AN ABSTRACT OF THE THESIS OF

Nathan J. Hostetter for the degree of Master of Science in Wildlife Science presented on December 8, 2009.

Title: Susceptibility of Juvenile Salmonids to Avian Predation: Are Caspian Terns and Double-crested Cormorants Only Taking the Sick and Injured?

Abstract approved:

Daniel D. Roby

The ability to non-destructively assess fish condition and subsequently track fish behavior and survival can be vital in understanding natural and anthropogenic stressors and sources of mortality, especially in populations of fish listed as threatened or endangered. I investigated the use of a quick, non-lethal, external examination technique to assess general health status of run-of-the-river juvenile steelhead (*Oncorhynchus mykiss*) migrating from the Snake River basin.

The relationship between external symptoms of captured fish (including body injuries, de-scaling, external symptoms of disease, fin damage, and ectoparasite infestations) and their health status was investigated through pathology analysis of a euthanized subsample of fish. I assessed the relative fitness of steelhead smolts assigned to various categories of health status by measuring the subsequent survival and susceptibility to avian predation of fish that were tagged with passive integrated transponder (PIT) tags and released unharmed. Histological analysis was conducted on 222 steelhead sacrificed at the juvenile collection facility of Lower Monumental Dam

(LMN) on the lower Snake River during steelhead out-migration in 2008; results indicated that external symptoms of disease, body injuries, de-scaling, and fin damage were all associated with increased prevalence of infectious pathogens.

Capture-recapture models for 14,177 steelhead PIT-tagged and released at LMN in 2007 and 2008 indicated that the presence of external symptoms of disease, body injuries, or de-scaling, but not fin damage, were associated with significantly reduced survival probabilities during either short-distance (ca. 119 Rkm) or long-distance (ca. 354 Rkm) migration. PIT tags from 3.0% and 1.9% of all released steelhead (n = 16,258) were recovered on a Caspian tern (*Hydroprogne caspia*) colony and a double-crested cormorant (*Phalacrocorax auritus*) colony, respectively, located < 79 Rkm downstream of release locations. A consistent factor relating susceptibility of steelhead to predation by both bird species was compromised health, particularly steelhead with external symptoms of disease and body injuries. River conditions, including decreased discharge and elevated water temperatures at the time of release, were also associated with increased susceptibility of steelhead to avian predation, but the strength of these explanatory factors differed between species of avian predator.

These results support the conclusion that external condition, measured non-destructively on individual fish, is associated with quantifiable differences in general health status and fitness of fish. Results also indicate that some reduction in avian predation on juvenile salmonids (*Oncorhynchus* spp.) may be accomplished by modifying hydrosystem operations. The higher susceptibility of unhealthy steelhead to avian predation suggests that a portion of any reduction in mortality due to avian predation will be compensated for by other sources of smolt mortality. The portion of

juvenile steelhead that are at greater risk of avian predation is small, however, based on

the small proportion of steelhead that exhibited visible symptoms of compromised health.

Susceptibility of Juvenile Salmonids to Avian Predation: Are Caspian Terns and Double-crested Cormorants Only Taking the Sick and Injured?

by
Nathan J. Hostetter

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented December 8, 2009
Commencement June 2010

<u>Master of Science</u> thesis of <u>Nathan J. Hostetter</u> presented on <u>December 8, 2009</u>.

APPROVED:

_____

Major Professor, representing Wildlife Science

_____

Head of the Department of Fisheries and Wildlife

_____

Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

_____

Nathan J. Hostetter, Author

ACKNOWLEDGMENTS

CONTRIBUTION OF AUTHORS

Dr. Daniel D. Roby (USGS-Oregon Cooperative Fish and Wildlife Research Unit, Oregon State University, Corvallis, OR) acquired funding, contributed to the study design, interpretation of results, and assisted in preparation of both manuscripts. Allen F. Evans (Real Time Research, Bend, OR) was a significant contributor at all stages of this study, including study design, field work, data processing and analysis, and interpretation of results. Ken Collis (Real Time Research, Bend, OR) contributed to the study design, field work, and interpretation of results. Mike Hawbecker (Real Time Research, Bend, OR) contributed to the study design, field work, and data processing. Benjamin P. Sandford (National Marine Fisheries Service, Pasco, WA) contributed to data processing, analysis, and interpretation of the Chapter 2 survival results. Dr. Frank J. Loge (Department of Civil and Environmental Engineering, University of California–Davis) contributed to study design, analysis, laboratory work, and interpretation of the pathology results in Chapter 2. Donald E. Thompson (Department of Civil and Environmental Engineering, University of California–Davis) contributed to field work, laboratory work, and interpretation of pathology results in Chapter 2.

TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDICES

CHAPTER 1

GENERAL INTRODUCTION

Nathan J. Hostetter

The Columbia River basin once supported vast numbers of anadromous salmon (*Oncorhynchus* spp.) and steelhead (*O. mykiss*), and one of the most productive salmon fisheries in the world (McClure et al. 2003). Declines of anadromous Pacific salmonid (*Oncorhynchus* spp.) populations in the Columbia River basin have prompted the listing of 13 of the 20 evolutionarily significant units (ESUs) from the basin as threatened or endangered under the United States Endangered Species Act (ESA) (Waples 1991, Good et al. 2005). Within the Columbia River basin, the majority of actions to restore salmonid populations have focused on mitigating the impacts of the so-called "four H's" - improving survival through the Hydrosystem, regulating human Harvest, modifying Hatchery practices, and restoring freshwater Habitat (Federal Caucus 2000). Mortality of juvenile salmonids associated with hydroelectric development in the Columbia River basin has been cited as a primary reason for declines in adult returns (Raymond 1979, Raymond 1988). Estimates of direct plus indirect salmonid mortality that approached 30% at a single hydropower project (dam and associated reservoir combined) have subsequently been reduced by numerous passage enhancements (Rieman et al. 1991, Mathur et al. 1996, Friesen and Ward 1999). However, mortality due to factors both directly and indirectly related to hydroelectric power development is still considered substantial (Budy et al. 2002).

Hydroelectric development in the Columbia River basin has greatly altered environmental conditions experienced by juvenile salmonids during their emigration through the hydrosystem. For instance, reduced water flow can delay downstream migration and prolong exposure of juvenile salmonids to predators within the hydrosystem (Raymond 1988, Deriso et al. 2001, Smith et al. 2002, Connor et al. 2003).

Increased concern regarding the impact of predation on juvenile salmonids prompted investigations into piscivorous fish (e.g., Beamesderfer et al. 1990, Rieman et al. 1991, Ward et al. 1995, Zimmerman 1999) and piscivorous birds (e.g., Collis et al. 2002, Roby et al. 2003, Ryan et al. 2003, Antolos et al. 2005) on ESA-listed salmonid populations in the Columbia River basin. Although predation by piscivorous fish and birds has not been implicated as a cause of salmonid declines in the Columbia River basin, some managers identify predation as a potentially significant limiting factor for recovery of threatened and endangered salmonid ESUs (NOAA 2004, NOAA 2007).

Substantial increases in the number of colonial nesting piscivorous waterbirds in the Columbia River basin and their impacts on salmonid populations over the past decade have been well documented (e.g., Collis et al. 2002, Roby et al. 2003, Good et al. 2007, Wiese et al. 2008). Increasing numbers of Caspian terns (*Hydroprogne caspia*) in the Columbia River estuary and their impact on threatened and endangered salmonid ESUs prompted a decision to manage this colony to reduce salmonid mortality in the estuary (Roby et al. 2002). Currently, management to relocate a portion of the Caspian terns nesting in the Columbia River estuary out of the Columbia River basin is being implemented, and additional management options to reduce predation on salmonids by piscivorous waterbirds are being investigated (Roby et al. 2002, USFWS 2006).

In addition to management efforts in the Columbia River estuary, consumption of juvenile salmonids by ring-billed gulls (*Larus delawarensis*) at Wanapum and Priest Rapids dams on the mid-Columbia River resulted in management to eliminate a gull (*Larus* spp.) breeding colony on a nearby island in the river (Ruggerone 1986, Pochop et al. 1998, York et al. 2000). Predation rates on juvenile salmonids by Caspian terns

nesting in the impoundment formed by McNary Dam on the Columbia River (hereafter referred to as McNary Pool) have also been quite high despite the small size of this colony compared to the Caspian tern colony in the Columbia River estuary (Antolos et al. 2005).

Despite multiple studies quantifying the number of juvenile salmonids consumed by various bird colonies (e.g., Collis et al. 2002, Roby et al. 2003, Antolos et al. 2005), our understanding of the environmental factors and individual fish characteristics that influence the susceptibility of juvenile salmonids to avian predation is extremely limited. Collis et al. (2002) found that the proportion of salmonids in piscivorous waterbird diets varied widely among piscivorous bird species and colony locations. Additionally, increased susceptibility of juvenile salmonids to avian predation has been attributed to differences in smolt behavior, physiology, condition, rearing environment, and size (Mesa et al. 1998, Collis et al. 2002, Schreck et al. 2006, Kennedy et al. 2007). Previous studies have demonstrated that susceptibility of juvenile salmonids to fish predation is influenced by river conditions associated with hydrosystem operations (e.g., Coutant 1973, Mesa 1994, Mesa and Warren 1997, Connor et al. 2003). Antolos et al. (2005) suggested that low river flows and reduced in-river salmonid abundance increased predation rates on juvenile salmonids by Caspian terns nesting on an island in the McNary Pool. However, studies directly investigating the potential influence of various environmental factors on avian predation rates are lacking. To date, studies to test the hypotheses from Antolos et al. (2005) and identify additional environmental factors associated with increased susceptibility of salmonids to avian predation have not been published.

Susceptibility of out-migrating juvenile salmonids to avian predation may also be influenced by individual fish characteristics. In their natural environments, fish are subjected to numerous stressors that impair physical condition and compromise overall health (Wedemeyer et al. 1984). Sub-lethal physiological effects of external trauma, ectoparasites, and skin diseases can affect survival through impairment of immune function (Peters et al. 1988, Maule et al. 1989, Arkoosh et al. 2006) or by altering other aspects of performance, such as predator avoidance (Olla et al. 1992, Mesa 1994, Mesa et al. 1994). Schreck et al. (2006) found suggestive evidence that differences among individual Chinook salmon (*O. tshawytscha*) smolts in the incidence and intensity of disease, plus physiological preparedness to enter saltwater, influenced susceptibility to Caspian tern predation in the Columbia River estuary. Kennedy et al. (2007) found similar relationships between juvenile steelhead physiology and susceptibility to avian predation, further supporting the hypothesis that salmonid susceptibility to avian predation in the Columbia River estuary is associated with the condition of individual fish.

Enhanced susceptibility of prey in substandard condition (weak, sick, stressed, etc.) to predation is widely accepted (Temple 1987). Detecting stress in fish can be difficult, however, and relating stress to overall health status of fish is even more complex, as complications from a stressor may not appear for some time after the stress event has occurred (Budy et al. 2002). Health status and stress levels of fish have been evaluated through numerous approaches at both the individual and population level, each with its own set of advantages and constraints, depending on particular objectives of the study. Sophisticated techniques, such as biochemical, physiological, and pathological

indices to health status, may be impractical for many studies due to cost, specialized training, instrumentation, and/or substantial time commitments required (Adams et al. 1993). In addition, assessing health status of fish populations often requires destructive sampling of individuals from the population of interest. Lethal collection of fish may not be appropriate for studies involving small populations, species listed as threatened or endangered, or if logistical constraints limit the time available to necropsy fish. Destructive sampling may also preclude tracking subsequent fish behavior, movements, or survival after release, which may be key to the research design.

Although Snake River steelhead have been the subject of extensive research, monitoring, and evaluation since development of the hydrosystem on the Snake River in the late 1960's (Schreck et al. 2006), little is known regarding the relationship between the characteristics of individual fish and their general health status or subsequent survival. Each year, thousands of juvenile salmonids emigrating from the Columbia River and Snake River basins are captured and externally examined at facilities associated with hydroelectric dams. During their out-migration, juvenile salmonids are commonly subjected to numerous stressors that can cause damage to the body and fins in a variety of ways. Overall, there is general agreement that fish condition and stress affect survival (Barton et al. 2002, Budy et al. 2002), but few studies have attempted to model and quantify the extent to which external indicators of fish condition and health are associated with subsequent survival of fish in a field setting.

This thesis investigates the influence of individual fish characteristics and river conditions on the survival of juvenile salmonids and their susceptibility to avian predation. Juvenile steelhead from the Snake River ESU and Caspian terns and double-

crested cormorants (*Phalacrocorax auritus*) nesting on islands in McNary Pool were used as models in this experiment. Snake River steelhead were selected for this study because this ESU is listed as threatened under the ESA, and data to assess mortality factors, such as avian predation, are needed to evaluate recovery options for this ESU. Additionally, juvenile steelhead were selected because prior research indicated they were the most susceptible salmonid species to avian predation in McNary Pool (Antolos et al. 2005).

The objective in Chapter 2 is to investigate whether external indicators of health status for out-migrating smolts, as measured by a quick, non-destructive examination procedure, were associated with the general health and fitness of juvenile steelhead from the Snake River basin. Relationships between external indicators and fitness of steelhead were inferred by assessing relative differences in pathogen prevalence and subsequent survival during out-migration for juvenile steelhead assigned to several categories of health status based on the presence or absence of external body injuries, de-scaling, externally-visible disease symptoms, fin damage, and ectoparasite infestations. We used juvenile run-of-the-river steelhead migrating from the Snake River basin that were captured at the juvenile collection facility of Lower Monumental Dam (LMN, Rkm 589) for this study. Juvenile steelhead implanted with passive integrated transponder (PIT) tags were tracked during their subsequent out-migration through the Columbia River hydrosystem to assess relationships between external symptoms and survival. In addition, a subsample of steelhead was euthanized and analyzed for the presence of pathogens known to infect salmonids throughout the Columbia River basin in order to investigate possible associations between steelhead external symptoms and pathogen prevalence.

In Chapter 3 I investigate how the susceptibility of juvenile Snake River steelhead to predation by piscivorous waterbirds is related to individual fish characteristics and river conditions. I used recoveries of smolt PIT tags from a Caspian tern colony and a double-crested cormorant colony located on islands in McNary Pool (< 79 Rkm from release locations) to identify those river conditions and individual smolt characteristics associated with increased susceptibility to avian predation. Steelhead characteristics that were evaluated included rearing type (hatchery or wild origin), size (fork length), and presence and severity of external symptoms of disease, injury, and stress (mentioned above). Environmental variables that were evaluated as part of this study included: (1) steelhead release location, (2) migration year, (3) prey abundance (number of in-river steelhead in the McNary Pool), (4) predator abundance (number of adult and juvenile Caspian terns or double-crested cormorants at the colonies on Crescent Island and Foundation Island, respectively), (5) water discharge (kcfs), (6) water temperature (^{o}C), and (7) water clarity (Secchi depth).

Overall, results from these two chapters enhance our understanding of how individual salmonid characteristics and river conditions influence juvenile survival, health status, and susceptibility to predation. This understanding can aid in developing effective recovery plans for ESA-listed salmonid populations from throughout the Columbia River basin.

LITERATURE CITED

Adams, S. M., A. M. Brown, and R. W. Goede. 1993. A quantitative health assessment index for rapid evaluation of fish condition in the field. Transactions of the American Fisheries Society 122:63-73.

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.

Arkoosh, M. R., A. N. Kagley, B. F. Anulacion, D. A. Boylen, B. P. Sandford, F. J. Loge, L. L. Johnson, and T. K. Collier. 2006. Disease susceptibility of hatchery Snake River spring-summer Chinook salmon with different juvenile migration histories in the Columbia River. Journal of Aquatic Animal Health 18:223-231.

Barton, B. A., J. D. Morgan, and M. M. Vijaya. 2002. Physiological and condition-related indicators of environmental stress in fish. Pp. 111-148 *in* S. M. Adams, editor. Biological indicators of aquatic ecosystem stress. American Fisheries Society, Bethesda, Maryland.

Beamesderfer, R. C., B. E. Rieman, L. J. Bledsoe, and S. Vigg. 1990. Management implications of a model of predation by a resident fish on juvenile salmonids migrating through a Columbia River reservoir. North American Journal of Fisheries Management 10:290-304.

Budy, P., G. P. Thiede, N. Bouwes, C. E. Petrosky, and H. Schaller. 2002. Evidence linking delayed mortality of Snake River salmon to their earlier hydrosystem experience. North American Journal of Fisheries Management 22:35-51.

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 loses of juvenile salmonids to avian predation. Transactions of the American Fisheries Society 131:537-550.

Connor, W. P., H. L. Burge, J. R. Yearsley, and T. C. Bjornn. 2003. Influence of flow and temperature on survival of wild subyearling fall Chinook salmon in the Snake River. North American Journal of Fisheries Management 23:362-375.

Coutant, C. C. 1973. Effect of thermal shock on vulnerability of juvenile salmonids to predation. Journal of the Fisheries Research Board of Canada 30:965-973.

Deriso, R. B., D. R. Marmorek, and I. J. Parnell. 2001. Retrospective patterns of differential mortality and common year-effects experienced by spring and summer Chinook salmon (*Oncorhynchus tshawytscha*) of the Columbia River. Canadian Journal of Fisheries and Aquatic Sciences 58:2419-2430.

Federal Caucus. 2000. Conservation of Columbia Basin fish: final basinwide salmon recovery strategy. Federal Caucus, Portland, Oregon.

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.

Good, T. P., R. S. Waples, and P. Adams (editors). 2005. Updated status of federally listed ESUs of West Coast salmon and steelhead. NOAA Technical Memorandum NMFS-NWFSC-66:598.

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.

Kennedy, B. M., W. L. Gale, and K. G. Ostrand. 2007. Relationship between smolt gill Na+, K+ ATPase activity and migration timing to avian predation risk of steelhead trout (*Oncorhynchus mykiss*) in a large estuary. Canadian Journal of Fisheries and Aquatic Sciences 64:1506-1516.

Mathur, D., P. G. Heisey, E. T. Euston, J. R. Skalski, and S. Hays. 1996. Turbine passage survival estimation for Chinook salmon smolts (*Oncorhynchus tshawytscha*) at a large dam on the Columbia River. Canadian Journal of Fisheries and Aquatic Sciences 53:542-549.

Maule, A. G., R. A. Tripp, S. L. Kaattari, C. B. Schreck, and S. L. Kaatari. 1989. Stress alters immune function and disease resistance in Chinook salmon (*Oncorhynchus tshawytscha*). Journal of Endocrinology 120:135-142.

McClure, M. M., E. E. Holmes, B. L. Sanderson, and C. E. Jordan. 2003. A large-scale, multispecies status assessment: anadromous salmonids in the Columbia River basin. Ecological Applications 13:964-989.

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., P. P. Thomas, M. G. Dena, and H. P. James. 1994. Are all prey created equal? A review and synthesis of differential predation on prey in substandard condition. Journal of Fish Biology 45:81-96.

Mesa, M. G., and J. J. Warren. 1997. Predator avoidance ability of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) subjected to sublethal exposures of gas-supersaturated water. Canadian Journal of Fisheries and Aquatic Sciences 54:757-764.

Mesa, M. G., T. P. Poe, A. G. Maule, and C. B. Schreck. 1998. Vulnerability to predation and physiological stress response in juvenile Chinook salmon (*Oncorhynchus tshawytscha*) experimentally infected with *Renibacterium salmoninarum*. Canadian Journal of Fisheries and Aquatic Sciences 55:1599-1606.

NOAA (National Oceanic and Atmospheric Administration) Fisheries. 2004. Biological opinion for consultation on remand for operation of the Columbia River Power System and 19 Bureau of Reclamation projects in the Columbia Basin, Portland, Oregon.

NOAA (National Oceanic and Atmospheric Administration) Fisheries. 2007. Draft biological opinion for consultation on remand for operation of the Columbia River Power System and 11 Bureau of Reclamation projects in the Columbia Basin and ESA section 10(a)(1)(A) permit for juvenile fish transportation program, Portland, Oregon.

Olla, B. L., M. W. Davis, and C. B. Schreck. 1992. Comparison of predator avoidance capabilities with corticosteroid levels induced by stress in juvenile coho salmon. Transactions of the American Fisheries Society 121:544-547.

Peters, G., M. Faisal, T. Lang, and A. Iman. 1988. Stress caused by social interaction and its effect on susceptibility to *Aeromonas hydrophila* infection in rainbow trout (*Salmo gairdneri*). Diseases of Aquatic Organisms 4:83-89.

Pochop, P. A., J. L. Cummings, C. A. Yoder, and J. E. Steuber. 1998. Comparison of white mineral oil and corn oil to reduce hatchability in ring-billed gull eggs. Proceedings of Vertebrate Pest Conference 18:411-413.

Raymond, H. L. 1979. Effects of dams and impoundments on migrations of juvenile Chinook salmon and steelhead from the Snake River, 1966 to 1975. Transactions of the American Fisheries Society 108:505-529.

Raymond, H. L. 1988. Effects of hydroelectric development and fisheries enhancement on spring and summer Chinook salmon and steelhead in the Columbia River basin. North American Journal of Fisheries Management 8:1-24.

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., K. Collis, D. E. Lyons, D. P. Craig, J. Y. Adkins, A. M. Myers, and R. M. Suryan. 2002. Effects of colony relocation on diet and productivity of Caspian terns. Journal of Wildlife Management 66:662-673.

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.

Ruggerone, G. T. 1986. Consumption of migrating juvenile salmonids by gulls foraging below a Columbia River dam. Transactions of the American Fisheries Society 115:736-742.

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.

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.

Smith, S. G., W. D. Muir, J. G. Williams, and J. R. Skalski. 2002. Factors associated with travel time and survival of migrant yearling Chinook salmon and steelhead in the lower Snake River. North American Journal of Fisheries Management 22:385-405.

Temple, S. A. 1987. Do predators always capture substandard individuals disproportionately from prey populations? Ecology 68:669-674.

USFWS (U.S. Fish and Wildlife Service). 2006. Record of decision: Caspian tern management to reduce predation of juvenile salmonids in the Columbia River estuary: Final Environmental Impact Statement. Portland, Oregon.

Waples, R. S. 1991. Definition of ''species'' under the Endangered Species Act: application to Pacific salmon. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-194.

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.

Wedemeyer, G. A., D. J. McLeay, and C. P. Goodyear. 1984. Assessing the tolerance of fish and fish populations to environmental stress: the problems and methods of monitoring. Pages 163-195 *in* V. W. Cairns, P. V. Hodson, and J. O. Nriagu, eds. Contaminant effects on fisheries. Wiley, New York.

Wiese, F. K., J. K. Parrish, C. W. Thompson, and C. Maranto. 2008. Ecosystem-based management of predator-prey relationships: Piscivorous birds and salmonids. Ecological Applications 18:681-700.

York, D. L., J. L. Cummings, J. E. Steuber, P. A. Pochop, and C. A. Yoder. 2000. Importance of migrating salmon smolt in ring-billed (*Larus delawarensis*) and California gull (*L. californicus*) diets near Priest Rapids Dam, Washington. Western North American Naturalist 60:216-220.

Zimmerman, M. P. 1999. Food habits of smallmouth bass, walleyes, and northern pikeminnow in the lower Columbia River basin during outmigration of juvenile anadromous salmonids. Transactions of the American Fisheries Society 128:1036-1054.

