

1988

The Breeding Ecology Of Pink Salmon (*Oncorhynchus Gorbuscha* Walbaum) From The Carp River, Eastern Lake Superior

Douglas Brian Noltie

Follow this and additional works at: <https://ir.lib.uwo.ca/digitizedtheses>

Recommended Citation

Noltie, Douglas Brian, "The Breeding Ecology Of Pink Salmon (*Oncorhynchus Gorbuscha* Walbaum) From The Carp River, Eastern Lake Superior" (1988). *Digitized Theses*. 1706.
<https://ir.lib.uwo.ca/digitizedtheses/1706>

This Dissertation is brought to you for free and open access by the Digitized Special Collections at Scholarship@Western. It has been accepted for inclusion in Digitized Theses by an authorized administrator of Scholarship@Western. For more information, please contact tadam@uwo.ca, wlsadmin@uwo.ca.

NOTICE

The quality of this microform is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us an inferior photocopy.

Previously copyrighted materials (journal articles, published tests, etc.) are not filmed.

Reproduction in full or in part of this microform is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30.

AVIS

La qualité de cette microforme dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de qualité inférieure.

Les documents qui font déjà l'objet d'un droit d'auteur (articles de revue, tests publiés, etc.) ne sont pas microfilmés.

La reproduction, même partielle, de cette microforme est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30.

THE BREEDING ECOLOGY OF
PINK SALMON (ONCORHYNCHUS GORBUSCHA WALBAUM)
FROM THE CARP RIVER, EASTERN LAKE SUPERIOR

by

Douglas B. Moltie

Department of Zoology

Submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy

Faculty of Graduate Studies
The University of Western Ontario
London, Ontario
January 1988

© Douglas B. Moltie 1988

Permission has been granted to the National Library of Canada to microfilm this thesis and to lend or sell copies of the film.

The author (copyright owner) has reserved other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without his/her written permission.

L'autorisation a été accordée à la Bibliothèque nationale du Canada de microfilmer cette thèse et de prêter ou de vendre des exemplaires du film.

L'auteur (titulaire du droit d'auteur) se réserve les autres droits de publication; ni la thèse ni de longs extraits de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation écrite.

ISBN 0-315-40783-2

ABSTRACT

Although inadvertently introduced to North America's Laurentian Great Lakes, pink salmon (Oncorhynchus gorbuscha) now constitute the world's only self-perpetuating freshwater population of this species. Their proliferation and growing impact on the extant fish fauna are elevating the species to one of considerable importance here. Despite this, the reproductive ecology of Great Lakes populations remains largely unknown. This study of the pink salmon breeding in the Carp River, a tributary to eastern Lake Superior, is a response to the need for this information. Considered are their upstream migration patterns, fish size and condition variation, migrant reproductive maturity and gonadal investment, male spawning performance, the determinants of male and female length of breeding life, rates of carcass recovery, and the wandering of spawners to other streams. Contrasts between Carp River and anadromous populations and between even- and odd-year runs into the same study stream are also emphasized.

Plasticity in the life histories of salmonid species is associated with the occurrence of alternative male breeding patterns. Because pink salmon display essentially invariable life histories, they seem unlikely to demonstrate similar breeding pattern diversity. Nonetheless, in behaviour studies some Carp River males

were seen to participate in spawnings by attempting to sneak fertilizations rather than by competing for access to females in characteristic salmonid fashion. These same individuals also resembled females in shape. Such behaviour was seen only at high spawner densities when single large males were apparently unable to monopolize nesting females. Consistent with these observations, morphological studies confirmed the occurrence of males which in shape resembled females more than did other males. Secondary sexual character development (hump size) was reduced in these individuals, likely as a result of their reduced condition. These female-like males did not differ from typical males in age, level of maturity, investment of biomass in testis, or length of breeding life. Thus, the occurrence of an alternative male breeding pattern in this population is interpreted as being a facultative response by males to reduced competitive ability.

ACKNOWLEDGEMENTS

In completing these studies, I drew on the talents, time, knowledge, and resources of many people. Foremost among these was my supervisor, Dr. Miles H.A. Keenleyside. He provided me far more than just the space in which to work and the finances with which to do it. His help in shaping and nurturing of the ideas contained between these covers and in refining their presentation has been much appreciated.

For the direction and assistance they provided along the way, I thank the members of my advisory committee: Drs. C.D. Ankney, D.M. Scott, and W-H. Kwain.

For field assistance, I am indebted to Frank Beletz, Dan Burton, Johnny Ellis, Josée Emerson, Nancy Kirkpatrick, Tammy McKellar, Elaine Noltie, Lionel Normand, and especially to Dan Robilliard whose pluck and perseverance I was able to take advantage of for an extended period.

My stay at the Silver Birch Lodge on the bank of the Carp River was made more pleasant by the company and interest shown by the following: Mrs. Edith Cox, Rod, Louanne and Tawney Cox, Jim and Millie Harvey, and Norman, Priscilla, Norman Jr., and Lisa Clement. The Carp River is certainly more theirs than mine, and I appreciated the loan of it.

Personnel at several agencies contributed materials, manpower, and ideas to the study. These included Dr. Tony Kwain, and Joe Cain, Lynn Golden, and Carlo Parker of the Ontario Ministry of Natural Resources, and Dr. J.J. Tibbles and Tom McAuley of the Sea Lamprey Control Centre in Sault Ste. Marie. Gaining a knowledge of the pink salmon literature was made possible in large part by the efforts of Agnes Kutas, Interlibrary Loans Officer at the University of Western Ontario's Sciences Library.

For their comraderie, I recognize the members of our laboratory group and the long-term inhabitants of the Collip Building. Of these, Simon Courtenay, Helene Dupuis, Greg Goff, Scott Hinch, Rob Mackereth, Bob Rangely, Mark Ridgway, Dan Robilliard, Keith Somers, and Peter Steele are of special note. From these individuals I have learned much, in part by osmosis, and in part by the friendly juxtaposition of ideas the challenging Collip environment seems to generate.

I am also grateful for the unfailing support of my wife, Elaine, and of my family, especially my parents, through the lengthy period required to finally arrive at this juncture. Their constant encouragement, understanding, and financial support made completing this work possible.

Final thanks is offered for the financial support this work received. Sources of funding included the 1984 Ontario Federation of Anglers and Hunters' Molson Research Grant in Sport Fisheries, an Ontario Ministry of Natural Resources Renewable Resources Research Grant, a Canadian Department of Fisheries and Oceans Science Subvention Grant, contributions from a Natural Sciences and Engineering Research Council of Canada (NSERC) operating grant awarded to my supervisor, Dr. Miles H.A. Keenleyside, and an NSERC Postgraduate Scholarship and Ontario Graduate Scholarships awarded to the author.

TABLE OF CONTENTS

Title Page	i
Certificate of Examination	ii
Abstract	iii
Acknowledgements	v
Table of Contents	viii
List of Tables	ix
List of Figures	xi
Preface	xii
Chapter 1	
General Introduction	1
References	7
Chapter 2	
Breeding Ecology of Pink Salmon (<u>Oncorhynchus gorbuscha</u>) from the Carp River, Eastern Lake Superior	12
Abstract	13
Introduction	14
Materials and Methods	16
Results	26
Discussion	67
Acknowledgements	83
References	84
Chapter 3	
Variation in Behaviour, Morphology and Ecology of Breeding Male Lake Superior Pink Salmon (<u>Oncorhynchus gorbuscha</u>)	110
Abstract	111
Introduction	112
Materials and Methods	117
Results	121
Discussion	145
Acknowledgements	150
References	150
Vita	165

LIST OF TABLES

Chapter 2

Table 1 Body length versus Julian date of catch relationships for male and female Carp River pink salmon 36

Table 2 Hourly catch frequencies of 1983 male and female Carp River pink salmon migrants during stream entry 38

Table 3 Mean body lengths of 1983 male and female Carp River pink salmon by hour of stream entry 40

Table 4 Yearly male and female Carp River pink salmon average lengths and weights 41

Table 5 Yearly body weight and body length relationships for Carp River pink salmon 43

Table 6 Comparison of secondary sexual character development in male and female Carp River pink salmon 46

Table 7 Between-year comparison of secondary sexual character development in male and female Carp River pink salmon 47

Table 8 Gonad maturity of male and female Carp River pink salmon 49

Table 9 Comparison of the unovulated and ovulated eggs of Carp River pink salmon females 51

Table 10 Secondary sexual character development in run- and pool-caught Carp River male and female pink salmon 54

Table 11	Comparison of ovary characteristics in Carp River female pink salmon	56
Table 12	Comparison of prespawning testis characteristics in Carp River male pink salmon	57
Table 13	Comparison of post-spawning testes in 1984 and 1985 male pink salmon	59
Table 14	Effect of spawner density on testis depletion in 1985 Carp River male pink salmon	61
Table 15	Determinants of length of breeding life in male and female Carp River pink salmon	64
Chapter 3		
Table 1	Studies of salmonid species in which alternative male breeding patterns occur	115
Table 2	Comparison of prespawning testes in typical and female-like pink salmon males	138
Table 3	Age distribution of Carp River female-like males	140
Table 4	Similarities in testis maturity, in typical and female-like Carp River male-pink salmon	142
Table 5	Comparison of post-spawning testes in typical and female-like Carp River male pink salmon	144

LIST OF FIGURES

Chapter 2

Figure 1 Carp River study site 18

Figure 2 1983 nightly catch numbers and associated environmental variables 28

Figure 3 1984 nightly catch numbers and associated environmental variables 31

Figure 4 1985 nightly catch numbers and associated environmental variables 34

Chapter 3

Figure 1 Relative positions of cluster and outlier males in a Carp River pink salmon spawning cluster 128

Figure 2 Discriminant function scores from 1984 and 1985 Carp River male and female morphological analyses 133

Figure 3 Plots of morphological variables for 1985 male, female, and female-like male Carp River pink salmon 136

PREFACE

"To be a philosopher is not merely to have subtle thoughts, nor even to found a school, but so to love wisdom as to live according to its dictates, a life of simplicity, independence, magnanimity and trust. It is to solve some of the problems of life, not only theoretically, but practically. The success of great scholars and thinkers is commonly a courtier-like success, not kingly, not manly."

Henry David Thoreau (1849).

A Week on the Concord and Merrimack Rivers,

"It may be quite misleading to presume to know what is in the mind of a salmon".

A.G. Huntsman (1945).

Trans. Am. Fish. Soc. 75: 257-266.

"...lugging a couple of salmon across country in a heavy tank of water may assist blood circulation, but it is bad for one's temper and not good for one's health".

G.M. King (1941).

The Field, April 19, pp. 496-497.

The author of this thesis has granted The University of Western Ontario a non-exclusive license to reproduce and distribute copies of this thesis to users of Western Libraries. Copyright remains with the author.

Electronic theses and dissertations available in The University of Western Ontario's institutional repository (Scholarship@Western) are solely for the purpose of private study and research. They may not be copied or reproduced, except as permitted by copyright laws, without written authority of the copyright owner. Any commercial use or publication is strictly prohibited.

The original copyright license attesting to these terms and signed by the author of this thesis may be found in the original print version of the thesis, held by Western Libraries.

The thesis approval page signed by the examining committee may also be found in the original print version of the thesis held in Western Libraries.

Please contact Western Libraries for further information:

E-mail: libadmin@uwo.ca

Telephone: (519) 661-2111 Ext. 84796

Web site: <http://www.lib.uwo.ca/>

CHAPTER 1

GENERAL INTRODUCTION

The introduction of species into previously Foreign habitats has been part of man's continuing history of impact on natural ecosystems. Although often inadvertent, such introductions have had drastic effects on native species (Taylor et al. 1984). A prime example has been the introduction of marine sea lamprey (Petromyzon marinus) to North America's Laurentian Great Lakes. Their parasitism was a major factor in the numerical decline of native salmonids, and has changed the Lakes' faunistic landscape substantially (Scott and Crossman 1973).

Recently, the Great Lakes ichthyofauna has seen the addition of yet another species of primarily marine origin, the pink salmon (Oncorhynchus gorbuscha Walbaum). Their inadvertent introduction resulted from attempts to establish a native fishery in Hudson Bay. Fertilized eggs from 1955 spawners were collected on the Lakelse River, a tributary of the Skeena River in northern British Columbia. These were held temporarily at the Horsefly Lake Hatchery near Quesnel, central B.C., and were then transferred to a hatchery on the Current River at Port Arthur (Thunder Bay), Ontario. Separate plants of eggs and fingerlings were made in Hudson Bay lowland streams in the spring of 1956. However, the waters of Hudson Bay proved too cold for the species and extensive surveys failed to locate any returning adults (Neave 1965; Munro 1967; Ricker and Loftus 1967; Kwain

1978, 1987; Aro 1979; Ryder and Edwards 1985).

Interest in transplanting pink salmon to Ontario waters subsequently waned. However, the species was restored to prominence after mature adults were recovered from Lake Superior tributaries in 1959 (Schumacher and Eddy 1960). The only known shipments of pink salmon to the watershed had been those to Port Arthur in 1955. Furthermore, pink salmon maintain a virtually invariable two-year life cycle across their native range (Bilton and Ricker 1965). Thus, the recoveries made in 1959 had likely arisen from undetected 1957 spawnings among feral individuals of the 1955 brood stock intended for Hudson Bay (Withler and Kwain 1984; Ryder and Edwards 1985). This situation was cause for concern among Great Lakes fisheries managers, since both Canada and the United States were bound by international agreement not to release exotic fish into the Great Lakes without prior consultation and approval (Snow 1984).

In tracing the fate of the young intended for Hudson Bay, it was discovered that three separate, previously unreported releases of pink salmon into Lake Superior had occurred. The first was of approximately 100 pink salmon fingerlings. These escaped directly into Lake Superior from containers being loaded onto aircraft preparing to leave Port Arthur for the plant sites (Schumacher and Eddy 1960; Munan 1967; Ryder and Edwards 1985). The second was of an additional 350 individuals which had

become mixed with lake trout (Salvelinus namaycush) in the Port Arthur hatchery, and which were subsequently released with them into Lake Superior at Pie Island, near today's Thunder Bay (Nunan 1967; Richey 1976; Arc 1979; Ryder and Edwards 1985).

The last and most substantial plant occurred after foul weather brought a premature halt to flights transporting the pink salmon fingerlings northwards. Three hatchery troughs of approximately 7,000 individuals each remained when flights ceased. The hatchery manager, loath simply to exterminate the leftovers, had them released into drains exiting the hatchery. These drains led into the nearby Current River, a Lake Superior tributary (Nunan 1967; Snow 1984; Ryder and Edwards 1985; Kwain 1987). Because the species was considered "obligately anadromous" at the time (Rounsefell 1958), the residual numbers were small and the risk of predation in the lake high, and since the young had not been imprinted on a home stream, their chances of survival were thought inconceivable.

Since these three accidental releases, however, the species has met with unanticipated success in the Great Lakes. Although still most abundant in Lake Superior where originally released, they have since spread through the entire Great Lakes system, reaching Lake Huron by 1969, Lake Michigan by 1973, Lakes Erie and Ontario by 1979, and recently Québec (Schumacher and Hale 1962;

Wagner and Stauffer 1975, 1982; Collins 1975; Emery 1981; Kwain and Lawrie 1981; Dermott 1982; Dermott and Timmins 1986; Dumont et al. 1988). Even-year runs have also developed, apparently the result of delayed maturation in some individuals (Kwain and Chappel 1978; Wagner and Stauffer 1980).

Despite indications that pink salmon elsewhere can survive a completely landlocked existence (Bakshtansky 1963), those of the Great Lakes form the only known self-perpetuating freshwater population in existence (Bolsowets 1978; Emery 1981; Kwain and Lawrie 1981; Kwain 1987). Since no additional plantings have occurred since 1956, natural reproduction has entirely sustained their increase. Pink salmon have been predicted to become the most abundant, naturally-reproducing salmonid in the Great Lakes before the year 2000 (Smith 1972). As such, populations in the Great Lakes present an interesting and important anomaly.

Despite their unheralded population explosion, "little is known regarding [pink salmon] ecology and population dynamics in the Great Lakes" (Bagdovits et al. 1986). Although unstudied, the conditions pertaining to spawning are considered the most likely to limit the abundance of these landlocked populations (Ryder and Edwards 1985; Kocik and Taylor 1987). Given this paucity of available information, the present work was initiated to investigate the general breeding ecology of spawning

Great Lakes pink salmon. The Carp River, a tributary of eastern Lake Superior, was selected as a study site. Preceding the work, this was one of the few Great Lakes streams known to support large enough runs in both even and odd years to permit data collection over several consecutive seasons. The results of this investigation constitute Chapter 2 of the thesis, and form the most fundamental contribution of the work.

In pink salmon, the breeding system has typically been considered one where males bearing well-developed secondary sexual characters compete for proximity to nesting females. However, my first season's work (1983) suggested instead that some Carp River males participated in spawnings by sneaking fertilisations. Such males also appeared to resemble females in their shape. Although alternative male breeding patterns occur widely in salmonids, especially among the remaining Oncorhynchus species (Gross 1984), reports of their occurrence in pink salmon were unknown when work on the Carp River began. Thus, as a second thrust to the research, I decided to investigate the possible existence of alternative male breeding patterns in Carp River spawners, emphasizing male behaviour, morphology, and breeding ecology. The outcome of this work constitutes Chapter 3 of the thesis.

References

- ARO, K.V. 1979. Transfers of eggs and young of Pacific salmon within British Columbia. Fish. Mar. Serv. Tech. Rep. 861: 147 p.
- BAGDOVITZ, M.S., W.W. TAYLOR, W.C. WAGNER, J.P. NICOLETTE, and G.R. SPANGLER. 1986. Pink salmon populations in the U.S. waters of Lake Superior, 1981-1984. J. Great Lakes Res. 12: 72-81.
- BAKSHANSKY, E.L. 1962. A pink salmon from a lake. Bull. PINRO 4: 46-47. Translated from Russian by Fish. Res. Board Can. Trans. Ser. 451: 3 p.
- BILTON, H.T., and W.E. RICKER. 1965. Supplementary checks on the scales of pink salmon (Oncorhynchus gorbuscha) and chum salmon (O. keta). J. Fish. Res. Board Can. 22: 1477-1489.
- COLLINS, J.J. 1975. Occurrence of pink salmon (Oncorhynchus gorbuscha) in Lake Huron. J. Fish. Res. Board Can. 32: 402-404.
- DERMOTT, R. 1982. Status of pink salmon (Oncorhynchus gorbuscha) in Lake Ontario, 1981. Can. MS Rep. Fish. Aquat. Sci. 1671: 7 p.
- DERMOTT, R.M., and C.A. TIMMINS. 1986. Occurrence and spawning of pink salmon, Oncorhynchus gorbuscha, in Lake Ontario tributaries. Can. Field-Nat. 100: 131-133.

DUMONT, P., J.F. BERGERON, P. DULUDE, Y. MAILHOT,
A. ROULEAU, G. OUELLET, and J-P. LEBEL. 1988.

Introduced salmonids: where are they going in Québec
watersheds of the Saint-Laurent River? Fisheries
(in press).

EMERY, L. 1981. Range extension of pink salmon
(Oncorhynchus gorbuscha) into the lower Great Lakes.
Fisheries 6: 7-10.

GROSS, M.R. 1984. Sunfish, salmon, and the evolution of
alternative reproductive strategies and tactics in
fishes. In Fish Reproduction: Strategies and
Tactics. Edited by G.W. Potts and R.J. Wootton.
Academic Press, London. pp. 55-75.

HONSOWETZ, D.C. 1978. The fish that fooled the experts.
Mich. Out-of-Doors 32: 34-35, 82.

KOCIK, J.F., and W.W. TAYLOR. 1987. Effect of fall and
winter instream flow on year-class strength of
Pacific salmon evolutionarily adapted to early fry
outmigration: a Great Lakes perspective. In Common
Strategies of Anadromous and Catadromous Fishes.
American Fisheries Society Symposium 1. Edited by
M.J. Dadswell, R.J. Klauda, C.M. Moffit,
R.L. Saunders, and R.A. Rulifson. American
Fisheries Society, Bethesda, MD. (in press).

KWAIN, W. 1978. Pink salmon are here to stay.
Ont. Fish. Wildl. Rev. 17: 17-19.

- 1987. Biology of pink salmon in the North American Great lakes. In Common Strategies of Anadromous and Catadromous Fishes. American Fisheries Society Symposium 1. Edited by M.J. Dadswell, R.J. Klauda, C.M. Moffit, R.L. Saunders, and R.A. Rulifson. American Fisheries Society, Bethesda, MD. (in press).
- KWAIN, W., and J.A. CHAPPEL. 1978. First evidence for even-year spawning pink salmon, Oncorhynchus gorbuscha, in Lake Superior. J. Fish. Res. Board Can. 35: 1373-1376.
- KWAIN, W., and A.H. LAWRIE. 1981. Pink salmon in the Great Lakes. Fisheries 6: 2-6.
- NEAVE, F. 1965. Transplants of pink salmon. Fish. Res. Board Can. MS Rep. (Biol.) 830: 1-35.
- MUNAN, P.J. 1967. Pink salmon in Lake Superior. Ont. Fish Wildl. Rev. 6: 9-14.
- RICHEY, D. 1976. Salmon surprise. Mich. Nat. Res. 45: 36, 38.
- RICKER, W.E., and K.H. LOFTUS. 1968. Pacific salmon move east. Ann. Rev. Fish. Coun. Can. 23: 37-39, 43.
- ROUNSEFELL, G.A. 1958. Anadromy in North American salmonidae. U.S. Fish Wildl. Serv. Fish. Bull. 58(131): 171-185.

- RYDER, R.A., and C.J. EDWARDS (eds.). 1985. A conceptual approach for the application of biological indicators of ecosystem quality in the Great Lakes basin. Report to the Great Lakes Science Advisory Board, International Joint Commission, Windsor, Ont. 169 p.
- SCHUMACHER, R.E., and S. EDDY. 1960. The appearance of pink salmon, Oncorhynchus gorbuscha (Walbaum), in Lake Superior. Trans. Am. Fish. Soc. 89: 371-373.
- SCHUMACHER, R.E., and J.G. HALE. 1962. Third generation pink salmon, Oncorhynchus gorbuscha (Walbaum), in Lake Superior. Trans. Am. Fish. Soc. 91: 421-422.
- SCOTT, W.B., and E.J. CROSSMAN. 1973. Freshwater fishes of Canada. Fish. Res. Board Can. Bull. 184: 1-966.
- SMITH, S.H. 1972. The future of salmonid communities in the Laurentian Great Lakes. J. Fish. Res. Board Can. 29: 951-957.
- SNOW, G. 1984. The 20,000 that got away. Topical 16:5.
- TAYLOR, J.N., W.R. COURTENAY, Jr., and J.A. McCANN. 1984. Known impacts of exotic fishes in the continental United States. In Distribution, Biology, and Management of Exotic Fishes. Edited by W.R. Courtenay, Jr., and J.R. Stauffer, Jr. Johns Hopkins University Press, Baltimore, MD. pp. 322-373.

- WAGNER, W.C., and T.M. STAUFFER. 1975. Occurrence of pink salmon in Michigan, 1963-1973. Mich. Dept. Nat. Res., Fish. Div., Tech. Rep. 75-3: 1-8.
- 1980. Three-year-old pink salmon in Lake Superior Trans. Am. Fish. Soc. 109: 458-460.
- 1982. Distribution and abundance of pink salmon in Michigan tributaries of the Great Lakes, 1967-1980. Trans. Am. Fish. Soc. 111: 523-526.
- WITHLER, F.C., and W. KWAIN. 1984. Survey of pink salmon in eastern Lake Superior, 1981. Can. Tech. Rep. Fish. Aquat. Sci. 1317: 35 p.

CHAPTER 2

Breeding Ecology of Pink Salmon (Oncorhynchus gorbuscha)

from the Carp River, Eastern Lake Superior

Abstract

This report describes ~~the~~ breeding ecology of the pink salmon (Oncorhynchus gorbuscha) which returned in 1983, 1984 and 1985 to spawn in the Carp River, an eastern Lake Superior tributary 70 km north of Sault Ste. Marie, Ontario. Nightly catch numbers varied with date, water temperatures, river discharge, and wind conditions, although the influence of these factors differed with sex and season. Upstream migration began at dusk each evening, perhaps in response to falling light levels. Spawners varied in size through the runs all years, but not in the same fashion from year to year. Spawner size and condition varied yearly in apparent response to prey abundance. Degree of secondary sexual character development, complete on stream entry, differed in even- and odd-year spawners in relation to condition. Males were usually spermiating on stream entry. Greater proportions of the females caught were unovulated, although not as often when caught further upstream or after time spent in the river. Fecundity and testis biomass differed between parent and presumed progeny generations. Within years, large males depleted their testis reserves more than did small males. Between years, the more numerous odd-year males depleted their testes more than those from the small even-year run. Length of breeding life was determined primarily by the

date fish sought access to the spawning grounds in both sexes. Increased spawner densities reduced length of breeding life only in females, and reduced male breeding performance within a season. The recovery rates of tagged male and female carcasses did not differ. Tagged fish wandered from the Carp River at a rate of at least 7%, many to spawn in adjacent streams. Although inter-year differences among these parameters are shown to be significant, much of the breeding ecology of these fish remains consistent with that exhibited by anadromous pink salmon populations.

Introduction

The pink salmon (Oncorhynchus gorbusha Walbaum) inhabiting the Laurentian Great Lakes constitute the world's only self-perpetuating, completely freshwater population of this species (Honsowets 1978; Emery 1981; Kwain and Lawrie 1981; Nicolette and Spangler 1986; Kwain 1987a). These populations were founded by an inadvertent release into Lake Superior in 1956 (Schumacher and Eddy 1960; MacKay 1963; Munan 1967; Ricker and Loftus 1968; Richey 1976; Kwain 1978, 1987a; Aro 1979; Kwain and Lawrie 1981; Snow 1984; Huggler 1985; Ryder and Edwards 1985). Since then, the species has colonized all five Great Lakes (Schumacher and Hale 1962;

Wagner and Stauffer 1975, 1982; Collins 1975; Reid 1980; Kwain and Lawrie 1981; Emery 1981; Dermott 1982; Dermott and Timmins 1986; Kwain 1987a). Natural reproduction has been solely responsible for their rapid increase, and in turn their growing impact on other Great Lakes fishes (Withler and Kwain 1984; Bagdovitz 1985; Huggler 1985; Ryder and Edwards 1985; Kocik and Taylor 1987a; Noltie 1987a). This growth is thought to be constrained primarily by limitations imposed during reproduction (Ryder and Edwards 1985; Nicolette and Spangler 1986; Kocik and Taylor 1987b). Despite this, the breeding ecology of Great Lakes pink salmon has just begun to receive attention (Kwain and Lawrie 1981; Kwain 1982; Nicolette 1983; Bagdovitz 1985; Kwain and Rose 1986; Nicolette and Spangler 1986).

Because little is yet known, I undertook the following three-year study of the breeding ecology of pink salmon in a Lake Superior tributary. Patterns of migration, migrant characteristics, their maturity, and breeding performance are given particular attention. These findings are contrasted with similar information for anadromous (North Pacific rim) pink salmon to assess whether conditions in this newly-adopted environment have influenced breeding.

Among anadromous populations, virtually all pink salmon exhibit fixed two-year life cycles (Bilton and Ricker 1965). Because those introduced to Lake Superior

were of the 1955 brood line, odd-year runs have since predominated in the Great Lakes. However, smaller even-year runs have also begun, these having recently arisen from individuals in which either delayed or precocious maturation occurred (Kwain and Chappel 1978; Wagner 1978; Wagner and Stauffer 1980; Nicolette 1984). In this study, even- and odd-year spawners from a river supporting annual runs are compared to see whether differences in their breeding ecology have arisen.

