VARIABILITY OF PINK SALMON FAMILY SIZE HAS IMPLICATIONS FOR CONSERVATION AND MANAGEMENT MODELS

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By

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ABSTRACT

In several populations of pink salmon, the short-term dynamics population size was related to both the mean and variance of individual family sizes, because not all families were equally productive. In the marine lifestage, population increases came disproportionately from the most productive families, especially in populations with the highest average marine survival. Moreover, the trait of marine survival itself had a statistically detectable genetic component. This implies that the most favored phenotypes change from generation to generation, and that the marine environment is unpredictable and changing. These results, together with laboratory studies of freshwater survival and measurements of wild pink salmon in Prince William Sound, Alaska, seemed to indicate that family-specific variation in marine survival and variation in egg retention within the redd were the most important potential influences on variation of pink salmon family size in the studied populations, when density was controlled to intermediate levels. These results provide more justification for maintaining stock sizes at intermediate or high levels, and for protecting metapopulation structure. These results also show the importance of variation and instability in the recruitment process of Pacific salmon, and highlight the inadequacy of current models of salmon recruitment, which emphasize stability and long-term averages.

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For Bev, Sigrid, and Beth

PREFACE

First, I thank Dr. Douglas Eggers for being my guide into the sciences of salmon biology and management, for years of stimulating conversations, smart criticism, and for many opportunities to grow and prosper. I thank Prof. Terry Quinn for guiding me into many new things over the last 18 years, this thesis being just one example. Prof. A.J. Gharrett has my great thanks for taking me on as a project, and successfully dealing with my stubbornness, willfulness, and strong aversion to authority. In the end, he was able to bring me to heel, teach me a great deal about genetics, and earn my respect. Prof. Bill Smoker has been a consistent scholarly advisor and ally throughout this enterprise, and I thank him for that and for his friendship. I thank Dr. Lev A. Zhivotovsky, especially for several important conversations when I first started on the second chapter. Profs. Gharrett, Smoker, and Quinn, and Drs. Zhivotovsky and Jerry Pella served as my committee, and I certainly extend them my thanks. My friend and colleague Sam Sharr helped with virtually every aspect of the work I did in Prince William Sound. Profs. Gharrett and Smoker's students collected the data that formed Chapter 4. Finally, I must thank Sigrid Dahlberg for so many things I don't even know where to start. The Alaska Department of Fish and Game supported me during my work on this degree.

Much of the work on my dissertation was done in collaboration with others. About two weeks after the wreck of the *Exxon Valdez* in 1989, I traveled to Prince William Sound with Doug Eggers, Chief Fisheries Scientist for the Alaska Department of Fish and Game, to begin planning for the evaluation of the effects of the resulting oil spill on fishery resources. Initially, Dr. Eggers and I started planning a series of studies with Alaska Department of Fish and Game staff – especially Sam Sharr, who at the time was the Commercial Fisheries Division's research project leader in Prince William Sound. In those first few days of planning, Alex Wertheimer and a number of his colleagues at the National Marine Fisheries Service helped refine the goals for an entire suite of pink salmon studies to be coordinated between ADF&G and the National Marine Fisheries Service. After several days of discussion, we jointly agreed to a series of related studies to be conducted cooperatively between the University of Alaska, the Alaska Department of Fish and Game, and the National Marine Fisheries Service. We agreed that to quantify the effects of the oil spill we needed to 1) develop improved estimates of pink salmon escapement for pre- and post-spill years, 2) measure egg (embryo) survival, 3) measure fry survival, 4) observe the near-shore condition and distribution of fry in Prince William Sound, 5) measure hatchery and wild salmon survival in the saltwater environment, and 6) survey the pink salmon habitat affected by the oil spill. The management of individual studies was assigned to Sam Sharr and Brian Bue, of the Alaska Department of Fish and Game, Alex Wertheimer and colleagues at the National Marine Fisheries Service, and Mark Willette of ADF&G and his collaborators at the University of Alaska Fairbanks.

Most of the field data that I used here (such as egg-dig data) were collected by technicians under the direction of Sam Sharr. The only data collection I directly supervised myself was the 1992 pink salmon radio-tagging data, which did not appear directly in this dissertation, but these data did affect the escapement estimates, which I used extensively. I developed the sampling plans for the coded-wire tagging studies, provided statistical consulting for the improved escapement estimates, and provided initial statistical consulting for the studies on fry and embryo studies, although Brian Bue assumed responsibilities for the statistical aspects of these fry and embryo studies once these studies became operational. I had no involvement in the planning or execution of the early marine studies, other than to share field staff and field resources.

After the first year of field studies, Dr. Phil Mundy and Prof. Ray Hilborn suggested tying these studies together through a run-reconstruction modeling effort, and a life-history model. The management of those projects was assigned to me. Profs. Terry Quinn and Jeremy Collie at the University of Alaska were contracted to do the run-reconstruction model, and I then began working with Sam Sharr, Brian Bue, Mark Willette, and Alex Wertheimer to assemble the data for the life history model. Alex directed me to some important literature that I was unaware of, and helped me refine what to include in this study. My contribution to the part of this work that appears in Chapter 2 was to (1) develop a plan for the coded wire tagging studies, (2) provide statistical advice and oversight of how to estimate most of the key statistics, (3) to assemble all of the data for the life history paper, (4) perform the reported analysis, (5) write the initial paper and serve as the corresponding author.

Profs. Gharrett and Smoker conceived the study that formed the basis for Chapter 3, and were responsible for collecting and assembling the original data set. Prof. Gharrett suggested this study to me, and pointed out that marine survival and family size should be considered inherited traits. Dr. Zhivotovsky suggested partitioning family size in survival into sequential life history stanzas, and suggested the approximations to the variance of family size. Based on these suggestions, I performed the analysis and wrote the paper that formed the basis of Chapter 4.

Prof. Gharrett's student Ivan Wang and Prof. Smoker's students Pat Malecha, and Kyle Hebert, collected the embryo-survival data sets, and all but one of the fecundity data sets that went into Chapter 4. Prof. Smoker collected the remaining fecundity data set. Prof. Gharrett suggested using these data for hypothesis tests for nonzero heritabilities in the freshwater environment. Not satisfied with the laboratory result, I decided to compare the laboratory studies of family-specific survival with the spatially clustered embryo and fry data that I had worked with previously in Prince William Sound. Those data on wild salmon had been collected by technicians working under the direction of Sam Sharr, and initially analyzed by Brian Bue. Steve Moffitt played an especially important role in the Prince William Sound data collection. I did all data analysis for Chapter 4, and I wrote this chapter.

Although Chapters 2 through 4 were published in, or submitted to, different journals, all were revised to conform to the suggested style provided in http://www.uaf.edu/gradsch/ThesisWorkbook.pdf .

Alas for you lawyers! You have taken away the key of knowledge. You did not go in yourselves, and those that were on their way in, you stopped.
— Luke 11:52

CHAPTER 1 -- INTRODUCTION

THE STORY OF TWO SALMON MANAGEMENTS

Lichatowich's (1999) history of the Pacific salmon in the Pacific Northwest takes the reader from 400 million years ago to the present. Beginning with the industrialization of the Pacific Northwest, he tells a story of overharvest, inability to control harvest rates directly, ideological dependence on hatchery technology, inability to recognize clear failure, and most importantly, the conversion of salmon habitat to other uses. The subtitle of Lichatowich's book, "A history of the Pacific salmon crisis," sets a tone that I think many people associate with the state of salmon and their management everywhere they occur, or once occurred, including Alaska, Canada, and the Russian Far East.

This account contrasts sharply with Royce's (1989) glowing description of the success of science and industry in Alaskan salmon management. Royce was a student of the Alaskan situation beginning in period of over harvests, ineffective management, and great public dissatisfaction, and his account was written near the peak of the value of the Alaskan salmon fishery. In describing changes in Alaska from the 1950s through the late

1980s, it seemed to Royce that salmon scientists and managers had achieved all their major goals: depleted runs were rapidly increasing – presumably because of the effects of management – the benefits of the resource were broadly distributed, and there was an effective management system in place with strong public support. In the late 1980s, the value of the resource was at an all-time high and the seafood harvesting industry was the largest private-sector employer in the Alaskan economy, both in terms of income and employment.

Alaska and the Pacific Northwest had similar pre-industrial histories with salmon management and human use, and in both regions people valued salmon and had complex property-rights systems and economies based on salmon (Lichatowich 1999). Starting in the 19th century, salmon were recognized as a valuable industrial resource to western industry, and an infrastructure to use Alaskan salmon as an industrial commodity began to develop. By about 1900, canning became the main means of preserving the salmon harvest, and the Federal Government was looking for ways to encourage an Alaskan salmon industry.

In 1897, The Federal Government sent the vessel *Albatross* to Alaska to survey the situation with the Alaska salmon fisheries under the command of Jefferson F. Moser. Moser (1899) provided a good characterization of the state of the fishery and the thinking of the salmon industry at the time. Referring to the 1897 fishing season, he says "the redfish (sockeye salmon) is the commercial fish, the other species being packed incidentally, or to fill up the quota when other kinds are scarce." Later in his report, he states that just over 75% of the 1897 pack was sockeye salmon, by weight, with just over 17% pack pink salmon. Even more interesting is his statement,

> Even when white men are met and questioned, information relating to the streams is difficult to obtain with any degree of exactness. The men at the head of the canneries know the cannery business thoroughly. They know how to get the fish to the canneries, pack them, case them for the market, and figure on the profits, but it is exceptionally rare to find one who has followed even his home stream to its sources and examined the lake system and the spawning grounds. This is not said in the sprit of criticism, for the cannerymen are interested only in obtaining fish, but to indicate the difficulty of gathering the information desired in our work, except by personal examination and investigation.

Even at this very early stage of the fishery development Moser observed depleted runs, and he could clearly see the need for conservation measures. Moser also noted how the new industrial fishery changed the status of fishery rights:

> Many disputes arise concerning the fisheries. A native, whose ancestors, and whose rights are respected by other natives, supplies a certain cannery with his catch, as possibly he has been doing for years. A rival cannery tells the native that he must sell his catch to it, and that otherwise their men will fish the native's stream. The result is over fishing, complaints, bad feelings, blows, and threats of bloodshed. So far as can be learned, there are no legal rights or title to any fishing-grounds in Alaska except what force or strategy furnish.

One of the first acts of federal management in 1896 forbade blocking or damming salmon streams, and forbade certain fishing practices (Moser 1899). Within a few years, federal law was to require any person, company, or corporation in Alaskan waters to establish a fish hatchery that would produce sockeye salmon fry at least four times the number of mature salmon taken each year. These early enhancement efforts were almost all failures, because the hatchery operators did not understand basic salmon biology (Ropel 1982).

The salmon trade concentrated in the hands of a few powerful fish packing companies. Large and efficient fish traps were introduced, and the Federal Government allowed exclusive fishing rights. Commercial catches increased to a peak of 126 million fish in 1936, and then declined. Detailed catch statistics for the commercial salmon fishery in Alaska are available from 1878 (Byerly et al. 1999), and these provide a long-term index that tell much of the story of salmon and salmon fisheries in Alaska.

Alexandersdottir (1987) divided the pre-statehood pink salmon fishery in Southeast Alaska into three periods (following Cooley 1963), which could be applied to the whole salmon fishery in Alaska. She describes 1900 to 1925 as the buildup period, when there was very little regulation of the fishery. This period ended with the White Act, passed in 1924, which halted fishing at the midpoint of the run – a disastrous policy from the point of view of preserving all genetic components of the run. The second period from 1925 to 1945 was a time when major fishing districts were defined, and a number of management measures and weekend fishing closures were introduced. Fishing effort increased up to 1930, when the number of fish traps was restricted. By the end of this period the runs were severely overfished and catch trends were on their way down. In the final period from 1946 to statehood – the period of decline – run timing had been substantially altered, some genetic stocks were gone, and the fishery had lost much of its value through depletion.

Because of resentment about the political power and exclusive fishery rights of the large packing companies, the narrow distribution of the benefits within Alaska, and resentment about the ineffectiveness of Federal management, control of salmon management was a major issue leading to Alaska's statehood in 1959. Evidence that these issues were strong political motivating forces can be seen in the Alaskan State Constitution. Article VIII deals with exclusively with Natural Resources. SECTION 15 of this article is titled "NO EXCLUSIVE RIGHT OF FISHERY." The new State government quickly outlawed fish traps, which were a powerful symbol of the period of Federal control, except for a single, small Federal reserve in Southeast Alaska. The new government launched a state fishery management system, with the principal goals of sustainable resource management, and broad distribution of the benefits.

This new management machinery had components that dealt with enforcement, research, management, permitting, and an explicitly political system for settling allocation disputes. The Alaska Board of Fisheries is a group of citizens chosen by the

Governor, and confirmed by the Alaskan State Legislature, with somewhat vaguely defined powers that overlap somewhat with those of the Alaska Department of Fish and Game. But the Board of Fisheries has the unambiguous role of approving fishery management plans into regulation, and, thereby, of settling allocation disputes between competing fishing groups. In 1947 prior to statehood, the fish-processing industry approached the University of Washington about beginning a program of research and recommendations for management, similar to the program that led to the International Pacific Halibut Commission – one of most visible symbols of success in fishery management. The early work by the Fisheries Research Institute at the University of Washington led to a system of escapement goals and a series of studies to optimize the yield from each major salmon stock in Alaska. The Ricker (1954) theory of stock and recruitment was an important organizing principle.

Run sizes increased following the move to state control, until 1970, when the run sizes dropped sharply. A report with the 1970 salmon forecast (Noerenberg and Seibel 1969) began with an optimistic statement about the value of management based on scientific principles, and stressed that harvests had seen a 25% increase over the pre-statehood period from 1951 to 1959. By 1975, the tone among salmon managers had changed from optimism to panic. The forecast report from that year (Seibel and Mecham 1975) is free of the talk about the success of scientific management, and this report makes clear that managers at the time placed great importance on the freshwater lifestage, and saw this lifestage as the primary source of variation in run size.

Following the drop in salmon production, Alaska launched two initiatives: it began a system of limited entry into the commercial fishery, and it began a large-scale hatchery building program. The originators of the hatchery program were convinced that they could intervene in the freshwater lifestage, and largely buffer the Alaskan salmon industry from variability in run sizes.