CHAPTER 2

RELATIONSHIP OF EXTERNAL FISH CONDITION TO PATHOGEN
PREVALENCE AND SUBSEQUENT SURVIVAL IN JUVENILE STEELHEAD

Nathan. J. Hostetter[1], A. F. Evans[2], D. D. Roby[1], K. Collis[2], M. Hawbecker[2], B. P.
Sandford[3], F. J. Loge[4], and D. E. Thompson[4]

[1]U.S. Geological Survey-Oregon Cooperative Fish and Wildlife Research Unit,
Department of Fisheries and Wildlife, 104 Nash Hall, Oregon State University, Corvallis,
OR 97331 USA

[2]Real Time Research, Inc., 52 S.W. Roosevelt Ave., Bend, OR 97702 USA

[3]National Marine Fisheries Service, 2725 Montlake Boulevard East, Seattle, WA 98112
USA

[4]Department of Civil and Environmental Engineering, University of California–Davis, 1
Shields Avenue, Davis, CA 95616 USA

ABSTRACT

The ability to non-destructively assess fish condition and subsequently track fish spatially and temporally can be vital in understanding sources of natural and anthropogenic stressors and mortality, especially in populations of fish listed as threatened or endangered. We investigated the use of a quick, non-lethal, external examination technique to identify general health status of run-of-the-river juvenile steelhead (*Oncorhynchus mykiss*) migrating from the Snake River basin. Relationships between external symptoms of captured fish (including body injuries, de-scaling, external symptoms of disease, fin damage, and ectoparasite infestations) and their health status were investigated through pathology analysis of collected fish and subsequent survival of released fish. Histological analysis of 222 euthanized steelhead captured at the juvenile collection facility of Lower Monumental Dam (LMN) on the lower Snake River during steelhead out-migration in 2008 indicated that external symptoms of disease, body injuries, de-scaling, and fin damage were associated with increased prevalence of infectious diseases. Capture-recapture models of 14,177 steelhead PIT-tagged and released at LMN in 2007 and 2008 indicated that the presence of external symptoms of disease, body injuries, or de-scaling, but not fin damage or ectoparasites, were associated with significantly reduced survival probabilities during either short-distance (ca. 119 Rkm) or long-distance (ca. 354 Rkm) migration. Overall, three of the five external symptoms evaluated by this study (i.e., external symptoms of disease, body injuries, and de-scaling) were significantly associated with increased pathogen prevalence and lower steelhead survival. These results support the conclusion that external condition, measured

non-destructively at the individual fish level, is associated with quantifiable differences in general health status of fish.

INTRODUCTION

Physiological stress associated with external damage can alter fish performance. In their natural environments, fish are subjected to numerous stressors that impair physical condition and overall health (Wedemeyer et al. 1984). Stress can overtax and compromise physiological and immunological systems, which in turn may reduce growth, impair reproduction, predispose fish to disease, and reduce the capability of fish to adapt to additional stressors (Adams 1990). External injuries and disease can reduce fish survival directly or through altering aspects of performance, such as depressing immunocompetence (Peters et al. 1988; Arkoosh 2006) or adversely affecting a fish's ability to avoid predators (Olla et al. 1992; Mesa 1994; Mesa et al. 1994) and cope with other environmental challenges (Schreck 1990; Pickering 1993; Wendelaar Bonga 1997). Overall, there is general agreement that fish condition and stress affect survival (Barton et al. 2002; Budy et al. 2002), but few studies have attempted to model and quantify the extent to which external condition is associated with subsequent survival of fish in a field setting.

Evaluating health status and stress levels of fish at the individual or population level has been attempted through numerous approaches, each with its own set of advantages and constraints, depending on the particular study objectives. Sophisticated techniques, such as biochemical, physiological, and pathological indices to health status, may be impractical for many studies due to cost, specialized training, instrumentation,

and/or substantial time commitments required (Adams et al. 1993). Goede and Barton (1990) addressed the need for a more pragmatic and inexpensive field technique to assess fish health by creating uniform evaluation procedures that incorporated quick and easily-measured organosomatic indices. This field necropsy technique, quantified by Adams et al. (1993), provided a health profile of fish populations based on anomalies observed in tissues and organs of sampled individuals that could subsequently be compared among sites, species, and years. Assessing health status of fish populations using methods developed by Adams et al. (1993), however, requires destructive sampling of a representative sample of the population of interest. Lethal collection of fish may not be appropriate nor the best alternative for studies involving small populations, species listed as threatened or endangered, or logistical constraints that limit time available to necropsy fish, or if tracking fish behavior, movements, or survival after release is the ultimate goal.

In the Pacific Northwest, declines of salmonid (*Oncorhynchus* spp.) populations over the past century have primarily been attributed to various human activities (Lichatowich 1999). Anadromous salmonids are vulnerable to a wide variety of anthropogenic factors in freshwater, estuarine, and ocean habitats due to their far-ranging distribution during their life history. Declines of salmonid populations from the Columbia River basin led the National Marine Fisheries Service (NMFS) to list 13 of 20 evolutionarily significant units (ESUs) of salmonids from the Columbia Basin as threatened or endangered under the United States Endangered Species Act (ESA), including the Snake River Steelhead ESU (*O. mykiss*) studied herein (Waples 1991; Good et al. 2005).

Each year, thousands of juvenile salmonids emigrating from the Columbia River and Snake River basins are captured and externally examined at facilities associated with hydroelectric dams. During their out-migration, juvenile salmonids are commonly subjected to numerous stressors that can cause damage to the body and fins in a variety of ways. Although Snake River steelhead have been the subject of extensive research, monitoring, and evaluation since the development of the Snake River hydrosystem in the late 1960's (Schreck et al. 2006), little is known regarding the relationship between the characteristics of individual fish and their general health status or subsequent survival.

The objective of the present study was to investigate whether external condition of out-migrating smolts, as measured by a quick, non-destructive examination procedure, was associated with the general health status and fitness of juvenile steelhead from the Snake River basin. Relationships between external condition and fitness of steelhead were inferred by assessing relative differences in pathogen prevalence and subsequent survival during out-migration for juvenile steelhead assigned to several categories of health based on the presence or absence of external body injuries, de-scaling, externally-visible disease symptoms, fin damage, and ectoparasite infestations.

METHODS

Fish capture, PIT-tagging, and examination

We used juvenile run-of-the-river steelhead migrating from the Snake River basin that were captured at the juvenile collection facility of Lower Monumental Dam (LMN, Rkm 589) for this study (Figure 2.1). Steelhead were sampled at least 5 days per week throughout the juvenile steelhead out-migration, beginning in early April and ending in

early July, in 2007 and 2008. In 2007, however, juvenile steelhead were only collected every third day throughout most of April.

Prior to sampling, daily captures of fish at LMN were held in a 7,500 liter holding tank with flow-through river water for up to 24 hours. Daily samples of captured juvenile steelhead were separated into small batches (10-50 fish) via a slide gate, anesthetized with MS-222, and tagged with a passive integrated transponder (PIT) tag via a modified hypodermic syringe with a 12-gauge needle (Prentice et al. 1990a; Prentice et al. 1990c; Nielson 1992). To reduce disease transmission, needles were soaked for a minimum of 10 min in 70% ethyl alcohol prior to PIT tag loading. Previous studies found no significant effects of PIT-tagging on survival of juvenile salmonids (Prentice et al. 1990c).

After a steelhead was PIT-tagged, it was placed in a sample-tray, measured (fork length, nearest mm), weighed (nearest gram), assigned as originating from a natural or hatchery rearing environment (presence of a clipped adipose fin or severe erosion of pectoral, pelvic, caudal, or dorsal fins), and examined for various external symptoms. Particular external symptoms investigated in this study included body injuries (hemorrhaging or scarring of the head, eye, operculum, or body), de-scaling (> 20% of body scales absent on at least one side), external symptoms of disease (bacterial, fungal, or viral infections), fin erosion (> 50% erosion or damage to at least one fin), and infestations of ectoparasites. To reduce handling time, digital photographs (Canon EOS Rebel Xti; 50mm lens) were taken of both sides of the steelhead to allow for detailed classification of external symptoms by type and severity after a steelhead was released. Digital photography, labeled with the same unique PIT tag code as the steelhead, was

downloaded into a computer and manually analyzed in a database specifically designed for this study.

Using a modified version of the procedure developed by Evans et al. (2004), steelhead also received an integrated condition rank (good, fair, or poor) based on the overall external condition of the fish (Table 2.1). The total time required to handle, PIT-tag, photograph, and examine a steelhead was, with few exceptions, $\leq$ 30 sec.

Survival analysis

Following the examination process, up to 300 PIT-tagged steelhead were placed in a 1,100 liter holding tank with flow-through river water for 4 to 18 hours, and then released as a group directly into the bypass river-return line leading to the dam's tailrace. Release times alternated between 18:00 - 23:00 PDT the same day as processing and 07:00 - 11:00 PDT the day following processing to reduce possible bias in survival associated with the time of day steelhead were released. All mortalities and ejected PIT tags were removed from the temporary holding tank prior to release and excluded from further analysis.

PIT-tagged steelhead released into the tailrace of Lower Monumental Dam can be detected when passing downstream juvenile bypass systems at Ice Harbor Dam (ICH), McNary Dam (MCN), John Day Dam (JDA), Bonneville Dam (BON), and, finally, by a net-mounted detector deployed by pair-trawlers in the Columbia River estuary (EST; Figure 2.1; Prentice et al. 1990b). Detection data from these locations were retrieved from the PIT Tag Information System (PTAGIS) maintained by the Pacific States Marine Fisheries Commission (PSMFC, Gladstone, Oregon). A detection history was constructed

to record where each unique PIT tag code was or was not detected. Relative survival probabilities for cohorts of steelhead, using both grouping and individual characteristics, were estimated using a Cormack-Jolly-Seber (CJS) capture-recapture model (Cormack 1964; Jolly 1965; Seber 1965) implemented in Program MARK (White and Burnham 1999).

Previous studies have suggested both environmental factors and individual characteristics can influence juvenile steelhead survival and detection probability at dams in the Columbia River and Snake River basins (Skalski 1998; Muir et al. 2001; Zabel et al. 2005; Plumb et al. 2006). To account for these possible sources of variation, we investigated factors other than external condition, including migration year, downstream detection location, rearing type, fork length, and run stage, prior to addressing our hypotheses regarding steelhead external condition. Run stage was separated into three time periods based on when the first 10% (early), middle 80% (peak), and last 10% (late) of all in-river juvenile steelhead passed LMN each year. These data were downloaded from the Data Access in Real Time (DART 1995) website maintained by the Columbia Basin Research group at the University of Washington, School of Aquatic and Fishery Sciences.

We used a multi-step approach to develop models investigating the association between steelhead external condition and apparent survival (φ). First, a set of *a priori* biological hypotheses regarding the influence of external condition on steelhead survival was developed. Next, we separated our analyses to investigate survival at two different migration distances: short-distance survival (LMN to MCN, ca. 119 Rkm) and long-distance survival (LMN to BON, the lowest dam on the Columbia River, ca. 354 Rkm).

Short-distance survival analysis incorporated all steelhead released from LMN, and detection histories from MCN and a pooled third occasion, which included all detection locations below MCN (JDA, BON, and EST) (Zabel et al. 2005). Long-distance survival analysis included all steelhead released from LMN and detection histories from BON and EST, which represented apparent survival through the remaining hydrosystem after steelhead migrated past LMN.

Next, we evaluated apparent survival and detection probability (p) models that included variables other than those pertaining to external symptoms of fish condition to develop a best approximating model for both short-distance and long-distance survival analyses (Burnham and Anderson 2002; hereafter referred to as the base model). Candidate base models for short-distance and long-distance survival could include variables for migration year (YR), run stage (RUN), fork length (LEN), and whether the steelhead was hatchery-reared or wild-origin (ORIGIN), all of which have been shown to influence juvenile salmonid survival in the Columbia River basin (Muir et al. 2001; Plumb et al. 2006; Zabel et al. 2005). A variable for detection location (LOC) was also included in all models to best estimate site-specific survival and detection probability at MCN and BON. Top base models for both short-distance and long-distance survival were then used as null models to investigate relationships between external symptoms and steelhead survival. Once top base models were selected, external symptom variables were individually added to the top short-distance and long-distance base models and ranked using Akaike's information criterion adjusted for small sample sizes (AIC$_c$) (Burnham and Anderson 2002).

Our overall modeling approach using Program MARK was to (1) develop *a priori* hypotheses regarding the effects of steelhead external condition, (2) evaluate goodness-of-fit and estimate an over-dispersion parameter (ĉ) for our global base model {(φ LOC*RUN*YR) p(LOC*RUN*YR)} using the boot-strap procedure in Program MARK and detection histories from MCN, JDA, BON, and EST, (3) correct the covariance matrices and AIC_c values for over-dispersion (ĉ = 1.48, 95% CI 1.45 to 1.51, 500 simulations) across all models, (4) determine the best detection probability (p) model using base model covariates and the global base model for survival, (5) determine the best base survival model using base model covariates and the top model structure for p, (6) individually add external condition variables to the top base model for apparent survival while holding the best detection probability model constant, and (7) evaluate the association between external condition and apparent survival by AIC_c model selection and odds ratios.

Due to the large number of variables investigated, the only interaction included in our *a priori* model set was year*run stage. Variation in river conditions and dam operations between years and stages of the run produced strong evidence in support of investigating this interaction in both detection probability and apparent survival models. Overall, this model selection structure allowed us to identify associations between steelhead external condition and apparent survival over two migration distances, after accounting for other expected sources of variation in steelhead detection and survival probabilities.

Pathology analysis

To investigate possible associations between steelhead external condition and pathogen prevalence, we euthanized (via a strike to the back of the head) a subset of anesthetized juvenile steelhead captured at LMN during the 2008 steelhead out-migration. Euthanized steelhead were then analyzed for the presence of numerous salmonid pathogens known to occur in the Columbia River basin (Arkoosh et al. 2004). We used histological methods to identify presence of mycotic (fungal) infections, *Saguinicola* spp. (digenean trematode), and gill amoebae. These tests were grouped into one category, hereafter referred to as infectious pathogen, and any steelhead that tested positive for at least one of these pathogens was classified as having an infectious pathogen. We also tested for the presence of two additional pathogens known to occur in the Columbia River basin, *Renibacterium salmoninarum* and Infectious Hematopoietic Necrosis Virus (IHNV), through polymerase chain reaction (PCR). *R. salmoninarum* is the causative agent of Bacterial Kidney Disease (BKD), a chronic, systemic infection of the kidney that is a virulent disease affecting populations of hatchery and wild salmonids in the Pacific Northwest (Fryer and Lannan 1993). IHNV affects wild-origin and hatchery-reared salmonids, and is a prevalent viral pathogen affecting salmonid populations in North America (LaPatra 1998).

The number of steelhead sampled for pathology analysis in a given week was designed to mimic the run timing and occurrence of particular external symptoms in steelhead passing LMN. However, the prevalence of particular external symptoms in steelhead collected for this analysis was different from the general in-river population

because we intentionally selected steelhead with various external symptoms to include in this analysis (Table 2.2 and 2.5).

Handling and external examination of steelhead destined for pathology analysis was identical to that of released steelhead, except that steelhead collected for pathology analysis were not PIT-tagged; instead, they were euthanized following external examination. After euthanasia, steelhead were immediately dissected, with sections of their gills and internal viscera (kidney, liver, spleen, heart, and gastrointestinal tract) placed in a tissue cassette. Tissue cassettes were uniquely labeled for each steelhead and then immersed in 10% neutral-buffered formalin with a final minimum volume of 1 part tissue to 10 parts formalin (Bancroft and Stevens 1994; Hopwood 1990; Presnell and Schreibman 1997). Sections of the integument, including fins, were collected and placed in the tissue cassette if there was any suggestion of injury or infection. Tissues were then fixed for a minimum of 72 h prior to further dissection and submission for routine histological processing, including paraffin embedding, sectioning at 5 μm, and staining with hematoxylin and eosin reagents (Bancroft and Stevens 1994; Presnell and Schreibman 1997). Electron-microscopic examination of tissues was used if further examination was warranted.

To investigate BKD and IHNV presence, a small (ca. 40 mg) piece of anterior head kidney was aseptically collected from each euthanized steelhead. Kidney samples were placed in 96-well plates containing RNAlater preservative (Qiagen, Valencia, CA), immediately placed on ice, and stored at -20°C within 3 hours. Samples remained stored at -20°C until nucleic acid extraction.

We evaluated differences in the prevalence of (1) infectious pathogens (mycotic infections, *Saguinicola* spp., and gill amoebae), (2) BKD, and (3) IHNV in cohorts of steelhead separated by the presence or absence of particular external symptoms using Pearson's χ^2 tests with Yates' continuity correction. Analyses were conducted using R statistical software (R 2008), with statistical significance set at $\alpha = 0.05$ for all tests.

Scope of inference

The scope of this study was limited to juvenile Snake River steelhead captured and released at LMN in 2007 and 2008. This study can provide support for the hypothesis that particular external symptoms are associated with variation in pathogen prevalence and survival in this population. Although the term survival is used throughout the paper, a more appropriate term may be "migration success," because steelhead unsuccessful in completing their migration, either due to death or residualizing in freshwater, were considered mortalities in this study. Predicting relationships between external condition and general health status of other fish species and populations will likely require further research and a more comprehensive analysis.

RESULTS

Fish condition

A total of 14,177 steelhead were PIT-tagged and released at Lower Monumental Dam (LMN) on the lower Snake River as part of this study (12,108 hatchery-reared and 2,069 wild origin). Although more steelhead were released in 2008 (n = 7,932) than in 2007 (n = 6,245), the incidence of de-scaling (ca. 6%), fin damage (ca. 82%), and

ectoparasites (ca. 2%) remained relatively constant across years (Table 2.2). In 2008, however, the prevalence of body injuries was 7% higher (χ^2 = 141.8, df = 1, P < 0.001), and the frequency of steelhead with external symptoms of disease was 3% lower (χ^2 = 72.5, df = 1, P < 0.001) than in 2007. Within season comparisons indicated that as the season progressed, there was an increased prevalence of body injuries (χ^2 = 207.6, df = 2, P < 0.001) and de-scaling (χ^2 = 72.4, df = 2, P < 0.001), while the proportion of steelhead with external disease symptoms decreased (χ^2 = 208.9, df = 2, P < 0.001, Table 2.2). Overall, fin damage was the most prevalent external symptom of those measured (82%), followed by body injuries (16%), de-scaling (6%), external disease symptoms (5%), and ectoparasites (2%; Table 2.2).

There was no difference between average fork length of steelhead captured in 2007 ($\bar{x}$ = 218 mm) and 2008 ($\bar{x}$ = 217 mm, P = 0.20). Length of hatchery-reared steelhead ($\bar{x}$ = 223 mm) was, however, 37 mm greater on average (95% CI: 36 to 39 mm, P < 0.001) than wild-origin steelhead ($\bar{x}$ = 186). Even though hatchery-reared steelhead were on average longer than wild-origin steelhead, there was large overlap in the range of fork lengths between these two rearing types (hatchery range = 132 to 375 mm, wild range = 134 to 354 mm).

Downstream detections of the 14,177 PIT-tagged steelhead released from LMN included 1,540 steelhead detected at MCN (11%), 1,680 steelhead detected at JDA (12%), 1,106 steelhead detected at BON (8%), and 163 steelhead detected at EST (1%).

Survival

The best base model for detection probability over short-distance migration included variables for detection location, fork length, and a year*run stage interaction {φ (LOC + LEN + YR*RUN + ORIGIN) p (LOC + LEN + YR*RUN)} (Appendix A). This base detection probability model indicated that detection probabilities were (1) specific to each run stage each year, and (2) decreased as steelhead fork length increased (β_{LEN} = -0.010, SE = 0.001, 95% CI: -0.013 to -0.007).

The top base model evaluating short-distance survival (i.e., models explaining variation in survival probability after controlling for variation in detection probability) included variables for detection location, fork length, rearing type, and a year*run stage interaction. This base model had strong support as the best base survival model as it was 5.2 AIC_c units better than the next best model (Appendix B). Results from the top base survival model indicated survival from LMN to MCN was (1) specific to each run stage each year, (2) increased as fork length increased (β_{LEN} = 0.011, SE = 0.003, 95% CI: 0.005 to 0.016), and (3) was higher for wild-origin steelhead than hatchery-reared steelhead (β_{ORIGIN} = 0.223, SE = 0.089, 95% CI: 0.048 to 0.397), after accounting for other variables.

The best detection probability base model for long-distance migration (LMN to BON) included variables for detection location, fork length, and a year*run stage interaction {φ (LOC + LEN) p (LOC + LEN + YR*RUN)} (Appendix A). Results from the best long-distance detection probability model indicated that detection probabilities were (1) specific to each run stage each year, and (2) increased with increasing fork length (β_{LEN} = 0.014, SE = 0.003, 95% CI: 0.009 to 0.020).

Model selection results suggested four competitive base models predicting long-distance survival, with the top survival base model including variables for detection location and fork length (Appendix B). We selected the top long-distance survival base model as the best long-distance survival base model from among the four competing models because it (1) had the lowest AIC_c value, (2) was 0.9 AIC_c units lower than the next competing model, (3) included only significant parameters for φ, and (4) competing models included additional non-significant variables. Results from the top long-distance survival base model indicated that survival from LMN to BON was inversely related to steelhead fork length (β_{LEN} = -0.007, SE = 0.003, 95% CI: -0.012 to -0.002). Selection of short-distance and long-distance survival base models that accounted for steelhead size, rearing type, and run stage support findings from previous studies that found juvenile salmonid survival is related to both individual fish characteristics and river conditions (Skalski 1998; Muir et al. 2001; Zabel et al. 2005; Plumb et al. 2006).

Results regarding our original hypotheses linking external symptoms to survival probabilities suggested that external symptoms of disease, body injuries, de-scaling, and integrated condition ranks were associated with reduced steelhead survival probabilities, after accounting for the other sources of variation in our base survival models. For short-distance survival, the model including external symptoms of disease had by far the most support of any model (AIC_c w = 1.0; Table 2.3a). Additionally, short-distance survival models that included body injuries and integrated condition ranks had greater support than the base short-distance survival model (43.7 and 2.7 AIC_c units better than the base survival model, respectively; Table 2.3a).

Similar to the short-distance survival models, the long-distance survival model incorporating external symptoms of disease had the most support of any long-distance survival model (AIC$_c$ w = 1.0; Table 2.3b). Long-distance survival models that included integrated condition ranks, de-scaling, or body injuries also had greater support than the base long-distance survival model (14.2, 1.9, and 0.2 AIC$_c$ units better than the base model, respectively; Table 2.3b). Overall, results suggested that including measurements of steelhead external symptoms, especially the presence of external symptoms of disease, body injuries, de-scaling, or an integrated condition rank, improved the ability of models to predict steelhead survival.

In addition to increased ability to explain variation in survival based on these external condition factors, parameter estimates of several types of external symptoms were related to significant reductions in steelhead survival probabilities. After accounting for other variables in the model, steelhead without external symptoms of disease were 4.3 times (95% CI: 3.1 to 6.0, $P < 0.001$) and 6.5 times (95% CI: 3.2 to 13.5, $P < 0.001$) more likely to survive short-distance and long-distance migrations, respectively. Steelhead without body injuries were 1.2 times more likely to survive short-distance migration (95% CI: 1.01 to 1.4, $P = 0.03$), but results were only suggestive for long-distance survival (1.2 times more likely, 95% CI: 0.9 to 1.6, $P = 0.14$), after accounting for the other variables in base models. De-scaling was not significantly related to short-distance survival ($P = 0.37$); however, steelhead without de-scaling were 1.5 times more likely to survive long-distance migration (95% CI: 1.0 to 2.4, $P = 0.05$), after accounting for the other variables in the base model (Table 2.4). Fin damage and ectoparasites, as measured by this study, had less support (higher AIC$_c$ values) than the base survival

model and parameter estimates for these variables were not significantly associated with decreased survival probabilities for either short-distance or long-distance migration (Table 2.3 and 2.4).

Estimates for integrated condition ranks suggested that steelhead classified as in poor condition were less likely than those classified as in good condition to survive either short-distance or long-distance migration. Steelhead in good condition were 1.8 times (95% CI: 1.5 to 2.1, $P < 0.001$) and 1.9 times (95% CI: 1.4 to 2.5, $P < 0.001$) more likely to survive short-distance and long-distance migration, respectively, than steelhead in poor condition, after accounting for other variables in the model. A difference in survival probabilities between steelhead in fair condition and those in good condition was not detected in short-distance survival models ($P = 0.51$), although there was a suggestive trend in long-distance survival models (1.2 times more likely, 95% CI: 1.0 to 1.5, $P = 0.09$, Table 2.4), after accounting for other variables in the respective best base models.

