Lewis River Fish Passage Subcommittee Meeting

Agenda

Thursday April 13, 2023
2:30 to 4:30 pm
Teams

2:30	**Introductions, Review Agenda and Approve Meeting Notes** • January, February, March meeting notes	All
2:35	**Design Team Updates**	Hansen/Higa/All
2:45	**Upstream Fish Passage Capacity Estimates**	Glaser/All
3:15	**Facility Alternative Analysis** • Draft Tables • Proposed revision to section 3 and addition of Appendix D to the Draft Elements Document • Merwin Downstream update • Next Steps	Olson/All
4:00	**2023 Yale Reservoir Fish Behavior Study**	Karchesky/All
4:20	**30% designs - Comment Response Matrix**	
4:25	**Next FPS meeting** – May 11th • Agenda	All
4:30	**Adjourn**	

PACIFICORP

Pacific Power |
Rocky Mountain Power
825 NE Multnomah, Suite 1800
Portland, Oregon 97232

FINAL Meeting Notes
Lewis River License Implementation
ACC Fish Passage Subcommittee Meeting
April 13, 2023
2:30 pm – 4:30 pm
MS Teams Meeting

Attendees

Christina Donehower – Cowlitz Indian Tribe
Amanda Farrar – Cowlitz PUD
Steve Manlow – LCFRB
Melissa Jundt – NOAA
Beth Bendickson – PacifiCorp
Mark Ferraiolo – PacifiCorp
Eric Hansen – PacifiCorp
Nathan Higa – PacifiCorp
Chris Karchesky – PacifiCorp
Erik Lesko – PacifiCorp
Todd Olson – PacifiCorp
Sam Gibbons – WDFW
Bryce Glaser – WDFW
Josua Holowatz – WDFW
Peggy Miller – WDFW
Erin Peterson – WDFW
Tyanna Blaschak – USDA-FS
Jeffrey Garnett – USFWS
Keely Murdoch – Yakama Nation Fisheries
Bill Sharp – Yakama Nation Fisheries

Introductions, Review Agenda and Approve Meeting Notes

Bryce Glaser, WDFW, reviewed the meeting agenda. Beth Bendickson, PacifiCorp, will send out the January and February 2023 meeting notes for final 7-day approval. If no additional comments are received, they will be considered final. The March meeting notes will be reviewed at the May meeting.

Design Team Updates

Eric Hansen, PacifiCorp, provided an update on the Yale downstream fish passage facility. We are developing the 60% design CAD drawings for the floating surface collector, intermediate sorting barge, and land-based sorting facility, all three of which are tied together near the powerhouse intake. The design team is working on the fish pump technical memo. Debris management discussions are continuing regarding the rake on the front for larger debris, how it will travel through the facility, and ultimate disposal on the backend of the FSC. While we realize that Yale reservoir does not have the same debris volume as Swift, we do recognize there will be some odd debris size and shape. We are nearing completion of getting sub-quotes in support of geotechnical, permitting, and specialty designs.

Nathan Higa, PacifiCorp, provided an update on Yale and Swift upstream facilities. For Yale, we are starting to work on the 60% design. We received attraction water supply (AWS) comments and are reconfiguring to provide more entrance flow. Preliminary modelling has been done. We are advancing on sorting/handling and refining no-touch processes. For Swift, we are working on fish ladder hydraulics and layout refinement. Including an attraction water canal pump station at 30 cfs minimum discharge facility; with the entrance area and how to mesh it in with the 100 cfs existing siphon.

Upstream Fish Passage Capacity Expansions

Bryce walked through an Upstream Fish Passage Capacity slide presentation (**Appendix A**).

<u>Comments</u>

- Chris Karchesky, PacifiCorp, asked if the assumed SAR of 15 percent used to estimate adult abundance was calculated with or without harvest? Bryce said without.
- Chris then clarified that EDT capacity estimate rather than abundance was used, and while he understands the disagreement, the capacity numbers do inherently provide more of a buffer than abundance as they represent maximum habitat capacity without density-dependent effects. Bryce replied that the EDT modeling exercise was more of a static assumed number; a single spawner-recruit curve point estimate instead of a range. The WDFW modelling exercise captures the variability in marine survival.
- Chris then asked about Bryce's comments about including a buffer for additional hatchery fish upstream during recolonization and once habitat was fully seeded. Bryce replied that in the longer term, more discussion is needed about how hatchery fish fit into upstream transport. In the short term, the current target is 9,000 adults above Swift Reservoir and any natural fish are back filled with hatchery fish to meet that goal. Bryce also indicated that sizing should include a buffer for resident fish and the response of resident fish is currently unknown. He went on to provide an example of sockeye (kokanee), which may eventually establish an anadromous run and the potential need to pass those fish.
- Based on the assumptions WDFW included in their model exercise, they recommended establishing a design capacity of 3,000 fish per day but hoped to get feedback and information from PacifiCorp on WDFW's modelling approach, and what can be achieved by increasing operational cycles, and what has been accomplished at the Merwin Trap.
- Chris acknowledged that the technical memo design documents did not do an adequate job in differentiating between design capacity vs. operational capacity. Design capacity is really intended to provide the design engineers with levels of magnitude for designing fish passage, holding, and processing infrastructure to accommodate expected or "normal" passage rates over a calendar year. Typically, design capacity accounts for how many fish can be processed, held, and transported over one operation cycle per day. Operational capacity accounts for how many operation cycles can be completed in one day. This includes how many trucks can you load, how fish can be processed, the use of additional staffing, and working longer. More discussion is needed on work rate and how that applies to the new upstream facilities. Chris also said one of the advantages of the upstream passage facilities upstream of Merwin Dam, is that they will be completely controlled systems. That is, we know everything that is coming into Merwin Reservoir because we will have transported them from the Merwin Trap. If we have a banner year, we can control where

fish go and change that based on adaptive management and harvest goals. We have a lot of flexibility at these facilities compared to the Merwin Trap which has open access to the Columbia River. The challenge is how do we work that flexibility into a realistic design capacity? He added that a facility designed for 3,000 to 5,000 fish per day is a really big facility. Bryce said they are concerned and that we should design for 3,000 but have some discussion on how to buffer with additional operational capacity.

- There was concern about using the Merwin Trap average collection numbers to estimate potential returns and therefore sizing collection capacity. We know we have had some challenges at Merwin Trap (capacity, mortality); a lot of hatchery fish are going upstream. Chris responded that the issues we have experience in the past at the Merwin Trap had nothing to do with design capacity, but rather the inability to transport surplus hatchery fish offsite to downstream hatcheries during peak migration periods. We will not have that issue upstream of Merwin Dam. Bryce asked about the maximum capacity at the Merwin Trap facility For perspective, Chris said he recalls that the Merwin Trap was designed for a little over 3,000 fish per day.
- Bryce said they would prefer to err on overbuilding than underbuilding. Chris did not disagree, but said with a design capacity of around 1,000 fish, we can have an operational capacity of 2-3 times that. It really boils down to staffing and how many trucks you can load in an hour and how far they need to go dump fish for a truck transport facility.

Todd Olson, PacifiCorp, and Chris both thanked Bryce for putting the presentation together in a thoughtful manner, and for providing the slides and paper for us to review.

Facility Alternative Analysis

Draft Tables

Todd walked through the updated tables distributed April 7, 2023. Peggy Miller, WDFW, clarified one of their comments. WDFW wanted to know how many times does PacifiCorp spill per month. Todd said it is usually about one time per year unless there is a rain on snow event. During an expected high flow event, we typically go into spill and then get out of it. Each year is different. Spill is pretty infrequent at these two locations. Bryce asked if there was a record of how many times it is occurred? Todd will check with the water management group and let the group know. He will also clean up the tables and send out a new version for review.

Proposed Revisions to the Draft Elements Document

Todd appreciated WDFW's review and comments for Section 3, Section 6, and the addition of Appendix D. He also revised the Merwin Downstream section to include Settlement Agreement language and the section was distributed for review on April 10, 2023.

While FERC was told we are working towards having a draft future fish plan by the end of April, he does not think we will make that date. His thought is to take the sections we have worked on and have everyone do a final review to feel comfortable with them and then move on. Ideally, it would be a draft out to this group. We can discuss it further at the May meeting and then look to finalize and provide it to the ACC with a decision document. Once approved, it would go to the Services for their agreement prior to going to FERC. The new goal is to finalize the document in

May. Bryce liked the idea of focusing on the individual sections to get them “across the finish line” now, and then work on the unresolved elements.

He will update it with any comments received and send out a new version which will have all the sections. He has been “piece parting” them as we review them. Bryce suggested a timeline table might be useful, maybe after the next version comes out.

Christina Donehower, Cowlitz Indian Tribe, asked if things are going smoothly, are we looking for ACC approval in June? Todd replied yes, with the understanding that we might need time for review at the May meeting. Hopefully, we can have something to the ACC in June for approval. She said they will not be able to approve anything without Tribal Council approval. She appreciated the ongoing status. Todd added that while FERC wants collective agreement, we all need to be on the same page. Peggy said their Assistant Attorney General will also need to review it, either between the time the ACC Fish Passage Group reviews it, before it goes to ACC, or after.

Next Steps

Review the April updates, previously distributed for discussion, at the May meeting.

2023 Yale Reservoir Fish Behavior Study

Chris shared the spring 2023 update.

30% Designs – Comment Response Matrix

Chris said, to date, he had not received any comments on the responses. As more things come to light, we can discuss anything that comes up.