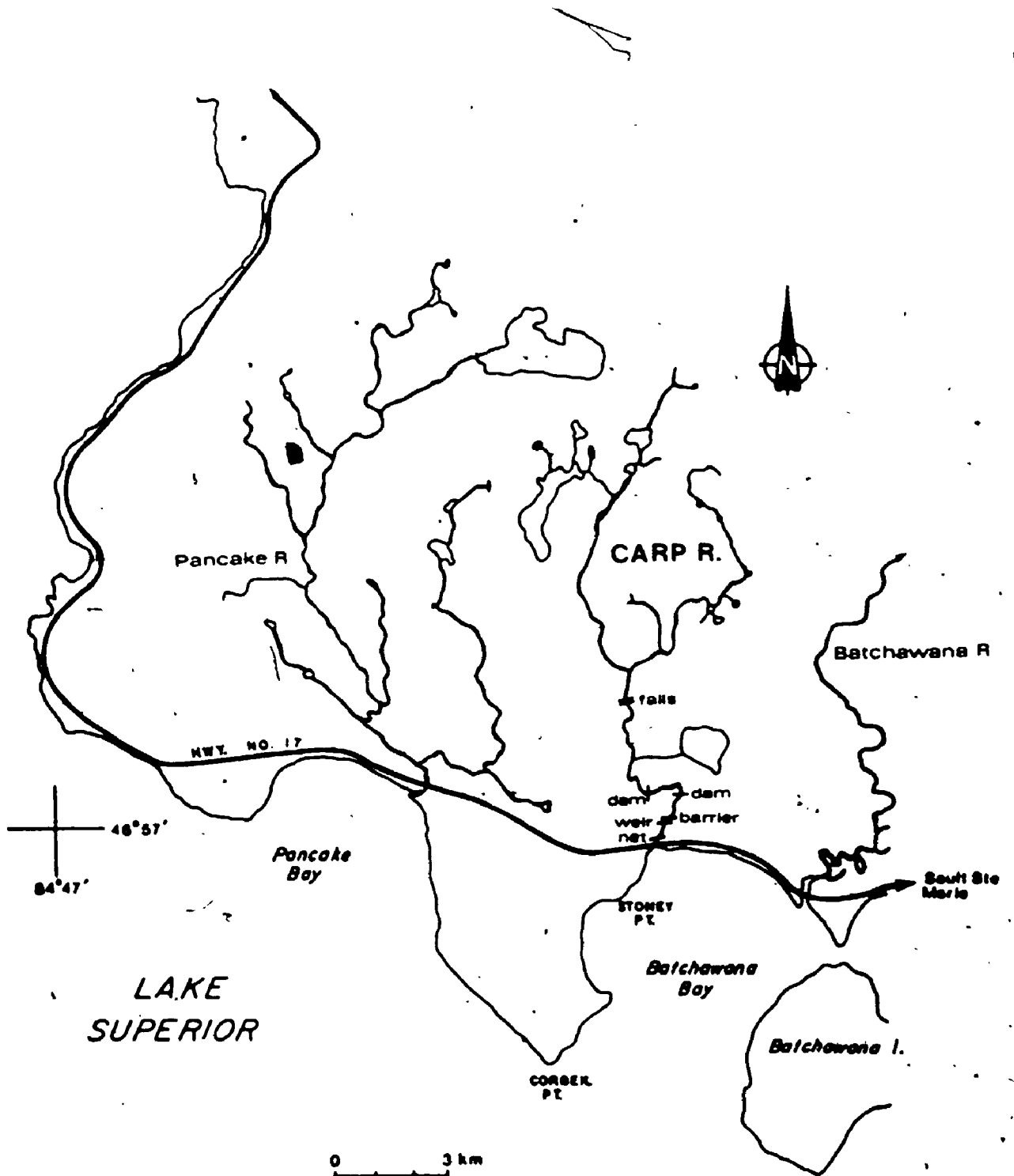
Because pink salmon are usually philopatric, returning to their natal streams to spawn, the fish studied in 1985 were likely the progeny of those studied in 1983. Therefore, these two runs are also contrasted in a comparison of presumed parents and progeny.

Materials and methods

Study site

The Carp River, an eastern Lake Superior tributary located 70 km northwest of Sault Ste. Marie, Ontario (46°57'N; 84°35'W; Fisher Township), was the chosen study site. The river empties into Batchawana Bay (Fig. 1) where pink salmon gather before entering the river to spawn (Withler and Kwain 1984). Bay characteristics are described by Thomas (1966), Kwain (1971), and Dermott (1984). The river drains an area of 75 km² and is fed by permanent lakes of the Canadian Shield (Fig. 1).

FIG. 1. Carp River study site, showing locations of net, weir, lamprey control barrier, beaver dams, impassable waterfalls, and adjacent streams. Modified from Kwain and Rose (1986).



Substrates in the lower drainage basin are unconsolidated, allowing rapid runoff and flooding after heavy rainfall. Beaver (Castor canadensis) dams restricted pink salmon to the first 4.5 km of streambed in 1983, and to areas below kilometer 2.7 in 1984 and during non-flood periods in 1985 (Fig 1.). A waterfall 10 km from the river mouth ultimately blocks further fish access upstream.

Carp River pink salmon spawned in stretches of gravel, separated downstream by areas of finer substrate at deep river bends or, further upstream, by runs of fast flow and cobble. The first gravelly spawning area occurred at kilometer 1.2 in 1983. Construction of a lamprey control barrier there that winter caused flooding of the next 600 m of spawning ground upstream. Spawning thus occurred only above kilometer 1.8 in 1984 and 1985.

Fish capture

Fish entering the stream in 1983 were captured live using a multifilament nylon gill net of 8.3 cm stretched mesh, 1.83 m deep. This was set 100 m upstream from the river mouth, typically from 1800 to 0100 h each evening. The net was lifted and cleared of fish hourly. When large catches occurred during one hour, the time the net was in place the next hour was reduced. The upstream migrants caught did not show spawning-related fin wear or body abrasion (i.e. were "prime").

Upstream migrants in 1984 were captured using a Y-shaped fish weir and box trap made of 5.1 cm square steel chain link fencing. This was installed just downstream from the lamprey barrier and spanned the entire stream. Fish were removed from the trap each morning. Undermining of the fence on September 11 and flooding on September 13-14 and 24-28, 1984 allowed some fish past the weir and into a pool below the lamprey barrier. These pool fish were stranded for an average of 8 days. On retrieval by gill net (that used in 1983), the catch dates of these individuals were back-dated to either September 13 or September 25. All pool fish were classified as either "worn" (exhibiting fin or body abrasions) or "prime" (free of wear). Trapped fish were free of such abrasions (i.e. were prime). River levels in 1984 were such that the leap over the lamprey barrier prevented pink salmon from surmounting it unassisted.

Fish were captured in 1985 as in 1984, although the weir was made instead of 3.8 cm square plastic fencing (Vexar^R; see Noltie 1987b). Floods in 1985 inundated the weir four times, and flows undermined it on four further occasions. These allowed large numbers of fish both into the lamprey barrier pool and onto the spawning grounds without having been counted, tagged, or measured. Some untagged fish were successfully retrieved from the lamprey barrier pool as in 1984, and were treated similarly. However, many others evaded capture and spent

their entire breeding lives in the pool. For the first flood of 1985, daily run numbers could be calculated afterwards by estimating the number of untagged migrants on the spawning grounds in proportion to the number of tagged fish present there. This estimate was then partitioned between the two flood dates, matching the male/female ratio to that in the run immediately before and after the flood. Similar estimates for subsequent floods could not be made, since which fish came from which flood could not be determined.

Fish measurements and recovery

Fish gill-netted in 1983 were sexed, then measured for body length (mid-eye to tip of compressed caudal fin) to the nearest mm using a measuring board. Total weight was measured with a spring balance to the nearest 10 g. Gamete release on applying gentle pressure to the abdomen was used to designate gonad maturity (spermiating/nonspermiating or ovulated/unovulated). After recording its hour of capture, each fish was uniquely marked with two 1.3 cm diameter Petersen disc tags (Floy Tag, Seattle, WA) wired through the nape, and was then released upstream. Pectoral fin clips were used instead to mark some fish during peak run periods. Others from an overwhelming catch on September 13 were simply counted and released. Samples of unspawned males and females of all sizes were killed by anesthetic overdose

and their gonads preserved in 10% formalin. Three months later these were weighed wet and then dried to asymptotic weight at 85°C for determination of gonad total, water, and dry weights (to the nearest 0.01 g). The preserved eggs from females were counted directly before drying. These gonad measurements were used in evaluating reproductive investment.

Assessment of 1984 fish paralleled that of 1983, although body length was measured from anterior orbit margin to tip of tail. Three sexually dimorphic characters were also measured: snout length (anterior orbit margin to tip of upper jaw), hump height (lateral line vertically to most dorsal extension of the back anterior to dorsal fin), and adipose fin length (anterior basal origin to distal lobe tip; see Moltie 1987c). These measurements were made to the nearest 0.1 mm using Vernier callipers. All fish were tagged with two 3.2 cm diameter Petersen disc tags affixed with wire, and were then released above the lamprey barrier. The carcasses of tagged fish captured prime were recovered daily from against the upstream side of the weir and on the spawning grounds. These were used to assess length of breeding life. To assess testis utilization, the post-spawning testes of prime males were removed and processed as described above for prespawning males in 1983.

Fish of 1985 were handled as in 1984, although an additional 4.0 cm anchor tag (Floy Tag) was applied

behind the dorsal fin to enhance carcass identification and nickle pins attached the Petersen discs. Because of the large run in 1985, some fish trapped at peak periods were simply counted, sexed, measured for total length and weighed. These were released above the upstream beaver dam (Fig. 1), an area which tagged fish released onto the spawning grounds typically could not reach. As in 1983, prespawning males and females in prime condition (the unspawned group) were killed on capture for assessment of gonad investment. Tagged males captured in prime condition were recovered daily as carcasses either on surveys of the spawning grounds or against the weir. Their post-spawning testes were processed as in 1984. The males collected from the spawning grounds (the "survey" group) had passed their entire breeding lives under conditions of natural spawner densities. Males collected from against the weir (the "fence" group) were ones which after their release had been swept by floods back over the lamprey barrier into the pool below. Densities in the pool were higher than on the spawning grounds because of the many untagged fish which had been stranded there with them. Nonetheless, fish did spawn in the pool, as evidenced by the body and fin wear on recovered carcasses, depleted testes in males, and the large numbers of eggs seen in the pool's downstream shallows.

Environmental data

Water temperatures, wind-generated turbulence in Batchawana Bay, and stream discharge were assessed each year as environmental factors which might influence nightly catches of pink salmon. River temperatures were measured to the nearest 0.1 C° with a continuously recording thermograph (Ryan Model J^R) installed at the lamprey barrier site. Batchawana Bay water temperatures were measured near the river mouth with a maximum-minimum thermometer. Daily means averaged highs and lows. Gaps in the temperature data resulted from vandalism of the recording devices. These data were replaced by estimates derived from daily mean air temperatures. These air temperatures were registered at the nearest Environment Canada climatological station at the Sault Ste. Marie airport, and were significantly correlated each season (all $r > 0.75$, all $p < 0.001$) with the recorded water temperatures.

As an indirect measure of Batchawana Bay turbulence, mean hourly wind speed and direction measurements (wind to nearest km/h, directions within standard 22.5° compass divisions) were obtained from the Sault Ste. Marie climatological station. Because of the bay's orientation (Fig. 1), only winds from the SW, SSW and S were considered. In 1983, two wind measurements (designated Day and Run) were calculated. Day wind summed the hourly windspeed recordings from 0600 h to the

time each night's gill netting ended. This gauged bay conditions from the end of the previous day's migration to the end of a particular night's sampling. Run wind summed windspeeds during the specific hours the gill nets were set each night. This gauged bay conditions while the entry of fish into the river was being monitored. In 1984 and 1985, Day wind summed windspeeds from end of run to end of run (0600 to 0600 h). Run wind summed windspeeds over the typical nightly migration period (1800 to 0400 h).

Daily Carp River discharge volumes in 1985 were calculated from water column heights. These were measured (± 0.1 cm) each morning from a staff gauge on the upstream side of the lamprey barrier. Height was converted to discharge using the barrier's width and contours (Hynes 1970). Discharge measurements for 1983 and 1984 could not be made directly because the lamprey barrier was absent in 1983 and a staff gauge was not installed until 1985. Instead, estimates of daily discharge were made using the highly significant ($r=0.9187$ $n=51$, $p<0.001$) relationship from 1985 between discharges in the Carp and the neighbouring Batchawana River (Fig. 1). The latter was monitored by a permanent Environment Canada stream gauge. This regression was: Carp River discharge = $-0.466 + 0.580(\text{Batchawana River discharge})^{0.5}$. Because flash flooding in the larger Batchawana River was less pronounced, the Carp River

flood peak of September 4, 1985 was substantially underestimated by an initial trial of this technique. This datum was subsequently dropped from the calculation of the regression reported. To avoid a similar underestimate for the flood of September 13, 1984, its discharge was estimated at 30% of that for the September 4, 1985 flood for which an actual discharge was known by comparing photographs of both.

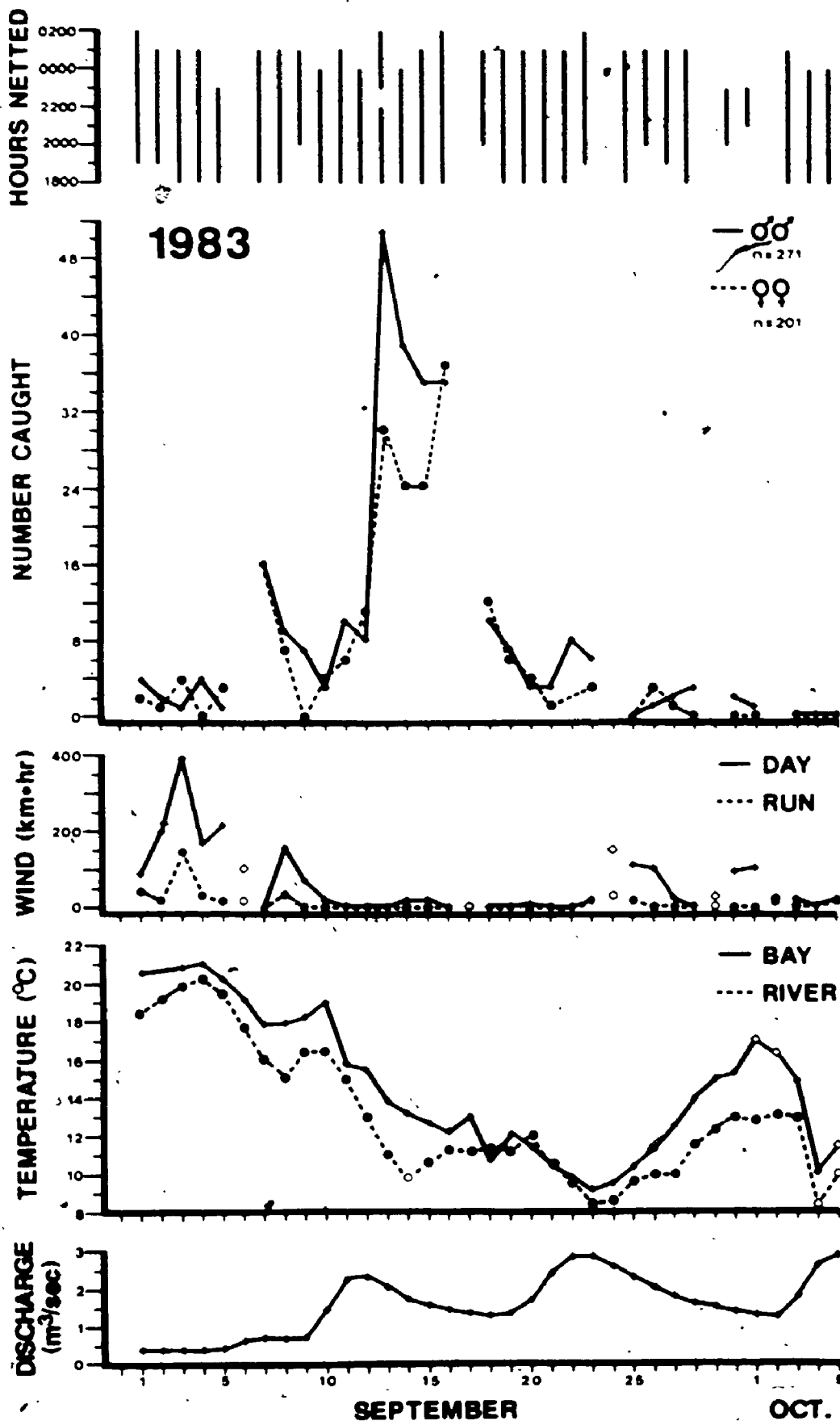
Results

Seasonal variation in nightly catch numbers

The upstream migration of Carp River pink salmon in 1983 (Fig. 2) was underway as netting operations commenced on September 1 at a day's mean river temperature of 18.5°C. The run continued until early October by which time river temperatures had fallen to 8.4°C. Multiple regression was used to evaluate possible associations between catch numbers and the environmental variables measured (Fig. 2).

As the dependent variable, residuals measuring the nightly departure of catch numbers from any underlying seasonal trend were calculated. To model this baseline pattern, Velleman and Hoaglin's (1981) "3RSSH twice" smoothing algorithm was applied to the catch data using MINITAB (MINITAB, Inc., 1985). Each sex was considered separately from its first to its last catch date, and

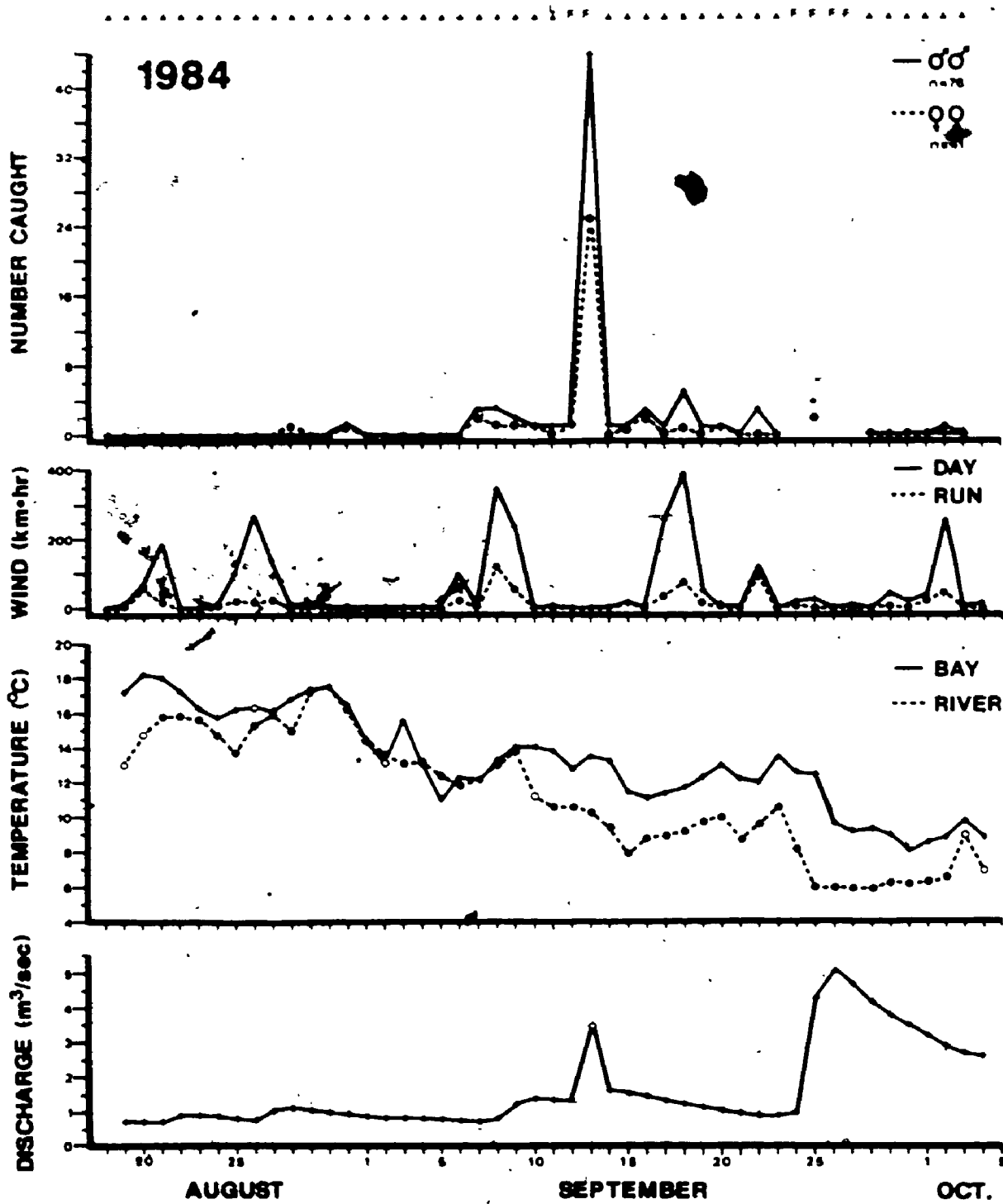
FIG. 2. Nightly catches of Carp River pink salmon and associated environmental variables in 1983. Blanks in top two panels indicate periods when foul weather prevented netting. See text for derivation of other variable values (open symbols = estimates). Wind: estimates for evenings when no netting occurred summed winds from 1800-0100 h (Run) and 0600-0100 h (Day).



dates on which netting did not occur were excluded. Nightly catch number residuals were thus the differences from this seasonal trend. As predictor variables, bay and river temperature and Carp River discharge data were used untransformed, while both the Day and Run wind measures were converted to ranks to reduce non-normality. Multiple regression analyses of the nightly catch number residuals against the five environmental variables proved non-significant for both males and females in 1983 (both $p < 0.25$). Thus, the abiotic variables considered did not appear to affect the 1983 nightly catch in either sex, given the regression sample sizes considered. The distribution of male and female catches through the season also did not differ (six sequential blocks of five sampling dates, 2x6 contingency table $\chi^2 = 2.66$, $p = 0.75$), despite more males than females being caught overall (271 and 201, respectively).

The pink salmon migration into the Carp River in 1984 spanned the 36 days from August 28 until October 2 (Fig. 3). Mean daily river temperatures were 15.0°C at the run's start and 6.4°C at run's end. Nightly catch numbers for both sexes were too small and intermittent to calculate smoothed seasonal trends. Thus, raw counts were used in an analysis otherwise identical to that of 1983. For males, the resulting multiple regression was: nightly catch number = $-13.67 + 10.006(\text{river discharge}) - 0.862(\text{bay temperature}) + 1.207(\text{river temperature}) +$

FIG. 3. Nightly catches of Carp River pink salmon and associated environmental variables in 1984. Top line: triangles denote days trap was in operation, F = flood when trap was inundated, L = leak when weir was partially undermined. See text for derivation of other variable values (open symbols = estimates).



1.054(Run wind rank) - 0.947(Day wind rank). The overall regression was significant ($F=4.79$, $n=25$, $p<0.01$), as were the effects of discharge ($t=4.52$, $p<0.001$) and both wind factors (both $t \geq 2.09$, both $p<0.02$). For females, the overall regression was not significant ($p>0.10$). These results indicate that in 1984, aspects of the abiotic environment mediated upstream migration in males. This could not be detected in females. Despite more males than females being caught overall in 1984 (76 and 41, respectively), the proportions of males and females did not differ through the three periods before, during, and after the September 13 flood (2x3 contingency table $\chi^2=0.77$, $p>0.50$).

In 1985, the run began August 24 and could last be monitored 41 days later on October 3 (Fig. 4). Mean daily river temperatures on these dates were 12.9°C and 9.5°C, respectively. Nightly catch numbers for each sex were sufficiently large that residuals could be determined. For males, nightly catch number variation was modelled by the equation: residual catch variation = -113.50 + 20.436(river discharge) + 20.146(bay temperature) - 15.998(river temperature) + 0.547(Run wind rank) + 0.740(Day wind rank). The overall regression was significant ($F=7.68$, $n=36$, $p<0.0005$), as were the effects of discharge ($t=5.94$, $p<0.001$) and bay temperature ($t=1.99$, $p=0.06$). For females, however, the regression was not significant ($p>0.10$). Thus, as in


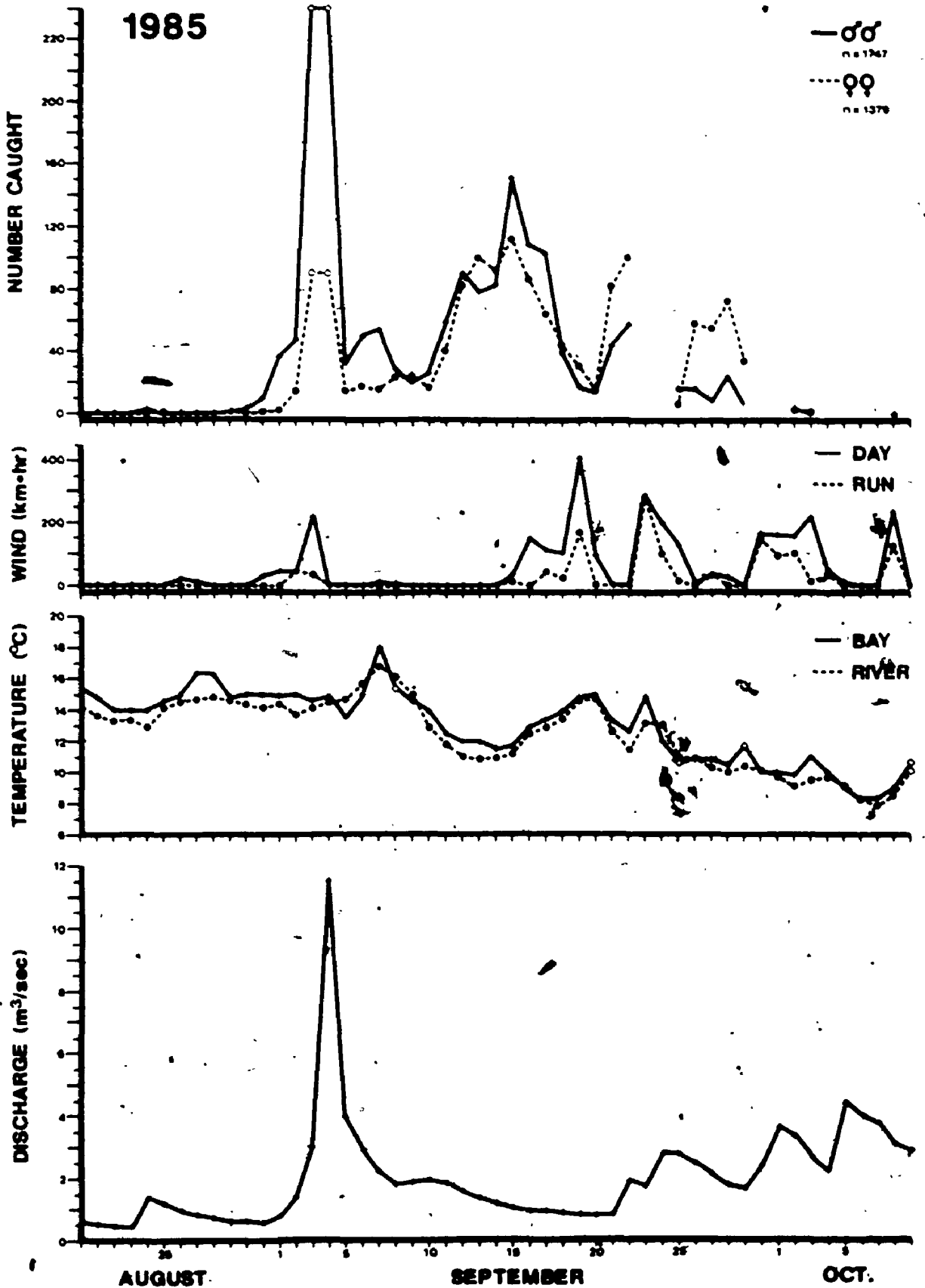


FIG. 4. Nightly catches of Carp River pink salmon and associated environmental variables in 1985. Top line: as per Fig. 3 legend. See text for derivation of other variable values (open symbols = estimates).