Pathology

We lethally collected 222 steelhead smolts between 24 April and 22 June, 2008. The majority (54%) of steelhead were collected during the peak of steelhead out-migration due to low availability of steelhead during early and late segments of the out-migration (Table 2.5). Of the 222 steelhead collected, 92 (41%) tested positive for an infectious pathogen (mycotic infections, *Saguinicola* spp., or gill amoebae), based on histological examination. Prevalence of infectious pathogens was highest in steelhead with external symptoms of disease (93%), followed by those with de-scaling (61%), body

injuries (54%), fin damage (46%), and ectoparasite infestations (18%). Of the five types of external symptoms investigated, four were significantly associated with increased prevalence of infectious pathogens (Figure 2.3). Steelhead with external symptoms of disease had the greatest relative increase in prevalence of infectious pathogens, as steelhead with external symptoms of disease had an infectious pathogen prevalence rate 70% higher than steelhead without external disease symptoms (95% CI: 60 to 80% higher, $P < 0.001$, df = 1). Other external symptoms associated with increased prevalence of infectious pathogens included body injuries (25% higher, 95% CI: 11 to 38% higher, $P < 0.001$, df = 1), de-scaling (25% higher, 95% CI: 9 to 42% higher, $P = 0.003$, df = 1), and fin damage (25% higher, 95% CI: 14 to 42% higher, $P < 0.001$, df = 1). The only type of external symptom not significantly associated with increased prevalence of infectious pathogens was ectoparasite infestations ($P = 0.20$, df = 1, Figure 2.3).

Using our *a priori* integrated condition ranks, poor condition steelhead had the highest prevalence of infectious pathogens (67%), followed by fair (26%) and good (16%) condition steelhead. Steelhead in poor condition had a significantly higher prevalence of infectious pathogens compared to steelhead in fair condition (51% higher, $P < 0.001$, df = 1) and steelhead in good condition (61% higher, $P < 0.001$, df = 1). The difference in prevalence of infectious pathogens between fair and good condition steelhead, however, was not significant ($P = 0.29$, df = 1).

Of the 222 steelhead tested for BKD using PCR, 8% (18 of 222 steelhead) tested positive. Prevalence of BKD ranged from 4% in steelhead with de-scaling to 9% in steelhead with ectoparasites. Differences in the prevalence of BKD were not significantly associated with any external symptoms or the integrated condition rank. IHNV was

detected in 5% of the 222 steelhead tested via PCR (10 of 222 steelhead) and, similar to

results for BKD, IHNV prevalence was not significantly associated with any external

symptoms or the integrated condition rank. Pathogen intensity (a semi-quantitative score)

of BKD or IHNV was not investigated because prevalence of these diseases in sampled

steelhead was low and not associated with any type of external symptom.

DISCUSSION

Overall, three of the five external symptoms evaluated by this study (i.e., external

symptoms of disease, body injuries, and de-scaling) were significantly associated with

higher pathogen prevalence and increased subsequent mortality in steelhead. These

results support the hypothesis that external symptoms, measured non-destructively in

individual fish, are associated with relative differences in general health status of fish.

While fin damage was associated with increased pathogen prevalence, it was not

associated with a significant reduction in survival. Ectoparasite infestations, as measured

in this study, were not related to either increased pathogen prevalence or decreased

survival. Therefore, associations between fin damage or ectoparasite infestations and

lower fitness were not demonstrated in this study.

Our results contribute to a growing body of evidence that suggests individual fish

characteristics, including external condition of a fish, are important variables when

evaluating survival in fish populations. Links between external symptoms and salmonid

survival in the Columbia River basin have previously been demonstrated in steelhead

kelts (Keefer et al. 2008). Additionally, Zabel et al. (2005) demonstrated the importance

of incorporating measurements of individual characteristics, such as length, in models predicting juvenile salmonid survival in the Columbia River basin.

Kostecki et al. (1987) also found reductions in survival probabilities associated with de-scaling in Atlantic salmon (*Salmo salar*) that had passed through a turbine at a hydroelectric dam. Necropsies of these Atlantic salmon, however, suggested scale loss was not the cause of death, as de-scaling was associated with internal injuries. The suggestion that de-scaling could be an external symptom of internal injuries aids in explaining why our results differed from those of other studies investigating survival and de-scaling. For instance, Bouck and Smith (1979) found no difference in freshwater survival of coho salmon (*O. kisutch*) after systematic scale removal in a laboratory setting. Discrepancies between our results and those of studies investigating the relationship between scale loss and survival may be because scale loss alone does not significantly decrease survival probabilities. Instead, external anomalies, such as de-scaling, body injuries, or external disease symptoms, may be an externally observable manifestation of internal injuries, trauma, or disease that can adversely affect fish health and survival at significant rates. Internal injuries associated with scale loss were probably not present in studies, such as Bouck and Smith (1979), which systematically removed fish scales, but were likely associated with the de-scaling observed in the present study.

Comparing our results with those of Bouck and Smith (1979) and Kostecki et al. (1987) exemplifies the strengths and weaknesses of using various external symptoms as a metric for general fish condition. Evaluating fish health status based solely on external criteria and measurements is advantageous with respect to ease, speed, uniform techniques, low cost, and an ability to relate fish condition to subsequent behavior,

movements, and survival post-release. The simplicity of this technique can be limiting, however, as correlations between external symptoms and pathogen prevalence or survival have little use as diagnostic tools. As described above, de-scaling may be related to reduced survival probability, but de-scaling *per se* may not be the cause of reduced survival. Instead, decreased survival probabilities associated with de-scaling and other external anomalies may be due to disruption of physiological processes (i.e., circulation, respiration, or osmoregulation) caused by trauma (Bouck and Smith 1979; Schreck 1990).

Likewise, this study identified relationships between external symptoms and prevalence of infectious pathogens, but our methods did not allow for conclusions regarding cause and effect relationships. In other words, we could not determine whether stress associated with external symptoms reduced immune response, thus increasing susceptibility to disease in steelhead. Alternatively, steelhead may have contracted an infectious pathogen that subsequently compromised the fish's innate ability to protect itself from additional external stressors. In addition, a third factor such as contaminant exposure, which was not investigated in this study, could reduce overall performance of steelhead, rendering them more susceptible to disease, external damage, and reduced survival (Arkoosh and Collier 2002). Because a fish's response to stress is limited by both internal and external constraints (Schreck 1981), it is likely that a complex set of interacting stressors was involved in degrading the general health of migrating juvenile steelhead.

Detecting stress in fish can be challenging, and relating stress to health status of fish is even more complex, as complications from a stressor may not appear for some

time after the stress-inducing event (Budy et al. 2002). External examination lacks the power to evaluate internal anomalies and symptoms of stress detectable through histological, physiological, or biochemical tests (Kostecki et al. 1987). In the end, use of external symptoms as a metric for evaluating general health status of fish is not meant to be diagnostic, but instead provide a quick, non-lethal technique to evaluate a fish's relative health status. Comparing the prevalence of particular external symptoms at various temporal or spatial scales can be used to better understand and predict differences in survival within and among fish populations. Overall, results from our study provide support for the hypothesis that non-lethal measurements of fish external condition are associated with relative differences in pathogen prevalence and survival of out-migrating juvenile steelhead.

CONSERVATION AND MANAGEMENT IMPLICATIONS

Fish populations are often behaviorally and physically heterogeneous, and this heterogeneity can lead to differential survival within a population. This study demonstrated that including various external measurements of steelhead condition, as measured by a quick, non-lethal, external examination, provided additional insight into the health and survival of migrating juvenile steelhead under various environmental conditions. Non-lethal examination techniques can be particularly important when working with species and populations that are listed as threatened or endangered. In this study, about 22% (3,136 of 14,177) of juvenile steelhead sampled at LMN in 2007 and 2008 possessed at least one of the three external symptoms associated with decreased survival (external symptoms of disease, body injuries, and de-scaling). However,

prevalence of external symptoms recorded at LMN may not fully represent the prevalence of these symptoms at other locations during steelhead out-migration. For instance, the prevalence of external symptoms of disease in juvenile steelhead sampled at LMN (~ 5%) only accounts for steelhead that survived to LMN and does not address the disproportionate percentage of diseased steelhead that likely died before reaching LMN. Increased mortality of diseased steelhead prior to arrival at LMN would imply that infectious diseases may be more prevalent and play a more significant role in juvenile steelhead mortality than results from this study suggest. Coordination of efforts to record the prevalence of various external symptoms across sampling locations within the Columbia River basin is needed to fully address questions regarding the influence of external symptoms on salmonid smolt survival.

The ability to non-lethally monitor relative changes in fish condition can improve our understanding of how various hydrosystem practices are associated with fish health and survival. For instance, we found that the prevalence of specific external symptoms (i.e., body injuries) varied between years and among stages of the run (Table 2.2); however, the causes of these differences were unknown. Ultimately, the probability of an individual steelhead surviving the juvenile life stage is likely determined by a complex set of interacting factors, including environmental conditions and individual fish characteristics. Understanding and addressing the causes of natural and anthropogenic stressors can increase the potential for management agencies to operate the hydrosystem in a manner that minimizes degradation of fish condition during juvenile salmonid out-migration. Improvements to fish passage that allow juvenile salmonids to successfully navigate the hydrosystem with minimal additional stress and allostatic load (McEwen and

Stellar 1993) would enhance salmonid survival through the hydrosystem and possibly

reduce delayed mortality after exiting the hydrosystem (Schreck et al. 2006). Increased

understanding of relationships among fish external condition, general health status, and

stress-induced mortality experienced during juvenile salmonid out-migration can aid

efforts aimed at reducing juvenile mortality and recovering ESA-listed stocks of Pacific

salmonids throughout the Columbia River basin.

LITERATURE CITED

Adams, S. M., editor. 1990. Biological indicators of stress in fish. American Fisheries Society, Symposium 8. Bethesda, Maryland.

Adams, S. M., A. M. Brown, and R. W. Goede. 1993. A quantitative health assessment index for rapid evaluation of fish condition in the field. Transactions of the American Fisheries Society 122:63-73.

Arkoosh, M. R., T. K. Collier. 2002. Ecological risk assessment paradigm for salmon: analyzing immune function to evaluate risk. Human & Ecological Risk Assessment 8:265.

Arkoosh, M. R., E. Clemons, A. N. Kagley, C. Stafford, A. C. Glass, K. Jacobson, P. Reno, M. S. Myers, E. Casillas, F. Loge, L. L. Johnson, and T. K. Collier. 2004. Survey of pathogens in juvenile salmon (*Oncorhynchus* spp.) migrating through Pacific Northwest estuaries. Journal of Aquatic Animal Health 16:186-196.

Arkoosh, M. R., A. N. Kagley, B. F. Anulacion, D. A. Boylen, B. P. Sandford, F. J. Loge, L. L. Johnson, and T. K. Collier. 2006. Disease susceptibility of hatchery Snake River spring-summer Chinook salmon with different juvenile migration histories in the Columbia River. Journal of Aquatic Animal Health 18:223-231.

Bancroft, J. D., and A. Stevens. 1994. Manual of histological techniques and their diagnostic applications, 2nd edition. Churchill Livingstone, Edinburgh, UK.

Barton, B. A., J. D. Morgan, and M. M. Vijaya. 2002. Physiological and condition-related indicators of environmental stress in fish. Pp. 111-148 *in* S. M. Adams, editor. Biological indicators of aquatic ecosystem stress. American Fisheries Society, Bethesda, Maryland.

Bouck, G. R., and S. D. Smith. 1979. Mortality of experimentally descaled smolts of Coho salmon (*Oncorhynchus kisutch*) in fresh and salt water. Transactions of the American Fisheries Society 108:67-69.

Budy, P., G. P. Thiede, N. Bouwes, C. E. Petrosky, and H. Schaller. 2002. Evidence linking delayed mortality of Snake River salmon to their earlier hydrosystem experience. North American Journal of Fisheries Management 22:35-51.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and inference: a practical information-theoretic approach, 2nd edition. Springer-Verlag, New York, New York.

Cormack, R. M. 1964. Estimates of survival from the sighting of marked animals. Biometrika 51:429-438.

DART (Columbia River Data Access in Real Time). 1995. Online interactive database of the Columbia Basin Research group. University of Washington School of Aquatic and Fishery Sciences.

Evans, A. F., R. E. Beaty, M. S. Fitzpatrick, and K. Collis. 2004. Identification and enumeration of steelhead kelts at a Snake River hydroelectric dam. Transactions of the American Fisheries Society 133:1089-1099.

Fryer, J. L., and C. N. Lannan. 1993. The history and current status of *Renibacterium salmoninarum*, the causative agent of bacterial kidney disease in Pacific salmon. Fisheries Research 17:15-33.

Goede, R. W., A. B. Bruce, and S. M. Adams. 1990. Organismic indices and an autopsy-based assessment as indicators of health and condition of fish. American Fisheries Society Symposium 8:93-108.

Good, T. P., R. S. Waples, and P. Admas (editors). 2005. Updated status of federally listed ESUs of West Coast salmon and steelhead. NOAA Tech. Memo NMFS-NWFSC-66:598.

Hopwood, D. 1990. Fixation and fixatives. Pp. 21-42 *in* J. D. Bancroft and A. Stevens, editors. Theory and practice of histological techniques. Churchill Livingstone, Edinburgh, UK.

Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika 52:225-247.

Keefer, M. L., R. H. Wertheimer, A. F. Evans, C. T. Boggs, and C. A. Peery. 2008. Iteroparity in Columbia River summer-run steelhead (*Oncorhynchus mykiss*): implications for conservation. Canadian Journal of Fisheries and Aquatic Sciences 65:2592-2605.

Kostecki, T., P. Clifford, S. P. Gloss, and J. C. Carlisle. 1987. Scale loss and survival in smolts of Atlantic salmon (*Salmo salar*) after turbine passage. Canadian Journal of Fisheries and Aquatic Sciences 44:210-214.

LaPatra, S. E. 1998. Factors affecting pathogenicity of infectious hematopoietic necrosis virus (IHNV) for salmonid fish. Journal of Aquatic Animal Health 10:121-131.

Lichatowich, J. 1999. Salmon without rivers: a history of the Pacific salmon crisis. Island Press, Washington D.C.

Maule, A. G., R. A. Tripp, S. L. Kaattari, C. B. Schreck, and S. L. Kaatari. 1989. Stress alters immune function and disease resistance in Chinook salmon (*Oncorhynchus tshawytscha*). Journal of Endocrinology 120:135-142.

McEwen, B. S., and E. Stellar. 1993. Stress and the individual: mechanisms leading to disease. Archives of Internal Medicine 153:2093-2101.

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., P. P. Thomas, M. G. Dena, and H. P. James. 1994. Are all prey created equal? A review and synthesis of differential predation on prey in substandard condition. Journal of Fish Biology 45:81-96.

Muir, W. D., S. G. Smith, J. G. Williams, E. E. Hockersmith, and J. R. Skalski. 2001. Survival estimates for migrant yearling Chinook salmon and steelhead tagged with passive integrated transponders in the lower Snake and lower Columbia rivers. North American Journal of Fisheries Management 21:269-282.

Nielson, L. A. 1992. Methods for marking fish and shellfish, American Fisheries Society. Special Publication 23, Bethesda, Maryland.

Olla, B. L., M. W. Davis, and C. B. Schreck. 1992. Comparison of predator avoidance capabilities with corticosteroid levels induced by stress in juvenile coho salmon. Transactions of the American Fisheries Society 121:544-547.

Peters, G., M. Faisal, T. Lang, and A. Iman. 1988. Stress caused by social interaction and its effect on susceptibility to *Aeromonas hydrophila* infection in rainbow trout (*Salmo gairdneri*). Diseases of Aquatic Organisms 4:83-89.

Pickering, A. D. 1993. Endocrine-induced pathology in stressed salmonid fish. Fisheries Research 17:35-50.

Plumb, J. M., R. W. Perry, N. S. Adams, and D. W. Rondorf. 2006. The effects of river impoundment and hatchery rearing on the migration behavior of juvenile steelhead in the Lower Snake River, Washington. North American Journal of Fisheries Management 26:438-452.

Prentice, E. F., T. A. Flagg, C. S. McCutcheon, D. F. Brastow, and D. C. Cross. 1990a. Equipment, methods and an automated data-entry station for PIT tagging. Pp. 335-340 *in* N. C. Parker, A. E. Giorgi, R. C. Heidinger, D. Jester, Jr., E. D. Prince, and G. A. Winans, editors. Fish-marking techniques. American Fisheries Society, Symposium 7, Bethesda, Maryland.

Prentice, E. F., T. A. Flagg, C. S. McCutcheon, and D. F. Brastow. 1990b. PIT-tag monitoring systems for hydroelectric dams and fish hatcheries. Pp. 323-334 *in* N. C. Parker, A. E. Giorgi, R. C. Heidinger, D. Jester, Jr., E. D. Prince, and G. A. Winans, editors. Fish-marking techniques. American Fisheries Society, Symposium 7, Bethesda, Maryland.

Prentice, E. F., T.A. Flagg, and C.S. McCutcheon. 1990c. Feasibility of using implantable passive integrated transponder (PIT) tags in salmonids. Pp. 317-322 *in* N. C. Parker, A. E. Giorgi, R. C. Heidinger, D. Jester, Jr., E. D. Prince, and G. A. Winans, editors. Fish-marking techniques. American Fisheries Society, Symposium 7, Bethesda, Maryland.

Presnell, J. K., and M. P. Schreibman. 1997. Humason's animal tissue techniques, 5th edition. Johns Hopkins University Press, Baltimore.

R Development Core Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Schreck, C. B. 1981. Stress and compensation in teleostean fishes: response to social and physical factors. Pp. 295-321 *in* A. D. Pickering, editor. Stress and fish. Academic Press, New York.

Schreck, C. B. 1990. Physiological, behavioral and performance indicators of stress. Pp. 29-37 *in* S. M. Adams, editor. Biological indicators of stress in fish. American Fisheries Society, Symposium 8, Bethesda, Maryland.

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.

Seber, G. A. F. 1965. A note on the multiple-recapture census. Biometrika 52:249-259.

Skalski, J. R. 1998. Estimating season-wide survival rates of outmigrating salmon smolt in the Snake River, Washington. Canadian Journal of Fisheries and Aquatic Sciences 55:761-769.

Waples, R. S. 1991. Definition of ''species'' under the Endangered Species Act: application to Pacific salmon. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-194.

Wedemeyer, G. A., D. J. McLeay, and C. P. Goodyear. 1984. Assessing the tolerance of fish and fish populations to environmental stress: the problems and methods of monitoring. Pp. 163-195 *in* V. W. Cairns, P. V. Hodson, and J. O. Nriagu, editors. Contamination effects on fisheries, Wiley, New York.

Wendelaar Bonga, S. E. 1997. The stress response in fish. Physiological Reviews 77:591-625.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:120-138.

Zabel, R. W., T. Wagner, J. L. Congleton, S. G. Smith, and J. G. Williams. 2005. Survival and selection of migrating salmon from capture-recapture models with individual traits. Ecological Applications 15:1427-1439.

Table 2.1. Criteria used for integrated condition ranks of juvenile steelhead captured at Lower Monumental Dam in 2007 and 2008.

Integrated rank	Criteria
Good	No noticeable external injury or symptoms of disease; de-scaling ≤ 10% of body surface
Fair	Minor scars or other closed external damage; de-scaling > 10% but ≤ 50% of body surface
Poor	Any steelhead with externally apparent fungal, parasitic, or bacterial infections, or de-scaling > 50% of body surface, or open external body lesions

Table 2.2. Summary of juvenile steelhead PIT-tagged and released from Lower Monumental Dam (LMN) in 2007 and 2008. Percentages represent prevalence of external symptoms during each stage of out-migration.

Run Stage	n	External Symptom Prevalence[a]				
		Body Injury	De-scaling	Disease	Ecto-parasites	Fin Damage
2007 Early	2,289	10%	3%	11%	1%	80%
2007 Peak	1,361	12%	6%	4%	1%	89%
2007 Late	2,595	14%	6%	3%	3%	85%
2008 Early	2,028	12%	3%	5%	3%	80%
2008 Peak	2,753	16%	6%	4%	2%	82%
2008 Late	3,151	27%	8%	2%	2%	79%
Total	14,177	16%	6%	5%	2%	82%

[a] See Methods for variable descriptions.
[b] Steelhead run stage was assigned based on when the first 10% (early), middle 80% (peak), and last 10% (late) of all in-river juvenile steelhead annually LMN in each year.

Table 2.3. Model selection results for models evaluating relationships between steelhead external symptoms and apparent survival for (a) short-distance (Lower Monumental Dam [LMN] to McNary Dam) and (b) long-distance (LMN to Bonneville Dam) survival analysis.

a. Short-distance survival

Rank	Model[a]	QAICc	K	ΔQAICc	W_i
1	BASE MODEL[b] + DISEASE	15202.33	18	0.00	1.00
2	BASE MODEL[b] + INTEGRATED CONDITION	15266.27	19	63.93	0.00
3	BASE MODEL[b] + BODY INJURIES	15307.27	18	104.94	0.00
4	BASE MODEL[b]	15309.92	17	107.59	0.00
5	BASE MODEL[b] + DE-SCALING	15311.12	18	108.79	0.00
6	BASE MODEL[b] + FIN DAMAGE	15311.81	18	109.48	0.00
7	BASE MODEL[b] + ECTOPARASITES	15311.88	18	109.55	0.00

b. Long-distance survival

Rank	Model[a]	QAICc	K	ΔQAICc	W_i
1	BASE MODEL[c] + DISEASE	6181.38	12	0.00	1.00
2	BASE MODEL[c] + INTEGRATED CONDITION	6203.73	13	22.35	0.00
3	BASE MODEL[c] + DE-SCALED	6216.02	12	34.64	0.00
4	BASE MODEL[c] + BODY INJURY	6217.78	12	36.41	0.00
5	BASE MODEL[c]	6217.96	11	36.58	0.00
6	BASE MODEL[c] + FIN DAMAGE	6219.43	12	38.06	0.00
7	BASE MODEL[c] + ECTOPARASITES	6219.96	12	38.59	0.00

[a] See Methods for variable descriptions.
[b] Short-distance base model = {φ(LOC+YR*RUN+LEN+ORIGIN) p(LOC+YR*RUN+LEN)}
[c] Long-distance base model = {φ(LOC+LEN) p(LOC+YR*RUN+LEN)}

Table 2.4. Estimated reduction in juvenile steelhead survival probabilities associated with presence of external symptoms. Relative decreases in short-distance (Lower Monumental Dam [LMN] to McNary Dam) and long-distance (LMN to Bonneville Dam) survival probabilities were estimated after accounting for other explanatory variables in the respective top base models for each distance. Upper (UCL) and lower (LCL) 95% confidence limits and *P*-values (*P*) of odds ratios are shown.

| | | | | | | Reduction in Survival | | | | |
| | | Short-distance[a] | | | | | Long-distance[a] | | | |
External Symptom[b]	n[c]	Odds ratio	LCL	UCL	*P*	Odds ratio	LCL	UCL	*P*
Body Injury	2,292	1.18	1.01	1.37	**0.03**	1.21	0.94	1.55	0.14
De-scaling	793	1.11	0.88	1.40	0.37	1.54	0.99	2.39	**0.05**
Disease	644	4.32	3.12	5.97	**< 0.001**	6.53	3.15	13.53	**< 0.001**
Ectoparasites	300	1.04	0.72	1.50	0.84	0.99	0.54	1.79	0.96
Fin Damage	11,632	0.97	0.83	1.14	0.73	1.10	0.86	1.40	0.77
Integrated Condition Rank[d]									
Fair	4,087	1.04	0.92	1.18	0.51	1.19	0.97	1.47	0.09
Poor	1,863	1.77	1.47	2.14	**< 0.001**	1.87	1.37	2.54	**< 0.001**

[a] See Methods for migration distances and descriptions.
[b] See Methods for external symptom descriptions.
[c] Number of PIT-tagged steelhead released from LMN in 2007 and 2008 exhibiting a particular external symptom.
[d] Odds ratios for integrated conditions are compared to steelhead ranked as in good condition.

Table 2.5. Summary of steelhead lethally collected at Lower Monumental Dam in 2008. Percentages represent prevalence of external symptoms in steelhead sampled during that time period.

