGA SAR.

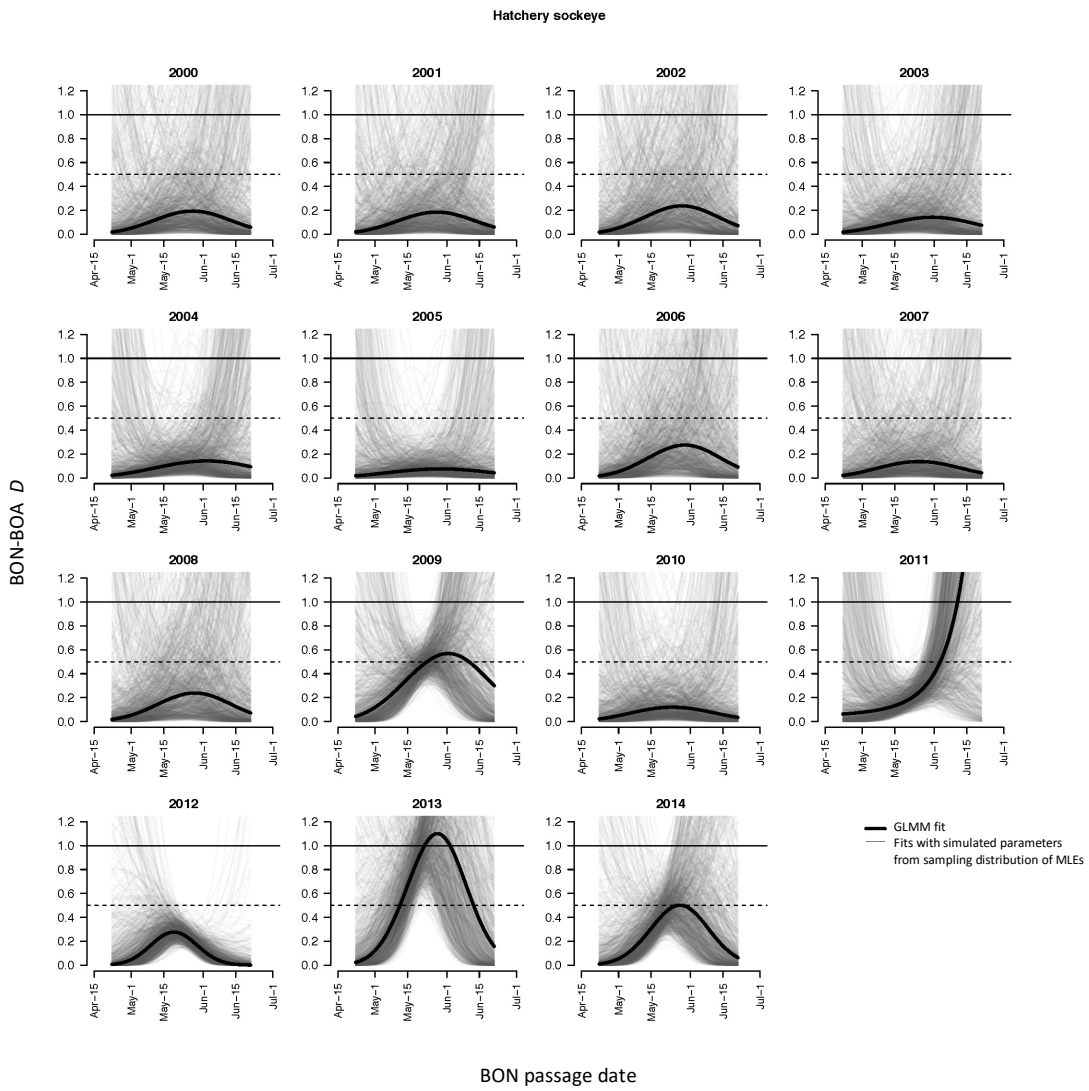


Figure 53. As Figure 33, except for hatchery sockeye *D*, and associated SARs in Figure 54.