1984, upstream migration by males was influenced more by environmental factors than was migration by females. The proportions of males and females caught also differed significantly through the periods of 13, 12 and 12 consecutive days which bracketed the three main peaks in 1985 catch numbers (Fig. 4). Males dominated early and females late in the run, with no difference in the middle period (2x3 contingency table $\chi^2=290.89$, $p<0.001$).

Size differences through the runs

Regressions of the body length of individuals against the Julian date each was caught were used to assess the existence of trends in the sizes of fish entering the Carp River across each season (Table 1). For each sex/year combination, the correlation coefficients indicate that fish size varied significantly with date (all $p<0.05$, except for 1984 males where $p=0.08$). Within years, no differences occurred between the male and female regression slopes (Table 1). Thus the size trends for each sex were similar. The results of subsequent tests of the regression intercepts and calculation of the adjusted mean body lengths (Table 1) are consistent with the finding that males were typically longer than females each year (see below).

To determine whether these size trends were consistent between seasons, comparisons of the three years' body length-versus-Julian date of catch

TABLE 1. Body length (BL, cm) versus Julian date of catch (JDC) relationships for male and female pink salmon entering the Carp River. Shown are correlation coefficients, sample sizes, results of covariance analyses between the sexes each year, and the mean lengths ($\bar{X} \pm 1$ S.E., cm) for each sex taken at comparable dates and after regressions adjusted to common slope.

Year	Sex	Regression	r	n	Slopes test	Intercepts test	Adjusted mean length
1983	Males	(BL) = -15.75 + 0.234(JDC)	0.2429	253	t=1.598 p>0.10	t=4.525 p<0.001	44.37 ± 0.26
	Females	(BL) = 16.78 + 0.100(JDC)	0.1449	189			42.53 ± 0.31
1984	Males	(BL) = 107.80 - 0.244(JDC)	0.2025	76	t=0.016 p>0.50	t=1.706 p>0.05	44.93 ± 0.53
	Females	(BL) = 105.54 - 0.241(JDC)	0.3647	41			43.39 ± 0.73
1985	Males	(BL) = 87.66 - 0.184(JDC)	0.3536	1042	t=-1.919 p>0.05	t=22.001 p<0.001	40.27 ± 0.09
	Females	(BL) = 76.96 - 0.148(JDC)	0.3899	989			38.72 ± 0.09

relationships were performed within each sex. These tests revealed significant among-year slope differences for both males and females (ANCOVAs, both $t \geq 18.622$, both $p < 0.0005$). For both sexes, SNK tests (Zar 1974) indicated that the positive slopes of the 1983 regressions differed significantly from the negative slopes for 1984 and 1985 (all $q \geq 5.862$, all $p < 0.001$), whereas the slopes for the latter two years did not differ in either sex (both $q \leq 1.788$, both $p > 0.20$). Thus, the trend of increasing sizes for both sexes through the 1983 run was the reverse of trends found in both sexes the subsequent two seasons.

Nightly migration patterns

Using the hourly catch records of 1983, the nightly pattern of fish movement into the Carp River was investigated. Upstream migration began in the early evening, abruptly increasing after nightfall and tapering off through the early morning hours (Table 2). This pattern suggests a relationship between decreasing light intensities and the start of instream movement. Throughout the 1983 season, the greatest number of fish was caught between 2000 and 2100 h (Table 2). However, subsequent time periods were sampled with somewhat less intensity because time was required to clear the net of catches made during preceding periods.

TABLE 2. Hourly catch frequencies of male and female pink salmon moving into the Carp River in 1983. Number of samples denotes frequency with which netting occurred in each time period over the entire run.

Time period	Time span	Males	Females	Total	‡	No. samples
1	1800 - 1900	2	0	2	0.4	21
2	1900 - 2000	2	4	6	1.3	25
3	2000 - 2100	60	48	108	22.9	29
4	2100 - 2200	63	37	100	21.2	30
5	2200 - 2300	46	39	85	18.0	29
6	2300 - 0000	53	35	88	18.6	27
7	0000 - 0100	33	26	59	12.5	22
8	0100 - 0200	12	12	24	5.1	4
Total		271	201	472	100.0	187

Comparing instream movement patterns between the sexes (Table 2), the proportions of males and females caught did not differ through the time periods sampled in 1983 (2x7 contingency table $\chi^2=2.86$, $p>0.75$, time periods 1 and 2 combined to increase cell sample sizes). A non-significant ($p>0.20$) correlation coefficient indicated no relationship between male body length and time period caught in 1983. In contrast, females were significantly larger ($r=0.1975$, $n=189$, $p<0.01$) the later in each evening's run they were caught [regression equation: female body length = $40.59 + 0.390(\text{time period number})$]. The mean lengths of fish caught in each time period (Table 3) illustrate these trends.

Differences in migrant size

Carp River pink salmon exhibited sex differences in size. Males in both 1983 and 1985 were, on average, significantly longer and heavier than females (Table 4). Sex differences were less pronounced in 1984 when sample numbers were relatively small (Table 4).

Yearly variation in size also occurred within both males and females (Table 4). Among-year analyses of variance revealed significant annual variation in body length and weight in each sex (all $F \geq 100.79$, all $p < 0.0005$). Pairwise comparisons between the years revealed that 1983 and 1984 fish were longer and heavier than fish of 1985 in both sexes (all $F \geq 30.39$, all

TABLE 3. Mean body lengths ($\bar{X} \pm 1$ S.E., cm) of 1983 male and female Carp River pink salmon by hour of stream entry. Sample sizes deviate from hourly run totals in Table 2 because some fish during peak run periods were released without taking their measurements.

Time period	Time span	Male body length	n	Female body length	n
1	1800 - 1900	51.70 \pm 0.90	2	-----	0
2	1900 - 2000	44.55 \pm 1.35	2	40.15 \pm 1.06	4
3	2000 - 2100	44.83 \pm 0.59	60	42.23 \pm 0.47	47
4	2100 - 2200	43.64 \pm 0.83	45	41.79 \pm 0.77	27
5	2200 - 2300	44.47 \pm 0.77	46	42.13 \pm 0.52	39
6	2300 - 0000	45.27 \pm 0.62	53	42.91 \pm 0.47	35
7	0000 - 0100	42.02 \pm 0.83	33	43.59 \pm 0.48	25
8	0100 - 0200	46.48 \pm 1.19	12	43.91 \pm 0.82	12
Total		44.41 \pm 0.31	253	42.52 \pm 0.23	189

TABLE 4. Yearly differences in Carp River pink salmon average ($\bar{X} \pm 1$ S.E.) body length (cm) and total body weight (kg) by sex. Shown also are results of analyses of variance comparing measures on adjacent lines. Only prime fish are considered each year.

Year	Sex	Body length	Weight	n
1983	Males	44.41 \pm 0.31	1.042 \pm 0.023	253
	Females	42.52 \pm 0.23	0.891 \pm 0.016	188
		F=20.83, p<0.0005	F=24.71, p<0.0005	
1984	Males	43.91 \pm 0.87	1.070 \pm 0.073	38
	Females	43.06 \pm 0.75	0.942 \pm 0.057	28
		F=0.50, p>0.25	F=1.71, p>0.10	
1985	Males	40.71 \pm 0.11	0.692 \pm 0.007	990
	Females	38.42 \pm 0.08	0.599 \pm 0.005	969
		F=273.31, p<0.0005	F=112.82, p<0.0005	

$p < 0.0005$). However, no differences in length or weight occurred within each sex between 1983 and 1984 individuals (all $F \leq 1.16$, all $p > 0.25$).

Condition

Males and females did not differ in condition (weight-at-length) in either 1983 or 1984. Covariance analysis revealed no significant slope or intercept heterogeneity in their condition relationships (Table 5). Male and female data were then combined for each year (Table 5) and the slopes of the two pooled condition regressions were examined for isometry (Ricker 1958). The regression slopes in both cases were significantly greater than 3 (both $t \geq 3.101$, both $p < 0.005$). Thus, long fish of each sex were more robust than short ones in both years.

In contrast, the two sexes in 1985 differed in condition. Females increased in weight more rapidly with increasing length than males (Table 5). The slope of the condition regression for males did not differ from 3 ($p > 0.50$), while for females it was significantly greater than 3 ($t = 5.371$, 967 df, $p < 0.001$). Thus, only females in 1985 exhibited greater robustness with increasing length.

Males differed in condition among the three years, as indicated by the heterogeneity in their condition relationship slopes (ANCOVA, $F = 5.24$, 2 and 1277 df, $p < 0.01$). Males of 1985 were in relatively poor

TABLE 5. Body weight (BW, kg) and body length (BL, cm) relationships for Carp River pink salmon in three years. Shown are correlation coefficients (all $p < 0.001$), sample sizes, and results of analyses of covariance comparing regressions on adjacent lines. Dashes denote inappropriate intercept test due to slope differences.

Year	Sex	Regression	r	n	Slopes test	Intercepts test
1983	Males	$\ln(\text{BW}) = -12.172 + 3.207 \ln(\text{BL})$	0.9721	253	$t = 1.120$ $p > 0.20$	$t = -1.083$ $p > 0.20$
	Females	$\ln(\text{BW}) = -11.779 + 3.105 \ln(\text{BL})$	0.9513	188		
	Both	$\ln(\text{BW}) = -12.043 + 3.174 \ln(\text{BL})$	0.9680	441		
1984	Males	$\ln(\text{BW}) = -12.573 + 3.326 \ln(\text{BL})$	0.9644	38	$t = 0.135$ $p > 0.50$	$t = 1.419$ $p > 0.50$
	Females	$\ln(\text{BW}) = -12.729 + 3.358 \ln(\text{BL})$	0.9721	28		
	Both	$\ln(\text{BW}) = -12.667 + 3.347 \ln(\text{BL})$	0.9659	66		
1985	Males	$\ln(\text{BW}) = -11.616 + 3.026 \ln(\text{BL})$	0.9230	990	$t = 3.916$ $p < 0.001$	-----
	Females	$\ln(\text{BW}) = -12.386 + 3.248 \ln(\text{BL})$	0.9143	969		

condition: pairwise comparisons between years using covariance analysis revealed that the condition regression slope for 1985 males was significantly lower than that for either 1983 or 1984 males (slope tests, both $t \geq 2.072$, both $p < 0.05$). However, males of 1983 and 1984 did not differ in condition, since neither the slopes nor the intercepts of their condition regressions differed significantly.

Females also showed significant between-year differences in condition. However, unlike males, this variation was reflected by heterogeneity in condition regression intercepts, not slopes (ANCOVA, $F=40.78$, 2 and 1181 df, $p < 0.0005$). Pairwise tests using covariance analysis revealed that 1985 females were in significantly poorer condition than those from 1983 or 1984 (intercepts tests, both $t \geq 3.554$, both $p < 0.001$). The adjusted mean weight of 1985 females was lower than for 1983 and 1984 females by 52.2 g and 33.5 g, respectively. Pairwise comparisons between 1983 and 1984 females, however, revealed no differences in either their condition regression slopes or intercepts.

Finally, fish captured from the lamprey barrier pool in 1984 and 1985 and classified as "worn" were excluded from these condition analyses. Significant differences in their condition relationships relative to "prime" fish were found for both males and females. This was likely the result of breeding activities.

Sexual dimorphism

In anadromous pink salmon, male spawners possess larger dorsal humps, and longer snouts and adipose fins than females (Davidson 1935; Beacham and Murray 1983, 1986). In Carp River fish, these characters also differed in size between males and females in 1984 and 1985 (Table 6). Relative to body length, covariance analyses both years revealed that hump size increased at a greater rate (different slopes), and adipose fin length was greater by a constant proportion (different intercepts), in males compared to females. Compared again to females, snout length was proportionally larger in 1984 males (different intercepts) but became increasingly large in males as size increased in 1985 fish (different slopes).

Of greater interest than these between-sex differences, the degree of secondary sexual character development differed between years in males and females. Hump development was proportionally greater in 1984 than in 1985 in both sexes: the intercepts and adjusted means for their respective character size-body length regressions differed significantly (ANCOVA results, Table 7). This less substantial hump development in 1985 fish corresponds to the reduced condition they displayed (see above). For snout length, the character length-body length regression for 1984 males was inclined significantly more steeply than for 1985 males (Table 7).

TABLE 6. Comparisons of the secondary sexual character development of male and female Carp River pink salmon. HH = hump height (cm), BL = body length (cm), SL = snout length (cm), AFL = adipose fin length (cm). Shown are correlation coefficients (all $p < 0.001$), sample sizes, and results of analyses of covariance comparing regressions on adjacent lines. Dashes denote inappropriate intercept tests due to slope differences.

Year	Character	Sex	Regression	r	n	Slopes test	Intercepts test
1984	Hump	Male	$\ln(HH) = -3.963 + 1.510 \ln(BL)$	0.9192	76	$t = 2.379$ $p < 0.02$	-----
		Female	$\ln(HH) = -3.006 + 1.173 \ln(BL)$	0.9121	41		
	Snout	Male	$\ln(SL) = -5.162 + 1.688 \ln(BL)$	0.9214	76	$t = 1.190$ $p > 0.20$	$t = 18.370$ $p < 0.001$
		Female	$\ln(SL) = -4.720 + 1.497 \ln(BL)$	0.9127	41		
1985	Hump	Male	$\ln(HH) = -3.925 + 1.471 \ln(BL)$	0.8276	1087	$t = 5.629$ $p < 0.001$	-----
		Female	$\ln(HH) = -3.267 + 1.222 \ln(BL)$	0.8012	1028		
	Snout	Male	$\ln(SL) = -4.285 + 1.458 \ln(BL)$	0.8264	1087	$t = 4.188$ $p < 0.001$	-----
		Female	$\ln(SL) = -3.781 + 1.251 \ln(BL)$	0.7259	1028		
Adipose fin	Male	$\ln(AFL) = -4.186 + 1.357 \ln(BL)$	0.7273	1080	$t = 0.410$ $p > 0.50$	$t = 41.329$ $p < 0.001$	
	Female	$\ln(AFL) = -4.466 + 1.378 \ln(BL)$	0.6603	1026			

TABLE 7. Between-year comparisons of relationships between body size and development of secondary sexual characters reported in Table 6. Shown are the results of covariance analyses between entries on adjacent lines and mean character sizes ($\bar{X} \pm 1$ S.E.) made at comparable body lengths using common slopes (adjusted means). Dashes denote inappropriate intercept test or where adjusted means could not be calculated due to slope differences or regression equivalence.

Sex	Character	Year	Slopes test	Intercepts test	Adjusted mean (cm)
Male	Hump	1984	t=0.492 p>0.50	t=10.782 p<0.001	5.10 \pm 1.01
		1985	1159 df	1160 df	4.58 \pm 1.00
	Snout	1984	t=2.721 p<0.01	-----	-----
		1985	1159 df		-----
Female	Hump	1984	t=0.443 p>0.50	t=7.464 p<0.001	3.57 \pm 1.02
		1985	1065 df	1066 df	3.29 \pm 1.00
	Snout	1984	t=1.663 p>0.05	t=-0.930 p>0.20	-----
		1985	1065 df	1066 df	-----

This suggests that 1985 males underwent less snout elongation. However, for females neither year's regression slopes nor intercepts differed for this character (Table 7). Between-year comparisons of adipose fin size are more fully explored in Noltie (1987c).

Reproductive maturity

Gonadal maturity was assessed in fish intercepted during their uninterrupted movement upstream each year, i.e. those netted in 1983 or trapped in 1984 and 1985 (designated as "run" fish). Virtually all run males caught each year were spermiating, whereas the proportion of run females caught whose eggs were ovulated varied from only 26 to 78% (Table 8). This difference between the sexes in the maturity of run fish was significant each year (1983 and 1985: both 2x2 continuity-corrected $\chi^2 \geq 142.56$, both $p < 0.001$; 1984: Fisher Exact test, $p < 0.001$). Between years, the proportions of fish captured immature varied only in females: more run females were captured with their eggs unovulated in 1983 and 1984 than in 1985 (1983 vs. 1985: 2x2 continuity-corrected $\chi^2 = 117.905$, $p < 0.001$; 1984 vs. 1985: Fisher Exact test, $p = 0.003$; 1983 vs. 1984: Fisher Exact test, $p = 0.764$).

Maturity in run females was not consistently size-related. Among 1983 run females, those with their eggs ovulated were significantly heavier than those whose

TABLE 8. Gonad maturity of male and female Carp River pink salmon. Mature = ovulated/spermiating. Immature = unovulated/nonspermiating. Run fish were caught either at the river mouth (1983) or just below the lamprey barrier (1984 and 1985). Pool fish were netted from the lamprey barrier pool some days past their run date.

Year	Sex	Catch location	Gonad condition			
			Mature		Immature	
			n	%	n	%
1983	Male	Run	144	99.3	1	0.7
	Female	Run	31	28.4	78	71.6
1984	Male	Run	29	100.0	0	0.0
		Pool	47	100.0	0	0.0
	Female	Run	5	33.3	10	66.7
		Pool	24	92.3	2	7.7
1985	Male	Run	1034	99.1	9	0.9
		Pool	45	100.0	0	0.0
	Female	Run	770	77.7	221	22.3
		Pool	37	94.9	2	5.1

eggs were not (ovulated: 937.3 ± 41.1 g; unovulated: 836.6 ± 26.6 g; $\bar{X} \pm 1$ S.E.; ANOVA, $F=4.19$, 1 and 106 df, $p<0.05$). However, parallel differences were not found in 1984 and 1985 run females (ANOVAs, both $p>0.25$). Because females which had ovulated were not always heavier than those which had not, the weight difference in 1983 was not attributable simply to the increase in female weight due to preovulatory egg hydration (see below).

Water uptake by the eggs at final maturation occurs in sockeye salmon (Oncorhynchus nerka) (Kisevetter 1948) and in other female teleosts (Wallace and Selman 1981; Wallace et al. 1987). Evidence of this phenomenon was sought among run females from 1985. Comparing the pre- and post-ovulatory females, significant differences occurred in the slopes of their egg water content-egg dry weight regressions (Table 9, bottom), the regression for the former lying above that for the latter. This suggests that the egg water content for preovulatory females had attained if not surpassed that for females that had ovulated. Thus, preovulatory females had matured to at least the stage of egg hydration at their capture. Differences in neither egg number nor ovary weight were responsible for this result, since females at both stages of maturity were similar in their fecundity- and egg wet weight-versus-somatic weight relationships (Table 9, top and middle).

TABLE 9. Comparison of the eggs of 1985 Carp River females which had or had not ovulated. TEN = total egg number, SW = somatic weight (g), EWW = egg wet weight (g), EWC = egg water content (g), EDW = egg dry weight (g). Shown are correlation coefficients (all $p < 0.002$), sample sizes, and results of covariance analyses comparing regressions on adjacent lines. Dashes denote inappropriate intercept test due to slope differences.

Gonad state	Regression	r	n	Slopes test	Intercepts test
Unovulated	TEN = 5.001 + 1.728(SW)	0.6804	18	t=0.360 p>0.50	t=1.321 p>0.10
Ovulated	TEN = -9.355 + 1.580(SW)	0.7430	51		
Unovulated	EWW = -19.281 + 0.263(SW)	0.7880	18	t=1.007 p>0.20	t=0.829 p>0.20
Ovulated	EWW = -2.690 + 0.219(SW)	0.8246	51		
Unovulated	EWC = 9.228 + 1.554(EDW)	0.9529	18	t=2.103 p<0.05	-----
Ovulated	EWC = 15.295 + 1.303(EDW)	0.9434	51		

Davidson and Vaughan (1941) observed that anadromous pink salmon occur in two maturation types. Those of the first type arrive at their natal stream in an immature condition and mature after stream penetration. Those of the second type arrive mature and almost immediately begin moving upstream. Two measures of maturity (gonad maturity and degree of secondary sexual character development) were examined to determine the maturation type of Carp River spawners. Assessments were made in 1984 and 1985 of both run fish and those captured from the lamprey barrier pool ("pool" fish). Had fish moving upstream (run fish) been immature, further ripening of their gonads and increased secondary sexual character development should have been detectable among pool fish after their period of temporary confinement.

In both years (Table 8), run females had ovulated in significantly smaller proportions than pool females (1984: Fisher Exact test, $p=0.001$; 1985: 2×2 continuity-corrected $\chi^2=5.55$, $p<0.025$). Likewise for males: although few run fish were nonspermiating, none captured after passing time in the pool remained immature (Table 8). This suggests that gonadal maturation was essentially complete in run males. It was nearly so in run females and was completed over the few days they were stranded in the pool. Thus, in contrast to run fish (see above), time spent in pool occupation erased differences between the sexes in the proportions of individuals found

mature and immature (Fisher Exact tests, 1984: $p=0.124$, 1985: $p=0.213$). The sizeable proportions of captured run females which had not ovulated suggests that many in an uninterrupted migration were likely to spend their first few days on the spawning grounds non-breeding, waiting to attain reproductive competence.

Regarding maturation from a morphological perspective, virtually no within-sex differences were evident in the secondary sexual character development of run and pool individuals from 1984 and 1985 (Table 10). Of all the comparisons performed, only that pertaining to male hump height in 1985 produced a significant result. However, the indicated difference was contrary to that predicted: the adjusted mean hump height for pool males was less than that for run males. These results indicate that the morphological maturation of upstream migrating fish of both years and both sexes had been completed before their capture. Although the morphological maturation was further advanced than the gonadal maturation in some fish, especially among females (see above), the time fish from the pool had spent there before being captured was sufficient to resolve this asynchrony.

Gonad investment

Both fecundity (total egg number) and egg wet weight increased directly with somatic weight (total body weight

TABLE 10. Comparisons of secondary sexual character development in run- and pool-caught Carp River pink salmon males and females. HH = hump height (cm), BL = body length (cm), SL = snout length (cm), AFL = adipose fin length (cm). Shown are regression correlation coefficients (all $p < 0.001$), sample sizes, and results of analyses of covariance between regressions on adjacent lines.

Year	Sex	Character	Condition	Regression	r	n	Slopes test	Intercepts test
1984	Male	Hump	Run	$\ln(\text{HH}) = -3.473 + 1.375 \ln(\text{BL})$	0.8926	29	$t = -1.084$	$t = -1.603$
			Pool	$\ln(\text{HH}) = -4.093 + 1.547 \ln(\text{BL})$	0.8819	47	$p > 0.20$	$p > 0.10$
	Snout	Run	$\ln(\text{SL}) = -5.030 + 1.656 \ln(\text{BL})$	0.8967	29	$t = -0.368$	$t = -0.713$	
		Pool	$\ln(\text{SL}) = -5.306 + 1.725 \ln(\text{BL})$	0.9333	47	$p > 0.50$	$p > 0.20$	
	Adipose fin	Run	$\ln(\text{AFL}) = -6.066 + 1.869 \ln(\text{BL})$	0.9306	29	$t = -0.606$	$t = -0.071$	
		Pool	$\ln(\text{AFL}) = -6.517 + 1.988 \ln(\text{BL})$	0.9225	47	$p > 0.50$	$p > 0.50$	
Female	Hump	Run	$\ln(\text{HH}) = -2.446 + 1.030 \ln(\text{BL})$	0.9110	15	$t = -0.907$	$t = -1.787$	
		Pool	$\ln(\text{HH}) = -3.083 + 1.191 \ln(\text{BL})$	0.9077	26	$p > 0.20$	$p > 0.05$	
	Snout	Run	$\ln(\text{SL}) = -4.336 + 1.396 \ln(\text{BL})$	0.9055	15	$t = -0.672$	$t = -0.052$	
		Pool	$\ln(\text{SL}) = -4.939 + 1.555 \ln(\text{BL})$	0.9083	26	$p > 0.50$	$p > 0.50$	
	Adipose fin	Run	$\ln(\text{AFL}) = -4.236 + 2.120 \ln(\text{BL})$	0.9077	15	$t = -1.940$	$t = -0.005$	
		Pool	$\ln(\text{AFL}) = -4.751 + 1.463 \ln(\text{BL})$	0.8222	26	$p > 0.05$	$p > 0.50$	
1985	Male	Hump	Run	$\ln(\text{HH}) = -3.870 + 1.456 \ln(\text{BL})$	0.8222	1042	$t = -0.066$	$t = 2.530$
			Pool	$\ln(\text{HH}) = -3.841 + 1.439 \ln(\text{BL})$	0.7797	45	$p > 0.50$	$p < 0.02$
	Snout	Run	$\ln(\text{SL}) = -4.288 + 1.459 \ln(\text{BL})$	0.8222	1042	$t = -0.114$	$t = -0.220$	
		Pool	$\ln(\text{SL}) = -4.356 + 1.478 \ln(\text{BL})$	0.8056	45	$p > 0.50$	$p > 0.50$	
	Adipose fin	Run	$\ln(\text{AFL}) = -4.173 + 1.354 \ln(\text{BL})$	0.7211	1035	$t = -0.759$	$t = -1.043$	
		Pool	$\ln(\text{AFL}) = -3.467 + 1.154 \ln(\text{BL})$	0.6197	45	$p > 0.20$	$p > 0.20$	
Female	Hump	Run	$\ln(\text{HH}) = -3.320 + 1.236 \ln(\text{BL})$	0.8031	989	$t = -1.910$	$t = -1.362$	
		Pool	$\ln(\text{HH}) = -2.186 + 0.925 \ln(\text{BL})$	0.7169	39	$p > 0.05$	$p > 0.10$	
	Snout	Run	$\ln(\text{SL}) = -3.790 + 1.253 \ln(\text{BL})$	0.7225	989	$t = -0.482$	$t = -0.109$	
Adipose fin	Run	$\ln(\text{SL}) = -3.439 + 1.155 \ln(\text{BL})$	0.7694	39	$p > 0.50$	$p > 0.50$		
Adipose fin	Run	$\ln(\text{AFL}) = -4.512 + 1.391 \ln(\text{BL})$	0.6603	987	$t = -1.910$	$t = -0.612$		
	Pool	$\ln(\text{AFL}) = -2.588 + 0.854 \ln(\text{BL})$	0.5339	39	$p > 0.05$	$p > 0.50$		

less preserved gonad wet weight) in 1983 and 1985 prime females (Table 11, top and middle). However, the fecundity relationships were relatively more variable (i.e. had lower correlation coefficients), likely due to the variation in egg size observed among females. Fecundities averaged 1256.4 ± 46.3 ($\bar{X} \pm 1$ S.E., $n=31$) in 1983, 764.6 ± 33.8 ($n=91$) in 1985.

No difference in the overall commitment of biomass to gonad could be detected between females from 1983 and 1985. Differences in their egg wet weight-versus-somatic weight or egg water content-versus-egg dry weight relationships were not evident (Table 11, middle and bottom). However, the partitioning of this investment into individual eggs did differ between parent and progeny generations. Females of 1985 increased in fecundity with increasing size at a significantly greater rate than did 1983 females (Table 11, top).

In males, their patterns of commitment of biomass to gonad also differed between parent and progeny generations. The testes of unspawned, prime males from 1983 and 1985 were not different in their relative water content to dry weight proportions (Table 12, bottom). Thus, gonad composition (relative sperm content) was similar in both generations. However, testis wet weight increased with somatic weight at a significantly greater rate (slopes differed) in 1985 than in 1983 males (Table 12, top).