Next FPS Meeting: May 11, 2023

Agenda Items

- Capacity Estimates
- Elements Document

Todd said the ACC discussed possibly meeting in person for the June meeting. He asked if this group would also consider that and if so, also moving the meeting time up a few hours to immediately follow the ACC meeting. Time for lunch would be allowed.

Lastly, Chris asked Josua Holowatz, WDFW, about his comment of “The tech memo has the average coho weight of 6 pounds. Columbia River commercial landings show an avg coho weight of just over 7 pounds.” Josua responded that the short term (less than 24 hours) holding criteria is based on poundage of fish given a certain volume of water. The design needs to take into account this larger body size. Josua added that the sizing the facility at 1,000 fish as far as 6 or 7 pounds, it would affect the sizing of the facility. Chris said that the 6 pound value was based on fish collected at Merwin Trap and did not include Jacks. Lewis River fish might be slightly smaller than those in the Columbia and asked Josua if he felt better if 7 pounds was used as a design number. Josua felt it would be more conservative. Chris said he will play with the numbers and we can have more discussion at a future meeting.

Action Items from April 11, 2023	**Status**
Beth will send out the January and February notes for final 7-day review.	**Complete**
Todd will talk to the PacifiCorp water management group and provide spill information to the group.	**Complete**
Review March 2023 meeting notes; any major items will be discussed at the May meeting.	
Clean up the tables and send out a new version for review	
Update the Elements document with any comments received and send out a new version which will have all the sections	
Action Items from March 9, 2023	
Review *30% Designs Comment Response Matrices*, distributed March 7, 2023, for discussion at the April meeting.	**Complete**
WDFW will perform an abundance modeling exercise.	**Complete**
Review and provide comments on the *Proposed Revision to Section 3* and the *Addition of Appendix D to the Draft Elements Document*, distributed March 8, 2023.	**Complete**

The meeting adjourned at 4:13 p.m.

Upstream Fish Passage Capacity

LEWIS FISH PASSAGE SUBGROUP

4/13/23

WDFW

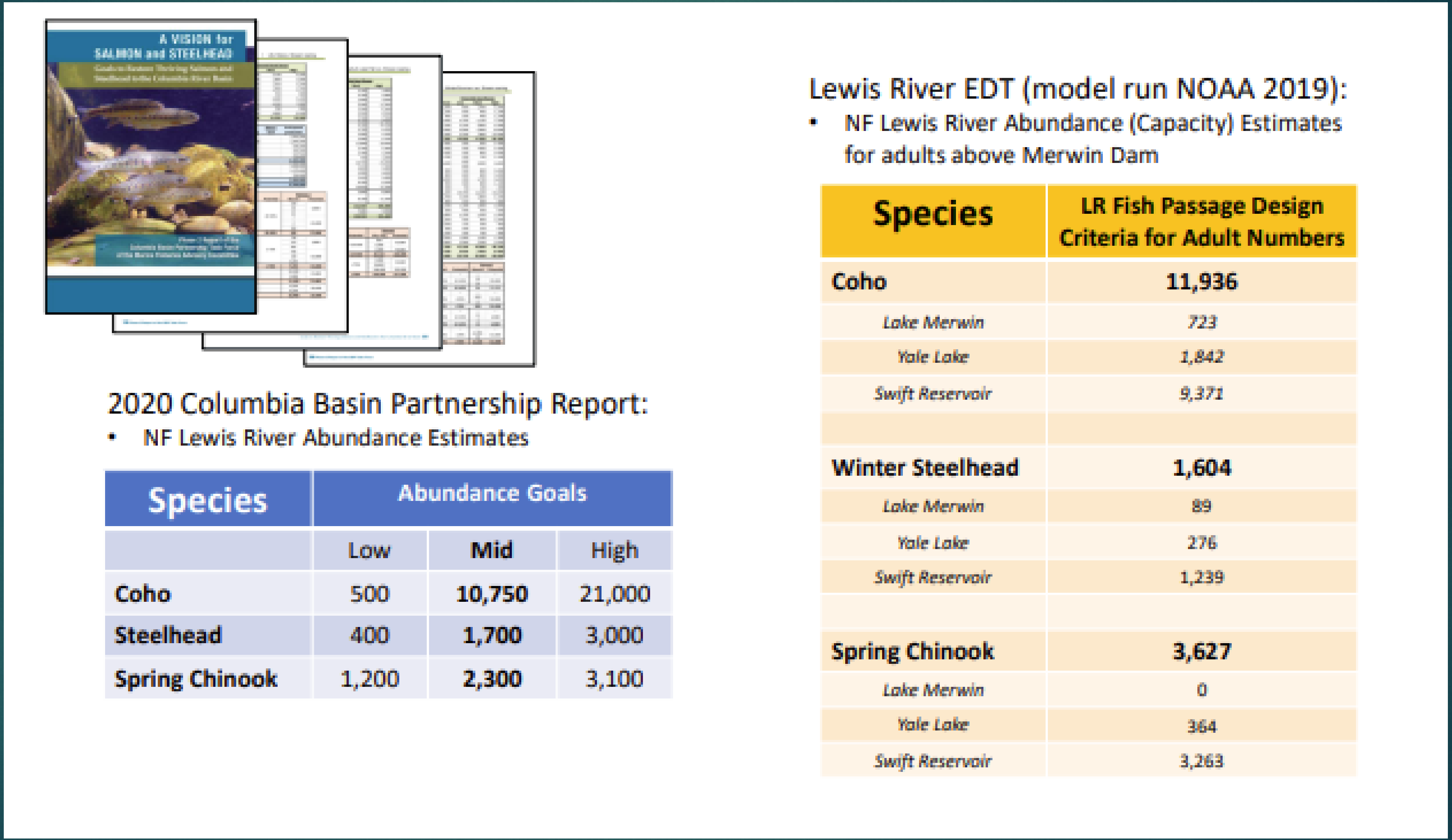
Goals and Key Question

- Goal:
  - Ensure safe, timely, effective fish passage.
    - Limited Delay.
    - Adequate attraction/holding capacity to handle peak fish abundance.
    - Ensure safe holding/handling to minimize injury/mortality (i.e. appropriate densities, DOs)
- What size of collection/trap facility is needed at Yale and Swift to adequately handle anticipated future fish return?
  - Primarily focused on coho, steelhead and spring Chinook.
  - May have other resident fish as well

Concerns.

- Don’t want an under-sized facility.
    - Excessive delays
    - Increased injury/mortality
    - Strained operational capacity
- Have ability to expand post-trap holding capacity, but getting the trap entrance, size and attraction (“front-door”) sized appropriately at the start is important.
- Don’t want to over-build facility.
    - Extra cost
    - Inefficient use of funds/resources

Proposed to date



A VISION for SALMON and STEELHEAD

2020 Columbia Basin Partnership Report:

- NF Lewis River Abundance Estimates

Species	**Abundance Goals**		
	Low	**Mid**	High
Coho	500	**10,750**	21,000
Steelhead	400	**1,700**	3,000
Spring Chinook	1,200	**2,300**	3,100

Lewis River EDT (model run NOAA 2019):

- NF Lewis River Abundance (Capacity) Estimates for adults above Merwin Dam

Species	**LR Fish Passage Design Criteria for Adult Numbers**
Coho	**11,936**
Lake Merwin	*723*
Yale Lake	*1,842*
Swift Reservoir	*9,371*
Winter Steelhead	**1,604**
Lake Merwin	89
Yale Lake	276
Swift Reservoir	1,239
Spring Chinook	**3,627**
Lake Merwin	0
Yale Lake	364
Swift Reservoir	3,263