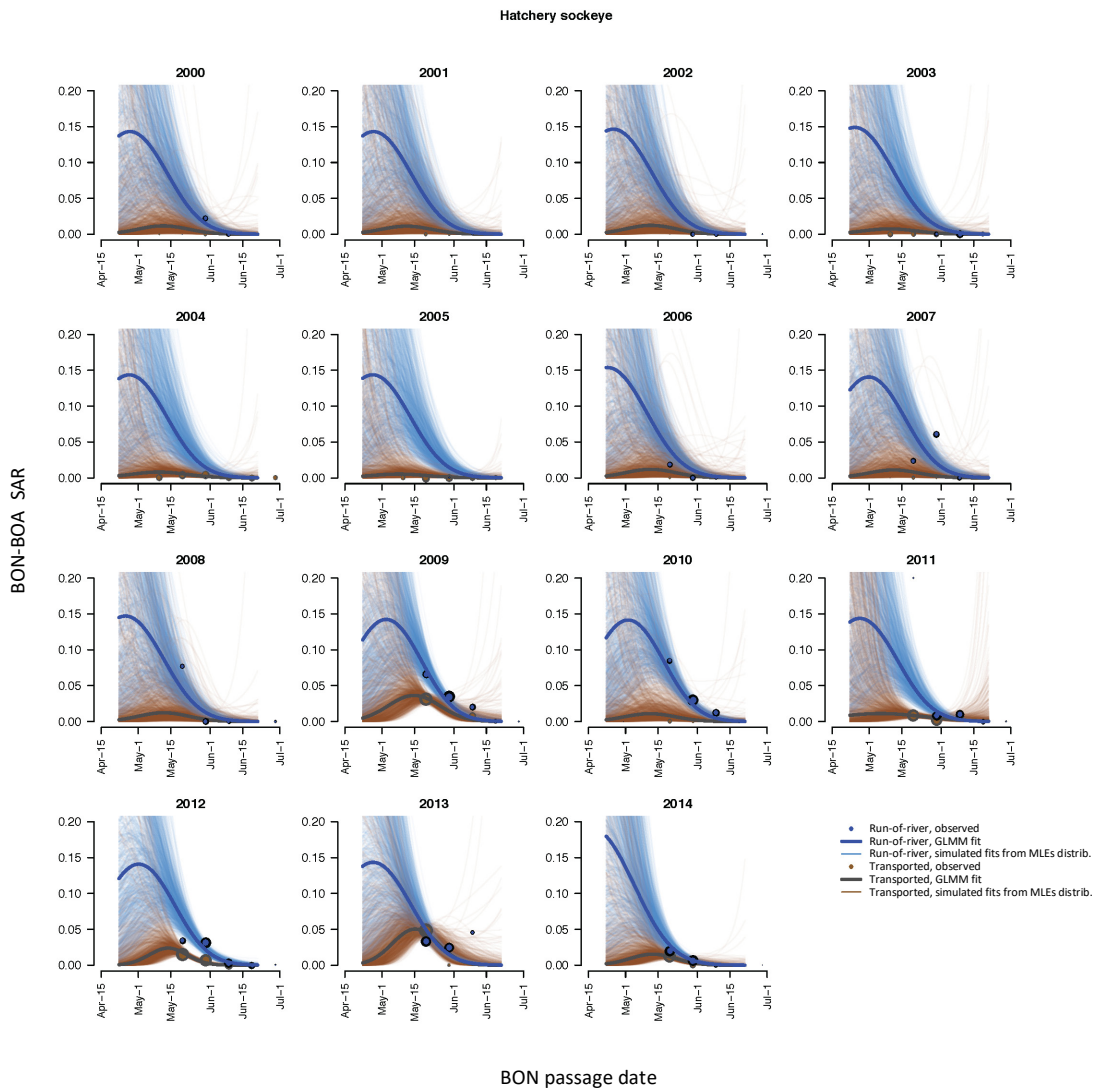


Figure 54. As Figure 34, except for hatchery sockeye BON-BOA SAR.