TABLE 11. Comparison of ovary characteristics for 1983 and 1985 Carp River pink salmon females. TEN = total egg number (n), SW = somatic weight (g), EWW = egg wet weight (g), EWC = egg water content (g), EDW = egg dry weight (g). Shown are correlation coefficients (all $p < 0.001$), sample sizes, and results of covariance analyses comparing regressions on adjacent lines. Dashes denote inappropriate intercepts test due to slope differences. Egg numbers for 1985 include both females whose eggs were and were not ovulated. However, the outcome of the comparison did not differ when only females yet to ovulate were considered. All other samples include only unovulated females. Untransformed data yielded the best regression fits.

Year	Regression	r	n	Slopes test	Intercepts test
1983	TEN = 741.745 + 0.715(SW)	0.5916	31	t=3.940 p<0.001	-----
1985	TEN = -66.685 + 1.744(SW)	0.7246	91		
1983	EWW = 12.493 + 0.227(SW)	0.8803	31	t=0.740 p>0.20	t=1.025 p>0.20
1985	EWW = -19.281 + 0.263(SW)	0.7880	18		
1983	EWC = 4.672 + 1.585(EDW)	0.9869	31	t=0.277 p>0.50	t=-1.048 p>0.20
1985	EWC = 9.228 + 1.554(EDW)	0.9529	18		

TABLE 12. Comparison of the testis characteristics for prespawning 1983 and 1985 Carp River pink salmon males. TWW = testis wet weight (g), SW = somatic weight (g), TWC = testis water content (g), TDW = testis dry weight (g). Shown are correlation coefficients (all $p < 0.001$), sample sizes, and results of covariance analyses comparing regressions on adjacent lines. Dashes denote inappropriate intercepts test due to slope differences.

Year	Regression	r	n	Slopes test	Intercepts test
1983	TWW = $11.808 + 0.045(SW)$	0.8706	48	$t=2.897$ $p < 0.005$	-----
1985	TWW = $-4.167 + 0.061(SW)$	0.8843	58		
1983	TWC = $3.446 + 3.076(TDW)$	0.9338	48	$t=1.257$ $p > 0.20$	$t=-1.091$ $p > 0.20$
1985	TWC = $8.199 + 2.790(TDW)$	0.9311	58		

Testis depletion between years

Spawner density is an important determinant of testis depletion in chum salmon (*Oncorhynchus keta*) (Schroder 1972, 1973; Chebanov 1979). However, only the effects of male size and sex ratio on this have been examined in pink salmon (Chebanov 1980a, 1982). Because Carp River spawner densities differed substantially between the 1984 and 1985 runs, how male testis depletion was affected could be examined. Since tagged carcass recoveries in 1984 were few, those retrieved from both the spawning grounds and against the weir were used. To produce a comparable sample, the 1985 recoveries from both sources were similarly combined.

Comparisons of the post-spawning testis weights of prime males from these two years were made relative to the prespawning total body weights of the same tagged fish. The bias arising from including the weight of the prespawning testes in the latter measure was minimal since testis weight comprises only a small fraction of total body weight in pink salmon males (Williams et al. 1986; Moltie et al. 1988). The testis wet weight-prespawning total body weight regression for 1984 males lay above and had a significantly greater slope than that for 1985 males (Table 13). This indicates that males from the small, even-year run died with relatively more residual testis biomass than did males from the large, odd-year run. However, the

TABLE 13. Comparison of the post-spawning testis characteristics of recovered Carp River pink salmon males from 1984 and 1985. TW = testis wet weight (g), PTBW = prespawning total body weight (g), TWC = testis water content (g), TDW = testis dry weight (g). Shown are correlation coefficients (all $p < 0.001$ except * where $p = 0.09$), sample sizes, and results of covariance analyses comparing regression slopes on adjacent lines. Dashes denote inappropriate intercepts test due to slope differences. Samples are of fence and survey males combined.

Year	Regression	r	n	Slopes test	Intercepts test
1984	TW = 6.174 + 0.039(PTBW)	0.5683*	10	t=3.774 p<0.001	-----
1985	TW = 1.244 + 0.012(PTBW)	0.3286	203		
1984	TWC = 5.728 + 4.155(TDW)	0.9685	10	t=0.6927 p>0.20	t=1.392 p>0.10
1985	TWC = 3.553 + 4.313(TDW)	0.9094	203		

similarity in the testis water-testis dry weight relationships (Table 13) indicates that similar concentrations of sperm remained in the testes of males from both years. Together, these results suggest that 1985 males spawning at high densities more fully depleted their testis reserves than did 1984 males.

Determinants of 1985 male spawning performance

The effect of spawner density could also be assessed among males within the 1985 season alone since densities were substantially lower on the spawning grounds than in the pool below the lamprey barrier. The testis depletion of tagged prime males recovered from these two areas differed substantially (Table 14). Although covariance analysis showed the slopes of their testis wet weight-versus-prespawning total body weight regressions to be similar ($p > 0.05$), the intercept for the fence male regression was significantly higher ($t = 3.483$, 200 df, $p < 0.001$) and their adjusted mean testis wet weight was 41% greater. This indicates that testis depletion was reduced among fence males, i.e. those spawning at elevated densities in the pool. Comparing the testis water-testis dry weight regressions for these individuals (Table 14), covariance analysis revealed that the intercept for the fence males was significantly higher than for the survey males ($t = 2.515$, 200 df, $p < 0.02$) and that their adjusted mean testis water weight was 10%

TABLE 14. Evaluation of the effect of spawner density on testis depletion in 1985 Carp River pink salmon males. TWW = testis wet weight (g), PTBW = prespawning total body weight (g), TWC = testis water content (g), TDW = testis dry weight (g). Shown are correlation coefficients (all $p < 0.02$) and sample sizes.

Year	Recovery group	Regression	r	n
1985	Unspawned	$TWW = -4.558 + 0.059(PTBW)$	0.8983	58
	Survey	$TWW = 2.926 + 0.007(PTBW)$	0.2627	86
	Fence	$TWW = 0.455 + 0.015(PTBW)$	0.3647	117
1985	Unspawned	$TWC = 8.199 + 2.790(TDW)$	0.9311	58
	Survey	$TWC = 3.014 + 4.427(TDW)$	0.9225	86
	Fence	$TWC = 4.033 + 4.192(TDW)$	0.9011	117

greater. Thus, the relative water content in the testes of fence males was greater than in the survey males. Given that the salmon testis becomes progressively more watery with disuse (Schroder 1975, 1976), the latter result is also consistent with a reduction in male spawning performance at higher spawner densities.

How fish size affected the testis depletion of males spawning at natural densities (survey males) was also examined in 1985. Compared against unspawned males (Table 14), covariance analysis revealed that the testis wet weight-prespawning total body weight regression for survey males differed significantly in slope ($t=9.700$, 140 df, $p<0.001$). The increasing divergence between these two regressions with increasing male size indicates that large males spawning under natural conditions expended relatively more of their testis contents than did small males in 1985. Considering the testis water-testis dry weight regressions for the unspawned and survey males (Table 14), the latter lay below and had a significantly greater slope than the regression for the unspawned males (ANCOVA, $t=2.578$, $df=140$, $p<0.02$). That the regressions intersected at increasing testis dry weights indicates that the more testis dry weight which survey males retained at death, the more their testis characteristics resembled those of unspawned males.

Length of breeding life

Length of breeding life in pink salmon is a potentially important correlate of reproductive success. For males, longer occupation of the breeding grounds may yield additional spawning opportunities. For females, guarding their redds longer reduces the likelihood of subsequent nest disturbance by other females nesting later in the season (van den Berghe and Gross 1986). For Carp River pink salmon, breeding life was measured as the total number of days prime fish survived after being caught, tagged, and released. Fish size and date of access to the spawning grounds were considered as possible correlates.

In 1984, length of breeding life in males increased with greater total length and earlier Julian date of catch (Table 15), although the effect of date of catch ($t = -2.58$, $p < 0.05$) was stronger than that of size ($t = 1.89$, $0.10 > p > 0.05$). For the small sample of 1984 females, however, the predictive equation was not significant overall (Table 15).

In 1985, the effect of spawner density on length of breeding life was also assessed. Males and females tagged prime were recovered dead either on the spawning grounds (survey fish) or from the pool below the lamprey barrier (fence fish). Fence fish experienced higher spawner densities than did survey fish. In males, length of breeding life decreased significantly with

TABLE 15. Predictive equations summarizing factors influencing length of breeding life of male and female Carp River pink salmon. \overline{LBL} = length of breeding life (days), JDC = Julian date of catch, TL = total length (cm). Recovery group denotes location of carcass recovery in 1985. 1984 carcasses were a mixture of fence and survey recoveries. Shown are correlation coefficients and associated sample sizes. Significant regression coefficients are underlined ($p < 0.05$). * denotes significant overall multiple regressions ($p < 0.05$).

Year	Sex	Recovery group	Regression	r	n
1984	Male	Mixed	$\overline{LBL} = 129.62 - 0.556(\overline{JDC}) + 0.527(TL)$	0.7958*	12
	Female	Mixed	$\overline{LBL} = -44.89 - 0.041(\overline{JDC}) + 1.609(TL)$	0.9808	4
1985	Male	Survey	$\overline{LBL} = 46.18 - 0.162(\overline{JDC}) + 0.149(TL)$	0.3263*	96
		Fence	$\overline{LBL} = 71.55 - 0.239(\overline{JDC}) + 0.012(TL)$	0.3198*	119
	Female	Survey	$\overline{LBL} = 142.89 - 0.527(\overline{JDC}) + 0.150(TL)$	0.5552*	104
		Fence	$\overline{LBL} = 80.02 - 0.248(\overline{JDC}) - 0.123(TL)$	0.3237*	111

increasing Julian date of capture in both recovery groups (Table 15). Because the effect of total length did not attain significance in either group, it was ignored in subsequent analysis. Comparison of the length of breeding life-versus-Julian date of catch regressions for survey and fence males by covariance analysis revealed no significant differences in either slopes or intercepts (Both $p > 0.25$). Furthermore, no differences in average length of breeding life occurred between them (ANOVA, $p > 0.25$; survey males: 11.08 ± 0.33 days; fence males: 11.10 ± 0.33 days; $\bar{X} \pm 1$ S.E.). Together, these results indicate that Julian date of catch was the only factor measured which had a significant effect on length of breeding life in males. Differences in spawner density had no detectable effect on these relationships.

For 1985 females, a rather different outcome resulted. Comparing the total length/Julian date of catch-versus-length of breeding life regressions for the survey and fence females (Table 15) revealed a significant interaction between date and group (ANCOVA, $F=10.10$, 1 and 207 df, $p=0.0017$). Mean length of breeding life also differed significantly between the two groups (ANOVA, $F=8.85$, 1 and 213 df, $p < 0.005$; survey females: 12.89 ± 0.45 days; fence females: 11.21 ± 0.36 days; $\bar{X} \pm 1$ S.E.). Together, these results indicate that length of breeding life and how it was determined differed between spawning environments in

females. The effect of density appears to have been more critical for females than for males, since neither fence nor survey males differed in length of breeding life.

Recovery rates

The recovery rates of anadromous pink salmon spawners are known to differ between males and females (Ward 1959; Helle *et al.* 1964). To test this in Carp River fish, the numbers of tagged carcasses from prime run males and females that were recovered in 1985 from the fence and survey (215 males and 215 females) were compared with the numbers tagged and released but not recovered (630 males and 625 females). No difference in proportions resulted (2x2 continuity-corrected $\chi^2=0.00024$, $p>0.975$). Thus, probability of carcass recovery was neither sex-related nor did it reflect sex differences in length of breeding life. The proportions of tagged males and females recovered against the weir and on spawning ground surveys (Table 15) also did not differ (2x2 continuity-corrected $\chi^2=0.46$, $p>0.25$).

Wandering

Not all fish tagged in the Carp River spawned there. In 1983, three fish were recovered by anglers from the adjacent Batchawana River (Fig. 1) an average of 21 days after being tagged, and showed evidence of having spawned there. Another was angled in the Pancake River (Fig. 1)

19 days after being tagged in the Carp River. Six further individuals were netted by commercial fishermen in Pancake Bay. Three others were recovered in Batchawana Bay in Ontario Ministry of Natural Resources experimental nets. Thus, at least 7.0% of fish initially entering the Carp River in 1983 (13 of 185 tagged individuals) left the stream, many to reproduce in adjacent watercourses. In 1985, tagged, spawning individuals were reported again from the Batchawana River, although tag returns were not provided.

Discussion

Seasonal variation in nightly catch numbers

In all three years of the study, the upstream migration of Carp River pink salmon spanned late August to early October (Figs. 2-4). Current evidence suggests that in pink salmon the timing of their return to their natal stream has a genetic component (Bans 1976; Taylor 1976, 1980). The similarity in annual timing of the Carp River's runs may thus relate to the genetic similarity of odd- and even-year Great Lakes populations (Garrett and Thomason 1987; Ihssen and Moltie, unpublished data), the latter having recently arisen from the former by delayed maturation in this typically biennial species (Wagner and Stauffer 1980; Kwain 1987a). The run timing of Carp River spawners also corresponds

with that of pink salmon from the Lakelse River, British Columbia, the forebears of these populations (Milne 1948; Aro and Shepard 1967; Ricker 1972; Kwain and Rose 1986). The water temperatures associated with each year's first and last catch of Carp River spawners were similar to those recorded in 1981 on the same stream (Kwain and Rose 1986) and elsewhere in southeastern Lake Superior (Nicolette 1983; Nicolette and Spangler 1986).

Nightly catch numbers were influenced by fluctuations in river discharge, wind, and water temperature (Figs. 2-4). However, the relative importance of these factors differed between the sexes some years and between years in males. This inconsistency may result from the stochastic nature of fluctuations in the abiotic environment within and between years. Differences in male and female migration timing, as occurs in anadromous spawners (see below), or the inability to detect relationships due to low regression sample sizes, might also be contributing factors. Previous work on runs into Lake Superior tributaries confirm that wind-generated turbulence (Kwain and Rose 1986) and river discharge (Nicolette 1983; Taylor 1984; Nicolette and Spangler 1986) influence the upstream movement of pink salmon. Kwain and Rose's (1986) daily wind index contains a bias, however. Because it was based on the standard 24-hour clock, winds were applied to an evening's run which in part were those influencing the

run of the previous evening. In the present study, winds were summed instead of time intervals which better reflected the fish's daily migration patterns.

These same three factors, river discharge, wind and water temperatures, also influence upstream movement in anadromous pink salmon. The importance of river discharge has been demonstrated many times (Jordan 1894; Pravdin 1929; Pritchard 1931, 1936, 1937; Davidson and Vaughn 1939a; Davidson *et al.* 1943; Kaganovskii 1949; Hunter 1959; Kirkwood 1962). The effect of temperature is also known to be significant (Kaganovskii 1949; Sheridan 1962, but see Pritchard 1936; Davidson *et al.* 1943; Hunter 1959), as is wind (Davidson and Christey 1938; Kaganovskii 1949; Dvinin 1952). This congruence is evidence that the migrations of anadromous and Great Lakes pink salmon are influenced by similar factors.

The increase in the proportion of females caught through the 1985 run confirms findings for other Lake Superior tributaries (Nicolette 1983; Nicolette and Spangler 1986), Withler and Kwain's (1984) offshore net samples, and Kwain and Rose's (1986) Carp River and nearby Pancake River entrance data. This aspect of Great Lakes pink salmon breeding ecology is also typical for anadromous populations from British Columbia (Pritchard 1931, 1937), Alaska (Davidson and Shostrom 1936; Davidson and Vaughn 1939b; Hutchinson 1944; Helle *et al.* 1964), the U.S.S.R. (Milovidova-Dubrovskaja 1937; Senko 1939;

Berg 1948; Kaganovskii 1949; Dvinin 1952; Birman 1958; Yefanov and Chupakhin 1982), and Japan (Ishida 1967). The smaller sample sizes obtained through the 1983 and 1984 Carp River runs (Figs. 2-4) may have prevented detecting changes in sex composition these years.

Size differences through the runs

In combined samples obtained at the mouths of the Carp and Pancake Rivers in 1981, Kwain and Rose (1986) found that larger males were captured as the run progressed, ending with a slight decrease in size, but that female size did not vary during the run. In this study, both males and females netted near the mouth of the Carp River were larger as the run progressed in 1983. However, the opposite held true for males and females trapped further upstream below the lamprey barrier in 1984 and 1985 (Table 1). Although construction of the lamprey barrier followed the 1983 run, and environmental conditions, capture methods and sampling locations differed each season, it is difficult to explain how these factors might cause size trends through the runs to differ from year to year. Because Kwain and Rose (1986) found that a lag of three to four days separated river mouth catches and upstream recaptures of the same tagged fish on the Carp River, it is possible that these fish do not maintain their run chronology after stream entry. Year to year switches may not be atypical, however:

opposite trends in the sizes of fish caught through runs in successive years in the same stream have also been recorded in anadromous pink salmon (Helle et al. 1964). The trends for runs into different streams may also vary, some increasing (Pritchard 1937), some decreasing (Semko 1939; Davidson and Vaughn 1941; Hoar 1951; Skud 1958; Hart 1973).

Nightly migration patterns

Across the 1983 season, no differences were found in the proportions of males and females caught each hour of the run (Table 2). This confirms Kwain and Rose's (1986) finding for 1981 fish on the same river. The rapid increase in the catch of both sexes at nightfall (Table 2) suggests that stream entry was cued by decreasing light intensity. This is also the case in other landlocked salmonids entering streams to breed (Munro and Balmain 1956; Lorz and Northcote 1965). Comparable studies of stream entrance timing in anadromous pink salmon populations are few. Pink salmon initiating their run into the Maleo River, a tributary of the U.S.S.R.'s Amur River, did so at night (Kuznetsov 1928). In contrast, Semko (1939) found that pink salmon entering the Bol'shaie River directly from the ocean did so mainly by day. Fish from the Thompson River, a tributary far up British Columbia's Fraser River, approached the spawning grounds predominantly by day as

well (Ward 1959). Thus, it is not clear whether the timing of river entry differs between lacustrine and anadromous populations. However, the constraints dictating the timing of pink salmon movements into the Carp River differ from those which apply to anadromous populations, since neither osmotic changes nor transitions between mainstem and tributary are involved in the former.

Differences in migrant size

Initial reports of the size of pink salmon from various Lake Superior tributaries indicated that, on average, even-year spawners were larger than odd-year spawners (Berg 1979; Kwain and Lawrie 1981). This alternation has not been consistent in more recent generations (Nicolette 1983; Bagdovits 1985; Wagner 1985; Bagdovits *et al.* 1986; Nicolette and Spangler 1986). That Carp River fish were smaller in 1985 than in either 1983 or 1984 (Table 4) continues this trend of more random seasonal differences. Moltie (1987a) outlines why these differences were unlikely to have resulted from differences in the capture methods used each year. Wagner (1985) confirms the similarity in sizes of fish from 1983 and 1984 in independent samples taken from other eastern Lake Superior pink salmon streams.

The diminished size of 1985 Carp River spawners (Table 4) may stem from decreased prey abundance.

Rainbow smelt (Osmerus mordax) are important prey for Great Lakes pink salmon in their second year (Kwain 1982; Withler and Kwain 1984; Huggler 1985; Kussall and Peebles 1986; Kocik and Taylor 1987b), and the abundance of smelt in Lake Superior, although variable from year to year (Anderson and Smith 1971), has recently been suggested to be on the decline (Bagdovitz 1985). Similar declines in the size of introduced chinook salmon (Oncorhynchus tshawytscha) occurred in landlocked New Hampshire lakes after smelt, the dominant prey species, became depleted (Hoover 1935). In other studies, the growth of Pacific salmon has been shown to correlate positively with water temperatures during the pelagic phase of their lives (Helle 1979; Beacham and Starr 1982). Thus, variation in the thermal and/or productivity conditions in Lake Superior may have also contributed to the yearly size differences in Carp River spawners.

Condition

Among females of all three years and males of 1983 and 1984, the slopes of their condition regressions (Table 5) exhibited positive allometry. In these groups, longer fish were more robust for their lengths than shorter fish. Although not well documented, Great Lakes pink salmon apparently feed primarily on various aquatic invertebrates and insects for much of their early lives (Kwain 1982; Nicolette 1983; Withler and Kwain 1984;

Bagdovits 1985; Ryder and Edwards 1985; Nicolette and Spangler 1986; Wilcock 1985; Kwain 1987a). However, in larger, second year individuals, rainbow smelt comprise substantially more of the diet, supplemented by alewife (Alosa pseudoharengus), and emerald shiners (Notropis atherinoides) (Kwain 1982; Withler and Kwain 1984; Huggler 1985; Ryder and Edwards 1985; Kocik and Taylor 1987b; Kwain 1987a). In both landlocked Atlantic salmon (Salmo salar) and lake trout (Salvelinus namaycush), condition has been shown to vary directly with the amount of rainbow smelt consumed (Bridges and Hambly 1971). Likewise, improved condition in longer pink salmon may be a reflection of increased fish content in the diet.

In 1985, males were in significantly poorer condition than females (Table 5). Reductions in condition might be more readily apparent in males if food became more limiting in 1985 because males typically grow faster than females (Table 4). In contrast, males and females of 1983 and 1984 did not differ in condition (Table 5), suggesting comparable exploitation of available food resources these years, i.e. when food may not have been as limiting as in 1985.

Sexual dimorphism

Maturing pink salmon mobilise and redeposit body reserves in undertaking their hump and snout development (Davidson 1935; Davidson and Shostrom 1936). Hump

heights in males and females were smaller in 1985 than in 1984 (Tables 6 and 7). Males also exhibited reduced snout development in 1985 (Tables 6 and 7). These results suggest that 1985 fish in poor condition (Table 5) could not devote as much somatic tissue to hump and snout growth as could fish in better condition from the previous year.

Reproductive maturity

In some anadromous pink salmon populations, reproductive maturity precedes stream entry (Davidson and Hutchinson 1942; Rounsefell 1958; Dye et al. 1986; McBride et al. 1986). In others, maturity occurs some weeks after they reach their home stream (Davidson and Shostrom 1936; Davidson and Vaughn 1939b; Berg 1948; Dvinin 1952; Ward 1959; Cameron 1968; Taylor 1976). In noting this dichotomy, Davidson and Vaughan (1941) and Davidson et al. (1943) concluded that pink salmon are of two migrant types. Carp River fish migrating upstream had completed their external metamorphosis (Table 10). The gonadal maturation in males was also virtually complete, and was soon to be so in females (Tables 8 and 9). Thus, these landlocked fish appear to belong to the first migrant type of Davidson and Vaughan (1941). That somewhat immature fish occurred predominantly among females is of interest. For males, reproductive competence upon stream entry ensures their immediate

capacity to compete successfully for fertilizations. For females, maturity on stream entry is likely not as crucial since they must first select a nest site and then complete its excavation.

Gonad investment

Both fecundity in females and testis biomass in males increased at a greater rate with increasing body size in 1985 than in 1983 Carp River spawners (Tables 11 and 12). These differences between presumed parent and progeny generations in the pattern of reproductive investment might stem simply from yearly differences in environment or in fish condition (Table 5). However, changing patterns of gonad and somatic weight variation may also be evidence of selection acting to optimize reproductive investment in these fish as they continue their adaptation to the Great Lakes. The fecundity relationships for female Lake Superior pink salmon from other years also exhibit substantial variation (Kwain 1982; Nicolette 1983; Bagdovits 1985; Bush 1985; Wagner 1985; Bagdovits et al. 1986; Nicolette and Spangler 1986).

Testis depletion between years

In Carp River pink salmon, competition for proximity to a nesting female typically results in the formation of a dominance hierarchy among males (Noltie 1986). This is

composed of a large lead male located closest to the female and successively smaller subsidiary males arrayed downstream. By being closer to the female, large male salmon obtain more fertilization opportunities than small males (Hanson and Smith 1967; Schroder 1973, 1976; Chebanov 1979, 1982). As a result, they also father more young (Chebanov 1979, 1980a; Schroder and Duker 1979; Schroder and Seeb 1979; Schroder 1981, 1982; Chebanov et al. 1983; Gross 1985; Maekawa and Onozato 1986; Hutchings and Myers 1987). This suggests why testis depletion was found to be greater in larger than in smaller males in this study (Table 14). Similar results were also reported by Chebanov (1979) for chum salmon. Also in Carp River pink salmon, the numbers of males accompanying nesting females were greater during the large run of 1985 than in the small run the previous year (Moltie 1988). Thus, the number of spawning males from 1985 could participate in was likely greater than in 1984, resulting in the greater degree of testis depletion 1985 males exhibited (Table 13).

Determinants of 1985 male spawning performance

The effects of variation in spawner densities in pink salmon have usually been assessed with respect to the efficiency of egg deposition by females or to subsequent embryo survivorship (e.g. McNeil 1964; Heard 1978; Nicolette and Spangler 1986). Evidence from the present

study suggests that the reproductive performance (testis depletion) of males may also suffer at substantially increased spawner densities (Table 14). In Carp River males whose spawning performance was reduced (i.e. 1985 pool males), the relative water content of their testes was greater (Table 14). This is consistent with Schroder's (1975, 1976) finding that in chum salmon the effect of lengthening freshwater occupation on the unused testis is an increase in water content, resulting in reduced fertility (Schroder 1981).

Length of breeding life

For males, increased spawner densities did not affect length of breeding life in 1985 (Table 15). For females, however, length of breeding life diminished. This difference between the sexes suggests that competition for spawning opportunities in 1985 may have been greater for females than for males. In contrast to the present findings, Chebanov (1980b) suggested that high spawner densities prolonged male life expectancy in an anadromous population, but provided no information as to how his experimental densities compared to those in nature. As found here, Senko (1939) and Ellis (1969) also attributed longer breeding lives in females to lower spawning ground densities in anadromous populations.

Early Carp River migrants survived longer than did late running individuals (Table 15). This has also been

documented in anadromous populations (Ward 1959; Helle et al. 1964; Helle 1970; Dangel and Jones 1987) and for other Pacific salmon species (Willis 1954; Killick 1955; McCart 1970; Neilson and Geen 1981; Neilson and Banford 1983, but see Schroder 1973). In this regard, Carp River spawners appear similar to anadromous Oncorhynchus species.

For Carp River spawners, date of catch was a more important determinant of length of breeding life than was fish total length (Table 15). This contrasts with findings for other salmon species in which size is the more important factor. In chum salmon, smaller males survive longer than do large ones (Chebanov 1979). In coho salmon (Oncorhynchus kisutch), larger fish survive longer on the spawning grounds, while season has no effect (van den Berghe and Gross 1986). This difference from other salmon species supports the contention of McBride et al. (1986) that the timing of pink salmon spawning and senescence is under sufficient genetic control that all other factors have relatively little influence on it.

The life expectancies recorded for Carp River pink salmon recovered on the spawning grounds (11-13 days) were comparable to those of anadromous individuals (Senko 1939; McNeil 1964; Helle et al. 1964; Dangel and Jones 1987). However, Kwain (1982) estimated that spawners in Lake Superior's Steel River survived on the

spawning grounds for less than 7 days. To what to attribute the shorter spawning life in Steel River fish is unknown. However, higher densities may have accompanied the much larger Steel River population of ca. 90,000 fish (Kwain 1982). If so, then shortened breeding lifespans may have resulted, as occurred in Carp River females which spawned at high densities in 1985 in the pool below the lamprey barrier.

For recoveries made on the Carp River spawning grounds, the length of breeding life in males was slightly shorter (11 days) than in females (13 days). This is consistent with the findings of Chebanov (1980a) for an anadromous pink salmon population in the Soviet Union. However, Dangel and Jones (1987) found that anadromous males and females in Alaska survived equally long on the spawning grounds. Thus, whether the differences in lifespan that Carp River males and females exhibited is typical cannot be determined. In other salmon species, males and females in kokanee and sockeye (McCart 1970) and coho salmon (van den Berghe and Gross 1986) exhibit similar lengths of breeding life. However, females outlive males in chinook (Neilson and Geen 1981), chum (Chebanov 1979), and in the coho salmon studied by Crone and Bond (1976). Males outlive females in sockeye (Killick 1955; Mathisen 1955) and in the chum salmon Schroder (1973) studied. Together, these findings

suggest that local conditions may contribute greatly to sex-specific spawning life expectancy in salmon species.

