



INDEPENDENT SCIENTIFIC ADVISORY BOARD

Predation Metrics Report

Developing and Assessing Standardized Metrics to
Measure the Effects of Predation on Columbia River
Basin Salmon and Steelhead

ISAB 2016-1

OCTOBER 5, 2016



Cover photos of California sea lions at East Mooring Basin, Astoria, Oregon, and Caspian tern by Tony Grover. Cover design by Eric Schrepel.



Independent Scientific Advisory Board

for the Northwest Power and Conservation Council,
Columbia River Basin Indian Tribes,
and National Marine Fisheries Service
851 SW 6th Avenue, Suite 1100
Portland, Oregon 97204

Kurt D. Fausch, Ph.D., Professor of Fisheries and Aquatic Sciences, Department of Fish, Wildlife, and Conservation Biology at Colorado State University, Fort Collins, Colorado

Stanley Gregory, Ph.D., Professor Emeritus of Fisheries at Oregon State University, Corvallis, Oregon

William Jaeger, Ph.D., Professor of Applied Economics at Oregon State University, Corvallis, Oregon (also serves on IEAB)

Cynthia Jones, Ph.D., Eminent Scholar and Professor of Ocean, Earth, and Atmospheric Sciences; Director of the Center for Quantitative Fisheries Ecology; and A.D. and Annye L. Morgan Professor of Sciences at Old Dominion University, Virginia

Alec G. Maule, Ph.D., Fisheries Consultant and former head of the Ecology and Environmental Physiology Section, United States Geological Survey, Columbia River Research Laboratory

Katherine W. Myers, Ph.D., Research Scientist (Retired), Aquatic and Fishery Sciences, University of Washington, Seattle, Washington

Gregory T. Ruggerone, Ph.D., (ISAB Chair) Fisheries Scientist for Natural Resources Consultants, Seattle, Washington

Laurel Saito, Ph.D., P.E., Nevada Water Program Director, The Nature Conservancy of Nevada, Reno, Nevada

Steve Schroder, Ph.D., (ISAB Vice-chair) Fisheries Consultant and Fisheries Research Scientist (Retired), Washington Department of Fish and Wildlife, Olympia, Washington

Carl J. Schwarz, Ph.D., Professor of Statistics and Actuarial Science at Simon Fraser University, Burnaby, British Columbia, Canada

Thomas Turner, Ph.D., Professor of Biology and Associate Dean for Research at the University of New Mexico, Albuquerque, New Mexico

Chris C. Wood, Ph.D., Research Scientist (Retired), Pacific Biological Station, Department of Fisheries and Oceans, Nanaimo, British Columbia, Canada (*ad hoc ISAB member*)

ISAB Ex Officios and Manager

Michael Ford, Ph.D., Director of the Conservation Biology Program at the Northwest Fisheries Science Center, Seattle, Washington

Nancy Leonard, Ph.D., Manager, Fish, Wildlife, and Ecosystem Monitoring and Evaluation, Northwest Power and Conservation Council, Portland, Oregon

Zach Penney, Ph.D., Fisheries Science Manager at the Columbia River Inter-Tribal Fish Commission, Portland, Oregon

Erik Merrill, J.D., Manager, Independent Scientific Review, Northwest Power and Conservation Council, Portland, Oregon

ISAB Predation Metrics Report: Developing and Assessing Standardized Metrics to Measure the Effects of Predation on Columbia River Basin Salmon and Steelhead

Contents

Acknowledgements.....	iv
Executive Summary.....	1
1. Introduction.....	3
2. Review Process.....	6
Sources of Information.....	6
Key Assumptions.....	7
Process for Evaluating Alternative Metrics.....	8
3. Why Compensation in Predation Mortality is Important to Developing a Predation Metric.....	12
Density Dependence.....	13
Selective Predation (see Chapter 8, Appendix A, for a detailed review and references)....	15
Selective predation by fishes.....	15
Selective predation by birds.....	16
Selective predation by marine mammals.....	16
Predator Switching to Different Prey.....	16
Estimating Compensation.....	19
4. Strategic Issues for Predation Metrics.....	23
What Salmon Life Stages and Predators Are Assessed by Predation Metrics?.....	23
What Management Concerns are Addressed by Predation Metrics?.....	24
5. A Life-Cycle Approach to Comparing Different Sources of Predation.....	28
6. Review of Three Alternative Metrics.....	31
Equivalence Factors (EF).....	32
Theoretical derivation.....	33
Establishing the relationship between abundances.....	37
Advantages/disadvantages of equivalence factors metrics.....	38
Delta Lambda ($\Delta\lambda$).....	39
Theoretical derivation.....	39
Using delta lambda to compare management actions.....	40
Advantages and disadvantages of delta lambda.....	41
Probability of Extinction in the Long-term.....	42
Choice of Suitable Predation Metrics.....	42

7. Conclusions and Recommendations	46
8. Appendices	47
Appendix A. Selective Predation.....	47
Selective predation by fishes.....	47
Selective predation by birds.....	49
Selective predation by marine mammals.....	51
Appendix B. Theoretical Issues in Estimating Compensation.....	53
Derivation of a key result for estimating covariance between overall survival and harvest/predation	55
Appendix C. Functional and Numerical Response of Predators.....	56
Functional responses.....	56
Numerical response of predators.....	59
Appendix D. Example Calculations with a Life-cycle Model.....	62
9. Literature Cited.....	68

List of Sidebars

Sidebar 2.1. Examples of Potential Alternative Predation Metrics from Briefings to the ISAB	8
Sidebar 2.2. A Hierarchical Approach to Evaluating Derivation Criteria	10
Sidebar 3.1. Functional and Numerical Responses.....	17

List of Tables

Table 3.1. Different types of individual-based data and associated statistical methods used to estimate the correlation between anthropogenic and natural mortality and the degree of compensation	19
Table 6.1 Comparison of four life-cycle models used to illustrate the impacts of changes in in-river survival.....	31
Table 6.2. Informal evaluation of three potential alternative predation metrics selected by the ISAB	43
Appendix Table D.1. Comparison of four life-cycle models used to illustrate the impacts of changes in in-river survival [same as Table 6.1]	62
Appendix Table D.2. Summary of number of fish at each stage in four life-cycle models	67

List of Figures

Figure 1.1. Map of the Columbia River Basin showing locations of major predator control projects and the Federal Columbia River Power System (FCRPS) dams.....	5
--	---

Figure 3.1. Stock-recruitment (S-R) relationships showing the relative effects of additive or compensatory predation mortality when density dependence is very weak or strong .. 14

Sidebar Figure 3.1. The general shapes of the three functional response curves and the corresponding percent mortality curve assuming constant abundance of predators..... 18

Figure 4.1. Life cycle of Columbia River anadromous Pacific salmonids 26

Figure 6.1. General definition of an equivalence factor (EF) to convert changes in abundance at one stage of a life cycle to changes in abundance at a second stage of the life cycle 33

Figure 6.2. Relationship between smolts at Lower Granite Dam (LGR) and returning adults at Bonneville for the four life-cycle models 35

Figure 6.3. Relationship between recruits (returning adults) and (parent) spawners for four life-cycle models..... 36

Appendix Figure C.1. The general shapes of the three functional response curves identified by Holling (1965) and the corresponding percent mortality curve assuming constant abundance of predators 57

Appendix Figure D.1. Simplified life-cycle model based on the Grande Ronde population ... 62

Appendix Figure D.2. Simplified life-cycle model based on the Grande Ronde population with an (arbitrary) addition of density dependence on production of age-3 adults 65

Acknowledgements

We gratefully acknowledge the many individuals who helped us complete this report.

Columbia River Basin researchers organized and provided excellent presentations, briefings, and discussions related to predation metrics used in their studies or potential metrics to be considered: Dave Roberts and John Skidmore (Bonneville Power Administration); Robert Lessard and Doug Hatch (Columbia River Inter-Tribal Fish Commission); Katie Barnas, Eric Ward, Michelle Wargo Rub, and Rich Zabel (NOAA/Northwest Fisheries Science Center); Mark Sorel (Ocean Associates Inc. contracted to NOAA/NWFSC); Adam Storch (Oregon Department of Fish and Wildlife); Dave Trachtenbarg (US Army Corps of Engineers); Don Lyons and Dan Roby (Oregon State University); Steve Williams (Pacific States Marine Fisheries Commission); Robin Brown (Oregon Department of Fish and Wildlife); Ken Collis and Allen Evans (Real Time Research); and Steve Haeseker (U.S. Fish and Wildlife Service).

Beth Sanderson (NOAA/NWFSC) was responsive to inquiries and added critical information and references for the report.

The ISAB coordinator and Ex Officio members helped define our review, organized briefings, provided context, researched data, and commented on drafts: Nancy Leonard (Council), Zach Penney (CRITFC), Mike Ford (NOAA), and Erik Merrill (ISAB Coordinator). Robert Lessard assisted Zach Penney in his role as Ex Officio and provided background information, data, and comments that improved our report.

Tony Grover, Council Fish and Wildlife Director, provided the cover photos, and Eric Schrepel, Council Web Specialist, designed the cover. The Council administrative staff supported our meetings and briefings, and Kendra Coles helped with final proofing of literature cited.

ISAB Predation Metrics Report: Developing and Assessing Standardized Metrics to Measure the Effects of Predation on Columbia River Basin Salmon and Steelhead

Executive Summary

At the [request](#) of the Northwest Power and Conservation Council, the Independent Scientific Advisory Board (ISAB) reviewed and recommended potential alternative metrics for evaluating and comparing the effects of predation at different stages in the life cycle of anadromous salmon and steelhead in the Columbia River Basin. This ISAB review is intended to inform a future technical workgroup charged with developing standardized predation metrics to help determine the effectiveness of predator management actions. Current predator control efforts in the Columbia River Basin intended to benefit salmon and steelhead include lethal removal of northern pikeminnow and northern pike and non-lethal and lethal methods to control avian predators (primarily ringed-bill and California gulls, Caspian terns, and double-crested cormorants) and pinnipeds (primarily California sea lions).

The ISAB's conclusions and recommendations are based on a targeted but not exhaustive literature review and a series of scientific and technical briefings by experts working in the Basin. The ISAB considered three types of alternative metrics: two are used to evaluate short-term effects of predation on salmon, and a third is used to examine long-term effects. The ISAB developed criteria that can be used to informally compare alternative metrics and a hierarchical approach for evaluating their usefulness.

At first glance, developing a metric to evaluate the consequences of predation on salmonid populations might seem straightforward. Predators take individuals from a population and cause a corresponding decline in salmonid abundance. However, it can be misleading to assume that mortality at each life stage accumulates additively over the salmonid life cycle if other factors *compensate* for this mortality.

The ISAB considers compensatory mortality the most important uncertainty to address when developing a predation metric. Compensatory mortality occurs when predation mortality at one life stage is offset to some degree by decreased mortality at the same or subsequent life stages. For example, a predator might eat injured or weak fish that would have died before reaching adulthood; therefore, controlling this predator would not result in more adult fish. The ISAB reviewed evidence for mechanisms of compensation, including (1) density dependent survival due to factors other than predation, (2) selective predation based on fish size and condition, (3) and switching behavior of predators, which may be caused by a change in abundances of alternative prey species or when secondary predators increase predation on salmon following control of the primary predator. Considerable compensation in predation-related mortality may occur between juvenile and adult life stages, but additional compensation may also occur during the subsequent spawner-to-smolt stage, indicating the need to consider predation within the context of the entire life cycle. Much of this compensation may stem directly from density dependence. For example, loss of 50% of a juvenile salmon population in response to predation or other factors would

likely reduce intraspecific competition for resources, potentially leading to increased growth and survival among the survivors.

A review and comparison of three alternative metrics using a standard set of evaluation criteria revealed that a single metric would not be adequate for evaluating all goals.

The ISAB recommends:

1. Using and further refining two types of metrics currently in use in the Basin:
 - (a) *Equivalence-factor metrics* (for example, adult equivalents), which can be used to compare the effects of predation on salmon and steelhead at different points in their life cycle.
 - (b) *Change in population growth rate metric* (also called *delta lambda*, $\Delta\lambda$), which can be used to compare how different predation scenarios affect rates of population recovery or decline.
2. Adjusting the *equivalence-factor metrics* and the *population growth rate metric* ($\Delta\lambda$) to account for assumed or estimated compensation in mortality.
3. Placing predation mortality in the context of a life-cycle model.

The ISAB concludes that individual metrics are useful, but metrics can be more informative when incorporated in a life-cycle model that can help disentangle multiple factors affecting salmon survival and interactions among those factors. Furthermore, such processes and interactions can be evaluated in modeled scenarios and verified with data. This approach could help guide research, monitoring, and evaluation of predation throughout the salmonid life cycle, both to provide the data necessary to parameterize and verify models, and to refine metrics. A significant challenge will be to estimate the degree of compensation associated with predation and predator control actions at different life stages. If estimates of compensation are not available, then assumptions about potential compensation should be considered when evaluating predator effects on salmon and steelhead populations and the benefits of predator control programs. Finally, the ISAB encourages the future workgroup charged with developing a standardized predation metric(s) to fully consider our recommended metrics and also explore additional alternative methods and metrics.

1. Introduction

The strategy for predator management in the Columbia River Basin under the Northwest Power and Conservation Council's 2014 Fish and Wildlife Program (the Program) is to "improve survival of salmon and steelhead and other native focal fish species by managing and controlling predation rates" ([Council Document 2014-12](#), pages 49-51). A general measure of the Program's Predator Management strategy calls for evaluation of predator-management actions in the Basin:

The federal action agencies, in cooperation with the Council, state and federal fish and wildlife agencies, tribes, and others, should convene a technical work group to: (a) determine the effectiveness of predator-management actions; and (b) develop a common metric to measure the effects of predation on salmonids, such as salmon adult equivalents, to facilitate comparison and evaluation against other limiting factors. Once developed and agreed upon, future predator-management evaluations funded by the action agencies should include a determination of the effectiveness of such actions and the common predation metric in their reports.

The Council's March 3, 2016, [review request letter](#) to the Independent Scientific Advisory Board (ISAB) calls for a review to "help inform future technical work group efforts" with regard to developing a common metric.¹ This metric and the associated monitoring should inform the effectiveness of predator management actions. As stated in the letter, "the Council requests that the ISAB recommend a common metric to measure the effects of predation on salmonids. Specifically, the Council encourages the ISAB to discuss alternative metrics and summarize the benefits and limitations of each as they relate to the goal of comparing different sources of predation across the salmon life cycle." The letter also notes that the Council has recommended deferment of the formation of a technical workgroup on predator-management issues until the ISAB can provide information to help inform the future workgroup's efforts.

Accordingly, the goal of this ISAB review is to address the Council's March 3, 2016 request. The aim is to consider standard, quantitative metrics that apply to any salmonid (salmon or steelhead) life stage, allowing for a comparison of predation mortality across the salmonid life cycle. The metric or metrics should serve multiple goals, such as evaluating predation as a factor limiting recovery, evaluating the effectiveness of predator management, and adjusting harvest levels to account for predation impacts. Significant fiscal and social costs are associated with predator management actions. This ISAB report addresses the question: What metric or metrics enable a comparison of various predator management actions (or inaction)? Since developing one standardized metric may not serve all purposes or be feasible with existing data, this ISAB review also describes general principles and criteria to consider when developing and choosing predation metrics and evaluates the pros and cons of alternative metrics.

¹ A metric is defined as "a value resulting from the reduction or processing of measurements." (Source: www.monitoringresources.org/Resources/Glossary/Index)

Predator management in the Columbia-Snake River Basin focuses on control of native species of predators of salmonids in habitats altered by the Federal Columbia River Power System (FCRPS) hydrosystem and at disposal sites of dredge spoils in the mid and lower Columbia River and estuary (Figure 1.1). Predation in these habitats affects 13 species² of Columbia River Basin salmon and steelhead listed for protection under the Endangered Species Act (ESA).

Major predator management efforts in the Basin currently include:

- lethal removal of northern pikeminnow (*Ptychocheilus oregonensis*) by sport-reward and dam-angling fisheries (www.pikeminnow.org; Storch et al. 2013)
- hazing, other deterrents, and lethal take of avian predators, primarily ringed-bill gulls (*Larus delawarensis*), California gulls (*Larus californicus*), and double-crested cormorants (*Phalacrocorax auritus*) at lower Snake and Columbia River dams (www.cbulletin.com/430260.aspx)
- non-lethal and lethal efforts to reduce the number of Caspian terns (*Hydroprogne caspia*) and double-crested cormorants on dredge spoil islands in the lower Columbia River and estuary (See US Army Corps of Engineers [USACE] web documents for [cormorants](#) and [terns](#))
- redistribution of Caspian terns from Goose and Crescent Island nesting colonies in the mid-Columbia River to other nesting sites in the western United States (see [USACE Inland Avian Predation Management Plan](#))
- non-lethal and lethal methods to control predation by pinnipeds, primarily California sea lions (*Zalophus californianus*), at Bonneville Dam (see [NOAA](#), [CRITFC](#), [ODFW](#), and [WDFW](#) web documents).

Management of nonnative fish predators of salmonids in habitats altered by the FCRPS is largely limited to changes in state fishing regulations (removal or increase in daily catch limits and possession limits and/or modified size limits) for a few species that support popular recreational fisheries, i.e., smallmouth bass (*Micropterus dolomieu*), walleye (*Sander vitreus*), northern pike (*Esox lucius*), and channel catfish (*Ictalurus punctatus*) (e.g., [ODFW](#) and [WDFW](#) regulations). Recent efforts are underway to control abundance and dispersal of northern pike in the Columbia Basin upstream from the anadromous salmonid zone (Bean 2015, ISRP 2016-6, 2016-7).

The organization and objectives of this ISAB Predation Metrics Report follow a logical path toward developing a predation metric. Chapter 2 describes the ISAB's methods and assumptions for this review. Chapter 3 provides an overview of the importance of compensatory mortality when developing a predation metric, including statistical issues. Chapter 4 reviews conceptual issues in managing predation. Chapter 5 reviews a life-cycle approach to comparing different sources of predation. Chapter 6 reviews the benefits and limitations of alternative metrics. Chapter 7 summarizes conclusions and provides recommendations. Chapter 8 (Appendices) provides detailed evidence for (1) compensatory mortality (Appendix 8A), (2) theoretical derivations of compensatory and additive predation mortality (Appendix 8B), (3) functional and numerical responses of

² As listed under the ESA, species is defined as a distinct population segment (DPS) or an Evolutionarily Significant Unit (ESU) for salmon. Source: NOAA Fisheries, [Protected Resources Glossary](#).

predators (Appendix 8C), and (4) example calculations with a life-cycle model (Appendix 8D). Chapter 9 lists all references cited in the report and appendices.

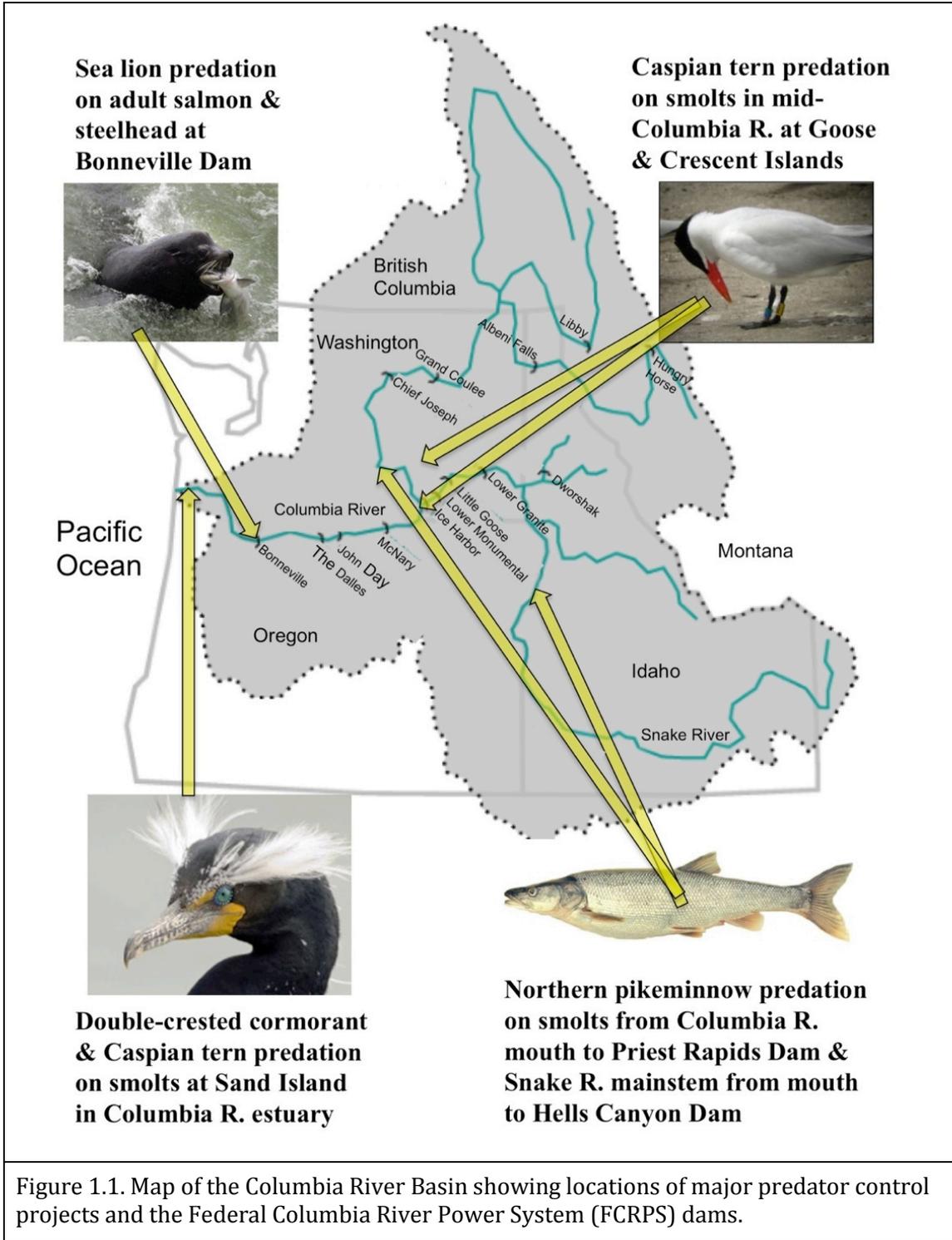


Figure 1.1. Map of the Columbia River Basin showing locations of major predator control projects and the Federal Columbia River Power System (FCRPS) dams.

2. Review Process

Sources of Information

The methods used by the ISAB to provide the requested independent scientific advice and recommendations followed the [ISAB's formal review procedures](#). Materials reviewed by the ISAB primarily included published scientific journal articles and unpublished reports (grey literature) by government agencies and other entities working in the Basin, as shown in citations in the text and list of references. Although an exhaustive review of the scientific literature on predation was beyond the scope of our assignment, the ISAB members were familiar with the foundational scientific literature on predation and computer search engines were used to find additional relevant sources of information from academic journals and the internet.

To obtain the most recent and relevant information, the ISAB also requested and received oral briefings by scientific and technical experts involved in the Basin's ongoing predator-control research, monitoring, and evaluation programs and projects. The briefings were held during three 1-day meetings of the ISAB in Portland, Oregon:

April 29, 2016

- *Incorporating predation into life-cycle models/Pinniped-predation mortality of adult Chinook salmon through the Columbia River estuary*, Rich Zabel, NOAA Fisheries, Northwest Fisheries Science Center (NWFSC) ([presentation](#))
- *Estimating consumption of Chinook salmon by predators, Salish Sea and coastwide*, Eric Ward, NOAA/NWFSC ([presentation](#))
- *Predation metrics, population dynamics, and resilience*, Robert Lessard, CRITFC ([presentation](#))

May 20, 2016

- *Tests of whether double-crested cormorants are an additive versus compensatory source of mortality for Snake River steelhead*, Steve Haeseker, Columbia River Fish and Wildlife Conservation Office, U.S. Fish and Wildlife Service ([presentation](#))

July 21, 2016

- *The Northern Pikeminnow Management Program: predation reduction based on science*, Adam Storch (ODFW) and Dave Roberts (BPA); Q and A: John Skidmore (BPA) and Steve Williams (PSMFC) ([presentation](#) [download and select "slideshow" view] and [audio](#))
- *What do we know about the role of nonnative fish in Pacific NW ecosystems?* Katie Barnas (NOAA/NWFSC) ([presentation](#) and [audio](#))
- *Adult spring/summer Chinook salmon estuarine and lower Columbia River survival and run timing*, Michelle Wargo Rub (NOAA-NWFSC) ([presentation](#) and [audio](#)); Q and A: Doug Hatch and Bob Lessard (CRITFC)
- *Avian predation metrics: colonial waterbird predation on juvenile salmonids from the Columbia Basin*, Allen Evans and Ken Collis (Real Time Research) ([presentation](#) and [audio](#))
- *Inland Avian predation management plan*. Dave Trachtenbarg (USACE, Walla Walla) ([presentation](#) and [audio](#))

The briefings provided information to the ISAB on the use of mathematical and statistical models to develop predation metrics, current metrics used by predator control programs in the Basin, and the use of tagging and tracking investigations to estimate and evaluate predator and salmonid prey abundance, predator-prey interactions, and salmonid migration timing and survival. The presenters were also invited to share relevant published and grey literature, to suggest potential metrics, and discuss the benefits and limitations of these metrics, as well as future sampling and data needs for developing predation metrics.

Key Assumptions

Past reviews by the ISAB/ISRP have highlighted many important assumptions that need to be considered when developing a predation metric, and these assumptions are addressed in greater detail throughout this report:

- Predators can have a significant impact on the survival of salmonids at all life stages [in both pristine and developed watersheds] ([ISAB 2015-1](#), p. 9, pp. 121-125; see Chapter 4).
- The overall impact of predators on a salmonid population depends on the feeding rate of individual predators [i.e., functional response], the number of predators, and the length of time the salmonids are vulnerable ([ISAB 2011-1](#), p. 80; [ISAB 2015-1](#), p. 9, p. 121; see Chapter 4). This combination of factors can be expressed as the total percent mortality for the prey population (see Chapter 8, Appendix C).
- Losses to predators early in the salmonid life history (e.g., from bird and fish predation) might be mitigated by lower mortality (i.e., compensatory) during later life stages, especially if predators selectively remove the most vulnerable individuals ([ISAB/ISRP 2016-1](#), p. 7, p. 40; see Chapters 3 and 4).
- Predation on adults during upstream migration (e.g., by sea lions) is of particular concern because it may reduce the potential spawning population more than an equivalent rate of predation at earlier life stages ([ISAB 2015-1](#), p. 9, pp. 123-124; see Chapter 4).
- Mortality caused by individual predators is typically depensatory; i.e., each predator kills a higher proportion of the prey population as prey abundance decreases. The impact on a prey population from individual predators decreases when more prey are available because the predators become satiated and reduce their feeding rate ([ISAB 2011-1](#), p. 54; [ISAB 2015-1](#), p. 121; see Chapter 3).
- The typical depensatory functional response of individual predators can be offset by an increase in the number of predators due to aggregation in the short term or increased predator reproduction and abundance in the long term. Thus, for example, large releases of hatchery fish can affect predation of natural-origin fish indirectly by influencing the behavior and dynamics of predator populations ([ISAB 2015-1](#), pp. 124-125; [ISAB/ISRP 2016-1](#), pp. 41-42). [This is an example of the “numerical response” of predators to prey density—see Appendix C.]
- The role of predators in maintaining community structure and ecological diversity is often poorly understood ([ISAB/ISRP 2016-1](#), pp. 40-41; see Chapter 4).
- The natural selection imposed by predators at any life stage prior to spawning could enhance (and may even be necessary to maintain) the fitness of wild salmon populations in the longer term ([ISAB 2011-1](#), pp. 47-57; see Appendix C). In some cases, this is well understood, as in the case of keystone predators.