Run Stage[b]	n	External Symptom Prevalence[a]				
		Body Injury	De-scaling	Disease	Ecto-parasites	Fin Damage
Early	29	34%	7%	24%	3%	79%
Peak	120	52%	22%	36%	3%	85%
Late	73	48%	29%	11%	10%	74%
Total	222	48%	22%	26%	5%	81%

[a] See Methods for variable descriptions.
[b] Steelhead run stage was assigned based on when the first 10% (early), middle 80% (peak), and last 10% (late) in-river juvenile steelhead migrated past LMN in 2008.
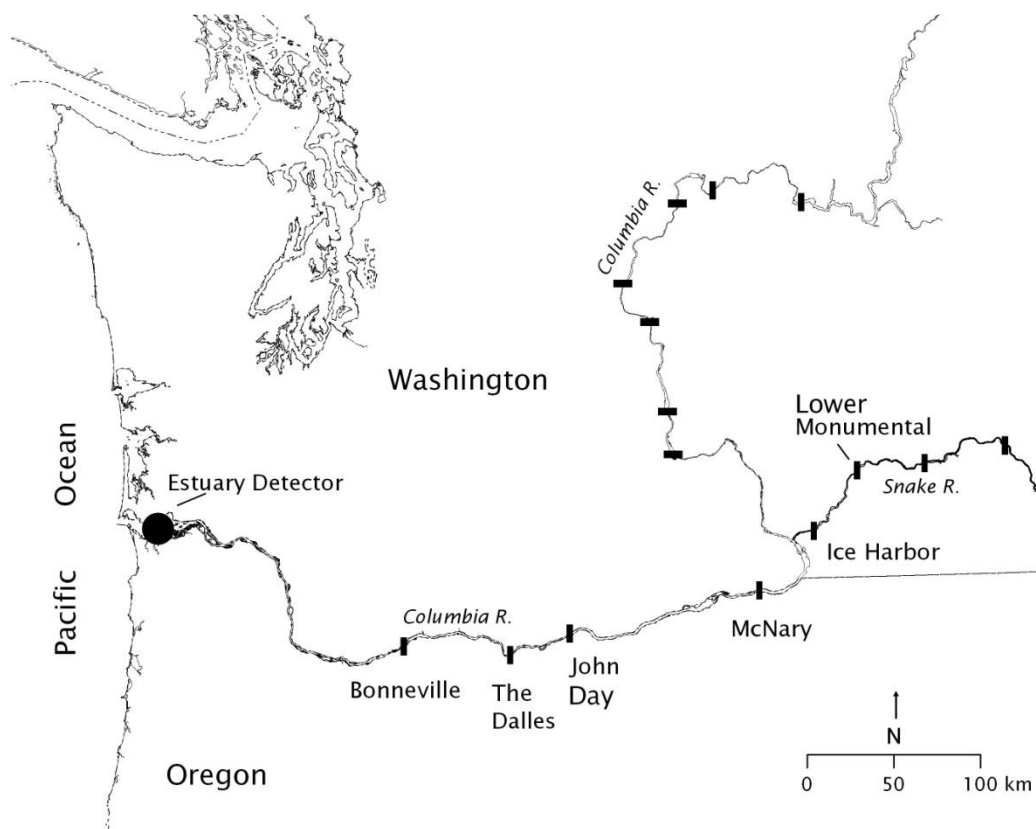
Figure 2.1. Map of the mainstem Snake and Columbia rivers with major hydroelectric dams denoted by bars. Juvenile steelhead PIT-tagged and released from Lower Monumental Dam were potentially detected as they passed Ice Harbor, McNary, John Day, and Bonneville dams, and finally by a net-mounted detector deployed from a pair-trawl in the estuary (dot).

Captured, PIT-tagged, evaluated, and released steelhead at Lower Monumental Dam

⬇

Retrieved steelhead detection histories from McNary, John Day, and Bonneville dams, and estuary trawl detector

⬇

Adjusted models for goodness-of-fit and over-dispersion (ĉ)

↙ ↘

Short-distance Survival: used detection histories from McNary Dam and combined John Day, Bonneville, and Estuary detections into joint third occasion	Long-distance Survival: used detection histories from Bonneville Dam and Estuary
⬇	⬇
Determined best detection probability model using global base survival model	Determined best detection probability model using global base survival model
⬇	⬇
Determined best base (no external symptom variables) survival model while using top detection probability model	Determined best base (no external symptom variables) survival model while using top detection probability model
⬇	⬇
Added external symptom variables to top base survival model	Added external symptom variables to top base survival model
⬇	⬇
Evaluated importance of external symptoms using AIC$_c$ and odds ratios	Evaluated importance of external symptoms using AIC$_c$ and odds ratios

Figure 2.2. Flow chart of methods used to evaluate associations between juvenile steelhead external symptoms and apparent survival from Lower Monumental Dam (LMN) to McNary Dam (short-distance) and LMN to Bonneville Dam (long-distance).
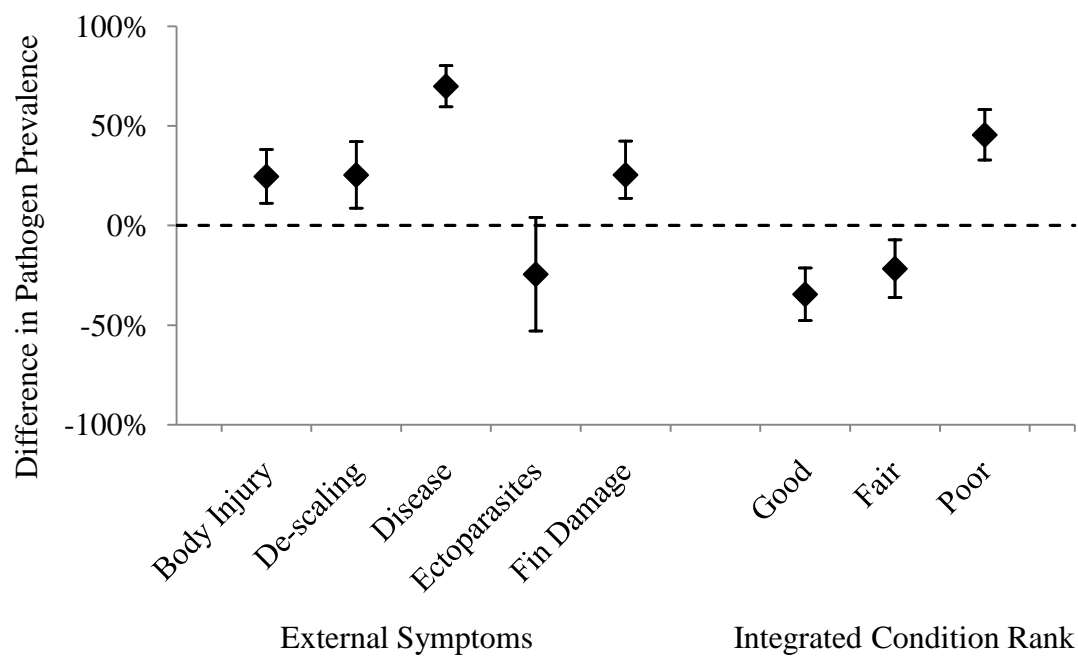
Figure 2.3. Difference in infectious pathogen prevalence of juvenile steelhead associated with presence of several types of external symptoms; data are from juvenile steelhead collected at Lower Monumental Dam in 2008. Error bars represent 95% confidence intervals of the difference. Dashed horizontal line represents zero difference between groups.

CHAPTER 3

FISH CHARACTERISTICS AND ENVIRONMENTAL CONDITIONS
INFLUENCING SUSCEPTIBILTY OF JUVENILE STEELHEAD
TO AVIAN PREDATION IN THE COLUMBIA RIVER

Nathan J. Hostetter[1], Allen F. Evans[2], Daniel D. Roby[1], Ken Collis[2], and Mike Hawbecker[2]

[1]U.S. Geological Survey-Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, 104 Nash Hall, Oregon State University, Corvallis, OR 97331 USA

[2]Real Time Research, Inc., 52 S.W. Roosevelt Ave., Bend, OR 97702 USA

ABSTRACT

Identification of individual fish characteristics and river conditions associated with higher susceptibility of juvenile salmonids (*Oncorhynchus* spp*.*) to predation can aid in recovery efforts for threatened salmonid populations throughout the Columbia River basin. To investigate these associations, run-of-the-river juvenile steelhead (*O. mykiss*) were captured, PIT-tagged, externally examined, and released at Lower Monumental and Ice Harbor dams on the lower Snake River during steelhead out-migration in 2007 and 2008. Overall, PIT tags from 3.0% and 1.9% of released steelhead (n = 16,258) were recovered on a Caspian tern (*Hydroprogne caspia*) colony and a double-crested cormorant (*Phalacrocorax auritus*) colony, respectively, located < 79 Rkm downstream of release locations. The size and condition of steelhead, as well as river conditions at the time of release, were all associated with steelhead susceptibility to avian predation, but the strength of these explanatory factors differed between avian predator species. Steelhead susceptibility to cormorant predation increased with increasing water temperature and was higher for steelhead released from the dam closer to the breeding colony. Increased susceptibility of steelhead to tern predation was instead most associated with decreasing water discharge. A consistent factor relating susceptibility of steelhead to predation by both bird species was the health status of steelhead, as indicated by the presence and severity of external symptoms of trauma, disease, and stress. Results suggest that some reduction in avian predation may be accomplished by modifying hydrosystem operations. The higher susceptibility of unhealthy steelhead to avian predation suggests, however, that a portion of this reduction in predation will be compensated for by other sources of smolt mortality.

INTRODUCTION

Population declines of anadromous Pacific salmonids (*Oncorhynchus* spp.) in the

Columbia River basin have prompted the listing of 13 of the 20 evolutionarily significant

units (ESUs) from the basin as threatened or endangered under the United States

Endangered Species Act (ESA) (Waples 1991, Good et al. 2005). The majority of

management actions to restore salmonid populations in the Columbia River basin have

focused on mitigating the impacts of the so-called "four H's" - improving survival

through the Hydrosystem, regulating human Harvest, modifying Hatchery practices, and

restoring freshwater Habitat (Federal Caucus 2000). Mortality of juvenile salmonids

associated with hydroelectric development in the Columbia River basin has been cited as

a primary reason for declines in adult returns (Raymond 1979, Raymond 1988).

Estimates of direct plus indirect salmonid mortality that approached 30% at a single

hydropower project (dam and associated reservoir combined) have subsequently been

reduced by numerous passage enhancements (Rieman et al. 1991, Mathur et al. 1996).

However, mortality due to factors both directly and indirectly related to hydroelectric

power development is still considered substantial (Budy et al. 2002).

Indirect mortality due to hydroelectric development includes reduced water flow,

delayed downstream migration, and prolonged exposure of juvenile salmonids to

predators within the hydrosystem (Raymond 1988, Deriso et al. 2001, Smith et al. 2002,

Connor et al. 2003). Increased concern regarding the impact of predation on juvenile

salmonids prompted investigations into piscivorous fish (e.g., Beamesderfer et al. 1990,

Rieman et al. 1991, Ward et al. 1995, Zimmerman 1999) and piscivorous birds (e.g.,

Collis et al. 2002, Roby et al. 2003, Ryan et al. 2003, Antolos et al. 2005) in the

Columbia River basin. Although predation by piscivorous fish and birds has not been

implicated as a cause of salmonid declines in the Columbia River basin, some managers

identify predation as a potentially significant limiting factor for recovery of threatened

and endangered ESUs of salmonids (NOAA 2004, NOAA 2007). Management efforts to

reduce the impacts of avian predation on survival of juvenile salmonids within the

Columbia River estuary have been and are currently being implemented (Roby et al.

2002, USFWS 2006). However, our understanding of the environmental factors and

individual fish characteristics that influence the susceptibility of juvenile salmonids to

avian predation is extremely limited. Understanding how susceptibility to avian predation

is related to the size and condition of smolts, plus river conditions during out-migration is

vital to evaluating the efficacy of management efforts to reduce the impacts of avian

predation and restore salmonid populations in the Columbia River basin.

Within salmonid populations, increased susceptibility to predation has been

attributed to differences in fish behavior, physiology, condition, rearing environment, and

size (Mesa et al. 1998, Collis et al. 2002, Schreck et al. 2006, Kennedy et al. 2007). The

theory that predators disproportionately prey on individuals in substandard condition

(weak, sick, stressed, inexperienced, etc.) is widely accepted (Temple 1987). Schreck et

al. (2006) found suggestive evidence that differences in the prevalence and intensity of

disease, plus physiological preparedness to enter saltwater, among individual Chinook

salmon (*O. tshawytscha*) smolts influenced susceptibility to Caspian tern (*Hydroprogne*

caspia) predation in the Columbia River estuary. Kennedy et al. (2007) found similar

relationships for juvenile steelhead (*O. mykiss*), further supporting the hypothesis that an

individual salmonid's susceptibility to avian predation in the Columbia River estuary is associated with condition of the fish.

In addition to characteristics of individual fish, environmental conditions experienced during juvenile salmonid out-migration can increase stress, reduce fish performance, and increase exposure to predators (Raymond 1979, Kareiva and Marvier 2000, Budy et al. 2002, Schreck et al. 2006). Several studies have suggested that the susceptibility of juvenile salmonids to fish predation is influenced by abiotic river conditions associated with hydrosystem operations (e.g., Coutant 1973, Mesa 1994, Mesa and Warren 1997, Connor et al. 2003). Factors such as turbidity (Gregory 1993, Gregory and Levings 1998, Korstrom and Birtwell 2006), discharge (Raymond 1979, Antolos et al. 2005), and water temperature (Coutant 1973, Wedemeyer et al. 1984, Barton et al. 1986, Marine and Cech 2004) have been shown to alter salmonid susceptibility to predation in either field or laboratory settings. Antolos et al. (2005) suggested that low river flows and reduced in-river salmonid abundance were associated with increased predation rates on salmonids by Caspian terns nesting on Crescent Island in the reservoir behind McNary Dam on the Columbia River (hereafter referred to as McNary Pool). However, studies to test the hypotheses from Antolos et al. (2005) and identify additional environmental factors associated with increased salmonid susceptibility to avian predation have not been published.

The study presented herein investigated how the susceptibility of juvenile steelhead to predation by piscivorous waterbirds is related to individual fish characteristics and river conditions. Juvenile steelhead from the Snake River ESU and colonies of Caspian terns and double-crested cormorants (*Phalacrocorax auritus*) nesting

on islands in McNary Pool were used as models in this experiment. Snake River steelhead were selected for this study because prior research suggested steelhead were the most vulnerable salmonid species to avian predation in McNary Pool (Antolos et al. 2005). In addition, the Snake River Steelhead ESU is listed as threatened under the ESA, and data to evaluate the impact of avian predation on this ESU are needed to evaluate recovery options.

Caspian terns and double-crested cormorants are the major source of avian predation on juvenile salmonids emigrating from the Columbia River basin (Collis et al. 2002). Caspian terns nesting on Crescent Island in McNary Pool forage primarily on juvenile salmonids (Collis et al. 2002, Antolos et al. 2005). Predation on juvenile salmonids by double-crested cormorants nesting on Foundation Island, also in McNary Pool, has become a concern to fisheries managers due to the prevalence of salmonids in cormorant diets and increasing numbers of passive integrated transponder (PIT) tags from salmonids smolts deposited on-colony (Collis et al. 2002, Collis et al. 2008). Finally, we selected bird colonies located in McNary Pool for this study due to their downstream proximity to steelhead release sites (< 79 Rkm).

METHODS

Study Area

Our research efforts focused on run-of-the-river juvenile steelhead migrating from the Snake River basin, which were guided into juvenile collection systems at either Lower Monumental Dam (LMN, Rkm 589) or Ice Harbor Dam (ICH, Rkm 538) on the lower Snake River, Washington, USA (Figure 3.1). We investigated two piscivorous

waterbird breeding colonies located on two different islands in McNary Pool, a Caspian tern colony on Crescent Island (Rkm 510), and a double-crested cormorant colony on Foundation Island (Rkm 518; Figure 3.1).

Fish capture, PIT-tagging, and external examination

Steelhead were captured for this study at least 5 days per week at LMN and 2 days per week at ICH in both 2007 and 2008. Sampling occurred throughout the juvenile steelhead out-migration, beginning in early April and ending in early July, or until capture numbers dropped below 100 steelhead per week. The lone exception to this capture schedule occurred at LMN in 2007, when juvenile steelhead were only captured every third day throughout most of April.

Prior to sampling, captured fish were held in a holding tank with flow-through river water for up to 24 hours. Daily captures of juvenile steelhead were separated into small batches (10-50 fish) via a slide gate, fully anesthetized with MS-222, and each fish was tagged with a PIT tag by abdominal injection using a modified hypodermic syringe with a 12-gauge needle (Prentice et al. 1990a, Prentice et al. 1990b, Nielson 1992). To prevent disease transmission, syringe needles were soaked for a minimum of 10 min in 70% ethyl alcohol prior to PIT tag loading. Previous studies have found no significant effects of PIT-tagging on subsequent survival of juvenile salmonids (Prentice et al. 1990a).

After a steelhead was PIT-tagged, it was placed in a sample-tray, measured (fork length, nearest mm), weighed (nearest gram), assigned as originating from either a wild-origin or hatchery-rearing environment (clipped adipose fin or severe erosion of dorsal,

pectoral, pelvic, and/or caudal fins), and examined for various external symptoms of health status. Categories of external symptoms included body injuries, de-scaling, external symptoms of disease, fin damage, and infestations of ectoparasites (Table 3.1). Using a modified version of a procedure developed by Evans et al. (2004), steelhead also received an integrated condition rank (good, fair, or poor) based on the overall external condition of the fish (Table 3.2). To reduce handling time, digital photographs (Canon EOS Rebel Xti; 50mm lens) were taken of each side of the steelhead, which allowed for detailed classification of external symptoms by type and severity after steelhead were released. Digital photographs, labeled with the same unique PIT tag code as the steelhead, were downloaded into a computer and analyzed in a database specifically designed for this study. The total time to handle, PIT-tag, photograph, and examine a steelhead was usually < 30 sec.

Following the examination process, daily groups of PIT-tagged steelhead were placed in a holding tank with flow-through river water for 1 to 18 hours, and then released as a group directly into the bypass river-return line leading to the dam's tailrace. Release times alternated between mornings and evenings to reduce possible bias in steelhead susceptibility to predation associated with time of day at release. Release times at LMN alternated between 18:00 - 23:00 PDT the day of processing and 07:00 - 11:00 PDT the day following processing. ICH release times alternated between 09:00 -13:00 PDT and 18:00 - 22:00 PDT the day of processing. All mortalities and ejected PIT tags were removed from temporary holding tanks prior to release and excluded from further analysis.

PIT tag recovery

PIT-tagged steelhead smolts were considered consumed by a Caspian tern nesting on Crescent Island or a double-crested cormorant nesting on Foundation Island if the unique PIT tag associated with a steelhead was detected on the Crescent Island tern colony or the Foundation Island cormorant colony, respectively. PIT tags were recovered from the tern and cormorant colonies each year, once birds dispersed following the nesting season. Detailed methods of PIT tag recovery can be found in Ryan et al. (2001, 2003) and are only briefly summarized here. On the tern colony, NOAA Fisheries personnel systematically scanned the tern nesting area for PIT tags using a flat-plate detector mounted on a 4-wheel-drive vehicle. Pole-mounted, hand-held transceivers were used to detect tags in areas inaccessible to the flat-plate detector. The thick woodland on Foundation Island did not allow for use of a vehicle; therefore, the entire cormorant colony was scanned using pole-mounted, hand-held transceivers.

Detection efficiency

PIT tag recoveries on bird colonies are minimum estimates of predation because (1) an unknown proportion of consumed tags are deposited off-colony, (2) deposited tags may be lost due to wind and water erosion, (3) some PIT tags are damaged to the point of being unreadable before or after they are deposited on the colony, and (4) detection efficiency of functioning PIT tags on the colony is less than 100% (Ryan et al. 2003). To better account for possible inter-annual differences in tag loss and damage, we annually measured detection efficiency by systematically sowing known PIT tags on both the tern and cormorant colonies, and then recovering these tags after the nesting season. To

investigate possible intra-seasonal variation in PIT tag detection efficiency, test tags were sown (1) prior to the birds' arrival on colony (March), (2) during egg incubation (May), (3) near chick fledging (June), and (4) once the birds had left the colony following the nesting season (late July to early August). We used logistic regression to estimate weekly detection efficiencies by interpolation. Weekly estimates of detection efficiency were then included as fixed effects in all models to account for seasonal variation in colony-specific detection efficiency.

Environmental variables

Previous studies have suggested that salmonid susceptibility to avian predation in the Columbia River basin may be influenced by individual fish characteristics and environmental conditions experienced during salmonid out-migration (Collis et al. 2001, Ryan et al. 2003, Antolos et al. 2005, Kennedy et al. 2007). Environmental factors evaluated as part of this study included: (1) steelhead release location (LOC), (2) migration year (YEAR), (3) prey abundance (estimated number of in-river steelhead in McNary Pool), (4) predator abundance (number of adult and juvenile Caspian terns or double-crested cormorants at the colonies on Crescent Island or Foundation Island, respectively), (5) water discharge (kcfs) from LMN (DISCHARGE), (6) water temperature (^{o}C) at LMN (TEMP), and (7) water clarity (Secchi depth in meters) in the Snake River (CLARITY).

Water clarity was estimated using averages of two to four Secchi measurements taken each week from a boat in the main channel of the Snake River just above the confluence of the Snake and Columbia rivers. Measurements of the number of juvenile

steelhead in-river, water discharge, and water temperature at LMN, ICH, and MCN were downloaded from the Data Access in Real Time (DART) website, maintained by the Columbia Basin Research group at the University of Washington, School of Aquatic and Fishery Sciences (www.cbr.wahington.edu/dart/). Discharge, water temperature, and water clarity variables were not correlated with one another (Pearson correlation coefficient, $R < 0.20$), but were correlated across recording locations (LMN, ICH, and MCN; Pearson correlation coefficient; $R > 0.80$). We decided to only use measurements of these three variables from LMN because of (1) high correlation between recording sites and (2) LMN was the site where most PIT-tagged steelhead were released.

Colony-specific weekly (Sunday through Saturday) predator abundance was estimated by averaging three to eight weekly counts of all adults and juveniles present on the Crescent Island tern and Foundation Island cormorant colonies. Additionally, we used the steelhead index from McNary Dam to estimate the number of in-river steelhead passing the two bird colonies each week. Because the McNary Dam steelhead index was only recorded every other day, we smoothed the data, and assigned a weekly (Sunday through Saturday) average of the number of in-river steelhead. The in-river steelhead index at McNary Dam is not an exact measurement of overall steelhead abundance in McNary Pool, but it does provide a quantitative estimate of large-scale changes in numbers of in-river juvenile steelhead (Figure 3.2).

Susceptibility to avian predation

We used a model selection approach to identify river conditions and individual fish characteristics that were associated with greater susceptibility of steelhead to

predation by Crescent Island terns or Foundation Island cormorants. We fit multiple

logistic regression functions:

$$\text{logit}(p_i) = \beta_0 + \beta_1 D_i + \beta_2 P_i + \beta_3 S_i + \ldots + \beta_p X_i$$

where p_i is the probability of being detected on-colony for steelhead i, β_0 is the

regression intercept, $\beta_1 D_i$ is the linear coefficient for the weekly colony-specific

detection efficiency for steelhead i, $\beta_2 P_i$ is the linear coefficient for the weekly colony-

specific predator abundance for steelhead i, $\beta_3 S_i$ is the linear coefficient for the weekly

in-river steelhead abundance for steelhead i, and $\beta_p X_i$ is the linear coefficient for the

independent explanatory variable X associated with steelhead i. Independent explanatory

variables included the river conditions and the individual fish characteristics described

above.