Max Daily Catch Rate

YUS TM01

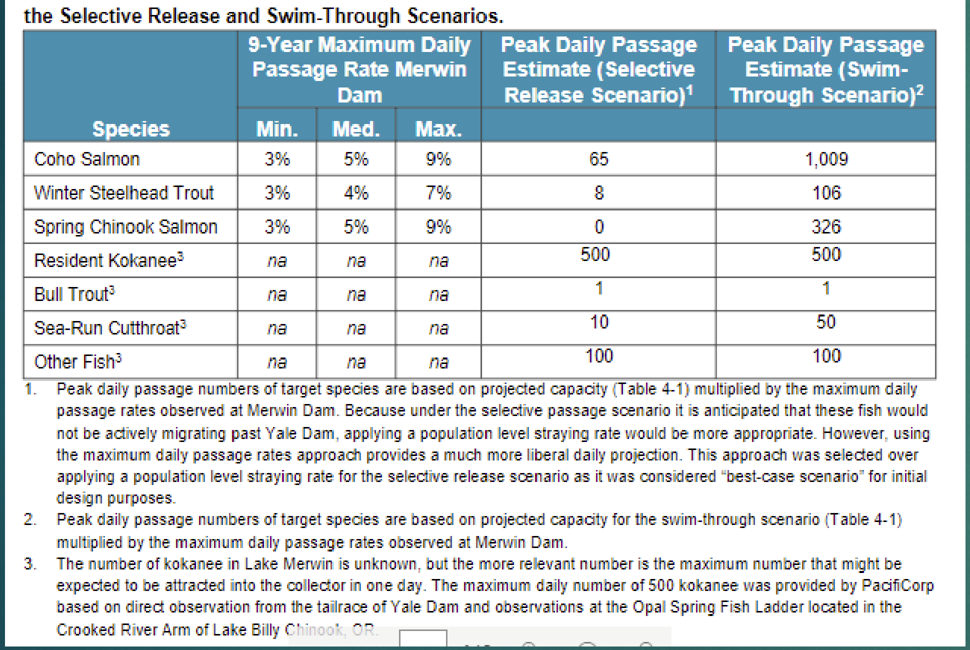
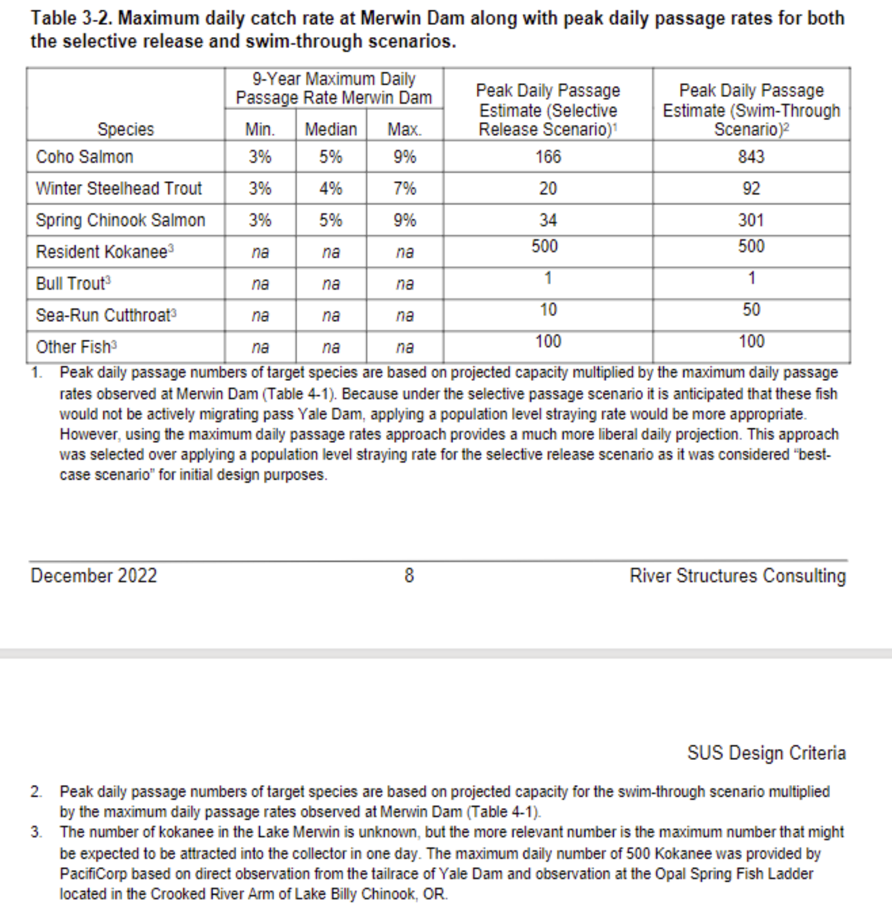


Table 4-2. Maximum Daily Catch Rate at Merwin Dam Along with Peak Daily Passage Rates for Both the Selective Release and Swim-Through Scenarios.

Species	9-Year Maximum Daily Passage Rate Merwin Dam			Peak Daily Passage Estimate (Selective Release Scenario)[1]	Peak Daily Passage Estimate (Swim-Through Scenario)[2]
	Min.	Med.	Max.		
Coho Salmon	3%	5%	9%	65	1,009
Winter Steelhead Trout	3%	4%	7%	8	106
Spring Chinook Salmon	3%	5%	9%	0	326
Resident Kokanee[3]	*na*	*na*	*na*	500	500
Bull Trout[3]	*na*	*na*	*na*	1	1
Sea-Run Cutthroat[3]	*na*	*na*	*na*	10	50
Other Fish[3]	*na*	*na*	*na*	100	100

1. Peak daily passage numbers of target species are based on projected capacity (Table 4-1) multiplied by the maximum daily passage rates observed at Merwin Dam. Because under the selective passage scenario it is anticipated that these fish would not be actively migrating past Yale Dam, applying a population level straying rate would be more appropriate. However, using the maximum daily passage rates approach provides a much more liberal daily projection. This approach was selected over applying a population level straying rate for the selective release scenario as it was considered "best-case scenario" for initial design purposes.
2. Peak daily passage numbers of target species are based on projected capacity for the swim-through scenario (Table 4-1) multiplied by the maximum daily passage rates observed at Merwin Dam.
3. The number of kokanee in Lake Merwin is unknown, but the more relevant number is the maximum number that might be expected to be attracted into the collector in one day. The maximum daily number of 500 kokanee was provided by PacifiCorp based on direct observation from the tailrace of Yale Dam and observations at the Opal Spring Fish Ladder located in the Crooked River Arm of Lake Billy Chinook, OR.

SUS TM01



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Species	9-Year Maximum Daily Passage Rate Merwin Dam			Peak Daily Passage Estimate (Selective Release Scenario)[1]	Peak Daily Passage Estimate (Swim-Through Scenario)[2]
	Min.	Median	Max.		
Coho Salmon	3%	5%	9%	166	843
Winter Steelhead Trout	3%	4%	7%	20	92
Spring Chinook Salmon	3%	5%	9%	34	301
Resident Kokanee[3]	*na*	*na*	*na*	500	500
Bull Trout[3]	*na*	*na*	*na*	1	1
Sea-Run Cutthroat[3]	*na*	*na*	*na*	10	50
Other Fish[3]	*na*	*na*	*na*	100	100

1. Peak daily passage numbers of target species are based on projected capacity multiplied by the maximum daily passage rates observed at Merwin Dam (Table 4-1). Because under the selective passage scenario it is anticipated that these fish would not be actively migrating pass Yale Dam, applying a population level straying rate would be more appropriate. However, using the maximum daily passage rates approach provides a much more liberal daily projection. This approach was selected over applying a population level straying rate for the selective release scenario as it was considered "best-case scenario" for initial design purposes.

December 2022 8 River Structures Consulting

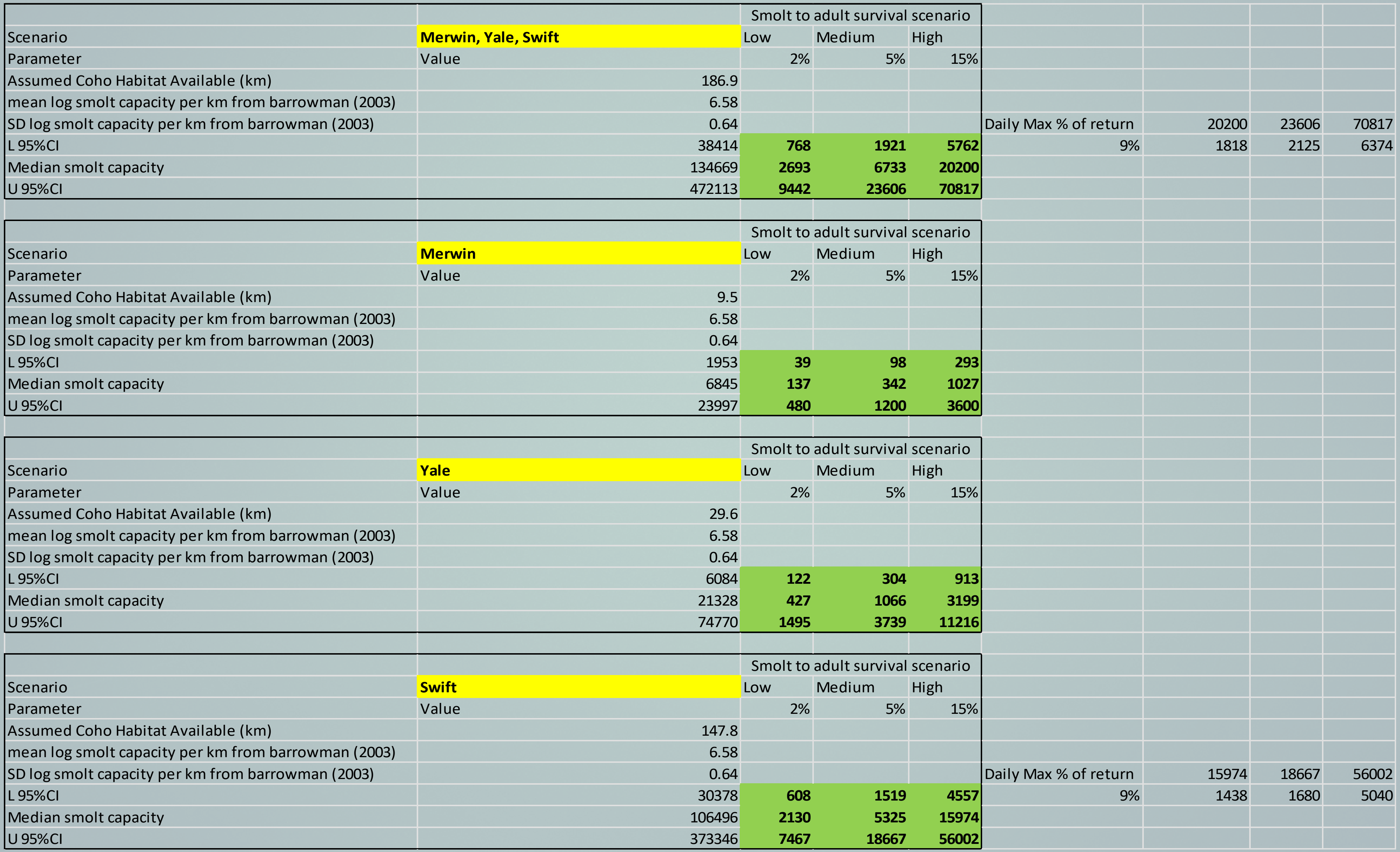
SUS Design Criteria

2. Peak daily passage numbers of target species are based on projected capacity for the swim-through scenario multiplied by the maximum daily passage rates observed at Merwin Dam (Table 4-1).
3. The number of kokanee in the Lake Merwin is unknown, but the more relevant number is the maximum number that might be expected to be attracted into the collector in one day. The maximum daily number of 500 Kokanee was provided by PacifiCorp based on direct observation from the tailrace of Yale Dam and observation at the Opal Spring Fish Ladder located in the Crooked River Arm of Lake Billy Chinook, OR.