In 1974, the Alaskan limited-entry system was viewed as both a conservation measure and a means to maintain a value of the resource for Alaskan citizens (Adasiak 1977). This system fixed the number of permits for access to the commercial fishery. The value of the permit could go up or down based on the health of the resource, and based on the health of the trade in fish. This created a proxy for ownership of the resource, and created a large economic incentive to preserve the health of the salmon stocks.

In 1971, the Alaska legislature created the Fisheries Rehabilitation, Enhancement, and Development Division (or FRED Division as it was known) to both promote and regulate enhancement. As in other places in the world, these enhancement efforts were heavily weighted toward hatcheries. One goal of this new hatchery division was to restore – through the use of hatcheries – the commercial salmon harvest to 100 million salmon. In the first twenty years, they constructed 20 hatcheries at a cost of $81 million, with operational costs many times that. In 1974, the Alaskan Legislature created a second hatchery program, which launched a new round of hatcheries, built and maintained by private non-profit corporations. In 1976 and 1977, a revolving aquaculture loan fund was created to provide funding for hatcheries. Eventually, the FRED was disbanded and the state-built hatcheries were handed over to private non-profit corporations. In 2000, there were two state-operated hatcheries and 31 private non-profit facilities in Alaska. Hatcheries have had their greatest effect in Prince William Sound with pink salmon and in Southeast Alaska with chum salmon. By 2000, biologists in Prince William Sound were forecasting a run of pink salmon that was almost 80% hatchery derived (Scott and Geiger 2000). Hilborn and Eggers (2000) speculated that the pink salmon hatcheries in Prince William Sound had merely resulted in a displacement of wild pink salmon, and that the number of pink salmon in the commercial harvest might be similar if the hatcheries had not been put there. Although Wertheimer et al. (2000) and others have challenged Hilborn and Eggers, the benefits and the costs of the Prince William Sound hatchery programs remain controversial.

The Alaska commercial harvest was 22 million Pacific salmon in 1974. From the mid 1970s to the present, run sizes, salmon survival, and sport and commercial fishery harvests have generally increased with commercial catches of 218 million salmon of all species in 1995 and 217 million in 1997.

The Paradigm of Salmon Management

Alaskan salmon managers have acted for decades on the belief that recruitment of Pacific salmon is generally predictable, following an underlying stock-recruitment law that states recruitment is maximized at intermediate stock size. Although many theoretical stock-recruit laws are available (Quinn and Deriso 1999), the Ricker model (1975) is the one most often applied to Pacific salmon. Traditional advice has been to estimate parameters of a Ricker model, and then proceed to find the harvest policy and specific escapements that will maximize the predicted yield for a stock whose recruitment is controlled by the estimated parameters (e.g., Bevan 1988), without regard to the potential loss that might come from model misspecification, sampling error of parameters, and so forth. This model has led fisheries management to focus narrowly on abundance alone (Ricker 1975, Walters and Collie 1988). Models used by conservation biologists in the analysis of the risk of extinction of populations (Ginzburg et al. 1982, Ferson et al. 1989, Dennis et al. 1991) are also based on abundance. However, in fisheries science some authors have argued that abundance is the single important parameter in fishery management models (e.g., Walters and Collie 1988).

Gulland (1988) expressed the mainstream view, but he seemed somewhat uncomfortable with it:

> The best initial approach in a particular situation remains that of plotting pairs of observed values of stock and recruitment, with the recognition that such a plot will

> exhibit a greater or lesser degree of scatter, due to the effect of environmental factors. In many stocks the dominant factor in determining the recruitment in any one year will be the environment...In principle the relation of main interest might be clarified by removing the effect of the environment. In practice, however, there are so many possible factors that might be relevant that it is easy to find some factor that has a high correlation with past recruitment...It would probably be optimistic to expect the situation to change much in the immediate future.

The notion of Maximum Sustainable Yield occurring at an optimal abundance comes directly from the use of this model to optimize yield from a single stock (Ricker 1975). Justification for other harvest policies, such as harvest rate-based policies, is often based on stochastic simulation of this model (e.g., Deriso 1985, Hilborn 1985, and many other possible citations). Walters (1986) and others have elevated the search for stock-recruit parameters – which he assumed to be unchanging – into one of the most important objectives of fisheries management.

In the Kuhnian sense (Kuhn 1962), the Ricker stock-recruit curve is the paradigm of salmon management in Alaska, and little research on salmon harvest policy has gained popular acceptance outside the perimeters of this paradigm. Over 20 years ago, as influential an author as Larkin (1977) called for a model with a more realistic acknowledgment of the dynamics and vicissitudes of the real world – including genetics – and recommended the retirement of the Maximum Sustainable Yield concept. He appeared to have some effect on the use of this concept in scientific publications, but as of 13 years ago, not in the area of policy analysis (Barber 1988).

The basic – and usually unquestioned assumption – implicit in the search for unchanging stock-recruit parameters, is that the present – and especially the future – is part of the same statistical universe as the recent past. Many researchers are so focused on a stock-recruit analytic framework that they see no way to provide advice on harvest policy without this reference to past stock-recruit data. For example, Hilborn and Walters (1992, p 241) state, "Any model for such synthesis must ultimately be tested by comparing its predictions to the observed overall relationship between stock and recruitment, so in the end there is no way to escape analysis of the overall relationship." In other words, they insist that advice on stock size and predictions about recruitment is consistent with past stock-recruit patterns.

Using computer simulation of the Ricker stock-recruit law, some investigators have concluded that salmon populations should be intentionally managed for fluctuation. Their reasoning is that to increase yield, intentional stock fluctuation is important to gain contrast in stock-recruit data. In principle, additional contrast will then lead to a better understanding of fixed, unchanging, parameters of the stock-recruit law (e.g., Walters 1986). Other authors believe that some attribute related to predicted yield is the one that should actually be maximized. For example, Deriso (1985) used economic arguments to recommend that the logarithm of the predicted yield should be maximized, and that this objective requires greater fluctuation in stock size than a fixed escapement policy provides.

It certainly seems that this generation of salmon scientists should be more concerned about having so much of their management advice based on a single optimization scheme – especially one that takes so little of the salmon's biology and life history requirements into account. Using Ricker stock-recruit relationships, Eggers (1993) showed that when management error is considered, harvest policies that increase stock-size fluctuation introduce an element of risk to yield not previously acknowledged. Schmidt et al. (1997) pointed out that fixed harvest rate-policies, which some authors have advocated based on simulations of Ricker stock-recruitment law, increase stock fluctuation and that this offers risks that cannot be uncovered or even understood by the study of theoretical stock-recruitment relationships. Snedaker and de Sylva (1994) showed how subtle the difference is between humorous parody and serious scientific advice when talking about the extremely narrowly focused optimization in fisheries – without regard to risk or obvious dangers.

By the 1990s, biologists were beginning to pay attention to the previously unobserved variability in the marine environment, and they were beginning to speculate on the role this variability had on fish populations (Quinn and Marshall 1989, Marshall 1992, Beamish and Bouillon 1995, Hare and Francis 1995, Adkison et al. 1996, Mantua et al. 1997, Gargett 1997, Beamish et al. 1998, and many others). In any event, some of the new thinking about salmon recruitment has shifted away from models that emphasize average recruitment and models that emphasize limitations in the freshwater environment, towards explaining variation induced by ocean-climate dynamics. Recent work on the concept of the regime shift shows why the Hilborn and Walters approach of validating a model for future production solely on the production pattern of the recent past should not be unquestioningly accepted. An extreme and untested hypothesis suggesting a possible need to unlink past and future stock-recruit patterns was put forward by Welch et al. (1998). Their hypothesis states an ocean environment hospitable to salmon will contract in the coming years due to global warming. Under this hypothesis, some Pacific salmon populations will undergo a steady decline in productivity. If Welch and his colleagues are correct, then a study of stock-recruit patterns using only past relationships will provide poor advice for the future, and the past relationships will overstate future production. A more plausible hypothesis, such as that put forward by Beamish et al. (1998), is that even if recruitment is controlled over short periods by a common stock-recruit function, these functions change at random, unpredictable intervals as a result of atmospheric forcing.

Beyond recognizing a need to maintain spawning stock size, habitat, and a vague recognition of the need to preserve productive stock groups, the actual mechanics of how surplus production is generated does not fit into current recruitment theory. Even though many authors have speculated that fishing may cause genetic changes, and therefore affect future yield, Conover and Munch (2002) have demonstrated "Darwinian consequences of selective harvest" in captive fish. Moreover, acknowledging that a changing environment plays a major role in yield trends is only now coming into fashion.

Although Kapuscinski and Lannan (1986), Gauldie (1991), Policansky (1993), and possibly others have attempted conceptual models of genetic fitness for fisheries managers, I know of no practical translation of genetic principles into specific advice about salmon harvest policy. However, over the last 100 years an enormous amount has been learned about salmon biology, salmon management, and the consequences of various policy actions.

Population Genetics and Salmon Management

Population genetics is the study of gene frequencies in a population of plants or animals, together with the study of the dynamics of those frequencies in the population over time. Fisher (1953) went so far as to suggest that from the genetics perspective, "The frequencies with which the different genotypes occur define the gene ratios characteristic of the population, so that it is often convenient to consider a natural population not so much as the aggregate of living individuals as a aggregation of gene ratios." A more fashionable term for the field of genetics that deals with the genetic dynamics of exploited populations in a changing environment would be *conservation genetics*, although I will use the older and more general term, *population genetics* to include both fields. Not surprisingly, much of genetic theory is based on simple probability theory, involving the sampling of dichotomous states (i.e., the binomial and similar probability distributions for discrete outcomes).

Fishery management is the application of scientific principles to the enterprise of fishing so as to bring about specific objectives. In their review of "genetics and fishery management" Allendorf et al. (1987) begin by noting that one of the most commonly used textbooks on the principles of fishery management has no chapter on genetics, and that genetics is only mentioned in the context of selective breeding of hatchery fish. So, as of 15 years ago, and probably today, the principles encompassing population genetics have not been well integrated into the field of fishery management.

Even so, fishery scientists have long been interested in blending genetics principles into fishery management and incorporating genetic principles into explanations of fish population dynamics. As influential an author as Larkin (1977) called for more biological realism in recruitment models by bringing in genetic concepts. This effort to incorporate genetics into population dynamics models has not been restricted to fisheries science (see, for example Lotka 1925, or Felsenstein 1988).

The field of genetics has had several important successes in supplying fisheries management tools for addressing mixed stock problems. Shacklee et al (1999) reviewed the use of genetics in Pacific salmon management. The development of large, shared databases of allozymes (allele forms that can be distinguished by protein electrophoresis) has proven to be an important tool for looking at the stability of gene frequencies, for looking at evolutionary history, and determining migration and straying patterns (Utter et al. 1987). More recently, DNA techniques are allowing population geneticists a means to look at reproductive isolation and gene flow and reproductive success (for example, Hendry et al. 2000 and Hendry 2001). Waples (1995) describes how genetics has provided tools for salmon recovery in the Pacific Northwest.

Population geneticists have made progress studying the Pacific salmon and other fishes, and geneticists have influenced the field of fishery management by contributing several important organizing concepts. One of the earliest and most important contributions of population genetic principles to fishery management was the development of the stock concept (reviewed by Geiger and Gharrett 1997), and the subsequent principle that phenotypic variation among stocks is partially genetically based, and that those differences should be preserved, to keep different habitats "productive." This provided a shared objective for population geneticists and fishery managers: the study of the differences among stocks, and a shared goal of maintaining the genetic basis for those differences.

One of the important concepts that will appear repeatedly in the following chapters is the idea of the *effective population size* (Wright 1931). One form of the basic idea can be developed from the notion that the frequency of alleles in a population will be affected (through sampling) by the size of the breeding population. That is, if breeding is random and mortality processes are independent of allelic states, then the frequency in a subsequent generation is approximately controlled by a binominal sampling process: if the frequency of some allele is p, and there are N_t individuals in the population, then the next generation will be formed from sampling the $2\ N_t$ total alleles, for a diploid species. If there are N_{t+1} individuals in the next generation, we might assume that the variance of the frequency in this next generation is $p(1-p)/(2\ N_t)$, based on the binominal distribution. Alternatively, we might admit that mortality, breeding, and family size is not random, so that the frequency of genes in the next distribution is more variable than the binomial distribution predicts. Wright introduced the quantity N_e, such that $p(1-p)/(2\ N_e)$ gives the actual variance of the allele frequency due to sampling from one generation to the next. To distinguish this form of effective population size it is called the *variance effective population size*. Note that for very, very large values of N_e the gene frequencies will not be influenced very much by the effects of sampling. However, for small values of N_e the gene frequencies will change due to sampling. This change in small populations is called *genetic drift*.

The way in which inbreeding distorts genetic frequencies is another line of population genetics inquiry. The Hardy-Weinberg principle is the name of an outcome from binominal probability theory that states that if the frequency some allele is p, under purely random sampling of genes from one generation to the next, the underlying mean proportions of genotypes will be given by p^2, $2p(1-p)$, and $(1-p)^2$. Inbreeding distorts these ratios. Wright (1931) formulated the problem, introducing a quantity f so that with inbreeding, the expected proportions of genotypes is given by,

$p^2(1-f)+fp$, $2p(1-p)(1-f)$, and $(1-p)^2(1-f)+f(1-p)$.

Wright also realized that groups of inbreeding animals might interact by exchanging migrants. He introduced the quantity m, which is the fraction of the population that is replaced by migrants. Then $N(1-m)$ is the number of breeding animals that originated in the population, and Nm is the number of migrants. Wright's f is related to m in that if m^2 is small, then

$$f \approx \frac{1}{4N_e m + 1}.$$

One important result this theory offers is that if m is much larger than $1/(4N_e)$, the subpopulation is essentially panmictic with the source of the migrants (Crow and Kimura 1970).

Then the quantities f, N_e, and other genetic quantities provide a means to conceptually describe how gene frequencies might change because of small population effects; m provides a means to conceptually describe how these frequencies might be stabilized by connecting small subpopulations into larger, linked metapopulations.

One of the other central organizing concepts of population genetics is the idea of *selection*: the process by which nature or man samples genes from one generation to the next in a way that favors some genes or gene combinations, and disfavors others. A closely related concept is that of *fitness*: the relative success an animal has at transmitting his or her genes to the next generation. In natural populations, selection acts on the actual physical characteristics of the animals: the phenotypes. The proportion of the phenotypic variation that is caused by additive genetic effects is called the heritability, h^2.