　　　　We considered a model including colony-specific detection efficiency, number of

birds on-colony, and in-river steelhead abundance as our null model (hereafter referred to

as the base model) due to the biological importance of these variables in predicting

steelhead susceptibility to avian predation. Explanatory variables included in the base

model were also included in all candidate models to account for variation in susceptibility

to avian predation associated with these variables prior to investigating relationships

between susceptibility to avian predation and explanatory variables of interest. Only

additive models were investigated (no interaction variables) due to the high number of

explanatory variables and the small proportion of PIT tags recovered on bird colonies

($\sim$ 2-3% per colony per year). Candidate models were ranked and compared using

Akaike's Information Criteria corrected for small sample size (AIC_c), AIC_c differences

(ΔAIC_c), and Akaike weights (w_i) (Burnham and Anderson 2002). Models with AIC_c values < 2 units from the best model were considered competing models. River condition variables and individual fish characteristic variables that were included in competing models were further investigated through probabilities, odds, and odds ratios. Evaluation of explanatory variables by AIC_c values, probabilities, and odds ratios allowed for identification of variables correlated with steelhead susceptibility to avian predation, while also assessing direction and strength of effects from significant explanatory variables. All analyses were conducted in SAS, Version 9.2 (SAS Institute, Inc.) with statistical significance set at $\alpha = 0.05$.

RESULTS

Steelhead capture and condition

A total of 16,258 steelhead were PIT-tagged and released from either LMN (n = 14,166) or ICH (n = 2,092) as part of this study. We released 7,085 PIT-tagged steelhead in 2007 and 9,173 in 2008. Released steelhead consisted of more hatchery-reared smolts (n = 13,903) than wild-origin smolts (n = 2,355), in agreement with the relative abundance of these two rearing types among run-of-the-river steelhead captured at LMN and ICH.

Fin damage was the most prevalent external symptom of compromised health (83%), followed by de-scaling (41%), body injuries (16%), external symptoms of disease (5%), and ectoparasite infestations (2%). Prevalence of body injuries was 7% higher in 2008 compared to 2007 ($\chi^2 = 132.9$, df = 1, $P < 0.001$). However, prevalence of several other external symptoms was lower in 2008 compared to 2007, including de-scaling

(13% lower, $\chi^2 = 272.1$, df = 1, $P < 0.001$), fin damage (4% lower, $\chi^2 = 42.5$, df = 1, $P < 0.001$), and external symptoms of disease (3% lower, $\chi^2 = 93.9$, df = 1, $P < 0.001$).

Average fork length of hatchery-reared steelhead ($\bar{x} = 223$ mm) was 20.5% greater than that of wild-origin steelhead ($\bar{x} = 185$ mm; 95% CI of difference: 20.0% to 21.1%, $P < 0.001$). Despite this difference, the range of fork lengths for hatchery-reared and wild-origin steelhead overlapped considerably (hatchery fork lengths = 132 - 375 mm, wild fork lengths = 134 - 354 mm).

Tag recoveries

Of the 16,258 PIT-tagged steelhead released as part of this study, we recovered 492 PIT tags (3.03%) on the Caspian tern colony at Crescent Island and 317 PIT tags (1.95%) on the double-crested cormorant colony at Foundation Island. Inter-annual differences in the proportion of PIT tags recovered on each bird colony were minor. On the Crescent Island tern colony, we recovered 213 (3.01%) and 279 (3.04%) of the 7,085 and 9,173 PIT-tagged steelhead released in 2007 and 2008, respectively. On the Foundation Island cormorant colony, we recovered 139 (1.96%) and 178 (1.94%) of the PIT-tagged steelhead released in 2007 and 2008, respectively.

There was a positive association between detection efficiency of PIT tags sown on the Crescent Island tern colony and Julian date, indicating that the probability of recovering a smolt PIT tag was higher for tags deposited on the tern colony late in the nesting season, both in 2007 ($\chi^2 = 140.9$, df = 1, $P < 0.001$) and in 2008 ($\chi^2 = 153.1$, df = 1, $P < 0.001$). No significant temporal trend in PIT tag detection efficiency was

found on the Foundation Island cormorant colony, either in 2007 ($\chi^2 = 1.8$, df = 1,

$P = 0.17$) or in 2008 ($\chi^2 = 3.3$, df = 1, $P = 0.07$, Appendix C).

Caspian tern predation

To investigate factors influencing the susceptibility of steelhead to Caspian tern

predation, we considered a base model that included PIT tag detection efficiency, number

of Caspian terns on the Crescent Island colony, and in-river steelhead abundance. Each of

these explanatory variables was statistically significant ($P < 0.01$) within the base model,

and suggestive ($P = 0.09$) to highly significant ($P < 0.0001$) in all competing models (i.e.,

those models within 2.0 AIC_c units of the top model), after accounting for other variables

in the models. Results from the top model and all competing models indicated that

steelhead susceptibility to predation by Crescent Island terns increased as the number of

terns on-colony increased and as in-river steelhead abundance decreased, suggesting

predator swamping at higher in-river steelhead abundances.

Model selection provided strong support for the hypothesis that individual

steelhead characteristics were related to steelhead susceptibility to tern predation. Two

models that included individual fish characteristics as explanatory variables were highly

competitive, with each model > 109 AIC_c units better than the base model at explaining

variation in the response variable. The top model for predicting steelhead susceptibility to

tern predation included variables for magnitude of body injuries and a quadratic function

of fork length. The only competing model ($\Delta AIC_c = 0.86$) included all variables in the

top model, plus a variable for rearing type (wild-origin vs. hatchery-reared; Table 3.3).

Steelhead fork length, specifically a quadratic function of fork length, appeared to be the most important individual fish characteristic in predicting steelhead susceptibility to tern predation, as it was present in all competing models and was highly significant ($P < 0.001$), after accounting for other variables in those models (Table 3.3 and 3.4). This result indicates that steelhead susceptibility to tern predation increased as steelhead fork length approached 203 mm, but decreased for longer steelhead. Additionally, after accounting for other variables in the top model, steelhead with severe body injuries were 1.5 times more susceptible to predation by terns compared to steelhead without body injuries (95% CI: 1.1 to 2.0, $\chi^2 = 5.9$, df = 1, $P = 0.02$). However, no difference in susceptibility to tern predation was detected between steelhead with moderate body injuries and those without body injuries ($\chi^2 = 0.6$, df = 1, $P = 0.45$; Table 3.4, Figure 3.3).

Rearing type (hatchery-reared vs. wild-origin) was included in a highly competitive model (Table 3.3), but was not significantly related to susceptibility of steelhead smolts to tern predation ($\chi^2 = 1.2$, df = 1, $P = 0.28$), after accounting for other variables in this model. Other than body injuries, no other type of external symptom was included in a competitive model or significantly associated with increased steelhead susceptibility to tern predation, after accounting for other variables in the respective best models; these external symptoms with no significant explanatory power included fin damage ($\chi^2 = 4.3$, df = 2, $P = 0.12$), external symptoms of disease ($\chi^2 = 1.3$, df = 2, $P = 0.53$), ectoparasite infestations ($\chi^2 = 2.8$, df = 2, $P = 0.24$), de-scaling ($\chi^2 = 5.5$, df = 3, $P = 0.14$), and integrated condition ranks ($\chi^2 = 4.0$, df = 2, $P = 0.13$).

In addition to individual steelhead characteristics, there was strong support for the hypothesis that river conditions were related to susceptibility of steelhead to tern

predation. Model selection indicated three competing models that included explanatory variables for river conditions, each > 45 AIC_c units better than the base model. Three river condition variables were present in all three competing models: migration year, discharge from LMN, and water clarity (Table 3.5). Steelhead susceptibility to predation by terns increased as discharge decreased ($\chi^2 = 9.3$, df = 1, $P = 0.002$), after accounting for other variables in the top model. Susceptibility to tern predation also increased with decreased water clarity (increased turbidity), but this relationship was not significant in the top model ($\chi^2 = 0.8$, df = 1, $P = 0.36$) or any competing model. Finally, after accounting for other variables in the top model, steelhead migrating in 2008 were 3.4 times more susceptible to predation by terns compared to steelhead migrating in 2007 (95% CI: 2.2 to 5.2, $\chi^2 = 29.1$, df = 1, $P < 0.0001$).

Water temperature and release site were not included in the top model, but each of these explanatory variables was present in models within 2.0 AIC_c units of the top model. Results for water temperature were suggestive of a positive correlation between water temperature and steelhead susceptibility to tern predation; however, this trend was not significant ($\chi^2 = 1.2$, df = 1, $P = 0.27$) after accounting for other variables in the best model that included water temperature. Similarly, release location was not significantly related to steelhead susceptibility to tern predation ($\chi^2 = 0.5$, df = 1, $P = 0.50$), after accounting for other variables in the respective best model.

Double-crested cormorant predation

To evaluate factors influencing the susceptibility of steelhead to double-crested cormorant predation, we considered a base model that included PIT tag detection

efficiency, number of double-crested cormorants on the Foundation Island colony, and in-river steelhead abundance. Model selection provided strong support for the hypothesis that individual fish characteristics were related to susceptibility of steelhead to cormorant predation. There were two competitive models that included individual fish characteristics, each > 30 AIC$_c$ units better than the base model. Explanatory variables for external symptoms of disease and rearing type were present in both competing models (Table 3.6), while the second best model (ΔAIC$_c$ = 1.49) also included a variable for fork length.

Model selection indicated that external symptoms of disease was the most important individual characteristic in predicting steelhead susceptibility to cormorant predation. A variable for external disease symptoms was present in all competing models (Table 3.6) and was highly significant ($P < 0.001$), after accounting for other variables in competing models. The probability of predation by cormorants for steelhead with moderate or severe external disease symptoms was 3.1 times greater (95% CI: 1.7 to 5.6, $\chi^2 = 13.6$, df = 1, $P < 0.001$) and 3.3 times greater (95% CI: 2.2 to 4.9, $\chi^2 = 34.5$, df = 1, $P < 0.0001$), respectively, than for steelhead without external disease symptoms (Table 3.7).

Rearing type was also included in all competitive models predicting steelhead susceptibility to cormorant predation, and suggested hatchery-reared steelhead were 1.5 times more susceptible to cormorant predation compared to wild-origin steelhead (95% CI: 1.0 to 2.1, $\chi^2 = 4.2$, df = 1, $P = 0.04$), after accounting for other variables in the top model. Integrated condition rank (good, fair, or poor) was significantly related to steelhead susceptibility to predation by Foundation Island cormorants ($\chi^2 = 24.4$, df = 2,

$P < 0.0001$), after accounting for other variables in the best model that included a

variable for integrated condition rank. According to this model, steelhead classified as in

poor condition were 2.0 times more susceptible to predation by Foundation Island

cormorants compared to steelhead classified as in good condition (95% CI: 1.5 to 2.6,

$\chi^2 = 22.2$, df = 1, $P < 0.0001$). However, no difference in steelhead susceptibility to

Foundation Island cormorant predation was detected between steelhead classified as in

good vs. fair condition ($\chi^2 = 0.03$, df = 1, $P = 0.86$), and integrated condition rank was not

included in any model in the set of competitive models ($\Delta AIC_c = 13.5$). Additional

external symptoms, including fin damage ($\chi^2 = 5.0$, df = 2, $P = 0.08$), body injuries

($\chi^2 = 2.8$, df = 2, $P = 0.25$), ectoparasites ($\chi^2 = 0.9$, df = 2, $P = 0.62$), and de-scaling

($\chi^2 = 1.5$, df = 3, $P = 0.69$), were not significantly related to susceptibility of steelhead to

predation by Foundation Island cormorants, after accounting for other variables in the

best models that included these variables.

Model selection also provided strong support for the hypothesis that steelhead

susceptibility to predation by double-crested cormorants was related to river conditions.

Four competitive models included explanatory variables for river conditions, each > 26

AIC_c units better than the base model (Table 3.8). Three river condition variables were

present in all four competing models: release site, migration year, and water temperature

(Table 3.8).

Susceptibility of steelhead to predation by Foundation Island cormorants

increased as water temperature increased ($\chi^2 = 6.8$, df = 1, $P = 0.009$), after accounting

for other variables in the top model. Also, susceptibility to cormorant predation was 2.4

times greater for steelhead migrating in 2008 compared to 2007 (95% CI: 1.5 to 3.6,

$\chi^2 = 15.6$, df $= 1$, $P < 0.0001$), after accounting for other variables in the model. This inter-annual difference in susceptibility to cormorant predation was similar to the inter-annual difference in susceptibility to tern predation. Susceptibility to cormorant predation was 1.6 times greater for steelhead released at ICH, the dam closer to the Foundation Island colony, compared to steelhead released at LMN (95% CI: 1.3 to 2.2, $\chi^2 = 12.4$, df $= 1$, $P < 0.001$), after accounting for other variables in the top model. Additionally, results from the top model indicated that steelhead susceptibility to predation by Foundation Island cormorants increased as the number of cormorants on-colony increased ($\chi^2 = 18.4$, df $= 1$, $P < 0.001$) and as in-river steelhead abundance decreased ($\chi^2 = 6.0$, df $= 1$, $P = 0.01$), after accounting for other variables in the top model. These results suggest predator swamping at higher in-river steelhead abundances, similar to the indication of predator swamping for Crescent Island terns.

Water clarity and discharge were not included in the top model for susceptibility to cormorant predation, but each of these explanatory variables was present in competitive models. Results suggest there was a positive correlation between water clarity and susceptibility of steelhead to predation by Foundation Island cormorants. However, this trend was not significant ($\chi^2 = 1.3$, df $= 1$, $P = 0.26$), after accounting for other variables in the best model that included water clarity. Similarly, discharge was not significantly ($\chi^2 = 1.0$, df $= 1$, $P = 0.31$) related to susceptibility of steelhead to cormorant predation, after accounting for other variables in the best model that included discharge.

DISCUSSION

The goal of our study was to determine whether individual fish characteristics and environmental variables influence the susceptibility of steelhead smolts to avian predation. We found that the size and condition of juvenile steelhead, as well as river conditions at the time of release, were related to a steelhead's probability of being eaten by an avian predator, but the strength of these explanatory factors differed between the two species of avian predator.

One consistent trend across both avian predators was the disproportionate consumption of steelhead in poorer health status (see Chapter 2). Increased susceptibility of prey in substandard condition is a widely accepted theory (Temple 1987), and has been well documented in fish predation studies (for review see Mesa et al. 1994). Our results indicated that steelhead in compromised health (Chapter 2) were more susceptible to avian predation compared to relatively healthy steelhead, regardless of the species of avian predator. Selective predation associated with individual steelhead characteristics and health status could result from several conditional events, including differences in predator-prey encounter rates, attack rates, and/or capture rates (Temple 1987). Individual prey in poor health could behave in such a manner as to enhance encounter rates with predators. Selective foraging by predators could enhance predator foraging efficiency (rate of successful attacks) due to less energy required to capture substandard individuals relative to that required to capture relatively healthy prey (Stephens and Krebs 1986). Finally, increased predation rates on prey in substandard condition could result from predators attacking all encountered individuals of the prey population equally, but with a higher capture rate when attacking individuals in poor health (Temple 1987).

Regardless of whether selective predation occurred prior to or after attacks were initiated, Caspian terns and double-crested cormorants disproportionately consumed steelhead in poorer health, which were less likely to survive even if they had not been consumed by these predators. This is strong support for the hypothesis that smolt mortality from avian predation is partly compensatory.

Individual fish characteristics other than health status were also related to increased steelhead susceptibility to avian predation, but the relevant fish characteristics varied by avian predator species. Our study documented that steelhead susceptibility to tern predation was greatest for steelhead with fork lengths near 203 mm, but was lower for steelhead that were larger or smaller. Size-dependent selection by various tern species (Subfamily: Sterninae), including Caspian terns (Baltz et al. 1979), crested terns (*Thalasseus bergii*) (McLeay et al. 2009), Forster's terns (*Sterna forsteri*) (Baltz et al. 1979), and roseate terns (*Sterna dougallii*) (Shealer 1998) has previously been documented. The hypothesis that piscivorous birds may be restricted by an upper limit of prey size was previously noted by Latta and Sharkley (1966), where girth, but not necessarily length, restricted fish consumption by another piscivorous waterbird, the common merganser (*Mergus merganser*). Decreasing salmonid susceptibility to predation by Caspian terns as smolt fork length decreases was previously hypothesized by Collis et al. (2001) and Ryan et al. (2003). These studies noted relative salmonid susceptibility to predation by Caspian terns in the Columbia River estuary was lower for juvenile Chinook and coho (*O. kisutch*) salmon, compared to the generally larger steelhead smolts. Caspian terns nesting in the McNary Pool were also found to disproportionately consume steelhead compared to the relatively smaller Chinook salmon (Antolos et al. 2005). Our

findings of size-dependent susceptibility of steelhead to Caspian tern predation supports

previous hypotheses that relative differences in susceptibility among salmonid ESUs are

due, at least in part, to size-dependent predation by Caspian terns.

Our results provide further support to the growing body of evidence that

behavioral and physical traits associated with hatchery-raised salmonids can enhance

susceptibility to predation compared to their wild-origin counterparts (Olla and Davis

1989, Johnsson and Abrahams 1991, Alvarez and Nicieza 2003, Fritts et al. 2007).

However, the results of the present study may not be applicable to predation by Caspian

terns and double-crested cormorants nesting at the much larger colonies in the Columbia

River estuary, because bird and fish behaviors can to be influenced by environmental

conditions specific to estuaries, such as salinity gradients and tidal cycles, which were not

evaluated in this study (Roby et al. 2002, Kennedy et al. 2007).

Overall, models incorporating explanatory variables for individual fish

characteristics were better than models incorporating explanatory variables for river

conditions at predicting steelhead susceptibility to predation by both Caspian terns and

double-crested cormorants, when all models accounted for predator abundance, prey

abundance, and colony-specific PIT tag detection efficiency. Greater support for

individual characteristic models could be due to either the importance of individual

characteristics in explaining fish susceptibility to avian predation, imperfect

representation of river conditions (especially when predation occurred over a large,

heterogeneous area), or both. Even with the imprecision inherent to the variables used as

indices for river conditions, models including river conditions had much more support

than the base models (> 26 AIC_c units better for both terns and cormorants), indicating

that river conditions were clearly associated with steelhead susceptibility to avian predation.

Results indicated that steelhead susceptibility to predation by both Foundation Island cormorants and Crescent Island terns was reduced when in-river steelhead abundances were high, likely due to predator swamping. Ryan et al. (2003) attributed a similar relationship between increased in-river steelhead abundance and reduced steelhead susceptibility to avian predation in the Columbia River estuary to a greater potential for predator satiation and an improved ability of schooling fish to avoid predation. In addition, this study also detected positive correlations between the number of birds on-colony and steelhead susceptibility to predation by Foundation Island cormorants and Crescent Island terns. The increased food demands of larger bird colonies, associated with more breeding pairs and metabolic requirements of more growing chicks (Roby et al. 2003), corresponded with the timing of steelhead out-migration through McNary Pool (Figure 3.2b, c, and d), and presumably underlies these relationships.

Additional associations between river conditions and steelhead susceptibility to avian predation were dependent on the species of avian predator, and commonality between the two predators was frequently lacking. Steelhead susceptibility to tern predation was most associated with decreased water discharge, which is correlated with water velocity, a key factor determining how quickly juvenile salmonids migrate through reservoirs and remain within foraging range of central place foraging predators (Berggren and Filardo 1993). No relationship between steelhead susceptibility to predation by double-crested cormorants and discharge was detected in this study; however, increased

susceptibility of steelhead to cormorant predation was instead associated with higher

water temperatures. Cormorants are pursuit-diving piscivores, and pursue their prey

underwater (Hatch and Weseloh 1999) where prey must avoid predation through

concealment or escape. Optimal salmonid performance is often associated with a narrow

temperature range and deviations from these temperatures can decrease fish performance

(Hokanson et al. 1977, Wedemeyer et al. 1984, Barton et al. 1986), including reduced

burst swimming ability (Marine and Cech 2004) or altered behavior (Coutant 1973).

Higher water temperatures may have contributed to increased steelhead susceptibility to

cormorant predation by reducing steelhead performance.

In addition to discharge and water temperature, turbidity was also present in

several competing models evaluating steelhead susceptibility to Caspian tern and double-

crested cormorant predation, although the trend for this relationship differed between the

two predator species. Our study suggested that steelhead susceptibility to double-crested

cormorant predation decreased as turbidity increased, while susceptibility to tern

predation increased as turbidity increased. This discrepancy may well be attributable to

differences in foraging mode between the two bird species. Unlike double-crested

cormorants, which are pursuit-divers, Caspian terns are plunge-divers that capture prey at

or near the water surface (Cuthbert and Wires 1999). Increased turbidity can decrease

susceptibility of fish species to predation by piscivorous fishes due to a hypothesized

reduction in predator-prey encounter rates (Gregory 1993, Gregory and Levings 1998, De

Robertis et al. 2003). Strod et al. (2008) found that higher turbidity reduced detection and

predation of fish by great cormorants (*Phalacrocorax carbo sinensis*), a pursuit-diver, in

a laboratory setting. Reduced sight distance associated with higher turbidity may decrease

encounter rates and hinder efficacy of pursuit-divers, like double-crested cormorants, while higher turbidity may be advantageous for plunge-divers because of decreased reaction times and reduced use of cover by salmonids in turbid water (Gregory 1993, Gregory and Levings 1998, Korstrom and Birtwell 2006).

The major inter-annual differences in steelhead susceptibility to predation from both avian predators are not easily interpreted. Results from the top models indicated that steelhead susceptibility to predation by both terns and cormorants was higher in 2008, when discharge was greater and water temperatures lower, compared to 2007 (Figure 3.2e and g). The inter-annual differences in steelhead susceptibility to avian predation may be attributable to between-year differences in the proportion of PIT-tagged steelhead that were released during the latter part of the out-migration; consistently higher numbers of steelhead smolts were PIT-tagged and released after May 20 in 2008 compared to 2007 (Figure 3.2a). Steelhead smolts out-migrating after the migration peak are particularly susceptible to avian predation because these fish migrate when in-river steelhead abundances are relatively low and food demands of piscivorous waterbird colonies are at their maximum due to caloric requirements of both adults and older chicks. Hence, the apparent higher steelhead susceptibility in 2008 compared to 2007 was likely due to inter-annual differences in the temporal distribution of released PIT-tagged steelhead, rather than higher steelhead predation rates by both terns and cormorants in 2008. The substantial inter- and intra-annual variation in environmental conditions during this two-year study makes the interpretation of variation in steelhead susceptibility to avian predation challenging; data from additional years will enhance understanding of associations between river conditions and steelhead susceptibility to avian predation.

Finally, we PIT-tagged and released steelhead at two locations on the lower Snake River to assess spatial differences in steelhead susceptibility to avian predation. No differences in susceptibility of steelhead to predation by Crescent Island terns were found between the two release locations, but steelhead released from ICH, the dam closer to the bird colonies, were significantly more susceptible to predation by Foundation Island cormorants. Predator foraging ecology, prey behavior, and environmental conditions could all contribute to differential susceptibility between release locations (Cuthbert and Wires 1999, Hatch and Weseloh 1999, Smith et al. 2002, Ferguson et al. 2005).

MANAGEMENT AND CONSERVATION IMPLICATIONS

Results from this study suggest that steelhead susceptibility to avian predation would decline with a reduction in the number of Caspian terns and double-crested cormorants nesting at their respective breeding colonies on Crescent Island and Foundation Island. Results also indicate that an increase in abundance of in-river migrating steelhead smolts would reduce steelhead susceptibility, presumably as a result of predator swamping. However, it also appears that hydrosystem operations and river conditions can influence the susceptibility of steelhead to avian predation. In particular, reductions in avian predation in the McNary Pool may be attainable through efforts to increase discharge and preclude high water temperatures.

Currently, management to move a portion of the Caspian terns nesting in the Columbia River estuary to alternative colony sites outside the Columbia River basin is being implemented, and research into additional management options to further reduce avian predation on juvenile salmonids is in progress (Roby et al. 2002, USFWS 2006).