WDFW Approach

- Agree with using the estimated Max Daily catch rate (i.e. peak surge rate) as the key design parameter
- Agree with Max daily passage rate at Merwin as an appropriate assumption
- Disagree that EDT Capacity or CBC Healthy Harvestable represent potential max abundance under full range of marine survival expectations.
  - EDT and CBC = avg abundance at recovery; don't account for variable SAR
  - Need facility with capacity for good SAR year at Recovery
- Reviewed species return overlap – not fully additive
  - Coho = fall returns; steelhead/spring Chinook = spring returns
- Focused on coho as highest abundance potential
- Utilized Barrowman et. al 2003
- Utilized marine survival range of 2%-15%
  - Higher than range provided for EDT modeling (1-9%)
  - Seen 1-10% in last decade; 15% is based on a plausible really good year.

Modeled Result – using Barrowman et al. 2003



		Smolt to adult survival scenario						
Scenario	**Merwin, Yale, Swift**	Low	Medium	High				
Parameter	Value	2%	5%	15%				
Assumed Coho Habitat Available (km)	186.9							
mean log smolt capacity per km from barrowman (2003)	6.58							
SD log smolt capacity per km from barrowman (2003)	0.64				Daily Max % of return	20200	23606	70817
L 95%CI	38414	**768**	**1921**	**5762**	9%	1818	2125	6374
Median smolt capacity	134669	**2693**	**6733**	**20200**				
U 95%CI	472113	**9442**	**23606**	**70817**				

		Smolt to adult survival scenario		
Scenario	**Merwin**	Low	Medium	High
Parameter	Value	2%	5%	15%
Assumed Coho Habitat Available (km)	9.5			
mean log smolt capacity per km from barrowman (2003)	6.58			
SD log smolt capacity per km from barrowman (2003)	0.64			
L 95%CI	1953	**39**	**98**	**293**
Median smolt capacity	6845	**137**	**342**	**1027**
U 95%CI	23997	**480**	**1200**	**3600**

		Smolt to adult survival scenario		
Scenario	**Yale**	Low	Medium	High
Parameter	Value	2%	5%	15%
Assumed Coho Habitat Available (km)	29.6			
mean log smolt capacity per km from barrowman (2003)	6.58			
SD log smolt capacity per km from barrowman (2003)	0.64			
L 95%CI	6084	**122**	**304**	**913**
Median smolt capacity	21328	**427**	**1066**	**3199**
U 95%CI	74770	**1495**	**3739**	**11216**

		Smolt to adult survival scenario						
Scenario	**Swift**	Low	Medium	High				
Parameter	Value	2%	5%	15%				
Assumed Coho Habitat Available (km)	147.8							
mean log smolt capacity per km from barrowman (2003)	6.58							
SD log smolt capacity per km from barrowman (2003)	0.64				Daily Max % of return	15974	18667	56002
L 95%CI	30378	**608**	**1519**	**4557**	9%	1438	1680	5040
Median smolt capacity	106496	**2130**	**5325**	**15974**				
U 95%CI	373346	**7467**	**18667**	**56002**				

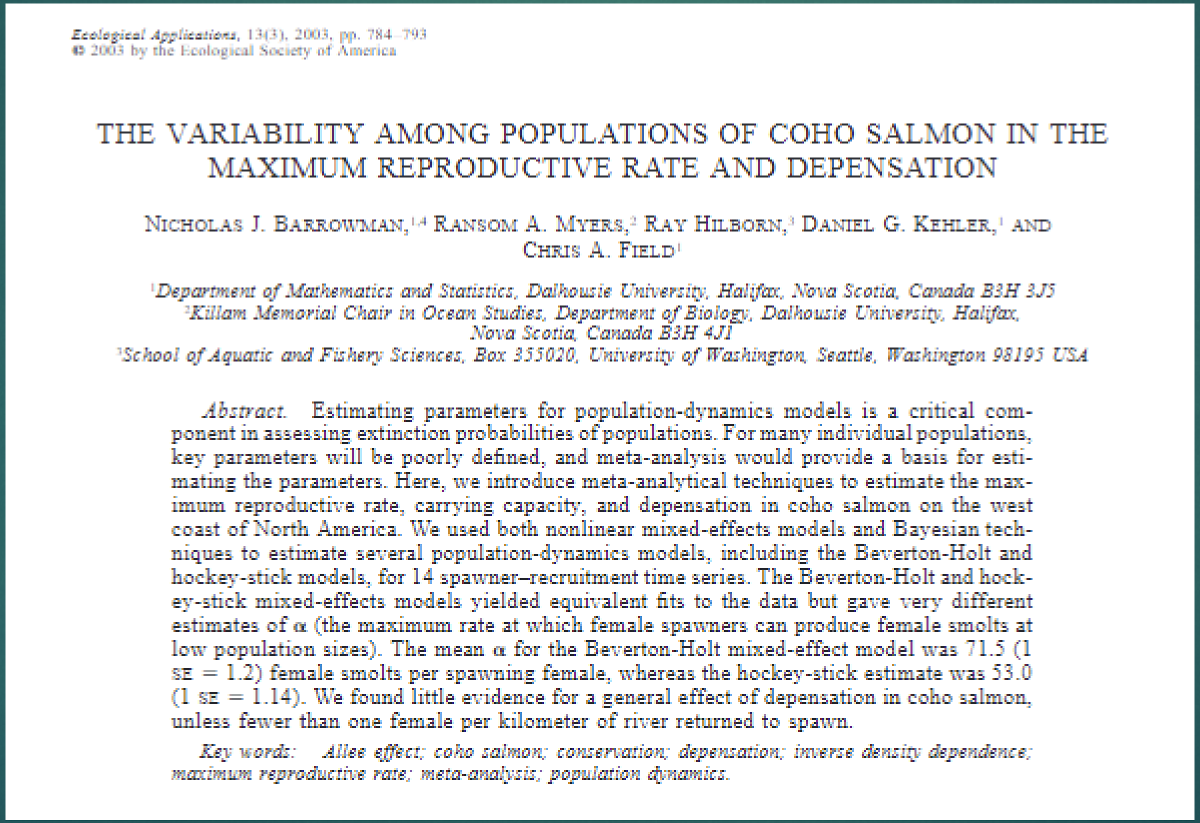
Recommendation for Yale/Swift

- Range of 1800 – 6300
  - Additional resident fish (i.e. kokanee)
  - Additional hatchery fish during recolonization/local adaptation

RECOMMENDATION: Design for max daily catch of 3000-5000

- Design for 3000 capacity with buffer provided by increased operational capacity (i.e. more cycles)
- Design for 5000 capacity – reduced need for operational capacity buffer

Questions??



Ecological Applications, 13(3), 2003, pp. 784–793

THE VARIABILITY AMONG POPULATIONS OF COHO SALMON IN THE MAXIMUM REPRODUCTIVE RATE AND DEPENSATION

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Chris A. Field[1]

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[2]*Killam Memorial Chair in Ocean Studies, Department of Biology, Dalhousie University, Halifax,*
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[3]*School of Aquatic and Fishery Sciences, Box 355020, University of Washington, Seattle, Washington 98195 USA*

Abstract. Estimating parameters for population-dynamics models is a critical component in assessing extinction probabilities of populations. For many individual populations, key parameters will be poorly defined, and meta-analysis would provide a basis for estimating the parameters. Here, we introduce meta-analytical techniques to estimate the maximum reproductive rate, carrying capacity, and depensation in coho salmon on the west coast of North America. We used both nonlinear mixed-effects models and Bayesian techniques to estimate several population-dynamics models, including the Beverton-Holt and hockey-stick models, for 14 spawner–recruitment time series. The Beverton-Holt and hockey-stick mixed-effects models yielded equivalent fits to the data but gave very different estimates of α (the maximum rate at which female spawners can produce female smolts at low population sizes). The mean α for the Beverton-Holt mixed-effect model was 71.5 (1 SE = 1.2) female smolts per spawning female, whereas the hockey-stick estimate was 53.0 (1 SE = 1.14). We found little evidence for a general effect of depensation in coho salmon, unless fewer than one female per kilometer of river returned to spawn.

Key words: Allee effect; coho salmon; conservation; depensation; inverse density dependence; maximum reproductive rate; meta-analysis; population dynamics.