When considering the population as a whole, the random quantity w is called the *Darwinian fitness* (Crow and Kimura 1970), and it is defined such that

$$N_{t+1} = N_t w_t.$$

Darwinian fitness derives from $w_{AA}N_{AA} + w_{Aa}N_{Aa} + w_{aa}N_{aa}$ (i.e. depends on genotypic frequencies and their fitness) with AA, Aa, and aa denoting genotype. If we define w_t^* as the multiloci extension over the entire genome, then note the similarity with the Ricker stock-recruit curve:

$$N_{t+1} = N_t\alpha\exp(-\beta N_t + \varepsilon_t),\ \text{such that } \varepsilon_t \sim N(0,\sigma),\ \text{cov}(\varepsilon_i,\varepsilon_j)=0,\ \text{and } \sigma>0.$$

Then the two theories intersect when $w_t^* = \alpha\exp(-\beta N_t + \varepsilon_t)$, although in the fisheries model the stock sizes prior to year t are irrelevant (for fixed α and β), whereas in the genetics model, much of the theory has to do with how past values of f, m, and especially N_e and the gene frequencies determine the value of w_t^*, for a particular environment. To combine population genetics and fishery population dynamics models an obvious starting point is break the Ricker multiplier into parts, and to allow α to be a time-dependent summary of the state of the stock. Letting θ_t denote a summary of the genetic information in the population at time t, then letting $\alpha(\theta_t)$ denote a factor for the underlying stock productivity (as a function of the stock's history), letting $\exp(-\beta N_t)$ denote a pure density-dependence factor, letting $\exp(\varepsilon_t)$ denote a random shock, then the population dynamics model could be joined with the genetics model. That is, $\alpha(\theta_t)\exp(\varepsilon_t)$ could be modeled to describe (1) the year-t genetic state of the population, (2) a random environment, and (3) an interaction between the genetic state (the allele frequencies) and the environment (and associated fitness) that will produce a new genetic state for year $t+1$.

Wright's writing in the 1930s was very much directed at examining the effects of genetic drift, while the other major figure of early 20th century genetics, Fisher, was more concerned about the effects of selection. A final population genetics concept that is relevant to the following chapters is Fisher's fundamental theorem of natural selection: rate of adaptive change in a population is proportional to the amount of genetic variation present (Price 1972). What this would seem to imply is that traits that are very important for fitness would have very little genetic variation, as these traits would have already been heavily selected for, draining the population of variation. Lande and Barrowclough (1987) stated, "Typical levels of heritability for many traits are of the order of 0.3 to 0.7;

however, for traits closely related to fitness, e.g., viability, litter size, etc, heritability values are often considerably lower."

Effective population size is one of the key concepts in 20th century genetics, and there is an enormous body of empirical work demonstrating its practical importance, starting with the work of Wright's collaborator, Dobzhansky, in the 1930s (see, for example, Lewontin et al. 1981), and in the field of salmon management see Waples (1990). While population size obviously has a role in a population's extinction probability (e.g., Ginzburg et al. 1982, Dennis et al. 1991, Wissel and Stocker 1991, and many others), authors such as Lande and Barrowclough (1987) formulated rules for the management of populations based on the effective population size. Many scientists studying salmon acknowledge the importance of the effective population size, but there is no consensus about specific, concrete advice to give fishery managers. Waples et al. (1990) stated "There are a variety of opinions regarding the minimum acceptable value of N_e, ..., almost certainly there is no single number that would apply to all species."

Population geneticists have had a very hard time making very specific predictions about effective population size in wild fishes, and then observing whether or not the predictions came true. Fish are mobile, very hard or impossible to distinguish individually, and unavailable for observation during most of their life. Mate selection, mortality and fitness processes, environmental change, inbreeding, are all essentially unobservable, as are fine-scale genetic relationships. Population geneticists are able to make extremely accurate predictions based on theory that has been validated on populations of *Drosophila sp.*, and other species, once values of key genetic parameters are known. However, in the case of salmon these parameters not usually known, and most specific predictions are unobservable as well. This has resulted in a lack of simple, easy-to-apply genetics procedures for fisheries management – although genetics has had outstanding success recommending simple procedures to the fields of animal husbandry and plant agriculture.

In contrast, fisheries management has recommended simple procedures such as Ricker analysis (Quinn and Deriso 1999), and the field of fisheries management has received widespread acceptance of these procedures within their own discipline. Moreover, academies have trained a large corps of technicians who are applying these procedures. It is unlikely that any omnibus procedure will be able to compete with the Ricker analysis for simplicity, ease of training technicians to carry out the mechanics, and the low cost of implementation. Still, fishery science should feel some embarrassment for not being more questioning about the limits of this technique, and not being more interested in the robustness of the advice it gives. My goal is to direct just a little attention away from the search for the underlying, stable, unchanging structure in salmon recruitment, and try to have a new look at the variation.

The Following Chapters

This dissertation began as three somewhat distinct studies of pink salmon biology and recruitment. The first was an examination of the effects of the Prince William Sound oil spill, the second a reanalysis of a very interesting and unique data set concerning family-specific marine mortality, and the third was a reanalysis of laboratory breeding studies. The Price William Sound study led to the first chapter, which started as an attempt to synthesize several studies about the oil spill's effects on wild pink salmon populations. Because pink salmon are so very hard to study in the wild, this study relied on average life history measurements from the literature, which stood in for unknown values or as benchmarks to see if our measurements seemed reasonable. In the end, one of the main outcomes of this study was an attempt to describe the average life history situation for Prince William Sound pink salmon. The second study started out as an attempt to characterize some average genetic parameters. The effective population size, which is discussed in detail in Chapters 3 and 4, is one way to quantify how much genetic variability a breeding population can hold. The ratio of effective population size to census population size can be very useful thing to know when making recommendations about population recovery, for example. This study was motivated by the thought that in the absence of specific information about a particular population, average values of this ratio for pink salmon might be useful to conservation biologists. But while working on

Chapter 3, my focus changed from characterizing averages to characterizing variation. Chapter 4 then became an attempt to have a glimpse at the answer to the question, why does family size vary? Of course, family size can vary for many reasons, which can change over time, and no attempt at this question can result in a full and complete answer. Still, an incomplete look at variation, in a few very specific cases, is progress. Whereas Chapters 2 through 4 are studies into pink salmon biology, in Chapter 5 I try apply this study of why things vary to the current canons of salmon management – especially to Ricker analysis. Finally, I will conclude by reflecting on the role of policy, and to the threats to sustainability of salmon in Alaska. My goal in this undertaking is to have a small glimpse into the biological underpinnings of pink salmon recruitment process, and contrast the guiding principles of salmon harvest management with what has recently been learned about the role of change and instability in recruitment.

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...One of our biologists was unable to find a single juvenile salmonid life form in Prince William Sound this spring.
— Former commissioner of Alaska Department of Fish and Game describing
the situation in Prince William Sound, following the Exxon Valdez oil spill

CHAPTER 2 -- A LIFE HISTORY APPROACH TO UNDERSTANDING PRINCE WILLIAM SOUND PINK SALMON[1]

INTRODUCTION

In the confusion following the *Exxon Valdez* oil spill, anything from no effect to devastation of pink salmon (*Oncorhynchus gorbuscha*) populations in the southwestern part of Prince William Sound seemed plausible. In the weeks following the spill, the Alaska Department of Fish and Game and the National Marine Fisheries Service initiated several studies to 1) develop improved estimates of pink salmon escapement for pre- and post-spill years, 2) measure egg (embryo) survival, 3) measure fry survival, 4) observe the near-shore condition and distribution of fry in Prince William Sound, 5) measure

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[1] This chapter is adapted from Geiger, H.J., B.G. Bue, Sam Sharr, A.C. Wertheimer, and T. Mark Willette. 1997. A Life History Approach to Estimating Damage to Prince William Sound Pink Salmon From the *Exxon Valdez* Oil Spill. *In* Rice, S.D, R.B. Spies, D.A. Wolfe, and B.A. Wright [eds.] *Exxon Valdez* Oil Spill Symposium Proceedings American Fisheries Society Symposium 18.

hatchery and wild salmon survival in the saltwater environment, and 6) survey the pink salmon habitat affected by the oil spill.

These studies have now documented contamination of embryos in oiled streams (Wiedmer et al. 1995), and juvenile salmon in the nearshore environment (Carls et al. 1995). The contamination has been linked to reduced survival in embryos in oiled streams (Bue et al. 1995) and to reduced growth of pink salmon in the marine environment (Willette 1995; Wertheimer and Celewycz 1995). The reduced growth in the early marine environment has, in turn, been linked to reduced marine survival (Willette 1995). Here, I synthesize the results of these studies of individual life history stages and estimate the loss of returning wild adult Prince William Sound pink salmon in years following the oil spill.

Pink salmon populations in Prince William Sound are not static. Powerful forces that may have affected them in recent years include the Alaskan earthquake of 1964, an increasingly intense commercial fishery, tremendous increases in hatchery production, and the *Exxon Valdez* oil spill. The earthquake of 1964 severely damaged some stocks and eliminated some runs entirely (Roys 1971). In the mid-1980s, large runs of hatchery-produced pink salmon began to equal and then far outnumber the wild salmon. Hatchery stocks are an important input to the commercial fishing industry, but from an ecological perspective, they are entirely different from the wild salmon. I focus on the wild salmon, which play an important role in the Prince William Sound ecosystem and an important economic role in the Prince William Sound fishing industry.

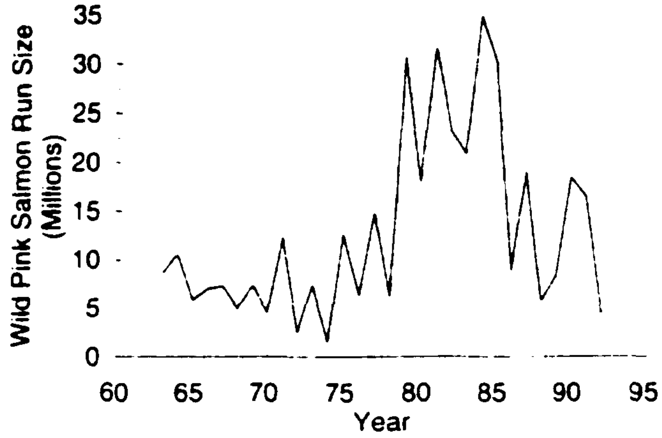

Figure 2.1. The estimated size of Prince William Sound wild pink salmon from 1963 to 1992.

The size of pink salmon runs to Prince William Sound has fluctuated wildly (Figure 2.1) in response to unobserved phenomena in the freshwater and marine environments. With this much background variability, even extremely large damage would be entirely undetectable using before-and-after comparisons of any function of population size. To gain statistical power I focused on the affected life history stages, looking for differences in life history statistics between groups of fish classified as oiled and unoiled in the same year. I refer to the summary of the life stage comparisons as the life history model.

I followed the 1988 brood year by estimating parental escapement, survival to emergence, and survival to emigration in 1989, measuring growth and survival of coded-wire tag groups as they migrated through the oil in the near-shore environment in the spring of 1989, and by measuring their final return numbers in 1990. I then continued with the odd-year line: following the 1989 brood year as they incubated in the oiled and unoiled streams in Prince William Sound, migrated in the relatively unoiled near-shore areas in 1990, and returned in 1991. The 1990 through 1992 brood years were followed in a similar manner up to the summer of 1992. At each life stage for the 1988 through 1992 brood years I summarized the evidence that the presence of oil reduced survival, and the evidence that a survival reduction was translated to reduced survival at the adult life stage as well. Figure 2.2 illustrates the life history pattern for pink salmon, showing the life stages, and points where oil detectably reduced survival in wild pink salmon.

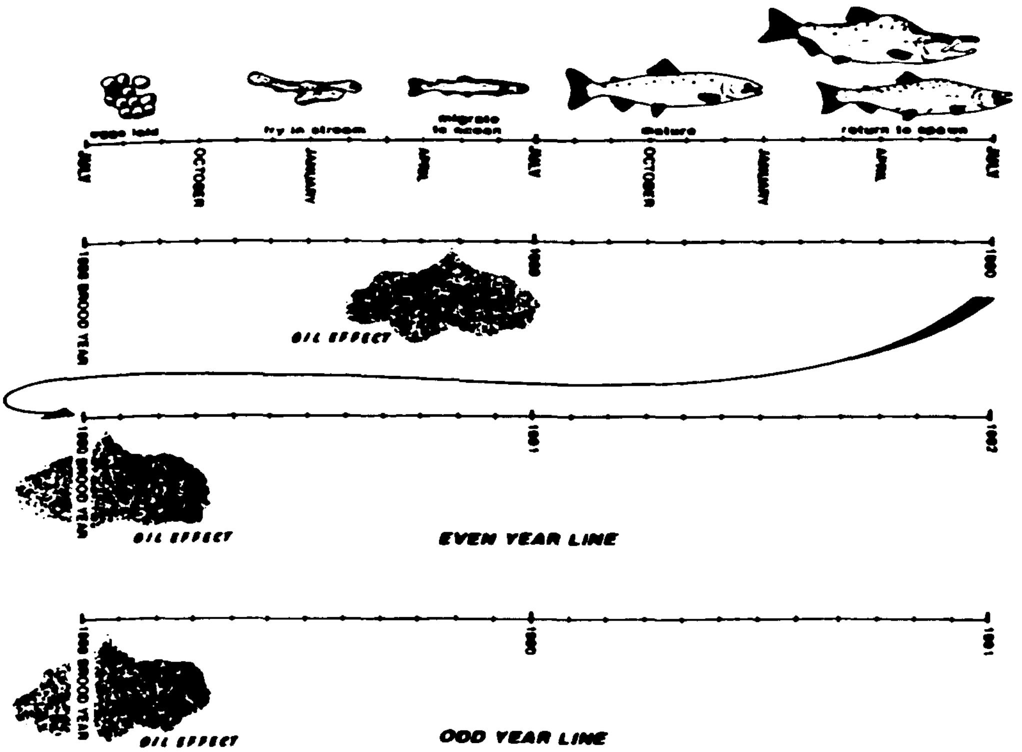

Figure 2.2. Pink salmon life history stages, with stages affected by oil denoted. "Oil effect" denotes detected effect at that lifestage.