The efficacy of predator control for efforts to restore salmonid populations in the Columbia River basin depends on whether reductions in smolt mortality due to avian predation are compensated for by other mortality factors. Increases in adult salmonid returns associated with reduced avian predation on juvenile salmonids would be diminished if some steelhead smolts consumed by avian predators would have died from other causes regardless (Schreck et al. 2006). Our results suggest that the efficacy of management actions to reduce avian predation may be discounted by the higher susceptibility of unhealthy steelhead to avian predation. This higher susceptibility indicates that smolt mortality due to avian predation is in part compensatory. However, the low prevalence of external symptoms of poor health in our samples of PIT-tagged steelhead, plus the recovery of PIT tags on-colony from steelhead that were classified as relatively healthy, suggests that a substantial proportion of smolt mortality due to avian predation is additive.

Empirical studies of predator-prey relationships that investigate the individual characteristics of prey and the environmental conditions at the time of predation provide important information for management decisions and practices (Mesa et al. 1994). Replication of this research with various salmonid ESUs and colonies of avian predators should clarify relationships among individual salmonid characteristics, river conditions, and susceptibility of out-migrating juvenile salmonids to avian predation. Identifying individual smolt characteristics and hydrosystem practices that affect smolt survival and susceptibility to predation can aid in development of management plans that benefit salmonid populations and contribute to recovery of Columbia Basin salmonid stocks currently listed as threatened or endangered under the ESA.

LITERATURE CITED

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.

Baltz, D. M., G. V. Morejohn, and B. S. Antrim. 1979. Size selective predation and food habits of two California terns. Western Birds 10:17-24.

Barton, B. A., C. B. Schreck, and L. A. Sigismondi. 1986. Multiple acute disturbances evoke cumulative physiological stress responses in juvenile Chinook salmon. Transactions of the American Fisheries Society 115:245-251.

Beamesderfer, R. C., B. E. Rieman, L. J. Bledsoe, and S. Vigg. 1990. Management implications of a model of predation by a resident fish on juvenile salmonids migrating through a Columbia River reservoir. North American Journal of Fisheries Management 10:290-304.

Berggren, T. J., and M. J. Filardo. 1993. An analysis of variables influencing the migration of juvenile salmonids in the Columbia River basin. North American Journal of Fisheries Management 13:48-63.

Budy, P., G. P. Thiede, N. Bouwes, C. E. Petrosky, and H. Schaller. 2002. Evidence linking delayed mortality of Snake River salmon to their earlier hydrosystem experience. North American Journal of Fisheries Management 22:35-51.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and inference - a practical information-theoretic approach, 2nd edition. Springer-Verlag, New York, New York.

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 loses of juvenile salmonids to avian predation. Transactions of the American Fisheries Society 131:537-550.

Collis, K., D. D. Roby, D. E. Lyons, Y. Suzuki, J. Y. Adkins, L. Reinalda, N. Hostetter, L. Adrean, M. Bockes, P. Loschl, D. Battaglia, T. Marcella, B. Cramer, A. F. Evans, M. Hawbecker, M. Carper, J. Sheggeby, and S. Sebring. 2009. Research, monitoring, and evaluation of avian predation on salmonid smolts in the lower and mid-Columbia River: 2008 final season summary. Project report submitted to Bonneville Power Administration and the U.S. Army Corps of Engineers, Portland, OR.

Connor, W. P., H. L. Burge, J. R. Yearsley, and T. C. Bjornn. 2003. Influence of flow and temperature on survival of wild subyearling fall Chinook salmon in the Snake River. North American Journal of Fisheries Management 23:362-375.

Coutant, C. C. 1973. Effect of thermal shock on vulnerability of juvenile salmonids to predation. Journal of the Fisheries Research Board of Canada 30:965-973.

Cuthbert, F. J., and L. R. Wires. 1999. Caspian tern (*Sterna caspia*). No. 403 *in* A. Poole, and F. Gill, editors. The Birds of North America. The Birds of North America Inc., Philadelphia, Pennsylvania.

DART. 1995. Columbia River data access in real time: online interactive database of the Columbia basin research group. University of Washington School of Aquatic and Fishery Sciences.

De Robertis, A., C. H. Ryer, A. Veloza, and R. D. Brodeur. 2003. Differential effects of turbidity on prey consumption of piscivorous and planktivorous fish. Canadian Journal of Fisheries and Aquatic Sciences 60:1517-1526.

Deriso, R. B., D. R. Marmorek, and I. J. Parnell. 2001. Retrospective patterns of differential mortality and common year-effects experienced by spring and summer Chinook salmon (*Oncorhynchus tshawytscha*) of the Columbia River. Canadian Journal of Fisheries and Aquatic Sciences 58:2419-2430.

Evans, A. F., R. E. Beaty, M. S. Fitzpatrick, and K. Collis. 2004. Identification and enumeration of steelhead kelts at a Snake River hydroelectric dam. Transactions of the American Fisheries Society 133:1089-1099.

Federal Caucus. 2000. Conservation of Columbia Basin fish: Final basinwide salmon recovery strategy. Federal Caucus, Portland, Oregon.

Ferguson, J. W., G. M. Matthews, R. L. McComas, R. F. Absolon, D. A. Brege, M. H. Gessel, and L. G. Gilbreath. 2005. Passage of adult and juvenile salmonids through federal Columbia River power system dams. NOAA Technical Memorandum NMFS-NWFSC-64.

Fritts, A. L., J. L. Scott, and T. N. Pearsons. 2007. The effects of domestication on the relative vulnerability of hatchery and wild origin spring Chinook salmon

(*Oncorhynchus tshawytscha*) to predation. Canadian Journal of Fisheries and Aquatic Sciences 64:813-818.

Good, T. P., R. S. Waples, and P. Adams (editors). 2005. Updated status of federally listed ESUs of West Coast salmon and steelhead. NOAA Technical Memorandum NMFS-NWFSC-66:598.

Gregory, R. S. 1993. Effect of turbidity on the predator avoidance-behavior of juvenile Chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 50:241-246.

Gregory, R. S., and C. D. Levings. 1998. Turbidity reduces predation on migrating juvenile Pacific salmon. Transactions of the American Fisheries Society 127:275-285.

Hatch, J. J., and D. V. Weseloh. 1999. Double-crested cormorant (*Phalacrocorax auritus*). No. 411 *in* A. Poole, and F. Gill, editors. The Birds of North America,. The Birds of North America Inc., Philadelphia, Pennsylvania.

Hokanson, K. E. F., C. F. Kleiner, and T. W. Thorslund. 1977. Effects of constant temperatures and diel temperature fluctuations on specific growth and mortality rates and yield of juvenile rainbow trout, *Salmo gairdneri*. Journal of the Fisheries Research Board of Canada 34:639-648.

Johnsson, J. I., and M. V. Abrahams. 1991. Interbreeding with domestic strain increases foraging under threat of predation in juvenile steelhead trout (*Oncorhynchus mykiss*): an experimental study. Canadian Journal of Fisheries and Aquatic Sciences 48:243-247.

Kareiva, P., and M. Marvier. 2000. Recovery and management options for spring/summer Chinook salmon in the Columbia River basin. Science 290:977.

Kennedy, B. M., W. L. Gale, and K. G. Ostrand. 2007. Relationship between smolt gill Na+, K+ ATPase activity and migration timing to avian predation risk of steelhead trout (*Oncorhynchus mykiss*) in a large estuary. Canadian Journal of Fisheries and Aquatic Sciences 64:1506-1516.

Korstrom, J. S., and I. K. Birtwell. 2006. Effects of suspended sediment on the escape behavior and cover-seeking response of juvenile Chinook salmon in freshwater. Transactions of the American Fisheries Society 135:1006-1016.

Latta, W. C., and R. F. Sharkey. 1966. Feeding behavior of the American merganser in captivity. Journal of Wildlife Management 30:17-23.

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.

Mathur, D., P. G. Heisey, E. T. Euston, J. R. Skalski, and S. Hays. 1996. Turbine passage survival estimation for Chinook salmon smolts (*Oncorhynchus tshawytscha*) at a large dam on the Columbia River. Canadian Journal of Fisheries and Aquatic Sciences 53:542-549.

McLeay, L. J., B. Page, S. D. Goldsworthy, T. M. Ward, and D. C. Paton. 2009. Size matters: variation in the diet of chick and adult crested terns. Marine Biology 156:1765-1780.

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., P. P. Thomas, M. G. Dena, and H. P. James. 1994. Are all prey created equal? A review and synthesis of differential predation on prey in substandard condition. Journal of Fish Biology 45:81-96.

Mesa, M. G., and J. J. Warren. 1997. Predator avoidance ability of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) subjected to sublethal exposures of gas-supersaturated water. Canadian Journal of Fisheries and Aquatic Sciences 54:757-764.

Mesa, M. G., T. P. Poe, A. G. Maule, and C. B. Schreck. 1998. Vulnerability to predation and physiological stress response in juvenile Chinook salmon (*Oncorhynchus tschawytscha*) experimentally infected with *Renibacterium salmoninarum*. Canadian Journal of Fisheries and Aquatic Sciences 55:1599-1606.

Nielsen, L. A. 1992. Methods for marking fish and shellfish. American Fisheries Society Special Publication, 23:104-109.

NOAA (National Oceanic and Atmospheric Administration) Fisheries. 2004. Biological opinion for consultation on remand for operation of the Columbia River Power System and 19 Bureau of Reclamation projects in the Columbia Basin, Portland, Oregon.

NOAA (National Oceanic and Atmospheric Administration) Fisheries. 2007. Draft biological opinion for consultation on remand for operation of the Columbia River Power System and 11 Bureau of Reclamation projects in the Columbia Basin and ESA section 10(a)(1)(A) permit for juvenile fish transportation program, Portland, Oregon.

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.

Prentice, E. F., T. A. Flagg, C. S. McCutcheon, D. F. Brastow, and D. C. Cross. 1990a. Equipment, methods and an automated data-entry station for PIT tagging. Pp. 335-340 *in* N. C. Parker, A. E. Giorgi, R. C. Heidinger, D. Jester, Jr., E. D. Prince, and G. A. Winans, editors. Fish-marking techniques. American Fisheries Society, Symposium 7, Bethesda, Maryland.

Prentice, E. F., T.A. Flagg, and C.S. McCutcheon. 1990b. Feasibility of using implantable passive integrated transponder (PIT) tags in salmonids. Pages 317-322 *in* N. C. Parker, A. E. Giorgi, R. C. Heidinger, D. Jester, Jr., E. D. Prince, and G. A. Winans, editors. Fish-marking techniques. American Fisheries Society, Symposium 7, Bethesda, Maryland.

Raymond, H. L. 1979. Effects of dams and impoundments on migrations of juvenile Chinook salmon and steelhead from the Snake River, 1966 to 1975. Transactions of the American Fisheries Society 108:505-529.

Raymond, H. L. 1988. Effects of hydroelectric development and fisheries enhancement on spring and summer Chinook salmon and steelhead in the Columbia River basin. North American Journal of Fisheries Management 8:1-24.

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., K. Collis, D. E. Lyons, D. P. Craig, J. Y. Adkins, A. Myers, and R. M. Suryan. 2002. Effects of colony relocation on diet and productivity of Caspian terns. Journal of Wildlife Management 66:662-673.

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.

Ryan, B. A., J. W. Ferguson, R. D. Ledgerwood, and E. P. Nunnallee. 2001. Detection of passive integrated transponder tags from juvenile salmonids on piscivorous bird colonies in the Columbia River basin. North American Journal of Fisheries Management 21:417-421.

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.

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.

Shealer, D. A. 1998. Size-selective predation by a specialist forager, the roseate tern. Auk 115:519-525.

Smith, S. G., W. D. Muir, J. G. Williams, and J. R. Skalski. 2002. Factors associated with travel time and survival of migrant yearling Chinook salmon and steelhead in the lower Snake River. North American Journal of Fisheries Management 22:385-405.

Stephens, D. W., and J. R. Krebs. 1986. Foraging theory. Princeton University Press, Princeton, New Jersey.

Strod, T., I. Izhaki, Z. Arad, and G. Katzir. 2008. Prey detection by great cormorant (*Phalacrocorax carbo sinensis*) in clear and in turbid water. Journal of Experimental Biology 211:866-872.

Temple, S. A. 1987. Do predators always capture substandard individuals disproportionately from prey populations? Ecology 68:669-674.

USFWS (U.S. Fish and Wildlife Service). 2006. Record of decision: Caspian tern management to reduce predation of juvenile salmonids in the Columbia River estuary: Final Environmental Impact Statement. Portland, Oregon.

Waples, R. S. 1991. Definition of ''species'' under the Endangered Species Act: application to Pacific salmon. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-194.

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.

Wedemeyer, G. A., D. J. McLeay, and C. P. Goodyear. 1984. Assessing the tolerance of fish and fish populations to environmental stress: the problems and methods of monitoring. Pp. 163-195 *in* V. W. Cairns, P. V. Hodson, and J. O. Nriagu, editors. Contaminant effects on fisheries. Wiley, New York.

Zimmerman, M. P. 1999. Food habits of smallmouth bass, walleyes, and northern pikeminnow in the lower Columbia River basin during outmigration of juvenile

anadromous salmonids. Transactions of the American Fisheries Society 128:1036-1054.

Table 3.1. Description, sample size (n), and prevalence (%) of external symptoms associated with steelhead captured at Lower Monumental and Ice Harbor dams in 2007 and 2008 (n = 16,258).

External Condition	n	%	Description
Body injury			
Absent	13,616	84%	No visible hemorrhaging, scarring, or other damage to the head, trunk, operculum, or eyes
Moderate	1,503	9%	Closed or healed scars to the head, trunk, operculum, or eyes
Severe	1,139	7%	Deformities, open wounds, or scarring on a large surface area of the head, trunk, operculum, or eyes
De-scaling			
< 5%	9,651	59%	De-scaling < 5% of body
5-20%	5,726	35%	De-scaling 5-20% of body
21-50%	808	5%	De-scaling 21-50% of body
> 50%	73	0.4%	De-scaling > 50% of body
Disease			
Absent	15,500	95%	No external symptoms of bacterial, fungal, or viral infections
Moderate	239	1%	Visible infection limited to one external area
Severe	519	3%	Visible infection in multiple areas or symptoms that suggest a systemic infection
Fin Damage			
Absent	2,819	17%	Fin wear and damage < 50% on any fin
Moderate	9,286	57%	Fin wear and damage > 50% on 1-2 fins
Severe	4,153	26%	Fin wear and damage > 50% on $\geq$ 3 fins
Parasites			
Absent	15,906	98%	No visible ectoparasites
Moderate	247	2%	Visible ectoparasites found in 1 area
Severe	105	1%	Visible ectoparasites in > 1 area or on gills

Table 3.2. Description, sample size (n), and prevalence (%) of integrated condition ranks associated with juvenile steelhead captured at Lower Monumental and Ice Harbor dams in 2007 and 2008 (n = 16,258).

Integrated Rank	N	%	Description
Good	9,399	58%	No noticeable external injury or symptoms of disease; de-scaling ≤ 10% of body surface
Fair	4,692	29%	Minor scars or other closed external damage; de-scaling > 10% but ≤ 50% of body surface
Poor	2,167	13%	Any steelhead with externally apparent fungal, parasitic, or bacterial infections, or de-scaling > 50% of body surface, or open body lesions

Table 3.3. Model selection results used to evaluate relationships between steelhead individual characteristics and susceptibility to predation by Crescent Island Caspian terns. Results from the five top models and the base model are shown.

Rank	Model[a]	K	AIC_c	ΔAIC_c	W_i
1	Base Model[b] + Length + Length^2 + Body Injury	8	3983.82	0.00	0.27
2	Base Model[b] + Length + Length^2 + Body Injury + H/W[c]	9	3984.68	0.86	0.17
3	Base Model[b] + Length + Length^2 + Fin Damage	8	3985.98	2.16	0.09
4	Base Model[b] + Length + Length^2	6	3986.23	2.41	0.08
5	Base Model[b] + Length + Length^2 + Integrated Condition	8	3986.33	2.51	0.08
37	Base Model[b]	4	4094.09	110.27	0.00

[a] See Methods for descriptions of each variable.

[b] Base model includes variables for colony-specific PIT tag detection efficiency, number of in-river steelhead, and number of Caspian terns on the Crescent Island colony.

[c] H/W = hatchery versus wild rearing types

Table 3.4. Odds ratios, upper and lower 95% confidence limits (UCL and LCL, respectively), and *P*-values (*P*) for the top model evaluating the relationship between individual characteristics of steelhead and susceptibility to predation by Crescent Island Caspian terns, after accounting for colony-specific PIT tag detection efficiency, number of steelhead in-river, and number of Caspian terns on the Crescent Island colony.

Variable[a]	Relative Predation Susceptibility			
	Odds Ratio	LCL	UCL	*P*
Body Injury: Moderate vs. Absent	0.89	0.64	1.23	0.45
Body Injury: Severe vs. Absent	1.45	1.07	1.97	**0.02**
Length [b]	3.97	2.66	5.94	**<0.0001**
Length^2 [b]	0.97	0.96	0.98	**<0.0001**

[a] See Methods for descriptions of variables.
[b] Odds ratios for length are associated with a 1-cm increase in fork length.

Table 3.5. Model selection results used to evaluate relationships between river condition factors and steelhead susceptibility to predation by Crescent Island Caspian terns. Results for the five top models and the base model are shown.

Rank	Model[a]	K	AIC_c	ΔAIC_c	W_i
1	Base Model[b] + Year + Discharge + Clarity	7	4047.13	0.00	0.38
2	Base Model[b] + Year + Discharge + Clarity + Temp	8	4047.90	0.77	0.26
3	Base Model[b] + Year + Discharge + Clarity + Loc	8	4048.66	1.53	0.18
4	Base Model[b] + Year + Discharge + Clarity + Temp + Loc	9	4049.24	2.11	0.13
5	Base Model[b] + Year + Clarity + Temp	7	4052.85	5.72	0.02
29	Base Model[b]	4	4094.09	46.96	0.00

[a] See Methods for variable descriptions.

[b] Base model includes variables for colony-specific PIT tag detection efficiency, number of in-river steelhead, and number of Caspian terns on the Crescent Island colony.

Table 3.6. Model selection results used to evaluate relationships between steelhead individual characteristics and susceptibility to predation by Foundation Island double-crested cormorants. Results from the top five models and the base model are shown.

Rank	Model[a]	K	AIC_c	ΔAIC_c	W_i
1	Base Model[b] + Diseased + H/W[c]	7	3073.52	0.00	0.48
2	Base Model[b] + Diseased + H/W[c] + Length	8	3075.01	1.49	0.23
3	Base Model[b] + Diseased	6	3076.12	2.60	0.13
4	Base Model[b] + Diseased + H/W[c] + Length + Length^2	9	3076.89	3.37	0.09
5	Base Model[b] + Diseased + Length	7	3078.03	4.51	0.05
28	Base Model[b]	4	3107.97	34.45	0.00

[a] See Methods for variable descriptions.

[b] Base model includes variables for colony-specific PIT tag detection efficiency, number of in-river steelhead, and number of double-crested cormorants on the Foundation Island colony.

[c] H/W = hatchery versus wild rearing types

Table 3.7. Odds ratios, upper and lower 95% confidence limits (UCL and LCL, respectively), and *P*-values (*P*) for the top model evaluating the relationship between individual characteristics of steelhead and susceptibility to predation by Foundation Island double-crested cormorants, after accounting for colony-specific PIT tag detection efficiency, number of steelhead in-river, and number of double-crested cormorants on the Foundation Island colony.

Variable[a]	Relative Predation Susceptibility			
	Odds ratio	LCL	UCL	*P*
Disease: Moderate vs. Absent	3.07	1.69	5.57	**< 0.001**
Disease: Severe vs. Absent	3.28	2.20	4.87	**< 0.0001**
Rearing: Hatchery vs. Wild	1.47	1.02	2.12	**0.04**

[a] See Methods for variable descriptions.

Table 3.8. Model selection results used to evaluate relationships between river condition factors and steelhead susceptibility to predation by Foundation Island double-crested cormorants. Results from five top models and the base model are shown.

Rank	Model[a]	K	AIC_c	ΔAIC_c	W_i
1	Base Model[b] + Loc + Year + Temp	7	3079.26	0.00	0.31
2	Base Model[b] + Loc + Year + Temp + Clarity	8	3079.52	0.26	0.27
3	Base Model[b] + Loc + Year + Temp + Discharge + Clarity	9	3080.52	1.26	0.17
4	Base Model[b] + Loc + Year + Temp + Discharge	8	3081.20	1.94	0.12
5	Base Model[b] + Loc + Year + Clarity	7	3083.49	4.23	0.04
29	Base Model[b]	4	3107.97	28.71	0.00

[a] See Methods for variable descriptions.