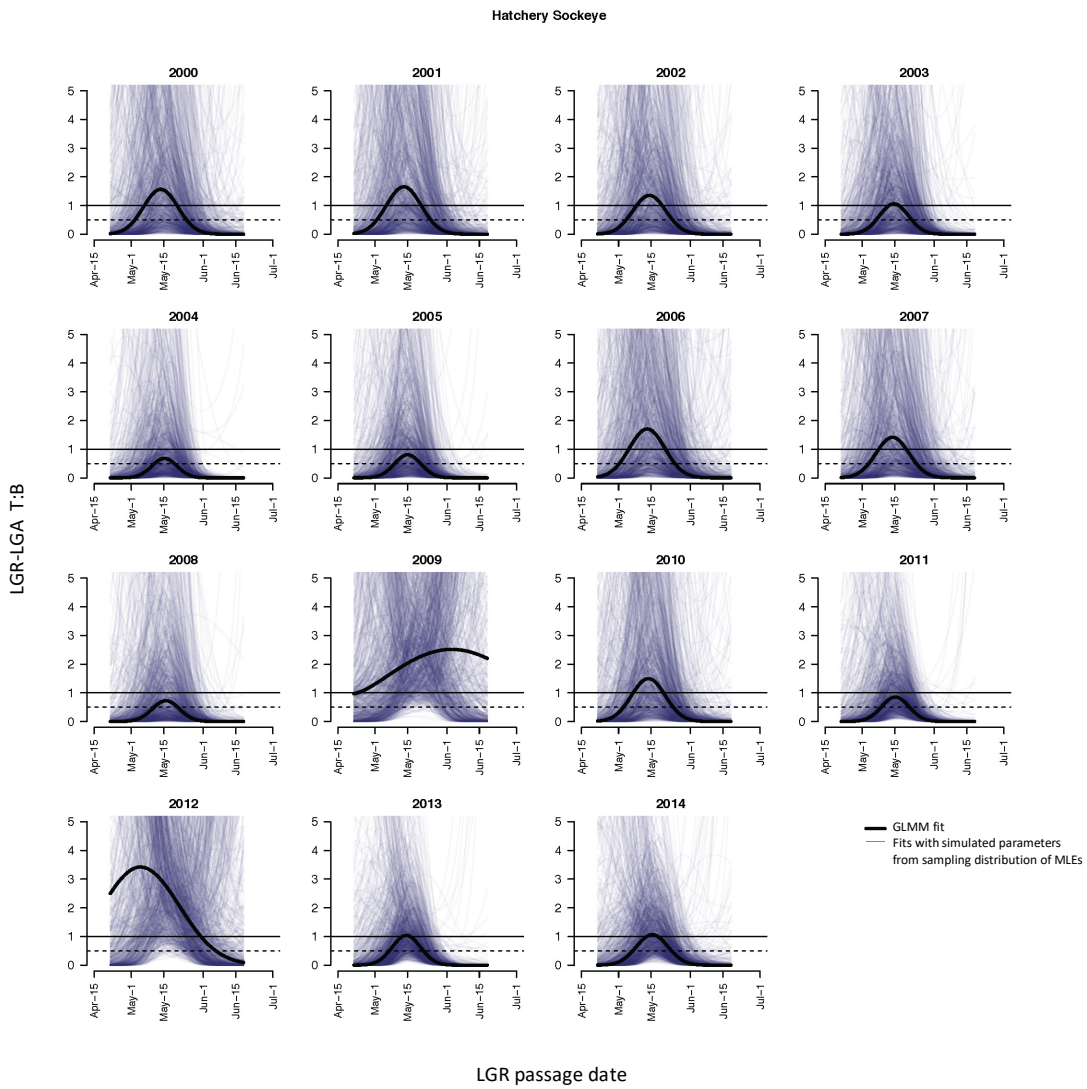


Figure 55. As Figure 35, except for hatchery sockeye T:B, and associated SARs in Figure 56.