Recovery rates

Male and female carcasses were recovered in equal proportions against the weir and on the spawning grounds in 1985 (Table 15). In contrast, Helle *et al.* (1964) found that weir recoveries favoured males in anadromous spawners, suggesting that males nearing death were more likely to drift downstream than females because they exhibit less attachment to sites on the spawning grounds. Because the weir Helle *et al.* (1964) monitored was almost three times further downstream from the spawning grounds (>1.6 km) than was that on the Carp River (0.6 km), sex-biased recovery rates may have been favoured there. However, in other pink salmon studies where carcasses were retrieved from the spawning grounds, Ward (1959) also recovered more females than males. Parallel results have been reported for recoveries of sockeye salmon carcasses from the spawning grounds too (Peterson 1954).

Wandering

Fish tagged in the Carp River wandered elsewhere at a rate conservatively estimated at 7%. This represents the first quantitative estimate of true wandering rates among Great Lakes pink salmon, since Kwain and Rose (1986) assessed downstream movement but not eventual recapture

elsewhere. Such high wandering rates are not known for anadromous pink salmon (Pritchard 1932, 1934, 1939, 1941, 1943, 1944; Clemens 1935; Clemens et al. 1939; Foerster 1943, 1944; Vernon 1962; Harry and Olson 1963; Helle 1966; Ishida 1966; Parker 1967; Aspinwall 1974; Withler 1982). Where wandering from Pacific tributaries does occur, however, suggestions are that donor and recipient streams must be in close proximity (Davidson 1934; Pritchard 1943; Semko 1954). Thus, the closeness of the the Carp River to adjacent streams (Fig. 1) may have contributed to the high wandering rates recorded from it. Kwain (1987a) suggests that such wandering might also result from overcrowding. Of interest, wanderers leaving the Carp River and entering the Pancake River did so against both the prevailing current flow of Lake Superior (Pycha et al. 1965) and the direction from which pink salmon initially approach the Carp River (Kwain and Lawrie 1981; Kwain and Rose 1986; Kwain 1987a).

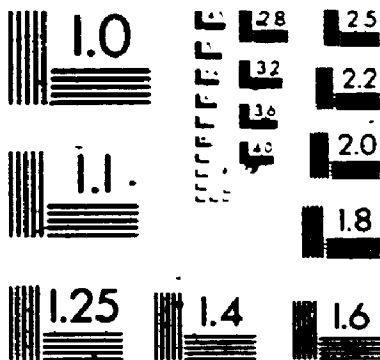
Conclusion

In previous reports, it has been suggested that Great Lakes pink salmon are but smaller versions of their anadromous conspecifics (Kwain 1982; Nicolette 1983; Nicolette and Spangler 1986). Much of the data presented here concerning the breeding ecology of Carp River spawners supports this contention. The obvious success of this species in a habitat previously considered

2

of / de

2



unsuitable (Rounsefell 1958) makes it an exciting study in local adaptation. Exploitation of Great Lakes pink salmon by sport and commercial interests has just begun, and has generated some debate (Wagner and Stauffer 1975; Richey 1976; Honscoewts 1978; Kwain 1978, 1987a,b; Reid 1980; Anonymous 1981, 1982, 1988; Emery 1981; Kwain and Lawrie 1981; Minns 1983; Kelso and Collins 1984; Thibert 1984; Withler and Kwain 1984; Huggler 1985; Kerr 1985a,b; Morgan 1985a,b; Nicolette and Spangler 1986; Rose 1986; Kocik and Taylor 1987b). Great Lakes pink salmon also threaten to invade Atlantic waters (Emery 1981; Prince 1984; Randall 1984; Snow 1984; Dermott and Timmins 1986; Kwain 1987a). Competition for food resources with other species of importance is already occurring (Lawrie and Rahrer 1972; Ryder and Edwards 1985; Kocik and Taylor 1987b). Management decisions appropriate to these concerns must be predicated on an adequate understanding of the species' biology. The present study represents one step towards providing the requisite information.

Acknowledgements

For their field assistance, I thank Daniel Burton, Johnny Ellis, Josée Emerson, Nancy Kirkpatrick, Tammy McKellar, Elaine Moltie, Lionel Normand, and especially Daniel Robilliard. T.C. McAuley of the Fisheries and Oceans Sea Lamprey Control Centre in Sault Ste. Marie

aided in the Carp River discharge conversions. P.J. McCurry of Environment Canada's Water Resources Branch in Guelph provided the Batchawana River discharge records. Elaine Moltie assisted with figure preparation. Financial support of this work came from NSERC and OGS scholarships to the author, grants from the Ontario Ministry of Natural Resources, the Canadian Department of Fisheries and Oceans, the Ontario Federation of Anglers and Hunters, and an NSERC operating grant to M.H.A. Keenleyside.

- ANDERSON, E.D., and L.L. SMITH, Jr. 1971. Factors affecting abundance of lake herring (Coregonus artedii Lesueur) in western Lake Superior. Trans. Am. Fish. Soc. 100: 691-707.
- ANONYMOUS. 1981. Lake Superior pinks. Sport Fish. Inst. Bull. 328: 6-7.
- 1982. Great Lakes pinks. Sport Fish. Inst. Bull. 334: 7.
- 1988. Pink salmon limit will be pursued. Angler and Hunter 12(4): 7.
- ARO, K.V. 1979. Transfers of eggs and young of Pacific salmon within British Columbia. Fish. Mar. Serv. Tech. Rep. 861: 147 p.

- ARO, K.V., and M.P. SHEPARD. 1967. Salmon of the North Pacific Ocean - Part IV Spawning populations of North Pacific salmon 5. Pacific salmon in Canada. Int. North Pac. Fish. Comm. Bull. 23: 225-327.
- ASPINWALL, N. 1974. Genetic analysis of North American populations of the pink salmon, Oncorhynchus gorbuscha, possible evidence for the neutral mutation-random drift hypothesis. *Evol.* 28: 295-305.
- BAGDOVITZ, M.S. 1985. Ecology and life history of pink salmon (Oncorhynchus gorbuscha) in selected Michigan tributaries to Lake Superior. M.Sc. thesis, Michigan State Univ., East Lansing, MI. 64 p.
- BAGDOVITZ, M.S., W.W. TAYLOR, W.C. WAGNER, J.P. NICOLETTE, and G.R. SPANGLER. 1986. Pink salmon populations in the U.S. waters of Lake Superior, 1981-1984. *J. Great Lakes Res.* 12: 72-81.
- BAMS, R.A. 1976. Survival and propensity for homing as affected by presence or absence of locally adapted paternal genes in two transplanted populations of pink salmon (Oncorhynchus gorbuscha). *J. Fish. Res. Board Can.* 33: 2716-2725.
- BEACHAM, T.D., and C.B. MURRAY. 1983. Sexual dimorphism in the adipose fin of Pacific salmon (Oncorhynchus). *Can. J. Fish. Aquat. Sci.* 40: 2019-2024.
- 1986. Sexual dimorphism in length of upper jaw and adipose fin of immature and maturing Pacific salmon (Oncorhynchus). *Aquacult.* 58: 269-276.

- BEACHAM, T.D., and P. STARR. 1982. Population biology of chum salmon, Oncorhynchus keta, from the Fraser River, British Columbia. Fish. Bull. 80: 813-825.
- BERG, L.S. 1948. Freshwater fishes of the U.S.S.R. and adjacent waters. 4th edition. Trans. from Russian by the Israel Program for Scientific Translations. Published by the National Science Foundation, Washington, D.C. and the Smithsonian Institute, 1962. 504 p.
- BERG, R.E. 1979. External morphology of the pink salmon, Oncorhynchus gorbuscha, introduced into Lake Superior. J. Fish. Res. Board Can. 36: 1283-1287.
- BILTON, H.T., and W.E. RICKER. 1965. Supplementary checks on the scales of pink salmon (Oncorhynchus gorbuscha) and chum salmon (O. keta). J. Fish. Res. Board Can. 22: 1477-1489.
- BIRMAN, I.B. 1958. On the occurrence and migration of Kamchatka salmon in the northwestern part of the Pacific Ocean. In Materialy po biologii morskovo perioda zhizni dalnevostochnykh lososei. VNIRO, Moscow. pp. 31-51. Transl. from Russian by Fish. Res. Board Can. Trans. Ser. 180: 1-24.
- BRIDGES, C.H., and L.S. HAMBLY. 1971. A summary of eighteen years of salmonid management at Quabbin Reservoir, Massachusetts. In Reservoir fisheries and limnology. American Fisheries Society Special

Publication 8. Edited by G.E. Hall. American Fisheries Society, Bethesda, MD. pp. 243-254.

BUSH, J.E. 1985. Determination of fertility in two and three-year-old pink salmon in a Minnesota tributary to Lake Superior. M.Sc. thesis, Univ. of Minnesota, St. Paul, MN. 73 p.

CAMERON, W.M. 1968. A preliminary investigation of the natural spawning, incubation and alevinage of the pink salmon (Oncorhynchus gorbuscha). Fish. Res. Board Can. MS Rep. 995: 1-25.

CHEBANOV, N.A. 1979. Behavior and mate selection among chum brood stock of different sizes with a predominance of males in the spawning grounds. Sov. J. Ecol. 10: 141-146.

----- 1980a. Spawning behavior of the pink salmon, Oncorhynchus gorbuscha. J. Ichthyol. 20: 64-73

----- 1980b. Materials on the assortive crossing and the role of sex ratio during the spawning period of the Pacific salmon. In Salmonid ecosystems of the North Pacific. Edited by W.J. McNeil and D.C. Himsworth. Oregon State University Press, Corvallis, OR. pp. 323.

----- 1982. Spawning behavior of the humpbacked salmon Oncorhynchus gorbuscha with different ratios of sexes at the spawning ground. Sov. J. Ecol. 13: 53-61.

- CHEBANOV, M.A., N.V. VARNAVSKAYA, and V.S. VARNAVSKIY. 1983. Effectiveness of spawning of male sockeye salmon, Oncorhynchus nerka (Salmonidae), of differing hierarchical rank by means of genetic-biochemical markers. J. Ichthyol. 23: 51-55.
- CLEMENS, W.A. 1935. Appendix 3. Report of the Pacific Biological Station Nanaimo, B.C. for 1934. Ann. Rep. Biol. Board Can. for 1934. pp. 24-34.
- CLEMENS, W.A., R.E. FOERSTER, and A.L. PRITCHARD. 1939. The migration of Pacific salmon in British Columbia waters. Amer. Assoc. Adv. Sci. Publ. 8: 51-59.
- COLLINS, J.J. 1975. Occurrence of pink salmon (Oncorhynchus gorbuscha) in Lake Huron. J. Fish. Res. Board Can. 32: 402-404.
- CRONE, R.A., and C.E. BOND. 1976. Life history of coho salmon, Oncorhynchus kisutch, in Sashin Creek, southeastern Alaska. Fish. Bull. 74: 897-923.
- DANGEL, J.R., and J.D. JONES. 1987. Southeast Alaska pink salmon total escapement and stream life. In Proceedings of the 1987 northeast Pacific pink and chum salmon workshop. Edited by P. Rigby. Alaska Dept. Fish Game, Juneau, AK. pp. 43-53.
- DAVIDSON, F.A. 1934. The homing instinct and age at maturity of the pink salmon (Oncorhynchus gorbuscha). Bull. U.S. Bur. Fish. 48: 27-39.

- 1935. The development of the secondary sexual characters in the pink salmon (Oncorhynchus gorbuscha). J. Morphol. 57: 169-183.
- DAVIDSON, F.A., and L.S. CHRISTEY. 1938. The migrations of pink salmon (Oncorhynchus gorbuscha) in the Clarence and Sumner Straits regions of southeastern Alaska. Bull. U.S. Bur. Fish. 48: 643-666.
- DAVIDSON, F.A., and S.J. HUTCHINSON. 1942. Natural reproduction of pink salmon studied at Little Port Walter, Alaska. Ecol. 23: 234-235.
- DAVIDSON, F.A., and O.E. SHOSTROM. 1936. Physical and chemical changes in the pink salmon during the spawning migration. U.S. Bur. Fish. Invest. Rep. 33: 1-37.
- DAVIDSON, F.A., and A.E. VAUGHN. 1939a. Cyclic changes in time of southeast Alaska pink salmon runs. Part 2. Pacific Fisherman (March): 40-42.
- 1939b. Cyclic changes in time of southeast Alaska pink salmon runs. Part 3. Pacific Fisherman (April): 39.
- 1941. Relation of population size to marine growth and time of spawning migration in the pink salmon (Oncorhynchus gorbuscha) of southeastern Alaska. J. Mar. Res. 4: 231-246.
- DAVIDSON, F.A., E. VAUGHAN, S.J. HUTCHINSON, and A.L. PRITCHARD. 1943. Factors influencing the

- upstream migration of the pink salmon (Oncorhynchus gorbuscha). Ecol. 24: 149-168.
- DERMOTT, R. 1982. Status of pink salmon (Oncorhynchus gorbuscha) in Lake Ontario, 1981. Can. MS Rep. Fish. Aquat. Sci. 1671: 7 p.
- 1984. Benthic fauna assemblages in Batchawana Bay, Lake Superior. Can. Tech. Rep. Fish. Aquat. Sci. 1265: 17 p.
- DERMOTT, R.M., and C.A. TIMMINS. 1986. Occurrence and spawning of pink salmon, Oncorhynchus gorbuscha, in (Lake Ontario tributaries. Can. Field-Nat. 100: 131-133.
- DVININ, P.A. 1952. The salmon of south Sakhalin. Izv. TINRO. 37: 69-108. Transl. from Russian by Fish. Res. Board Can. Trans. Ser. No. 120: 47 p.
- DYE, H.M., J.P. SUMPTER, U.H.M. FAGERLUND, and E.M. DONALDSON. 1986. Changes in reproductive parameters during the spawning migration of pink salmon, Oncorhynchus gorbuscha (Walbaum). J. Fish. Biol. 29: 167-176.
- ELLIS, R.J. 1969. Return and behavior of adults of the first filial generation of transplanted pink salmon, and survival of their progeny, Sashin Creek, Baranof Island, Alaska. U.S. Fish. Wildl. Serv. Spec. Sci. Rep. Fish. 589: 1-13.

- EMERY, L. 1981. Range extension of pink salmon (Oncorhynchus gorbuscha) into the lower Great Lakes. Fisheries 6: 7-10.
- FOERSTER, R.E. 1943. Appendix 4. Report for 1942 of the Pacific Biological Station, Nanaimo, B.C. Ann. Rep. Fish. Res. Board Can. for 1942. pp. 20-24.
- 1944. Appendix 4. Report for 1943 of the Pacific Biological Station, Nanaimo, B.C. Ann. Rep. Fish. Res. Board Can. for 1943. pp. 22-26.
- GHARRETT, A.J., and M.A. THOMASON. 1987. Genetic changes in pink salmon (Oncorhynchus gorbuscha) following their introduction into the Great Lakes. Can. J. Fish. Aquat. Sci. 44: 787-792.
- GROSS, M.R. 1985. Disruptive selection for alternative life histories in salmon. Nature 313: 47-48.
- HANSON, A.J., and H.D. SMITH. 1967. Mate selection in a population of sockeye salmon (Oncorhynchus nerka) of mixed age-groups. J. Fish. Res. Board Can. 24: 1955-1977.
- HARRY, G.Y., Jr., and J.M. OLSON. 1963. Straying of pink salmon to Sashin Creek Little Port Walter Bay. Auke Bay Biol. Lab. MS Rep. 63-3: 1-9.
- HART, J.L. 1973. Pacific fishes of Canada. Fish. Res. Board Can. Bull. 180: 1-740.
- HEARD, W.R. 1978. Probable case of streambed overseeding - 1967 pink salmon, Oncorhynchus gorbuscha, spawners

- and survival of their progeny in Sashin ~~Alaska~~
southeastern Alaska. Fish. Bull. 76: 569-582.
- HELLE, J.H. 1966. Behavior of displaced adult pink salmon. Trans. Am. Fish. Soc. 95: 188-195.
- 1970. Biological characteristics of intertidal and fresh-water spawning pink salmon at Olsen Creek, Prince William Sound, Alaska, 1962-63. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 602: 1-19.
- 1979. Influence of marine environment on age and size at maturity, growth, and abundance of chum salmon, Oncorhynchus keta (Walbaum), from Olsen Creek, Prince William Sound, Alaska. Ph.D. thesis; Oregon State Univ., Corvallis, OR. 129 p.
- HELLE, J.H., R.S. WILLIAMSON, and J.E. BAILEY. 1964. Intertidal ecology and life history of pink salmon at Olsen Creek, Prince William Sound, Alaska. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 483: 1-26.
- HOAR, W.S. 1951. The chum and pink salmon fisheries of British Columbia 1917-1947. Fish. Res. Board Can. Bull. 90: 1-46.
- HONSOWETS, D.C. 1978. The fish that fooled the experts. Mich. Out-of-Doors 32: 34-35, 82.
- HOOVER, E.E. 1936. Contributions to the life history of the chinook and landlocked salmon in New Hampshire. Copeia 1936: 193-198.

- HUGGLER, T. 1985. Michigan's pink pussler. Mich. Nat. Res. (September/October): 12-17.
- HUNTER, J.G. 1959. Survival and production of pink and chum salmon in a coastal stream. J. Fish. Res. Board Can. 16: 835-886.
- HUTCHINGS, J.A., and R.A. MYERS. 1987. Egg fertilization by mature male parr in competition with anadromous male Atlantic salmon (Salmo salar) during spawning. In Reproductive physiology of fish 1987. Proceedings of the 3rd international symposium on reproductive physiology of fish, St. John's, Newfoundland, Canada, August 2-7, 1987. Edited by D.R. Idler, L.W. Crim, and J.M. Walsh. Marine Sciences Research Laboratory, Memorial University of Newfoundland, St. John's, Nfld. pp. 131.
- HUTCHINSON, S.J. 1944. Port Walter evidence points to fewer pinks in 1944 for southeast Alaska generally. Pacific Fisherman (February): 37, 39.
- HYNES, H.B.M. 1970. The ecology of running waters. University of Toronto Press, Toronto, Ont. 555 p.
- ISHIDA, T. 1966. Salmon of the north Pacific Ocean - Part III A review of the life history of north Pacific salmon 2. Pink salmon in the far east. Int. North Pac. Fish. Comm. Bull. 18: 29-39.
- 1967. Salmon of the north Pacific Ocean - Part IV Spawning populations of north Pacific salmon

2. Pink salmon in the far east. Int. North Pac. Fish. Comm. Bull. 23: 9-22.
- JORDAN, D.S. 1894. Salmon and trout of the Pacific coast. Calif. State Board Fish. Comm. 13th Biennial Rep. for 1893-1894: 125-141.
- KAGANOVSKII, A.G. 1949. Some problems of the biology and population dynamics of pink salmon. Isv. TINRO 31: 3-57. In Pacific salmon: selected articles from Soviet periodicals translated from Russian. Published for the National Science Foundation, Washington, D.C., and the Department of the Interior by the Israel Program for Scientific Translations, Jerusalem. 1961. pp. 127-183.
- KELSO, J.R.M., and R.H. COLLINS. 1984. An attempt at assessing abundance and distribution of pink salmon (*Oncorhynchus gorbuscha*) prior to their entry of spawning streams. Can. MS Rep. Fish. Aquat. Sci. 1772: 16 p.
- KERR, J. 1985a. Pinks: threat or benefit? Ont. Out-of-Doors 17(5): 12-14.
- 1985b. Year of the pink. Ont. Out-of-Doors 17(7): 36-39.
- KILLICK, S.R. 1955. The chronological order of Fraser River sockeye salmon during migration, spawning and death. Int. Pac. Salmon Fish. Comm. Bull. 7: 1-95.

- KIRKWOOD, J.B. 1962. Inshore-marine and freshwater life history phases of the pink salmon, Oncorhynchus gorbuscha (Walbaum), and the chum salmon, O. keta (Walbaum), in Prince William Sound, Alaska. Ph.D. thesis, Univ. of Louisville, Louisville, KY. 300 p.
- KIZEVETTER, I.V. 1948. Changes in chemical composition of the body of red (sockeye) salmon. Izv. TINRO 27: 29-42. In Pacific salmon: selected articles from Soviet periodicals translated from Russian. Published for the National Science Foundation, Washington, D.C., and the Department of the Interior by the Israel Program for Scientific Translations, Jerusalem. 1961. pp. 86-100.
- KOCIK, J., and W.W. TAYLOR. 1987a. Diet and movements of age-1+ pink salmon in western Lake Huron. Trans. Am. Fish. Soc. 116: 628-633.
- 1987b. Effect of fall and winter instream flow on year-class strength of Pacific salmon evolutionarily adapted to early fry outmigration: a Great Lakes perspective. In Common strategies of anadromous and catadromous fishes. American Fisheries Society Symposium 1. Edited by M.J. Dadswell, R.J. Klauda, C.M. Moffit, R.L. Saunders, and R.A. Rulifson. American Fisheries Society, Bethesda, MD. (in press).

KUSNETSOV, I.I. 1928. Some observations on the propagation of the Amur and Kamchatka salmon. Izv. Tikhookean. nauchno-issled. Stantsii. 2(3): 3-195. Trans. from Russian by N.B. Motkin, Int. Pac. Sal. Fish. Comm., Seattle, WA., March 19, 1947. 249 p.

KWAIN, W. 1971. Life history of rainbow trout (Salmo gairdneri) in Batchawana Bay, eastern Lake Superior. J. Fish. Res. Board Can. 28: 771-775.

----- 1978. Pink salmon are here to stay. Ont. Fish Wildl. Rev. 17: 17-19.

----- 1982. Spawning behavior and early life history of pink salmon (Oncorhynchus gorbuscha) in the Great Lakes. Can. J. Fish. Aquat. Sci. 39: 1353-1360.

----- 1987a. Biology of pink salmon in the North American Great Lakes. In Common strategies of anadromous and catadromous fishes. American Fisheries Society Symposium 1. Edited by M.J. Dadswell, R.J. Klauda, C.M. Moffit, R.L. Saunders, and R.A. Rulifson. American Fisheries Society, Bethesda, MD. (in press).

----- 1987b. Record size of freshwater pink salmon. N. Am. J. Fish. Manage. 7: 302-303.

KWAIN, W., and J.A. CHAPPEL. 1978. First evidence for even-year spawning pink salmon, Oncorhynchus gorbuscha, in Lake Superior. J. Fish. Res. Board Can. 35: 1373-1376.

- KWAIN, W., and A.H. LAWRIE. 1981. Pink salmon in the Great Lakes. Fisheries 6: 2-6.
- KWAIN, W., and G.A. ROSE. 1986. Spawning migration of Great Lakes pink salmon (Oncorhynchus gorbuscha): size and sex distributions, river entrance and exit. J. Great Lakes Res. 12: 101-108.
- LAWRIE, A.H., and J.F. RAHRER. 1972. Lake Superior: effects of exploitation and introductions on the salmonid community. J. Fish. Res. Board Can. 29: 765-776.
- LORZ, H.W., and T.G. NORTHCOTE. 1965. Factors affecting stream location, and timing and intensity of entry by spawning kokanee (Oncorhynchus nerka) into an inlet of Nicola Lake, British Columbia. J. Fish. Res. Board Can. 22: 665-687.
- MacKAY, H.H. 1963. Fishes of Ontario. Bryant Press Limited, Toronto, Ont. 300 p.
- MAEKAWA, K., and H. ONOZATO. 1986. Reproductive tactics and fertilization success of mature male Miyabe charr, Salvelinus malma miyabei. Env. Biol. Fish. 15: 119-129.
- MATHISEN, O.A. 1955. Studies on the spawning biology of the red salmon, Oncorhynchus nerka (Walbaum) in Bristol Bay, Alaska with special reference to the effect of altered sex ratios. Ph.D. thesis, Univ. of Washington, Seattle, WA. 285 p.

- McBRIDE, J.R., U.H.M. FAGERLUND, H.M. DYE, and J. BAGSHAW. 1986. Changes in structure of tissues and in plasma cortisol during the spawning migration of pink salmon, Oncorhynchus gorbuscha (Walbaum). J. Fish. Biol. 29: 153-166.
- MCCART, P.J. 1970. A polymorphic population of Oncorhynchus nerka at Babine Lake, B.C. involving anadromous (sockeye) and non-anadromous (kokanee) forms. Ph.D. thesis, Univ. of British Columbia, Vancouver, B.C. 135 p.
- MCNEIL, W.J. 1964. Radd superimposition and egg capacity of pink salmon spawning beds. J. Fish. Res. Board Can. 21: 1385-1395.
- MILNE, D.J. 1948. The growth, morphology and relationship of the species of Pacific salmon and the steelhead trout. Ph.D. thesis, McGill Univ., Montreal, PQ. 101 p.
- MILOVIDOVA-DUBROVSKAIA, N.V. 1937. Materials on the biology and fishery of Primorskii pink salmon. Izv. TINRO 12: 101-114.
- MINITAB, Inc. 1985. Minitab reference manual. Minitab, Inc., State College, PA. 232 p.
- MIMMS, C.K. 1983. Analysis of pink salmon information needs in the Great Lakes. Report to the Joint Department of Fisheries and Oceans/Ontario Ministry of Natural Resources Fisheries Research Committee.

- Great Lakes Fish. Res. Branch, Canada Centre for
Inland Waters, Burlington, Ont. 31 p.
- MORGAN, R. 1985a. Pink salmon: to dip or...not to dip.
Angler and Hunter 9(9): 13.
- 1985b. Pink salmon. Angler and Hunter
10(2): 28.
- MUNRO, W.R., and K.H. BALMAIN. 1956. Observations on
the spawning runs of brown trout in the South Queich,
Loch Leven. Scottish Home Dept., Freshw. Salmon
Fish. Res. 13: 3-17.
- MUZZALL, P.M., and C.R. PEBBLES. 1986. Helminths of
pink salmon, Oncorhynchus gorbuscha, from five
tributaries of Lake Superior and Lake Huron.
Can. J. Zool. 64: 508-511.
- NEILSON, J.D., and C.E. BANFORD. 1983. Chinook salmon
(Oncorhynchus tshawytscha) spawner characteristics in
relation to redd physical features. Can. J. Zool.
61: 1524-1531.
- NEILSON, J.D., and G.H. GEEN. 1981. Enumeration of
spawning salmon from spawner residence time and
aerial counts. Trans. Am. Fish. Soc. 110: 554-556.
- NICOLETTE, J.P. 1983. Population dynamics of pink
salmon in selected Minnesota tributaries to Lake
Superior. M.Sc. thesis, Univ. of Minnesota,
St. Paul, MN. 94 p.

- 1984. A 3-year-old pink salmon in an odd-year run in Lake Superior. N. Am. J. Fish. Manage. 4: 130-132.
- NICOLETTE, J.P., and G.R. SPANGLER. 1986. Population characteristics of adult pink salmon in two Minnesota tributaries to Lake Superior. J. Great Lakes Res. 12: 237-250.
- NOLTIE, D.B. 1987a. Incidence and effects of sea lamprey (Petromyzon marinus) parasitism on breeding pink salmon (Oncorhynchus gorbuscha) from the Carp River, eastern Lake Superior. Can. J. Fish. Aquat. Sci. 44: 1562-1567.
- 1987b. Fencing material and methods for effectively trapping and holding pink salmon. N. Am. J. Fish. Manage. 7: 159-161.
- 1987c. Sex and year comparisons of Lake Superior pink salmon (Oncorhynchus gorbuscha) adipose fins. J. Great Lakes Res. 13: 272-278.
- 1988. Variation in behaviour, morphology and ecology among male Lake Superior pink salmon Oncorhynchus gorbuscha. Chapter 3, this volume.
- NOLTIE, D.B., J.F. LEATHERLAND, and M.H.A. KEENLEYSIDE. 1988. Epizootics of thyroid hyperplasia in Lake Superior and Lake Erie pink salmon (Oncorhynchus gorbuscha Walbaum). Can. J. Zool. (accepted).
- NUMAN, P.J. 1967. Pink salmon in Lake Superior. Ont. Fish Wildl. Rev. 6: 9-14.