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NICHOLAS J. BARROWMAN,[1,4] RANSOM A. MYERS,[2] RAY HILBORN,[3] DANIEL G. KEHLER,[1] AND CHRIS A. FIELD[1]

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[2]*Killam Memorial Chair in Ocean Studies, Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada B3H 4J1*
[3]*School of Aquatic and Fishery Sciences, Box 355020, University of Washington, Seattle, Washington 98195 USA*

Abstract. Estimating parameters for population-dynamics models is a critical component in assessing extinction probabilities of populations. For many individual populations, key parameters will be poorly defined, and meta-analysis would provide a basis for estimating the parameters. Here, we introduce meta-analytical techniques to estimate the maximum reproductive rate, carrying capacity, and depensation in coho salmon on the west coast of North America. We used both nonlinear mixed-effects models and Bayesian techniques to estimate several population-dynamics models, including the Beverton-Holt and hockey-stick models, for 14 spawner–recruitment time series. The Beverton-Holt and hockey-stick mixed-effects models yielded equivalent fits to the data but gave very different estimates of α (the maximum rate at which female spawners can produce female smolts at low population sizes). The mean α for the Beverton-Holt mixed-effect model was 71.5 (1 SE = 1.2) female smolts per spawning female, whereas the hockey-stick estimate was 53.0 (1 SE = 1.14). We found little evidence for a general effect of depensation in coho salmon, unless fewer than one female per kilometer of river returned to spawn.

Key words: Allee effect; coho salmon; conservation; depensation; inverse density dependence; maximum reproductive rate; meta-analysis; population dynamics.

INTRODUCTION

A key ecological issue—perhaps the fundamental one in the estimation of extinction probabilities—is the nature of population dynamics at low population sizes. For fish, population dynamics are often described using well-known models, such as the Beverton-Holt (Beverton and Holt 1957) and more recently, the hockey stick and its generalizations (Barrowman and Myers 2000). These models estimate the maximum reproductive rate, i.e., the rate at which spawners can produce replacement spawners at low population sizes without fishing. When considering extinction dynamics, specifying the maximum reproductive rate and modeling depensation allows us to determine the capacity for growth and the speed with which populations recover from reduced sizes.

Usually, we lack any information at low population sizes, so that the estimation of extinction probabilities is extremely difficult. However, for coho salmon, a relatively large number of data sets are available in which the production of smolts is estimated at low population abundance. Unfortunately, these time series are generally short and vary in quality.

We contend that, in order to make progress, information from many populations must be combined. This may be viewed as a form of meta-analysis. To do this, we must abandon the pretense that ecological parameters among populations are unrelated, and instead model them as being drawn from a common distribution. In statistical terms, rather than treating ecological parameters as population-specific values to be separately estimated, i.e., as fixed effects, we treat them as coming from a probability distribution with mean and variance to be estimated, i.e., as random effects. The resulting models are known as mixed-effects models or hierarchical models.

Meta-analytic investigations in ecology may have several different goals: to obtain overall estimates of ecological parameters, to explore heterogeneity in the information provided by different populations, and to provide predictions regarding populations for which no direct data are available. Additionally, mixed-effects models for meta-analysis can provide improved population specific estimates.

The chief goal of this work is to develop meta-analytical methods for the estimation of extinction probabilities under various management actions. We have had very good success using a meta-analytic approach on a variety of other problems (Myers et al. 1995*a*, Myers and Barrowman 1996, Myers 1997), and have

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completed two recent meta-analytical studies for sockeye salmon (Myers et al. 1997*a*, 1998).

Here, we extend existing approaches to combining population parameters among populations, and apply these methods to coho salmon populations. We standardized all the populations considered so that they are all in the same units. This allows all the parameters to be compared among populations. In previous approaches, e.g., Liermann and Hilborn (1997), only a subset of population parameters were treated as comparable among populations.

Our analysis models the freshwater portion of coho life history, so that this information can be combined with independent data on survival at sea to produce improved management models. For example, in Southern British Columbia, coho salmon catches and escapements have declined in the last 20 years and there has been considerable disagreement on the causes of these declines (Walters 1993, Walters and Ward 1998, Beamish et al. 1999). However, it is clear that salmon survival at sea has greatly declined in recent years (Bradford et al. 2000). Our analysis of their freshwater survival can produce estimates of the mean and variation among populations, which can then be combined with long term data on survival at sea. Furthermore, we can produce improved population-specific estimates for individual rivers.

DATA

Our primary source of data is the compilation by Bradford et al. (1997). We have also obtained several more unpublished sources of data (Pacific Biological Station, Nanaimo, British Columbia, Canada, Salmon Archive, BL/2/5). In all, we have data on 14 populations of coho salmon. An in-depth analysis of these and related data is in Bradford et al. (2000).

We will estimate the production of female smolts per female spawner. Note, however, that our spawner units are always the number of female spawners per kilometer of stream, and the units for recruits are the number of female smolts produced per kilometer of stream. The lengths of streams ranged from ~1 km to 92 km, with a median of 7 km. Also, we assume that the sex ratio of smolts is 1:1 (Dittman et al. 1998). This puts data from all streams in common units, thus allowing comparisons among streams.

SPAWNER–RECRUITMENT MODELS

We extend the nonlinear mixed model approach used by Myers et al. (2001) to include a wider range of spawner–recruitment functions and depensation. Let $R_{i,t}$ be recruitment in units of female smolts from cohort t from population i, and let $S_{i,t}$ be the number of female spawners that produced those smolts. For coho salmon, we primarily consider models in which recruitment is a nondecreasing function of spawner abundance, in contrast to models that display overcompensation such as the Ricker model. Coho salmon juveniles are territorial (Sandercock 1991), and little density-dependent mortality appears to occur until territories have filled the habitat, i.e., the stream (Bradford et al. 1997, 2000, Barrowman and Myers 2000). In this case, we would expect survival to remain relatively constant until the habitat was close to being full, and then survival would decrease. This would result in recruitment being proportional to spawner abundance at low spawner abundance, and then leveling off at higher spawner abundance. We consider four spawner–recruitment functions (Fig. 1). In each case, the parameters of the function must be positive.

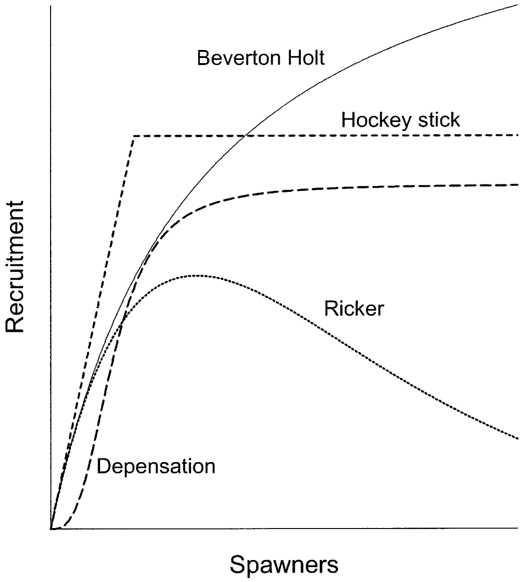

FIG. 1. The four spawner–recruitment curves considered in this paper.

The Beverton-Holt model,

$$R_{i,t} = \frac{\alpha_i S_{i,t}}{1 + (S_{i,t}/K_i)}$$

seems to match the general compensatory population dynamics of coho salmon. The parameter α_i gives the slope at the origin, and is the maximum reproductive rate when multiplied by natural survival at sea. The parameter K_i is the spawner abundance corresponding to half the asymptotic recruitment (carrying capacity.) Barrowman and Myers (2000) showed that, for a single population, the Ricker model often gives more reasonable extrapolations of the slope at the origin than does the Beverton-Holt. Of the models considered, only the Ricker model shows overcompensation, i.e., recruitment declines at high spawner abundances. Barrowman and Myers (2000) and Bradford et al. (2000) also proposed the hockey-stick model:

$$R_{i,t} = \alpha_i \min(S_{i,t}, S_i^*)$$

where S_i^* is the spawner abundance at which density dependence has an effect. Barrowman and Myers

(2000) showed that the hockey-stick model typically gives reasonable extrapolations of the slope at the origin as well as matching the population dynamics of coho salmon. They also proposed two generalizations of the hockey stick that allow for a smoother transition between density-independent mortality and density-dependent mortality: the quadratic hockey stick (not presented here), and the smoother logistic hockey stick,

$$R_{i,t} = \alpha_i \theta_i \mu_i (1 + e^{-1/\theta_i}) \times \left\{ \frac{S_{i,t}}{\theta_i \mu_i} - \log\left[\frac{1 + e^{(S_{i,t} - \mu_i)/(\theta_i \mu_i)}}{1 + e^{-1/\theta_i}} \right] \right\}. \qquad (1)$$

where θ_i is a smoothness parameter and μ_i is the inflection point of spawner abundance (Barrowman and Myers 2000).

A number of authors have expressed concern about depensatory dynamics (Courchamp et al. 1999, Stephens and Sutherland 1999). Myers et al. (1995*a*) investigated depensation for 128 fish populations using a modification of the Beverton-Holt model, which we call the type-1 depensatory Beverton-Holt model:

$$R_{i,t} = \frac{\alpha_i S_{i,t}^{\delta_i}}{1 + S_{i,t}^{\delta_i}/K_i}$$

where δ_i controls the extent of depensation. The parameter α_i has dimensions of recruitment per spawner in all of the models. Except for the depensation model, α_i gives the slope of the function at $S_{i,t} = 0$; it is crucial to setting the limits of overfishing (Mace 1994, Myers and Mertz 1998).