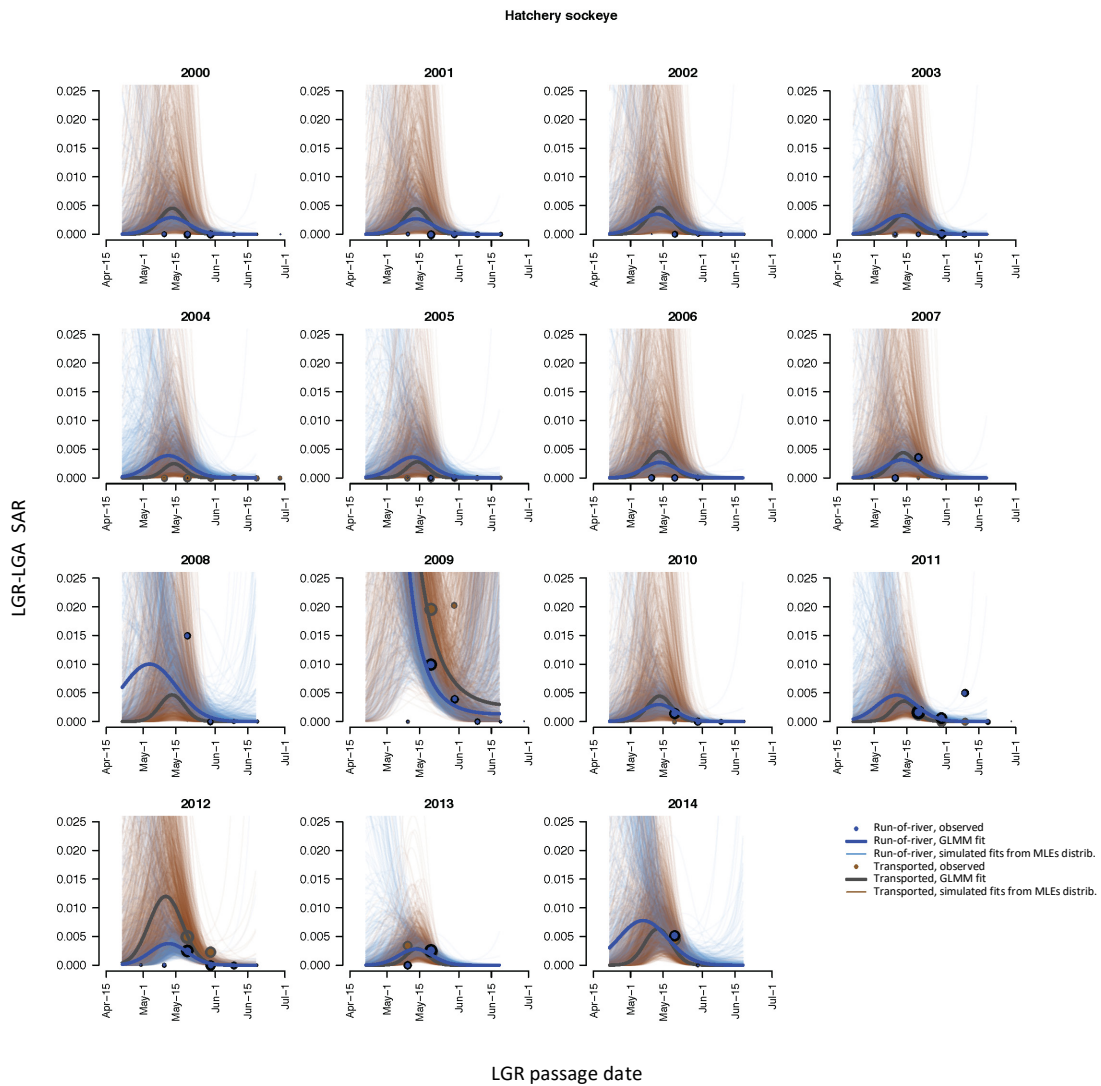


Figure 56. As Figure 36, except for hatchery sockeye LGR-LGA SAR.

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