If the oil spill reduced survival at an early juvenile life stage, the final return of adult salmon could have remained unaffected because of compensatory mortality: mortality that increases when density is high, and decreases when density is low. In her review of the pink salmon literature, Alexandersdottir (1987) cited Heard's (1978) work in Sashin Creek in Southeast Alaska in 1967 and Donnelly's (1983) work in Kodiak to conclude compensatory mortality was linked to an overabundance of spawners, and density-dependent survival could be a factor from spawning to outmigration.

If compensatory mortality effects are negligible at a particular lifestage and all subsequent lifestages, then estimating the effects of the oil spill are straightforward: the estimated proportional loss of production can simply be the measure of decrease in estimated survival at that lifestage. Alternatively, if compensatory mechanisms exist, the loss of production from the oil spill will be overestimated by assuming oil-induced mortality translates directly into reduced adult production. I examined the available evidence that compensatory mortality could be caused by oil-induced loss of production.

The effect of the *Exxon Valdez* oil spill on any important part of the biota will never be known exactly. Unfortunately, the failure to precisely measure injury from the oil spill is sometimes confused with justification for concluding the injury is nonexistent. Similarly, the ability to statistically detect some aspect of injury is sometimes confused with significance in a larger biological sense. Rather than perform a statistical test of the hypothesis that pink salmon populations were completely unchanged by the oil spill, I viewed my responsibility as to identify the biologically -- not statistically -- important sources of mortality, and provide the most reasonable estimates of the magnitude of loss, in units of adult salmon, consistent with the information available to us.

METHODS

Prince William Sound Fishing Districts, Stocks and Stock Size Estimates

Prince William Sound is divided into nine fishing districts, which correspond to stocks for the purposes of fisheries management (Figure 2.3). In much of the discussion, I will be restricting our focus to the Southwest Fishing District, where the greatest damage to freshwater spawning habitat occurred (Middleton et al. 1992). I used total production and revised estimates of district-specific escapement from a database maintained by the Alaska Department of Fish and Game in Cordova, Alaska. The data were the most current as of June of 1993.

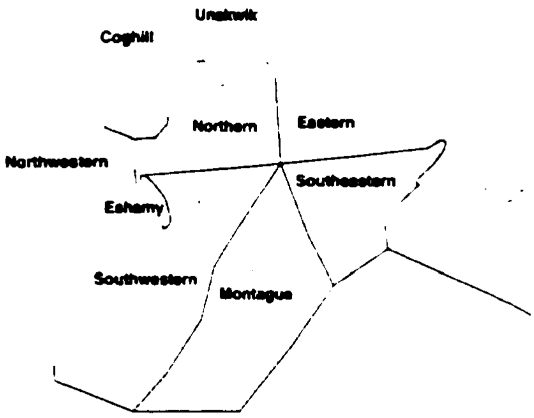

Figure 2.3. Map of Prince William Sound showing the fishing districts.

Life History Parameters, Statistics, and Estimators

Let y_{t+2} represent the subsequent Prince William Sound wild pink salmon production in year $t+2$ from an escapement of x_t spawners in brood year t. Let s_t represent the random variable that summarizes survival and fecundity. This is commonly called return per spawner and is usually expressed as some function of previous escapement (e.g., Ricker 1975). I was interested in the life history steps underlying the return per spawner when escapement has been restricted to approximately what managers considered optimal. Formally, the process is described by

$$y_{t+2} = s_t x_t \, . \qquad (2.1)$$

In year $t+2$, Prince William Sound salmon management attempts to harvest all of the return except a fixed escapement goal, x_{goal}. Due to management error, the actual escapement is x_{t+2}, and the process repeats.

In years when the oil spill reduced survival, let p_t be the fraction of the total number of eggs from brood year t that were potentially affected by oil sometime in their life. Let s'_t be the return per spawner reflecting the reduction due to the oil spill, including the effects of compensatory mortality.

In years when a fraction of the potential production is reduced by an oil-spill effect, I assumed production was given by

$$y_{t+2} = [(1 - p_t)s_t + p_t s'_t]x_t . \qquad (2.2)$$

Notice the quantity $(1-p_t)$ is the fraction of eggs unaffected by oil. s_t is the return per spawner, so that $(1-p_t)s_t x_t$ denotes the production from unoiled streams; similarly, $p_t s'_t x_t$ denotes the production from oiled streams, and production from both sources equals the total production.

In actual practice, managers observe $\hat{x}_t$, some function of x_t, where the function describes observational error. Similarly, $\hat{y}_{t+2}$ denotes the estimated total run, consisting of the catch, which is approximately known, and the estimated escapement.

To estimate parameters, I first assumed no strong compensatory mortality mechanisms, or at least no compensatory mortality after the affected life stage. Without reference to stochastic models, I estimate parameters in equations (2.1) and (2.2) algebraically: assuming that s'_t is approximately equal to s_t multiplied by the estimated amount survival was reduced.

Letting r_t denote the survival in oiled areas expressed as a fraction of potential survival at each affected life stage, estimates of s'_t and s_t were found as follows by replacing elements in equation (2.2) with their estimates and solving,

$$\hat{s}_{t'} = \hat{s}_t \hat{r}_t ,$$

and, then from (2.2),

$$\hat{s}_t = \frac{\hat{y}_{t+2}}{\hat{x}_t}((1 - \hat{p}_t) + \hat{p}_t \hat{r}_t)^{-1} .$$

Production, expressed in units of adult salmon that would have returned had there been no oil spill, was then estimated by

$$\hat{y}_{nooil\,t+2} = \hat{s}_t \hat{x}_t ,$$

and the estimated loss in broodyear t, at the adult population level, is given by

$$\hat{L}_t = \hat{y}_{nooil\,t+2} - \hat{y}_{t+2} .$$

To estimate typical values of s_t, for the purpose of projecting future production from the 1991 and 1992 escapements, I considered the median recruits-per-spawner from

1963 to 1987. Information on the steps that lead to s_t from the pink salmon literature was used to provide additional justification for this estimate. Five stochastic steps lead to the return-per-spawner value, s_t: 1) the fraction of the run consisting of females, denoted Fem_t, 2) the average fecundity per female, denoted Fec_t, 3) the fraction of the potential egg deposition that is actually deposited, denoted Dep_t, 4) the survival from eggs deposited to emergence, denoted Seg_t and 5) the marine survival, denoted Smr_t. The overall return per spawner, s_t, is simply the product of each of these stochastic outcomes:

$$s_t = Fem_t \, x \, Fec_t \, x \, Dep_t \, x \, Seg_t \, x \, Smr_t \, . \tag{2.3}$$

The Fraction of the Potential Egg Deposition in Oiled Streams

Estimates of the fraction of eggs in oiled streams were obtained by estimating the fraction of streams affected by oil and adjusting for the relative egg density in oiled streams. I assumed that only streams in the Southwest Fishing District were affected, ignoring some oiling on Montague Island and elsewhere.

To estimate the fraction of pink salmon spawning streams affected by oil, I needed a sample of streams with information on oiling level and information on egg density for each stream in the sample. In 1991, the aerial survey of spawning escapement was expanded to include a representative sample of oiled and control streams. To determine which streams in the 1991 aerial survey were affected by oil, I referred to Middleton et al. (1992), personal field observations, and conversations with other observers. In general, if a stream was classified as *Heavy* through *Very Light* in Middleton et al. I considered it an oiled stream. In cases where Middleton et al. disagreed with our field observations, I relied on our observations. The peak spawner density from this survey was used as a proxy for the egg density in each stream in this survey. To estimate the fraction of the potential egg deposition in the Southwest Fishing District that incubated in oiled streams, I calculated the weighted average of the proportion of streams classified as oiled in the 1991 survey, using the peak aerial escapement count in the 1991 aerial survey as the weights. Then, to estimate the fraction of the entire potential egg deposition in the whole sound affected by oil, I multiplied this weighted average by the fraction of the entire escapement that was in the Southwest Fishing District.

Oil-Induced Mortality in the Freshwater Stage

Let m_v be the underlying mortality rate of juveniles, at some life stage, with oiling level v. If this is the only affected lifestage, then the ratio of survival at each lifestage to the potential survival, defined as r above, is found by

$$r = \frac{(1 - m_{oil})}{(1 - m_{unoil})}. \tag{2.4}$$

To estimate *r*, I substituted the unweighted estimated average mortality in the embryos into equation (2.4), using data described in Bue et al. (1995). Average mortality was not weighted by total eggs deposited at tide stage because estimates of total eggs deposited by tide stage were unavailable to us.

Table 2.1. Estimated overall embryo mortalities from oiled and control sites in Prince William Sound, with estimated percentage reduction in survival in oiled areas, by brood year. The estimates are based on unweighted average mortalities by tide stage from data described in Bue et al. (1995).

Brood Year	Oiled Sites	Control Sites	Survival in Oiled Areas as Percent of Potential Survival
1989	0.174	0.104	92%
1990	0.295	0.195	88%
1991	0.433	0.221	73%
1992	0.450	0.250	73%

The Fraction Exposed in the Early Marine Stage

The fraction of eggs that could eventually be affected by exposure to oil in any life stage up through the early marine environment was the most difficult parameter to estimate. In the end, I simply used the estimated fraction of the 1988 escapement that was in the Southwestern Fishing District, knowing that fry that emerged anywhere in the Southwestern Fishing District in 1989 were a short distance from exposure once they emigrated into the marine environment. I know from Willette (1995) that some fish from unoiled areas emigrated into oiled marine areas and vice versa.

RESULTS

Willette (1995) estimated that fry from unoiled areas that reared in oiled near-shore environments in 1989 experienced a marine survival of 72% of their unoiled potential, based on coded-wire tagging studies from the Wallace H. Noerenberg Hatchery.

I estimated that the survival from egg deposition to the fry stage was 92% of its potential in oiled areas for the 1989 brood year, and 88% of its potential for the 1990 brood year (Table 2.1). Bue et al. (1995) found statistically detectable excess mortalities in the eyed-embryo stage, which they attributed to oil-spill effects, but they failed to find statistically detectable effects in the pre-emergent fry stage of development. The estimates of the proportional reduction in survival of oiled eggs, relative to control eggs, together with estimates of overall embryo-stage mortality for oiled and unoiled streams are provided in Table 2.2. Statistically detectable elevated mortalities were also noted by Bue et al. (1995) between oiled and unoiled sites for the 1991 and 1992 brood years.

Three pink salmon life stages were judged to have had a measurable oil-spill effect (Figure 2.2).

Based on the field surveys, I estimated that the fraction of pink salmon spawning streams contaminated with oil was 31% of all spawning streams in the Southwest Fishing District. Unoiled streams had larger average peak escapement counts than oiled streams, meaning that 31% may overstate the proportion of eggs affected in the Southwest Fishing District. When I used peak spawner density from the 1991 aerial escapement survey as a proxy for egg density, as described above, an estimated 20% of the potential egg deposition in the Southwest Fishing District was associated with streams classified as oiled. Using escapement information to estimate the fraction of the potential egg deposition in the entire sound potentially affected by oil in the freshwater stage, the estimate never exceeded 6% of the eggs (Table 2.2).

Estimated Adult Salmon that Failed to Return

In 1990, total production of wild pink salmon was estimated at 18.40 million from an escapement of 4.99 million in the 1988 brood year. I assumed that 32% of the potential 1988 brood year was exposed to oil effects, using the proportional escapement in the Southwest Fishing District, as described above. Based on the observed reduction in marine survival of coded-wire tagged fish from Willette (1995), I estimated the proportional reduction in survival was 72%, as described above. Substituting these estimates for the appropriate quantities in equation (2.2) yields

$$18.40=((1-0.32)s_{1988}+0.32(s_{1988}\cdot 0.72))\cdot 4.99.$$

Solving for s_{1988} produced an estimated return per spawner in the absence of oil of 4.06. Applying this return per spawner to the 1988 escapement produced an estimate of 20.26 million adults that would have returned in the absence of oil. By subtraction, the estimated loss of adult pink salmon in 1990 was approximately 1.86 million. Key statistics and results for the 1988 through 1991 brood years are provided in Table 2.2. Using the same reasoning, I estimated that the loss of adult pink salmon was approximately 60 thousand and 70 thousand for the 1989 and 1990 brood years, respectively.

Table 2.2. Estimates of oil spill-induced losses of adult production with other important statistics for brood years 1988, 1989, and 1990; the expected future losses for brood years 1991 and 1992 are based on the assumption that the genetic damage hypothesis is correct. Losses are expressed in units of million adults that fail to return two years following the brood year. The estimated return per spawner is the estimate for what would have been possible without the oil spill. Estimated production is for all of Prince William Sound.

	Estimated for Broodyear			Projected for Broodyear	
Statistic	1988	1989	1990	1991	1992
Soundwide Escapement (millions)	4.99	6.89	6.18	9.66	2.71
Escapement to Southwest District (millions)	1.61	1.91	1.77	2.21	0.81
Subsequent production (millions)	18.40	16.54	4.50	---	---
Estimated return per spawner in absence of oil	4.06	2.41	0.74	1.79[2]	1.79[2]
Percent of PED potentially affected by oil	32%	6%	6%	5%	6%
Estimated survival of oil-affected fish relative to non-oiled fish	72%	92%	88%	73%	73%
Estimated production without oil spill effects (millions)	20.26	16.60	4.57	17.30	4.85
Estimated loss of returning adult fish (millions)	1.86	0.006	0.07	0.24	0.08
Loss as percent of potential production in Southwest district	28%	1%	6%	6%	5%

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[2] Median value for brood years 1963 - 1987

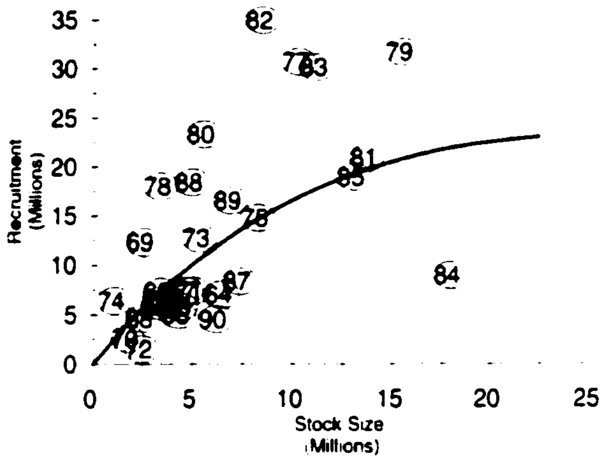

Figure 2.4. Stock-recruitment history for Prince William Sound pink salmon. The numbers denote the brood year.