- PARKER, R.R. 1967. Contributions of the 1964 brood year of Bella Coola pink salmon to fisheries and escapements of the central British Columbia area. Fish. Res. Board Can. MS Rep. 935: 1-19.
- PETERSON, A.E. 1954. The selective action of gillnets on Fraser River sockeye salmon. Int. Pac. Salmon Fish. Comm. Bull. 5: 1-101.
- PRAVDIN, I.F. 1929. Morphometrical characteristics of the west Kamchatka humpback salmon. Izv. Tikhook. Nauchno-Promyslovoi Stanstii 4: 1-150.
- PRINCE, L. 1984. The exotic migrants of the Great Lakes. Ont. Out-of-Doors 16(7): 39, 71-72.
- PRITCHARD, A.L. 1931. A report of the pink salmon investigations in British Columbia. Fish. Res. Board Can. Prog. Rep. Pac. 10: 5-9.
- 1932. The return of marked pink salmon in 1932. Fish. Res. Board Can. Prog. Rep. Pacific Biol. Sta., Nanaimo B.C., and Fish. Exper. Sta., Prince Rupert, B.C. 15: 10-11.
- 1934. The recovery of marked pink salmon in 1934. Fish. Res. Board Can. Prog. Rep. Pac. 22: 17-18.
- 1936. Factors influencing the upstream spawning migration of the pink salmon, Oncorhynchus gorbuscha (Walbaum). J. Biol. Board Can. 2: 383-389.

- 1937. Variation in the time of run, sex proportions, size and egg content of adult pink salmon (Oncorhynchus gorbuscha) at McClinton Creek, Masset Inlet, B.C. J. Biol. Board Can. 3: 403-416.
- 1939. Homing tendency and age at maturity of pink salmon (Oncorhynchus gorbuscha) in British Columbia. J. Fish. Res. Board Can. 4: 233-251.
- 1941. The recovery of marked Masset Inlet pink salmon during the season of 1940. Fish. Res. Board Can. Prog. Rep. Pac. 48: 13-17.
- 1943. Results of the 1942 pink salmon marking at Morrison Creek, Courtenay, B.C. Fish. Res. Board Can. Prog. Rep. Pac. 57: 8-10.
- 1944. Return of two marked pink salmon (Oncorhynchus gorbuscha) to the natal stream from distant places in the sea. Copeia 1944: 80-82.
- PYCHA, R.L., W.R. DRYER, and G.R. KING. 1965. Movements of hatchery-reared lake trout in Lake Superior. J. Fish. Res. Board Can. 22: 999-1024.
- RANDALL, R.G. 1984. First record of a pink salmon (Oncorhynchus gorbuscha) in the Miramichi River, New Brunswick. Nat. can. 111: 455-457.
- REID, D. 1980. The first pinks in Lake Erie. Ont. Fish. Wildl. Rev. 19: 2-5.
- RICHEY, D. 1976. Salmon surprise. Mich. Nat. Res. 45: 36, 38.

- RICKER, W.E. 1958. Handbook of computations for biological statistics of fish populations. Fish. Res. Board Can. Bull. 119: 1-300.
- 1972. Hereditary and environmental factors affecting certain salmonid populations. In The stock concept in Pacific salmon. Edited by R.C. Simon and P.A. Larkin. H.R. MacMillan Lectures in Fisheries, Univ. of British Columbia, Vancouver, BC. pp. 19-160.
- RICKER, W.E. and K.H. LOFTUS. 1968. Pacific salmon move east. Ann. Rev. Fish. Council. Can. 23:37-39,43.
- ROSE, R. 1986. Southern fisheries report. Angler and Hunter 10(4): 30.
- ROUNSEFELL, G.A. 1958. Anadromy in North American Salmonidae. U.S. Fish Wildl. Serv. Fish. Bull. 58(131): 171-185.
- RYDER, R.A., and C.J. EDWARDS (eds.). 1985. A conceptual approach for the application of biological indicators of ecosystem quality in the Great Lakes basin. Report to the Great Lakes Science Advisory Board. International Joint Commission, Windsor, Ont. 169 p.
- SCHRODER, S.L. 1972. Effects of density on the spawning success of chum salmon (*Oncorhynchus keta*) - a progress report. In Proceedings of the 1972 northeast Pacific pink salmon workshop. Edited by J.E. Bailey. Alaska Dept. Fish Game Info. Leaflet 161. pp. 91-100.

- 1973. Effects of density on the spawning success of chum salmon (Oncorhynchus keta) in an artificial spawning channel. M.Sc. thesis, Univ. of Washington, Seattle, WA. 78 p.
- 1975. Assessment of production of chum salmon fry from the Big Beef Creek spawning channel. Ann. Rep., Anadromous Fish Project AFC-67, Fish. Res. Inst., Univ. of Washington, Seattle, WA. FRI-UW-7513. 53 p.
- 1976. Some observations concerning mate selection patterns found in chum salmon. In Proceedings of the 1976 northeast Pacific pink and chum salmon workshop. Edited by G.K. Gunstrom. Alaska Dept. Fish Game. pp. 140-151.
- 1981. The role of sexual selection in determining overall mating patterns and mate choice in chum salmon. Ph.D. thesis, College of Fisheries, Univ. of Washington, Seattle, WA. 274 p.
- 1982. The influence of intrasexual competition on the distribution of chum salmon in an experimental stream. In Proceedings of the salmon and trout migratory behavior symposium. Edited by E.L. Brannon and E.O. Salo. University of Washington Press, Seattle, WA. pp. 275-285.
- SCHRODER, S.L., and G.J. DUKER. 1979. Assessment of production of chum salmon fry from the Big Beef Creek spawning channel. Ann. Rep., Anadromous Fish Project

AFC-82, Fish. Res. Inst., Univ. of Washington,
Seattle, WA. FRI-UW-7909. 14 p.

SCHRODER, S.L., and J. SEEB. 1979. Potential genetic contribution of satellite males in chum salmon demes. In Proceedings of the 1978 northeast Pacific pink and chum salmon workshop. Edited by J.C. Mason. Pacific Biological Station, Nanaimo, B.C. pp. 397-402.

SCHUMACHER, R.E., and S. EDDY. 1960. The appearance of pink salmon, Oncorhynchus gorbuscha (Walbaum), in Lake Superior. Trans. Am. Fish. Soc. 89: 371-373.

SCHUMACHER, R.E., and J.G. HALE. 1962. Third generation pink salmon, Oncorhynchus gorbuscha (Walbaum), in Lake Superior. Trans. Am. Fish. Soc. 91: 421-422.

SEMKO, R.S. 1939. The Kamchatka pink salmon. Isv. TINRO 16: 1-111. Trans. from Russian by Fish. Res. Inst., Univ. of Washington, Seattle, WA. 117 p.

----- 1954. The stocks of west Kamchatka salmon and their commercial utilization. Isv. TINRO 41: 3-109. Trans. from Russian by Fish. Res. Board Can. Trans. Ser. 288: 131 p.

SHERIDAN, W.L. 1962. Relation of stream temperatures to timing of pink salmon escapements in southeast Alaska. In Symposium on pink salmon. Edited by M.J. Wilimovsky. H.R. MacMillan Lectures in Fisheries, Univ. of British Columbia, Vancouver, B.C. pp. 87-102.

- SKUD, B.E. 1958. Relation of adult pink salmon size to time of migration and freshwater survival. *Copeia* 1958: 170-176.
- SNOW, G. 1984. The 20,000 that got away. *Topical* 16: 5.
- TAYLOR, S.G. 1976. Marine survival of the fry of early and late spawning pink salmon produced in a gravel incubation hatchery at Auke Creek, Alaska. In *Proceedings of the 1976 northeast Pacific pink and chum salmon workshop*. Edited by G.K. Gunstrom. Alaska Dept. Fish Game. pp. 188-195.
- 1980. Marine survival of pink salmon fry from early and late spawners. *Trans. Am. Fish. Soc.* 109: 79-82.
- TAYLOR, W.W. 1984. Population dynamics and yield potential of Lake Superior pink salmon (*Oncorhynchus gorbuscha*). Project Number R/GLF-15, Volume 2, Michigan Sea Grant College, East Lansing, MI. pp. 326-346.
- THIBERT, J. 1984. Pink paradise. *Angler and Hunter* 8(10): 22-24.
- THOMAS, M.L.H. 1966. Benthos of four Lake Superior bays. *Can. Field-Nat.* 80: 200-212.
- van den BERGHE, E.P., and M.R. GROSS. 1986. Length of breeding life of coho salmon (*Oncorhynchus kisutch*). *Can. J. Zool.* 64: 1482-1486.

- VELLEMAN, P.F., and D.C. HOAGLIN. 1981. Applications, basics, and computing of exploratory data analysis. Duxbury Press, Boston, MA. 354 p.
- VERNON, E.H. 1962. Pink salmon populations of the Fraser River system. In Symposium on pink salmon. Edited by N.J. Wilimovsky. H.R. MacMillan Lectures in Fisheries, Univ. of British Columbia, Vancouver, B.C. pp. 53-58.
- WAGNER, W.C. 1978. A three-year-old pink salmon from Lake Superior. Mich. Dep. Nat. Res., Fish. Div., Fish. Res. Rep. 1861: 1-7.
- 1985. Size, age, and fecundity of pink salmon in Michigan. Mich. Dep. Nat. Res., Fish. Div., Fish. Res. Rep. 1933: 1-13.
- WAGNER, W.C., and T.M. STAUFFER. 1975. Occurrence of pink salmon in Michigan, 1963-1973. Mich. Dept. Nat. Res., Fish. Div., Tech. Rep. 75-3: 1-8.
- 1980. Three-year-old pink salmon in Lake Superior tributaries. Trans. Am. Fish. Soc. 109: 458-460.
- 1982. Distribution and abundance of pink salmon in Michigan tributaries of the Great Lakes, 1967-1980. Trans. Am. Fish. Soc. 111: 523-526.
- WALLACE, R.A., and K. SELMAN. 1981. Cellular and dynamic aspects of oocyte growth in teleosts. Amer. Zool. 21: 325-343.

- WALLACE, R.A., K. SELMAN, M.S., GREELEY, JR., P.C. BEGOVAC, Y-W. P. LIN, R. McPHERSON, and T.R. PETRINO. 1987. Current status of oocyte growth. In Reproductive physiology of fish 1987. Proceedings of the 3rd international symposium on reproductive physiology of fish, St. John's, Newfoundland, Canada, August 2-7, 1987. Edited by D.R. Idler, L.W. Crim, and J.M. Walsh. Marine Sciences Research Laboratory, Memorial University of Newfoundland, St. John's, Nfld. pp. 167-177.
- WARD, F.J. 1959. Character of the migration of pink salmon to Fraser River spawning grounds in 1957. Int. Pac. Salmon Fish. Comm. Bull. 10: 1-70.
- WILCOCK, B. 1985. Pink salmon explosion. Angler and Hunter 16(3): 26.
- WILLIAMS, I.V., J.R. BRETT, G.R. BELL, G.S. TRAXLER, J. BAGSHAW, J.R. McBRIDE, U.H.M. FAGERLUND, H.M. DYE, J.P. SUMPTER, E.M. DONALDSON, E. BILINSKI, H. TSUYUKI, M.D. PETERS, E.M. CHOROMANSKI, J.H.Y. CHENG, and W.L. COLERIDGE. 1986. The 1983 early run Fraser and Thompson River pink salmon; morphology, energetics and fish health. Int. Pac. Salmon Fish. Comm. Bull. 23: 1-55.
- WILLIS, R.A. 1954. The length of time that silver salmon spend before death on the spawning grounds at Silver Creek, Wilson River, in 1951-52. Oregon Fish. Comm. Res. Briefs 5: 27-31.

- WITHLER, F.C. 1982. Transplanting Pacific salmon.
Can. Tech. Rep. Fish. Aquat. Sci. 1079: 27 p.
- WITHLER, F.C., and W. KWAIN. 1984. Survey of pink
salmon in eastern Lake Superior, 1981. Can. Tech.
Rep. Fish. Aquat. Sci. No. 1317: 35 p.
- YEFANOV, V.N., and V.M. CHUPAKHIN. 1982. The dynamics
of some population indices of pink salmon,
Oncorhynchus gorbuscha, from Iturup (Kuril Islands).
J. Ichthyol. 22: 42-50.
- ZAR, J.H. 1974. Biostatistical analysis.
Prentice-Hall, Inc. Englewood Cliffs, NJ. 620 p.

CHAPTER 3

Variation in Behaviour, Morphology and Ecology

of Breeding Male Lake Superior

Pink Salmon (Oncorhynchus gorbuscha)

Abstract

The breeding of male pink salmon (Oncorhynchus gorbuscha) from the Carp River, eastern Lake Superior, was assessed during the small even-year and large odd-year runs of 1984 and 1985, respectively. In behaviour studies, males were observed in 1985 which resembled females in shape and which participated in spawnings by sneaking rather than by competition for proximity to females. In 1984, during which females nested in relative isolation and single large males monopolized access to them, males attempting to sneak fertilizations were not observed. Thus, the occurrence of such behaviour appears to have been related to spawner densities. Morphological studies in 1985 confirmed the occurrence of males which in shape resembled females more than did other males. In these individuals, secondary sexual character development (hump height) occurred to a lesser degree relative to their body lengths than in typical males. These female-like males were also characterized by having low weights for their lengths (poor condition). Female-like males were not distinct from more typical males in their morphology, but appeared instead as extremes within the range of male shape variation. Female-like males were reproductively mature, had returned at ages typical for this population, and committed biomass to gonad no differently than did typical males. Likewise, their

spawning performance did not differ from typical males, as assessed by comparison of the amount of gonad they retained unspawned at death and by their spawning ground life expectancy. Together, these results provide further evidence that male pink salmon exhibit alternative breeding tactics. However, these putative tactics appear due more to proximate reasons than to divergent life history strategies as in other salmonid species.

Introduction

Alternative breeding patterns have been defined as "any discontinuous variation in an aspect of reproductive behavior among one sex in a single population with associated differences in the behavior's costs and benefits" (Austad 1984). Much recent work in behavioural ecology has been directed towards establishing a theoretical framework to explain this phenomenon within animal species (e.g. see *American Zoologist* special issue 24(2), 1984). In fishes, studies of male centrarchids and salmonids have figured prominently in this regard (Keenleyside 1972; Gross 1979, 1980a,b, 1982, 1984, 1985; Dominey 1980, 1984; Gross and Charnov 1980; Maekawa 1983; Montgomery 1983; Maekawa and Hino 1986a,b; Maekawa and Onozato 1986; van den Berghe and Gross 1986; Hutchings and Myers 1987; Montgomery et al. 1987).

In Pacific salmon (genus Oncorhynchus), males generally seek fertilizations in two ways. These are termed here as the "cluster" and "outlier" tactics. Differences in male location and proximity relative to the prespawning female distinguish the two. Cluster males are those which congregate in a group behind a female which has established her nesting territory. When egg deposition appears imminent, cluster males rush upstream into the nest and close ranks around the female. Fertilization is achieved by some or all releasing sperm. Males closer to the female preceding nest entry are more apt to be adjacent to her at egg deposition, increasing their fertilization success (Schroder and Duker 1979; Schroder and Seeb 1979; Schroder 1981; Chebanov et al. 1983; Maekawa and Hino 1986a; Maekawa and Onosato 1986). Thus, competition among males for position within the downstream cluster is usually intense.

Outlier males seek fertilizations differently. Instead of competing for a position among the typically larger and more combative cluster males, they hold solitary positions apart from the cluster but adjacent to the nest. From here, outlier males sneak fertilizations by darting laterally into the nest at egg deposition, securing positions closer to the female than do some cluster males approaching her from downstream. By this means, outlier males may obtain fertilizations without incurring the costs of competition that cluster males do.

To date, the occurrence of both these breeding patterns has been documented within populations of five of the six Oncorhynchus species (Table 1). In some species, differences in male breeding pattern appear from these studies to be related to life history variation. In coho salmon, outlier males ("jacks") are small individuals which mature precociously. In chinook, masu and sockeye salmon, outlier males are smaller individuals which have matured after spending greater proportions of their lives in the less productive waters of lakes or streams. In the remaining species, the chum salmon, males adopt the cluster or outlier tactic more facultatively, in response to the sizes and ages of the individuals they face in competition. Common to all five species, however, is that the outlier males are at a disadvantage in male-male competition because of their small size. Outlier males may also resemble females in shape and commit relatively greater amounts of biomass to testes than cluster males (Robertson 1957; Smirnov 1959).

In contrast to their five congeners, the size variation and life history differences which seem to promote the occurrence of alternative male breeding patterns are substantially more constrained in pink salmon (Oncorhynchus gorbuscha). This species displays a virtually invariant life cycle, almost all spawners being biennials which go to sea in the spring of their first year and return mature in the autumn of their second

TABLE 1. Studies of Pacific salmon species in which alternative male breeding behaviours have been observed, or where small, precociously mature males implicate their likely occurrence. Reference list is not exhaustive.

Species	Reference
chinook <u>Oncorhynchus tshawytscha</u>	Rutter 1904 Robertson 1957 Gebhards 1960 Smirnov 1962, 1975 Flain 1970 Scott and Crossman 1973 Hankin and McKelvey 1985
chum <u>O. keta</u>	Schroder 1972, 1973, 1976, 1981 Schroder and Duker 1979 Schroder and Seeb 1979
coho <u>O. kisutch</u>	Briggs 1953 Shapovalov and Taft 1954 Robertson 1957 Hager and Noble 1976 Gross 1984 van den Berghe and Gross 1986
masu <u>O. masou</u>	Ohno 1932 Smirnov 1962, 1963 Nikolsky 1963 Utoh 1976 Komiyama, in Maekawa 1983
sockeye <u>O. nerka</u>	Evermann 1897 Smirnov 1959, 1963 Hanson and Smith 1967 Krokhin 1967 McCart 1969, 1970

(Bilton and Ricker 1965). Thus, the occurrence of alternative male breeding patterns appears somewhat unlikely in this species. Nonetheless, recent work suggests that pink salmon males may indeed exhibit different breeding patterns in some populations (Chebanov 1982; Keenleyside and Dupuis 1988a). Davidson (1935) and Davidson and Shostrom (1936) documented the occurrence of male pink salmon whose humps were noticeably small for their lengths but whose snout development was typical for males of their size. Males which are "female-like" in their morphology have also been found elsewhere, the suggestion being that "mimicking" females assists them in avoiding competition and in sneaking fertilizations. (Kirkwood 1962; Beacham and Murray 1985).

Despite these indications, the occurrence of alternative male breeding patterns in pink salmon has not been the subject of specific investigation. Furthermore, the few comparisons made of the males of the two purported patterns have been of limited scope. In the following, I report on a broader study of this phenomenon in *O. gorbuscha*. Its objectives were twofold: (1) to seek within a single stream, over successive years, evidence of behavioural and morphological variation among males consistent with the occurrence of alternative breeding patterns, and (2) to establish what the differences in male breeding pattern might be due to;

and whether these differences are reflected in aspects of their breeding ecology.

Materials and Methods

The pink salmon studied were 1984 and 1985 spawners from the Carp River ($46^{\circ}57'N$; $84^{\circ}35'W$), an eastern Lake Superior tributary 70 km north of Sault Ste. Marie, Ontario. These are part of the entirely freshwater population which arose from an accidental introduction into the Great Lakes in 1956 (Kwain 1987a).

Data of two sorts were collected: behavioural and morphological. Both collections began by capturing upstream migrants. Most were intercepted before reaching the spawning grounds using a Y-shaped weir and box trap. This was erected 1.2 km upstream of the river mouth, just below a permanent lamprey control barrier. The remaining captures were made by gill net. This was used when floods and undermining allowed fish past the weir and stranded them between it and the lamprey barrier. Because gill netting required a return to near-normal flows, fish were stranded for varying durations. Long-stranded fish exhibited scratches, lower caudal fin and lower jaw wear, and had diminished in condition (weight-at-length) (Moltie, unpubl. data). These fish were omitted from subsequent analyses where body or gonad weights were involved. In 1984 virtually the entire run

(117 fish; 76 males and 41 females) was captured. However, the 2115 fish caught in 1985 (1087 males and 1028 females) represented only about 25% of the total run, based on estimates of odd-year run size in the Carp River (Kwain and Rose 1986; Kwain 1987a). The remaining 1985 fish evaded capture during floods and reached the spawning grounds untagged.

To assess morphology, four characters of captured males and females were measured: (1) body length, from anterior orbit margin to the upper tip of the compressed caudal fin; (2) snout length, from anterior orbit margin to the tip of the upper jaw; (3) hump height, perpendicular from the lateral line to the highest point on the back anterior to the dorsal fin; (4) total body weight. Sex was determined by gonete extrusion or by abdominal palpation. In males, the results of attempts to extrude gonetes were also used to assess their reproductive maturity (spermiating or non-spermiating). Each fish was also examined for evidence (wounds, scars or superficial marks) of parasitism by sea lamprey, *Petromyzon marinus* (see Moltie 1987) and for the occurrence of thyroid hyperplasia (overt or cryptic) (see Moltie 1988a; Moltie et al. 1988). All captured fish were tagged with numbered 3.2 cm diameter Petersen disc tags, plus 4.0 cm long anchor tags in 1985 (Floy Tag, Seattle, WA). Some prespawning males in 1985 were killed for testis wet and dry weight determinations

(see Moltie 1988b for methods). None were killed in 1984 because the total run was so small. Once tagged, males and females were released above the lamprey barrier. The spawning grounds beyond were surveyed daily for the spawned-out carcasses of tagged males and females. Male carcasses were dissected and their spawned-out testes removed for assessment of testis depletion.

Most Lake Superior pink salmon mature at the end of their second year. However, small numbers do mature as either one- or three-year-olds (Wagner 1978, 1985; Wagner and Stauffer 1980; Nicolette 1983, 1984; Kwain and Kerr 1984; Bagdovitz 1985; Bush 1985; Bagdovitz et al. 1986; Nicolette and Spangler 1986; Kwain 1987a,b). Given the potential importance of life history variation in this study, ages were assessed in selected males. Scales and vertebral centra were both used. Scales were taken from each fish's flank at capture. Later, after washing and drying, acetate impressions of the scales were made and ages read from them. To obtain centra, the heads and first few vertebrae from either males killed before spawning or collected as carcasses afterwards were retained frozen. Later, the first 10-15 cranial vertebrae were removed, trimmed of flesh, and dried for 24 h. Dermestid beetles cleaned the bones. The centra were then softened for 8 h in water, separated, and the fascia individually removed. Soaking for approximately 1 h in 3% sodium hypochlorite solution (50% Javex[®];

50% water) removed remaining soft tissue. The cones of each centrum were then buffed with a cotton swab and the neural and haemal arches removed to facilitate drying. Reading of transverse sections of the centra was performed against a dark background using a dissecting microscope and reflected fibre optics lighting.

Behavioural observations were made only of pink salmon preparing to spawn. Because the purpose of these observations was to determine whether males exhibited alternative male fertilisation tactics and to summarize the behaviours involved, the data collected were primarily descriptive. Observations were made from the nearest stream bank 3 to 5 m away (sometimes with aid of binoculars), and were recorded either by direct transcription or with a video camera (using a zoom lens). These observations were made in the late afternoons and early evenings of 22 different dates both years. These hours were independent of time spent reviewing the video tapes and of the daily stream surveys on which brief observations of spawning clusters were also made. Because so many 1985 fish had evaded capture during floods, most males observed were untagged and unknown morphologically. Thus, their sizes and degree of hump development relative to males they were associated with were assessed by eye. Counts of cluster sizes, the numbers of males not associated with females (lone males), and the activities of males whose tags

could be identified were also determined where possible during daily spawning ground surveys.

Results

Behaviour

Spawners were few in 1984, so that nesting females were both scarce and isolated. On the 22 dates in 1984 when nesting females were found during daily spawning ground surveys, 22 of a sample of 28 (78.6%) were not within sight of another nesting female. Cluster formation around nesting females in 1984 appeared to be actively discouraged by large, single males with well-developed humps which monopolized them and dispersed potential cluster members. Females were accompanied by only single males in 60.7% of the 28 spawning groups observed. Clusters of two, three or four or more males accompanied females in 17.9, 14.3 and 7.1% of the remaining groups, respectively. The clusters that did form were more prevalent where two or more females were in close proximity (<5 m apart): only 36.4% of the 22 isolated (>15 m apart) nesting females were accompanied by clusters of males, whereas clusters formed around half of the 6 females which nested near other nesting females.

Where males could be identified by their tags on the spawning grounds in 1984, those seen at least once accompanying nesting females were of significantly

greater body length than were those observed only as lone individuals (males with females: 47.41 ± 0.86 cm, $n=21$; lone males: 43.05 ± 1.77 cm, $n=10$; $\bar{X} \pm 1$ S.E.; ANOVA $F=6.30$, $p<0.025$). Lone males were common in 1984. Of 86 observations of the activities of individual males, 50% were not actively associated with a nesting female. A higher proportion of unpaired males would be expected if, as observed, single large males forced others away from the females they controlled.

In contrast to 1984, spawning clusters formed much more often in 1985. Single males appeared unable to monopolize nesting females. In a sampling of 134 nesting females in 1985, the number of consorting cluster males averaged 3.43 (S.E.=0.13). Where males could be identified by their tags, the body lengths of those seen at least once accompanying nesting females and those only observed as lone individuals did not differ (males with females: 41.52 ± 0.40 cm, $n=71$; lone males: 41.22 ± 0.74 cm, $n=20$; $\bar{X} \pm 1$ S.E.; ANOVA $F=0.12$, $p>0.25$). Similar sizes between lone males and those accompanying females would be expected where large "lead" males (the dominant cluster male nearest the female) could not prevent cluster formation. Under such conditions, lone males are likely to be those in transition from one cluster to another. Of 443 observations of the activities of individual males, only 20% were lone. Relative to cluster males, lone males were

significantly less common in 1985 compared to 1984 (2x2 continuity-corrected $\chi^2=32.83$, 1 df, $p<0.001$).

The behaviour of males from 33 clusters was observed for a total of 43 h over the two study seasons. Cluster males first joined a female as she began nest excavation. Over time, cluster membership grew and the positions males secured within them stabilized. The positions males held within clusters were size-related. In 96.4% of a sampling of 56 clusters, the lead male appeared to be as large or larger than all other males in his group. The position he occupied was to the side and slightly downstream from the female. Subsidiary males occupied staggered positions downstream from the primary pair, usually in order of decreasing size. Only when the largest male showed considerable body or fin wear did it not hold the lead position.

Among cluster males, especially subsidiary individuals, proximity to the female was gained by jockeying for improved position. The lead male's position was constantly contested. Attempts by subsidiary males to usurp positions nearer the female incited male-male interaction. For example, when the side of the female unoccupied by the lead male was approached by a subsidiary individual, the lead male quickly crossed over the female's tail to block access to the interloper. A general reshuffling of cluster positions resulted, restoring the staggered arrangement

of the cluster. Lead males challenged by other males of similar size participated in extended parallel swim displays. Here, both individuals swam rapidly upstream beside one another, matching one another's speed and direction. During such displays, a subsidiary male moved up beside the female until the lead male's return.

Besides interacting among themselves, prespawning cluster males directed behaviours towards their female. The most prominent was the body quiver. In performing this, a lead male swam upstream beside his female, whereupon the entire length of his body trembled spasmodically. Body quivers varied in intensity. Females made no obvious response to this display. Subsidiary males quivered only when allowed beside the female. In 102 occurrences in 14 clusters, less than 2% of the quivers recorded were performed by other than the lead male.