- Predicting the impact of predation on prey populations is complicated, especially if other factors [such as climate] are expected to change beyond historical norms ([ISAB/ISRP 2016-1](#), p. 7, pp. 39-40; see Chapter 4).

Process for Evaluating Alternative Metrics

An evaluation of the pros and cons of the many potential predation metrics and numerous ways to derive them was beyond the scope of this report. For example, a list of metrics that we developed from presentations at the April, May, and July 2016 briefings of the ISAB, while relatively long, includes only a small number of the potential metrics that might be considered (Sidebar 2.1). Nevertheless, the ISAB assumed that this list includes many or most of the potential alternative metrics that might be considered by the future workgroup assigned to this task. Many of the metrics listed in Sidebar 2.1 are special cases of the same general types of metrics. For example, both compensation-adjusted adult equivalents and recruits per spawner (R/S) are special cases of equivalence factors (see Chapter 6). No single metric can address all management concerns (e.g., short-term effects of predation on salmonid harvest opportunity and spawning abundance or long-term effects on salmonid population viability and ecosystem resilience and sustainability; see Chapters 4 and 6). We focused specifically on metrics that would facilitate comparison of different sources of predation across the salmonid life cycle, as well as comparison of the effects of predation with other limiting factors. Thus, the ISAB selected a small subset of alternative metrics considered most likely to be useful for evaluating short-term effects of predation on salmonids (equivalence factors and change in population growth rate) and long-term effects (probability of extinction) (Sidebar 2.1).

Sidebar 2.1. Examples of Potential Alternative Predation Metrics from Briefings to the ISAB.

[Metrics in bold font were selected by the ISAB for evaluation in Chapter 6.]

Metrics to evaluate short-term effects:

- **Compensation-adjusted adult equivalents (AEQ) (S. Haesecker, R. Zabel, and A. Evans and K. Collis presentations)**
- **Productivity (changes in recruits per spawner, R/S, at low abundance) (R. Zabel presentation)**
- Change in average survival for individual populations (R. Zabel presentation)
- Percent survival improvement (R. Zabel presentation)
- **Change in annual population growth rate ($\Delta\lambda$ or delta lambda) (A. Evans and K. Collis presentation)**
- Change in smolt-to-adult returns (SARs) (A. Evans and K. Collis presentation)
- Change in adult salmon survival from estuary to Bonneville Dam (M. Wargo Rub presentation)
- Change or trend in predation rate (number or % prey consumed per unit time) (B. Lessard, R. Zabel, A. Storch and D. Roberts, D. Trachtenberg, and A. Evans and K. Collis presentations)
- Change in cumulative survival relative to predation rate (A. Evans and K. Collis presentation)

- Consumption rates (change in a predator's rate of prey consumption per unit time with change in prey density) by ESU/DPS, predator colony, river reach (D. Trachtenbarg, A. Evans and K. Collis presentations)
- Change in percent composition (frequency and/or weight) of salmonids in predator diets (D. Trachtenbarg, A. Evans and K. Collis, K. Barnas presentations)
- Change in number of juvenile salmonids consumed (K. Barnas)
- Percentage of juvenile salmonid run consumed (K. Barnas)
- Change or trend in exploitation rate (% of predators removed by recreational fishing per unit time) (A. Storch and D. Roberts presentation)
- Percent change in salmonid abundance after 50% reduction in predators (R. Zabel presentation)

Metrics to evaluate long-term effects (population viability metrics):

- **Change in probability of extinction of salmonid ESU or DPS (abundance falls to zero) (R. Zabel presentation)**
- Change in long-term mean abundance (number of adult spawners) (R. Zabel presentation)

Although the ISAB received oral briefings about multi-species predator-prey, food web, and ecosystem models such as Ecopath/Ecosim and the Atlantis model during the preparation of this report (Ward [presentation](#)), metrics from these models were not assessed. Most of these models are production models with applicability to ocean system dynamics. Such models are currently not appropriate for assessing predation simultaneously at spatially discrete locations and life history stages of Columbia River salmon and steelhead. Harvey and Kareiva (2005) did apply the Ecopath/Ecosim model to John Day Reservoir to examine predation effects of multiple types of predators and produced counterintuitive results regarding predation by non-indigenous predators (see Predator Switching, Chapter 3). Appropriate parameterization of these complex models requires a large amount of data and assumptions, and they can be difficult to verify with field data. However, anadromous fish are affected by both freshwater and ocean predation, and, as suggested by Hunsicker et al. (2011), future development of life-cycle models and these larger scale ecosystem models could evolve to enable more comprehensive assessment of multi-species predator-prey interactions.

The ISAB developed a list of qualitative criteria for informal evaluation of alternative metrics:

- *Wide use*: Is the metric in wide use (in the Basin or elsewhere) as a predation metric or as a metric for some other limiting factor?
- *User friendly*: Is the metric conceptually easy for people to understand and communicate?
- *Relevant*: Is the metric relevant to management or policy makers? For example, would the metric help resource managers understand whether they are meeting their management objectives (predator control, salmonid harvest management, salmonid recovery)? Are there relevant and widely-used thresholds, benchmarks, or ranges for the metric?
- *Comparison/evaluation*: Can the metric be used for comparisons among different predator control measures throughout the salmonid life cycle and to limiting factors other than predation?

- *Scientific/statistical soundness*: Are the metric and its underlying assumptions scientifically and statistically sound? For example, does the metric account for other mortality factors? Does the metric account for compensatory (vs. additive) mortality at the same or subsequent salmonid life stages (see Chapter 3)?
- *Scale*: Can the metric be applied to measure predation effects at different spatial/temporal scales? Can the metric be applied to different levels of biological organization, e.g., population, distinct population segments (DPS³), evolutionarily significant units (ESU⁴), and major population groups (MPG)?
- *Derivation*: Is the metric easy to derive? Is the metric conceptually feasible to derive? Can the metric be derived given the current data/computer software available? We addressed this criterion to the extent possible, given that an evaluation of the types and quality of data available for deriving predation metrics was beyond the scope of this review. We used a hierarchical approach to evaluating derivation criteria (see Sidebar 2.2).
- *Cost*: Will it be costly to obtain data? Although a review of cost was beyond the scope of this review, we assumed that if sufficient data are lacking at this time and if derivation involves a sophisticated modeling effort, then the metric would be costly to develop.

To facilitate comparison among potential alternative metrics, the ISAB listed answers to criteria questions for all evaluated metrics: yes (y), no (blank), or a question mark if the ISAB's information was insufficient. These were listed in a single table, accompanied by a more detailed explanation for each metric in the text (see Table 6.2). The ISAB's final recommendations on standardized metrics were based on these criteria, as well as results discussed in other chapters of the report.

Sidebar 2.2. A Hierarchical Approach to Evaluating Derivation Criteria

Derivation of predation metrics can be evaluated using an informal hierarchical approach with increasing levels of complexity (simple, intermediate, complex). Here, we provide a hierarchical example for three potential metrics of adult equivalents (AEQ) at Bonneville Dam (BON):

Example 2.1. Simple AEQ Metric: "Average" adults at BON (averaged over all flow conditions, ocean conditions, etc., and ignoring compensatory responses)

³ **Distinct population segment (DPS)**: A listable entity under the ESA that meets tests of discreteness and significance according to U.S. Fish and Wildlife Service and NOAA Fisheries policy. A population is considered distinct (and hence a "species" for purposes of conservation under the ESA) if it is discrete from and significant to the remainder of its species based on factors such as physical, behavioral, or genetic characteristics, it occupies an unusual or unique ecological setting, or its loss would represent a significant gap in the species' range. Source: www.westcoast.fisheries.noaa.gov.

⁴ **Evolutionarily significant unit (ESU)**: A group of Pacific salmon or steelhead trout that is (1) substantially reproductively isolated from other conspecific units and (2) represents an important component of the evolutionary legacy of the species. Source: www.westcoast.fisheries.noaa.gov.

- Easy to derive? Yes. This metric is derived by summing Total Adult Returns over many brood years and divide by the Sum of Total Smolts over the same brood years to get an average conversion factor based on tagged smolts;
- Conceptually feasible? Yes. We need many years of data spanning different flow and ocean conditions and removals by predation or harvest;
- Derived using current data? Yes, simple AEQs have been measured for smolts for many years.

Example 2.2. Intermediate AEQ Metric: Adults at BON adjusted for flow conditions and ocean conditions, but not adjusted for compensatory responses.

- Easy to derive? Moderate. This metric requires a regression model relating adult returns to smolts that includes covariates;
- Conceptually feasible? Yes. We need many years of data spanning different flows and ocean conditions;
- Derived using current data? Yes? It is not clear, however, if we have enough contrast in flow conditions that span different ocean conditions to account for flow and ocean effects.

Example 2.3. Complex AEQ Metric: Adults at BON adjusted for river flow and ocean conditions, and adjusted for compensatory responses (e.g., see life-cycle model approach in Chapter 5 and 6).

- Easy to derive? No. A sophisticated modeling effort is needed to statistically estimate the various effects.
- Conceptually feasible? Yes. We need many years of data spanning different flows, ocean conditions, and predation. A specialized capture-recapture design as outlined in Péron (2013) will be needed;
- Derived using current data? No, measures of predation on tagged smolts are limited; we need better data to allow partitioning of smolt survival among hydrosystem, estuary, and ocean habitats and, most importantly, to estimate compensatory response (or lack thereof) in these habitats; and the number of adult returns may be so small that noise will overwhelm the model.

3. Why Compensation in Predation Mortality is Important to Developing a Predation Metric

At first glance, developing a metric to evaluate the consequences of predation on salmonid populations might seem straightforward. Predators take individuals from a population and cause a corresponding decline in salmonid abundance. This type of mortality in which the influence of mortality at one life stage can be added directly to mortality in subsequent life stages is known as *additive mortality*. However, assigning a predator with a specified effect, for example, on adult salmon and steelhead counts at Bonneville Dam, based only on the number of prey consumed will be erroneous if other factors compensate for this mortality. Three primary mechanisms leading to *compensatory mortality* are (1) density dependent survival due to factors other than predation, (2) selective predation, and (3) predator switching from one prey species to another. In this chapter, we explain how these mechanisms lead to compensation and briefly summarize the supporting evidence. More detailed evidence for compensation in predation mortality and citations to the literature are provided in Appendix A. This evidence shows that compensatory mortality introduces important complications that must be considered when developing a predation metric that links predation on salmonids at one life stage to the overall impact on the population. Statistical issues to consider when estimating compensatory mortality are also addressed in this chapter.

It is important to note that compensation associated with density dependence could apply to any source of mortality, including mortality associated with the hydrosystem. For example, the benefits of improving salmon survival through the hydrosystem could be constrained by strong density dependence in the estuary. Non-random mortality associated with dam passage, if any, could also lead to compensation. The concept of compensatory versus additive mortality is important to consider when evaluating sources of mortality and actions to reduce mortality on salmon populations. This is one reason why the ISAB ([2015-1](#)) emphasized the need to consider density dependence in the Columbia Basin.

The idea that mortality associated with predation might be compensated by reduced mortality from other causes (e.g., other predators) dates back at least to the 1930s (e.g., [Errington's papers](#)). However, most estimates of survival benefits to salmon from predator control projects in the Columbia Basin have not directly addressed uncertainty related to compensation or, as in the case of some projects, have assumed that predation mortality is completely additive (0% compensatory mortality; e.g., Antolos et al. 2005; Good et al. 2007). Several avian predation studies have estimated survival benefits to salmon from a reduction in avian predation over a range of possible compensation levels (Roby et al. 2003, Lyons 2010, Lyons 2011a,b; Lyons et al. 2014b). Lyons et al. (2014b) cite a growing body of evidence that avian predation mortality is only partially additive, e.g., as the predation of smolts in poor physical condition, as observed by Schreck et al. (2006) and Hostetter et al. (2012), is expected to be compensatory. Additionally, Wiese et al. (2008) provided evidence that bird removal in the upper Columbia Basin may reduce predation on pikeminnow and salmonids, but may ultimately lead to a net decline in salmonid smolt abundance because of increased abundance of pikeminnow.

Lyons et al. (2014b) stated, "Perhaps the most critical uncertainty for assessing potential benefits to salmonid populations from reduced cormorant predation on juveniles [salmon and steelhead] is the degree to which other mortality factors later in the life history might

compensate for reductions in mortality due to cormorant predation.” To address this uncertainty, Haeseker (2016 [presentation](#)) tested whether predation mortality on juvenile steelhead by double-crested cormorants is additive or compensatory. Preliminary findings indicated strong compensation, but interpretation of these findings should consider statistical issues discussed below (see section below: Statistical issues in estimating compensation). Lastly, although Evans et al. (2016b) found that most emigrating smolts were in good condition, they suggested future tagging studies could “more rigorously” address all types of condition-dependent predation mortality. In other words, tagging operations should randomly select fish for tagging rather than excluding fish that appear to be unhealthy (Haeseker 2016 [presentation](#)).

Density Dependence

Density dependent mortality is a form of compensatory mortality. A review of density dependence by the ISAB, while not exhaustive, considers how mortality imposed by predators is related to prey density and summarizes findings about the overall impact of major predators on Columbia River salmon populations ([ISAB 2015-1](#), pages 121-125). This review found evidence of depensatory⁵ (the opposite of compensatory) mortality caused by predators feeding on juvenile salmonids, but life cycle recruitment relationships indicated that density dependence over the entire life cycle remains strongly compensatory.

Typically, stock-recruitment relationships from one juvenile salmonid life stage to another are not linear but curve towards a maximum value as density increases (Figure 3.1). In this case, mortality is compensated by reduced competition for resources among the survivors, leading to reduced predation effects on recruitment compared to completely additive mortality (Ward and Hvidsten 2011). Also, if the stock-recruitment curve is dome-shaped, implying overcompensation, then predation at high density may in fact increase recruitment (Figure 3.1b). Thus, the impact that predators have on recruitment and population growth is not determined simply by the number of prey consumed if this mortality is compensated by greater survival after the predation event (Ward and Hvidsten 2011).

When thinking about the relationship between density dependence and predation it is useful to recognize that juvenile salmon and steelhead are often competing for limited resources. If some juveniles are removed from a population by predators, then intra- and inter-specific competition is reduced, potentially leading to improved growth and survival. As a result, an increase in growth and body size could be an important compensatory response in salmon populations subjected to predation and other sources of mortality (Ward and Hvidsten 2011).

The ISAB examined evidence for density dependence among salmonids in the Columbia Basin and our report ([2015-1](#)) provides insight into species, populations, and life stages

⁵ Depensatory density dependence (*depensation*), in which a population’s growth rate *decreases* at low densities, is opposite to what is typically expected. Depensatory mortality occurs when predators tend to kill a fixed *number* of prey, leading to a higher percentage of the population killed at lower densities ([ISAB 2015-1](#)).

where mortality caused by predation (or other factors) may be compensated by density dependence. Relatively strong density dependence was documented in nearly all Chinook and steelhead populations where data were available. Evidence for density dependence was observed during the spawner-to-smolt life stage (e.g., growth, emigration, and survival) and from the spawner-to-spawner stage (entire life cycle). Relatively little quantitative investigation of density dependence has occurred during smolt emigration in the mainstem Columbia River and in the estuary and ocean, although density dependence could be caused by high food demand of smolts during emigration ([ISAB 2011-1](#)) and density dependence in the estuary is assumed to occur by groups that rehabilitate estuarine habitat ([ISAB 2015-1](#)).

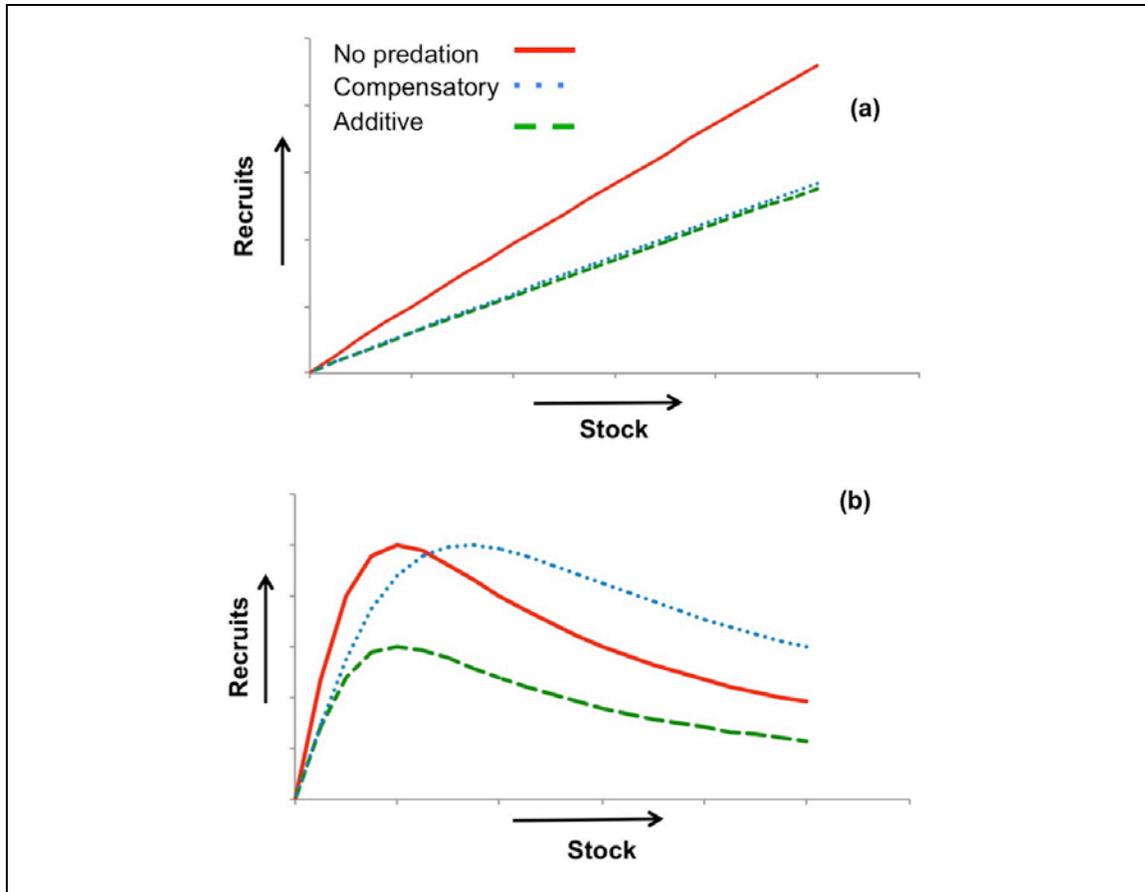


Figure 3.1. Stock-recruitment (S-R) relationships showing the relative effects of additive or compensatory predation mortality when density dependence is very weak (panel a) or strong (panel b). The effects of additive and compensatory mortality are approximately equal in a population when density-dependent mortality is weak (panel a). When strong density dependent mortality occurs in a population (e.g., overcompensation in Ricker-type recruitment; panel b), compensatory mortality at high stock levels can potentially increase the number recruits produced over what would have been achieved if no predation had occurred (panel b). This potential benefit from predation (or harvest) would not occur if recruitment reflected a Beverton-Holt relationship that does not exhibit overcompensation (see [ISAB 2015-1](#)). Fewer recruits are produced at all stock levels when the population experiences additive mortality (panel b). Compensatory mortality in this example does not consider selectivity by the predator for less fit individuals. Source: Figure 8.5 from Ward and Hvidsten (2011).

The information provided by the ISAB ([2015-1](#)) and the numerous investigations referenced in the document indicates that predation mortality is likely to be compensated by density dependence to some degree during the spawner to smolt stage and perhaps during smolt emigration and passage through the estuary. During the adult stage, prespawner mortality may be compensatory in response to stress and reduced access to cold-water refugia ([ISAB 2014-4](#) and references within). Furthermore, depending on the number of spawners, compensatory effects that ameliorate predation (and harvest) may occur during the subsequent spawner-to-smolt stage. The interaction between predation mortality and density dependence during subsequent life stages highlights the need for a life-cycle approach, as discussed in Chapters 5 and 6 and in Appendix D.

Selective Predation (see Chapter 8, Appendix A, for a detailed review and references)

Knowledge about the selectivity of a predator for its prey is critical for evaluating predator impacts on the population dynamics of the prey species. In the absence of other sources of compensation such as density dependence, non-selective (e.g., random) predation will be additive because its effect on abundance at subsequent stages is proportional to the numbers (and percentage) of the prey species consumed by the predator. If, on the other hand, predators select individuals that would otherwise be more likely to survive to the reproductive stage (e.g., large salmonids), then the effect of predation on the prey species is compensatory because survival probabilities (at the population level) at subsequent stages will decrease. Conversely, if predators select less fit individuals, then the effect of predation will be compensatory. Selective predation is an important mechanism that may contribute to compensatory mortality. For example, many studies indicate smaller salmon smolts have lower survival rates at sea (see Appendix A), suggesting that selective predation on smaller salmonids in the Basin will be compensated to some extent by size-dependent mortality at sea.

The importance of selective predation when evaluating potential effects of a predator species on salmonid populations was recognized by Columbia Basin scientists more than 20 years ago (Mesa et al. 1994). Here, we present conclusions stemming from our limited review of literature in the Columbia Basin and elsewhere to identify whether or not fishes, birds, and marine mammals tend to randomly consume salmonid prey or whether predators select salmonids that possess specific attributes. Details of this review along with references are provided in Chapter 8 (Appendix A).

Selective predation by fishes

Most piscivorous fishes tend to select smaller than average salmonids and fish that are less healthy. Domesticated hatchery salmonids may be consumed by piscivorous fishes more than wild salmonids, although this type of selective predation may be offset by the larger body size of hatchery salmonids compared to wild salmonids. In most situations, selective predation by piscivorous fishes will lead to compensatory mortality which ameliorates the adverse effect of predation on a salmonid population to some extent.

Selective predation by birds

A salmonid's susceptibility to bird predation is complicated by a variety of behavioral and physical traits, including body size and condition, migration timing, abundances of salmonids and alternative prey, and predator-specific foraging techniques and behaviors. Steelhead, especially hatchery steelhead, tend to be selected by birds more than other species of salmon, possibly in response to their surface orientation and larger size. Caspian terns consume larger than average salmonids (up to about 200 mm), whereas cormorants are less influenced by salmonid size and may readily consume salmonids up to about 300 mm. Fish in poor condition are selectively consumed by birds, but these fish represent a small percentage of total salmonid abundance in the Columbia Basin.

In conclusion, the degree of compensatory versus additive mortality in response to predation by birds is complex because, depending on species, birds may selectively consume salmonids that are larger than average size, smaller than average size, or unhealthy, or consumption of salmonids may be non-selective.

Selective predation by marine mammals

Large mammals such as killer whales and bears have the ability to preferentially select large versus small salmon, but current evidence in the Columbia River suggests that pinnipeds may select smaller salmon such as jacks. Pinnipeds in the Basin and killer whales (*Orcinus orca*) outside the Basin selectively consume Chinook salmon. The timing of pinnipeds residing in the Columbia River leads to higher predation on spring versus summer Chinook salmon and on early components of salmon populations within those races. More research is needed to evaluate selective foraging by pinnipeds on adult salmon to determine whether or not predation mortality may be compensatory or additive.

Predator Switching to Different Prey

Additional mechanisms involving predator behavior could also lead to compensatory mortality following predation on Columbia River salmonids. These mechanisms involve the numerical and functional responses of the predators to abundances of salmon populations and other prey (see Sidebar 3.1). Here we briefly describe how numerical and functional responses may lead to compensatory mortality.

Weise et al. (2008) evaluated diet and predation rates by several bird species on salmonids in the upper Columbia River in relation to a predator control program (hazing and shooting birds). The birds switched from consuming salmonids during the smolt migration to juvenile pikeminnow after the smolt migration period. The investigators concluded that allowing the birds to remain in the system rather than culling them led to a large net savings in salmonid smolts because the birds ate pikeminnow that would have eventually consumed smolts. Ultimately, the investigators recommended non-lethal methods (wires at dams and hazing) to reduce predation on smolts by birds while maintaining bird predation on piscivorous pikeminnow.

We offer another hypothetical example of compensatory interactions by two or more predators to illustrate how predator control efforts could lead to unintended and difficult to

anticipate consequences. In this example, a sharp decline in the abundance of one key predator (e.g., via predator removal) and the associated decline in predation on salmonids could be offset by increased predation by other predators, leading to little change in predation rates on salmonids. This situation could arise if the secondary predator(s) were able to increase their feeding rate in the absence of the primary predator either because interference between species would be reduced or because a higher density of salmonids would become available following the reduction in predation by the primary predator. The latter mechanism would require a Type III functional response to prey density, which is described in more detail in Sidebar 3.1 and Appendix C. An overall increase in predation by all secondary predator(s) (as opposed to increased predation rate by individual predators) could also occur if more predators entered the Columbia Basin to feed on salmonids after the initial primary predator was removed (numerical response).

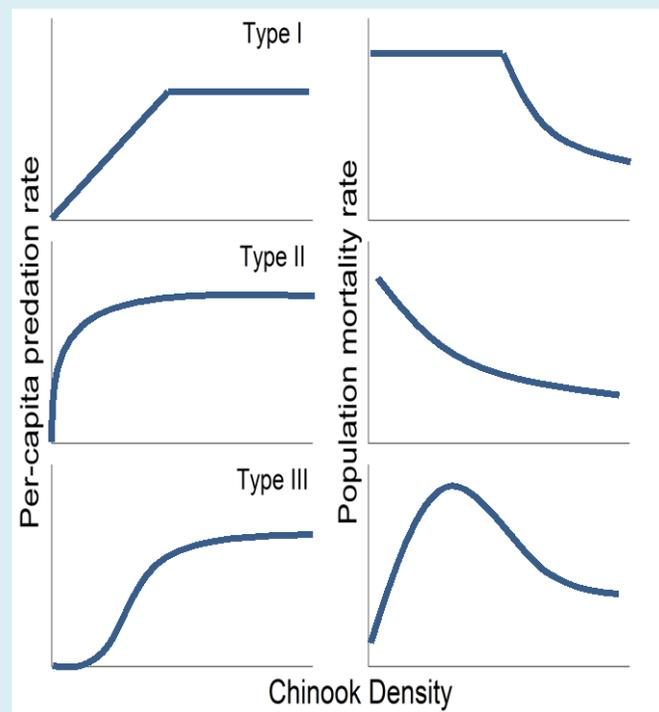
This hypothetical example has been modeled for several non-native (smallmouth bass, walleye, channel catfish) and native predators (pikeminnow, terns) of juvenile Chinook and steelhead in the John Day reservoir using Ecopath with Ecosim (Harvey and Kareiva 2005). This approach used a functional response that allows prey to alternate between “vulnerable” and “invulnerable” states to predation. A key finding was that the pikeminnow predator control program produced a 27% reduction in smolts eaten by pikeminnow, but this immediate mortality estimate was compensated by an increase in predation by non-native predators and birds that were not managed. Ultimately, total smolt predation declined less than 11% rather than 27% because of responses by other predators in the John Day reservoir.

Given the practical implications of different functional response curves, it seems important to develop such relationships for the principal salmon predators in the Columbia River (e.g., Petersen and DeAngelis 1992). Predation can then be examined within a life-cycle model and/or a community-based Ecopath/Ecosim model. Regarding the predation metric, a key issue is whether predators have a Type III or modified Type II response to salmon abundance such that predator control leads to higher predation rates on salmon by an uncontrolled predator. Consequently, data or metrics that allow researchers to develop such relationships should certainly be among those that are considered by researchers and managers that are involved with salmon management and predator control.