Compensatory Mortality

I found no evidence that compensatory mortality mechanisms operate on the scale of variation induced by oil-spill effects. Figure 2.4 shows the new stock-recruitment history using the revised estimates of escapement. Although compensatory mortality mechanisms may control production in Prince William Sound at escapement extremes – such as when escapement reaches 20 million – for the important brood years of 1988, 1989, and 1990, the escapement remained very near what managers have traditionally thought of as optimum (the escapement goal in the old index-units can be found in Geiger and Savikko 1991; an escapement goal has not yet been formulated in the units of the revised escapement estimates).

To see if compensatory mortality was operating during the embryo stage, I examined estimated egg survival, up to the time the survey was conducted, as a function of observed egg density for 1989, 1990, and 1991. Although some slight compensatory mortality might have occurred as densities exceed 2,500 eggs per unit of surface area (0.186 m^2) in the lower tide stages in 1989, overall no strong compensation was observed. I was unable to detect a relationship between egg density and the empirical logit (Agresti 1990) of the egg survival (analysis of covariance, *P-val* = 0.3135) after adjusting for year, tide stage, and oiling level.

If oil-induced mortality is strongly compensated for in the pre-emergent fry stage, then the proportion of live fry would be strongly inversely related to the proportion of live eggs. Figure 2.5 shows this relationship for the 1989 through 1991 fry dig studies. These graphs show considerable mortality and variation in mortality from site to site, yet the measured mortality is low in the fry stage, irrespective of the mortality between egg deposition and the fry stage. Thus, no compensatory mortality was seen in this life stage.

To look for compensatory mortality in the marine life stages, I examined Prince William Sound pink salmon hatchery production as a function of fry released (from data supplied by Doug Eggers, Alaska Department of Fish and Game, and recent estimates from Prince William Sound hatchery operators). The number of fry emigrating from freshwater systems shows a strong linear relationship to the number of returning adults, within the range of 0 to approximately 600 million hatchery fry (Figure 2.6). The slope of a smooth line through these data is approximately 5% – a reasonable average survival for pink salmon (Heard 1991). These data indicate no compensatory survival mechanisms in the marine lifestages.

In summary, I found no evidence that oil-induced mortality in either the freshwater or the marine environment would be compensated for by density dependent mechanisms in Prince William Sound pink salmon populations.

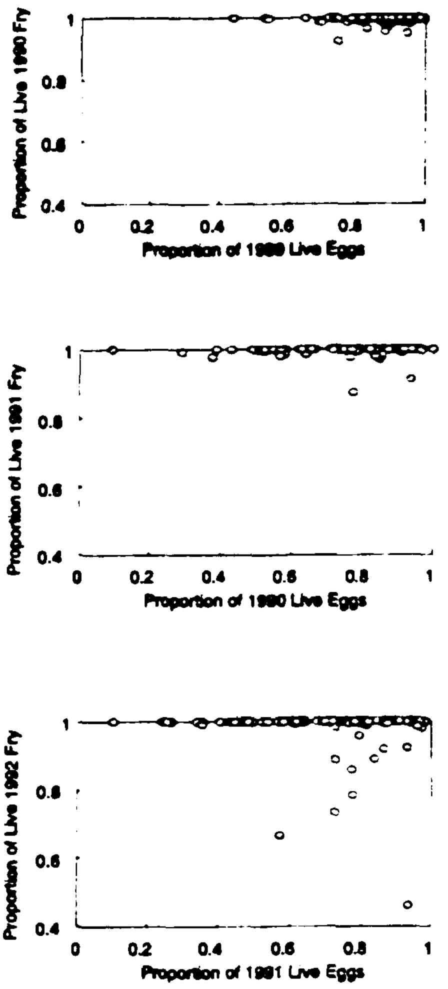

Figure 2.5. Proportion of live fry paired with the previous proportion of live eggs for years 1989 through 1991.

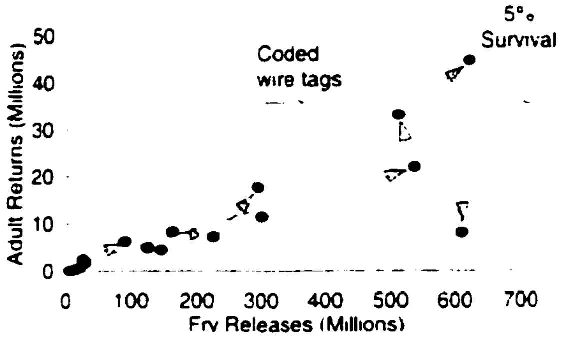

Figure 2.6. Production of pink salmon from Prince William Sound hatcheries as a function of fry released from 1975 brood year to 1990 brood year. Arrows denote time sequence of the observations. Coded-wire tags were first introduced into the estimation process for the 1985 brood year.

Typical Life History Values and the 1991 and 1992 Brood years

The annual return per spawner is a random variable in equation (2.1). This random variable results from the realization of five previous stochastic steps, as described above. Table 2.3 shows our best estimate of approximate typical values for life history parameters at each of these steps from various sources in the pink salmon literature, and from post-spill, unpublished coded-wire tagging studies of wild pink salmon (data available from the Alaska Department of Fish and Game, Cordova, Alaska). These estimates led to the impression that typically, about 1.65 recruits per spawner are generated from an escapement near the optimum level. Using the revised estimates of escapement, the median return per spawner from the 1963 to 1987 brood year was 1.79.

The life history parameters from Table 2.3 lead to a similar picture of the typical return-per-spawner values that have been observed recently in Prince William Sound. However, this image is quite different from the one based on previous escapement estimates (Heard 1991), where the typical return per spawner is thought to be closer to 4.0. I assumed 1.79 returns per spawner as a typical value, in the absence of oil-spill effects, for projection of future production at the time this report was originally prepared in June of 1993. The projected returns for the 1991 and 1992 brood years are 17.3 million and 4.9 million, in the absence of oil-spill effects. If the estimated egg-stage survival ratio between oiled and control areas represents persistent oil-spill effects, the projected return is reduced by approximately 240 thousand and 80 thousand for the 1991 and 1992 brood years, respectively.

Table 2.3. Life history survival and fecundity values from the pink salmon literature. Let *Fem* be the fraction of the run consisting of females, *Fec* the average fecundity per female, *Dep* the fraction of the potential egg deposition that is actually deposited, *Seg* is the survival from eggs to emergence, *Smr* is the marine survival, and $s_t = Fem_t\ Fec_t\ Dep_t\ Seg_t\ Smr_t$.

Life Stage	Conversion			Next Stage	Typical Value	Source
Escapement	times	*Fem*	=	*Females*;	*Fem* ≈ 0.5	Assumed
Females	times	*Fec*	=	*PED* ;	*Fec* ≈ 1875	Heard(1991)
PED	times	*Dep*	=	*AED* ;	*Dep* ≈ 0.44	Heard(1991)
AED	times	*Seg*	=	*Fry*;	Seg ≈ 0.20	Estimated by eye from data in Ignell (1988)
Fry	times	*Smr*	=	*Adults*;	*Smr* ≈ 0.02	Unpublished coded-wire tag data from M. Willette, ADF&G, Cordova, Alaska
Escapement	times	*s*	=	*Adults*;	s≈1.65	By multiplication

DISCUSSION

The studies I examined indicate that the *Exxon Valdez* oil spill did result in a detectable loss of wild adult pink salmon. That conclusion by itself is not of much value without some measure of the magnitude of the loss, and a context in which to view the magnitude. I estimated nearly two million adult pink salmon failed to return from the 1988 brood year in 1990 because of oil-induced mortality. This loss may have been over a quarter of the potential wild production in the Southwest Fishing District. Unless I have considerably underestimated the injuries in the 1989 and 1990 brood years, the loss of adult salmon was measurable, but small relative to other human-induced mortality, such as that caused by the commercial fishery. I concluded that the proportion of adult pink salmon missing from these brood years was less than 10% of the potential wild production in the Southwest Fishing District, and less than 2% of the potential wild production in the entire sound.

The 1990 pink salmon harvest was a record catch at approximately 44.2 million pink salmon (Geiger and Savikko 1991). The large harvest in 1990 legitimately helps makes the point that the *Exxon Valdez* oil spill did not devastate or cripple the commercial fishery following the year of the spill. However, the commercial harvest in 1990 is a poor indicator of effect of the oil spill on the wild pink salmon resource in the affected areas of Prince William Sound. The survival of the 1988 brood year was strengthened by favorable near-shore conditions for pink salmon fry – a conclusion based on measured zooplankton abundance (Jeff Olsen, Prince William Sound Aquaculture Corporation, personal communication). The size of the harvest of wild salmon is masked by the harvest of hatchery salmon, which provide a wholly different ecological role in Prince William Sound. Well before the oil spill, the total catch of salmon in Prince William Sound was expected to increase throughout the 1980s because of increasing hatchery production. In 1989, fry from the 1988 brood year of wild salmon were joined by 507 million hatchery fry, the second largest release of pink salmon fry into Prince William Sound at that time.

Even though the salmon hatcheries largely masked the effect of oil on the wild salmon resource that returned in 1990, the oil had a detectable effect on the hatchery resource as well (Willette 1995). Of the total 507 million hatchery pink salmon released in 1989, 160 million fry were from the Armin F. Koerning Hatchery, which sits just off the path of the oil in the southwestern portion of the Sound. Based on the observed growth reductions in Willette (1995), and based on Willette's size survival relationships, the potential loss of the hatchery resource in 1990 is in units of millions of adult salmon. The overall estimated survival for the 1988 brood year, which returned in 1990, was 4.24% for the Armin F. Koerning Hatchery. The survival at the Wallace H. Noerenberg Hatchery, a similar hatchery, but further from the path of the oil, had an estimated survival of 8.49% (unpublished data available from the Alaska Department of Fish and Game, Cordova, Alaska) – approximately twice as large. The estimated survivals in years without an oil influence for the Armin F. Koerning and Wallace H. Noerenberg hatcheries were 6.8% and 8.8%, respectively, in 1987 (Peltz and Geiger 1990); 4.52% and 4.99%, respectively, in 1991; and 2.08% and 0.94%, respectively, in 1992 (unpublished data). Although not compelling in themselves, these data certainly are not in conflict with presumed large numbers of missing adult salmon that would have returned to the Armin F. Koerning Hatchery in 1990.

We also concluded that some wild adult salmon that would have returned in 1991 and 1992 from the 1989 and 1990 brood years were lost due to the oil spill. The primary mechanism of the loss was decreased embryo-stage survivals. The presence of oil is known to elevate juvenile salmon mortality (Moles et al. 1987). This appears to have happened in the contaminated streams in Prince William Sound, yet relatively few streams were oiled -- approximately 31% of the streams, by our criteria, in that part of Prince William Sound most affected by oil. The oiled streams tended to face north, and were generally in the southwestern part of the Sound. The oiled streams had a lower density of spawners when the density was observed in 1991.

We compared our estimates of the spatial distribution of the oil contamination to those in presented in other studies, including those sponsored by the Exxon Corporation. Maki et al. (1995) estimated that 14% of the streams in the affected area were oiled, but they considered a larger affected area than I did, including the Eshamy and Montague fishing districts. I found no classification disagreement in our sample with that of Bue et al. (1995). I did find two streams (16760 and 16610) out of 10 that were in both our sample and that of Brannon et al. (1995), which they considered unoiled yet I considered lightly or very lightly oiled. Moderate errors in the spawner density in these streams, moderate errors in number of streams oiled, or even moderate errors in the ratio of survival in oiled and unoiled streams would not have affected the larger conclusions about the result of egg-stage damage in the 1989 through 1992 brood years: the lost wild adult salmon probably was far less than 10% of the potential wild adult production in the Southwest Fishing District, and less than a few percent of the wild potential production in the entire sound.

The most serious criticism of these estimates is that our assumed fraction of fish exposed in the near-shore environment is little more than a guess. Most authors believe the most critical period for pink salmon survival is when the fish first enter the marine environment (e.g., Alexandersdottir 1987, Heard 1991). Carls et al. (1995) showed that juvenile salmon were contaminated, and Willette (1995) observed the reduced growth and survival that might have been predicted from an understanding of pink salmon biology. Even without an exact count of the number of fish exposed, because of the extent of the oiling of the marine environment, I surmised the greatest potential for damage to wild pink salmon resulting from the *Exxon Valdez* oil spill came from exposure in the critical near-shore environment.

The second most serious criticism of this study is that I may have missed large, delayed mortality in the marine life stage in brood years after 1988, and may have missed mortality in the fry stages in all brood years. Direct examination of pre-emergent fry in oiled streams by Wiedmer et al. (1995) showed damage in individual pre-emergent fry from oiled streams. Unfortunately, Wiedmer et al. provided no quantitative assessment.

The most important question about pink salmon unanswered in this study is why the estimated egg-stage mortality did not converge to control levels -- but instead became more dissimilar in 1991 and 1992. The egg-stage effects I attributed to the oil spill could simply reflect natural differences in sites. Bue et al. (1995) explained why this is unlikely, and they speculate that the difference may be due to genetic damage. This hypothesis seems a reasonable, if untested explanation, but this explanation is far from certain. *Exxon Valdez* oil was shown to cause chromosome aberrations in larval herring that incubated in oiled areas in Prince William Sound, and these aberrations were reproduced in laboratory studies (Biggs et al. 1995; Hose et al. 1996).

Taking all these uncertainties into consideration, I have attempted to gauge the order of magnitude of the wild pink salmon injury for each brood year, leaving the question of the larger significance of this loss for someone else. Even so, this study points to the large potential for loss of adult salmon resulting from contamination in the early marine life stage. It is this point, in particular, I hope is not lost when planning for and evaluating future oil spills in Alaska.

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It's an ocean filled with tears, and sorrow to fill the sea; an ocean full of tears, cried by fools like me.

— Northwest blues singer Paul deLay

CHAPTER 3 -- VARIABILITY OF FAMILY SIZE AND MARINE SURVIVAL[3]

INTRODUCTION

The prevailing view in fisheries science is that the most important population parameter is abundance. Fisheries management and harvest decisions are based on abundance (Ricker 1975, Walters and Collie 1988), as are models used by conservation biologists in the analysis of the risk of extinction of populations (Ginzburg et al. 1982, Ferson et al. 1989, Dennis et al. 1991). For family size defined as the number of returning adult breeders per number of parents, abundance is just the product of family size and the number of breeders in the previous generation. In other words, abundance is equivalent to average family size for fixed breeding numbers.