Cluster males also responded to the behaviour of their female. As nest excavation neared completion, the female swam slowly upstream along the nest floor, probing the substrate with her anal fin. When hesitation accompanied the passage of her vent over the nest's deepest part, cluster males rushed forwards to join her, the lead male on one side, the foremost subsidiary male on the other, and the remaining males flanking this trio. The female then continued upstream, rose up, circled back around the nest, and returned to where she had started.

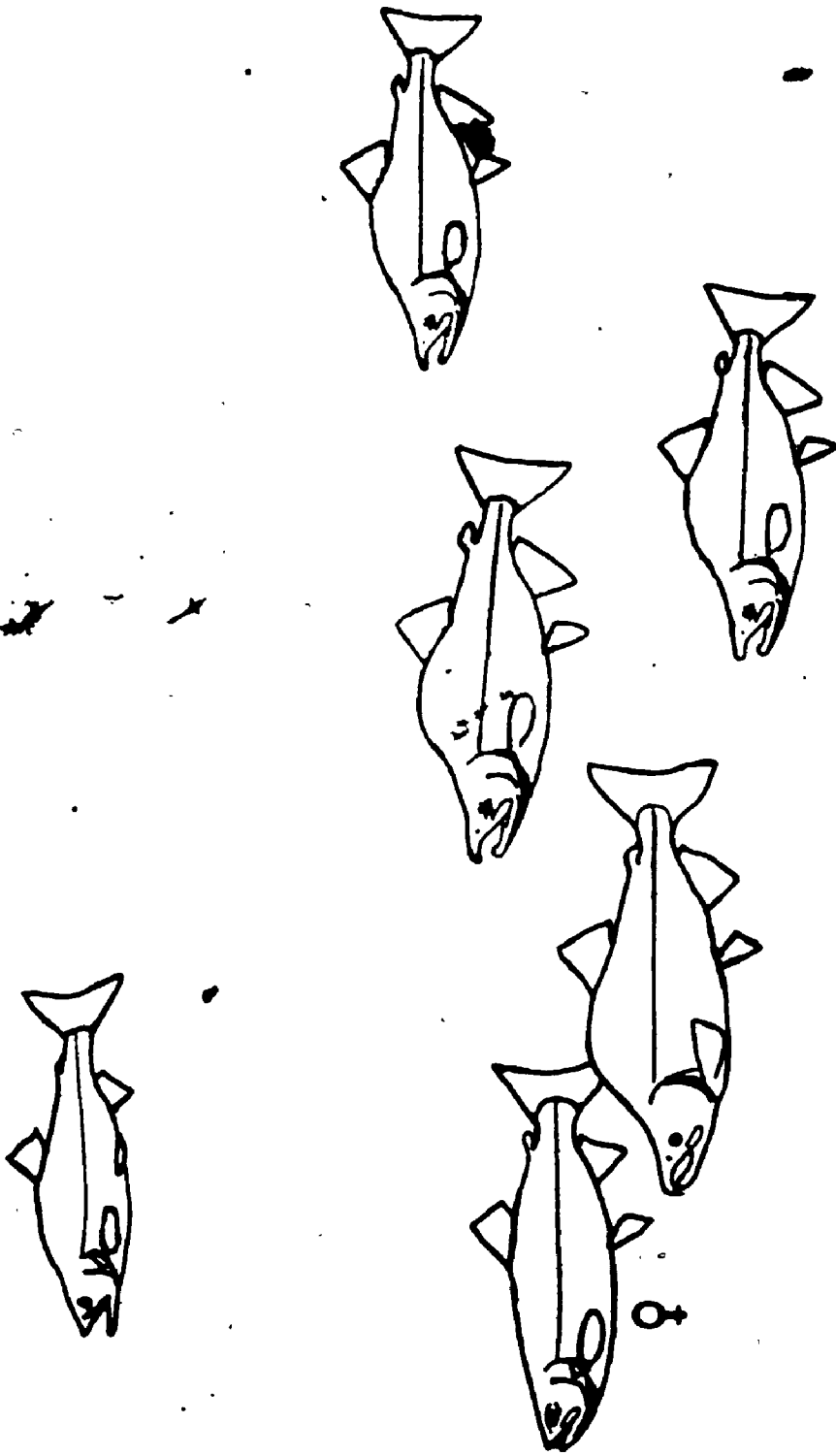
Cluster males separated, and then reformed the downstream cluster. Females repeated this probing, interspersed with nest excavation, until egg deposition eventually occurred. Egg deposition appeared to differ from probing only in that a female hesitated longer, gaped, and shed eggs. Milt was shed as the males surrounding her gaped in response. However, whether all males gaped and released sperm could not be seen. Afterwards, the female immediately began nest covering. Most males stayed with the female, although large ones sometimes left soon after.

The above describes spawnings involving only cluster males. However, some clusters in 1985 were accompanied by an outlier male. Twenty-three such clusters received 32 h of observation. The average number of cluster males comprising these groups was 3.41 (S.E.=0.33). Single outlier males accompanied them in all but one instance where two outliers joined a cluster of 7 males. Outliers always appeared to be the smallest of the males attending a given female. However, they were not necessarily the size of the smallest males in the population. Because they also exhibited relatively small humps, outlier males resembled females in shape and were occasionally mistaken for females by the observer. Outlier males appeared smaller and less well-humped than the terminal cluster males they accompanied. Never were large males with well-developed humps seen as outliers.

Outlier males were substantially different in how they associated with females. They did not join spawning clusters proper, but positioned themselves lateral to the females, 1 to 1.5 m away, close to the substrate (Fig. 1). Outlier males maintained their distance, briefly approaching the prespawning female only when the cluster males were momentarily absent or when the female probed the nest substrate. Outlier males approached by a cluster member avoided confrontation by fleeing. Nonetheless, they returned quickly after leaving their positions, and were persistent in their association with particular clusters. Neither bites by outlier males towards cluster males nor parallel swims with them were observed. Outlier males were not seen to quiver towards females. Females were usually territorial only towards other females, and towards cluster males only when they aggregated over a female's nest for an extended period. However, outlier males also elicited territorial defense from females on occasion, indicating possible gender misidentification.

Outlier males also differed from cluster males in their response to impending egg deposition. Instead of rushing upstream from the rear, they darted laterally towards the female as she settled into the nest. By this means, outlier males could precede subsidiary cluster males into the nest, especially those holding cluster positions furthest downstream. Positions next to the

FIG. 1. Outline drawing of the relative positions of cluster and outlier males in a Carp River pink salmon spawning group. Arrow denotes direction of current flow. See text for further description.



lead male or beside the female with the lead male opposite could thus be obtained. In 14 cases (25% of the cluster numbers observed), actual egg depositions were seen. Here, outlier males appeared to obtain positions as close to females as they did during preliminary egg deposition sequences. Because egg deposition occurred at dusk, video tapes of the spawnings could not be made. Thus, exactly how close outlier males got to females at fertilization could not be ascertained.

The association of outlier males with nested females varied with spawner density. Where nesting females were concentrated and male densities were high in 1985, clusters formed despite the efforts of lead males. At such densities, lead males did not make extended forays from the females they guarded, presumably because other males would quickly occupy their positions. Increased densities resulted in frequent male-male interactions and constant turmoil on the spawning grounds. Outlier males were apparently able to hide amidst this confusion and maintain associations with particular spawning blusters. The outlier tactic was also favoured by the locations of some nests. Where nests were close to shore or mid-stream gravel bars, outlier males stayed in the shallows, and aggression towards them could only originate from one side.

In contrast, persistent association of outlier males was not observed in 1984 when densities were low,

although small males were temporarily seen around females at times. Similarly, large clusters accompanied by outlier males were also not seen around the few isolated nests which occurred in 1985.

Morphology

Because most fish in 1985 escaped tagging, the observations of outlier males almost all came from morphologically unknown individuals. This precluded direct comparison of the characteristics of confirmed outlier and cluster males. However, behavioural observations did suggest that the outlier males were also those which resembled females in shape.

In an attempt to corroborate these observations, males resembling females in their morphology were sought from among the 1984 and 1985 spawners. Within each year, discriminant analysis was used to determine how distinguishable the sexes were. The morphological measurements considered were body length and hump height, these being greater in males than in females on average (Moltie 1988b). Transformation (natural logarithms) linearized the relationships between these two variables. A priori group membership (true males and females) was designated based on gonad characteristics.

In 1984 fish, this analysis produced a discriminant function representing a gradient between fish whose humps were small for their body lengths (the females) and fish

whose humps were large (the males) (Fig. 2 top). There was no overlap in the distributions of male and female discriminant function scores (Fig. 2 top). Thus, discrimination between the sexes was complete in this small sample ($\chi^2=199.36$, $df=2$, $p<0.0001$). Classifying the fish according to sex on this axis produced no erroneous assignments. Thus, males were clearly separable from females on the basis of their morphology in 1984.

The same procedure was applied to 1985 fish. Although significant separation of the sexes was achieved ($\chi^2=2973.2$, $df=2$, $p<0.0001$), the resulting discriminant function did not completely distinguish all males from females in this larger sample. Parts of the distributions of male and female discriminant function scores overlapped (Fig. 2 bottom). This indicates that some 1985 males did indeed resemble females in their morphology. This finding is consistent with the behavioural observation that some 1985 males (those which demonstrated the outlier fertilization tactic) resembled females in physiognomy.

Inspection of the distribution of 1985 male discriminant function scores (Fig. 2 bottom) reveals that male variation in morphology was continuous. Because males resembling females did not form a distinct group, a subset for further study was selected arbitrarily. Males were designated as "female-like" if they were among the

FIG. 2. Frequency distributions of male (black bars) and female (open bars) discriminant function scores from the 1984 (top) and 1985 (bottom) Carp River pink salmon morphological analyses. Smaller bars superimposed where distributions overlap. Group centroids shown on the abscissa. Standardized canonical discriminant function coefficients:

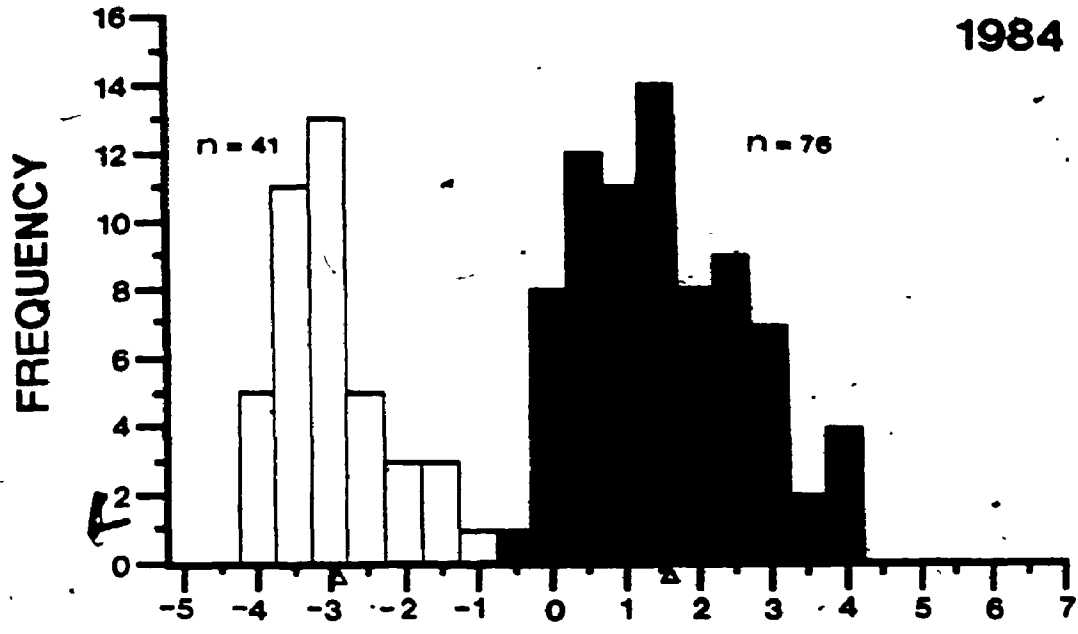
$$1984 \ln(\text{hump height}) = 2.46095$$

$$\ln(\text{body length}) = -2.19338$$

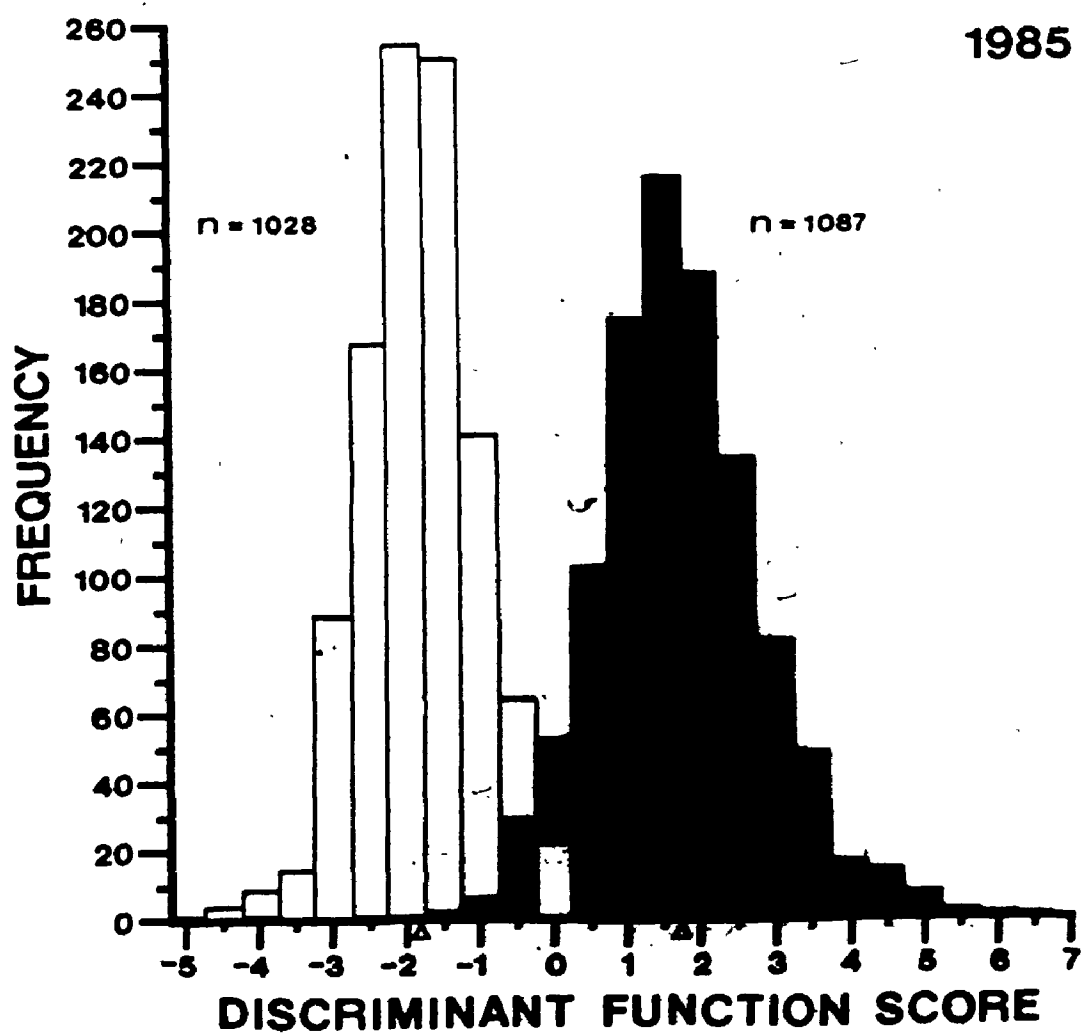
$$1985 \ln(\text{hump height}) = -1.69763$$

$$\ln(\text{body length}) = -1.18626$$

1984



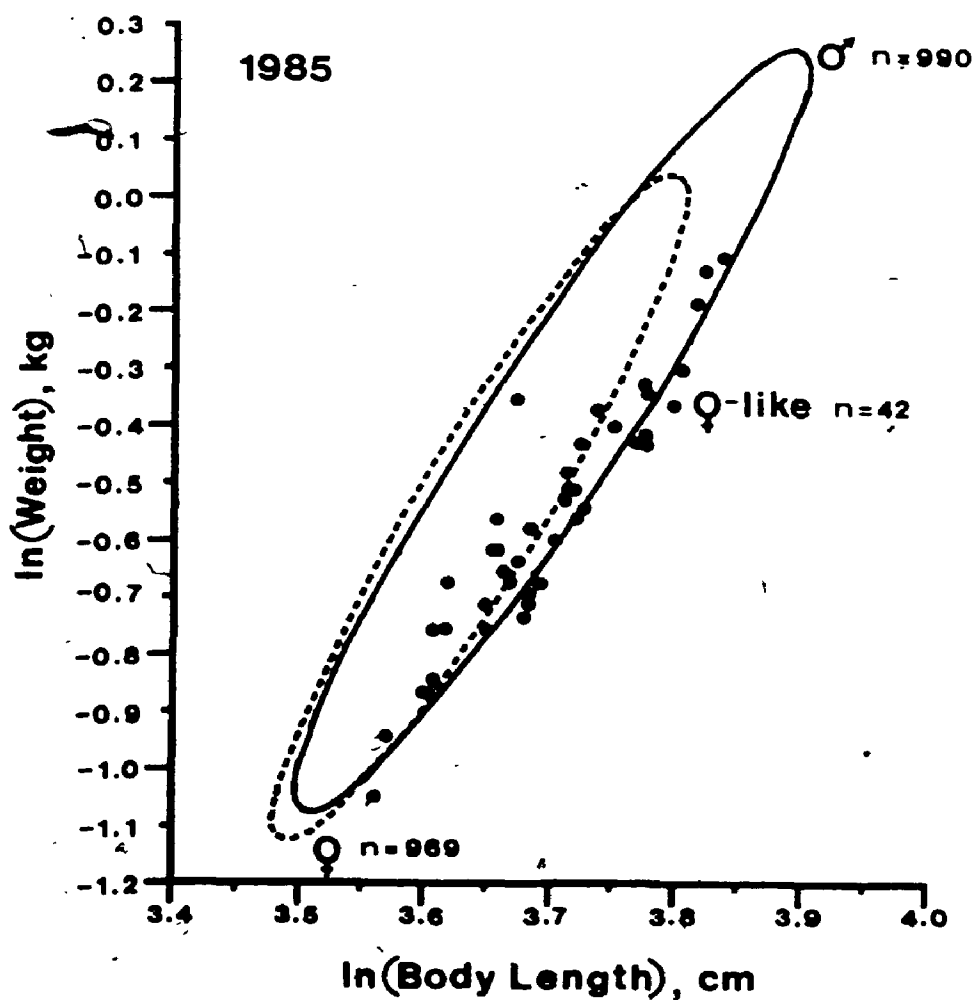
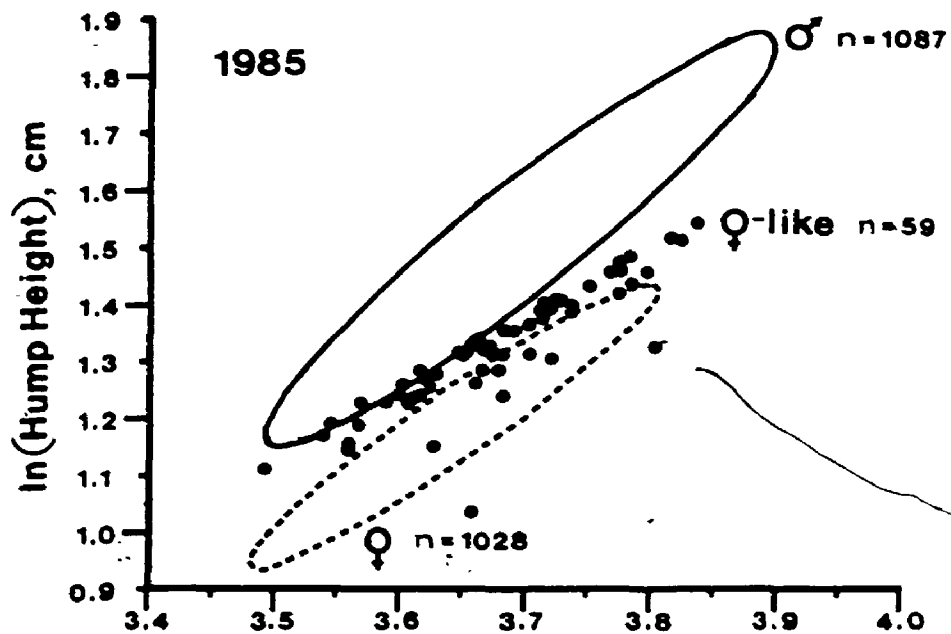
1985



5.4% of males (n=59) which had a greater probability of being classified female than male on the discriminant function. Those remaining were termed "typical" males. The morphological characteristics of the individuals allocated to these two subsets were explored further using a bivariate plot of the data (Fig. 3 top). Here, 95% confidence ellipses summarize the relationship between hump height and body length for all males and females, respectively. Superimposed are the data for the 59 female-like males. This display shows clearly that those males designated as female-like resembled true females because their humps were smaller for their body lengths than for typical males.

In pink salmon, hump development results from the redistribution of somatic tissue in males (Davidson 1935; Davidson and Shostrom 1936). Males designated as female-like may thus have displayed small humps simply because they had less body mass to reallocate [i.e. they were in relatively poor condition (weight-at-length)]. To explore this possibility, the lengths and weights of the males designated as typical and female-like were compared. Although analysis of variance revealed no body length differences (typical males: 40.71 ± 0.11 cm, n=949; female-like males: 40.54 ± 0.45 cm, n=42; $\bar{X} \pm 1$ S.E.; $F=0.10$, $p>0.25$), typical males were significantly heavier than female-like males (typical males: 696 ± 7 g; female-like males: 582 ± 20 g;

FIG. 3. Bivariate plots of the relationships between morphological variables for all male (solid ellipses), female-like male (points), and female (dashed ellipses) 1985 Carp River pink salmon. Data summarized as 95% confidence ellipses for ease of display. See text for further explanation.



$F=11.20$, $p<0.0005$). Bivariate plots relating total body weight and body length (Fig. 3 bottom) also indicate that female-like males were light for their lengths (i.e. were in poor condition). This outcome suggests that the resemblance of some males to females stemmed from their diminished condition, preventing them from developing humps of sizes typical for their body lengths.

The possibility that typical and female-like males made different investments of biomass in gonad before spawning was investigated first by comparing their $\ln(\text{testis total weight})$ -versus- $\ln(\text{somatic weight})$ (=total less testis total weight) regressions. Tests of slope and intercept differences (Table 2) indicated that the two subsets of males did not differ in relative gonad biomass. For these same individuals, comparison of their testis water weight-dry weight relationships (an assessment of the potential genetic material both types had available for fertilizations) also revealed no differences (Table 2).

Age assessments were used to determine whether males designated as female-like had distinctive life histories. Scales alone were available from 27 female-like males which were captured but whose carcasses were never recovered. Both scales and centra were acquired from 31 carcass recoveries. My confidence in the scale ages I assigned these female-like males was minimal: the scale margins were often so badly resorbed that one year's

TABLE 2. Comparison of pre-spawning testes in pink salmon males designated as typical and female-like. TTW = testis total weight (g), SW = somatic weight (g), TWM = testis water weight (g), TDW = testis dry weight (g). Shown are the regression coefficients (all $p < 0.005$), sample sizes, and results of covariance analyses comparing regressions listed on adjacent lines.

Male designation	Regression	X	n	Slope test	Intercept test
Typical	$\ln(\text{TTW}) = 3.119 + 1.028 \ln(\text{SW})$	0.8643	43	$t=0.460$ $p>0.50$	$t=0.696$ $p>0.20$
Female-like	$\ln(\text{TTW}) = -4.367 + 1.224 \ln(\text{SW})$	0.8958	8		
Typical	$\ln(\text{TWM}) = 1.757 + 0.794 \ln(\text{TDW})$	0.9268	43	$t=1.603$ $p>0.10$	$t=0.292$ $p>0.50$
Female-like	$\ln(\text{TWM}) = 2.033 + 0.553 \ln(\text{TDW})$	0.9573	8		

growth may have been completely lost. Furthermore, some scales exhibited an apparent check part way through what I interpreted as the first year's growth, although no cutting over of circuli occurred. Regardless, I gave scale ages to all, designating fish as 1+ if any hint of a substantial widening between the circuli occurred after the first definite winter check. In contrast, the centra generally exhibited four clear concentric bands, a central translucent one, the next narrow and opaque, the third translucent, and the last wide and opaque. My ability to distinguish these marks confidently was much greater than for the more ambiguous scales.

From scales alone, the resulting age distribution (Table 3 left) contained an appreciable number of 0+ individuals (26% 15 of 58), the proportions of which did not differ between the scale-only and scale-plus-centra samples (2x2 continuity-corrected $\chi^2=0.83$, $df=1$, $p>0.25$). Parallel age determination by the centra, however, resulted in a uniform 1+ age distribution (Table 3 right), significantly different from the scale-aged results on the same fish (Fisher Exact test, $p=0.024$). This latter evidence indicates that males designated as female-like were all in their second year. Their age at maturity thus did not differ from the pattern exhibited by most Lake Superior pink salmon. Age determination using scales proved inadequate to accurately assess this fact.

TABLE 3. Age distributions of males designated as female-like as assessed by scales and centra.

Sample	Age by structure (y)			
	Scales		Centra	
	0+	1+	0+	1+
Scales only	9	18	-	--
Scales + centra	6	25	0	31

Breeding ecology

To further compare males designated as typical and female-like, aspects of their breeding ecology were examined. For each male and female caught by trapping in 1985, its Julian catch date denoted when access to the spawning grounds was sought. Analysis of variance showed that mean catch date differed significantly among typical males, female-like males, and females (typical males: 256.50 ± 0.20 , $n=938$; female-like males: 259.23 ± 1.07 , $n=40$; females: 260.95 ± 0.22 , $n=952$; $\bar{X} \pm 1 \text{ S.E.}$; $F=110.73$, $p<0.0005$). In pairwise comparisons, SNK tests (Zar 1974) revealed that the mean catch date for males designated as typical differed significantly from female-like males and from females (both $p<0.01$). However, female-like males and females did not differ in mean catch date ($p>0.05$). These results indicate that female-like males and females approached the spawning grounds at similar times.

To determine whether males designated as female-like differed from typical males in maturity, the testis ripeness of all males was assessed at capture (Table 4). Female-like males were no more often immature (non-spermiating) than were typical males (Fisher Exact test, $p=0.0816$). Thus, the resemblance of female-like males and females could not be attributed to a preponderance of immature individuals among the former.

Table 4. Similarities in testis maturity in pink salmon males designated as typical and female-like. See text for details of significance tests.

Male designation	Testis maturity	
	Spermiating	Non-spermiating
Typical	1021	7
Female-like	57	2

In 1985, the time males occupied the spawning grounds was determined from tagged individuals recovered as spawned out carcasses on the daily surveys. Males designated as female-like and typical did not differ in their spawning ground residencies (typical males = 10.14 ± 0.35 days, $n=90$; female-like males = 8.75 ± 0.86 days, $n=8$; $\bar{X} \pm 1$ S.E.; $F=1.35$, 1 and 96 df, $p=0.50$).

The testes of spawned-out, tagged males retrieved as carcasses from the spawning grounds were examined to assess testis depletion. Males designated as typical and female-like did not differ in either the slopes or the intercepts of (a) their testis dry weight versus total pre-spawning body weight or (b) their testis water weight versus testis dry weight relationships (Table 5). Thus, males designated as female-like had depleted their sperm supplies to the same degree as had typical males. The shortcomings of using total pre-spawning body weight in the former comparison are recognized, but no other measure of body weight was common to both pre- and post-spawning males.