Sidebar 3.1. Functional and Numerical Responses

To understand how predation shapes salmonid populations, the functional and numerical responses of predators to varying abundances of salmonids need to be determined. The functional response describes the mean number of prey eaten per predator per unit of time in relation to prey density, and the numerical response describes how the number of predators varies in relation to prey density (Solomon 1949, Holling 1959a,b). The total number of salmon eaten by a predator species per unit time equals the predation rate times the abundance of the predator. This information can be used to address the major question of how predation mortality varies with salmon abundance. Examination of functional and numerical responses of predators highlights the dynamic and often non-linear effects of predation on salmon populations. See Appendix C for details and examples.

Three basic predation responses are shown in Sidebar Figure 3.1. A Type I functional response is linear at low to mid prey densities and then abruptly becomes constant at high prey densities. In a Type II response, prey mortality increases with prey density and gradually reaches an asymptote (predator saturation) at high prey densities. Predators approach saturation gradually because prey consumption is affected by handling time, digestion, and satiation effects, and switching from one prey species to another one does not occur. A Type III response curve is S-shaped. Mortality is low at low prey densities until a threshold density of prey is reached and then increases sharply at mid densities until it gradually reaches an asymptote. Holling (1959b) attributes the slow rise of predation versus prey density to a learning curve, as when developing a search image. When enough of a certain prey are present to be more easily identified as food, then the predator begins to select for that prey.



Sidebar Figure 3.1. The general shapes of the three functional response curves (left column) and the corresponding percent mortality curve assuming constant abundance of predators (right column). Source: Zabel 2016 ([presentation](#)).

The shape of the total response curve (functional response x numerical response) determines how prey density affects the percentage of salmon killed by the predator population and thus, how predation will affect the dynamics of the prey population (Sidebar Fig. 3.1, right column). A Type II total response is "depensatory" and can potentially lead to the extinction of a prey population (zero recruits) at low stock levels if the percentage of the prey population eaten by the predator population is high (Peterman and Gatto 1978, Ward and Hvidsten 2011). Type III responses can lead to "multiple domains of stability" such that populations may become trapped at small population sizes (Peterman 1977, Peterman and Gatto 1978). A Type III response can lead to compensation, as described in the main text. Evidence indicates that predators show a

variety of responses, but most fishes and birds feeding on juvenile salmon exhibit Type III responses when more than one species of prey is available (Peterman and Gatto 1978, Petersen and DeAngelis 1992).

Estimating Compensation

Rather surprisingly, there is not a large amount of statistical literature on methods to test compensatory vs. additive mortality hypotheses on survival using marked individuals, and most of the work has been applied to bird populations (e.g., waterfowl). Péron (2013) summarized seven types of studies that have been considered (Table 3.1).

Table 3.1. Different types of individual-based data and associated statistical methods used to estimate the correlation between anthropogenic and natural mortality and the degree of compensation. Source: Table 1 in Péron (2013). *C* indicates the rate of "compensation-additivity" and varies between 0 (complete additivity) and 1 (complete compensation) and can be interpreted as the proportion of fluctuations in predation mortality around its average that are compensated.

Abbreviation	Type of data	Estimated parameters	Parameters to be estimated separately	Upward sampling bias on <i>C</i>	Downward competition bias on <i>C</i>	References
CR	Capture-recovery data with only one type of recoveries	S, r	λ, n_0	Y	Y	Brownie & Pollock (1985); Williams, Nichols & Conroy (2002) Appendix S1, part 1
CR-H	Capture-recovery data plus a measure of anthropogenic mortality rate	$S, r, b, E(n_0)$	$\text{Var}(n_0)$	Y	Y	Barker, Hines & Nichols (1991); Gauthier <i>et al.</i> (2001) Appendix S1, part 2
IPM	Capture-recovery data plus population surveys	S, r	λ, n_0	(Y)	Y	Besbeas <i>et al.</i> (2002); Péron, Nicolai & Koons (2012)
CRP	Capture-recovery and Capture-recapture data	n, h	n_0	Y	Y	Servanty <i>et al.</i> (2010)
CRR	Capture-recovery data with two (or more) types of recoveries	n, h	n_0	Y	Y	Schaub & Lebreton (2004) Appendix S1, part 3
CP-H	Capture-recapture data with a measure of anthropogenic mortality rate	$S, b, E(n_0)$	$\text{Var}(n_0)$	N	Y	Veran <i>et al.</i> (2007); Rolland, Weimerskirch & Barbraud 2010;
KF	Known-fate data (telemetry, radiotracking)	$n, h, b, E(n_0)$	$\text{Var}(n_0)$	N	Y	Heisey & Patterson (2006); Creel & Rotella (2010) Appendix S1, part 2

S stands for annual survival, *r* for recovery probability, *n* for annual natural mortality, *h* for annual anthropogenic mortality, λ for mark reporting rate (for animals dead from the anthropogenic source) and n_0 for annual natural mortality in the absence of anthropogenic mortality. *E* and *Var* stand for expected value and temporal variance, respectively, when only one of these quantities is involved. In the 'bias' columns, Y (Y) and N, respectively, indicate that a bias is systematically present, not systematically present (there is sampling covariance but it may vary in direction) or is absent. More details about the statistical methods are found in the quoted references (among others).

Here we summarize examples of three common study approaches for estimating compensation.

1. One of the first attempts to quantify additive and compensatory mortality was a paper by Burnham and Anderson (1984). Their analysis was based on earlier work that modeled North American mallard duck populations. Mallards are banded on breeding grounds in North America and band-returns are reported by hunters. While the survival over all causes of mortality S_i can be estimated fairly easily based on returns of banded birds from hunters, it is not possible to estimate the kill rate directly based solely on hunter returns because not

all killed birds are reported. There may also be further mortality (e.g., from crippling the birds) that is not reported. Consequently, independent estimates of the reporting and crippling rates are needed to convert the reported number of killed birds to the total kill and hence to decompose survival over all causes into its constituent parts. Lebreton (2005) noted that uncertainty in these estimates leads to the “error in variables” problem in regression (where X values are uncertain) and tends to bias the estimates of additivity effects toward compensatory effects.

2. Schaub and Lebreton (2004) developed a model where recoveries from several different causes of mortality are available and does not require information outside the capture-recapture data. However, the cause of death of any recovered individual must be known. They used the example of banding studies on storks where recovered storks were classified as dying from contact with power-lines or from other causes.⁶ Two sources of mortality are modeled and the correlation between the two mortality rates provides information about compensation. However, a sophisticated statistical model (e.g., a Bayesian state-space model) is needed to separate the process correlation (the compensation) from sampling correlation (artifacts of the data collection process). Nevertheless, even with these approaches there is an intrinsic bias in the underlying correlation parameter due to the competing risks; this bias can be substantial and again points towards compensation (see below).

3. Seding et al. (2010) and Servanty et al. (2010) further develop this Bayesian state-space approach with random components for the sources of mortality which allows for estimation of the process correlation (free of bias caused by sampling correlations). Servanty et al. (2010) further include a Bayesian prior probability distribution for natural survival in the absence of the competing mortality to account for both the sampling correlation and the intrinsic bias. They applied their model to wild boar (*Sus scrofa scrofa*) to assess if harvesting is compensatory to natural mortality. In their model, live recaptures were combined with harvest due to hunting (rather than having recoveries from two sources of mortality as in Schaub and Lebreton [2004]). The Servanty model is likely the most suitable for assessing compensation in smolts as they pass through the hydrosystem where some recoveries from avian predation can be obtained by searching nesting grounds for Passive Integrated Transponder (PIT)-tags; smolts that die from natural causes are never seen; and there are multiple chances to detect smolts as they pass through the hydrosystem.

The following statistical issues are important to consider:

(a) *Heterogeneity can mimic compensation.* Apparent compensation can occur that is an artifact of heterogeneity in vital rates among individuals (Lebreton 2005). For example, suppose a population of 1000 individuals consists of 500 “non-vulnerable” individuals with a natural survival probability of 0.8 and 500 “vulnerable” individuals with a survival probability of 0.2. The average natural survival probability (at the population level) is 0.5. Now suppose that predation in the vulnerable segment is 0.30 versus 0.10 in the non-vulnerable segment. The average predation probability (at the population level) is 0.2. The approximate number of survivors after predation and then followed by natural mortality is 430 for a combined survival of 0.430 (200 animals eaten by predators and 370 dying from other natural causes). An additive mortality hypothesis, ignoring heterogeneity, would

⁶ As in all banding studies, only a small number of all deaths are actually reported.

predict that $1000 \times (1-0.2) \times 0.5 = 400$ animals would be expected to survive (with 200 animals eaten by predators and 400 dying from other natural causes). There is an apparent compensation of 30 animals that is due strictly to heterogeneity in the vital rates.

(b) Separation of process correlation vs. sampling correlation as a measure of compensation. It is tempting to simply plot two estimated time series of natural and harvest probabilities against each other to assess correlation. Unfortunately, such a simple analysis fails to account for the difference between process and sampling correlation.

Process correlation is the underlying relationship between the two probabilities and is a measure of compensation. Sampling correlation is an artifact of the estimation process. For example, in capture-recapture studies it is relatively simple to estimate combined survival (over all causes of mortality). When one partitions this combined survival into constituent components, there is a sampling correlation induced because the two separate survivals must combine to give the overall survival. So if the estimate of the survival due to one component increases, the survival due to the other component must decrease in order to keep the combined estimate consistent. This leads to a negative sampling correlation in the survival (and mortality) components, which looks like compensation. This artifact is known as sampling correlation.⁷

Sophisticated random effect models (typically fit using Bayesian methods) are needed to separate the process and sampling correlations.

(c) Intrinsic bias in correlation due to competing risks. As noted by Schaub and LeBreton (2004) and Servanty et al. (2010), competing sources of mortality can operate over a long time period. Hence the number of animals at risk during this time period is affected by both sources of mortality, and so a negative correlation (i.e., apparent compensation) occurs even when the two cause-specific mortalities are additive. An example of competing risks is gauntlet predation where different sources of mortality (the different predators) operate sequentially. Now, if one source of mortality is higher, then the number of animals at risk to the other source of mortality is reduced and so the number of animals dying from the second source of mortality is also reduced. The size of the bias can be computed (see Schaub and LeBreton, 2004, Appendix B) but requires an estimate of natural mortality without the competing risks, e.g. from a non-exploited population. Competing risks of death modeling (Quinn and Deriso 1999, Heisey and Patterson 2006) may provide a simple, heuristic conceptual and quantitative approach for assessing the interactions of multiple competing predators and other sources of mortality on survival and abundance of salmonids (Hilborn et al. 2012).

Péron (2013) summarizes the direction of sampling and intrinsic bias on estimates of compensation under seven different capture-recapture studies (Table 3.1). Note that Péron (2013) calls the intrinsic bias the “competition” bias.

(d) Contrast needed. It is impossible to distinguish between compensation and additivity if the underlying sources of mortality (e.g., natural and predation probabilities) are constant

⁷ This is similar to what happens when fitting regression lines. If the estimated slope is increased, then the estimated intercept must decrease, leading to negative sampling correlation between estimates of the slope and intercept even if the slope of the line is positive.

over time. Some variation is needed in either or both of the sources of mortality. As in most statistical models, larger contrasts (e.g., ranges in predation or natural mortality) lead to more precise estimates of the compensatory response. If there is no temporal variation in either source of mortality, then it is impossible to separate the survival probabilities. This has implications when assessing compensatory mortality on outgoing smolts in the Columbia River where system operations can keep smolt mortality relatively constant underlying water conditions. This may have the impact of reducing the contrast in natural mortality that will make it more difficult to detect compensatory behavior. Similarly, as shown by Péron (2013), the relative variation in natural and harvest/predation mortality can limit the degree of compensation possible.

4. Strategic Issues for Predation Metrics

What Salmon Life Stages and Predators Are Assessed by Predation Metrics?

The ISAB has not comprehensively reviewed the impacts of predation on Columbia River salmon, but we have summarized some existing knowledge in our reports on food webs ([ISAB 2011-1](#)) and density dependence ([ISAB 2015-1](#)), and we provide a brief summary here for context. Our reviews indicate that most research on the impacts of predation on salmonid populations have focused on three groups of (non-human) predators: (1) freshwater fishes (primarily native northern pikeminnow but also non-native smallmouth bass, walleye and channel catfish); (2) piscivorous water birds (primarily Caspian terns and double-crested cormorants but also California gulls, ring-billed gulls and the American white pelican); and (3) marine mammals (primarily California sea lions and Steller sea lions (*Eumetopias jubatus*) at Bonneville Dam and in the lower river and estuary). Little is known about the impact of fish, bird, and marine mammal predators on Columbia River salmon and steelhead during coastal marine and open ocean life stages ([ISAB 2011-1](#)).

Among freshwater fish predators, northern pikeminnow kill the highest proportion of juvenile salmonids migrating down the lower Columbia and lower Snake rivers (Friesen and Ward 1999). Pikeminnow are abundant in most reservoirs and appear to aggregate in the tailraces of dams, where they feed on salmon smolts that become disoriented after passing dams (Poe et al. 1991, Ward et al. 1995), and at sites where hatchery-origin salmonids are released (Collis et al. 1995). Raymond et al. (1996) estimated that prior to initiation of a control program, pikeminnow killed 8% of the roughly 200 million juvenile salmonids (both hatchery and wild) that migrated downstream in the Basin each year. The pikeminnow removal program, initiated in 1990, appears to have progressively reduced mortality on juvenile salmonids by 25% after 5 to 6 years (Friesen and Ward 1999) and by about 40% after 19 years (to an annual mortality of 5%) (summarized in [ISAB 2011-1](#)). However, these estimates of reduction in salmon mortality assume that predation by other fishes (e.g., smallmouth bass, walleye, and channel catfish) has not increased over the period of pikeminnow control.

Among waterbirds, Caspian terns and double-crested cormorants kill the most salmonid smolts, primarily in the estuary and mainstem of the Columbia River (Collis et al. 2002). Roby and Collis (2009) estimated that Caspian terns and double-crested cormorants nesting on East Sand Island killed 15-20 million smolts or about 15% of all juvenile salmonids reaching the estuary during the 2009 out-migration. Combined predation probabilities by terns, cormorants, gulls, and pelicans nesting near the Snake and Columbia river confluence were also estimated to be substantial; minimum combined predation probabilities by these species ranged from 1.4% for Snake River fall Chinook salmon to 13.2% for upper Columbia River steelhead (Evans et al. 2012). Predation probabilities have likely been reduced by recent actions to reduce nesting abundance both in the estuary (e.g., East Sand Island) and at inland nesting locations (e.g., Goose and Crescent islands), and to provide alternative nesting sites out of the Basin. Nevertheless, a new study with Juvenile Salmon Acoustic Tagging System (JSATS) tags (in addition to PIT tags used in previous studies) indicated that avian predation probabilities by all birds (combined) feeding on juvenile salmon traveling through the lower Snake River and the lower and middle Columbia River in 2012 and 2014 ranged from 6% to 28% of tagged steelhead, 3% to 9% of tagged yearling Chinook, and 1% to 5% for tagged subyearling Chinook (Evans et al. 2016b).

Pinnipeds consume adult spring Chinook salmon returning to the Columbia River, and predation rates have been relatively high in recent years. Three species of pinnipeds frequent the estuary and adjacent ocean: Pacific harbor seal (*Phoca vitulina*), California sea lion, and Steller sea lion. Recent tagging studies by NOAA indicate that after accounting for estimates of human fishing mortality and post-release mortality caused by the sampling gear, the weighted mean annual survival of spring Chinook migrating upstream from the Lower Columbia estuary past Bonneville Dam declined steadily from 90% in 2010 to 59% in 2014, but increased to 72% in 2015 (Wargo Rub 2016, [presentation](#) and [audio](#)). The declining survival rates mirror the growing presence of sea lions and seals in the estuary. The number of sea lions identified at haul-out sites near Astoria increased steadily from 2010 to 2015, and the peak count was 10 times greater in 2015 than in 2010 (Wargo Rub 2014, [presentation](#)).

Much less is known about the impact of fish, bird, and marine mammal predators on Columbia River salmon and steelhead during coastal marine and open ocean life stages ([ISAB 2011-1](#)). While predation mortality is generally assumed to be the proximate cause of ocean mortality of salmon and steelhead, which frequently exceeds 95% of smolts entering the ocean (CSS 2015), direct observations of predation mortality in the ocean are extremely rare. Detecting and understanding marine predator-prey interactions, which may be influenced by density-dependent effects and varying responses of predators and prey, are major challenges (see Chapter 6). Continued monitoring and simulation modeling will be needed to understand these mechanisms.

A critical uncertainty discussed in [ISAB/ISRP 2016-1](#) is that predicting how predators will impact salmonid populations is particularly difficult when factors that affect the number of predators, or the density and vulnerability of the prey, are changing beyond historical norms. Continuing trends in climate change, human population growth, and the abundance of non-native species are all expected to alter freshwater and ocean habitat conditions for salmon beyond historical norms. Climate and ocean conditions are well known to affect the distribution and presumably abundance of marine predators and their prey, both in the short-term (e.g., El Nino) and the long-term (e.g., Pacific Decadal Oscillation). As well, the continuing spread of non-native predators of salmon (e.g., walleye, smallmouth bass, channel catfish, northern pike) within the Columbia River basin is now widely recognized as a potential threat to salmon recovery (e.g., Sanderson et al. 2009), and one that warrants further investigation ([ISAB/ISRP 2016-1](#)). On the other hand, an ECOSIM model developed explicitly to simulate the effects of removing non-native fish predators from John Day Reservoir suggests that benefits for salmon survival might be partly or totally offset by indirect food web interactions, and were subtle compared to the effects of native predator management (Harvey and Kareiva 2005, discussed in more detail in Chapter 3).

What Management Concerns are Addressed by Predation Metrics?

Harvest opportunity - Fisheries and (non-human) predation both reduce the number of salmon within a given cohort that might otherwise survive to spawn. In this sense, predators can compete with human fishers by removing salmon that might otherwise be available for harvest. Different predator species can also compete with one another, as seen in the complex interactions among avian predators foraging on migrating smolts (Evans et al. 2016a).

Predation on adult salmon during their return migration (e.g., by sea lions) typically reduces the harvestable population more than an equivalent rate of predation at earlier life stages. Losses to predators early in the salmonid life history (e.g., from bird and fish predation) can be offset by reduced (compensatory) mortality during later life stages, especially if predators selectively remove the most vulnerable individuals ([ISAB 2015-1](#)). This critical issue of “compensation” is discussed in detail in Chapters 3 and 8 (Appendix A).

By the time adult salmon enter the Columbia River estuary, they have already survived a myriad of hazards in both freshwater and marine environments. They have also attained their maximum size and value for in-river human harvest. Accordingly, the change in the number of adults (from the number in absence of predation) passing Bonneville Dam would be a convenient standard metric for evaluating the impacts of predation on harvest opportunity above Bonneville.

Spawning abundance - The annual abundance of spawning adults is an important measure of abundance in assessing the status of a salmon population. Especially for Pacific salmon that die after spawning, the number of individuals within any given cohort surviving to contribute to the next generation is at its minimum just prior to spawning. Minimum absolute abundance is critical to assessing future status because small populations are more vulnerable than large populations to all causes of extinction risk, especially genetic losses and demographic uncertainty (Shaffer 1981). For this reason, change in the annual number of spawning adults (again from the number in the absence of predation) for each Evolutionarily Significant Unit (ESU) or Major Population Group (MPG) could be a useful standard metric for evaluating the impacts of predation on Endangered Species Act (ESA)-listed species.

Spawning numbers will differ from adult numbers at Bonneville Dam to the extent that mortality occurs during upstream migration. Mammalian predators (e.g., bears) are known to kill adult salmon in tributaries. Pre-spawning mortality associated with stressful conditions and disease can also be high (>50%) in some areas in some years (discussed in [ISAB 2014-4](#), pp. 11-13). Both these sources of mortality represent additional opportunities for compensation when adult salmon density affects the mortality probability. For example, Roumasset and Caudill (2013) found that fish density and warm water temperatures on spawning grounds were positively associated with pre-spawning mortality rate.

Viability of salmon populations - Although mortality from predation (or harvest) reduces spawning abundance, it does not follow that predators always reduce the future abundance or viability of a salmon population. Indeed, the concept of sustainable fisheries is that removing (even adult) fish from an abundant population can increase rather than decrease total abundance of juveniles in the next generation because of density dependence (see [ISAB 2015-1](#)). In other words, fisheries can be sustained because compensatory mortality in the next phase of the life cycle is able to maintain smolt production despite (or because of) the reduced number of spawning adults. A life cycle perspective (Figure 4.1) helps to explain how fish and bird predation on juveniles and human harvests of adults have conceptually similar impacts on population viability even though the mechanisms and life stages for compensation are likely different.

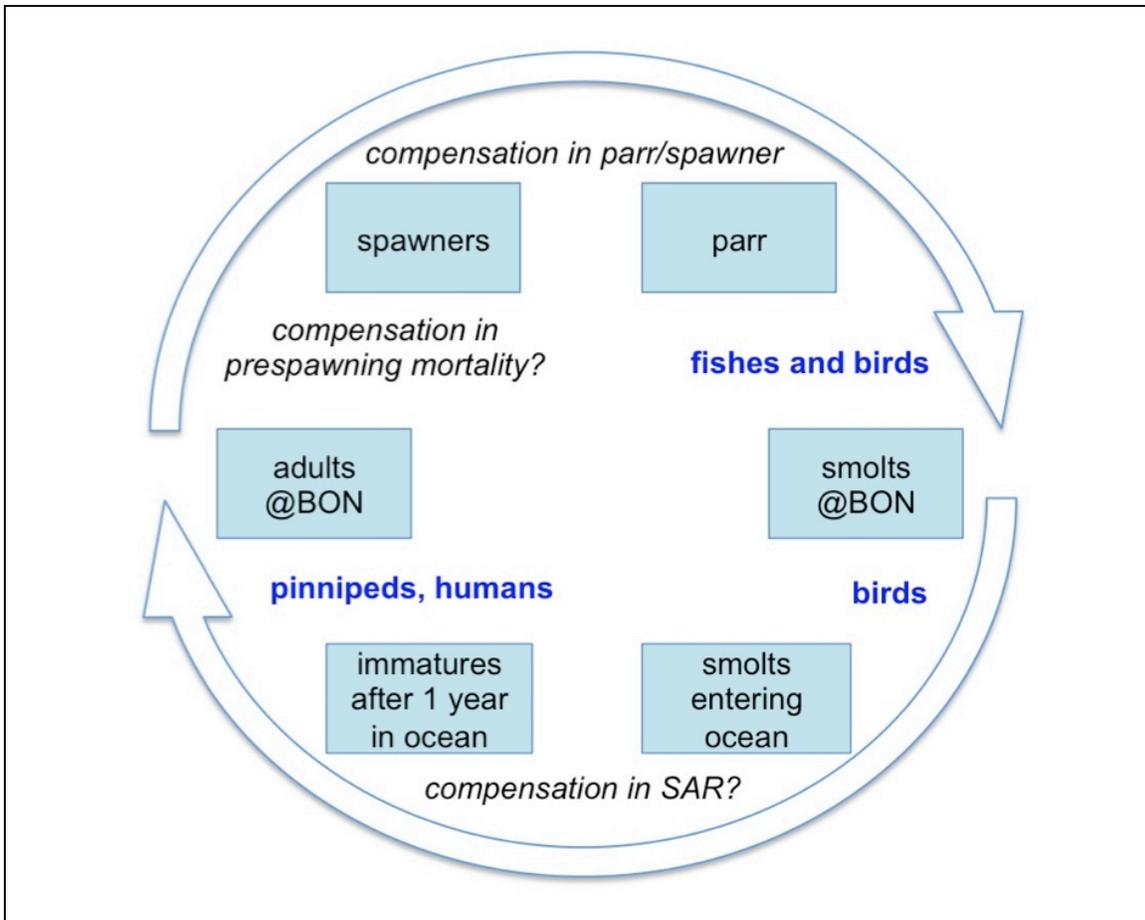


Figure 4.1. Life cycle of Columbia River anadromous Pacific salmonids showing key life history stages (boxes), predators of greatest management concern (blue font), and known and likely opportunities for compensatory mortality (italics). BON = Bonneville Dam (see Figure 1.1), SAR = smolt-to-adult return.

To compare how predation mortality at different stages influences the productivity and viability of salmon populations, a different metric is needed—one that can account for compensation over the entire life cycle. NOAA has developed a number of candidate metrics based on life-cycle models to assess the status of ESA-listed populations (e.g., McClure et al. 2000, 2003; Zabel et al. 2013). These methods are presented in Chapter 5.

Resilience and sustainability of ecosystem - The role of predators in maintaining community structure and ecological diversity is sometimes poorly appreciated. The fact that a typical Pacific salmon lays thousands of eggs, of which the vast majority die or are eaten at later life stages, indicates that salmonids have evolved to survive as prey species within a complex food web. Contemporary ecological thinking that focuses on the food webs involved in nutrient recycling and energy flow in ecosystems (e.g., [ISAB 2011-1](#)) often cautions against removal of predators (Patton 2011). Predator control programs can have counterintuitive and unintended consequences for both the target populations and other predator and prey species. For example, reducing avian predation on bass and pikeminnow to increase juvenile salmon survival may inadvertently increase the abundance of bass and pikeminnow, thereby increasing predation by these species on juvenile salmonids and

partially undermining existing efforts to reduce pikeminnow populations in parts of the Basin (Weise et al. 2008).

Lessard et al. (2005) describe the extreme uncertainty associated with any policy aimed at controlling complex interactions that determine extinction risk for focal species and argue that such policies should be treated as management experiments that include comparisons with appropriate controls and monitoring. These ecological and evolutionary perspectives suggest that additional metrics may be required to compare the consequences of selectively removing predators to increase salmonid abundance or the viability of salmonid populations.

5. A Life-Cycle Approach to Comparing Different Sources of Predation

Managers and scientists may compare the consequences of predation at one life stage to those by a different predator at another life stage. An intuitively attractive approach to make this comparison is to use existing information about average survival rates between successive life stages to convert losses from predation into losses of standardized “adult equivalents” counted at Bonneville Dam. Hypothetically, if smolt-to-adult return (SAR) survival (from Bonneville to Bonneville) has averaged 1% over the recent record for the population in question, then on average, 100 smolts have been required to produce one adult at Bonneville. By this calculation, the loss of 100 smolts to avian predators would be equivalent to the loss of one adult to a sea lion at Bonneville. Considerable data exist to calculate these conversion rates, at least within the recent range of salmon and predator abundances. The main tasks here would be to calculate and document survival probabilities between successive life stages by species, life history and area as illustrated below (see Example calculations with a life-cycle model).

Calculating adult equivalents based on average survival rates is certainly useful as a first approximation, but several issues complicate this conversion and may lead to erroneous values. The method implicitly assumes that cumulative losses from predation are additive throughout the smolt-to-adult period so that survival probabilities at successive stages can be multiplied to determine survival over many life stages. However, the probability of surviving through a life stage is unlikely to be independent of what has already happened at earlier life stages for two reasons. First, individual smolts vary widely in their health and susceptibility to predation. Other things being equal, selective removal of unhealthy or vulnerable smolts in one life stage will tend to improve the average health or decrease the average vulnerability of fish entering subsequent stages, thereby compensating to some extent for increased mortality in the earlier life stage. This issue of predator selectivity is reviewed in more detail in Chapters 3 and 8 (Appendix A). Second, survival probability will also change as prey density changes, both through compensation due to intraspecific competition and the behavioral responses of predators (discussed in Chapter 3). The consequences of such compensation are illustrated for a hypothetical example in Appendix D. More complicated models and a better understanding of these issues would be required to predict the degree of compensation that will arise from significant changes to predation rates in particular life stages (see Chapter 6).