A second way to introduce depensation into a spawner–recruitment model is through multiplication by a term of the form

$$\frac{S_{i,t}}{S_{i,t} + d_i}.$$

We call models altered in this way type-2 depensatory models. The parameter d_i controls the extent of depensation; the original function is obtained when $d_i = 0$. The depensation parameter can be thought of as the number of female spawners per kilometer of stream needed to reduce the expected number of recruits by 50% relative to a model without depensation. This parameterization was used to obtain depensatory versions of the Beverton-Holt and logistic hockey-stick models.

INDIVIDUAL MODEL FITS

We will assume that within a population there is no autocorrelation in the recruitment residuals among years during the freshwater life-history stage (Bradford 1999). We also assume that the log-transformed deviations from the spawner recruitment curve are normal (Myers et al. 1999). Individual maximum likelihood fits of the Beverton-Holt model to these data are shown in Fig. 2.

The data sets vary tremendously in terms of information content due to differences in sample size and the configuration of spawner observations. The data for two rivers, Bingham Creek and Qualicum River, suggest that the slope at the origin is arbitrarily large, i.e., $\alpha_i = \infty$ or equivalently $1/\alpha_i = 0$. Defining $\pi_i = 1/\alpha_i$, it can be shown (Barrowman 2000) that for $\hat{\pi}_i = 0$ to be a least-squares estimate of π_i, it is necessary that

$$\sum_{j=1}^{n_i} \log(R_{i,j}/\tilde{R}_i)/S_{ij} \geq 0$$

where $\tilde{R}_i$ denotes the geometric mean of the observed recruitments in population *i*. Indeed this condition holds for Bingham Creek and Qualicum River, and in both cases, when α_i is not constrained to be positive, a numerical optimizer converges to a negative estimate. We conclude that, for these cases, the likelihood is maximized by an infinite slope at the origin. However, this is not credible: there cannot be more female smolts than the number of eggs produced by a female spawner, which though large (~3500), is certainly finite.

A formal model selection criterion can be used to choose the ''best'' model for the coho spawner-recruitment data. The Akaike Information Criterion (AIC) is commonly used for this purpose. Since each of the three models has the same number of parameters (two), choosing the model with the largest log likelihood is equivalent to using the AIC for model selection (Table 1).

In only one case (Deer Creek) is the maximized log likelihood for the Ricker model larger than that for the Beverton-Holt model. Summing the individual maximized likelihoods (last line of Table 1) shows that the Beverton-Holt model provides much better overall fitting of the data than the Ricker model. The comparison between the Beverton-Holt and the hockey-stick model is more equivocal. The AIC favors the Beverton-Holt for seven of the populations and the hockey stick for the other seven. For several populations, however, the maximized likelihood for the hockey stick is considerably larger than that for the Beverton-Holt.

MODELS

Mixed-effects Models

Our goal is to examine fits of spawner-recruitment models simultaneously for all 14 rivers; we thus need to consider the patterns of deviations of the observations of recruitment from the mean behavior model. Previous work has shown that, in the marine environment, recruitment deviations are correlated at separations of roughly 500 km (Myers et al. 1995*b*, 1997*b*) compared to <50 km in the freshwater environment (Myers et al. 1997*b*). These results apply for coho salmon, for which freshwater survival is almost independent among years for populations >20 km apart, but marine survival is correlated at a much greater spatial scale (Bradford 1999). Thus, in what follows we will assume that deviations from the spawner–recruitment relation-

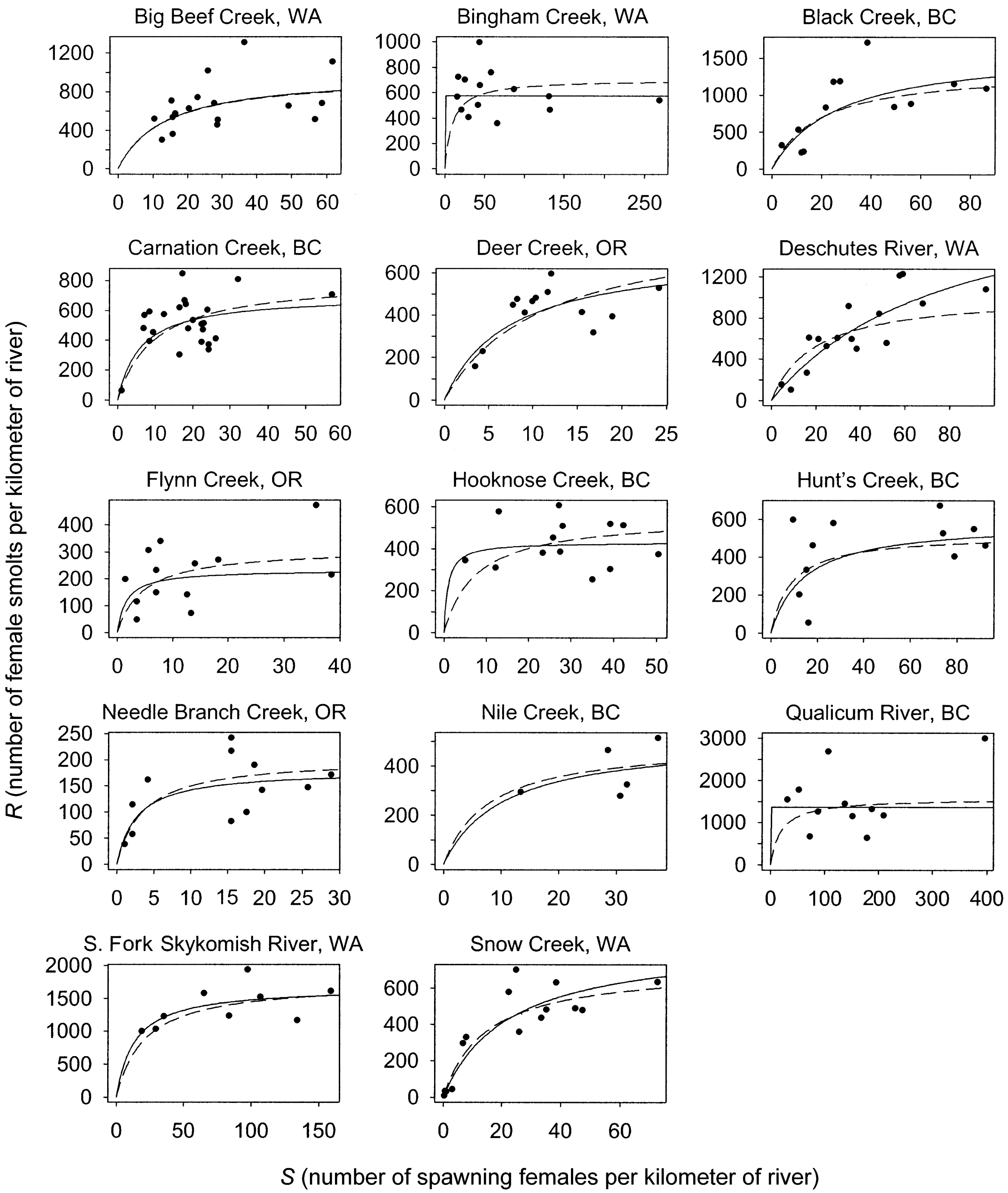

FIG. 2. Coho salmon data with superimposed fitted curves from individual maximum-likelihood fits of the Beverton-Holt model assuming a lognormal recruitment distribution (solid curves) and empirical Bayes curves from a mixed-model fit (dashed curves). Abbreviations are: WA, Washington State, OR, Oregon; and BC, British Columbia.

ship are independent among populations for the freshwater part of the life history.

Our contention is that focusing on one population at a time can be misleading. In this section, we shall demonstrate how this can be avoided by incorporating the estimation of a spawner–recruitment model into a nonlinear mixed-effects model. Myers et al. (1999) used a similar approach for the Ricker model; however, thanks to the linearity of the Ricker model on the log scale, they were able to use linear mixed-effects models. As noted earlier, the Ricker model exhibits overcompensation. Therefore, for coho salmon, the Beverton-Holt

TABLE 1. Maximized log likelihoods for each of the coho salmon populations using the Ricker, Beverton-Holt, or hockey-stick models.

Population	Ricker	Beverton-Holt	Hockey stick
Big Beef Creek, WA	−4.6	−4.2	−4.2
Bingham Creek, WA	−7.2	0.3	0.3
Black Creek, BC	−5.3	−4.9	−4.4
Carnation Creek, BC	−12.4	−8.9	−5.6
Deer Creek, OR	3.5	2.5	7.6
Deschutes River, WA	−4.3	−3.8	−4.7
Flynn Creek, OR	−12.1	−9.7	−10.2
Hooknose Creek, BC	−0.8	1.0	1.1
Hunt's Creek, BC	−8.9	−8.2	−8.5
Needle Branch Creek, OR	−3.4	−2.1	−1.1
Nile Creek, BC	2.7	3.6	3.5
Qualicum River, BC	−8.1	−4.5	−4.5
S. Fork Skykomish River, WA	5.4	7.3	5.7
Snow Creek, WA	−4.9	−4.5	−3.4
Sum	−60.5	−36.3	−28.6

Note: The final row of the table gives the sum of the individual maximized log likelihoods for each model, providing an indication of which model provides the best overall fits.

model seems more appropriate, necessitating the use of nonlinear mixed-effects models.