[b] Base model includes variables for colony-specific PIT tag detection efficiency, number of steelhead in-river, and number of double-crested cormorants on the Foundation Island colony.
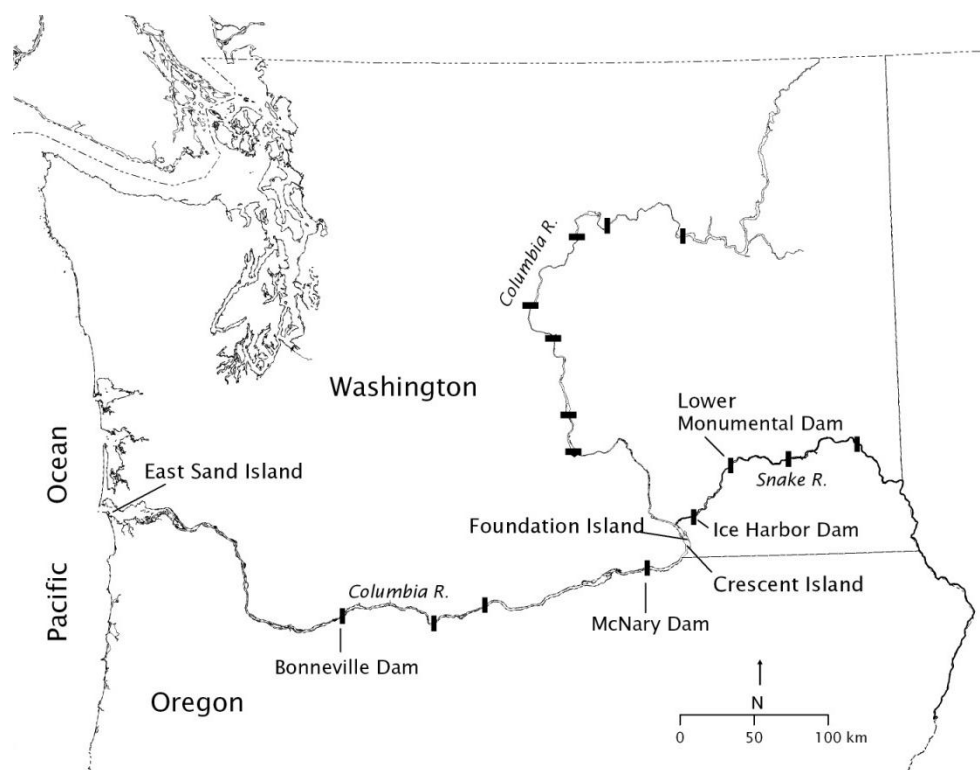
Figure 3.1. Map of the mainstem Columbia and Snake rivers showing major hydroelectric dams (bars), the Caspian tern colony (Crescent Island) and double-crested cormorant colony (Foundation Island) investigated in this study, and locations of additional bird colonies and dams mentioned in the text.

a.

b.

c.

d.

e.

f.

g.
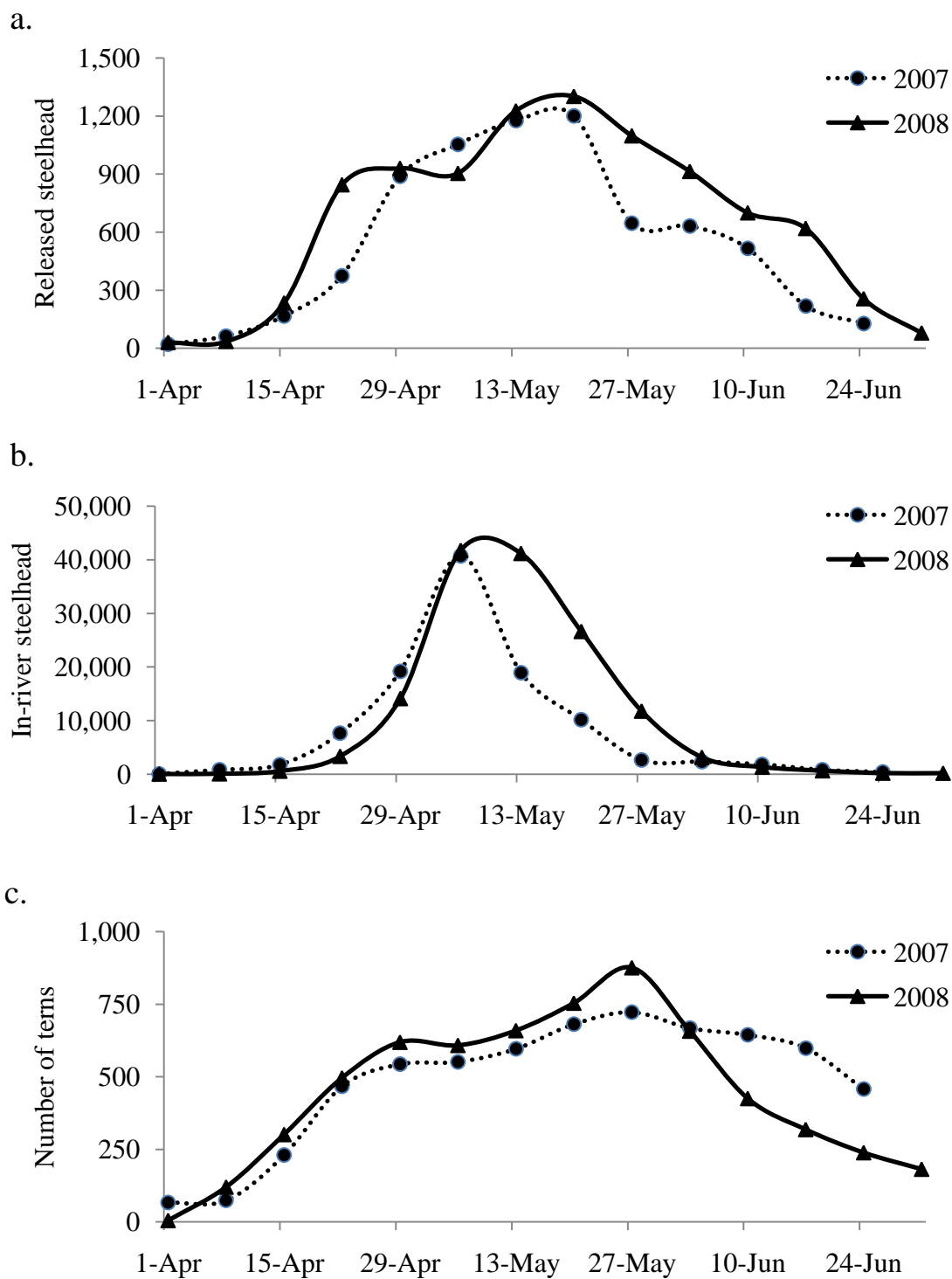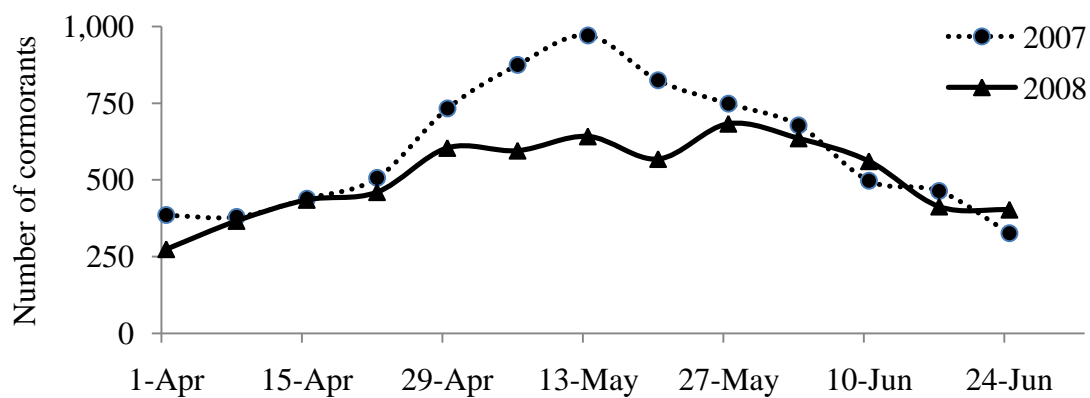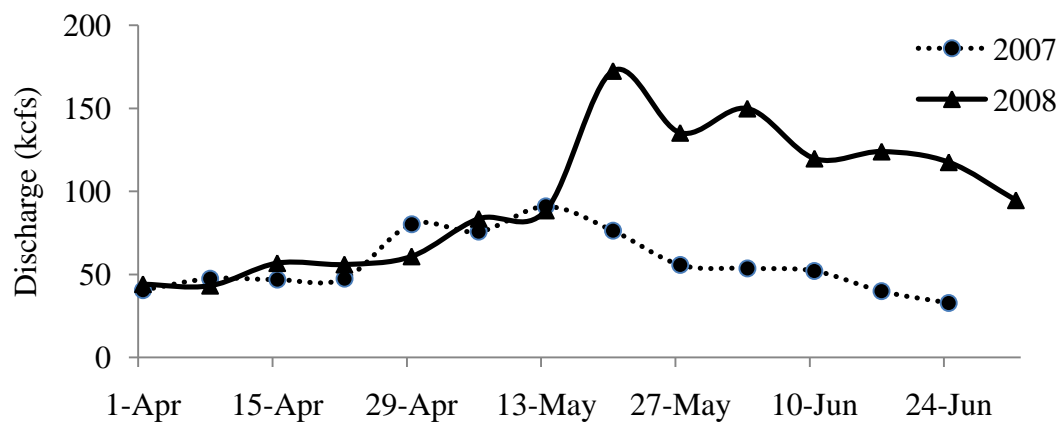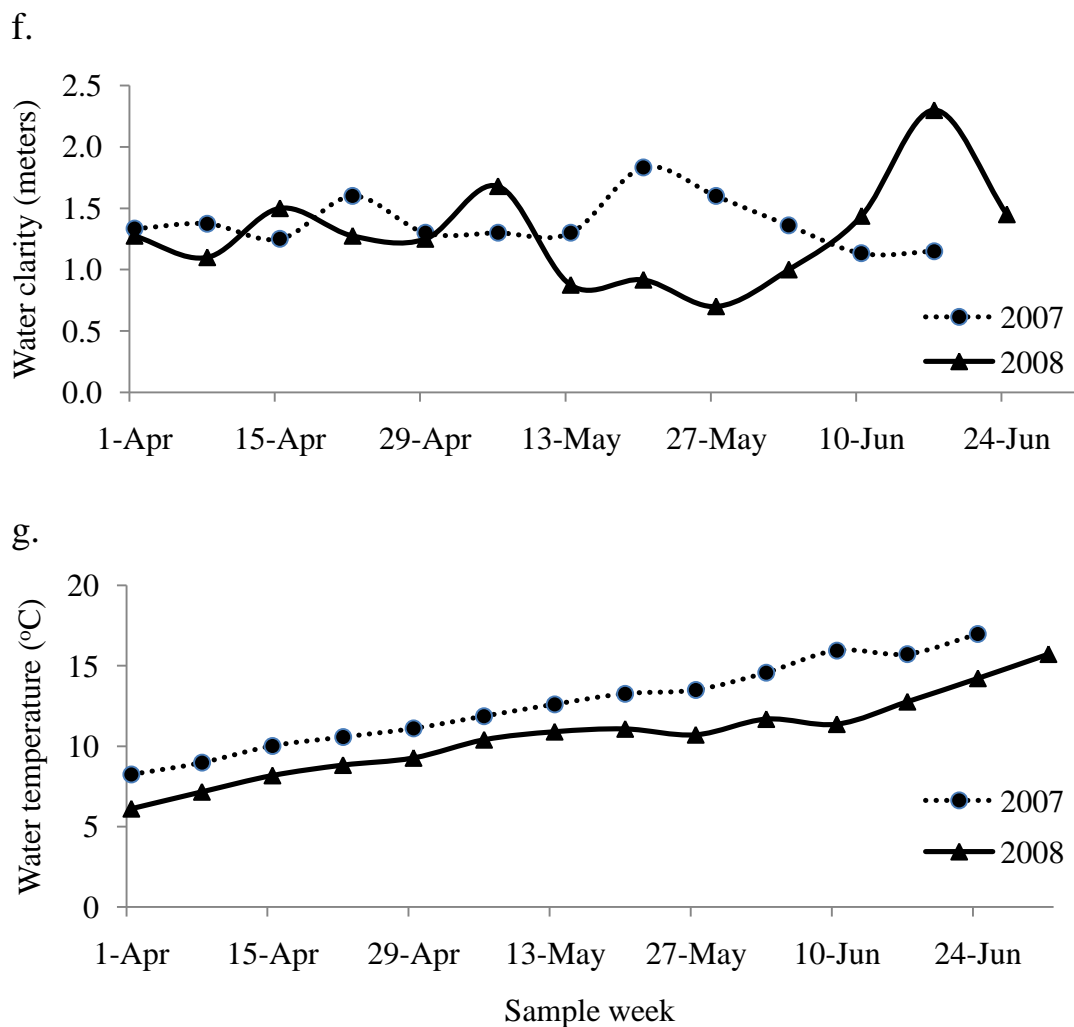
Figure 3.2. Weekly averages of (a) number of steelhead PIT-tagged and released as part of this study, (b) number of in-river steelhead as measured at McNary Dam, (c) number of Caspian terns on the Crescent Island colony (adults + juveniles), (d) number of double-crested cormorants on the Foundation Island colony (adults + juveniles), (e) water discharged (kcfs) from Lower Monumental Dam (LMN), (f) water clarity (Secchi reading in meters) measured at the confluence of the Snake and Columbia rivers, and (g) water temperature (^{o}C) measured at LMN. Data points are plotted on the first day of each sample week. See Methods for complete variable descriptions.
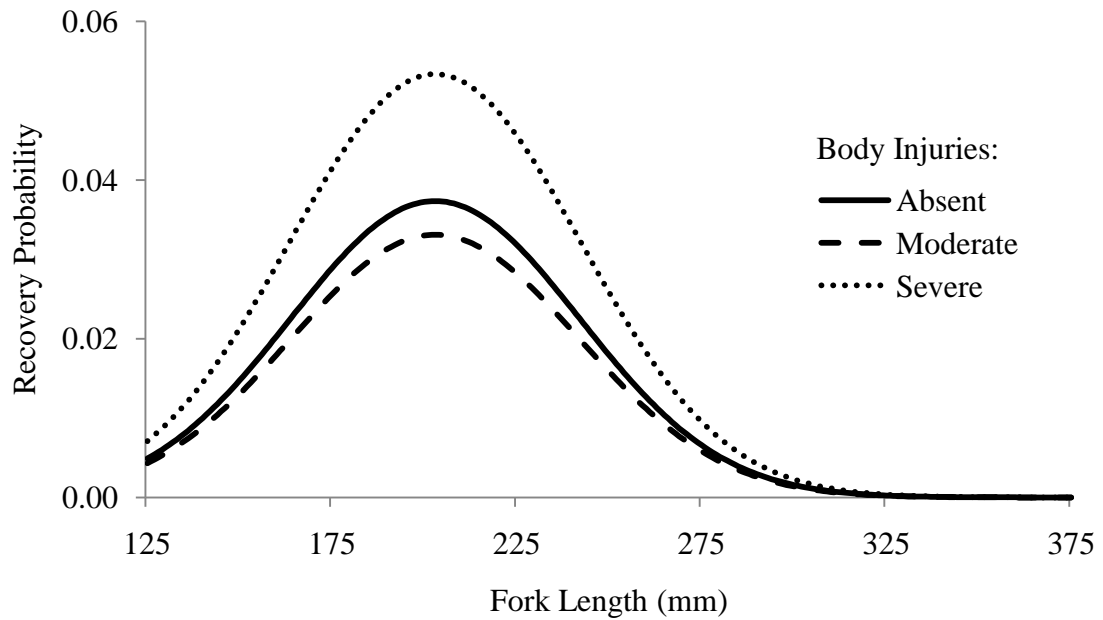
Figure 3.3. Regression lines from the top model predicting susceptibility of PIT-tagged juvenile steelhead released at Lower Monumental and Ice Harbor dams in 2007 and 2008 (n = 16,258) to predation by Crescent Island Caspian terns. Regression lines were calculated while other variables in the top model (colony-specific PIT tag detection efficiency, number of steelhead in-river, and number of Caspian terns on the Crescent Island colony) were held constant at their respective median values.

CHAPTER 4

SYNOPSIS, CONCLUSIONS, AND CONSERVATION APPLICATIONS

Nathan J. Hostetter

Management efforts to restore Pacific salmonids (*Oncorhynchus* spp.) have incorporated various strategies to reduce mortality and stress to juveniles during freshwater life stages. Efforts to restore evolutionarily significant units (ESUs; Waples 1991) of salmonids in the Columbia River basin) that are listed as threatened or endangered under the U.S. Endangered Species Act (ESA) have focused on the causes of salmonid population declines (i.e., overharvest, habitat destruction, hydropower development). Mortality factors that were not the original cause of declines, but may limit recovery of certain ESUs (i.e., hatchery production, predation) have also received conservation attention. Although predation on juvenile salmonids by piscivorous fish and birds has not been implicated as a cause of salmonid declines, some managers identify predation as a potentially significant limiting factor in recovery of ESA-listed salmonids (NOAA 2004, NOAA 2007). Several studies have quantified the number of juvenile salmonids consumed by various piscivorous bird colonies throughout the Columbia River basin (e.g., Collis et al. 2002, Roby et al. 2003, Ryan et al. 2003, Antolos et al. 2005); however, our understanding of the environmental factors and individual fish characteristics that influence the susceptibility of juvenile salmonids to avian predation is extremely limited. To address this paucity of knowledge, we investigated how survival, pathogen prevalence, and susceptibility to avian predation of migrating juvenile steelhead (*O. mykiss*) were associated with individual fish characteristics and river conditions.

Relationships between the external condition of steelhead smolts and their fitness were inferred by assessing relative differences in pathogen prevalence and subsequent survival during out-migration. Juvenile steelhead were assigned to several categories of health based on the presence or absence of external body injuries, de-scaling, externally-

visible symptoms of disease, fin damage, and ectoparasite infestations. My results indicated that external symptoms of disease, body injuries, and de-scaling were associated with reduced fitness in juvenile steelhead. For instance, steelhead with external symptoms of disease, body injuries, or de-scaling were more likely to carry infectious diseases and less likely to survive out-migration compared to steelhead without these conditions. The smolt PIT-tags recovered on a Caspian tern (*Hydroprogne caspia*) colony and on a double-crested cormorant (*Phalacrocorax auritus*) colony in the mid-Columbia River indicated that steelhead condition was also associated with susceptibility to avian predation; both avian predators disproportionately consumed steelhead in poorer health status.

Errington (1956) discussed the importance of changes in vulnerability when considering predation in animal populations. Compensation for mortality caused by predation is of strong interest to managers when evaluating the efficacy of predator control programs. Compensation for reduced predation mortality by increased mortality from other causes (e.g., other predators, disease, etc.) weakens the effectiveness of predator control (Banks 1999). In the Columbia River basin, the efficacy of predator control to restore salmonid populations depends on whether reductions in smolt mortality due to avian predation are compensated by other mortality factors. Increases in adult salmonid returns associated with reduced avian predation would be diminished if some steelhead consumed by avian predators would have died from other causes regardless (Schreck et al. 2006). Our results suggest that the effectiveness of management actions to reduce avian predation may be partially discounted by the higher susceptibility of unhealthy steelhead to avian predation. This higher susceptibility indicates that smolt

mortality due to avian predation is at least in part compensatory. However, several factors preclude this study from determining what percentage of salmonid mortality due to avian predation was compensatory, a factor of interest to fisheries managers (Roby et al. 2003).

First, the small proportion of juvenile steelhead displaying symptoms of poorer health suggests that the contribution of unhealthy steelhead to the total number of smolts consumed by avian predators is relatively minor, even though unhealthy smolts were more susceptible to avian predation. This observation implies that the majority of smolt mortality due to avian predation is additive. However, methods used by this study were not designed to determine if an individual steelhead smolt was healthy; health status was assigned relative to comparison groups. Therefore, steelhead classified as relatively healthy actually consisted of both healthy and unhealthy individuals. For example, 23% of a sample of steelhead classified as healthy (e.g., those without external symptoms of disease) tested positive for an infectious disease. Long-distance survival probabilities for smolts classified as healthy were as low as 50% in some groups. Our inability to completely address this within-group variation in fitness based on external appearance illustrates how methods that evaluate fish condition through categorical comparisons (e.g., steelhead with disease symptoms vs. steelhead without disease symptoms) greatly oversimplifies a complex continuum. The inability of this study to assign a quantitative estimate of individual steelhead fitness and reliably assign a health condition to each smolt indicates that any estimate of the level of compensatory mortality associated with avian predation would be inaccurate and likely an underestimate.

My results, however, do support the paradigm that predators disproportionately prey on individuals in substandard condition (*sensu* Temple 1987). Increased susceptibly

of steelhead in poorer health status is a principle that likely extends to predation by other colonial waterbirds throughout the Columbia River basin. However, some results of the present study may not be as widely applicable. For instance, fish behavior can be influenced by dynamic environmental conditions specific to estuaries, such as salinity gradients and tidal cycles. The increased stress associated with these transitions may differ between hatchery-reared and wild-origin salmonids (Kennedy et al. 2007). Therefore, although differences in susceptibility to avian predation between hatchery and wild steelhead were observed in the present study, further investigation into these relationships in the Columbia River estuary is warranted. Similarly, replication of this work involving various salmonid ESUs and bird colonies throughout the Columbia River basin will determine whether the results from this study can be generalized.

CONSERVATION APPLICATIONS

This study demonstrated that external fish condition, measured non-destructively at the level of the individual fish, was related to the general health status and fitness of migrating juvenile steelhead. The ability to non-lethally monitor relative changes in fish condition can improve our understanding of how various hydrosystem practices are associated with fish health and survival. Understanding causes of natural and anthropogenic stressors can increase the potential of management agencies to operate the hydrosystem in a manner that minimizes degradation of fish condition during and immediately following juvenile migration through the hydrosystem.

Currently, management to move a portion of the Caspian terns nesting in the Columbia River estuary to alternative colony sites outside the Columbia River basin is

being implemented, and research into management options to further reduce salmonid predation by piscivorous waterbirds is in progress (Roby et al. 2002, USFWS 2006). Our results indicate that steelhead susceptibility to avian predation would decline with a reduction in the number of Caspian terns and double-crested cormorants nesting at their respective breeding colonies on Crescent Island and Foundation Island in the mid-Columbia River. Additionally, an increase in abundance of in-river migrating steelhead smolts would reduce steelhead susceptibility to avian predation, presumably as a result of predator swamping. Our results also suggest that reductions in avian predation in McNary Pool may be attainable through efforts to increase discharge and preclude high water temperatures. However, evaluation of management options to reduce avian predation and increase juvenile salmonid survival must account for the higher susceptibility of unhealthy steelhead to avian predation. This higher susceptibility indicates that smolt mortality due to avian predation is partly compensatory; however, the level of compensation has yet to be identified.

Empirical predator-prey studies that investigate prey characteristics and environmental conditions at or near the time of predation provide important information applicable to management decisions and practices (Mesa et al. 1994). Replication of the present study with various salmonid ESUs and colonies of avian predators should reduce some of the ambiguity in our results and clarify relationships among individual smolt characteristics, river conditions, and susceptibility of out-migrating juvenile salmonids to avian predation. Identifying individual smolt characteristics and hydrosystem practices that affect smolt survival and susceptibility to predation can aid in development of management plans that benefit entire salmonid populations and contribute to recovery of

Columbia Basin salmonid stocks currently listed as threatened or endangered under the

ESA.

LITERATURE CITED

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.

Banks, P. B. 1999. Predation by introduced foxes on native bush rats in Australia: do foxes take the doomed surplus? Journal of Applied Ecology 36:1063-1071.

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 loses of juvenile salmonids to avian predation. Transactions of the American Fisheries Society 131:537-550.

Errington, P. L. 1956. Factors limiting higher vertebrate populations. Science 124:304-307.

Kennedy, B. M., W. L. Gale, and K. G. Ostrand. 2007. Relationship between smolt gill Na+, K+ ATPase activity and migration timing to avian predation risk of steelhead trout (*Oncorhynchus mykiss*) in a large estuary. Canadian Journal of Fisheries and Aquatic Sciences 64:1506-1516.

Mesa, M. G., P. P. Thomas, M. G. Dena, and H. P. James. 1994. Are all prey created equal? A review and synthesis of differential predation on prey in substandard condition. Journal of Fish Biology 45:81-96.

NOAA (National Oceanic and Atmospheric Administration) Fisheries. 2004. Biological opinion for consultation on remand for operation of the Columbia River Power System and 19 Bureau of Reclamation projects in the Columbia Basin, Portland, Oregon.

NOAA (National Oceanic and Atmospheric Administration) Fisheries. 2007. Draft biological opinion for consultation on remand for operation of the Columbia River Power System and 11 Bureau of Reclamation projects in the Columbia Basin and ESA section 10(a)(1)(A) permit for juvenile fish transportation program, Portland, Oregon.

Roby, D. D., K. Collis, D. E. Lyons, D. P. Craig, J. Y. Adkins, A. Myers, and R. M. Suryan. 2002. Effects of colony relocation on diet and productivity of Caspian terns. Journal of Wildlife Management 66:662-673.

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.

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.

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.

Temple, S. A. 1987. Do predators always capture substandard individuals disproportionately from prey populations? Ecology 68:669-674.

USFWS (U.S. Fish and Wildlife Service). 2006. Record of decision: Caspian tern management to reduce predation of juvenile salmonids in the Columbia River estuary: Final Environmental Impact Statement. Portland, Oregon.

Waples, R. S. 1991. Definition of ''species'' under the Endangered Species Act: application to Pacific salmon. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-194.

BIBLIOGRAPHY

Adams, S. M., editor. 1990. Biological indicators of stress in fish. American Fisheries Society, Symposium 8. Bethesda, Maryland.

Adams, S. M., A. M. Brown, and R. W. Goede. 1993. A quantitative health assessment index for rapid evaluation of fish condition in the field. Transactions of the American Fisheries Society 122:63-73.

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.

Arkoosh, M. R., T. K. Collier. 2002. Ecological risk assessment paradigm for salmon: analyzing immune function to evaluate risk. Human & Ecological Risk Assessment 8:265.

Arkoosh, M. R., E. Clemons, A. N. Kagley, C. Stafford, A. C. Glass, K. Jacobson, P. Reno, M. S. Myers, E. Casillas, F. Loge, L. L. Johnson, and T. K. Collier. 2004. Survey of pathogens in juvenile salmon (*Oncorhynchus* spp.) migrating through Pacific Northwest estuaries. Journal of Aquatic Animal Health 16:186-196.

Arkoosh, M. R., A. N. Kagley, B. F. Anulacion, D. A. Boylen, B. P. Sandford, F. J. Loge, L. L. Johnson, and T. K. Collier. 2006. Disease susceptibility of hatchery Snake River spring-summer Chinook salmon with different juvenile migration histories in the Columbia River. Journal of Aquatic Animal Health 18:223-231.

Baltz, D. M., G. V. Morejohn, and B. S. Antrim. 1979. Size selective predation and food habits of two California terns. Western Birds 10:17-24.

Bancroft, J. D., and A. Stevens. 1994. Manual of histological techniques and their diagnostic applications, 2nd edition. Churchill Livingstone, Edinburgh, UK.

Banks, P. B. 1999. Predation by introduced foxes on native bush rats in Australia: do foxes take the doomed surplus? Journal of Applied Ecology 36:1063-1071.