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[3] This chapter is adapted from Geiger, H.J., W.W. Smoker, L.A. Zhivotovsky and A.J. Gharrett. 1997. Variability of Family Size and Marine Survival in Pink Salmon Has Implications for Conservation Biology and Human Use. Canadian Journal of Fisheries and Aquatic Sciences 54(11): 2684-2690.

Little attention has been directed toward how family size varies in fish populations or how this variation indexes the amount of genetic variation that can be carried by a population. Although this variability has not been used explicitly in models of population dynamics or risk assessment, its importance has been acknowledged in conceptual models (Gilpin and Soulé 1986, Kapuscinski and Lannan 1986). Below I present a context for relating family-specific survival variation at different life-history stanzas to the genetic concept of effective population size, and I present an example where the population increased largely by increasing the variance of family size – not by a uniform increase in family size across most families.

In the extreme, either variation in anadromous salmon family size reflects only random influences or this variation reflects differing genetic approaches to survival in the marine environment. To test the hypothesis that family size is random, and not related to genetic information passed on from parents, I directly observed the number of pink salmon (*Oncorhynchus gorbuscha*) offspring, marked and tagged by family, surviving to return to their natal site in Southeast Alaska. By following the fate of families with more than one dam (female parent) per sire (male parent), I was able to use standard analysis of variance techniques to test for a genetic (sire) component to survival and family size (Falconer 1989). If half siblings with the same sire but different dams have survival and family size that is more alike than fish with different dams and sires, then it would seem that survival and family size is genetically influenced. To the degree that survival tended to be more similar between half sibling groups with the same sire than among family groups with different parents, I interpreted this similarity to be evidence of genetic influence on average family size and survival. These comparisons of survival similarity were formalized into standard statistical hypothesis tests.

Theoretical Background

Our notation describes the size of populations and the properties of the families of individuals in those populations. Let N_t denote the number of adult breeders in a spawning population of pink salmon in generation t. Let k denote the random variable that describes the number of adult spawners produced in some family in generation t, and let $\bar{k}$ and $v(k)$ denote the mean and variance of family size. In our notation, $v()$ denotes the observed variance among the families actually present, and $V()$ denotes variance with respect to some probability distribution.

Crow and Morton (1955) called the ratio $R_k = v(k)/\bar{k}$ the index of variability and described its calculation from adult progeny, from egg production, and from sampling variance in gene frequency. They showed that under random survival the index of variability tends to 1. In populations where the entire family survives or not as a unit, they show this ratio tends to $\bar{k}_{early} + v(\bar{k}_{early})/\bar{k}_{early}$, where *early* denotes a lifestage occurring before the family-specific mortality. Even though both theoretical and observed values outside these limits are possible, the value of 1 for random survival, and the value given by $\bar{k}_{early} + v(\bar{k}_{early})/\bar{k}_{early}$ for complete familial survival or mortality provide theoretical lower and upper reference values on the index of variability for populations with given fecundity and other parameters.

To consider populations that are intermediate between Crow and Morton's reference values, suppose each family is formed by a unique male and female pairing, and each family has a unique underlying probability distribution for family size. Let λ_i denote the underlying mean of family size for the i^{th} family, and assume that conditioned on λ_i, the family size, k_i, is generated by a Poisson distribution. Then for the i^{th} family, the actual family size, k_i, is a random variable with mean and variance λ_i. Let λ_i follow some distribution with probability density function $g(\lambda_i)$, and note that k_i, the actual family size for the i^{th} family, is then generated by a compound distribution (Titterington et al. 1985).

I am not assuming that the actual family size follows any particular distribution. However, if the variance of λ_i is zero, then the observed family size, k_i, follows a Poisson distribution, and differences in family size are due to purely random processes not indexed by individual family. Alternatively, if the variance of λ_i is large, then the distribution of the actual family size is indexed by family. In this case, the distribution of actual family sizes has a greater variance than the Poisson distribution with the same mean, but I don't know to what extent this variation is due to genetic causes. For example, some redds within a stream could be destroyed by ice or other random environmental catastrophe, and this will increase the non-genetic familial variation. If salmon could be raised in a uniform environment, so as to eliminate non-genetic sources of familial variation, then remaining variation would be largely due to genetic causes. Either way, to the extent the variation in λ_t increases, the variance of family size increases. When this happens, the effective population size (Wright 1931, Crow and Kimura 1970) will decrease relative to the population census, as will the amount of genetic variation the population can carry.

Using E( ) to denote mathematical expectation, the unconditional mean of k_t must equal the mean of λ_t, since

$$E(k_t)=E(E(k_t \mid \lambda_t))=E(\lambda_t).$$

To find an expression for the variance of k_t, in terms of the variance of λ_t, note that $V(k_t|\lambda_t) = \lambda_t$ is the Poisson variance. Then, using the well known result (e.g., Lindgren 1993)

$$V(x)=V(E(x \mid y))+E(V(x \mid y)),$$

we can find $V(k)$ as

$$\begin{aligned} V(k_t)&=V(E(k_t \mid \lambda_t))+E(V(k_t \mid \lambda_t)) \\ &=V(\lambda_t)+E(\lambda_t). \end{aligned} \tag{3.1}$$

Recalling that λ_i is the expected underlying number of offspring from the i^{th} family, let r_i denote the expected number of offspring that survive to some lifestage, such as entry into the marine environment. Now, let s_i be the underlying survival for this family in the next lifestage, so that

$$\lambda_i = s_i r_i .$$

We assume that s_i and r_i are independent, so that for C_s and C_r denoting the respective coefficients of variation, then using Goodman's (1960) formula for the variance of the product of independent random variables,

$$V(\lambda_i) = E(s_i)^2 V(r_i) + V(s_i) E(r_i)^2 + V(s_i) V(r_i) .$$

Now, substituting this expression into equation (3.1), dividing by $E(k_i)$, and omitting the subscript, that indexes the family

$$\frac{V(k)}{E(k)} = \frac{E(\lambda) + V(\lambda)}{E(\lambda)}$$

$$\frac{V(k)}{E(k)} = 1 + \left[\frac{(E(s))^2 V(r)}{E(sr)} + \frac{(E(r))^2 V(s)}{E(sr)} + \frac{V(r)V(s)}{E(sr)}\right]$$

$$\frac{V(k)}{E(k)} = 1 + E(sr)\left[\frac{(E(s))^2 V(r)}{(E(s))^2 (E(r))^2} + \frac{(E(r))^2 V(s)}{(E(s))^2 (E(r))^2} + \frac{V(r)V(s)}{(E(s))^2 (E(r))^2}\right]$$

$$\frac{V(k)}{E(k)} = 1 + E(\lambda)\left[(C_r^2 + C_s^2 + (C_r C_s)^2\right]$$

$$\frac{V(k)}{E(k)} = 1 + E(k)\left[(C_r^2 + C_s^2 + (C_r C_s)^2\right].$$

So this shows how the variance-mean ratio with respect to a probability distribution is a related to variability in survial at each life stage. If $k \approx E(k)$, $v(k) \approx V(k)$, and $V(k)/E(k) \approx v(k)/\bar{k}$, then the variance-mean ratio with respect to a probability distribution, or the actual index of variability in a population might be inflated by (1) family-specific influences that cause the number of recruits *to* the marine lifestage to vary, or by (2) family-specific influences on survival *in* the marine lifestage. In the absence of family-specific influences, this ratio is 1.

METHODS

Identifying Families of Anadromous Salmon

In September 1982, 22 female pink salmon (dams) were crossed with 33 males (sires) in a factorial design (Figure 3.1) with eleven replicated crosses of two females with three males. Dams and sires that were judged to be fully mature were chosen and mated at random on each day that spawning occurred. All of the offspring of one female failed to survive incubation, probably because that female was not fully mature on the day she was spawned; this failed family was not included in subsequent analyses. In 1983 and 1984, similar crosses were performed, except that in these years two dams were nested within each sire (Figure 3.2), and that two temporally-spaced runs (Smoker et al. 1994, Smoker et al. 1998) were sampled each year. I considered this arrangement as five distinct groups of salmon for this study: 1) 1982 late, 2) 1983 early, 3) 1983 late, 4) 1984 early, and 5) 1984 late. In the 1983 early and late groups, 60 females were crossed with 30 males; in the 1984 early group, 66 females were crossed with 33 males; and in the 1984 late group, 54 females were crossed with 27 males. In each group, the offspring from at least one, but no more than three, sire-dam crosses failed to thrive for reasons having to do with artificial culture; these failed offspring were not included in subsequent analyses. The total eggs for each individual female were divided into two approximately equal groups; each group was then fertilized, and assigned at random to a cell in an incubator. After emergence and tagging with a group-specific half-length coded wire tag (Thrower and Smoker 1984), all groups were placed into a common holding tank until release. The juveniles were counted and released to the ocean prior to their first exogenous feeding, at about 0.25g wet body weight. Surviving adult fish were intercepted and counted at a trap 16 months later as they entered fresh water. All pink salmon were native to Auke Creek, Alaska (Taylor 1980, Gharrett and Smoker 1993). The mating experiments, incubation, release, and recovery occurred at Auke Creek, in Auke Creek water.

Individual pink salmon families (offspring from the same dam-sire pair) were monitored for survival to return based on the recovery of coded wire tags. A total of 300 individual pink salmon families were tagged as larvae (unfed fry), in the five groups. I considered marked individuals a random sample from the total offspring surviving to that time, and C_r, the coefficient of variation of recruitment to the marine life stage, was held to a minimum by striving to tag and release 1,000 juveniles per family.

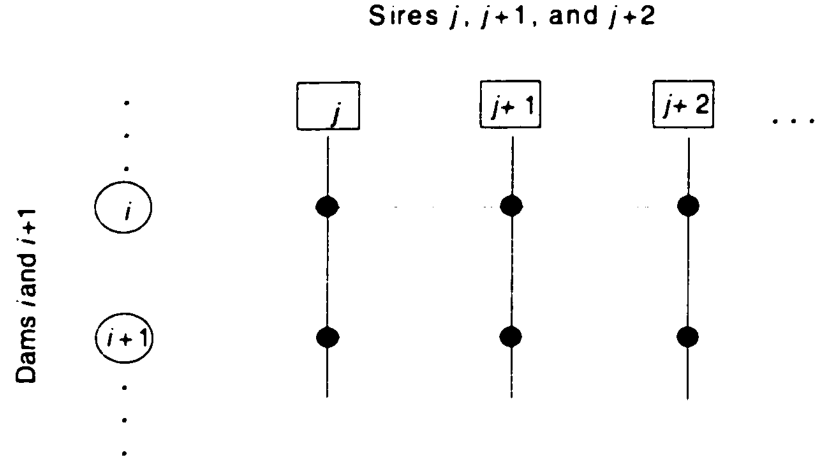

Figure 3.1. Diagrammatic representation of the mating design for the early 1982 run. Sires (males) are shown as square boxes, and dams (females) are shown as circles. Each sire was to be mated with two dams, and each dam was mated with three sires. This created six half-sib groups per replicate.

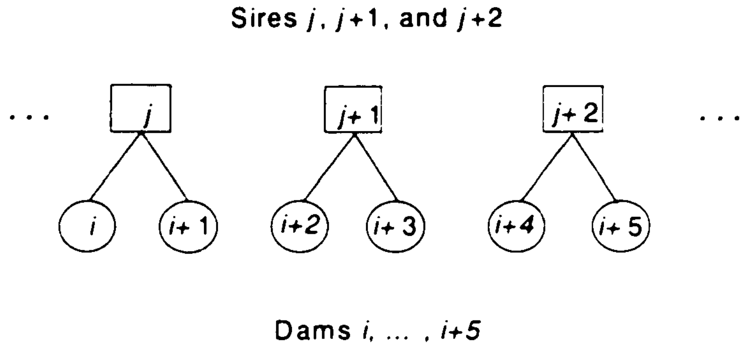

Figure 3.2. Diagrammatic representation of the mating design for the 1983 and 1984 early and late runs. Sires (males) are shown as square boxes, and dams (females) are shown as circles. Each sire was to be mated with two dams, creating a nested design, with two half-sib groups per sire.

Computation

As a variance stabilizing measure, release and return numbers were converted to the empirical logit (Agresti 1990) for each dam-sire cross. The empirical logit then became the trait of interest. Analysis of variance was used to estimate variance components. The usual *F*-test for a sire effect was used to detect an additive genetic component to the variation in the trait (Becker 1984). Because of the relatively small sample sizes, and the lack of information on the size of the effect, all tests were performed at the 0.10 level of significance (Tacha et al. 1982).

The size of a particular dam's family was not independent of the size of the family with the same sire but different dam (see Figures 3.1 and 3.2) – complicating the computation of variance of the number of offspring per family. In other words, the offspring numbers in half-sib family groups were correlated, which could result in an underestimate of variance in family size. For the 1982 families, the mean and variance of the family size were considered to be functions of the dam, and offspring numbers were summed over sire only after I failed to find a statistically significant sire effect ($P > 0.95$). In the 1983 and 1984 families, dams were randomly divided into two groups so that no sire was crossed with more than one dam in each group. I then calculated the mean and variance for each group, and then averaged the mean and variance over the groups.

RESULTS AND DISCUSSION

The index of variability increased as family size increased; similarly, the sire effects became more evident (significance probability decreased) as family size increased (Table 3.1). The sire effect in the analysis of variance table measures the genetic influences on the variability of the trait of interest (e.g. Falconer 1989, Becker 1984). Two groups had statistically significant sire effects (Table 3.2). The logit of marine survival, and by implication C_v, can have a non-zero genetic component in pink salmon – survival and family size are traits that can be inherited.

Family size for the five release groups appeared more dispersed than the Poisson distribution would provide, although family size did not seem to consistently follow any obvious distribution (Fig. 3.3). The Poisson distribution has a single parameter for both the mean and variance; data with a variance far in excess of the mean are sometimes described as overdispersed relative to the Poisson distribution. The two release groups with the highest survival, that is the 1983 early and 1983 late, had the greatest overdispersion and the largest average family sizes.