We begin by developing a nonlinear mixed-effects model for the Beverton-Holt, and later generalize to the other spawner–recruitment models. Suppose we have M populations and suppose that for population i we have n_i observations. We assume additive normal observational errors in log recruitment, i.e., for the Beverton-Holt model,

$$R_{i,t} = \frac{\alpha_i S_{i,t}}{1 + (S_{i,t}/K_i)} e^{\varepsilon_{i,t}}$$

where $\varepsilon_{11}, \ldots, \varepsilon_{Mn_M} \overset{\text{i.i.d.}}{\sim} N(0, \sigma^2)$. Dividing by α_i, we obtain

$$R_{i,t} = \frac{S_{i,t}}{1/\alpha_i + S_{i,t}/(R_{\max,i})} e^{\varepsilon_{i,t}}. \tag{2}$$

Note that $R_{\max,i} \equiv \alpha_i K_i$ is the asymptotic level of median recruitment. We prefer this parameterization because the asymptotic recruitment is well determined for many of the coho populations and has a direct biological interpretation.

Mixed models make additional assumptions by treating some or all of the parameters in Eq. 2 as random effects. Different versions of such models and the methods used for fitting them are discussed in the Appendix. Briefly, the basic model we use (model II) treats the logarithms of both α_i and $R_{\max,i}$ as being normally distributed.

Other models

We fitted models analogous to model II for the Ricker and logistic hockey-stick model with a smoothness parameter, θ, initially of 10. We also fitted three-parameter versions of model II for the type-l and type-2 depensatory Beverton-Holt models and the logistic hockey-stick model. In each of these cases, we assumed that there was no among-population correlation in population parameters.

RAINDROP PLOTS

To display our results we use the recently introduced raindrop plot (N. Barrowman and R. Myers, *unpublished manuscript*). The raindrop plot provides a graphical gauge of the relative plausibility of different values, and is useful when conventional point estimates of parameters with confidence limits are not adequate. Conventional estimates are not appropriate when the likelihood is not approximately normal, as can occur with small sample sizes or nonlinear models. To understand how the individual raindrop shapes are obtained, consider Fig. 3, showing the profile log likelihood for α for Hunt's Creek, British Columbia.

A modification of the scheme for producing raindrop shapes can be used to display meta-analytic summaries showing confidence regions for the mean, estimated random-effect distributions, and Bayesian posterior and predictive distributions. In place of the log likelihood, we use the log-probability density. In other words, we use a raindrop based on the log density over the highest density region (Hyndman 1996).

RESULTS

We fitted nonlinear mixed models using the Beverton-Holt, logistic hockey-stick, and depensation spawner–recruitment models. Fitting was performed using the NLME software in S-PLUS (Statistical Sciences, Seattle, Washington, USA), which implements the method of Lindstrom and Bates (1990). The Beverton-Holt mixed model, described in detail earlier (model II), produced very reasonable individual estimates of log α and asymptotic recruitment (Fig. 2).

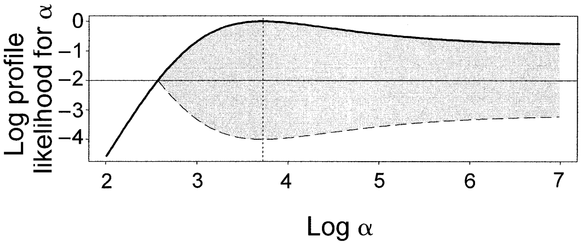

FIG. 3. Profile log likelihood for α for Hunt's Creek, British Columbia, showing how the raindrop shape is obtained. The profile log likelihood (solid curve) has been graphed with its maximum (indicated by the dotted vertical line) equal to 0. A drop in the log likelihood of ~2 (indicated by the horizontal line) is significant at the 0.05 level. In this case, the ~95% confidence interval for log α ranges from ~2.5 to infinity. By reflecting the part of the curve above −2 about the horizontal line, we obtain a symmetric region (shaded in the figure). The height of the region at a particular value of log α relative to the maximum height gauges the relative plausibility of that value.

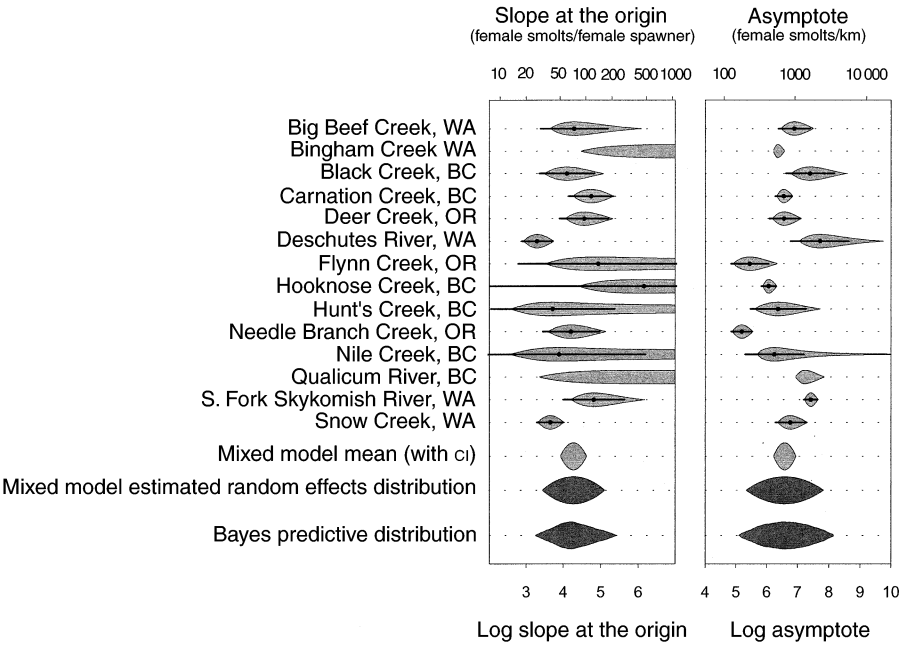

FIG. 4. Raindrop plots for the slope at the origin, α, and asymptotic level, R_{max}, in the Beverton-Holt model for the 14 coho salmon populations, together with meta-analytic summaries. The light-shaded raindrop shape for each population depicts a profile-likelihood-based 95% confidence interval for α for that population. The superimposed dot is the maximum-likelihood estimate obtained by nonlinear regression. Note that for two populations, convergence of the nonlinear least-squares algorithm was not obtained because of ''ramping'' behavior in the likelihood surface. In cases where convergence was obtained, an approximate asymptotic 95% confidence interval (based on nonlinear least squares theory) around the estimate is shown. The asymptotics are often poor in that the asymptotic confidence interval often does not match the profile-likelihood-based interval well. The three taller raindrop shapes at the bottom are meta-analytic summaries from the nonlinear mixed model, and should be interpreted differently from the raindrops for individual populations. The ''mixed model mean (with CI)'' represents the estimated mean log α from the mixed model with a 95% confidence interval obtained from the asymptotic standard error of the mean. The two bottom raindrop shapes are shown darker to emphasize that they represent distributions: in place of the log likelihood, we use the log probability density, with a cutoff corresponding to a probability of 0.95. The ''mixed-model estimated random effects distribution'' represents the normal distribution with mean given by the estimated mean log α from the mixed model, and variance given by the estimated variance of log α obtained from the mixed model. The ''Bayes predictive distribution'' represents the induced prior from the Bayesian analysis (Efron 1996).

Raindrop plots for each population of log α and asymptotic recruitment (Fig. 4) show the relative information content provided by each data set and their relation to the estimated means of the respective parameters. Maximum-likelihood estimates of the variability among populations (the ''mixed-model estimated random-effects distribution'') of log α and asymptotic recruitment are also depicted.

The Beverton-Holt mixed model produced estimates of the mean (among populations) of log α and asymptotic recruitment larger than the hockey-stick model (Table 2). Thus, even though the models fit the data

TABLE 2. Comparison of model fits.

Model	Maximized approximate log likelihood	Log α			Log R_{max}			Log depensation parameter		
		Mean	SE	SD	Mean	SE	SD	Mean	SE	SD
Beverton-Holt (BH)	−116.1	4.27	0.18	0.43	6.58	0.18	0.64			
Logistic hockey stick (LHS)	−116.4	3.97	0.13	0.32	6.35	0.17	0.62			
Type-1 depensatory BH	−116.1	4.08	0.22	0.38	6.51	0.18	0.61	0.13	0.10	0.03
Type-2 depensatory BH	−115.9	4.34	0.21	0.40	6.57	0.19	0.63	−2.01	1.52†	1×10^{-7}
Type-2 depensatory LHS	−116.3	3.99	0.15	0.33	6.35	0.17	0.61	−3.29	3.77†	0.003

Notes: SE, standard error of estimated mean; SD, standard deviation of random effect. Note that for the depensation models, α does *not* have the interpretation of slope at the origin. The logistic hockey stick (LHS) and its depensatory version both used a smoothness parameter θ = 10.

† The maximum-likelihood estimates are not normally distributed. Treating depensation as a fixed effect and examining profile likelihoods reveals an undefined lower boundary and a 95% upper boundary (from a χ^2 approximation) of −0.38 for the Beverton-Holt (BH) model and −0.73 for the LHS model.