Barton, B. A., C. B. Schreck, and L. A. Sigismondi. 1986. Multiple acute disturbances evoke cumulative physiological stress responses in juvenile Chinook salmon. Transactions of the American Fisheries Society 115:245-251.

Barton, B. A., J. D. Morgan, and M. M. Vijaya. 2002. Physiological and condition-related indicators of environmental stress in fish. Pp. 111-148 *in* S. M. Adams, editor.

Biological indicators of aquatic ecosystem stress. American Fisheries Society, Bethesda, Maryland.

Beamesderfer, R. C., B. E. Rieman, L. J. Bledsoe, and S. Vigg. 1990. Management implications of a model of predation by a resident fish on juvenile salmonids migrating through a Columbia River reservoir. North American Journal of Fisheries Management 10:290-304.

Berggren, T. J., and M. J. Filardo. 1993. An analysis of variables influencing the migration of juvenile salmonids in the Columbia River basin. North American Journal of Fisheries Management 13:48-63.

Bouck, G. R., and S. D. Smith. 1979. Mortality of experimentally descaled smolts of Coho salmon (*Oncorhynchus kisutch*) in fresh and salt water. Transactions of the American Fisheries Society 108:67-69.

Budy, P., G. P. Thiede, N. Bouwes, C. E. Petrosky, and H. Schaller. 2002. Evidence linking delayed mortality of Snake River salmon to their earlier hydrosystem experience. North American Journal of Fisheries Management 22:35-51.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and inference - a practical information-theoretic approach, 2nd edition. Springer-Verlag, New York, New York.

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 loses of juvenile salmonids to avian predation. Transactions of the American Fisheries Society 131:537-550.

Collis, K., D. D. Roby, D. E. Lyons, Y. Suzuki, J. Y. Adkins, L. Reinalda, N. Hostetter, L. Adrean, M. Bockes, P. Loschl, D. Battaglia, T. Marcella, B. Cramer, A. F. Evans, M. Hawbecker, M. Carper, J. Sheggeby, and S. Sebring. 2009. Research, monitoring, and evaluation of avian predation on salmonid smolts in the lower and mid-Columbia River: 2008 final season summary. Project report submitted to Bonneville Power Administration and the U.S. Army Corps of Engineers, Portland, OR.

Connor, W. P., H. L. Burge, J. R. Yearsley, and T. C. Bjornn. 2003. Influence of flow and temperature on survival of wild subyearling fall Chinook salmon in the Snake River. North American Journal of Fisheries Management 23:362-375.

Cormack, R. M. 1964. Estimates of survival from the sighting of marked animals. Biometrika 51:429-438.

Coutant, C. C. 1973. Effect of thermal shock on vulnerability of juvenile salmonids to predation. Journal of the Fisheries Research Board of Canada 30:965-973.

Cuthbert, F. J., and L. R. Wires. 1999. Caspian tern (*Sterna caspia*). No. 403 *in* A. Poole, and F. Gill, editors. The Birds of North America. The Birds of North America Inc., Philadelphia, Pennsylvania.

DART. 1995. Columbia River data access in real time: online interactive database of the Columbia basin research group. University of Washington School of Aquatic and Fishery Sciences.

De Robertis, A., C. H. Ryer, A. Veloza, and R. D. Brodeur. 2003. Differential effects of turbidity on prey consumption of piscivorous and planktivorous fish. Canadian Journal of Fisheries and Aquatic Sciences 60:1517-1526.

Deriso, R. B., D. R. Marmorek, and I. J. Parnell. 2001. Retrospective patterns of differential mortality and common year-effects experienced by spring and summer Chinook salmon (*Oncorhynchus tshawytscha*) of the Columbia River. Canadian Journal of Fisheries and Aquatic Sciences 58:2419-2430.

Errington, P. L. 1956. Factors limiting higher vertebrate populations. Science 124:304-307.

Evans, A. F., R. E. Beaty, M. S. Fitzpatrick, and K. Collis. 2004. Identification and enumeration of steelhead kelts at a Snake River hydroelectric dam. Transactions of the American Fisheries Society 133:1089-1099.

Federal Caucus. 2000. Conservation of Columbia Basin fish: Final basinwide salmon recovery strategy. Federal Caucus, Portland, Oregon.

Ferguson, J. W., G. M. Matthews, R. L. McComas, R. F. Absolon, D. A. Brege, M. H. Gessel, and L. G. Gilbreath. 2005. Passage of adult and juvenile salmonids through federal Columbia River power system dams. NOAA Technical Memorandum NMFS-NWFSC-64.

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., J. L. Scott, and T. N. Pearsons. 2007. The effects of domestication on the relative vulnerability of hatchery and wild origin spring Chinook salmon (*Oncorhynchus tshawytscha*) to predation. Canadian Journal of Fisheries and Aquatic Sciences 64:813-818.

Fryer, J. L., and C. N. Lannan. 1993. The history and current status of *Renibacterium salmoninarum*, the causative agent of bacterial kidney disease in Pacific salmon. Fisheries Research 17:15-33.

Goede, R. W., A. B. Bruce, and S. M. Adams. 1990. Organismic indices and an autopsy-based assessment as indicators of health and condition of fish. American Fisheries Society Symposium 8:93-108.

Good, T. P., R. S. Waples, and P. Adams (editors). 2005. Updated status of federally listed ESUs of West Coast salmon and steelhead. NOAA Technical Memorandum NMFS-NWFSC-66:598.

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.

Gregory, R. S. 1993. Effect of turbidity on the predator avoidance-behavior of juvenile Chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 50:241-246.

Gregory, R. S., and C. D. Levings. 1998. Turbidity reduces predation on migrating juvenile Pacific salmon. Transactions of the American Fisheries Society 127:275-285.

Hatch, J. J., and D. V. Weseloh. 1999. Double-crested cormorant (*Phalacrocorax auritus*). No. 411 *in* A. Poole, and F. Gill, editors. The Birds of North America,. The Birds of North America Inc., Philadelphia, Pennsylvania.

Hokanson, K. E. F., C. F. Kleiner, and T. W. Thorslund. 1977. Effects of constant temperatures and diel temperature fluctuations on specific growth and mortality rates and yield of juvenile rainbow trout, *Salmo gairdneri*. Journal of the Fisheries Research Board of Canada 34:639-648.

Hopwood, D. 1990. Fixation and fixatives. Pp. 21-42 *in* J. D. Bancroft and A. Stevens, editors. Theory and practice of histological techniques. Churchill Livingstone, Edinburgh, UK.

Johnsson, J. I., and M. V. Abrahams. 1991. Interbreeding with domestic strain increases foraging under threat of predation in juvenile steelhead trout (*Oncorhynchus mykiss*): an experimental study. Canadian Journal of Fisheries and Aquatic Sciences 48:243-247.

Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika 52:225-247.

Kareiva, P., and M. Marvier. 2000. Recovery and management options for spring/summer Chinook salmon in the Columbia River basin. Science 290:977.

Keefer, M. L., R. H. Wertheimer, A. F. Evans, C. T. Boggs, and C. A. Peery. 2008. Iteroparity in Columbia River summer-run steelhead (*Oncorhynchus mykiss*): implications for conservation. Canadian Journal of Fisheries and Aquatic Sciences 65:2592-2605.

Kennedy, B. M., W. L. Gale, and K. G. Ostrand. 2007. Relationship between smolt gill Na+, K+ ATPase activity and migration timing to avian predation risk of steelhead trout (*Oncorhynchus mykiss*) in a large estuary. Canadian Journal of Fisheries and Aquatic Sciences 64:1506-1516.

Korstrom, J. S., and I. K. Birtwell. 2006. Effects of suspended sediment on the escape behavior and cover-seeking response of juvenile Chinook salmon in freshwater. Transactions of the American Fisheries Society 135:1006-1016.

Kostecki, T., P. Clifford, S. P. Gloss, and J. C. Carlisle. 1987. Scale loss and survival in smolts of Atlantic salmon (*Salmo salar*) after turbine passage. Canadian Journal of Fisheries and Aquatic Sciences 44:210-214.

LaPatra, S. E. 1998. Factors affecting pathogenicity of infectious hematopoietic necrosis virus (IHNV) for salmonid fish. Journal of Aquatic Animal Health 10:121-131.

Latta, W. C., and R. F. Sharkey. 1966. Feeding behavior of the American merganser in captivity. Journal of Wildlife Management 30:17-23.

Lichatowich, J. 1999. Salmon without rivers: a history of the Pacific salmon crisis. Island Press, Washington D.C.

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.

Mathur, D., P. G. Heisey, E. T. Euston, J. R. Skalski, and S. Hays. 1996. Turbine passage survival estimation for Chinook salmon smolts (*Oncorhynchus tshawytscha*) at a large dam on the Columbia River. Canadian Journal of Fisheries and Aquatic Sciences 53:542-549.

Maule, A. G., R. A. Tripp, S. L. Kaattari, C. B. Schreck, and S. L. Kaatari. 1989. Stress alters immune function and disease resistance in Chinook salmon (*Oncorhynchus tshawytscha*). Journal of Endocrinology 120:135-142.

McClure, M. M., E. E. Holmes, B. L. Sanderson, and C. E. Jordan. 2003. A large-scale, multispecies status assessment: anadromous salmonids in the Columbia River basin. Ecological Applications 13:964-989.

McEwen, B. S., and E. Stellar. 1993. Stress and the individual: mechanisms leading to disease. Archives of Internal Medicine 153:2093-2101.

McLeay, L. J., B. Page, S. D. Goldsworthy, T. M. Ward, and D. C. Paton. 2009. Size matters: variation in the diet of chick and adult crested terns. Marine Biology 156:1765-1780.

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., P. P. Thomas, M. G. Dena, and H. P. James. 1994. Are all prey created equal? A review and synthesis of differential predation on prey in substandard condition. Journal of Fish Biology 45:81-96.

Mesa, M. G., and J. J. Warren. 1997. Predator avoidance ability of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) subjected to sublethal exposures of gas-supersaturated water. Canadian Journal of Fisheries and Aquatic Sciences 54:757-764.

Mesa, M. G., T. P. Poe, A. G. Maule, and C. B. Schreck. 1998. Vulnerability to predation and physiological stress response in juvenile Chinook salmon (*Oncorhynchus tschawytscha*) experimentally infected with *Renibacterium salmoninarum*. Canadian Journal of Fisheries and Aquatic Sciences 55:1599-1606.

Muir, W. D., S. G. Smith, J. G. Williams, E. E. Hockersmith, and J. R. Skalski. 2001. Survival estimates for migrant yearling Chinook salmon and steelhead tagged with passive integrated transponders in the lower Snake and lower Columbia rivers. North American Journal of Fisheries Management 21:269-282.

Nielsen, L. A. 1992. Methods for marking fish and shellfish. American Fisheries Society Special Publication, 23:104-109.

NOAA (National Oceanic and Atmospheric Administration) Fisheries. 2004. Biological opinion for consultation on remand for operation of the Columbia River Power System and 19 Bureau of Reclamation projects in the Columbia Basin, Portland, Oregon.

NOAA (National Oceanic and Atmospheric Administration) Fisheries. 2007. Draft biological opinion for consultation on remand for operation of the Columbia River Power System and 11 Bureau of Reclamation projects in the Columbia Basin and ESA section 10(a)(1)(A) permit for juvenile fish transportation program, Portland, Oregon.

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. B. Schreck. 1992. Comparison of predator avoidance capabilities with corticosteroid levels induced by stress in juvenile coho salmon. Transactions of the American Fisheries Society 121:544-547.

Peters, G., M. Faisal, T. Lang, and A. Iman. 1988. Stress caused by social interaction and its effect on susceptibility to *Aeromonas hydrophila* infection in rainbow trout (*Salmo gairdneri*). Diseases of Aquatic Organisms 4:83-89.

Pickering, A. D. 1993. Endocrine-induced pathology in stressed salmonid fish. Fisheries Research 17:35-50.

Plumb, J. M., R. W. Perry, N. S. Adams, and D. W. Rondorf. 2006. The effects of river impoundment and hatchery rearing on the migration behavior of juvenile steelhead in the Lower Snake River, Washington. North American Journal of Fisheries Management 26:438-452.

Pochop, P. A., J. L. Cummings, C. A. Yoder, and J. E. Steuber. 1998. Comparison of white mineral oil and corn oil to reduce hatchability in ring-billed gull eggs. Proceedings of Vertebrate Pest Conference 18:411-413.

Prentice, E. F., T. A. Flagg, C. S. McCutcheon, D. F. Brastow, and D. C. Cross. 1990a. Equipment, methods and an automated data-entry station for PIT tagging. Pp. 335-340 *in* N. C. Parker, A. E. Giorgi, R. C. Heidinger, D. Jester, Jr., E. D. Prince, and G. A. Winans, editors. Fish-marking techniques. American Fisheries Society, Symposium 7, Bethesda, Maryland.

Prentice, E. F., T. A. Flagg, C. S. McCutcheon, and D. F. Brastow. 1990b. PIT-tag monitoring systems for hydroelectric dams and fish hatcheries. Pp. 323-334 *in* N. C. Parker, A. E. Giorgi, R. C. Heidinger, D. Jester, Jr., E. D. Prince, and G. A. Winans, editors. Fish-marking techniques. American Fisheries Society, Symposium 7, Bethesda, Maryland.

Prentice, E. F., T.A. Flagg, and C.S. McCutcheon. 1990c. Feasibility of using implantable passive integrated transponder (PIT) tags in salmonids. Pp. 317-322 *in* N. C. Parker, A. E. Giorgi, R. C. Heidinger, D. Jester, Jr., E. D. Prince, and G. A. Winans, editors. Fish-marking techniques. American Fisheries Society, Symposium 7, Bethesda, Maryland.

Presnell, J. K., and M. P. Schreibman. 1997. Humason's animal tissue techniques, 5th edition. Johns Hopkins University Press, Baltimore.

R Development Core Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Raymond, H. L. 1979. Effects of dams and impoundments on migrations of juvenile Chinook salmon and steelhead from the Snake River, 1966 to 1975. Transactions of the American Fisheries Society 108:505-529.

Raymond, H. L. 1988. Effects of hydroelectric development and fisheries enhancement on spring and summer Chinook salmon and steelhead in the Columbia River basin. North American Journal of Fisheries Management 8:1-24.

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., K. Collis, D. E. Lyons, D. P. Craig, J. Y. Adkins, A. Myers, and R. M. Suryan. 2002. Effects of colony relocation on diet and productivity of Caspian terns. Journal of Wildlife Management 66:662-673.

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.

Ruggerone, G. T. 1986. Consumption of migrating juvenile salmonids by gulls foraging below a Columbia River dam. Transactions of the American Fisheries Society 115:736-742.

Ryan, B. A., J. W. Ferguson, R. D. Ledgerwood, and E. P. Nunnallee. 2001. Detection of passive integrated transponder tags from juvenile salmonids on piscivorous bird colonies in the Columbia River basin. North American Journal of Fisheries Management 21:417-421.

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.

Schreck, C. B. 1981. Stress and compensation in teleostean fishes: response to social and physical factors. Pp. 295-321 in A. D. Pickering, editor. Stress and fish. Academic Press, New York.

Schreck, C. B. 1990. Physiological, behavioral and performance indicators of stress. Pp. 29-37 in S. M. Adams, editor. Biological indicators of stress in fish. American Fisheries Society, Symposium 8, Bethesda, Maryland.

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.

Seber, G. A. F. 1965. A note on the multiple-recapture census. Biometrika 52:249-259.

Shealer, D. A. 1998. Size-selective predation by a specialist forager, the roseate tern. Auk 115:519-525.

Skalski, J. R. 1998. Estimating season-wide survival rates of outmigrating salmon smolt in the Snake River, Washington. Canadian Journal of Fisheries and Aquatic Sciences 55:761-769.

Smith, S. G., W. D. Muir, J. G. Williams, and J. R. Skalski. 2002. Factors associated with travel time and survival of migrant yearling Chinook salmon and steelhead in the lower Snake River. North American Journal of Fisheries Management 22:385-405.

Stephens, D. W., and J. R. Krebs. 1986. Foraging theory. Princeton University Press, Princeton, New Jersey.

Strod, T., I. Izhaki, Z. Arad, and G. Katzir. 2008. Prey detection by great cormorant (*Phalacrocorax carbo sinensis*) in clear and in turbid water. Journal of Experimental Biology 211:866-872.

Temple, S. A. 1987. Do predators always capture substandard individuals disproportionately from prey populations? Ecology 68:669-674.

USFWS (U.S. Fish and Wildlife Service). 2006. Record of decision: Caspian tern management to reduce predation of juvenile salmonids in the Columbia River estuary: Final Environmental Impact Statement. Portland, Oregon.

Waples, R. S. 1991. Definition of ''species'' under the Endangered Species Act: application to Pacific salmon. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-194.

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.

Wedemeyer, G. A., D. J. McLeay, and C. P. Goodyear. 1984. Assessing the tolerance of fish and fish populations to environmental stress: the problems and methods of monitoring. Pp. 163-195 *in* V. W. Cairns, P. V. Hodson, and J. O. Nriagu, editors. Contaminant effects on fisheries. Wiley, New York.

Wendelaar Bonga, S. E. 1997. The stress response in fish. Physiological Reviews 77:591-625.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:120-138.

Wiese, F. K., J. K. Parrish, C. W. Thompson, and C. Maranto. 2008. Ecosystem-based management of predator-prey relationships: Piscivorous birds and salmonids. Ecological Applications 18:681-700.

York, D. L., J. L. Cummings, J. E. Steuber, P. A. Pochop, and C. A. Yoder. 2000. Importance of migrating salmon smolt in ring-billed (*Larus delawarensis*) and California gull (*L. californicus*) diets near Priest Rapids Dam, Washington. Western North American Naturalist 60:216-220.

Zabel, R. W., T. Wagner, J. L. Congleton, S. G. Smith, and J. G. Williams. 2005. Survival and selection of migrating salmon from capture-recapture models with individual traits. Ecological Applications 15:1427-1439.

Zimmerman, M. P. 1999. Food habits of smallmouth bass, walleyes, and northern pikeminnow in the lower Columbia River basin during outmigration of juvenile anadromous salmonids. Transactions of the American Fisheries Society 128:1036-1054.

APPENDICES

Appendix A. Model selection results for models investigating steelhead PIT tag detection probability (p) using base model covariates and a highly parameterized base survival model (φ). Short-distance survival (a) represents survival from Lower Monumental Dam (LMN) to McNary Dam (ca. 119 Rkm), and long-distance survival (b) represents survival from LMN to Bonneville Dam (ca. 354 Rkm). All models < 7 AIC_c units from the top model are shown.

a. Short-distance survival

Rank	Model[a]	$QAIC_c$	K	$\Delta QAIC_c$	W_i
1	{φ(LOC+YR*RUN) p(LOC+LEN+YR*RUN)}	15327.34	15	0.00	0.40
2	{φ(LOC+YR*RUN) p(LOC+LEN +YR*RUN+ORIGIN)}	15328.71	16	1.37	0.20
3	{φ(LOC+YR*RUN) p(LOC+LEN +YR+RUN)}	15329.16	13	1.82	0.16
4	{φ(LOC+YR*RUN) p(LOC+LEN +RUN)}	15329.47	12	2.13	0.14
5	{φ(LOC+YR*RUN) p(LOC+LEN+ YR+RUN+ORIGIN)}	15330.38	14	3.04	0.09

b. Long-distance survival

Rank	Model[a]	$QAIC_c$	K	$\Delta QAIC_c$	W_i
1	{φ(LOC+YR*RUN) p(LOC+LEN +YR*RUN)}	6221.34	15	0.00	0.50
2	{φ(LOC+YR*RUN) p(LOC+LEN +YR*RUN+ORIGIN)}	6221.71	16	0.37	0.42
3	{φ(LOC+YR*RUN) p(LOC+LEN +YR+RUN)}	6226.31	13	4.97	0.04
4	{φ(LOC+YR*RUN) p(LOC+LEN +YR +RUN+ORIGIN)}	6226.78	14	5.44	0.03

[a] See Methods for variable descriptions.

Appendix B. Model selection results for models investigating steelhead apparent survival (φ) using base model covariates and top base model structure for PIT tag detection probability (p). Short-distance survival (a) represents survival from Lower Monumental Dam (LMN) to McNary Dam (ca. 119 Rkm), and long-distance survival (b) represents survival from LMN to Bonneville Dam (ca. 354 Rkm). All models < 7 AIC_c units from the top model are shown.

a. Short distance survival

Rank	Model[a]	$QAIC_c$	K	$\Delta QAIC_c$	W_i
1	{φ(LOC+LEN +YR*RUN+ORIGIN) p(LOC+LEN +YR*RUN)}	15309.92	17	0.00	0.93
2	{φ(LOC+LEN +YR*RUN) p(LOC+LEN +YR*RUN)}	15315.14	16	5.22	0.07

b. Hydrosystem survival

Rank	Model[a]	$QAIC_c$	K	$\Delta QAIC_c$	W_i
1	{φ(LOC+LEN) p(LOC+LEN+YR*RUN)}	6217.96	11	0.00	0.24
2	{φ(LOC+LEN+ORIGIN) p(LOC+LEN+YR*RUN)}	6218.82	12	0.85	0.16
3	{φ(LOC+LEN +YR*RUN) p(LOC+LEN+YR*RUN)}	6219.05	16	1.09	0.14
4	{φ(LOC+LEN +YR) p(LOC+LEN+YR*RUN)}	6219.43	12	1.46	0.12
5	{φ(LOC+LEN +YR*RUN +ORIGIN) p(LOC+LEN+YR*RUN)}	6220.12	17	2.15	0.08
6	{φ(LOC+LEN +RUN) p(LOC+LEN+YR*RUN)}	6220.57	13	2.61	0.07
7	{φ(LOC+YR*RUN+ORIGIN) p(LOC+LEN+YR*RUN)}	6221.09	16	3.13	0.05
8	{φ(LOC+YR*RUN) p(LOC+LEN+YR*RUN)}	6221.34	15	3.38	0.04
9	{φ(LOC+LEN +YR+RUN) p(LOC+LEN+YR*RUN)}	6222.47	14	4.51	0.03
10	{φ(LOC+LEN +YR+RUN+ORIGIN) p(LOC+LEN+YR*RUN)}	6223.43	15	5.47	0.02
11	{φ(LOC+ORIGIN) p(LOC+LEN+YR*RUN)}	6223.56	11	5.59	0.01
12	{φ(LOC+YR+ORIGIN) p(LOC+LEN+YR*RUN)}	6224.39	12	6.43	0.01
13	{φ(LOC) p(LOC+LEN+YR*RUN)}	6224.46	10	6.50	0.01
14	{φ(LOC+YR+RUN+ORIGIN) p(LOC+LEN+YR*RUN)}	6224.75	14	6.79	0.01

[a] See Methods for variable descriptions.

Appendix C. Parameter estimates, standard errors (SE), χ^2 statistics, and *P*-values from logistic regression models used to calculated weekly colony-specific PIT tag detection efficiencies for (a) Crescent Island Caspian terns in 2007, (b) Crescent Island Caspian terns in 2008, (c) Foundation Island double-crested cormorants in 2007, and (d) Foundation Island double-crested cormorants in 2008.

a. Crescent Island Caspian tern colony, 2007

Parameter	df	Estimate	SE	χ^2	*P*
Intercept	1	-0.240	0.117	4.16	0.041
Sample Week	1	0.145	0.012	140.91	<.0001

b. Crescent Island Caspian tern colony, 2008

Parameter	df	Estimate	SE	χ^2	*P*
Intercept	1	-0.907	0.137	43.99	<.0001
Sample Week	1	0.161	0.013	153.12	<.0001

c. Foundation Island double-crested cormorant colony, 2007

Parameter	df	Estimate	SE	χ^2	*P*
Intercept	1	1.220	0.175	48.69	<.0001
Sample Week	1	-0.022	0.017	1.85	0.174

d. Foundation Island double-crested cormorant colony, 2008

Parameter	df	Estimate	SE	χ^2	*P*
Intercept	1	1.329	0.156	72.85	<.0001
Sample Week	1	-0.028	0.015	3.26	0.071