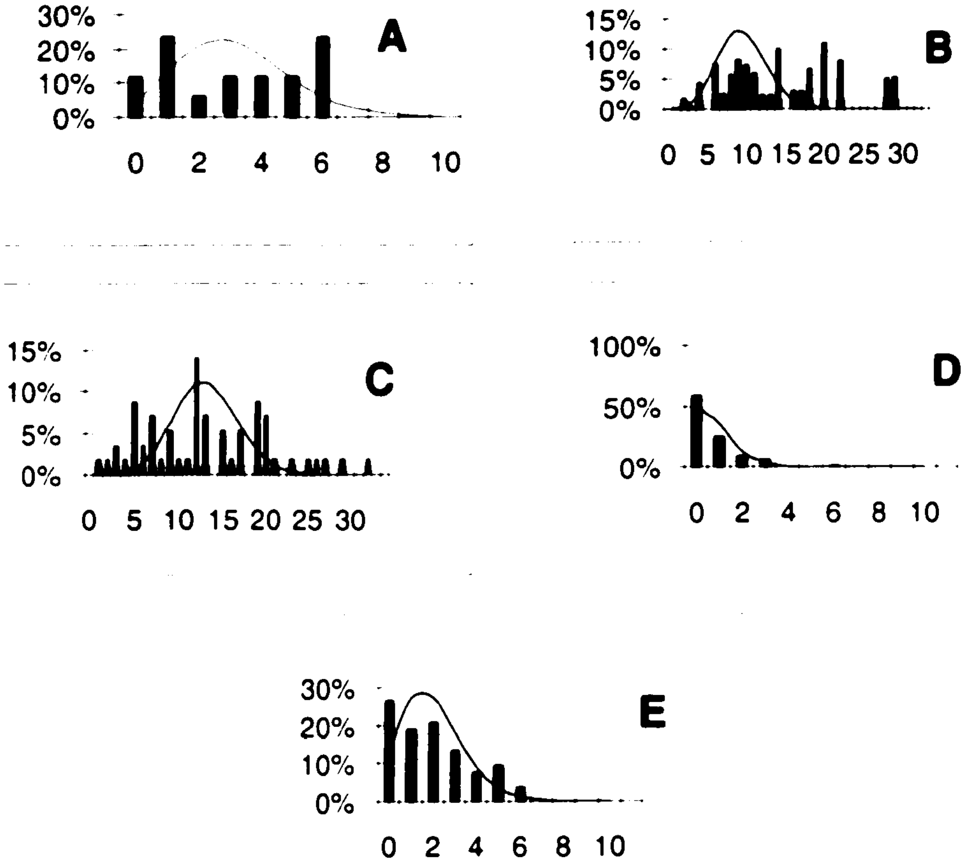

Figure 3.3. The distribution of individual family sizes (the number of returning offspring per family on the x axis) for each female for each of five runs of pink salmon returning to Auke Creek, Alaska; for A, the 1982 late run; for B, the 1983 early run; for C, 1983 late run; for D, the 1984 early run; and for E, the 1984 late run. The vertical bars show the actual distribution of offspring for each female. The lines show the shape of a Poisson distribution with the same mean as the observed average family size. Vertical axis is percentage observed for each family size.

Table 3.1. Seven statistics of interest on survival among pink salmon families released into the Pacific Ocean in five distinct groups. As a variance stabilizing measure, release and return numbers were converted to the empirical logit for each dam-sire cross; the empirical logit of survival then became the trait of interest. Sire significance probability is the result of an *F*-test of no sire effect. Mean survival represents survival from emigration into the marine water until adult return. Mean family size is the total number of adult breeders returning divided by the number of females in the parent year. The index of variability is the variance of family size divided by the mean family size, and plays an important role in determining the genetic quantity called the effective population size. The index at release was calculated just before release to the ocean, the "predicted index" is a theoretical value generated by scaling release statistics under the assumption that marine survival is purely random, and not family-specific. The index at return was calculated in the breeding population of mature spawners. Note that the actual index is uniformly larger than the "predicted index," strongly suggesting family-specific mortality processes in the marine lifestage. Under the hypothesis that marine mortality was completely family specific, a comparable predicted index would be near 800.

Statistic	1982 Early	1983 Early	1983 Late	1984 Early	1984 Late
Sire significance probability	0.97	0.07	0.008	0.85	0.71
Mean Survival	0.003	0.012	0.019	0.001	0.002
Mean Family Size at Return	2.8	9.3	13.2	0.7	2.0
Mean Family Size at Release	942	772	706	630	838
Release Index of Variability	162	97.3	110.7	104.7	101.5
"Predicted Index" at Return	1.48	2.16	3.05	1.12	1.24
Final Index of Variability	1.77	4.97	4.03	2.45	1.58

Table 3.2. Analysis of variance tables for the logit of marine survival of pink salmon returning to Auke Creek, Alaska. Families were individually tagged with coded-wire tags for one run in 1982 and each of two runs, an early and a late run, in 1983 and 1984. In 1982, sire and dams were crossed in a factorial design. In 1983 and 1984, families had a single dam (mother), but sires (fathers) were mated with two dams, creating a nested design. Not all crosses had offspring surviving to release.

Source	df	Sum of Squares	Mean Squares	Significance Probability
1982 Late Run				
Total	58	39.2439		
Sire	32	14.8873	0.4652	0.970
Error	26	24.3566	0.9368	
1983 Early Run				
Total	58	41.083		
Sire	29	26.1007	0.9000	0.070
Error	29	14.9824	0.5166	
1983 Late Run				
Total	56	10.7643		
Sire	29	7.9117	0.2728	0.008
Error	27	2.8526	0.1056	

Table 3.2 (continued)

Source	df	Sum of Squares	Mean Squares	Significance probability
1984 Early Run				
Total	58	50.2969		
Sire	29	20.3541	0.7019	0.848
Error	29	29.9428	1.0325	
1984 Late Run				
Total	58	42.9130		
Sire	29	19.2798	0.6648	0.706
Error	29	23.6332	0.8149	

These results provide several refinements to our understanding of pink salmon biology. Specifically, these results provide (a) insight into the effective population size (Wright 1931), a familiar genetic parameter describing the amount of genetic variability that a population can retain; (b) evidence for a genetic component to marine survival in some environments; and (c) the observation that in the groups of salmon I studied, the index of variability increased with the mean family size at return.

I implicitly assumed that the salmon were not affected by residual nongenetic, family-specific influences on survival in the marine environment. Siblings that were incubated together could conceivably remain together in the marine environment and be subjected to common mortality, or prerelease handling could have had a large family-specific post-release effect on survival. I assume that these possibilities are remote, but in any case, they would not have produced the results I observed. The nested design used in the breeding experiment would have prevented most non-genetic influences from affecting the statistical hypothesis tests of genetic influence on survival. The statistical hypothesis tests were based on the sire effects. That is, the *F*-statistic in question was inflated by a consistent commonality among the survival of half-siblings with the same sire – but not the same dam, same incubator, and so forth.

Recall that $R_k = v(k)/\bar{k}$; for populations that are expanding or contracting, Kimura and Ohta (1971) give the following formula for the variance effective population size,

$$N_e(t) = \frac{(N_{t-1} - 1)\bar{k}}{R_k + 1}.$$

In populations that are neither expanding nor contracting, the average family size, $\bar{k}$, must be equal to 2. Assuming no familial mortality and random mating, the variance in the family size must also be approximately 2 (Crow and Kimura 1970), so that $R_k \approx 1$

and $N_e \approx N_{t-1} - 1$. However, I observed indices of variability approximately twice as large as this model predicts, even when variation in recruitment to the marine life stage was artificially held to a minimum. In wild populations, C_r is probably very high if for no other reason than the physical proximity that eggs from a single family have in the redd. With the index of variability near 2, the effective population size will be near 2/3 of the breeding population size. If there is a weak association between $\bar{k}$ and $v(k)/\bar{k}$, and little familial variation in recruitment to the marine lifestage, hypothetical N_e/N_t ratios will slowly decline to less than 0.4 over the range of family sizes that I observed (Fig. 3.4). In wild pink salmon populations, we can expect N_e/N_t to be far less than 2/3, because of familial variation in recruitment to the marine environment.

The theoretical benchmark value of a mean and variance of family size of 2, applies to completely random fecundity, random egg deposition success, and random survival at each lifestage – a biologically unrealistic benchmark. A more realistic benchmark is found by letting the index e denote a time event when the average family size and variance are calculated at an early life stage, and letting the index l denote a time event when these statistics are calculated at a later life stage. Then if survival is completely random between time e and time l, Crow and Morton (1955) show

$$\frac{\frac{v_l}{\bar{k}_l} - 1}{\bar{k}_l} = \frac{\frac{v_e}{\bar{k}_e} - 1}{\bar{k}_e},$$

or,

$$\frac{v_l}{\bar{k}_l} = \bar{k}_l \left[\frac{\frac{v_e}{\bar{k}_e} - 1}{\bar{k}_e} \right] + 1 \; . \qquad (3.2)$$

Alternatively, if survival works on the family as unit, then

$$\frac{v_e}{\bar{k}_e} + \bar{k}_e = \frac{v_l}{\bar{k}_l} + \bar{k}_l \; .$$

or,

$$\frac{v_l}{\bar{k}_l} = \frac{v_e}{\bar{k}_e} + \bar{k}_e - \bar{k}_l \, . \qquad (3.3)$$

The 1982 early population had an index of variability of 162 at release, but the other four populations had the index of variability at release held very close to 100 (the largest deviation in the latter four populations was 10.7); the median variance-to-mean ratio at release as was 104.7, or essentially 100, and the mean family size was 773 (Table 3.1). Substituting a value of $\bar{k}_l = 2$ into equations (3.2) and (3.3), and solving for the index of variation at return, under the hypothesis of a purely random environment, with no family-specifics of any kind, we expect a variance-mean ratio of 1.24 to 1.33, for an average of 2 breeders surviving. The ratio would tend to approximately 870 for survival completely determined by family membership, with random survival acting to allow a family to survive or perish as a unit. In other words, if the observed ratios at return are near or larger than, say 500, we can conclude that in the marine life stage, survival is acting almost entirely at the family level, but if this ratio is less than say, 2 or so, mortality in the marine environment is working mostly at the level of the individual, and not the family – which is what I would expect. Substituting the actual mean family size at return for $\bar{k}_t$ in equation (3.2) results in predicted indices that are slightly, but uniformly, smaller than the actual observed values (Table 3.1). As expected, these results suggest a very large role for randomness in determining final family size. However, these results also show a family-specific effect consistently across each of the five populations.

Or another way to look at this is to ask the question, given that pink salmon may at least occasionally experience density-dependent population-size regulation (McNeil 1964), why has selection not increased the productivity of the stock by favoring those fish with higher marine survival, and reduced the genetic component of variation to undetectable levels? The answer must be that the favored phenotypes change between generations, and that eliminating genetic variation in this trait can have a big effect on stock productivity. Evidence of this is supplied by McIntyre et al. (1988), who artificially selected individuals for increased marine survival in four successive broods of a coho salmon (*O. kisutch*). The authors reported that marine survival in the selected line decreased compared to a control line, presumably because of the loss of genetic variation.

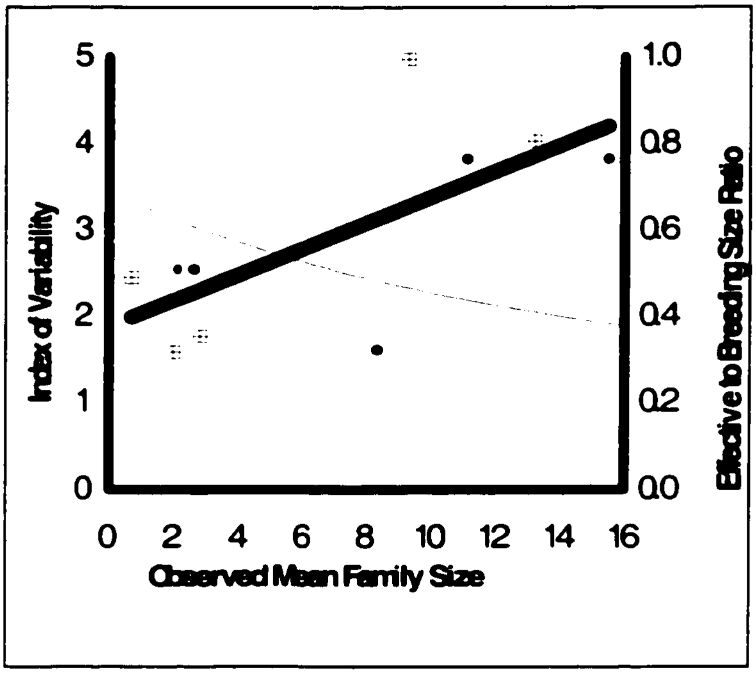

Figure 3.4. Index of variability for experimentally produced salmon (left axis), as a function of mean family size, and estimated N_e/N ratios. Because of similar handling in early lifestages, these fish have a minimum of familial variation of recruitment to the marine lifestage. Boxes represent the five groups of Auke Creek pink salmon. Filled dots represent observations of coho salmon by Simon et al. (1986). In all cases, the index of variability exceeded 1. Functional relationships between family size and index of variability are unknown, and surely differ among species, times, locations. Because of the limited sample sizes, a single linear smoothing is provided using the estimated regression of the Auke Creek pink salmon and Simon et al. coho salmon (the thick line). Based on this regression relationship, a hypothetical N_e/N_t relationship is plotted (the dashed line, right axis) as a function of mean family size for population sizes large enough that $N_e \approx N_t - 1$, and assuming no familial variation in recruitment to the marine lifestage. Estimated regression parameters for the equation $y = \hat{a} + \hat{b}x$ are $\hat{a} = 1.88$ and $\hat{b} = 0.150$ for combined data (shown), $\hat{a} = 2.03$, and $\hat{b} = 0.102$ for the coho salmon data and $\hat{a} = 1.69$, and $\hat{b} = 0.227$ for the pink salmon data.

If marine survival of salmon cannot be increased by selection, any surplus of animals available for human use comes from a changing and unpredictable fraction of the population. A genetic component of marine survival and a changing environment underscore the importance for fitness of genetic variability in exploited or recovering salmon populations.