Life-cycle modeling has become an invaluable tool for managing species that have distinct life stages. A major advantage of life-cycle models is that they can be used to estimate or simulate cumulative impacts across several life stages based on a variety of performance metrics. NOAA is coordinating an effort to develop life-cycle models for salmonid populations in the Columbia River as a tool to translate changes in demographic rates (survival, capacity, or fecundity) at specific life stages into overall measures of population viability (e.g., long-term abundance, productivity, or probability of extinction) (e.g., Zabel et al. 2013). The Comparative Survival Study (CSS) has also developed a separate life-cycle model to examine mechanisms of mortality originating within the hydrosystem (CSS 2015), focusing primarily on survival after the smolt stage and the consequences for smolt-to-adult return survival (SAR) and adult production.

Both the NOAA and CSS life-cycle models involve survival computations that predict how changes in the abundance of a cohort at one life stage will affect its abundance at a subsequent life stage. In other words, these models already incorporate data or assumptions that are required to convert impacts of predation at one life stage to corresponding impacts at another. Moreover, both models are designed to facilitate comparison of population projections under alternative management scenarios. Explicit attempts to use these models to assess the impacts of manipulating predation rates have not yet been published (at the time of writing), but NOAA scientists have begun using them to explore the consequences of reducing predation by birds and pinnipeds for the viability of ESA-listed populations (Zabel 2016 [presentation](#)). Accordingly, the ISAB believes it would be advantageous to consider and choose among predation metrics that are already explicitly represented within life-cycle models that have already been developed.

It should be noted that, to date, the life-cycle modeling efforts by NOAA and CSS scientists have allowed (and estimated) compensation only within the spawner-to-smolt life stages. Thus, their findings are subject to the same criticisms mentioned with respect to calculating adult equivalents based on average SARs. Chapter 8 (Appendix D) provides four simple examples that consider only compensation from density dependence to illustrate the sometimes counterintuitive insights that are possible from computations based on a life-cycle approach.

A related, but simpler quantitative approach ($\Delta\lambda$ or delta lambda metric; see a more detailed discussion in Chapter 6) has been used over the last decade as an expedient way to compare the relative value of management options to reduce predation (Roby et al. 2003, Good et al. 2007, Lyons et al. 2011a,b, 2014a,b). This $\Delta\lambda$ approach takes advantage of the fact that deterministic age-structured matrix models have already been developed under NOAA's Cumulative Risk Initiative (CRI) to estimate the average annual population growth rate (λ) for threatened and endangered ESUs of salmonids. Most ESUs appear to require 5–15% increases in the current λ value to recover and become viable (i.e., so that $\lambda > 1$; e.g., to increase lambda from 0.8 to 1 requires a 25% increase in current lambda; McClure et al. 2003). Although estimating λ is challenging (Kareiva et al. 2000), the $\Delta\lambda$ approach can still be useful for comparing the relative value of alternative recovery actions in terms of the predicted increase in λ . Moreover, the $\Delta\lambda$ metric can be calculated directly from expected changes in annual survival rate (after mortality from all sources) if one knows the average generational time for the population or ESU (McClure et al. 2003).

Several potential recovery actions have been evaluated with the $\Delta\lambda$ metric. Although these analyses are somewhat dated, they are useful examples of how the $\Delta\lambda$ metric could be applied to evaluate alternative management actions including predator control. Altered management of the Columbia and Snake rivers hydropower system (the cumulative impact of over 100 specific actions) could potentially achieve 3–15% improvements in λ , depending on the salmonid ESU (NMFS 2000a). Breaching four dams on the Snake River might increase λ by 6–27% for the Snake River spring–summer Chinook ESU, depending on assumptions regarding hydropower system induced mortality in smolts that occurs after they pass through the hydropower system (NMFS 2000a). Complete elimination of harvest could increase λ by 4–12% for steelhead and 1–30% for Chinook salmon (depending on ESU) when compared with harvest levels of the 1980s and early 1990s (McClure et al. 2003). The northern pikeminnow management program has reduced predation by an estimated 3.8 million smolts per year (Friesen and Ward 1999), which might have increased λ by 0.4–0.7% if this mortality is completely additive (Roby et al. 2003). This and many of

the earlier studies using this metric assumed no density dependence, which we know is not correct for most populations examined ([ISAB 2015-1](#), [ISAB/ISRP 2016-1](#)).

More recently the $\Delta\lambda$ metric has been used to compare the relative impacts of predation on juvenile salmon by Caspian terns and double-crested cormorants assuming no other mortality factors would compensate for the complete elimination of predation of smolts by these birds. Completely eliminating predation by Caspian terns nesting at Goose Island (in Potholes Reservoir near Othello, WA) was identified as the single most beneficial control action in that it could potentially increase λ values for Upper Columbia River steelhead by up to 4.2% (for hatchery smolts) or 3.2% (for wild smolts) (Lyons et al. 2011a,b). Similarly, completely eliminating predation by double-crested cormorants nesting on East Sand Island could potentially increase λ by 0.4 to 1.1% for Chinook salmon ESUs originating upstream of Bonneville Dam or from the Upper Willamette Basin, 1.6% for the Snake River sockeye salmon ESU, and 1.8 to 2.1% for steelhead DPSs originating upstream of Bonneville Dam (Lyons et al. 2014a,b). However, if even a moderate (50%⁸) level of compensatory smolt mortality occurred in response to complete elimination of mortality due to cormorant predation, the increase in λ would drop below 1% for Chinook and sockeye salmon ESUs but remain at 0.9 to 1.1% for steelhead DPSs (Lyons et al. 2014a,b). Thus, a critical and unknown factor in applying this and other metrics is the extent to which other predators or other forms of mortality will compensate for targeted reductions in predation by focal predators.

⁸ The approximate benefit from predator reduction is 50% of that assumed by additive mortality.

6. Review of Three Alternative Metrics

This chapter reviews the benefits and limitations of three alternative metrics among many that were discussed during ISAB briefings (see Chapter 2 for a description of review methods). We focused specifically on metrics that would facilitate comparison among different sources of predation across the salmonid life cycle, as well as comparison of the effects of predation with other limiting factors. Two of these metrics (equivalence factors and delta lambda, $\Delta\lambda$) are useful for evaluating different management actions over the short term (typically within one generation). Equivalence factors can be computed between any two life-stages and include, as a special case, adult equivalents. Recruits-per-spawner (also denoted as recruits/spawner) is also an equivalence factor (i.e., recruit equivalents expressed as a proportion of the number of parent spawners). Equivalence-factor metrics can incorporate density dependence at any point between the two life stages. The $\Delta\lambda$ metric captures changes over the entire life cycle (typically assuming no density-dependent effects) and requires only knowledge of changes in survival rate.

After briefly describing the theoretical development of equivalence factor metrics (Equivalence Factors section) and the $\Delta\lambda$ metric (delta lambda section), we illustrate their use with numerical examples from four life-cycle models for Chinook salmon based on the Grande Ronde population with parameter values extracted from the latest Comparative Survival Study report (CSS 2015; see Chapter 8, Appendix D for details). The four models differ in the life stages at which density dependence occurs or in values of in-river survival achieved by controlling predation on smolts (Table 6.1).

Table 6.1 Comparison of four life-cycle models used to illustrate the impacts of changes in in-river survival via predator control on subsequent stages in the life cycle if there is no density dependence after in-river survival is increased (M2 vs. M1) and if there is additional density dependence after in-river survival (M4 vs. M3). See Chapter 8, Appendix D.			
Model	Density-dependent survival during spawning/rearing	In-river survival increased by predator control	Density-dependent survival within the estuary
M1	x		
M2	x	x	
M3	x		x
M4	x	x	x

A third metric (probability of extinction) is examined after the EF and $\Delta\lambda$ metrics. This metric can be used to evaluate management actions over the long term (i.e., many generations in the future). It requires a more sophisticated life-cycle model to include stochasticity (random processes) both in transitions among life stages and in the impacts of external factors (e.g., ocean conditions) on the life cycle.

Equivalence Factors (EF)

As noted previously, equivalence factors (EF) include two metrics commonly used in the Basin.

The concept of adult equivalents (AEQ) is widely accepted and applied by fishery scientists and management agencies to evaluate the impacts of ocean fishing on salmon stocks, particularly Chinook salmon. The Council's request letter to the ISAB specifically identifies *adult equivalents* as an example of a potential predation metric for consideration. As explained in the ISAB's Harvest Management Report, "since Chinook salmon are harvested [in the ocean] at various ages and stages of maturity, exploitation rates are commonly expressed in terms of adult equivalents for this species to provide a consistent basis for monitoring fishery impacts over time. Adult equivalents are derived by multiplying the number of fish from a given stock and age harvested by a particular fishery by the appropriate adult-equivalence factor, the probability that a fish that is alive at a given age would survive to return to its river of origin to spawn in the current or any future year, in the absence of fishing" ([ISAB 2005-4](#)).

Simple AEQ metrics (not adjusted for other sources of mortality or compensation) have been used to a limited extent in the Basin to evaluate predation effects on salmonids. For example, AEQ metrics were used to explain impacts on tribal harvests of predation on salmon and steelhead smolts as they migrate downstream through the FCRPS and lower Columbia River and estuary below Bonneville Dam (e.g., [Lumley 2013](#), [Columbia River Treaty Tribes 2014](#)). In these examples, the equivalent number of adult salmonids that would be available for tribal harvests if not lost to predators at an earlier life stage can be derived by multiplying the number of smolts lost to predation by an assumed (1%)⁹ smolt-to-adult survival.

Recruits per spawners is another metric commonly used in the Columbia Basin to determine the annual productivity of a population under current conditions (and at the current density). Measures of productivity are useful for monitoring status and trends. Here the number of recruits (typically total adult returns before fishing mortality) is simply normalized (divided by) the number of parent spawners. Thus, derivation of a recruit per spawner equivalence metric follows the same logic as for AEQ.

⁹ This report uses a variety of assumed smolt-to-adult survival rates to demonstrate concepts. Survival rates may vary considerably depending on species, population, and year. Other documents should be consulted for specific survival rate information. In this example, AEQ is defined as 1 adult per 100 smolts.

Theoretical derivation

The EF is computed as the ratio of changes in abundance at one life stage to changes in abundance in another life stage in response to an action such as predator control. The EF is defined as:

$$EF = \frac{\Delta_{\text{Abundance at Lifestage 2}}}{\Delta_{\text{Abundance at Lifestage 1}}}$$

Conceptually, the EF depends on the relationship between abundances at the two life stages (Figure 6.1). The ratio of the differences in abundance at the two life stages is the average slope between the curve relating the abundances at the two life stages. For small changes in abundance in the first life stage, the EF is very close to the tangent line (the derivative of the curve). For larger changes in abundance, the EF is the average tangent line.

If the relationship between the abundances at the two life stages is nonlinear (as in a recruit-spawner curve that reflects density dependence), then the EF could change depending on where the change in abundance occurs. For example in Figure 6.1, the EF could be positive, negative, or zero depending on where the changes in abundance in the first life stage occur.

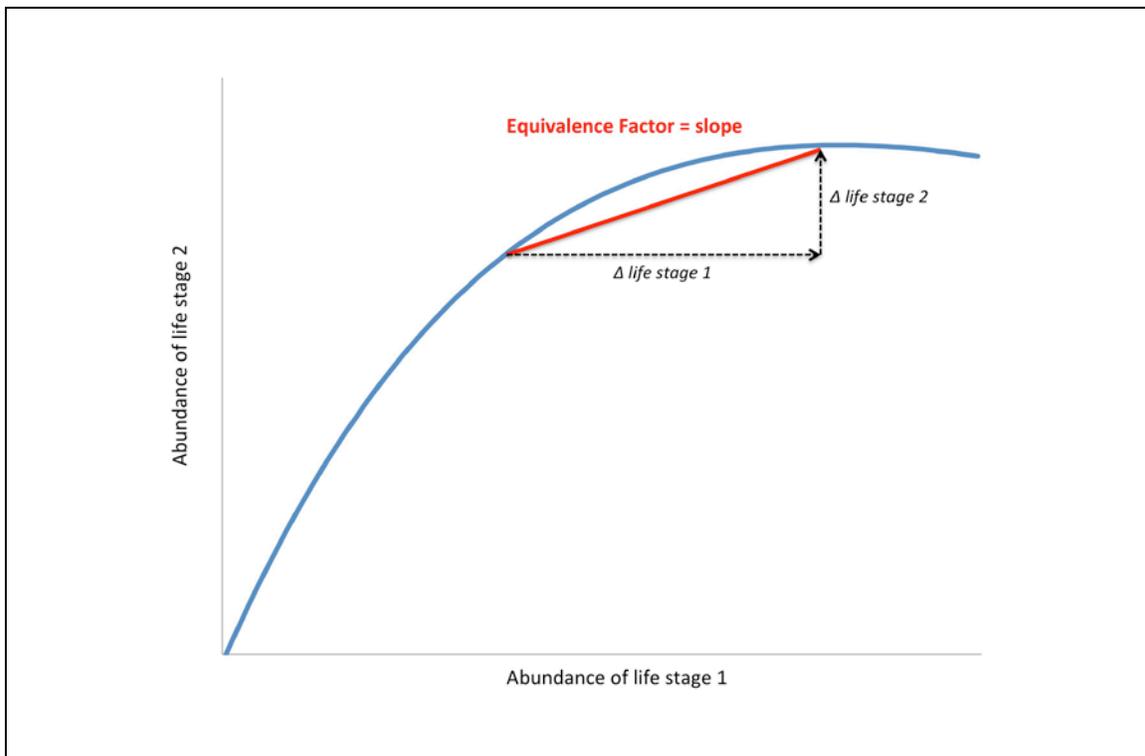


Figure 6.1. General definition of an equivalence factor (EF) to convert changes in abundance at one stage of a life cycle to changes in abundance at a second stage of the life cycle. For a change in abundance of just one fish at life stage 1, the EF will correspond closely to the derivative of the relationship (slope of the tangent line). If the relationship is nonlinear, the EF will depend on the abundance at which changes occur.

The key to computing the EF is the relationship between the two abundances. For example, consider plots of the relationship between the number of smolts produced and the number of adults returning to Bonneville from models M1 and M2 (Figure 6.2). For models M1 and M2 (Chapter 8, Appendix D), there is no density dependence or compensatory behavior between these two life stages, and so the relationship between abundance at the two life stages is a straight line. Also, because the intercept must be zero (i.e., no smolts produced means no spawning adults), the fitted line between adults at Bonneville and smolts at LGR is:

$$\text{Adults at Bonneville} = 0 + 0.042 \times \text{LGR smolts}$$

In the simple case of a linear relationship, the EF is easy to compute. In this case, the two abundances have a simple relationship:

$$\text{Abundance}_2 = \beta_0 + \beta_1 \text{Abundance}_1$$

and $EF = \beta_1 = 0.042$. That is, each smolt added (or lost) after LGR leads to an increase (or decrease) of 0.042 adults at Bonneville because the smolt to adult survival rate is 4.2% and there is no compensatory mortality associated with predation.

For models M3 and M4 (Chapter 8, Appendix D), density dependence in the estuary affects recruitment to age-3 in the ocean. Consequently, the relationship between abundances is nonlinear. However, the density-dependent effect is quite weak, and so a simple EF computed using an average slope over the range of smolt values may still be adequate (Figure 6.2).

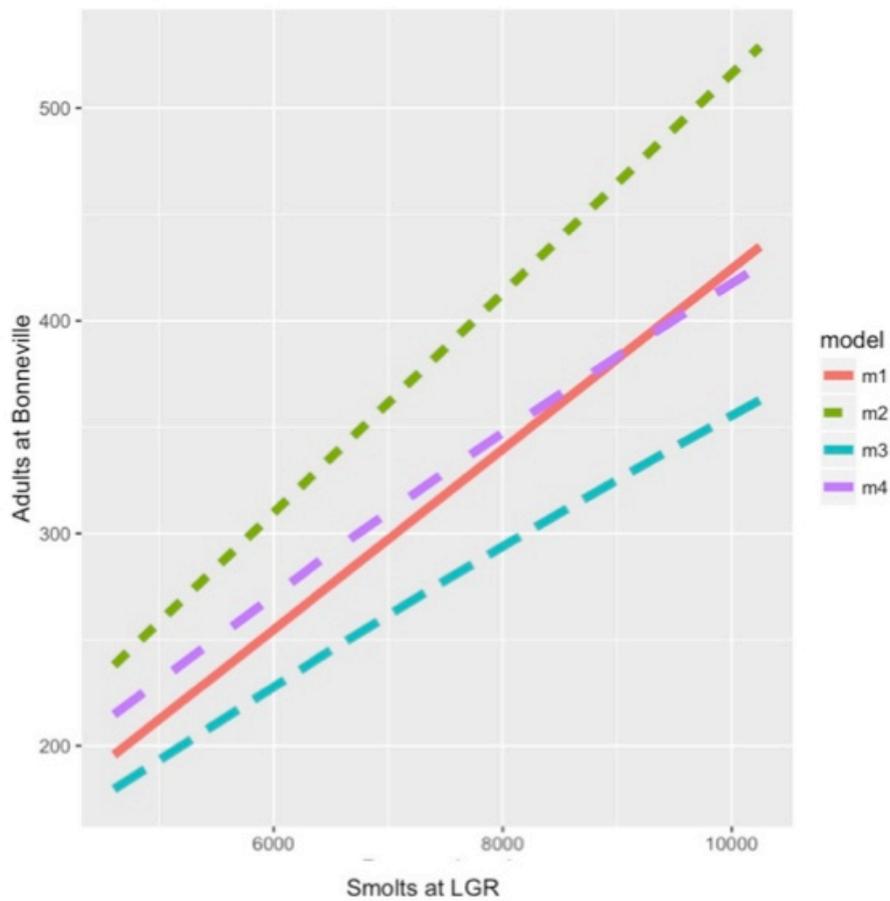


Figure 6.2. Relationship between smolts at Lower Granite Dam (LGR) and returning adults at Bonneville for the four life-cycle models considered in Chapter 8, Appendix D). See Table 6.1 for descriptions of each model.

In cases where density dependence and/or compensatory dynamics are important during the interval between the two life stages, then the relationship between abundances at the respective life stages is likely to be highly nonlinear. If complete compensation occurs between the two life stages, such as when predators eat only moribund prey, then the slope of the line (and the EF) will be zero. There is no simple way to compute an EF without looking at the relationship between the abundances at the two points in the life cycle. However, compensatory responses associated with predator selectivity and predator switching may be difficult to fully assess using this approach. It should be noted that in cases of very nonlinear relationships, both the life stage at which the change in abundance is to occur and the magnitude of the change are important, i.e., the average slope could be quite different from the tangent line.

An EF based on recruits per spawner may also be calculated as an alternative metric that reflects the change in productivity associated with predation and predator control. Recruits/spawner relationships can be used in two different ways. First, if the action affects the number of spawners, then a stock-recruitment curve can be used to estimate the effect

of the actions on recruitment. For example, the relationship between the number of parent spawners and subsequent adult returns (recruits) without fishing mortality is shown in Figure 6.3 for each of the four models described in Appendix D. The slope of the curve is not constant, and now the effects of density dependence (mostly in the production of smolts) is quite noticeable and the EF varies depending on the parent spawner density for which it is computed. For example, in model 3, the effect of adding 400 new spawners when there are 1600 spawners is quite different (virtually no impact on recruits and R/S) compared to adding 100 new spawners when there are only 400 spawners (many more recruits and higher R/S).

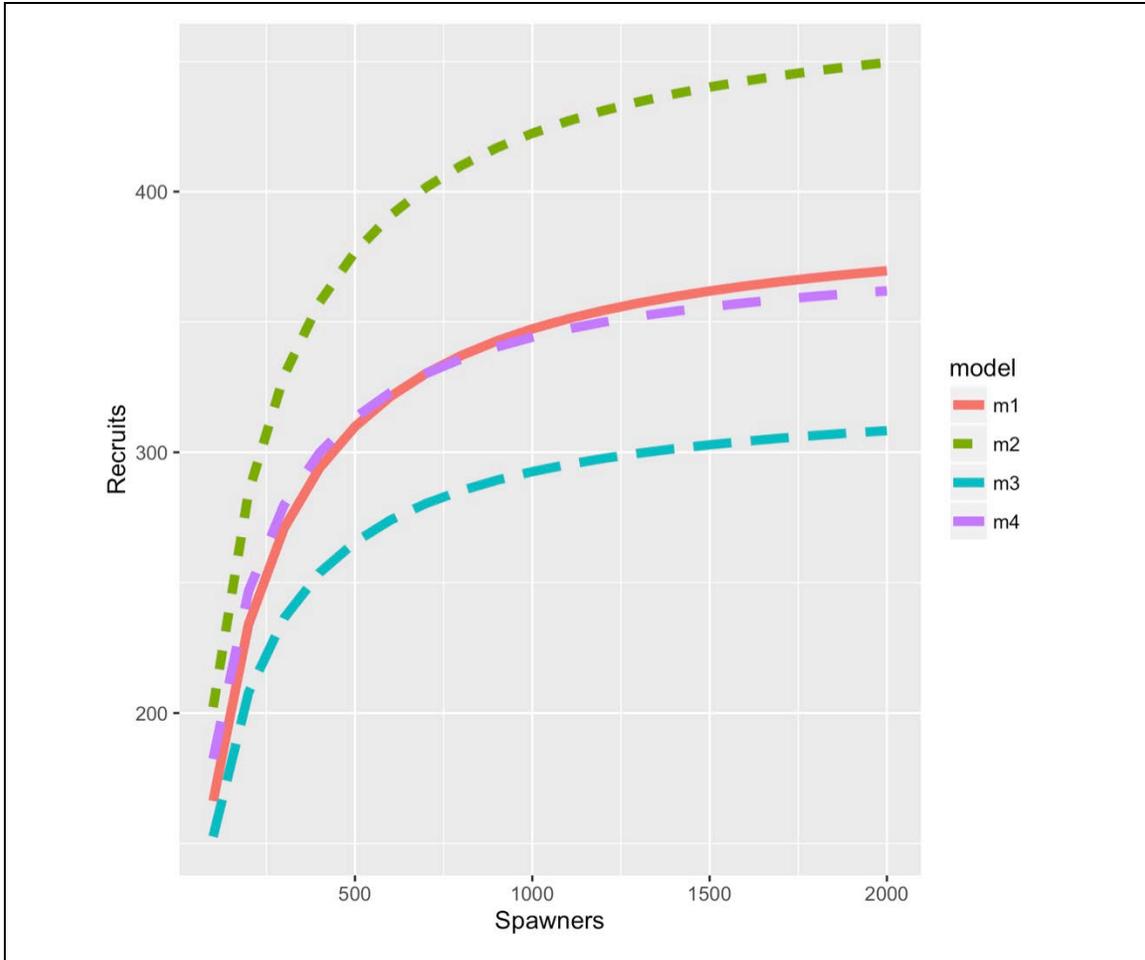


Figure 6.3. Relationship between recruits (returning adults) and (parent) spawners for the four life-cycle models considered in Chapter 8, Appendix D.

Second, it may be of interest to know how many more adult recruits can be expected to return under the same scenario of predator control given the same number of parent spawners yielding a change in the recruits-per-spawner:

$$\Delta R/S = \frac{\Delta_{\text{Abundance of returning spawners}}}{\Delta_{\text{Abundance of smolts in river}} \times \text{Original number of spawners}}$$

In this usage, one is interested in the shift (up or down) of the recruits-spawner relationship when predator control improves survival at a particular life stage. This approach is primarily relevant when the number of parent spawners would remain relatively constant; otherwise a shift in parent spawners will strongly affect the metric.

Values in Figure 6.3 can be used to estimate the change in the recruits/spawner when predator controls are introduced. For example, suppose that there are 500 parent spawners. Under model M1 (no predator control), approximately 310 recruits are estimated when $R/S=0.62$. Under Model M2 (predator control resulting in increased in-river survival), the number of recruits increases to 375 and $R/S=0.75$. The number of recruits/spawner increases from 0.62 to 0.75 when predator controls are introduced into the river and the number of parent spawners is constant.

Establishing the relationship between abundances.

The key for using an EF approach is knowing the relationship between the two points in the life cycle. This relationship between abundances can be established in many ways. Empirical data on the abundances at the various points in the life cycle will not all lie on simple curves, so appropriate statistical methods will be required to fit the curve. The EF is then found directly from the fitted curve. A key advantage to this approach is that the empirical fit automatically includes density dependence or other compensatory responses in the relationship.

Some common statistical problems that may occur with this approach, and that will require careful use of statistical methods are:

- Lack of contrast. It is quite difficult to fit a curve if the range of abundances on the X axis is quite small.
- Non-normal errors. The distribution of residuals about the fitted line could have a skewed distribution (e.g., log-normal shape).
- Error-in-variables. If the abundances on the X axis are uncertain (i.e., estimated), severe biases can occur in determining the functional relationship.
- Effects of confounding variables. The observed relationship may be influenced by other covariates, some of which may be unobserved. The EF implicitly assumes no changes in these covariates. This is especially true when data collected from one time period under certain climate conditions will be used to determine EF for another time period under different climate conditions.

The ISAB report on density dependence has a brief discussion of the difficulties in fitting these types of curve ([ISAB 2015-1](#)).

Obtaining these empirical relationships will be *challenging*. For example, while the Columbia River Basin has an extensive PIT tagging program tracking survival (and abundance of tagged groups of fish), there is little work in deriving estimates of *total* smolt abundance moving through the hydrosystem. Consequently, while changes in abundance for the PIT tagged group are known, the scaling factor to place these on the abundance curve is unknown. This is particularly problematic if the relationship between abundances is highly nonlinear. If linear, then the EF is directly obtainable from survival rates which are more easily found from capture-recapture studies.

In lieu of empirical relationships, life-cycle models are useful tools, especially when data are fragmented or are lacking for various life stages (e.g., number of adults at age 3 in the ocean). By making some broad assumptions, life-cycle models can piece together information from disparate studies into a coherent framework. The obvious dangers in using such a model are that the broad assumptions are not tenable and it is more difficult to obtain measures of uncertainty about the EF. A simple example of a life-cycle model is given in Chapter 8, Appendix D.

Because EF can be derived from the underlying survival probabilities, statistical methods can be employed to estimate the EF based on the relationships between natural and harvest/predation mortality. During a briefing to the ISAB, a compensation-adjusted AEQ metric was suggested (Haeseker 2016 [presentation](#)). This methodology would have the advantage of not needing abundance estimates but would require sophisticated modeling efforts that are statistically challenging (see below for example calculations with a life-cycle model: Chapter 8, Appendix D). Scientific and statistical soundness of a compensation-adjusted AEQ metric relies on the underlying assumptions, methods, and quality of the data used to derive the metric and adjust for compensation (see Chapter 3 for a review of statistical issues). Notable challenges are that the metric requires estimation of a mortality source or index and compensation level (direct or sensitivity analysis), and may need to account for positive correlations among life stages (Haeseker 2016 [presentation](#)). Data available from avian and northern pikeminnow predator control projects in the Basin appear to be of sufficient quality to derive adult equivalents but may not be sufficient for direct estimates of compensation. Estimates of smolt-to-adult survival are available from the [Fish Passage Center](#), but adult survival estimates from the estuary to Bonneville Dam are limited (only Chinook salmon, 2010-present; Wargo Rub 2016 [presentation](#) and [audio](#)). Because of data limitations and the complexity of life-cycle modeling, this metric may be costly. However, once the model is developed and additional years of data are collected for pinnipeds and non-indigenous predators, the use of compensation-adjusted AEQ metric(s) will likely be relatively cost-effective.