Although lamprey parasitism was known to reduce condition (Moltie 1987), only 8.5% (5 of 59) of males designated as female-like bore lamprey-inflicted marks. Overt thyroid hyperplasia was also associated with reduced condition (Moltie 1988a; Moltie et al. 1988). However, its occurrence in males designated as

TABLE 5. Comparison of post-spawning testes in pink salmon males designated as typical and female-like. TDW = testis dry weight (g), TPBW = total pre-spawning body weight (g), TWW = testis water weight (g). Shown are the regression coefficients (* denotes $p \leq 0.05$), sample sizes, and results of covariance analyses comparing regressions listed on adjacent lines.

Male designation	Regression	r	n	Slope test	Intercept test
Typical	$\ln(\text{TDM}) = -4.640 + 0.634 \ln(\text{TPBW})$	0.2408*	79	t=0.350 p>0.50	t=1.028 p>0.20
Female-like	$\ln(\text{TDM}) = -7.469 + 1.130 \ln(\text{TPBW})$	0.4604	9		
Typical	$\ln(\text{TWW}) = 2.064 + 0.624 \ln(\text{TDM})$	0.8556*	79	t=1.227 p>0.20	t=0.341 p>0.50
Female-like	$\ln(\text{TWW}) = 2.028 + 0.348 \ln(\text{TDM})$	0.6648*	9		

female-like (32.3%; 19 of 59) and typical (36.1%; 371 of 1028) did not differ (2x2 continuity-corrected $\chi^2=0.22$, $p>0.50$). Thus, female-like morphology appears not to have been simply a manifestation of having sustained parasitism or of thyroid dysfunction.

Discussion

The information presented above indicates that a small proportion of spawning pink salmon males seek fertilizations using an alternative breeding tactic. These outlier males resembled females in their appearance (Fig. 1). Consistent with these observations, morphological analyses revealed the existence of males whose female-like shape related to their minimal hump development (Figs. 2 and 3). As a result of flooding, the bulk of the behavioural observations had to be obtained from untagged fish. Thus, the synonymy of outlier and female-like males could not be firmly established. This represents a shortcoming to the present work, but provides an obvious avenue for future research.

In some salmonid species, game theory (Maynard Smith 1982) offers an explanation for how dichotomies in male breeding pattern are perpetuated. Males exist as markedly different types in an evolutionarily stable mix of pure strategies within populations (Gross 1984, 1985;

Maekawa and Hino 1986b). Being equal in fitness, disruptive selection acts to reinforce their contrasting fertilization tactics, life histories, relative gonad investments and differences in morphology.

From evidence collected in the present study, the dichotomy in breeding tactics that male pink salmon exhibit does not appear consistent with a mixed ESS interpretation. Although outlier males resembling females did occur, individuals shown to be female-like in shape were not morphologically distinct from typical males. Furthermore, males which were female-like were no different from other males in their prespawning gonad investment, age at maturity, degree of testis depletion or length of breeding life, the latter two being components of fitness (Gross 1985).

Males in other salmonid species exhibit alternative breeding patterns facultatively, primarily when they find themselves at a competitive disadvantage (e.g. Jonsson and Hindar 1982). Here, males adopt the outlier tactic to make the best of a bad situation, and seek fertilizations using the second of two tactics available to them within a single conditional strategy (Dawkins 1980; Gross 1984). In a similar fashion, male pink salmon maturing at relatively low body weights for their sizes (low condition) and which therefore undergo minimal hump development as a result (appear female-like) may be predisposed to employ the outlier fertilization tactic to

overcome the competitive disadvantage they likewise face. That relative weight is an important determinant of competitive ability in fish has been demonstrated in experiments by Barlow (1983), Enquist and Jakobsson (1985), and Enquist et al. (1987). Tests of whether pink salmon males can switch between tactics and the heritability of the morphological characteristics rendering males as female-like would be useful further investigations in this species.

It was of interest to note that the outlier male tactic and males of female-like morphology were only detected among 1985 spawners. During the small run of 1984, the relative isolation of individual nesting females and their monopolization by single large males likely served to minimize the success of the outlier tactic. Males were also in good condition in 1984 (Moltie 1988b) and individuals which were female-like in morphology were not found. In contrast, the higher spawner densities in 1985 inhibited the monopolization of females. Cluster formation and mass spawning appeared to facilitate successful sneak fertilization. Furthermore, 1985 males were in substantially poorer condition than both females of that year and males from former years (Moltie 1988b). As a result, some males matured in 1985 with relatively minimal secondary sexual character development and thus appeared female-like. Together, these between-year differences suggest that both high

spawner densities and low condition in males are important proximate factors for the occurrence of alternate male breeding patterns in *O. gorbuscha*. The necessity of heightened breeding population densities for alternative male breeding tactics to be demonstrated and to be effective has also been alluded to in a wide range of fish species (Gebhardt 1960; Warner and Robertson 1978; Warner and Hoffman 1980; Kodric-Brown 1981; Schroder 1981; Chebanov 1982; Fahy and Nixon 1982; Dominey 1984). Notable also is that the only other evidence to date of alternative breeding patterns in male pink salmon have come from studies of Pacific populations conducted during the years when spawners were also most abundant (Kirkwood 1962; Beacham and Murray 1985; Keenleyside and Dupuis 1988a).

Also of interest are the similarities in aspects of the spawning behaviours exhibited or elicited by outlier males in this study and in other salmonid species where alternative male breeding patterns occur. That outliers are attacked frequently has been recorded many times, as has their avoidance of direct competition for mates by quickly retreating from attacking cluster males (Jones and King 1952; Hanson and Smith 1967; McCart 1970; Maekawa 1983). Despite such aggression, however, outlier males are persistent in their association with clusters (Jones and King 1952; Jones 1959, McCart 1970). As in pink salmon, the female-like appearance of outlier males

in other species may explain why nesting females attack them (Hanson and Smith 1967; McCart 1970; Schroder 1981; Maekawa 1983). As here, Kirkwood (1962) and Keenleyside and Dupuis (1988a) observed that the male pink salmon which females chased were smaller than most others and did not have definite male secondary sexual characteristics. Keenleyside and Dupuis (1988a) also made no note of female-like males quivering to females, performing parallel swim displays, or biting in response to attacks by cluster males.

Finally, aspects of the spawning behaviour of Pacific pink salmon have been documented by a variety of authors (Kusnetsov 1928; Semko 1939; Wickett 1959; Sheridan 1960; Kirkwood 1962; Strelakova 1963; Cameron 1968; Kamyshnaya and Smirnov 1968; Heard 1972; Smirnov 1975; Chebanov 1980, 1982; Keenleyside and Dupuis 1988a,b). However, the present work represents the only consideration to date of the breeding behaviour of pink salmon from the Great Lakes. Despite the novelty of their adopted habitat, the breeding habits of Great Lakes pink salmon appear to differ little from those of their anadromous conspecifics. In this aspect of their ecology, the suggestion that the differences between Great Lakes and Pacific pink salmon occur primarily in their size at maturity (Kvain 1982; Nicolette 1983) appears to be valid.

Acknowledgements

For their field assistance, I thank Daniel Burton, Johny Ellis, Josée Emerson, Nancy Kirkpatrick, Tammy McKellar, Elaine Moltie, Lionel Normand and Daniel Robilliard. Financial support of this work came from NSERC and OGS scholarships to the author, grants from the Ontario Ministry of Natural Resources, the Department of Fisheries and Oceans, the Ontario Federation of Anglers and Hunters, and an NSERC operating grant to M.H.A. Keenleyside. The cooperation of OMNR personnel in Sault Ste. Marie is gratefully acknowledged.

References

- AUSTAD, S.N. 1984. A classification of alternative reproductive behaviors and methods for field-testing ESS models. Amer. Zool. 24: 309-319.
- BAGDOVITZ, M.S. 1985. Ecology and life history of pink salmon (Oncorhynchus gorbuscha) in selected Michigan tributaries to Lake Superior. M.Sc. thesis, Michigan State Univ., East Lansing, MI. 64 p.
- BAGDOVITZ, M.S., W.W. TAYLOR, W.C. WAGNER, J.P. NICOLETTE, AND G.R. SPANGLER. 1986. Pink salmon populations in the U.S. waters of Lake Superior, 1981-1984. J. Great Lakes Res. 12: 72-81.

- BARLOW, G.W. 1983. Do gold Midas cichlid fish win fights because of their color, or because they lack normal coloration? *Behav. Ecol. Sociobiol.* 13: 197-204.
- BEACHAM, T.D., AND C.B. MURRAY. 1985. Variation in length and body depth of pink salmon (Oncorhynchus gorbuscha) and chum salmon (O. keta) in southern British Columbia. *Can. J. Fish. Aquat. Sci.* 42: 312-319.
- BILTON, H.T., AND W.E. RICKER. 1965. Supplementary checks on the scales of pink salmon (Oncorhynchus gorbuscha) and chum salmon (O. keta). *J. Fish. Res. Board Can.* 22: 1477-1489.
- BRIGGS, J.C. 1953. The behavior and reproduction of salmonid fishes in a small coastal stream. *Calif. Dept. Fish Game Fish Bull.* 94: 1-62.
- BUSH, J.E. 1985. Determination of fertility in two and three-year-old pink salmon in a Minnesota tributary to Lake Superior. M.Sc. thesis, Univ. of Minnesota, St. Paul, MN. 73 p.
- CAMERON, W.M. 1968. A preliminary investigation of the natural spawning, incubation and alevinage of the pink salmon (Oncorhynchus gorbuscha). *Fish. Res. Board Can. MS Rep.* 995: 1-25.
- CHEBANOV, N.A. 1980. Spawning behavior of the pink salmon, Oncorhynchus gorbuscha. *J. Ichthyol.* 20: 64-73.

1982. Spawning behavior of the humpbacked salmon Oncorhynchus gorbuscha with different ratios of sexes at the spawning ground. Sov. J. Ecol. 13: 53-61.

CHEBANOV, M.A., N.V. VARNAVSKAYA, AND V.S. VARNAVSKIY.

1983. Effectiveness of spawning of male sockeye salmon, Oncorhynchus nerka (Salmonidae), of differing hierarchical rank by means of genetic-biochemical markers. J. Ichthyol, 23: 51-55.

DAVIDSON, F.A. 1935. The development of the secondary sexual characters in the pink salmon (Oncorhynchus gorbuscha). J. Morphol. 57: 169-183.

DAVIDSON, F.A., AND O.E. SHOSTROM. 1936. Physical and chemical changes in the pink salmon during the spawning migration. U.S. Bur. Fish. Invest. Rep. 33: 1-37.

DAWKINS, R. 1980. Good strategy or evolutionarily stable strategy? p. 331-367 In G.W. Barlow and J. Silverberg [eds.] Sociobiology: beyond nature/nurture. Westview Press, Boulder, CO.

DOMINEY, W.J. 1980. Female mimicry in male bluegill sunfish - a genetic polymorphism? Nature 284: 546-548.

1984. Alternative mating tactics and evolutionarily stable strategies. Amer. Zool. 24: 385-396.

- ENQUIST, M., AND S. JAKOBSSON. 1986. Decision making and assessment in the fighting behaviour of Nannacara anomala (Cichlidae, Pisces). Ethol. 72: 143-153.
- ENQUIST, M., T. LJUNGBERG, AND A. SANDOR. 1987. Visual assessment of fighting ability in the cichlid fish Nannacara anomala. Anim. Behav. 35: 1262-1264.
- EVERMANN, B.W. 1897. A report upon salmon investigations in the headwaters of the Columbia River, in the state of Idaho, in 1895, together with notes upon the fishes observed in that state in 1894 and 1895. Bull. U.S. Fish Comm. for 1896 16: 149-202.
- FAHY, E., AND J.J. NIXON. 1982. Spawning trout in eastern Connemara. Fish. Bull. (Dublin) 6: 1-11.
- FLAIN, M. 1970. Precocious male quinnat salmon Oncorhynchus tshawytscha (Walbaum) in New Zealand. N.S. J. Mar. Freshw. Res. 4: 217-222.
- GEBHARDS, S.V. 1960. Biological notes on precocious male chinook salmon parr in the Salmon River drainage, Idaho. Prog. Fish-Cult. 22: 121-123.
- GROSS, M.R. 1979. Cuckoldry in sunfishes (Lepomis: Centrarchidae). Can. J. Zool. 57: 1507-1509.
- 1980a. Sexual selection and the evolution of reproductive strategies in sunfishes (Lepomis: Centrarchidae). Ph.D. thesis, Univ. of Utah, Salt Lake City, UT. 330 p.

- 1980b. Cuckoldry and parental care in sunfishes - is there an equilibrium? *Amer. Zool.* 20: 826.
1982. Sneakers, satellites and parentals: polymorphic mating strategies in North American sunfishes. *Z. Tierpsychol.* 60: 1-26.
1984. Sunfish, salmon, and the evolution of alternative reproductive strategies and tactics in fishes. p. 55-75 In G.W. Potts and R.J. Wootton [eds.] *Fish reproduction: strategies and tactics.* Academic Press, London.
1985. Disruptive selection for alternative life histories in salmon. *Nature* 313: 47-48.
- GROSS, M.R., AND E.L. CHARNOV. 1980. Alternative male life histories in bluegill sunfish. *Proc. Natl. Acad. Sci. U.S.A.* 77: 6937-6940.
- HAGER, R.C., AND R.E. NOBLE. 1976. Relation of size at release of hatchery-reared coho salmon to age, size, and sex composition of returning adults. *Prog. Fish-Cult.* 38: 144-147.
- HANKIN, D.G., AND R. MCKELVEY. 1985. Comment on fecundity of chinook salmon and its relevance to life history theory. *Can. J. Fish. Aquat. Sci.* 42: 393-394.
- HANSON, A.J., AND H.D. SMITH. 1967. Mate selection in a population of sockeye salmon (*Oncorhynchus nerka*)

- of mixed age-groups. J. Fish. Res. Board Can. 24: 1955-1977.
- HEARD, W.R. 1972. Spawning behavior of pink salmon on an artificial redd. Trans. Am. Fish. Soc. 101: 276-283.
- HUTCHINGS, J.A., AND R.A. MYERS. 1987. Egg fertilization by mature male parr in competition with anadromous male Atlantic salmon (Salmo salar) during spawning. p. 131 In D.R. Idler, L.W. Crim and J.M. Walsh [eds.] Reproductive physiology of fish 1987. Proceedings of the 3rd international symposium on reproductive physiology of fish, St. John's, Newfoundland, Canada, August 2-7, 1987. Marine Sciences Research Laboratory, Memorial University of Newfoundland, St. John's, Nfld.
- JONES, J.W. 1959. The salmon. Collins, London. 192 p.
- JONES, J.W., AND G.M. KING. 1952. The spawning of the male salmon parr (Salmo salar Linn. juv.). Proc. Zool. Soc. London 122: 615-619.
- JONSSON, B., AND K. HINDAR. 1982. Reproductive strategy of dwarf and normal Arctic charr (Salvelinus alpinus) from Vangsvatnet Lake, western Norway. Can. J. Fish. Aquat. Sci. 39: 1404-1413.
- KAMYSHENAYA, M.S., AND A.I. SMIRNOV. 1968. Natural reproduction of pink salmon acclimatized in the watersheds of the Barents and White seas. Rybn.

- Khoz. 44: 18-20. (Trans. from Russian by Fish. Res. Board Can. Trans. Ser. 1215, 1969).
- KEENLEYSIDE, M.H.A. 1972. Intraspecific intrusions into nests of spawning longear sunfish (Pisces: Centrarchidae). *Copeia* 1972: 272-278.
- KEENLEYSIDE, M.H.A., AND H.M.C. DUPUIS. 1988a. Courtship and spawning competition in pink salmon (*Oncorhynchus gorbuscha*). *Can. J. Zool.* (in press).
- 1988b. Comparison of digging behavior by female pink salmon (*Oncorhynchus gorbuscha*) before and after spawning. *Copeia* (in press).
- KIRKWOOD, J.B. 1962. Inshore-marine and freshwater life history phases of the pink salmon, *Oncorhynchus gorbuscha* (Walbaum), and the chum salmon, *O. keta* (Walbaum), in Prince William Sound, Alaska. Ph.D. thesis, Univ. of Louisville, Louisville, KY. 300 p.
- KODRIC-BROWN, A. 1981. Variable breeding systems in pupfishes (Genus *Cyprinodon*): adaptations to changing environments. p. 205-235 In R.J. Naiman and D.L. Solts [eds.] *Fishes in North American deserts*. John Wiley & Sons, Inc., New York, NY.
- KROKHIN, E.M. 1967. A contribution to the study of dwarf sockeye *Oncorhynchus nerka* Walb., in Lake Dalnee (Kamchatka). *Vopr. Ikhtiol.* 7: 433-445. (Trans. from Russian by Fish. Res. Board Can. Trans. Ser. 986, 1967).

- KUZNETSOV, I.I. 1928. Some observations on the propagation of the Amur and Kamchatka salmon. Izv. Tikhook. nauchno-issled. Stantsii. 2(3): 3-195. (Trans. from Russian by N.B. Notkin, Int. Pac. Salmon Fish. Comm., Seattle, WA, March 19, 1947. 249 p.).
- KWAIN, W.H.. 1982. Spawning behavior and early life history of pink salmon (Oncorhynchus gorbuscha) in the Great Lakes. Can. J. Fish. Aquat. Sci. 39: 1353-1360.
- 1987a. Biology of pink salmon in the North American Great Lakes. In M.J. Dadswell, R.J. Klauda, C.M. Moffit, R.L. Saunders and R.A. Rulifson [eds.] Common strategies of anadromous and catadromous fishes. American Fisheries Society Symposium 1. American Fisheries Society, Bethesda, MD. (in press).
- 1987b. Record size of freshwater pink salmon. N. Am. J. Fish. Manage. 7: 302-303.
- KWAIN, W., AND S.J. KERR. 1984. Return of 1-year-old pink salmon in Michipiooten River, eastern Lake Superior. N. Am. J. Fish. Manage. 4: 335-337.
- KWAIN, W., AND G.A. ROSE. 1986. Spawning migration of Great Lakes pink salmon (Oncorhynchus gorbuscha): size and sex distributions, river entrance and exit. J. Great Lakes Res. 12: 101-108.
- MAEKAWA, K. 1983. Streaking behaviour of mature male parrs of the Miyabe charr, Salvelinus malma miyabei, during spawning. Jap. J. Ichthyol. 30: 227-234.

MAEKAWA, K., AND T. HINO. 1986a. Alternative reproductive tactics of lacustrine Miyabe charr and anadromous Dolly Varden. p. 948-949 In T. Uyeno, R. Arai, T. Taniuchi and K. Matsuura [eds.] Indo-Pacific fish biology: proceedings of the second international conference on Indo-Pacific fishes. Ichthyological Society of Japan, Tokyo, Japan.

1986b. Spawning behaviour of Dolly Varden in southeastern Alaska, with special reference to the mature parr. Jap. J. Ichthyol. 32: 454-458.

MAEKAWA, K., AND H. ONOZATO. 1986. Reproductive tactics and fertilization success of mature male Miyabe charr, Salvelinus malma miyabei. Env. Biol. Fish. 15: 119-129.

MAYNARD SMITH, J. 1982. Evolution and the theory of games. Cambridge University Press, Cambridge. 224 p.

MCCART, P. 1969. Digging behaviour of Oncorhynchus nerka spawning in streams at Babine Lake, British Columbia. p. 39-51 In T.G. Northcote [ed.] Symposium on salmon and trout in streams. H.R. MacMillan Lectures in Fisheries, Univ. of British Columbia, Vancouver, B.C.

1970. A polymorphic population of Oncorhynchus nerka at Babine Lake, B.C. involving anadromous (sockeye) and non-anadromous (kokanee) forms. Ph.D. thesis, Univ. of British Columbia, Vancouver, B.C. 135 p.

- MONTGOMERY, W.L. 1983. Parr excellence. *Nat. Hist.* 92: 58-67.
- MONTGOMERY, W.L., G.E. GOSLOW, Jr., K.B. STALEY, AND J.R. MILLS. 1987. Alternative mating behaviors of male Atlantic salmon (*Salmo salar*), with special reference to mature male parr. p. 232-238 In W.J. Matthews and D.C. Heins [eds.] *Community and evolutionary ecology of North American stream fishes*. University of Oklahoma Press, Norman, OK.
- NICOLETTE, J.P. 1983. Population dynamics of pink salmon in selected Minnesota tributaries to Lake Superior. M.Sc. thesis, Univ. of Minnesota, St. Paul, MN. 94 p.
1984. A 3-year-old pink salmon in an odd-year run in Lake Superior. *N. Am. J. Fish. Manage.* 4: 130-132.
- NICOLETTE, J.P., AND G.R. SPANGLER. 1986. Population characteristics of adult pink salmon in two Minnesota tributaries to Lake Superior. *J. Great Lakes Res.* 12: 237-250.
- NIKOLSKY, G.V. 1963. *The ecology of fishes*. Academic Press, London. 352 p.
- MOLTIE, D.B. 1987. Incidence and effects of sea lamprey (*Petromyzon marinus*) parasitism on breeding pink salmon (*Oncorhynchus gorbusha*) from the Carp River, eastern Lake Superior. *Can. J. Fish. Aquat. Sci.* 44: 1562-1567.

1988a. Differences in breeding Lake Superior pink salmon (Oncorhynchus gorbuscha) associated with variation in thyroid hyperplasia. Can. J. Zool. (accepted).

1988b. Breeding ecology of pink salmon (Oncorhynchus gorbuscha from the Carp River, eastern Lake Superior. Chapter 2, this volume.

NOLTIE, D.B., J.F. LEATHERLAND, and M.H.A. KEENLEYSIDE.

1988. Epizootics of thyroid hyperplasia in Lake Superior and Lake Erie pink salmon (Oncorhynchus gorbuscha Walbaum). Can. J. Zool. (accepted).

OHNO, I. 1934. Life-history of Oncorhynchus masou found in the waters of Hokkaido. Proc. 5th Pac. Sci. Congr., 1933, vol. 5, sect. B6, no. 28, p. 3785-3786.

ROBERTSON, O.H. 1957. Survival of precociously mature king salmon male parr (Oncorhynchus tshawytscha juv.) after spawning. Calif. Fish Game 43: 119-130.

RUTTER, C. 1904. Natural history of the quinnat salmon. A report on investigations in the Sacramento River 1896-1901. U.S. Fish Comm. Bull. for 1902 2: 65-141.

SCHRODER, E.L. 1972. Effects of density on the spawning success of chum salmon (Oncorhynchus keta) - a progress report. p. 91-100 In J.E. Bailey [ed.] Proceedings of the 1972 northeast Pacific pink salmon workshop. Alaska Dept. Fish Game Info. Leaflet 161.

1973. Effects of density on the spawning success of chum salmon (Oncorhynchus keta) in an artificial spawning channel. M.Sc. thesis, Univ. of Washington, Seattle, WA. 78 p.

1976. Some observations concerning mate selection patterns found in chum salmon. p. 140-151. In G.K. Gunstrom [ed.] Proceedings of the 1976 northeast Pacific pink and chum salmon workshop. Alaska Dept. Fish Game.

1981. The role of sexual selection in determining overall mating patterns and mate choice in chum salmon. Ph.D. thesis, Univ. of Washington, Seattle, WA. 274 p.

SCHRODER, S.L., AND G.J. DUKER. 1979. Assessment of production of chum salmon fry from the Big Beef Creek spawning channel. Ann. Rep., Anadromous Fish Project AFC-82, Fish. Res. Inst., Univ. of Washington, Seattle, WA. FRI-UW-7909. 14 p.

SCHRODER, S.L., AND J. SEEB. 1979. Potential genetic contribution of satellite males in chum salmon demes. p. 397-402. In J.C. Mason [ed.] Proceedings of the 1978 northeast Pacific pink and chum salmon workshop. Pacific Biological Station, Nanaimo, B.C.

SCOTT, W.B., AND E.J. CROSSMAN. 1973. Freshwater fishes of Canada. Fish. Res. Board Can. Bull. 184: 966 p.

- SEMKO, R.S. 1939. The Kamchatka pink salmon. *Izv. TINRO* 16: 1-111. (Trans. from Russian by Fish. Res. Inst., Univ. of Washington, Seattle, WA. 117 p.).
- SHAPOVALOV, L., AND A.C. TAFT. 1954. The life histories of the steelhead rainbow trout (Salmo gairdneri gairdneri) and silver salmon (Oncorhynchus kisutch) with special reference to Waddell Creek, California, and recommendations regarding their management. Calif. Dept. Fish Game Fish Bull. 98: 1-303.
- SHERIDAN, W.L. 1960. Frequency of digging movements of female pink salmon before and after egg deposition. *Anim. Behav.* 8: 228-230.
- SMIRNOV, A.I. 1959. Differences in the biology of reproduction and development of residual or dwarf sockeye and anadromous sockeye (Oncorhynchus nerka (Walbaum)). *Nauch. Dokl. Vysshei Shkoly, Biol. Nauki* 3: 59-65. (Trans. from Russian by Fish. Res. Board. Can. Trans. Ser. 266, 1960).
1962. Reproductive ecology of masu (Oncorhynchus masu (Brevoort)). *Dokl. Akad. Nauk S.S.S.R.* 143: 1449-1452. (Trans. from Russian by *Dokl. Biol. Sci. Sect.* 142-147: 334-336, 1962-63).
1963. Production of sperm by the Pacific Ocean Oncorhynchus salmon. *Vopr. Ikhtiolog.* 3: 64-98. (Trans. from Russian by U.S. Env. Protection Agency, TR-79-0612).

1975. The biology, reproduction and development of the Pacific salmon. *Izv. Mosk. Univ.* 335 p. (Trans. from Russian by Can. Fish. Mar. Serv. Transl. Ser. 3861, 1976).

STREKALOVA, I.I. 1963. Observations on spawning of pink salmon Oncorhynchus gorbuscha (Walbaum) and chum salmon Oncorhynchus keta (Walbaum) in the My River (Amur estuary). *Vopr. Ikhtiol.* 3:256-265. (Abstr. Trans. from Russian by Biol. Abstr. 45, No. 67517, 1964).

UTOH, H. 1976. Study of the mechanism of differentiation between the stream resident form and the seaward migratory form in masu salmon, Oncorhynchus masou Brevoort: I. Growth and sexual maturity of precocious masu salmon parr. *Bull. Fac. Fish. Hokkaido Univ.* 26: 321-326.

van den BERGHE, E.P., AND M.R. GROSS. 1986. Length of breeding life of coho salmon (Oncorhynchus kisutch). *Can. J. Zool.* 64: 1482-1486.

WAGNER, W.C. 1978. A three-year-old pink salmon from Lake Superior. *Mich. Dept. Nat. Res., Fish. Div., Fish. Res. Rep.* 1861: 1-7.

1985. Size, age, and fecundity of pink salmon in Michigan. *Mich. Dept. Nat. Res., Fish. Div., Fish. Res. Rept.* 1933: 1-13.

WAGNER, W.C., AND T.M. STAUFFER. 1980. Three-year-old pink salmon in Lake Superior tributaries. Trans. Am. Fish. Soc. 109: 458-460.

1982. Distribution and abundance of pink salmon in Michigan tributaries of the Great Lakes, 1967-1980. Trans. Am. Fish. Soc. 111: 523-526.

WARNER, R.R., AND S.G. HOFFMAN. 1980. Local population size as a determinant of mating system and sexual composition in two tropical marine fishes (Thalassoma spp.). Evol. 34: 508-518.

WARNER, R.R., AND D.R. ROBERTSON. 1978. Sexual patterns in the labroid fishes of the western Caribbean, I: The wrasses (Labridae). Smith. Contrib. Zool. 254: 1-27.

WICKETT, W.P. 1959. Observations on adult pink salmon behaviour. Fish. Res. Board Can. Prog. Rep. Pac. Coast Sta. 113: 6-7.

ZAR, J.H. 1974. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, NJ. 620 p.