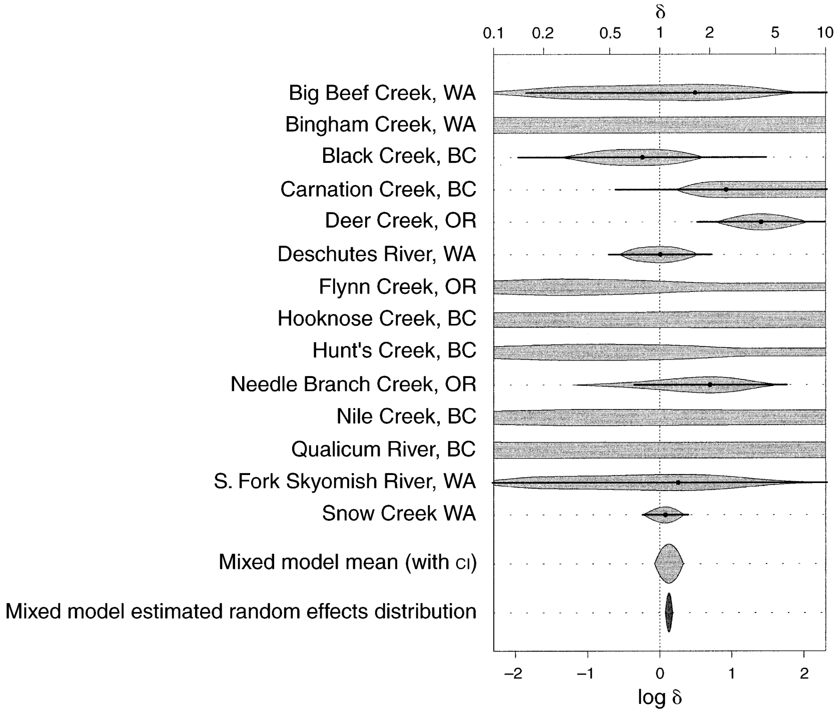

FIG. 5. Raindrop plot for the depensation parameter, δ, for the type-l depensatory Beverton-Holt model for the 14 coho salmon populations, together with meta-analytic summaries (see Fig. 4 for details).

equally well, the hockey-stick model suggests that coho should be managed much more conservatively than does the Beverton-Holt model. The random-effects distribution is shifted up for the Beverton-Holt compared to the hockey-stick model. However, both models predict roughly the same lower limit for α: 95% of the populations are estimated to have an α between 30 and 169 for the Beverton-Holt model, while the range for the hockey stick is between 28 and 68.

We do not give details on the Ricker model for reasons given earlier. Note, however, that the maximized log likelihood of the Ricker mixed model was very similar to that of other models fit to the data (Table 2).

DEPENSATION MODELS

In the nonlinear mixed models previously discussed, there were two random effects, the log slope at the origin, log α, and the log asymptotic level. For the depensation models, we also treated log δ or log d as a random effect. Note that for these models, α can no longer be interpreted as the slope at the origin.

Most data sets contained almost no information on depensation (Fig. 5), and in no case was the addition of depensation in the mixed-effect model close to being statistically significant by a likelihood ratio test. Also, in all cases, the mean level of depensation estimated was very small.

The other two models of depensation, the depensatory Beverton-Holt and depensatory hockey stick, show similar results (Table 2). In each case, they show that the mean depensation appears to occur only at very low population densities, i.e., at 0.13 and 0.037 female spawners per kilometer of river. Even the upper 95% confidence limit for the mean depensation (derived from the profile log likelihood) is $d = 0.68$ females per kilometer of river, and $d = 0.48$, respectively (Table 2). This implies that, on average, depensation can only occur at very low population densities. At these population densities, some streams used in the analysis would have no fish at all, so that depensation would occur trivially.

BAYESIAN ANALYSIS AND ROBUSTNESS ANALYSIS

For robustness, we repeated the above analyses using a fully Bayesian analyses. In general, we found the results similar to the mixed-model results, so we only give the results for the Beverton-Holt model in detail. Vague priors were used for the means of log α and log K (normal with mean 0 and variance 10 000). Approximately uninformative priors for the variance components were specified in terms of precision = 1/variance, using a gamma distribution with shape parameter 0.001 and scale parameter 1000. Markov chain Monte Carlo (MCMC) sampling was performed with BUGS software (Bayesian inference Using Gibbs Sampling; Gilks et al. 1994, 1996). For this model, BUGS uses Metropolis-within-Gibbs sampling, which requires bounded ranges for the log α_i and log K_i random effects. The ranges applied were (0.5, 10) for log α; and (−30, 30) for log K_i. Neither the priors used nor the bounded ranges applied had a strong influence on the results.

The Bayes predictive distribution was calculated for the slope at the origin and the asymptote (Fig. 4). In both cases, the fully Bayes predictive distributions are wider than the mixed-model estimate of the random-effects distribution. This is expected for theoretical reasons, i.e., the fully Bayes predictive distribution incorporates all of the uncertainty in the parameter estimates (Efron 1996). However, the Bayes predictive distributions are only slightly wider than the mixed-model estimates, which suggests that the simpler-to-calculate mixed-model estimates are adequate approximations. Similar results were obtained for other models.

For robustness, we also considered a variety of modifications of the mixed-effects models: alternative estimates of smoothness for the logistic hockey stick and correlations among the random effects. In no case did these modifications significantly improve the fit, or lead to any important changes in the results.

DISCUSSION

In this paper, we carried out parallel analyses using nonlinear mixed-effects models and fully Bayes approaches, extending the nonlinear mixed-model approach used by Myers et al. (2001) to include a wider range of spawner–recruitment functions and depensation. A related model for depensation was developed by Liermann and Hilborn (1997), however their approach differed in two important ways. First, they treated only a subset of population parameters as comparable among populations. Second, rather than a mixed-model or fully Bayes approach, they used a hybrid Bayesian approach involving several approximations. Notably, the nonlinear mixed-effects model approach we have described is much simpler to implement.

Critical to our analysis is that all model parameters are in units that can be compared among populations. The α is in units of female smolts produced per female spawner, $R_{\max}$ is in units of female smolts produced per kilometer of river, and the depensation parameter is either a dimensionless number (δ) or the spawner abundance per kilometer of river, for which the expected recruitment is one-half what it would be if there were no depensation (d). This ‘‘unit comparability’’ is indispensable for meta-analytic models. Model fits to individual rivers can produce nonsensical results, e.g., infinite α or carrying capacity (Barrowman and Myers 2000).

This study shows that the choice of model can markedly affect ones interpretation of the data, even though the goodness of fit of the models are almost identical. The Beverton-Holt mixed-effects model shows a median slope of 71.5 female smolts to female spawners, while the logistic hockey stick shows a median slope of 53. This difference has important consequences for the estimation of extinction probabilities, and for the optimal management of the species. Since it is hard to imagine how density dependence could keep increasing at very low densities, the hockey-stick estimate may be preferred.

The individual and mixed-model fits were dramatically different. For example, in Table 1, the sum of the maximized likelihoods for the hockey-stick model was greater than for the Beverton-Holt fits. However, this was not the case in the overall fit of the mixed-effect models, which gave virtually identical fits (Table 2). This difference is important, and the mixed effects results are probably more biologically and statistically meaningful because they incorporate realistic constraints on the differences among populations.

The estimate of the mean log α depends upon whether a depensatory model is used (Table 2). In other words, the estimation of log α is not independent of the estimation of the depensatory term. This creates a problem if empirically derived prior distributions for depensation are applied to models in which the parameters were estimated in the absence of a depensatory term. For example, Liermann and Hilborn (1997) produced predictive distributions for depensation, which could theoretically be used as priors in a Bayesian risk assessment. What is actually needed in this case is a joint prior for the depensatory parameter and log α, thus magnifying the complexity of the problem considerably. Although the effect of including a depensatory factor on the estimation of α is small in our case, the estimates of the mean do differ in the depensatory and nondepensatory models (Table 2). This problem is more acute with modifications of the Beverton-Holt than the hockey stick.

CONCLUSIONS

Meta-analytic techniques provide a way to obtain estimates for populations where little is known. In the case of the coho salmon, we were able to obtain estimates of α, the rate at which female spawners can produce female smolts at low population sizes (and thus critical to predicting extinction) for each stream, as well as an estimate of the variance of α. This information could be incorporated directly into an extinction model, thus overcoming the difficulties highlighted by Routledge and Irvine (1999) about imprecise predictions.

We also have provided an improved approach to estimating depensation. Our estimates of depensation provide much-improved quantitative information compared to previous approaches. For example, we have obtained estimates of the population size where depensation will occur, whereas previous approaches have provided much less useful information (Myers et al. 1995*a*).

Also, we have demonstrated that you cannot estimate depensation independently from other model parameters. That is, models that include a depensation parameter change the meaning of the other parameters, and the parameters cannot be considered independent a priori. This results in a difficulty in practice in applying Bayesian population dynamic models that include depensation.

Considerable effort has been devoted to the development of both analytical and simulation models that estimate extinction probabilities of natural populations (Lande 1993, Ludwig 1996, Fagan et al. 1999). On the whole, these models suffer from a lack of plausible parameter values, as there is often very little data available. Instead, parameters are drawn from distributions without firm empirical bases and the conclusions are difficult to apply in specific cases (Foley 1994, Johst and Wissel 1997). This problem is particularly acute for parameters that describe population dynamics at low population sizes. Moreover, it is the dynamics at low sizes that are of greatest import when estimating extinction risk.

Meta-analytic techniques are crucial for estimating the among-population variability in population parameters, which are needed for conservation and management models. With these techniques, we have the capability of estimating not only the means of ecological parameters, but their spread as well. The populations whose parameters are at the extremes, and which may be more susceptible to extinction, may be the ones we care about the most.

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APPENDIX

A description of models and methods for combining population dynamics data is available in ESA’s Electronic Data Archive: *Ecological Archives* A013-012-A1.