Advantages/disadvantages of EF metrics

The greatest benefits of EF metrics are conceptual, communicative, and comparative. The concept is simple to comprehend and to communicate. The metric helps people to understand the impact of predation across life stages (smolt vs. adult). Thus, the effect of predator control can then be compared with the EF of other actions. The metric is relevant to management and policy makers and can be applied at the population level, providing a convenient basis for harvest decisions and predator control rules.

It should be noted, however, that EF metrics might not be suitable for comparing alternative management scenarios in which compensation arises from predator behavior (e.g., selectivity or switching). If the relationship between abundances at two life stages (e.g., Fig. 6.1) is nonlinear only due to density dependence, then the relationship will be useful for predicting the change in abundance at life stage 2 regardless of the management action used to change abundance at life stage 1. In contrast, if the nonlinearity arises from predator selectivity, then the same relationship cannot be expected to predict the outcome of different management scenarios if one involves removal of the selective predator and the other involves removal of other sources of non-selective mortality. In such cases, a more

sophisticated model would be required to evaluate alternative scenarios.

Delta Lambda ($\Delta\lambda$)

Another popular metric to assess the impact of changes in survival on salmonids (e.g., due to predation management) is the delta lambda ($\Delta\lambda$) approach. The basis to this approach is a deterministic, age-structured population growth model that excludes compensatory responses.

Theoretical derivation

The derivation starts with a deterministic model that computes the reproductive rate; i.e., on average, how many new smolts are produced in the next generation from a single smolt. For example, paralleling the life-cycle model used earlier:

$$R_0 = d_j s_0 F_3 d_s R + d_j s_0 (1 - F_3) s_3 F_4 d_s R + d_j s_0 (1 - F_3) s_3 (1 - F_4) s_4 d_s R$$

where d_j is the in-river survival rate; s_0 is the survival rate from Bonneville to age-3; F_3, F_4 are the maturation rate of age-3 and age-4 fish (all remaining fish at age 5 return to spawn); s_3, s_4 are the survival rates from age-3 to age-4 and from age-4 to age-5; d_s is in-river survival and survival from Bonneville to the spawning ground; and R is the average number of smolts produced per returning spawner. A value of $R_0 < 1$ indicates that the population is not self-reproducing and declining; a value of $R_0 > 1$ indicates that the population is tending to increase.

Note that while the equation for R_0 above was developed in terms of a smolt-to-smolt life cycle, a mathematically equivalent equation could be derived for a spawner-to-spawner life cycle (i.e., the order of the factors within each term makes no difference).

Because the reproductive rate operates over several years, the annual population growth rate can be approximated by

$$\lambda = R_0^{1/G}$$

where G is the generation time typically defined as *the age at which members of a given cohort are expected to reproduce*. For illustrative purposes, we used 5 years as the generation time in the examples below.

The proportional change in the population growth rate in response to a change in survival that appears in all terms of R_0 (such as the in-river survival rate) can be estimated as follows:

$$\Delta\lambda = \frac{\lambda_{new} - \lambda_{old}}{\lambda_{old}} = \frac{\lambda_{new}}{\lambda_{old}} - 1 = \left(\frac{R_{0,new}}{R_{0,old}} \right)^{1/G} - 1 = \left(\frac{d_j^{new}}{d_j^{old}} \right)^{1/G} - 1$$

because all other terms factor out in the ratio of the R_0 's and cancel. In this case, the *only* information needed is the change in the in-river survival rate. Of course, in-river survival could be partitioned into finer components to investigate the impact of improvements in specific aspects of the in-river experience.

So returning to the simple life-cycle model M1, a change in the in-river survival from 0.37 to 0.45 results in:

$$\Delta\lambda = \left(\frac{0.45}{0.37}\right)^{1/5} - 1 = .04$$

or a 4% increase in the annual population growth rate regardless of the number of spawners on the spawning ground. The life-cycle model M1 when run for one generation, forecasts a change from 257 to 313 spawners. A change in the population growth rate from equilibrium ($\lambda = 1$) to $\lambda = 1.04$ is a 4% change as well. Both AEQ and $\Delta\lambda$ methods will yield identical results because neither model assumes density dependence between LGR-smolts at Lower Granite Dam and adults at Bonneville.

Now consider the life-cycle model M3 which assumes density dependence in the estuary and is closer to capacity constraints. Delta lambda of 0.04 is unchanged, but the life-cycle model predicts a one-generation increase in spawners from 212 to 252 or a change in population growth from equilibrium ($\lambda = 1$) to $\lambda = 1.035$ for a 3.5% change in the population growth rate.

The $\Delta\lambda$ approach can also be used if the population is actually in a short-term decline. For example, if the number of spawners is increased to 1000 in model M1, the next generation is forecast to have only 293 spawners ($\lambda = 0.78$) because of density dependence during the spawner to smolt stage; if the in-river survival is then increased to 0.45, the next generation is forecast to have 344 spawners ($\lambda = 0.81$). Hence the change in population growth is $(0.81-0.78)/0.78$ or 3.8%. In this case, both populations are declining (population growth rates below 1), but the rate of decline has "improved" with the increase in in-river survival.

So at first approximation, $\Delta\lambda$ may be a suitable metric, but it will become more and more unreliable as density dependence or other forms of compensation predominate and are not accounted for in other ways.

Using delta lambda to compare management actions

While $\Delta\lambda$ does not have a simple interpretation to "convert" a fish from one part of the life cycle to another part of the life cycle, it can be used to compare the relative benefit of different management actions (particularly if the common survival terms are partitioned into finer components), albeit with the caveats above.

We can compare $\Delta\lambda$ resulting from improvement in in-river survival (Model M2 vs. M1) to the management action of eliminating harvest of adults returning to the spawning ground. We earlier saw that changing the in-river survival from 0.37 to 0.45 results in:

$$\Delta\lambda = \left(\frac{0.45}{0.37}\right)^{1/5} - 1 = .04$$

or a 4% increase in the annual population growth rate.

Currently, Model M1 has a 15% harvest rate, so the (returning) in-river survival is $1 - 0.15$ or 0.85. If harvest is reduced to 0%, the (returning) in-river survival is $1 - 0.00$ or 1.0.

Now

$$\Delta\lambda = \left(\frac{1-0.00}{1-0.15}\right)^{1/5} - 1 = \left(\frac{1.00}{0.85}\right)^{1/5} - 1 = .033$$

and one would conclude that the change in in-river survival is more beneficial than the change in harvest. But, as noted earlier, the improvement in the number of fish associated with changes in in-river survival cannot be easily estimated because total smolt abundance is typically not estimated.

Similarly, if predation is assumed to be the only cause of mortality during a narrowly defined life stage when smolts are exposed to predation, then the initial annual survival rate (S_i) is estimated by calculating one minus the currently documented predation rate (Lyons et al. 2014). Changes in λ can be estimated for a range of potential final annual survival rates (S_f); the change is equivalent to one minus the expected future predation rate by the given predator species. Thus, the potential benefits of different management alternatives that might produce a range of reductions in predation (and a corresponding range of increases in juvenile survival) can be quickly estimated and compared.

However, such an evaluation ignores the impacts of compensation, including density dependence. To account for compensation, one could incorporate adjustments to the survival rate after the management action, e.g., assume that compensation will eliminate half of the improvements due to a reduction in predation as a sensitivity analysis.

Advantages and disadvantages of delta lambda

The key advantage of the $\Delta\lambda$ approach is that the impact on population growth can be approximated by knowing only changes to the survival rates without having to know values of the other parameters, unlike the life-cycle model where all parameters must be estimated. The key disadvantages are that this approach will *not* work for changes in survival that are not common to all terms in the model, such as s_3, s_4 and cannot easily include compensatory mortality or density dependence. For example, the $\Delta\lambda$ approach treats a proportional change in the in-river survival or the same proportional change in survival of adults as they return to the spawning grounds as being equivalent because there is no opportunity for density dependence or compensatory responses. Similarly, a proportional change in the survival rates appears to have the same benefit regardless of whether the population on the spawning grounds is far from or at capacity.

The $\Delta\lambda$ metric may provide a suitable approximation if the impacts of compensation or density are small. Alternatively the impact of the management action may be adjusted (before calculating $\Delta\lambda$) to reflect compensation based on other assumptions or analyses. The $\Delta\lambda$ approach could also be extended to explicitly account for density dependence or compensatory responses by building a population matrix model (Caswell 2001) where the terms in the matrix include compensatory/density effects. This is equivalent to the life-cycle model considered previously. However, density dependence and other compensatory behavior need to be strong before the two approaches provide substantially different results.

Probability of Extinction in the Long-term

The two previous metrics (equivalence factors and $\Delta\lambda$) are best used for short-term impact of management actions as they both rely on deterministic models for forecasting impacts of changes. However, all populations are subject to both demographic stochasticity (if 100 fish each have a probability of survival of 0.50, then the actual number of fish that survive would vary above and below the expected value of 50), and environmental stochasticity (long- and short-term climate fluctuations, changes in ocean conditions, etc. cause survival probabilities to vary). Thus, while the growth rate may indicate a growing population, stochastic events could extirpate the population.

The probability of extinction can be used as a metric to compare the long-term performance of management actions. A management action that leads to a large reduction in the probability of extinction is preferable to another action that leads to a smaller reduction (all else being equal).

The only feasible way to estimate the probability of extinction in the long-term is via a simulation study where random processes are incorporated into a life-cycle (or similar) model. Then population trajectories can be predicted in simulated scenarios under different management actions, and the associated probability of extinction (proportion of trajectories in which abundance falls to 0) or quasi-extinction (abundance falls below some threshold) can be estimated.

These types of models will require much information to reliably estimate the expected values for parameters (e.g., survival rates, productivity, etc.) and how they can vary over time. A first step is to develop simple life-cycle models to conduct sensitivity analyses to indicate which parts of the model need to be expanded.

Choice of Suitable Predation Metrics

The suitability of predation metrics depends on a number of factors as summarized in Table 6.2. Here we focus on evaluating two equivalence factor metrics (AEQ and R/S) and the $\Delta\lambda$ metric. We did not give further consideration to the probability of extinction metric because it is too onerous for many management applications and is still in development as a predation metric in the Basin (e.g., Zabel et al. 2016). Nonetheless, the probability of extinction metric may be useful when examining predation effects on ESA-listed stocks.

Table 6.2. Informal evaluation of three potential alternative predation metrics selected by the ISAB: AEQ @ BON = adult equivalents at Bonneville Dam (BON) (number of adults), $\Delta\lambda$ = change in population growth rate (% increase per unit time), R/S = net recruits per spawner (number of adult recruits per spawner). Note that both AEQ @ BON and R/S are both equivalence factor metrics. The metrics are evaluated based on ISAB judgments (“yes” (y), “no” (blank) or “uncertain” (?)) about the usefulness of the computed metric for three cases: 1 = simple (no other mortality factors or compensation in predation mortality), 2 = intermediate (additional mortality factors but no compensation), 3 = complex (both for other mortality factors and compensation). See methods (Chapter 2) for explanation of evaluation criteria.

Evaluation Criteria	Alternative metrics and case								
	AEQ @ BON			$\Delta\lambda$			R/S		
	1	2	3	1	2	3	1	2	3
Wide use	y	y		y	y		y	y	
User friendly	y	y	y				y		
Relevance for:									
Predator control	y	y	y	y	y			y	y
Salmonid harvest	y	y	y	y	y		y	y	y
Salmonid conservation	y			y	y		y	y	y
Benchmark	y			y	y		y	y	y
Comparison & evaluation									
Predation at other life stages	y	y	y	y/n*	y/n*	y/n*	y	y	y
Other limiting factors	y	y	y	y	y	y	y	y	y
Scientific & statistical soundness	y	y	y	y	y	y	y	y	y
Scale									
Spatial/temporal	y	y	y	y	y	y	y	y	y
Biological	y	y	y	y	y	y	y	y	y
Derivation									
Easy to derive	y	y		y	y		y	y	
Feasible to derive	y	y	y	y	y	y	y	y	y
Available data/software	y	?		y	?	?	y	y	
Costly to obtain data?		y	y		y	y		y	y

* As outlined in the text, the $\Delta\lambda$ metric works best for components that are common to all subsequent life stages equally (e.g., in-river survival), but not for isolated components (e.g., selective harvest only of age-4 fish). Delta lambda is not specific to spawners or smolts and is equivalent for all parts of the life cycle.

First and foremost, both the equivalence factor and $\Delta\lambda$ metrics (and perhaps others) can be useful for evaluating the performance of management actions with respect to the abundance or productivity of salmon populations (e.g., how many more fish return to spawn as given by the equivalence factors) and population recovery (does the management action improve the population growth rate as given by $\Delta\lambda$). An equivalence factor metric alone may be sufficient if the population is healthy and interest lies, for example, primarily in increased harvest opportunities. However, both metrics are likely needed in the case of endangered populations so that an improvement in adult returns or spawners can be put into context. Notice that either metric, by itself is not sufficient. Knowledge that population numbers would increase or that the change in the population growth rate is positive does not indicate that the population is not endangered: any metric needs to be placed into context.

The conceptual basis for equivalence factors is easy to understand—how many more fish at a subsequent life stage are produced (or lost) per additional fish saved (or lost) at this life stage.

The conceptual basis for $\Delta\lambda$ is much more complex. Delta lambda only informs about the *relative change* in the growth rate, but, on its own, provides no information on the actual population growth rate. So $\Delta\lambda$ may indicate that a management action results in a positive *increase* in the growth rate but does not inform if this increase will result in an overall growing population. As well, the $\Delta\lambda$ value is a proportion (or percentage) applied to a rate (which looks like a proportion) and so can be confusing. For example, increasing $\Delta\lambda$ by 5% when the base survival rate is 0.40 actually increases survival to only 0.42 (assuming a generation time of one year).

The $\Delta\lambda$ value applies to the population trajectory as a whole and will apply to adults at Bonneville, spawners, smolts at Lower Granite Dam, smolts at Bonneville Dam, age-3 fish, etc.

The choice of stages in the life cycle for which an EF is computed depends on the context. So while the increase in the number of adults at Bonneville (AEQ) is important for questions about in-river harvest, it would fail to acknowledge that the population may be at capacity on the spawning grounds and so additional spawners are not beneficial (or potentially counter-productive if overcompensation is strong).

Consequently, multiple EF values may be needed, including an equivalence factor that is based upon the entire life cycle (e.g., spawner to spawner) which can then provide information on the actual population growth rate, and the reproductive value of fish at that particular life stage. Using changes in recruits/spawner (or spawner/spawner) as a metric for the effects of predator control may be a useful summary measure for evaluating long-term viability (similar to $\Delta\lambda$) because if the value of spawner/spawner over time is < 1 , the population must be in decline, while spawner/spawner > 1 indicates potential for rebuilding. However, this metric ignores the actual numerical response, so an increase in the recruit/spawner of 1.5 when the underlying original spawner abundance is 10 is quite different than if the original spawner abundance is 1000 given demographic and environmental stochasticity that is always present.

The computation of EF and $\Delta\lambda$ metrics share important strengths and limitations. Both AEQ and $\Delta\lambda$ metrics can (in theory) be computed in cases with and without

density/compensatory responses. Both metrics attempt to identify marginal benefits from management actions, i.e., assuming that all other conditions remain constant. However, neither metric will indicate how the equilibrium population is expected to shift in response to changes in in-river survival (as shown in Appendix D). While our numerical example showed a compounded benefit in changes in in-river survival, this is attributable to the assumed (Beverton-Holt) density dependent relationship. It is quite possible that an opposite effect could occur if a Ricker relationship exists. Similarly, neither metric can account for other changes, such as predator shifting to a different prey in response to changes in prey numbers.

The EF and $\Delta\lambda$ metrics will both give “equivalent” answers when applied to populations with no density or compensatory responses. Both metrics can be easily computed with information on changes in survival at a particular life stage without having to build an entire life-cycle model. Hence for simple cases the data requirements are fairly modest—just estimates of survival and proposed change in survival rate at that particular life stage.

If density/compensatory responses are present, then simple computation of the metrics ignoring such effects will likely overstate any benefit. But, it also seems likely that unless compensation/density effects are strong, that the approximate answers ignoring these effects may be sufficient to compare different management actions. While the actual numerical value from the metric may be (slightly) biased, the relative comparison among different management actions might be relatively unaffected. A logical next step after such an analysis would be to conduct a sensitivity analysis to estimate the potential magnitude of bias given a plausible range of compensation at each life stage.

There does not appear to be a simple way to modify either metric to account for strong density/compensatory responses in life stages other than moving to a full life-cycle model (at least between the two life stages for equivalence factors). This may require more data and sophisticated statistical methods to estimate the density/compensation response.

While point estimates of the average value of the metric may be relatively easy to obtain, estimating the uncertainty due to both estimation error and demographic and environmental stochasticity (randomness) is much more complex. This likely will require a full life-cycle model where such variation can be simulated. If stochasticity is being considered, then metrics such as extinction risk can also be evaluated.

7. Conclusions and Recommendations

The ISAB concludes that individual metrics are useful, but metrics can be more informative when incorporated in a life-cycle model that can help disentangle multiple factors affecting salmon survival and interactions among those factors. Furthermore, such processes and interactions can be evaluated in modeled scenarios and verified with data. This approach could help guide research, monitoring, and evaluation of predation throughout the salmonid life cycle, both to provide the data necessary to parameterize and verify models, and to refine metrics. A significant challenge will be to estimate the degree of compensation associated with predation and predator control actions at different life stages. If estimates of compensation are not available, then assumptions about potential compensation should be considered when evaluating predator effects on salmon and steelhead populations and the benefits of predator control programs. Finally, the ISAB encourages the future workgroup charged with developing a standardized predation metric(s) to fully consider our recommended metrics and also explore additional alternative methods and metrics.

The ISAB recommends:

1. Using and further refining two types of metrics currently in use in the Basin:
 - (a) *Equivalence-factor metrics* (for example, adult equivalents), which can be used to compare the effects of predation on salmon and steelhead at different points in their life cycle.
 - (b) *Change in population growth rate metric* (also called *delta lambda*, $\Delta\lambda$), which can be used to compare how different predation scenarios affect rates of population recovery or decline.
2. Adjusting the *equivalence-factor metrics* and the *population growth rate metric* ($\Delta\lambda$) to account for assumed or estimated compensation in mortality.
3. Placing predation mortality in the context of a life-cycle model.

8. Appendices

Appendix A. Selective Predation

Chapter 3 briefly describes why compensatory mortality is important to developing a predation metric. Selective predation is one of several key mechanisms that may lead to compensatory mortality. In Appendix A, we briefly review literature in the Columbia Basin and elsewhere to identify whether or not fishes, birds, and marine mammals tend to randomly consume salmonid prey or whether predators select salmonids that are more fit or less fit. Appendix A provides additional detail and references for the summary of selective predation presented in Chapter 3.

In this assessment, we assume that larger-than-average individuals of the same species are more likely to survive. This assumption is based on observations of size-selective mortality of Pacific salmon smolts entering the ocean: larger individuals tend to have higher survival (Beamish et al. 2004, Duffy and Beauchamp 2011, Ruggerone et al. 2013, Thompson and Beauchamp 2014). Also, larger adult salmon have higher reproductive potential. Large adult female salmon tend to have larger, more numerous eggs and can deposit those eggs deeper in the gravel where risk of scouring is reduced compared with smaller salmon (Steen and Quinn 1999, Quinn 2005). Larger adult male salmon are typically more successful at mating and passing along genes than smaller salmon. As expected, survival to the adult stage is typically lower for juveniles with body injuries, fin damage, and external signs of disease (Hostetter et al. 2011, 2012; Evans et al. 2014, 2016a).

Selective predation by fishes

Many piscivorous fish studies have been conducted in the Columbia River Basin, including several studies of selective predation on juvenile salmonids. Poe et al. (1991) reported that northern pikeminnow selectively consumed smaller salmonids in John Day Reservoir and that maximum size of salmonids consumed by pikeminnow increased linearly with length of pikeminnow. Nearly all juvenile salmonids were vulnerable to pikeminnow longer than 375 mm, but larger smolts experienced less risk. The investigators rarely observed salmonids that had been physically injured by turbine passage in the stomachs of predators. The percentage of migrating salmon smolts consumed by pikeminnow, walleye, and bass in the John Day Reservoir was considerably higher in August (61% of smolt migration) compared with April to June (7-11%), indicating predation was higher on subyearling versus yearling Chinook salmon (Rieman et al. 1991).

Muir et al. (2006) estimated the proportion of fish in the pikeminnow (freshwater) and Pacific hake (*Merluccius productus*, a highly abundant marine species that sometimes feeds on salmon smolts in the Columbia River plume) populations below Bonneville Dam that were sufficiently large to capture and consume juvenile Chinook salmon. They reported that wild Chinook salmon were vulnerable to a larger abundance of predators than hatchery salmon because wild salmon were 25-28 mm smaller. Furthermore, post-hydro-system predation mortality was potentially higher for transported salmon than for in-river migrants because transported fish were smaller. Transported fish had 2-4 weeks less time to grow in the river (in-river fish grew ~5-8 mm) and migrated through the estuary at an earlier time period when smolt density was lower and less likely to "swamp" predators.

ODFW and BPA have implemented a major pikeminnow predator control program for many years, but the program has not recently evaluated whether or not pikeminnow in the river selectively consume large or small salmonids, less healthy salmonids, or if they tend to select one salmon species over another (Storch et al. 2016 [presentation](#)).

Fritts and Pearsons (2006) examined size-dependent predation by smallmouth bass in the lower Yakima River. Smallmouth bass selected smaller than average salmon even though bass can potentially consume salmon sizes up to about 57% of their fork length. The maximum size ratio declined at larger bass sizes. Smallmouth bass generally ate salmonids at lengths that were less than 50% of the maximum potential length and that averaged 25% of predator length. Salmonids that were 100 mm or larger were rarely consumed. The proportion of smallmouth bass that contained salmonid prey decreased with increasing bass size; most salmonids were consumed by bass that were less than 250 mm.

Several studies of selective predation in the Columbia Basin were conducted in controlled laboratory conditions as a means to evaluate the effect of an environmental stressor or hatchery rearing environment. Juvenile fall Chinook salmon from the Hanford Reach were subjected to acute thermal stress in the laboratory and predation by smallmouth bass, but the single temperature exposure did not increase vulnerability to predation (Mesa et al. 2002). Juvenile Chinook salmon were subjected to stressors designed to simulate routine hatchery practices (multiple handlings) or dam passage, then exposed to predation by pikeminnow in a laboratory (Mesa 1994). Stressed salmon were consumed more frequently by pikeminnow compared with unstressed salmon during the first hour of exposure to pikeminnow, but this effect was not evident during longer exposures (24 hours). Juvenile Chinook salmon experimentally exposed to *Renibacterium salmoninarum*, the causative agent of bacterial kidney disease (BKD), were eaten in significantly greater numbers (2:1) than control salmon by pikeminnow or smallmouth bass (Mesa et al. 1998). Steelhead fry raised from eggs of wild parents survived better than hatchery fry when exposed to predation by sculpins, suggesting an effect from hatchery domestication (Berejikian 1995). Experience, in the form of 50-minute visual exposure to sculpin predation on "sacrificial" steelhead trout, improved the ability of fry from wild and hatchery populations to avoid predation by sculpin: wild-experienced fry were eaten in the fewest number of trials followed by wild-naive, hatchery-experienced, and hatchery-naive fry. Additional studies indicate hatchery salmon may be more vulnerable to predators than wild salmon due to domestication (Olla and Davis 1989, Johnsson et al. 1996, Olla et al. 1998, Alvarez and Nicieza 2003, Yamamoto and Reinhardt 2003), but larger size of hatchery salmon may reduce this vulnerability (Debes and Hutchings 2014).

Studies beyond the Columbia Basin

Fishes that consume salmonids are typically limited by their gape and/or ability to capture large prey, leading to selective predation on smaller than average juvenile salmonids. Reviews by Juanes (1994) and Sogard (1997) confirm that piscivorous fishes typically select smaller than average prey even though predators may consume juvenile salmon up to ~50% of their body length. Mean prey size may increase with predator size, but predator selection of prey sizes is typically a passive process mediated by differential size-based capture success rather than active preference. The influence of prey size on capture success is likely to be most important for small predator-prey size ratios (i.e., when prey are a large proportion of predator size), where a small change in prey size can result in a large change in capture success. This suggests that a slight increase in growth of prey may convey significant survival advantage.

Although reduced capture success of predators feeding on larger salmonids typically leads to size biased mortality of smaller salmonids, other factors may ultimately influence the outcome of size-selective predation, indicating the need to evaluate selective predation rather than rely on generalizations. In the Wood River Lakes, Alaska, Arctic char aggregate in rivers that connect the lakes to feed on emigrating age-1 and age-2 sockeye salmon smolts (Ruggerone and Rogers 1984). For a number of years in the 1970s and early 1980s, the Alaska Department of Fish and Game used a purse seine to capture, hold, and then live-release char from pens after the sockeye smolt migration ended. Most sockeye smolts emigrated during the darkest part of the night and were smaller than smolts that migrated during twilight and daylight. Char actively fed upon smolts during twilight hours, but feeding activity clearly declined during the darkest part of the night when numerous smaller smolts typically migrated (e.g., char no longer leapt from the water every few seconds while attacking smolts). Although char probably had lower capture success on large smolts, the overall result of the char feeding periodicity and smolt migration pattern was selection by char of larger than average sockeye salmon smolts.

A number of studies beyond the Columbia Basin have also examined the effects of abiotic factors (e.g., temperature, toxic chemicals) or parasites on the susceptibility of salmonids to predation. Elevated water temperature (17-20°C, 21-24°C versus 13-16°C) increased the vulnerability of juvenile Chinook salmon to predation (Marine and Cech 2004). Juvenile coho exposed to low-level copper were unresponsive to their chemosensory environment and were more vulnerable to predation by cutthroat trout (McIntyre et al. 2012). Juvenile pink and chum salmon parasitized by sea lice were more vulnerable to predation by coho salmon than non-parasitized juveniles (Krkosek et al. 2011).

Selective predation by birds

A number of studies in the Columbia Basin indicate a fish's susceptibility to bird predation is related to behavioral and physical traits, including fish size and condition, run-timing, abundances of salmonids and alternative prey, and predator-specific foraging techniques and behaviors (Collis et al. 2001, Ryan et al. 2003, Antolos et al. 2005, Lyons et al. 2014a,b, Evans et al. 2016a, Weitkamp et al. 2016). Most piscivorous bird studies in the Columbia Basin have involved Caspian terns, double-crested cormorants, and gulls.

Caspian terns are highly selective for prey compared with double-crested cormorants. Terns disproportionately consume steelhead compared with yearling and subyearling salmon (Collis et al. 2001, Antolos et al. 2005, Evans et al. 2016a). Terns also select larger salmonids within a given species, e.g., the odds of Caspian tern predation on spring/summer Chinook salmon increased by 12% for every 10 mm increase in fork-length (Evans et al. 2016a). Susceptibility of steelhead to Caspian tern predation also increased with increasing fork length up to 202 mm but then decreased for longer steelhead (Hostetter et al. 2012). The relatively high susceptibility of steelhead to predation by terns may reflect the large size and surface orientation of steelhead, and feeding near the surface by the plunge-diving terns. Hatchery spring/summer Chinook salmon are more vulnerable to predation by terns than their wild counterparts in the river. ESA-listed and non-listed salmonids appear to be equally vulnerable to predation by Caspian terns and cormorants in the estuary (Collis et al. 2012).

Double-crested cormorants also disproportionately consume steelhead compared with yearling Chinook salmon (Collis et al. 2001). However, there was no evidence of size-selectivity in double-crested cormorants on PIT-tagged juvenile salmonids and no evidence of greater susceptibility of hatchery versus natural salmonids. Additionally, in contrast to Caspian terns, double-crested cormorants consumed smolts in proportion to their relative availability, not absolute abundance (Lyons et al. 2014). Changes in absolute abundance of alternative prey, both marine and freshwater/estuarine forage fishes, influenced how much cormorants relied on salmonids as prey. Lyons et al. (2014a,b) concluded that environmental conditions that influence abundances of alternative prey for cormorants were more important than colony size during their study period. In contrast to double-crested cormorants, Brandt's cormorants consumed few salmonids.

Fish condition influences susceptibility to predation by piscivorous birds. Preliminary evidence suggests that at least some smolt mortality is influenced by differential predation by avian predators on Chinook salmon infected with *Renibacterium salmoninarum* and possessing low smoltification levels (relatively low gill Na⁺/K⁺-ATPase activity) (Schreck et al. 2006). Susceptibility of Snake River steelhead to predation by Caspian terns was greater for juveniles showing degraded external condition (e.g., body injuries, descaling, external signs of disease, fin damage, and ectoparasite infestations) (Hostetter 2009, Hostetter et al. 2011, 2012; Evans et al. 2014). The higher susceptibility of unhealthy steelhead to avian predation implies compensatory mortality. However, the portion of unhealthy juvenile steelhead that are at greater risk of avian predation is reportedly small, based on the small proportion of steelhead that exhibited visible symptoms of compromised health.

Consumption of dead or moribund salmonids below turbines could bias interpretation of predation rates, i.e., complete compensation. However, no JSATS tags were recovered on bird colonies from the release of 373 dead, tagged smolts into the tailraces of McNary and John Day dams, providing evidence that dead smolts were not more susceptible to consumption by piscivorous colonial waterbirds in the tailrace of dams compared to their live counterparts (Hughes et al. 2013 and Skalski et al. 2015 in Evans et al. 2015). Gulls are the primary bird species feeding immediately below dams.

Transportation of salmonids in barges around dams may increase the susceptibility of some species to predation by cormorants. Transported Snake River fall Chinook and sockeye salmon were disproportionately consumed by double-crested cormorants compared with in-river migrants during 2006-2015 (Evans et al. 2016a,b). This may reflect lower fish condition, increased residence time in the estuary, abundance, and spatial distribution. In contrast, there was some evidence that in-river steelhead and in-river spring/summer Chinook were disproportionately consumed by Caspian terns and double-crested cormorants compared with transported fish, but results were not consistent across all weeks and years.

Many of the bird predation studies rely upon the recovery of salmon tags on the bird colonies, so the findings are only related to those species and stocks that have been tagged. Genetic analysis of prey consumed by terns and cormorants since 2006 provides a more comprehensive view of salmonids consumed by birds (Lyons et al. 2014a,b; Kuligowski et al. 2016; Weitkamp et al. 2016). This type information is especially important when comparing species composition in the diet of birds with all fish species available to birds and evaluating the influence of alternative marine and freshwater species on the predation

rates of birds on salmonids. As noted above, consumption of salmonids by cormorants depends on the abundance of alternative prey (Lyons et al. 2014a,b).

Studies beyond the Columbia Basin

A wealth of important findings about predation by birds in the Columbia River has been reported. Therefore, the ISAB spent little effort to gather information outside of the Columbia Basin. However, Tucker et al. (2016) provides some relevant information on selectivity of abundant rhinoceros auklets (*Cerorhinca monocerata*, a pursuit diving predator) foraging on pink, sockeye, and chum salmon off coastal British Columbia. Auklets preyed on small individuals in poor condition (low weight at length) and consistently selected them at levels higher than their relative availability. Sockeye salmon were selected more than pink and chum salmon relative to their respective abundances, but the authors were uncertain why this species selectivity occurred.

Selective predation by marine mammals

Research in the lower Columbia River and estuary suggests that pinnipeds (California sea lion, Steller sea lion, and harbor seal) selectively consume adult salmon below Bonneville Dam (Wargo Rub 2016 [presentation](#) and [audio](#), Zabel 2016 [presentation](#); Wargo Rub and Gilbreath 2016, project [website](#)). Predation on adult spring/summer Chinook salmon occurs primarily from March to May when California sea lions are abundant in the estuary and lower river. This timing has a strong influence on the species and stocks of salmonids consumed by California sea lions. Among Chinook salmon populations, spring Chinook salmon are exposed to predation more than summer Chinook salmon, and within each population, early-arriving Chinook are more vulnerable than later arriving Chinook. Earlier arriving populations—such as the Tucannon, Lookingglass, Catherine Creek, and upper Grande Ronde population in the Snake River and Methow River and Leavenworth Hatchery stocks in the upper Columbia—tend to have higher mortality attributed to predation compared with other spring/summer Chinook salmon populations. Fin-clipped Chinook salmon tend to have higher survival than unclipped fish, but this finding likely reflects migration timing of clipped versus unclipped fish, according to the investigators.

Size dependent mortality has been observed in the estuary and lower Columbia River: smaller Chinook salmon have higher mortality (Wargo Rub 2016 [presentation](#) and [audio](#)). Early maturing jack Chinook salmon (one winter in the ocean) had higher mortality, but the investigators wondered if this might be an artifact of higher straying by jack salmon. However, Quinn and Fresh (1984) reported that straying of spring Chinook returning to the Cowlitz River was positively correlated with age, indicating that jack salmon probably stray less not more. Although adult spring/summer Chinook salmon were targeted by most California sea lions, approximately 15% of the sea lions consumed only salmon smolts (Wargo Rub 2016 [presentation](#) and [audio](#)). Alternative prey, such as smelt during the early season, shad in the late season or anchovy, likely influence the degree of predation on salmonids. Harbor seals are abundant and known to prey on adult and juvenile salmon, but little is known about selectivity and predation rates by seals in the Columbia estuary and lower river.

The investigators have not detected selective predation on tagged and released salmon that might be more vulnerable to predation after handling than non-tagged salmon (Wargo Rub 2016 [presentation](#) and [audio](#)). Radio-tags have been used to avoid the potential "dinner-bell effect" that may be associated with some acoustic tags (Berejikian et al. 2016).

Studies beyond the Columbia Basin

Resident killer whales are important predators on maturing salmon in coastal marine waters. Chinook salmon are selectively consumed compared with other salmon species, apparently because Chinook salmon are large and have relatively high lipid content (Ford and Ellis 2006, Ford et al. 2010; Hanson et al. 2010, Adams et al. 2016). Killer whales tend to select larger Chinook salmon (Ford et al. 2010). Chum salmon, which are the second largest salmon, are consumed when they are abundant whereas smaller salmon (pink, sockeye, and coho) are consumed less frequently (Ford and Ellis 2006).

Bears are significant predators on spawning salmon, although predation by bears is likely infrequent in the Columbia Basin. In a small stream in Alaska, brown bears selectively killed large versus small sockeye salmon, and the degree of selectivity across 20 years of investigation depended on salmon density (Ruggerone et al. 2000, Cunningham et al. 2013, Quinn et al. 2014). Bears selectively killed male versus female salmon even though bears targeted the eggs in female salmon. Strong compensatory predation was observed, e.g., 92% of sockeye spawners were killed when 505 salmon entered the creek declining to 16% when approximately 16,000 spawners were present. However, life-cycle recruitment of sockeye salmon was compensatory, indicating that compensation at other life stages overwhelmed compensatory predation by the bears.

Appendix B. Theoretical Issues in Estimating Compensation

Overall annual survival (S) can be written as

$$S = 1 - n - h$$

where n is the natural mortality and h is the mortality due to harvest/predation. Both h and n may vary over time. Péron (2013) shows that the correlation between n and h can be written as (see B.1):

$$\text{corr}(n, h) = -\frac{\text{cov}(S, h)}{\sqrt{\text{Var}(h)\text{Var}(n)}} - \sqrt{\frac{\text{Var}(h)}{\text{Var}(n)}}$$

where $\text{cov}(S, h)$ is the covariance between overall survival and predation and quantifies the extent to which overall survival depends on predation; $V(h)$ is the variance in predation; $\text{Var}(n)$ is the variance in natural mortality. All variances are over time and not over individuals.

As shown by Péron (2013), there are five possible outcomes:

(a) Over compensation:¹⁰

$$\text{corr}(n, h) < -\sqrt{\frac{\text{Var}(h)}{\text{Var}(n)}}$$

This occurs if annual survival increases with increasing predation. For example, in populations with a size hierarchy where larger animals have a higher survival rate, removing the larger animals may reduce competition against the small animals leading to improved survival rates of the smaller fish and a potential net improvement in population survival.

(b) Complete compensation:

$$\text{corr}(n, h) = -\sqrt{\frac{\text{Var}(h)}{\text{Var}(n)}}$$

Annual survival is independent of predation ($\text{cov}(S, h) = 0$). Note that if $\text{Var}(n) < \text{Var}(h)$, then complete compensation is impossible. Some care is needed to distinguish between conditional and unconditional independence. For example, gauntlet fisheries have conditionally independent harvest/predation rates, but their unconditional harvest/predation rates are not independent. Predation on unburied salmon eggs is an example of complete compensation as unburied eggs are not expected to survive (Moyle 1977 as cited by Ward and Hvidsten 2011). In the Columbia, predation on dead or moribund salmonids below dams is another example (see Chapter 3, Selective Predation).

¹⁰ The term "over compensation" here should not be confused with the term "overcompensation" used by Ricker to describe declining recruitment of salmonids at high abundances (see [ISAB 2015-1](#)).

(c) Incomplete compensation:

$$-\sqrt{\frac{\text{Var}(h)}{\text{Var}(n)}} < \text{corr}(n,h) < 0$$

The reduction in annual survival probability is smaller than the change in the predation probability. Incomplete compensation (also called compensatory mortality) occurs when predation is biased toward individuals that possess traits or behaviors that increase the likelihood of predation. Aggressive foraging behavior and relatively small size are examples of attributes that may lead to incomplete compensation, as both could lead to higher predation rates.

(d) Complete additivity:

$$\text{corr}(n,h) = 0$$

Changes in predation are independent of changes in natural mortality. Both sources of mortality add to each other without interfering with each other.

(e) Over-additivity:

$$\text{corr}(n,h) > 0$$

The rate of compensation-additivity (C) is defined as:

$$C = -\text{corr}(n,h) \sqrt{\frac{\text{Var}(n)}{\text{Var}(h)}} \approx -\frac{\partial n}{\partial h}$$

where values of C above 1 indicate overcompensation; values below 0 indicate over additivity; 0 indicates complete additivity; and 1 indicates complete compensation. It can be roughly interpreted as the proportion of the fluctuations of the predation mortality about its average that are compensated.

An example of over-additivity is when predators select larger than average size salmonid smolts, which typically have high survival rates. If the smaller surviving fish do not have increased survival (assuming little or no density dependence at this life stage), then removing larger salmonids would have a larger than average negative impact. As predation rates (h) go up, natural mortality (n) also increases which is a positive correlation between h and n .

Derivation of a key result for estimating covariance between overall survival and harvest/predation

From $S = 1 - n - h$ we have $S + n + h = 1$

Consequently,

$$\text{Var}(S + n + h) = 0$$

$$\text{Var}(S) + \text{Var}(n) + \text{Var}(h) + 2 \text{cov}(S, n) + 2 \text{cov}(S, h) + 2 \text{cov}(n, h) = 0$$

$$[\text{Var}(S) + V(n) + 2 \text{cov}(S, n)] + V(h) + 2 \text{cov}(S, h) + 2 \text{cov}(n, h) = 0$$

$$\text{Var}(S + n) + V(h) + 2 \text{cov}(S, h) + 2 \text{cov}(n, h) = 0$$

$$\text{Var}(1 - h) + V(h) + 2 \text{cov}(S, h) + 2 \text{cov}(n, h) = 0$$

$$\text{Var}(h) + V(h) + 2 \text{cov}(S, h) + 2 \text{cov}(n, h) = 0$$

$$2 \text{Var}(h) + 2 \text{cov}(S, h) + 2 \text{cov}(n, h) = 0$$

$$\text{Var}(h) + \text{cov}(S, h) + \text{cov}(n, h) = 0$$

This then gives the key result:

$$\text{cov}(n, h) = -\text{Var}(h) - \text{cov}(S, h)$$

$$\frac{\text{cov}(n, h)}{\sqrt{\text{Var}(n)\text{Var}(h)}} = -\frac{\text{Var}(h)}{\sqrt{\text{Var}(n)\text{Var}(h)}} - \frac{\text{cov}(S, h)}{\sqrt{\text{Var}(n)\text{Var}(h)}}$$

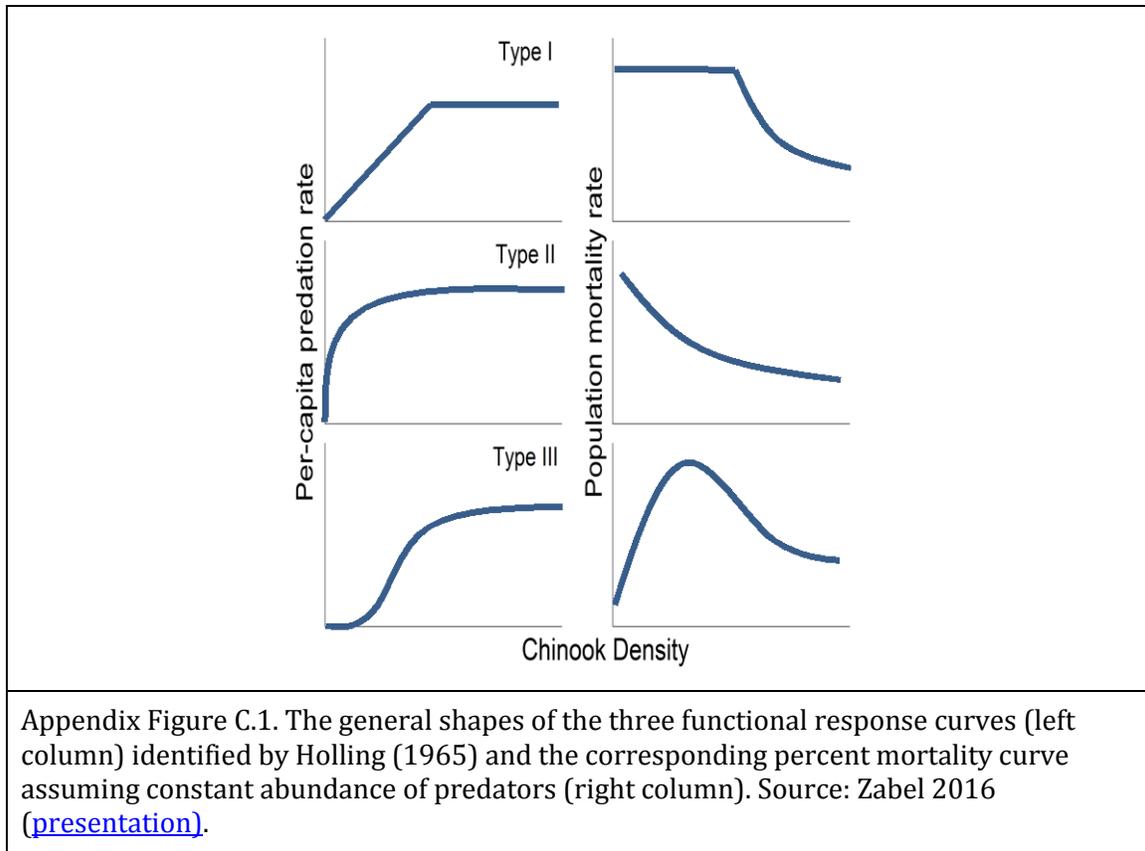
$$\text{cor}(n, h) = -\sqrt{\frac{\text{Var}(h)}{\text{Var}(n)}} - \frac{\text{cov}(S, h)}{\sqrt{\text{Var}(n)\text{Var}(h)}}$$

Appendix C. Functional and Numerical Response of Predators

The functional and numerical response of predators to varying abundances of salmonids is critical to the understanding of predation effects on salmonid populations. The functional response describes the mean number of prey eaten per predator per unit time in relation to prey density, and the numerical response describes how the number of predators varies in relation to prey density (Solomon 1949, Holling 1959a,b). The total number of salmon eaten by a predator species per unit time equals the predation rate times the abundance of the predator. This information can be used to address the major question of how predation mortality varies with salmon abundance. We offer this brief review of functional and numerical responses of predators to highlight the dynamic and often nonlinear effects of predation on salmon populations. As briefly noted in Chapter 3 (and below), some functional and numerical responses can lead to compensatory mortality. However, most functional and numerical responses describe immediate predation rates and additional evaluation of predator selectivity and density dependence must be conducted to determine whether mortality is additive or compensatory.

Functional responses

In the late 1950s and the 1960s, C.S. Holling developed an integrated approach to understand the dynamics of predation on prey populations (Holling 1959a,b; Holling 1965). He concentrated on the functional response of a predator to prey densities, while accounting for predator and prey types. A simplification of his classification portrays three predation responses (Appendix Figure C.1). A Type I functional response is linear at low to mid prey densities and then abruptly becomes constant at high prey densities. In subsequent use, it is sometimes portrayed as entirely linear through a range of prey densities. In a Type II response, prey mortality increases with prey density and gradually reaches an asymptote (predator saturation) at high prey densities (Appendix Figure C.1). Predators approach saturation gradually because prey consumption is affected by handling time, digestion, and satiation effects, and switching from one prey species to another one does not occur. A Type III response curve is sigmoidal (Appendix Figure C.1). Mortality is low at low prey densities until a threshold density of prey is reached and then increases sharply at mid densities until it gradually reaches an asymptote. Similar to the Type II response, predator saturation is gradually achieved and is mediated by handling time, digestion, and satiation. Holling (1959b) attributes the slow rise of predation versus prey density to a learning curve, what might be referred to as developing a search image. When enough of a certain prey are present to be more easily identified as food, then the predator begins to select for that prey. Ricker (1948) noted a similar switching between prey. When young sockeye salmon were in low density, northern pikeminnow used alternate prey, and then switched back to sockeye salmon as they became more abundant. A predator that switches between prey species may also display a "modified" Type II response in which essentially none of the alternative prey (e.g., salmon) are eaten until a threshold prey density is reached (Peterman and Gatto 1978).



The type of functional response exhibited by a predator can have a substantial effect on a prey population. For example, if predators are opportunistic and take a particular prey even when it is rare (a Type II response) then a disproportionate impact on the prey population is likely to occur (Peterman and Gatto 1978, Ward and Hvidsten 2011). A Type II functional response can lead to the extinction of a prey population (zero recruits) at low stock levels because the percentage of the prey population eaten by the predator population is very high (Appendix Figure C.1, right column). Fundamentally, a Type II functional response is depensatory and inherently destabilizing when the prey population is declining. Type II functional responses are often associated with relatively sedentary and opportunistic generalist predators (Ward and Hvidsten 2011).

Type III and modified Type II functional responses can lead to "multiple domains of stability" such that populations may become trapped at small population sizes (Peterman 1977, Peterman and Gatto 1978). This effect is most easily shown by plotting percent mortality of the prey in relation to prey density or abundance (Appendix Figure C.1, right column). As the prey population begins to grow from small numbers, it encounters a higher and higher mortality rate that inhibits recovery. Recovery is possible when the prey population exceeds a threshold and the mortality rate begins to decline. Peterman and Gatto (1978) concluded that the shape of the population mortality rate relationship can have important implications for salmon management. As noted in Chapter 3, the shape of the population mortality relationship can influence compensation. For example, removal of one predator on salmon could lead to increased salmon abundance and therefore switching behavior and increased predation by another predator that exhibits a Type III or modified Type II response.

There is a limited amount of published literature that addresses functional responses of salmonid predators in the Columbia River Basin. An individual-based model was used to evaluate predation by northern pikeminnow on juvenile salmonids in the Columbia River (Petersen and DeAngelis 1992). Type II and Type III functional responses fit the field data best, but it was not possible to distinguish between these two models. The authors concluded that pikeminnow were feeding on patches of salmonids in the river. To our knowledge, this is the only published study of the functional response of a salmonid predator in the Columbia River Basin.

Peterman and Gatto (1978) provide an excellent review of functional responses of salmon predators for investigations published through 1978. Some salmon predator relationships suggested a Type III or modified Type II functional response, but percent mortality was difficult to access because changes in predator abundances were not fully documented. Typically, predators were not being swamped by prey. They conclude that predators of juvenile salmon, such as fish and birds, show a variety of responses, but Type III responses are most common when more than one prey is available. When relating functional responses to salmon management, Peterman and Gatto (1978) conclude that “if these predators have a Type III or modified Type II responses, many salmon enhancement projects may only increase the proportion of salmon fed to predators instead of increasing the proportion caught by fishermen.”

Studies of salmonids in other locations provide some insights into functional responses of predators. Arctic char (*Salvelinus alpinus*) feeding on sockeye salmon smolts (*Oncorhynchus nerka*) in Little Togiak River, Alaska, exhibited a Type II functional response, where vulnerability of smolts may be greater at lower migration densities depending on the numerical response of char (Ruggerone and Rogers 1984). Cutthroat trout (*Oncorhynchus clarkii*) predation on steelhead parr in an experimental stream best fit a Type I functional response (Tatara et al. 2011). However, the study included both hatchery reared and wild parr, with wild parr having a higher growth rate. This allowed the wild parr to outgrow the predation field and, even though consumption was linear to abundance, hatchery fish accounted for most of the cutthroat diet. Light levels appear to change the functional response of young kokanee salmon (*Oncorhynchus nerka*) to daphnia (*Daphnia ambigua*) (Koski and Johnson, 2001). At lower light levels fingerlings had a Type I response, while at greater light levels it was easier for them to search, and then they exhibited a Type II response. In studying the complex dynamics of brown trout (*Salmo trutta*) predation on vendace (*Coregonus albula*) in Finnish lakes, Heikinheimo (2001) tested to see if the functional response of the predator might explain some of the vendace population dynamics. Heikinheimo compared only the Type II and III responses in his model with a combination of two predator species, brown trout and perch. The importance of the functional response of the predator was especially pronounced on prey species with dome-shaped stock recruit relationships. The importance placed on each predator differed depending on the type of functional response exhibited, sometimes making it a minor influence on prey persistence and sometimes major. The value of these types of simulations is that they allow us to see the potential impacts that predators may have on prey and ecosystem.

Studies of non-salmonid species also provide insight into functional responses. Data that linked the abundance of western Atlantic cod (*Gadus morhua*) and the amount of cod in seal diets was best described as a Type II functional response, demonstrating an asymptote

(O'Boyle and Sinclair 2012). A newer study modeled the prey consumption of grey seals (*Halichoerus grypus*) on eastern Atlantic cod, again based on diet studies (Smout et al. 2014). However, in this study Smout et al. modeled a multi-species functional response and compared how well the data fit a type II or III response. They conclude that there is better evidence of a Type III response where seals engage in prey switching. A study of grey gurnard (*Eutrigla gurnadus*) predation on cod (Floeter et al. 2005) gave more nuanced results than either study above. Although they modeled a Type II functional response, their simulations matched observations as long as the predator field abundance stayed constant, but fit much less well otherwise. Moreover, they felt that there was insufficient data to discriminate between a Type II or III response.

In trying to understand the ecosystem effects of fishing on Steller sea lion decline in the Gulf of Alaska, Gaichas et al. (2011), explored the effect of functional responses on model performance. They found no simple relationship explained abundances of many species and that the model fit an array of scenarios of climate, fishing, and predator-prey interactions. Not only are predator-prey interactions dependent on the ecosystem in which they exist but also they are dependent on the predator's ontogenic stage of life. Gape limitations and reaction distances determine the number and types of prey that can be taken at each life stage. Nonetheless, even at different life stages with different prey, all of the tested life stages showed an asymptotic number of prey eaten with increased prey density, a Type II functional response.

Statistical methods to determine functional response curves. Ecologists have been using functional response curves and expanding upon the ideas first produced by Holling for over four decades. Statistical methods have been developed that can: (a) determine the type of curve that is exhibited by a functional response, i.e., is it a Type II or III response curve, (b) compare functional response curves produced by different predators, or by the same predator at different ages or sizes, and (c) refine the parameters used in the mechanistic models that define a functional response (Juliano 2001). Bayesian methods have also been developed that allow investigators to examine multispecies functional responses (MSFR) in generalist predators (Smout et al. 2010). To model the effects of such predators, it is necessary to describe how they respond to the abundance levels of all their prey species. For instance, we might expect that the consumption of any one type of prey would be influenced by its availability, plus the availability of other potential prey species (Smout et al. 2010).

Given the practical implications of different functional response curves, it seems important to develop such relationships for the principal salmon predators in the Columbia River. Regarding the predation metric, a key issue is whether predators have a Type III or modified Type II response to salmon abundance such that predator control leads to higher predation rates on salmon by an uncontrolled predator. Consequently, data or metrics that allow researchers to develop such relationships should certainly be among those that are considered by researchers and managers that are involved with salmon management and predator control.

Numerical response of predators

The second component of predation is the numerical response (Solomon, 1949), which is composed of a demographic response (individual fish growth and reproduction of

predators) and an aggregation response; i.e., predators aggregate where prey are concentrated. The numerical response must be considered in determining the total impact that predators will have on prey population abundance. Early pioneers in predator-prey modeling developed the equations of the effect of the number of predators on prey and prey density. The most well-known of these are the Lotka-Volterra equations which predict oscillations in predator abundance that follows a $\frac{1}{4}$ cycle after the prey abundance cycle. MacLulich (1937) illustrated this with snowshoe hare and lynx data from Canada, and several studies illustrate the same phenomena for host-parasitoid relations. The stability of the model depends on the amplitude of the cycles, with greater amplitude resulting in a higher chance of extirpation of either the predator or prey or both.

Generalist predators (i.e., species with a varied diet such as pinnipeds, colonial waterbirds, and northern pikeminnow) are of particular concern for Columbia River salmon. Generalist predators may diminish or eradicate cyclical interactions between specialist predators and their prey, maintain prey populations at low densities placing them into predator pits, and drive some prey populations to extinction (Peterman 1977, Smout et al. 2010). The likelihood of these effects depends upon the form of the predator's functional and numerical responses (Smout et al. 2010).

Demographic response. If a predator specializes in one type of prey, numerical increases and declines in predator and prey abundance will cycle through time. If on the other hand, a predator is an opportunistic generalist, population crashes in one of its prey species will not likely affect its overall abundance. Such predators, if they remain abundant and forage opportunistically, are more likely to depress salmon populations than those that decline in abundance when salmon become rare (Ward and Hvidsten 2011). Examples of opportunistic predators in the Columbia Basin include gulls (Wiese et al. 2008) and pinnipeds (Wargo Rub 2016 [presentation](#) and [audio](#)).

Demographic response becomes more problematic when prey do not respond cyclically (Nowak et al. 2008). When Lotka-Volterra equations include logistic growth for the prey population, i.e., population growth rate decreases as the population approaches the maximum number of individuals that the environment can support, and an asymptote for the functional response from the predator, both predator and prey populations become more stable and follow damped oscillations in abundance (Begon et al. 1996). However, Solomon (1949) noted that the laboratory experiments that were the basis of this theory had to be strongly manipulated to yield cycles (prey or predators were added during the experiments) and that few examples could be observed in nature. He also noted that any density-dependent population control would also occur in predators. The best model fit to the longest run of Luckinbill's (1973) classic lab experiments included Type III functional response and a delayed numerical response by the predator (Harrison 1995). The simple predator-prey model was expanded by Spencer and Collie (1995) to include an alternate prey source for a marine piscivore. They did state that the model results presented an "interesting management problem of finding the optimal combination of fishing mortality rates for the two species." Bonsall and Hassell (2007) provide a recent review on the theory of predator-prey interaction and recent developments.

Aggregation response. The spatial distribution of predators and prey also impact the population growth of both. Because laboratory experiments often resulted in extirpation of either the predator or prey or both, Huffaker (1958) investigated spatial distribution of two mite species, a prey species that ate oranges and a predator mite on those prey. He found

that prey were consistently extirpated whenever predators could move freely. Only when prey were given refuges (by restricting predator movement using Vaseline paths) were both species able to persist for long periods of time. Solomon (1949) also mentioned this as a controlling factor in predator-prey interactions. Further research has confirmed the value of spatially heterogeneous habitats and metapopulations to provide persistence of populations (see Jones 2006 for a review). Solomon (1949) saw that populations of both predators and prey maintained less variable population abundances in complex ecosystems in which there were multiple prey and predator species that stabilized interactions.

The other consideration in the spatial distribution of predator and prey concerns the movement of predators into areas of higher prey densities. The Ideal Free Distribution hypothesis of Fretwell and Lucas (1970) states that animals will migrate from areas of high food resource and high animal density to areas with lower resources and animal densities such that the resource per animal is equal across space (Ward and Hvidsten 2011). Predators on salmon respond to increased salmon abundance by aggregating. When this happens to small populations it can be destabilizing as predators can move between patches of prey.

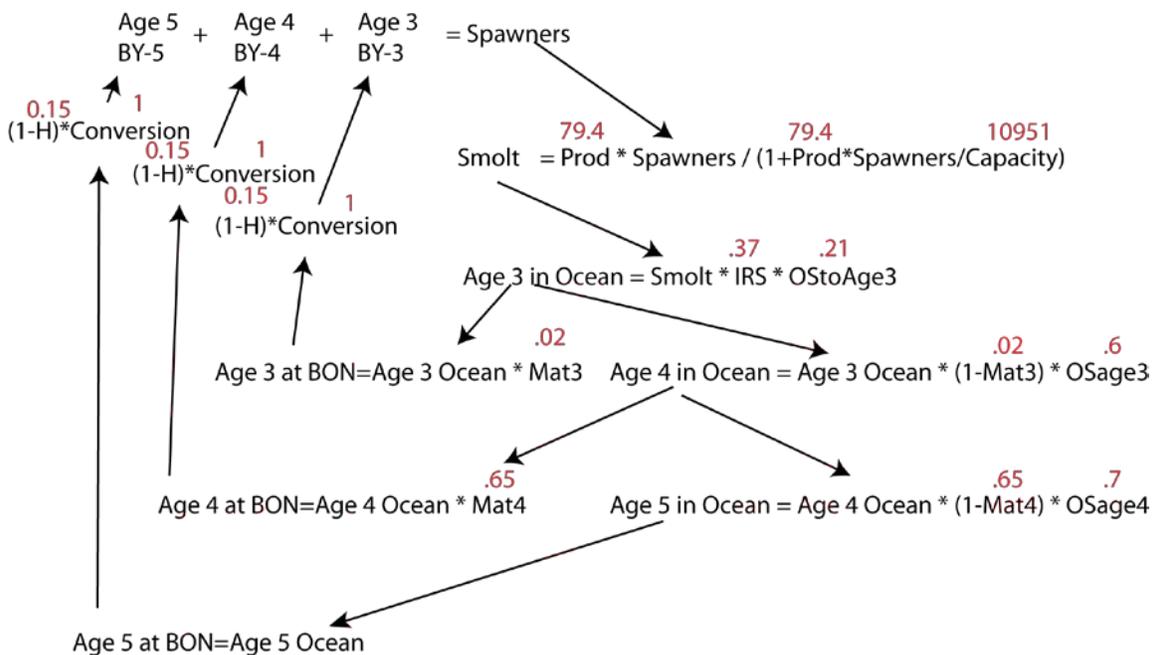
How predators are distributed over space can also influence their impact on salmon populations. Those that are spatially ubiquitous will exert disproportionate effects on small populations, much like a Type II functional response (Ward and Hvidsten 2011). Predators that are dispersed and fail to aggregate until prey are concentrated and abundant may instead exert stabilizing density dependent mortality (Ward and Hvidsten 2011). An example of this type of aggregated behavior was observed by Middlemas et al. (2006). They found that harbor seal abundance in a Scottish river system increased with the abundance of returning Atlantic salmon (*Salmo salar*). Dietary analyses performed on seal scats collected over the course of the salmon run indicated that a Type III functional response existed between seals and Atlantic salmon.

Appendix D. Example Calculations with a Life-cycle Model

Consider a simplified life-cycle model for Chinook based on the Grande Ronde population with parameter values extracted from the latest CSS report. Appendix Figure D.1 shows a diagram of the (simplified) life cycle. Smolts are counted at Lower Granite Dam (LGR) and Bonneville Dam. We consider four different versions of the life-cycle model as summarized in Appendix Table D.1. Appendix Table D.2 presents a summary of the equilibrium conditions for all four models.

Appendix Table D.1. Summary of four life-cycle models used to illustrate the impacts of changes in in-river survival via predator control on subsequent stages in the life cycle where there is no density dependence following in-river movement (M2 vs M1) and where there is further density dependence (M4 vs M3). [This table is the same as Table 6.1.]

Model	Density Dependent Spawning/rearing	Increased in-river survival via predator control	Density dependent estuary early-ocean survival
M1	x		
M2	x	x	
M3	x		x
M4	x	x	x



Appendix Figure D.1. Simplified life-cycle model based on the Grande Ronde population with parameter values (red) extracted from the CSS (2015). This is the model M1. The model has been simplified by ignoring transport of smolts in-river. LGR smolts are produced from spawners (top line, middle in diagram) that are produced from previous brood years using a Beverton-Holt density dependence relationship with a productivity

(Prod) of 79.4 smolts/spawners and a capacity (Capacity) of 10,951 smolts. The smolts travel downstream to Bonneville with an in-river survival probability (IRS) of 0.37 and an estuary and early-ocean survival of 0.21 to age-3 (OSToAge3). At age-3, 2% mature (Mat3) and return to Bonneville (BON). There is a 0.60 survival probability from age-3 to age-4 (OSage3), at which time 65% of age-4 fish return to spawn (Mat4). There is a 0.70 survival probability from age-4 to age-5 (OSage4) and all remaining adult fish return to Bonneville at age-5. The in-river harvest (H) is 15% and 100% conversion (probability of returning to natal spawning ground) of the remaining fish to the spawning grounds is assumed. Note that a single brood-year of smolts contributes adults at ages 3, 4, and 5 on the spawning ground in different years. Demographic stochasticity has been ignored; i.e., there is no random variation assumed around the population transitions.

Model M1 (see Appendix Figure D.1). At equilibrium, each brood year starts with 257 spawners consisting of 9 age 3, 180 age 4, and 68 age 5 fish on the spawning ground. With 257 spawners, 7137 Lower Granite (LGR) smolts are produced (on average) using the Beverton-Holt density dependence relationship:

$$\text{Smolts} = \frac{79.4 \times \text{Spawners}}{1 + \frac{79.4 \times \text{Spawners}}{10951}}$$

These smolts migrate through the hydrosystem with an in-river survival of 0.37. The estuary and early ocean survive to age-3 in the ocean is of 0.21 giving 555 fish at age-3 in the ocean.

Then 2% of the fish mature at age-3, and return to Bonneville (BON) (11 fish); 15% are harvested; and with an assumed 100% survival from BON to the spawning grounds, there are again 9 age-3 fish on the spawning ground.

Similarly, of the 98% that do not mature, the ocean survival is 60% giving 326 age-4 fish in the ocean. Then 65% mature and return to BON (212 fish), 15% are harvested and all remaining fish (180 fish) return to the spawning ground as age-4 fish.

Finally, the remaining fish in the ocean have a 70% survival and all return to BON at age-5 (80 fish), of which 15% are harvested and the remaining fish survive to the spawning ground (68 fish).

The system is in equilibrium with a self-sustaining population of 257 spawners which produce 7137 smolts, which survive and produce 257 spawners (in total over the 3 year classes).

Because there is no density dependence anywhere in the system except on the spawning grounds in this model, it takes an average of 24 LGR smolts to produce one adult fish at BON, or each LGR-smolt produces 0.042 adult fish at BON.

The 7137 LGR-smolts travel in-river to BON and, on average, 2640 survive. Here it takes an average of 8.74 smolts at Bonneville (BON-smolts) to produce an adult at Bonneville or each BON-smolt is worth 0.11 adults at BON. A BON-smolt is more “valuable” than a LGR-smolt.

Similarly, these 2640 BON-smolts produce 555 age-3 fish. At age-3, it takes an average of 1.83 age-3 fish to produce one adult at Bonneville, or each age-3 fish is worth 0.68 adult fish at Bonneville. An age-3 fish is more “valuable” than a smolt.

Model M2. Reducing mortality anywhere in the system results in a direct corresponding increase in the number of adults returning to BON. For example, suppose that the hydrosystem survival is increased from 0.37 to 0.45 thereby increasing the number of BON-smolts from 2641 (7137×0.37) to 3211 (7137×0.45), an increase of 570 BON-smolts. Because it takes an average of 8.74 BON-smolts to produce one adult fish at Bonneville, this implies that another 65 spawning adults at Bonneville should be produced. Indeed, the life-cycle model predicts that the 257 spawners will again produce 7137 LGR-smolts, but the increased in-river survival increases the number of adults returning to BON by $0.45/0.37=1.22$ (22%) to 13/258/97 age 3/4/5 fish for a total increase in adults returning to BON from 302 to 368 (also a 22% increase). There is 15% harvest, and all remaining fish survive to give an apparent 22% increase in the total number of spawners to 313 (assuming that the age distribution does not change).

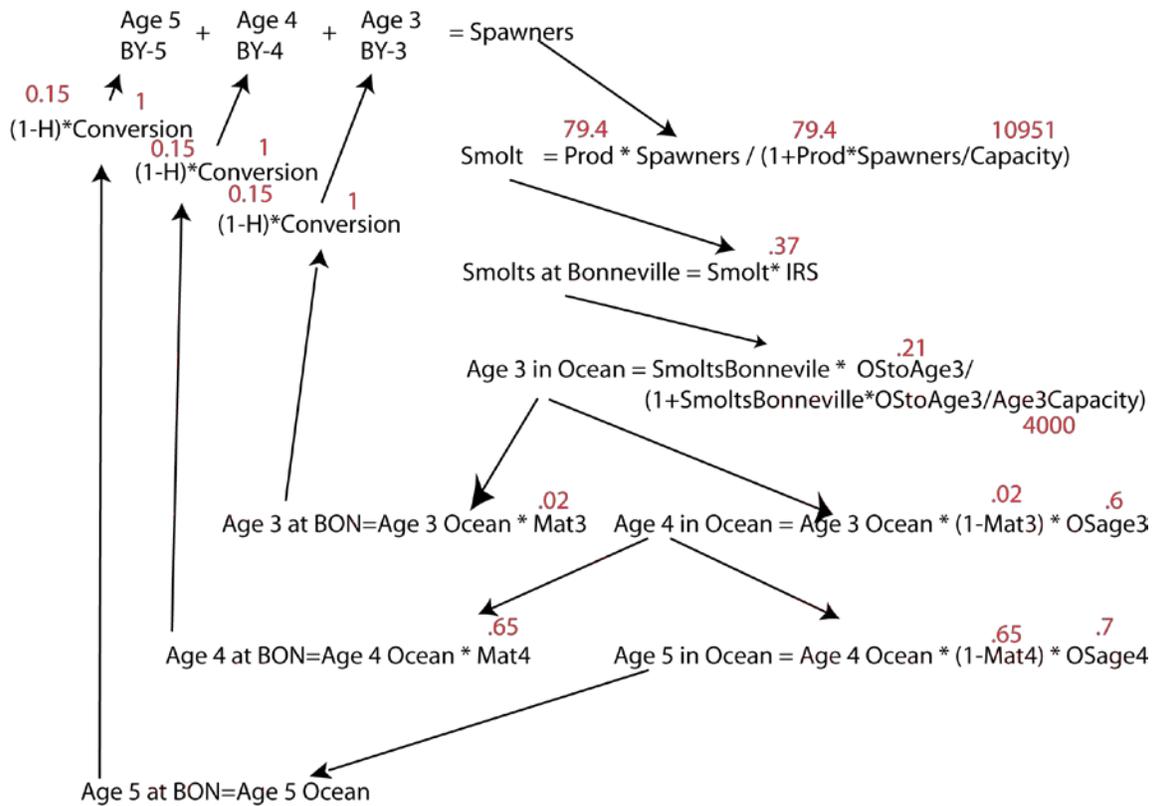
However, because there are more spawners, they always produce more LGR-smolts according to the Beverton-Holt relationship, and so this is not the new equilibrium. The new equilibrium is 343 spawners (i.e., a 33% increase from the previous equilibrium) now producing 7815 LGR-smolts (which is only an increase of 10% in LGR-smolts). So a 22% increase in the in-river survival leads to 33% increase in the equilibrium point, which seems counterintuitive, but according to Beverton-Holt relationships, more spawners always produce more LGR-smolts, albeit at a declining rate. So in fact, reducing mortality anywhere in the system, leads to a larger than corresponding increase in the equilibrium. Simple predation metrics may not capture this feedback effect.

At equilibrium, the life-cycle models predict that one LGR-smolt must produce, on average, one LGR-smolt in the next generation. It takes an average of 9 BON-smolts to produce one new adult in the next generation, at equilibrium in both Model M1 and M2 because the models are identical following passage out from Bonneville. However, once the feedback mechanism and density dependence are accounted for, an increase by 22% in the number of adults that make it to Bonneville and to the spawning grounds only increases total LGR-smolt production by 10% ($7815/7137$). It would seem disappointing that substantially more fish spawn without a corresponding increase in LGR-smolt production, but production of smolts is constrained by the capacity of the system via density dependence.

Model M3. Adding density dependence or compensatory mortality elsewhere in the system complicates matters considerably. For example, suppose that there is density dependence in the number of age-3 fish that can be produced, due for example to constraints in the estuary after Bonneville. A revised life-cycle model is shown in Appendix Figure D.2 where survival to age-3 in the ocean is limited, again by a Beverton-Holt relationship following survival of smolts to Bonneville.¹¹

¹¹ This is a highly simplified example. Capacity constraints in the estuary will operate over multiple populations.

$$Age3 = \frac{.389 \times SmoltsBonneville}{1 + \frac{.389 \times SmoltsBonneville}{4000}}$$



Appendix Figure D.2. Simplified life-cycle model based on the Grande Ronde population with parameter values (red) extracted from CSS (2015) *with an (arbitrary) addition of density dependence on production of age-3 adults*. This is model M3. The model has been simplified by ignoring transport of smolts in-river. Smolts at Lower Granite (LGR-smolts) are produced from spawners (top line, middle in diagram) that are produced from previous brood years using a Beverton-Holt density dependence relationship with a productivity (Prod) of 79.4 smolts/spawners and a capacity of 10,951 smolts. The LGR-smolts travel downstream to Bonneville (BON) with an in-river survival probability (IRS) of 0.625. Survival to age-3 is governed by a Beverton-Holt density dependence relationship with a base survival from BON-smolts of 0.389 (OStoAge3) and a capacity of 4000 age-3 adults (Age3Capacity). At age-3, 2% mature (Mat3) and return to BON. There is a 0.60 survival probability from age-3 to age-4 (OSage3), of which 65% of age-3 fish mature (Mat4) and return to spawn. There is a 0.70 survival probability from age-4 to age-5 (OSage4) and all remaining adult fish return to BON at age-5. The in-river harvest (H) is 15% and 100% conversion (probability of returning to natal spawning ground) of the remaining fish to the spawning grounds is assumed. Note that a single brood-year of LGR-smolts contributes adults at ages 3, 4, and 5 on the spawning ground in different years. Demographic stochasticity has been ignored, i.e. there is no random variation assumed around the population transitions.

At equilibrium, each brood year starts with 212 spawners consisting of 8 age-3, 149 age-4, and 56 age-5 fish on the spawning ground. With 212 spawners, 6645 LGR-smolts are produced (on average) using the Beverton-Holt density dependence relationship seen earlier. These smolts then migrate through the hydrosystem with a survival of 0.37 giving 2459 BON-smolts. A density dependent relationship in the estuary with a base survival to age-3 in the ocean of 0.21 and a capacity of 4000 fish gives 457 fish at age-3 in the ocean.

Then 2% mature at age-3, and return to Bonneville as adult; 15% are harvested; the remaining all survive the upstream mitigation from Bonneville to the spawning grounds, giving again 8 age-3 fish on the spawning ground.

Similarly, of the 98% that don't mature, the ocean survival is 60% giving 269 age-4 fish in the ocean. Then 65% mature and return to Bonneville (175 fish) of which 15% are harvested and the remainder return to the spawning ground as age-4 fish.

Finally, the remaining fish in the ocean have a 70% survival and all return to Bonneville (66 fish), of which 15% are harvested and the remainder convert to the spawning ground.

The system is in equilibrium with a self-sustaining population of 212 spawners who produce 6645 LGR-smolts, which survive and produce 212 spawners (in total over the 3 year classes).

Because of density dependence in the estuary, it now takes more LGR-smolts to produce a returning adult at Bonneville compared to Model M1, and so a LGR-smolt is less valuable in Model M3 compared to Model M1. However, an age-3 adult is equally valuable for all model because there is no density dependence from this age onward until the next spawner to smolt stage.

Now, if the in-river survival rate increases from by 0.37 from 0.45 (a 22% increase), there are 22% more smolts that reach Bonneville, i.e. from 2459 to 2990, but because of density dependence at age-3, the number of age-3 adults only increases from 457 to 542 (only a 19% increase) and the number of adults returning to Bonneville and the number of spawners also increases by only 19%. In the absence of density-dependence to age-3, it took an average of 9 BON-smolt to produce one adult fish at Bonneville (0.11 adults/smolt), and this conversion factor is consistent regardless of the number of smolts in the system. In the presence of density-dependence at age-3, an additional 531 BON-smolts produced only another 47 adults at Bonneville, or 11 smolts/adults, or 0.09 adults/smolt. This conversion factor will decline further if the number of BON-smolts increases even more. In general, an outgoing BON-smolt is less "valuable" in the presence of density dependence in the estuary compared to the same outgoing smolt in the absence of density dependence at age-3.

Model M4. The new equilibrium with the increased in-river survival rate and density dependence in the estuary is 272 spawners producing 7277 LGR-smolts, or an increase in the equilibrium by 28% in the number of spawners. There is only a 10% increase in overall LGR-smolt production even though the number of BON-smolts increases by 22% with the increased in-river survival. Some of the increase survival in-river is "wasted" (i.e. compensated) by the density dependence further in the estuary.

Appendix Table D.2. Summary of number of fish at each stage in the four life-cycle models with three conversion factors at the end of the table. The four models are used to illustrate the impacts of changes in in-river survival via predator control on subsequent stages in the life cycle if there is no density dependence after in-river survival (M2 vs. M1) and if there is density dependence after in-river survival (M4 vs. M3).

	M1	M2	M3	M4
	In-river survival = 0.37	In-river survival = 0.45	In-river survival = 0.37	In-river survival = 0.45
	Unlimited estuary capacity for smolts	Unlimited estuary capacity for smolts	Limited estuary capacity of 4000 age-3 fish	Limited estuary capacity of 4000 age-3 fish
Spawners (age 3, 4, 5)	257 = 9 + 180 + 68	343 = 13 + 240 + 90	212 = 8 + 149 + 56	272 = 10 + 190 + 72
Smolts at LGR	7137	7815	6645	7277
Smolts at BON	2640	3517	2459	3275
Age 3 ocean fish	555	738	457	587
Age 3 adults at Bonneville	11	15	9	12
Age 3 spawners on spawning grounds	9	13	8	10
Age 4 ocean fish	326	434	269	345
Age 4 adults at Bonneville	212	282	175	224
Age 4 spawners on spawning grounds	180	240	149	190
Age 5 ocean fish	80	106	66	85
Age 5 adults at Bonneville	80	106	66	85
Age 5 spawners on spawning grounds	68	90	56	72
Total adults at Bonneville	302	403	250	320
Smolt -> Adult at BON	.042 adults/smolt 24 smolt/adult	.052 adults/smolt 19 smolt/adult	0.037 adult/smolt 27 smolt/adult	.044 adults/smolt 23 smolt/adult
Smolt at BON -> Adult at BON	0.11 adults/smolt 8.7 smolt/adult	0.11 adults/smolt 8.7 smolt/adult	0.10 adults/smolt 9.8 smolt/adult	0.97 adults/smolt 10.3 smolt/adult
Age 3 -> Adult at BON	0.54 adults/age 3 adult 1.8 age 3 adult/adult			

9. Literature Cited

- Adams, J., I.C. Kaplan, B. Chasco, K.N. Marshall, A. Acevedo-Gutiérrez, E.J. Ward. 2016. A century of Chinook salmon consumption by marine mammal predators in the Northeast Pacific Ocean. *Ecological Informatics* 34: 44–51.
- Alvarez, D., and A.G. Nicieza. 2003. Predator avoidance behaviour in wild and hatchery-reared brown trout: the role of experience and domestication. *Journal of Fish Biology* 63: 1565-1577.
- Antolos, M., D.D. Roby, D.E. Lyons, K. Collis, A.F. Evans, M. Hawbecker, and B.A. Ryan. 2005. Caspian tern predation on juvenile salmonids in the mid-Columbia River. *Transactions of the American Fisheries Society* 134: 466–480.
- Beamish, R.J., C. Mahnken, and C.M. Neville. 2004. Evidence that reduced early marine growth is associated with lower marine survival of coho salmon. *Transactions of the American Fisheries Society* 133: 26–33.
- Bean, N.J. 2015. Box Canyon Reservoir northern pike mechanical suppression project: summary of 2012-2015 project results. Prepared by Kalispel Tribe of Indians for the Northwest Power and Conservation Council.
- Begon, M., M. Mortimer, and D.J. Thompson. 1996. *Population ecology: a unified study of animals and plants*. Third Edition. Blackwell.
- Berejikian, B. 1995. The effects of hatchery and wild ancestry and experience on the relative ability of steelhead trout fry (*Oncorhynchus mykiss*) to avoid a benthic predator. *Canadian Journal of Fisheries and Aquatic Sciences* 52: 2476-2482.
- Berejikian, B.A., M.E. Moore, S.J. Jeffries. 2016. Predator–prey interactions between harbor seals and migrating steelhead trout smolts revealed by acoustic telemetry. *Marine Ecology Progress Series* 543: 21–35.
- Bonsall, M. B., and M. P. Hassell. 2007. Predator-prey interactions. Pages 46-61 in R. M. May and A. R. McLean, editors. *Theoretical ecology: principles and applications*. 3rd edition. Oxford University Press, Oxford, U.K.
- Burnham, K.P., and D.R. Anderson. 1984. Test of compensatory vs. additive hypotheses of mortality in mallards. *Ecology* 63: 105-112.
- Caswell, H. 2001. *Matrix population models: construction, analysis, and interpretation*, Second Edition. Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts
- Collis, K., R.E. Beaty, and B.R. Crain. 1995. Changes in catch rate and diet of northern squawfish associated with the release of hatchery-reared juvenile salmonids in a Columbia River reservoir. *North American Journal of Fisheries Management* 15: 346-357.
- Collis, K., D.D. Roby, D.P. Craig, B.A. Ryan, and R.D. Ledgerwood. 2001. Colonial waterbird predation on juvenile salmonids tagged with passive integrated transponders in the Columbia River estuary: vulnerability of different salmonid species, stocks, and rearing types. *Transactions of the American Fisheries Society* 130: 385–396.
- Collis, K., D.D. Roby, D.P. Craig, S. Adamany, J.Y. Adkins, and D.E. Lyons. 2002. Colony size and diet composition of piscivorous waterbirds on the lower Columbia River: implications for losses of juvenile salmonids to avian predations. *Transactions of the American Fisheries Society* 131:537-550.

- Collis, K., D.D. Roby, K.W. Larson, L.J. Adrean, K. Nelson, A.F. Evans, D. Battaglia, D.E. Lyons, T. Marcella, and A. Patterson. 2012. Trends in Caspian tern nesting and diet in San Francisco Bay: Conservation implications for terns and salmonids. *Waterbirds* 35: 25-34.
- CSS [Comparative Survival Study]. 2015. Comparative Survival Study of PIT-tagged spring/summer/fall Chinook, summer steelhead, and sockeye 2015 Annual Report, December 2014-November 2015, BPA Contract 70765, BPA Project 1996-020-00. 496 pp. Available at: http://www.fpc.org/documents/CSS/CSS_2105AnnualReport.pdf
- Cunningham, C.J., G.T. Ruggerone, and T.P. Quinn. 2013. Size-selectivity of predation by brown bears depends on the density of their sockeye salmon prey. *American Naturalist* 181:663-673.
- Debes, P.V., and J.A. Hutchings. 2014. Effects of domestication on parr maturity, growth, and vulnerability to predation in Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences* 71: 1371-1384.
- Duffy, E.J., and D.A. Beauchamp. 2011. Rapid growth in the early marine period improves the marine survival of Chinook salmon (*Oncorhynchus tshawytscha*) in Puget Sound, Washington. *Canadian Journal of Fisheries and Aquatic Sciences* 68: 232-240.
- Evans, A.F., N.J. Hostetter, K. Collis, D.D. Roby, D.E. Lyons, B.P. Sandford, R.D. Ledgerwood, and S. Sebring. 2012. A system-wide evaluation of avian predation on juvenile salmonid in the Columbia River Basin based on recoveries of passive integrated transponder tags. *Transactions of the American Fisheries Society* 141: 975-989.
- Evans, A.F. N.J. Hostetter, K. Collis, D.D. Roby and F.J. Loge. 2014. Relationship between juvenile fish condition and survival to adulthood in steelhead. *Transactions of the American Fisheries Society* 143: 899-909.
- Evans, A., Q. Payton, A. Turecek, B. Cramer, K. Collis, D. Roby, P. Loschl, L. Sullivan, M. Weiland, J. Skalski, and R. Townsend. 2015. Avian predation on juvenile salmonids in the Columbia River: a spatial and temporal analysis of impacts in relation to fish survival. Final Technical Report submitted to Grant County Public Utility District No. 2. Available on-line at www.birdresearchnw.org.
- Evans, A.F, Q. Payton, B.M. Cramer, K. Collis, D.E. Lyons, and P. J. Loschl. 2016a. Predation impacts on juvenile salmonids by double-crested cormorants and Caspian terns nesting on East Sand Island in the Columbia River Estuary. Final technical report submitted to the U.S. Army Corps of Engineers in partial fulfillment of Contract No. W912EF-14-D-0004, Task Order No. 0004.
- Evans, A.F., Q. Payton, A. Turecek, B. Cramer, K. Collis, D.D. Roby, P.J. Loschl, L. Sullivan, J. Skalski, M. Weiland, and C. Dotson. 2016b. Avian predation on juvenile salmonids: spatial and temporal analysis based on acoustic and passive integrated transponder tags, *Transactions of the American Fisheries Society* 145: 860-877.
- Floeter, J. A. Kempf, M. Vinther, C. Schrum, and A. Temming. 2005. Grey gurnard (*Eutrigla gurnadus*) in the North Sea: an emerging key predator? *Canadian Journal of Fisheries and Aquatic Sciences* 62: 1853-1864.
- Ford, J.K., and G.M. Ellis. 2006. Selective foraging by fish-eating killer whales *Orcinus orca* in British Columbia. *Marine Ecology Progress Series* 316: 185-199.
- Ford, J.K.B, B.M. Wright, G.M. Ellis, and J.R. Candy. 2010. Chinook salmon predation by resident killer whales: seasonal and regional selectivity, stock identity of prey, and consumption rates. Department of Fisheries and Oceans Canadian Science Advisory Secretariat Research Document 2009/101. iv + 43 p. Available at: www.dfo-mpo.gc.ca/csas-sccs/

- Fretwell, S.D., and H.L. Lucas. 1970. On territorial behavior and other factors influencing habitat distribution in birds I. Theoretical development. *Acta Biotheoretica* 19: 16-36.
- Friesen, T. A., and D. L. Ward. 1999. Management of northern pikeminnow and implications for juvenile salmonid survival in the Lower Columbia and Snake Rivers. *North American Journal of Fisheries Management* 19: 406-420.
- Fritts, A.L., and T.N. Pearsons. 2006. Effects of predation by nonnative smallmouth bass on native salmonid prey: the role of predator size and prey size. *Transactions of the American Fisheries Society*. 135: 853-860.
- Gaichas, S.K., K.Y. Aydin, and R.C. Francis. 2011. What drives dynamics in the Gulf of Alaska? Integrating hypotheses of species, fishing, and climate relationships using ecosystem modeling. *Canadian Journal of Fisheries and Aquatic Sciences* 68: 1553-1578.
- Good, T.P., M.M. McClure, B.P. Sandford, K.A. Barnas, D.M. Marsh, B.A. Ryan, and E. Casillas. 2007. Quantifying the effect of Caspian tern predation on threatened and endangered Pacific salmon in the Columbia River estuary. *Endangered Species Research* 3: 11-21.
- Hanson, M.B., R.W. Baird, J.K. Ford, J. Hempelmann-Halos, D.M. Van Doornik, J.R. Candy, C.K. Emmons, G.S. Schorr, B. Gisborne, K.L. Ayres, S.K. Wasser, K.C. Balcomb, K. Balcomb-Bartok, J.G. Sneva, and M.J. Ford. 2010. Species and stock identification of prey consumed by endangered southern resident killer whales in their summer range. *Endangered Species Research* 11: 69-82.
- Harrison, G. W. 1995. Comparing predator-prey models to Luckinbill's experiment with *Didinium* and *Paramecium*. *Ecology* 76: 357-374.
- Harvey, C.J., and P.M. Kareiva. 2005. Community context and the influence of non-indigenous species on juvenile salmon survival in a Columbia River reservoir. *Biological Invasions* 7: 651-663.
- Heikinheimo, O. 2001. Effects of predation on the low-density dynamics of vendace: significance of the functional response. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 1909-1923.
- Heisey, D.M., and B.R. Patterson. 2006. A review of methods to estimate cause-specific mortality in presence of competing risks. *The Journal of Wildlife Management* 70: 1544-1555.
- Hilborn, R., S.P. Cox, F.M.D. Gulland, D.G. Hankin, N.T. Hobbs, D.E. Schindler, and A.W. Trites. 2012. The effects of salmon fisheries on southern resident killer whales: final report of the Independent Science Panel. Prepared with the assistance of D.R. Marmorek and A.W. Hall, ESSA Technologies Ltd., Vancouver, B.C. for National Marine Fisheries Service (Seattle, WA) and Fisheries and Oceans Canada (Vancouver, BC). xv + 61 pp. + Appendices.
- Holling, C.S. 1959a. Some characteristics of simple types of predation and parasitism. *Canadian Entomologist* 91(7): 385-398.
- Holling, C.S. 1959b. The components of predation as revealed by a study of small mammal predation on European pine sawfly. *Canadian Entomologist* 92: 293-320.
- Holling, C.S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. *Memoirs of the Entomological Society of Canada* 45:5-60.
- Hostetter, N.J. 2009. Susceptibility of juvenile salmonids to avian predation: are Caspian terns and double-crested cormorants only taking the sick and injured? Master of Science thesis. Oregon State University, Corvallis, Oregon.

- Hostetter, N.J., A.F. Evans, D.D. Roby, K. Collis, M. Hawbecker, B.P. Sandford, D.E. Thompson, and F.J. Loge. 2011. Relationship of external fish condition to pathogen prevalence and out-migration survival in juvenile steelhead. *Transactions of the American Fisheries Society* 140: 1158-1171.
- Hostetter, N.J., A.F. Evans, D.D. Roby, and K. Collis. 2012. Susceptibility of juvenile steelhead to avian predation: the influence of individual fish characteristics and river conditions. *Transactions of the American Fisheries Society* 141: 1586-1599.
- Huffaker, C.B. 1958. Experimental studies on predation: dispersion factors and predator-prey oscillations. *Hilgardia* 27(14): 343-383.
- Hughes, J.S., M.A. Weiland, C.M. Woodley, G.R. Ploskey, S.M. Carpenter, M.J. Hennen, E.F. Fischer, G.W. Batten III, T.J. Carlson, A.W. Cushing, Z. Deng, D.J. Etherington, T. Fu, M.J. Greiner, M. Ingraham, J. Kim, X. Li, J. Martinez, T.D. Mitchell, B. Rayamajhi, A. Seaburg, J.R. Skalski, R.L. Townsend, K.A. Wagner, and S.A. Zimmerman. 2013. Survival and passage of yearling and subyearling Chinook salmon and steelhead at McNary Dam, 2012. Pacific Northwest National Laboratory, Final Report PNNL-22788, Richland, Washington to the U.S. Army Corps of Engineers, Walla Walla District, Walla Walla, Washington.
- Hunsicker, M.E., L. Ciannelli, K.M. Bailey, J.A. Buckel, J.W. White, J.S. Link, T.E. Essington, S. Gaichas, T.W. Anderson, R.D. Brodeur, K.S. Chan, K. Chen, G. Englund, K.T. Frank, V. Freitas, M.A. Hixon, T. Hurst, D.W. Johnson, J.F. Kitchell, D. Reese, G.A. Rose, H. Sjodin, W.J. Sydeman, H.W. van der Veer, K. Vollset, and S. Zado. 2011. Functional responses and scaling in predator-prey interactions of marine fishes: contemporary issues and emerging concepts. *Ecology Letters* 14: 1288-1299.
- ISAB (Independent Scientific Advisory Board). 2005-4. Report on harvest management of Columbia River salmon and steelhead. Northwest Power and Conservation Council, Portland, Oregon. ISAB Report 2005-4. Available at www.nwcouncil.org/fw/isab/isab2005-4.
- ISAB (Independent Scientific Advisory Board). 2011-1. Columbia River Food Webs: Developing a broader scientific foundation for fish and wildlife restoration. Northwest Power and Conservation Council, Portland, Oregon. ISAB Report 2011-1. Available at www.nwcouncil.org/fw/isab/isab2011-1.
- ISAB (Independent Scientific Advisory Board). 2014-4. Review of NOAA Fisheries' viable salmonid population (VSP) modeling of Willamette River spring Chinook populations. Northwest Power and Conservation Council, Portland, Oregon. ISAB Report 2014-4. Available at www.nwcouncil.org/fw/isab/isab2014-4.
- ISAB (Independent Scientific Advisory Board). 2015-1. Density dependence and its implications for fish management and restoration programs in the Columbia River. Northwest Power and Conservation Council, Portland, Oregon. ISAB Report 2015-1. 246pp. Available at www.nwcouncil.org/fw/isab/isab2015-1.
- ISAB/ISRP (Independent Scientific Advisory Board/Independent Scientific Review Panel). 2016-1. Critical uncertainties for the Columbia River Basin Fish and Wildlife Program. Northwest Power and Conservation Council, Portland, Oregon. ISAB Report 2016-1. 162pp. Available at www.nwcouncil.org/fw/isab/isabisrp2016-1.
- ISRP (Independent Scientific Review Panel). 2016-6. Final Review of Lake Roosevelt Northern Pike Suppression Proposal (1994-043-00). Northwest Power and Conservation Council, Portland, Oregon. ISRP report 2016-6. Available at www.nwcouncil.org/fw/isrp/isrp2016-6.

- ISRP (Independent Scientific Review Panel). 2016-7. Review of Box Canyon Northern Pike Suppression Progress Report (#2007-149-00). Northwest Power and Conservation Council, Portland, Oregon. ISRP report 2016-7. Available at www.nwcouncil.org/fw/isrp/isrp2016-7.
- Johnsson, J.I., E. Petersson, E. Jönsson, B.T. Björnsson, and T Järvi. 1996. Domestication and growth hormone alter antipredator behaviour and growth patterns in juvenile brown trout, *Salmo trutta*. Canadian Journal of Fisheries and Aquatic Sciences 53: 1546-1554.
- Juanes, F. 1994. What determines prey selectivity in piscivorous fishes? Pages 79-100 in D.J. Stouder, K.L. Fresh, and R.J. Feller, editors. Theory and application in fish feeding ecology. University of South Carolina Press, Columbia, South Carolina.
- Jones, C.M. 2006. Chapter 4: Estuarine and diadromous fish metapopulations. Pages 119-156 in J.P. Krtizer and P.F. Sale, editors. Marine metapopulations. Academic Press.
- Juliano, S.A. 2001. Nonlinear curve fitting: predation and functional response curves. Pages 178-196 in S.M. Scheiner and J. Gurevitch, editors. Design and analysis of ecological experiments, second edition. Oxford University Press, New York, New York.
- Kareiva, P., M. Marvier, and M. McClure. 2000. Recovery and management options for spring/summer Chinook salmon in the Columbia River Basin. Science (Washington, D.C.) 290: 977-979.
- Koski, M.L. and B.M. Johnson. 2001. Functional response of kokanee salmon (*Oncorhynchus nerka*) to *Daphnia* at different light levels. Canadian Journal of Fisheries and Aquatic Sciences 59: 707-716.
- Krkosek, M., B.M. Connors, H. Ford, S. Peacock, P. Mages, J.S. Ford, A. Morton, J.P. Volpe, L.M. Dill, and M.A. Lewis. 2011. Fish farms, parasites and predators: implications for salmon population dynamics. Ecological Applications 21: 897-914.
- Kuligowski, D., L. Weitkamp, C. Roegner, D. Roby, K. Collis, D. Lyons, D. Van Doornik, L. Reinalda, A. Evans, T. Marcella, P. Loschl, and D. Teel. 2016. Genetic analysis of Caspian tern (*Hydroprogne caspia*) and double-crested cormorant (*Phalacrocorax auritus*) salmonid depredation in the Columbia River estuary 2006-2013. PowerPoint presentation at Columbia River Estuary Conference. Available at: www.estuarypartnership.org.
- Lebreton, J.D. 2005. Dynamical and statistical models for exploited populations. Australian and New Zealand Journal of Statistics 47: 49-63.
- Lessard, R.B., S. Martell, C.J. Walters, T.E. Essington, and J.F.K. Kitchell. 2005. Should ecosystem management involve active control of species abundances? Journal 10: 1. Available at: www.ecologyandsociety.org/vol10/iss2/art1.
- Luckinbill, L. S. 1973. Coexistence in laboratory populations of *Paramecium aurelia* and its predator *Didinium nasutum*. Ecology 54: 1320-1327.
- Lyons, D.E. 2010. Bioenergetics-based predator-prey relationships between piscivorous birds and juvenile salmonids in the Columbia River estuary. Unpubl. Ph.D. dissertation, Oregon State University, Corvallis, Oregon. Available at www.birdresearchnw.org.
- Lyons, D.E., D.D. Roby, A.F. Evans, N.J. Hostetter, and K. Collis. 2011a. Benefits to Columbia River anadromous salmonids from potential reductions in avian predation on the Columbia Plateau. Report submitted to the U.S. Army Corps of Engineers, Walla Walla District. Bird Research Northwest. Available at www.birdresearchnw.org.

- Lyons, D.E., D.D. Roby, J.Y. Adkins, P.J. Loschl, L.R. Kerr, T.K. Marcella, A.F. Evans, N.J. Hostetter, K. Collis, D.R. Kuligowski, and B.P. Sandford. 2011b. Impacts of piscivorous birds on native anadromous fishes in the mid-Columbia River. Pages 49-80 in Roby, D.D. (ed.). Impacts of avian predation on salmonid smolts from the Columbia and Snake rivers: A synthesis report to the U.S. Army Corps of Engineers, Walla Walla District. Available at www.birdresearchnw.org.
- Lyons, D.E., A.F. Evans, N.J. Hostetter, A. Piggott, L. Weitkamp, T.P. Good, D.D. Roby, K. Collis, P.J. Loschl, B. Cramer. 2014a. Factors influencing predation on juvenile salmonids by double-crested cormorants in the Columbia River Estuary: a retrospective analysis. Prepared for the U.S. Army Corps of Engineers, Portland District.
- Lyons, D.E., D.D. Roby, A.E. Evans, N.J. Hostetter, and K. Collis. 2014b. Benefits to Columbia River anadromous salmonids from potential reductions in predation by double-crested cormorants nesting at the East Sand Island Colony in the Columbia River Estuary. Final Report to the U.S. Army Corps of Engineers, Portland District. 64 pp.
- MacLulich, D.A. 1937. Fluctuations in the numbers of the varying hare (*Lepus americanus*). University of Toronto Studies, Biology Series.43: 1-136.
- Marine, K.R, and J.J. Cech. 2004. Effects of high water temperature on growth, smoltification, and predator avoidance in juvenile Sacramento River Chinook salmon. North American Journal of Fisheries Management 24: 198-210.
- McClure, M., B. Sanderson, E. Holmes, C. Jordon, P. Kareiva, and P. Levin. 2000. A standardized quantitative analysis of risks faced by salmonids in the Columbia River Basin. National Marine Fisheries Service, Northwest Fisheries Science Center, Seattle, Washington.
- McClure, M. M., E. E. Holmes, B. L. Sanderson, and C. E. Jordan. 2003. A large-scale, multi-species status assessment: anadromous salmonids in the Columbia River. Ecological Applications 13: 964-989.
- McIntyre, J.K., D.H. Baldwin, D.A. Beauchamp, and N.L. Scholz. 2012. Low-level copper exposures increase visibility and vulnerability of juvenile coho salmon to cutthroat trout predators. Ecological Applications 22: 1460-1471.
- Mesa, M.G. 1994. Effects of multiple acute stressors on the predator avoidance ability and physiology of juvenile Chinook salmon, Transactions of the American Fisheries Society 123: 786-793.
- Mesa, M. G., T. P. Poe, D.M. Gadomski, and J.H. Petersen. 1994. Are all prey created equal? A review and synthesis of differential predation on prey in substandard condition. Journal of Fish Biology 45:sA: 81-96.
- Mesa, M.G., T.P. Poe, A.G. Maule, and C.B. Schreck. 1998. Vulnerability to predation and physiological stress responses in juvenile Chinook salmon (*Oncorhynchus tshawytscha*) experimentally infected with *Renibacterium salmoninarum*. Canadian Journal of Fisheries and Aquatic Sciences 55: 1599-1606.
- Mesa, M.G., L.K. Weiland, and P. Wagner. 2002. Effects of thermal stress on the survival, predator avoidance, and physiology of juvenile fall Chinook salmon. Northwest Science 76: 118-128.
- Middlemas, S.J., T.R. Barton, J.D. Armstrong, and P.M. Thompson. 2006. Functional and aggregative responses of harbor seals to changes in salmonid abundance. Proceedings of the Royal Society B 273: 193-198.
- Moyle, P.B. 1977. In defense of sculpins. Fisheries 2: 20-23.

- Muir, W.D., D.M. Marsh, B.P. Sandford, S.G. Smith, and J.G. Williams. 2006. Post-hydropower system delayed mortality of transported Snake River stream-type Chinook salmon: Unraveling the mystery. *Transactions of the American Fisheries Society* 135: 1523-1534.
- NMFS. 2000a. Biological opinion for reinitiation of consultation on operation of the Federal Columbia River Power System. National Marine Fisheries Service, Northwest Region, Portland, Or.
- Nowak, E.M., T.C. Theimer, and G.W. Schuett. 2008. Functional and numerical responses of predators: Where do vipers fit in the traditional paradigms? *Biological Reviews* 83: 601-620.
- O'Boyle, R., and M. Sinclair. 2012. Seal-cod interactions on the Eastern Scotian Shelf: reconsideration of modelling assumptions. *Fisheries Research* 115-116: 1-13.
- Olla, B.L., and M.W. Davis. 1989. The role of learning and stress in predator avoidance of hatchery-reared coho salmon (*Oncorhynchus kisutch*) juveniles. *Aquaculture* 76: 209-214.
- Olla, B.L., M.W. Davis, and C.H. Ryer. 1998. Understanding how the hatchery environment represses or promotes the development of behavioral survival skills. *Bulletin of Marine Science* 62: 531-550.
- Patton, D.R. 2011. Forest wildlife ecology and habitat management. CRC Press, Boca Raton.
- Péron, G. 2013. Compensation and additivity of anthropogenic mortality: life-history effects and review of methods. *Journal of Animal Ecology*, 82: 408-417.
- Péron, G., C.A. Nicolai, and D.N. Koons. 2012. Demographic response to perturbations: the role of compensatory density dependence in a North American duck under variable harvest regulations and changing habitat. *Journal of Animal Ecology* 80: 960-969.
- Peterman, R.M. 1977. A simple mechanism that causes collapsing stability regions in exploited salmonid populations. *Journal of the Fisheries Research Board of Canada* 34: 1130-1142.
- Peterman, R.M., and M. Gatto. 1978. Estimation of Functional Responses of Predators on Juvenile Salmon. *Journal of the Fisheries Research Board of Canada* 35: 797-808.
- Petersen, J.H., and D.L. DeAngelis. 1992. Functional response and capture timing in an individual-based model: predation by northern squawfish (*Ptychocheilus oregonensis*) on juvenile salmonids in the Columbia River. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 2551-2565.
- Poe, T.P., H.C. Hansel, S. Vigg, D.E. Palmer, and L.A. Prendergast. 1991. Feeding of predaceous fishes on out-migrating juvenile salmonids in John Day Reservoir, Columbia River. *Transactions of the American Fisheries Society* 120:405-420.
- Quinn, T.J., and R. Deriso. 1999. Quantitative fish dynamics. Oxford University Press, New York, NY.
- Quinn, T.P. 2005. The behavior and ecology of Pacific salmon and trout. University of Washington Press, Seattle.
- Quinn T.P., and K. Fresh. 1984. Homing and straying in Chinook salmon (*Oncorhynchus tshawytscha*) from Cowlitz River Hatchery, Washington. *Canadian Journal of Fisheries and Aquatic Sciences* 41: 1078-1082.
- Quinn, T.P., C.J. Cunningham, J. Randall, and R. Hilborn. 2014. Can intense predation by bears exert a compensatory effect on recruitment in a Pacific salmon population? *Oecologia* 176: 445-456.

- Raymond, H.L., R.C.P. Beamesderfer, D.L. Ward, and A.A. Nigro. 1996. Evaluation of the biological basis for a predator control program on northern squawfish (*Ptychocheilus oregonensis*) in the Columbia and Snake rivers. *Canadian Journal of Fisheries and Aquatic Sciences* 53: 2898-2908.
- Ricker, W.E. 1948. The consumption of young sockeye salmon by predacious fishes. *Journal of the Fisheries Research Board of Canada*.
- Rieman, B.E., R.C. Beamesderfer, S. Vigg, and T.P. Poe. 1991. Estimated loss of juvenile salmonids to predation by northern squawfish, walleyes, and smallmouth bass in John Day Reservoir, Columbia River. *Transactions of the American Fisheries Society* 120: 448-458.
- Roby, D.D., and K. Collis. 2009. Research, monitoring and evaluation of avian predation on salmonids smolts in the lower and mid-Columbia River. Draft 2009 Annual Report. Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon, USA.
- Roby, D.D., D.E. Lyons, D.P. Craig, K. Collis, and G.H. Visser. 2003. Quantifying the effect of predators on endangered species using a bioenergetics approach: Caspian terns and juvenile salmonids in the Columbia River estuary. *Canadian Journal of Zoology* 81: 250-265.
- Roumasset, A., and C. Caudill. 2013. Prespawn mortality of Upper Willamette River spring Chinook salmon: Associations with stream temperature, watershed attributes and environmental conditions on the spawning grounds. In 2012 Willamette Basin Fisheries Science Review. Oregon State University and the US Army Corps of Engineers, Corvallis, Oregon.
- Ruggerone, G.T., and D.E. Rogers. 1984. Arctic char predation on migrating sockeye smolts at Little Togiak River, Alaska. *Fishery Bulletin* 82: 401-410.
- Ruggerone, G.T., R. Hansen, and D. Rogers. 2000. Selective predation by brown bears (*Ursus arctos*) foraging on spawning sockeye salmon. *Canadian Journal of Zoology* 78:6:974-981.
- Ruggerone, G.T., B.A. Agler, L. Wilson, and E.V. Farley, Jr. 2013. Size-selective mortality of Bristol Bay sockeye smolts in relation to smolt characteristics, ocean conditions, and sockeye salmon productivity. *North Pacific Anadromous Fish Commission Technical Report* 9: 210-213.
- Ryan, B.A., S.G. Smith, J.M. Butzerin, and J.W. Ferguson. 2003. Relative vulnerability to avian predation of juvenile salmonids tagged with passive integrated transponders in the Columbia River estuary, 1998–2000. *Transactions of the American Fisheries Society* 132:275–288.
- Sanderson, B. L., K. A. Barnas, and M. Rub. 2009. Non-indigenous species of the Pacific Northwest: an overlooked risk to endangered fishes? *BioScience* 59:245-256.
- Schaub, M., and J.D. Lebreton, 2004. Testing the additive versus the compensatory hypothesis of mortality from ring recovery data using a random effects model. *Animal Biodiversity and Conservation* 27: 73-85.
- Schreck, C.B., T.P. Stahl, L.E. Davis, D.D. Roby, and B.J. Clemens. 2006. Mortality estimates of juvenile spring-summer Chinook salmon in the lower Columbia River and estuary, 1992-1998: Evidence for delayed mortality? *Transactions of the American Fisheries Society* 135: 457-475.
- Sedinger, J.S., G.C. White, S. Espinosa, E.T. Partee and C.E. Bruan. 2010. Assessing compensatory versus additive harvest mortality: an example using greater sage-grouse. *Journal of Wildlife Management* 74: 326-332.
- Servanty S., R. Choquet, E. Baubet, S. Brandt, J. Gaillard, M. Schaub, C. Toigo, J. Lebreton, M. Buoro, and O. Gimenez. 2010. Assessing whether mortality is additive using marked animals: a Bayesian state-space modeling approach. *Ecology* 91: 1916-1923.
- Shaffer, M.L. 1981. Minimum population sizes for species conservation. *BioScience* 31: 131-134.

- Skalski, J.R., R. Townsend, J.M. Lady, M.A. Timko, L.S. Sullivan, and K. Hatch. 2015. Survival of acoustic-tagged steelhead and yearling Chinook salmon smolts through the Wanapum–Priest Rapids Project in 2014. Final Report submitted by Columbia Basin Research, University of Washington, Seattle, and Blue Leaf Environmental, Ellensburg, Washington to Grant County Public Utility District, Ephrata, Washington.
- Smout, S., C. Asseburg, J. Matthiopoulos, C. Fernandez, S. Redpath, S. Thirgood, and J. Harwood. 2010. The functional response of a generalist predator. *PLoS One* 5(5): e10761. Doi:10.1371/journal.pone.0010761.
- Smout, S., A. Rindorf, P.S. Hammond, J. Harwood, and J. Matthiopoulos. 2014. Modelling prey consumption and switching by UK grey seals *ICES Journal of Marine Science* 71(1): 81-89.
- Sogard, S.M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bulletin of Marine Science* 60: 129-1157.
- Solomon, M.E. 1949. The natural control of animal populations. *Journal of Animal Ecology* 18(1): 1-35.
- Spencer, P.D., and J.S. Collie. 1995. A simple predator-prey model of exploited marine fish populations incorporating alternative prey. *ICES Journal of Marine Science* 53: 615-628.
- Steen, R.P., and T.P. Quinn. 1999. Egg burial depth by sockeye salmon (*Oncorhynchus nerka*): implications for survival of embryos and natural selection on female body size. *Canadian Journal of Zoology* 77: 836–841.
- Storch, A.J., C. Mallette, and S. Williams. 2013. Northern pikeminnow management program evaluation 1/1/2013 - 12/31/2013. Annual Research, Monitoring, and Evaluation Report for Bonneville Power Administration, Portland, Oregon. Project No. 1990-077-00.
- Tatara, C.P., S.C. Riley, and B.A. Berejikian. 2011. Effects of hatchery fish density on emigration, growth, survival, and predation risk of natural steelhead parr in an experimental stream channel. *North American Journal of Fisheries Management* 31(2): 224-235.
- Thompson, J.N., and D.A. Beauchamp. 2014. Size-selective mortality of steelhead during freshwater and marine life stages related to freshwater growth in the Skagit River, Washington. *Transactions of the American Fisheries Society* 143: 910-925.
- Tucker, S., J.M. Hipfner, and M. Trudel. 2016. Size- and condition-dependent predation: a seabird disproportionately targets substandard individual juvenile salmon. *Ecology* 97: 461–471.
- Ward, D.L., J.H. Petersen, and J.J. Loch. 1995. Index of predation on juvenile salmonids by northern squawfish in the lower and middle Columbia River and in the lower Snake River. *Transactions of the American Fisheries Society* 124: 321–334.
- Ward, D.M., and N.A. Hvidsten. 2011. Predation: compensation and context dependence, Chapter 8. Pages 199-220 in O. Aas, S. Einum, A. Klemetsen, and J. Skurdal (editors). *Atlantic salmon ecology*, First Edition, Wiley-Blackwell.
- Weitkamp, L.A., T.P. Good, D.E. Lyons, and D.D. Roby. 2016. The influence of environmental variation on the Columbia River estuarine fish community: implications for predation on juvenile salmonids. *North Pacific Anadromous Fish Commission Bulletin* 6: in press.
- Wiese, F.K., J.K. Parrish, C.W. Thompson, and C. Maranto, C. 2008. Ecosystem-based management of predator–prey relationships: piscivorous birds and salmonids. *Ecological Applications*, 18: 681–700. doi:10.1890/06-1825.1.

Yamamoto, T, and U.G. Reinhardt. 2003. Dominance and predator avoidance in domesticated and wild masu salmon *Oncorhynchus masou*. Fisheries Science 69: 88-94.

Zabel, R., T. Cooney, C. Jordan, R.W. Carmichael, B.C. Jonasson, E.W. Sedell, T.L. Hoffnagle, J. White, C. Beasley, M. Nahorniak, C. McGrath, J. Benjamin, J. Jorgensen, A. Murdoch, J. Cram, C. Paulsen, L.G. Crozier, N. Kendall, W.P. Connor, W. Young, R. Perry, K.F. Tiffan, M. Newsom, R. Bellmore, C. Snow, R.B. Lessard, C. Justice, I. Courter, C. Frederiksen, E. Buhle, A.H. Fullerton, P. Moran, D. Van Doornik, E. Ward, and M. Scheuerell. 2013. Life-cycle models of salmonid populations in the interior Columbia River: understanding the connection between impacts & salmon survival. June 28, 2013 Draft, NOAA Fisheries, Northwest Fisheries Science Center, Seattle, Washington. 428 pp. Available at: www.nwfsc.noaa.gov.