Loss of genetic variation can reduce survival and mean fitness (Falconer 1989). Several recent studies provide examples of inbreeding, and its associated loss of genetic variation, leading to detectably reduced survival in vertebrates in natural habitats (Jimenez et al. 1994, Keller et al. 1994). Ryman (1970) reported lower recapture frequencies in inbred families of Atlantic salmon (*Salmo salar*) and indicated a likely additive genetic component of variation of recapture frequencies.

In the only other study I know of in which family size was directly observed in Pacific salmon, Simon et al. (1986) tagged 158 families of hatchery-produced coho salmon (*O. kisutch*) over five years, and reported the index of variability of family size. They also noted an increase in the variance of family size as a function of mean family size, and observed that the family size distribution did not fit any simple distribution, such as the Poisson. Their observations closely agree with ours (Figure 3.4). The index of variability was always larger than one, and increased with average family size – a result consistent with Crow and Morton's (1955) findings with fruit flies.

Our finding that $v(k)/\bar{k}$ is larger than 1 is consistent with studies of other species. A value of $v(k)/\bar{k}$ nearly as high as 15 was reported by Begon (1977) in a laboratory study of the fruit fly (*Drosophila subobscura*). Nozawa (1972) reported effective population size estimates of 20% to 76% of the breeding population size in Japanese macaque (*Macaca* sp.). Ryman et al. (1981) simulated populations of moose (*Alces alces*) and white tail deer (*Odocoileus virginianus*) and speculated that effective population sizes would be between 20% to 42% of total populations under various harvest strategies that did not alter sex ratios. Frankham (1995) recently provided a review of N_e/N in a large number of different species, including insects, mollusks, fishes and other vertebrates, and plants; this review included estimates of 0.9 for rainbow trout (*O. mykiss*) but 0.013 to 0.043 for chinook salmon (*O. Tshawytscha*). Nunney (1995) proposed that the ratio of effective population size to breeding size "is expected to be higher than 0.5" in populations with overlapping generations, but that the lack of overlapping generations creates "an increased likelihood of extremely low values (i.e., $N_e/N < 0.25$)."

In summary, I showed that the variation in family size of anadromous salmon is a function of two potentially important factors: 1) familial recruitment to the marine lifestage, and 2) the subsequent familial survival in the marine environment. I then detected familial differences in marine survival in the populations of pink salmon I studied, and linked familial variation in family size to genetic causes. By observing the association between average family size, and variance in family size we find a link between population increase (or exploitable production, surplus to breeding needs) and genetic variability in the population. The important biological conclusion is that some part of the breeding population is the most productive, and that this productive segment is both changing and unpredictable. Thus, population dynamics models that only incorporate abundance will fail to predict decreases in stock productivity as a consequence of actions that maintain abundance in the short term, but decrease genetic variability.

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It's pretty hard to hurt yourself with a chum salmon.

— Prof. Lewis Haldorson in a lecture to his ichthyology students in the fall of 1995

CHAPTER 4 -WHAT CAUSES VARIABILITY IN PINK SALMON FAMILY SIZE?[4]

INTRODUCTION

Although average family size determines recruitment in a single generation, the genetic dynamics of a population depend strongly on the variability in the family size. High values of the variance of family size mean that a relatively small number of families "effectively" contribute genetically to the next generation. This notion is formalized in a family of genetic concepts grouped under the heading of *effective population size*. Effective population size influences such things as how much genetic variation can be maintained over generations, hence the degree to which evolution will allow the population to respond to change, and the magnitude of random genetic drift. Let $\bar{k}$ and $v(k)$ denote the mean and variance of family size in some population, and let N_{t-1} denote

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[4] This chapter is adapted from Geiger, H.J., I. Wang, P. Malecha, K. Hebert, W.W. Smoker, and A.J. Gharrett, *in progress*. What causes variability in pink salmon family size?

the breeding population size in the previous generation. The *variance effective population size* (N_{ev}: Crow and Kimura 1970) is expressed in terms of both the variance of family size and the mean family size.

$$N_{ev} = \frac{(N_{t-1} - 1)\bar{k}}{v(k)/\bar{k} + 1}.$$

The ratio of the variance to the mean of family size, which appears in the denominator of N_{ev}, is sometimes called the index of variability (Crow and Morton 1955). For small breeding population sizes, the index of variability assigns a measure to the amount of genetic variability a population can hold. Recruitment, population increases or decreases, fishery yield, and the index of variability are all determined by a combination of fecundity and family-specific survival, which may result from genetic differences or spatial clustering of families in an environment with spatially correlated mortality pressures.

Variability in traits closely linked to survival seems to be maintained in Pacific salmon because variability is such an important feature of their environment. McIntyre et al. (1988) artificially selected families for increased marine survival in four successive generations of a coho salmon (*Oncorhynchus kisutch*) line; marine survival in the selected line decreased compared to a control line, presumably because of the loss of genetic variation. Previously, Geiger et al. (1997) showed that in pink salmon (*O. gorbuscha*) populations the genetic trait of marine survival varied among families within a given environment. Selection appears to stabilize some quantitative traits related to survival in wild populations of Pacific salmon, but also to prevent too fine a stabilization in some survival-related traits (review by Taylor 1991). Many traits under genetic control have been shown to be linked to survival or fitness. For example, embryo development rate (in freshwater) has been linked with survival-related events in Pacific salmon life histories (Brannon 1987, Hebert et al. 1998, a review by Gharrett and Smoker 1993a, Smoker et al. 1998, McGregor et al. 1998). Therefore, variation of development rate among families will induce variation of family size.

In pink salmon, family-specific mortality is, at times, caused by influences in the freshwater life stage (e.g., Fukushima et al. 1998) related to the spatial clustering of eggs from the same mother. DeVries (1997) concluded that egg-deposition depth represents a tradeoff of maternal energy uses, and that burial depth is positively correlated with maternal body size and that deeper burial protects eggs from scouring loss. He also speculated that pink salmon may require especially deep deposition for their size because of the hydrological features of their spawning habitat. It is then reasonable to speculate that maternal choices about redd location, construction, and depth will also induce a component of variation in family size.

For Pacific salmon, it is convenient and natural to divide the lifetime survival process into sub-processes in the freshwater lifestage, and sub-processes in the later marine lifestage. Here we have divided pink salmon life history into four life history stanzas: (1) fecundity, (2) egg deposition and egg loss from the redd, (3) freshwater survival, and (4) marine survival. Although these stanzas are not entirely independent, this approximation allows a detailed study of life history and makes the study of variation in family size tractable. Geiger et al. (1997) showed that population increases were accompanied by a greater variance of family size. Here we used similar techniques to examine familial links to freshwater survival and fecundity. To do this we reanalyzed the results of genetic breeding experiments on laboratory populations of pink salmon that had been conducted for other purposes. We then examined freshwater survival measurements – for those eggs and embryos that were retained in redds – from field studies of wild pink salmon populations in Prince William Sound, Alaska to see if these approximately agreed with our laboratory values. Our purpose is to assemble data sets that relate family-specific survival with variation in family size in the freshwater environment and to compare patterns of this variation with patterns of variation in other determinants of family size, such as survival in the marine environment and fecundity.

METHODS

Notation and Concepts

For the ith family, let k_i denote the random family size. Let f_i denote the fecundity of the mother, let r_i denote the fraction of the total eggs both deposited and then retained in the redd, let q_i denote the freshwater survival of the emergent fry within the redd, and let s_i denote the marine survival of emigrant fry. Considering family size in this way allows partitioning the variation of family size because $k_i = f_i r_i q_i s_i$. Let $E(k_i)$ denote the expectation, $V(k_i)$ denote the variance of family size, and in the notation of Goodman (1960) let $G(x)$ denote the square of the coefficient of variation (i.e., $G(k_i) = V(k_i)/ E(k_i)^2$). As a first order approximation, assume that f_i, r_i, q_i, and s_i are nearly independent. Then using Goodman's (1960) result,

$$\begin{aligned}
V(k_i) &= V(f_i r_i q_i s_i) \\
&= E(k_i)^2[G(f_i) + G(r_i) + G(q_i) + G(s_i) \\
&\quad + G(f_i)G(r_i) + G(f_i)G(q_i) + G(f_i)G(s_i) \\
&\quad + G(r_i)G(q_i) + G(r_i)G(s_i) + G(q_i)G(s_i) \\
&\quad + G(f_i)G(r_i)G(q_i) + G(f_i)G(r_i)G(s_i) + G(f_i)G(q_i)G(s_i) + G(r_i)G(q_i)G(s_i) \\
&\quad + G(f_i)G(r_i)G(q_i)G(s_i)].
\end{aligned}$$

Goodman (1960) stated that in cases with "small" values of $G(x)$, it is common to approximate the variance with $E(k)^2[G(f)+G(r)+G(q)+G(s)]$, ignoring the terms involving products; the inaccuracy will be on the order of $(G(f)^{-1}+G(r)^{-1}+G(q)^{-1}+G(s)^{-1}+1)^{-1}$. Below we will estimate the magnitudes of $G(f)$, $G(q)$ – the ratios of the variance to squared means – for fecundity and freshwater rearing survival – and compare these values to estimates of $G(s)$ from Geiger et al. (1997).

Laboratory Studies and Statistical Methods

We obtained laboratory observations of freshwater survival in four experimental groups of pink salmon native to Auke Creek, Alaska (Taylor 1980, Gharrett and Smoker 1993b) and one experimental group from Macaulay Hatchery in Juneau, Alaska.

In some experimental studies, dams and sires were organized into family units by mating experiments designed to estimate sire effects (Gharrett and Smoker 1993b; Falconer 1989, Becker 1984). These studies of survival make up data sets labeled Set A through Set E; an additional data set labeled Set F contains measurements of fecundity only. Family survival was estimated as the surviving eggs for each dam, divided by the number of eggs that female had in all incubator rearing compartments, and the dam was used to define and index the family.

Data Set A and Set B represent even-year broodline crosses between 40 mature pink salmon females with 40 mature males from Auke Creek. The Set A cross was made on 29 August, 1996. The cross was a replicated incomplete-factorial mating design: two males were crossed with two females in all four possible ways to produce paternal half-sib families. This basic mating unit was repeated twenty times to mate all individuals. Embryos of each family were divided, by eye, into two equal proportions; each replicate was placed in a randomly assigned (by a pseudo-random number algorithm) compartment within one of two vertical incubator stacks of FAL Heath (tm) incubators. For our analysis the replicates were combined. The stacks each held sixteen incubating trays divided into 10 roughly equal sized compartments by separate acrylic dividers. Loading densities were approximately 200 eggs/compartment. This process was repeated on September 1 and 2, 1997 for the odd-year broodline cross, and is represented as Set B.

Data Sets C and D were generated as part of a study of heritability of embryonic development, and the descriptions of the crosses, handling, and populations are described in Hebert (1994) and Hebert et al. (1998). The crosses were a nested hierarchical mating design (Becker 1984), mating 40 sires with 80 dams. Each male fertilized eggs from two females (two dams nested within each sire) to create 80 half-sib families in August and September of 1991.

Data set E was generated from salmon gametes obtained from Macaulay Hatchery on 31 August 1996 in Juneau, Alaska. Again, crosses of sires with dams followed the same nested hierarchical mating design used for data Sets C and D. Thirty males were mated with 60 females; sperm from a single male fertilized eggs from each of two females, creating 60 half-sib families. Each full-sib family (single male mated to single female) was split into two replicate lots and randomly placed into two of 120 compartments of FAL Heath™ incubator trays. For our analysis, the observations of survival in the two replicates of each family were combined.

To improve the statistical properties, the quantitative trait that we analyzed for statistical hypothesis tests was the empirical logit of survival (Agresti 1990). For n_i the number of eggs incubated, and x_i the number that survived from the ith family, the empirical logit was calculated as $l_i = \ln((x_i + ½)/(n_i - x_i + ½))$. Sire effects were isolated by means of analysis of variance (Becker 1984), and all analyses of variance and statistical tests (based on the F-statistic) described below relate to the logit of survival as the trait of interest. Variance components were estimated from random effects models, and F-statistics were generated by constructing the error term based on expected mean squares (e.g. Neter et al. 1985). The means and squared coefficients of variation we report were calculated in units of eggs, proportional survival, or number of surviving animals.

For Sets C-E, (replicate nested mating design) we avoided treating half-sib groups (same sire, different dam) as independent statistical units in the calculation of among-family variance, by dividing each data set in half (by sire) so that we had two dependent data subsets containing only independent observations for each family in the subset (single sire and single dam crosses). We then separately calculated survival within, and variance among, full-sib groups in each data subset. The squared coefficients of variation (i.e., estimated values of $G(x)$), were averaged over the two subset estimates. Dam-specific fecundity estimates were made for Sets B-F. The fecundity data were calculated either by a hand-count of all eggs (Set F), or volumetric methods with counted samples (other data sets). The data set labeled Set F represents a hand-count of eggs from 258 Auke Creek females maturing in 1985.

Field Studies

Data collection methods for the field studies in which embryos and larval fry were collected from stream gravels with hydraulic samplers (i.e. pumped jets of water) are described in detail in Bue et al. (1996). Graphical summaries of these data are presented in Geiger et al. (1996). In the field studies, 25 streams within western Prince William Sound, Alaska, were selected to represent salmon spawning streams either affected by the *Exxon Valdez* oil spill in March of 1989 or not affected by the floating oil. Samples of spawning habitat were stratified by elevation. Within each stream and within each stratum, separate transects across the stream were located for embryo and fry samples. Embryo sampling was conducted in late September to mid October, and fry samples were collected the following March. Most transects were approximately 30 m long, although some transect sizes were adjusted to fit into riffle spawning areas within the streams. Along each transect, 14 separate digs, or holes, were located approximately systematically. At each dig, the basic data were counts of live and dead embryos, or counts of live and dead fry pumped out of the gravel. Nearly all salmon and debris from decaying dead salmon within an approximately 0.183 m^2 area were pumped out of the gravel at each dig-unit. Fry were sometimes killed by the pumping and retrieval, so fry with signs of decay were counted as dead but newly dead fry were counted as live. The data were collected in 1989, 1990, and 1991. Salmon embryos deposited in sub-tidal reaches of streams were underrepresented by this sampling effort because no samples were taken below an elevation approximately 2 m above the mean high tide. The unit of observation for our purpose was the transect, and our data is summarized over the 14 digs/transect. No attempt was made to determine family relationships, and the sampling was only meant to represent spatial mortality processes on a scale that would approximate scales of processes that affect clusters of siblings.

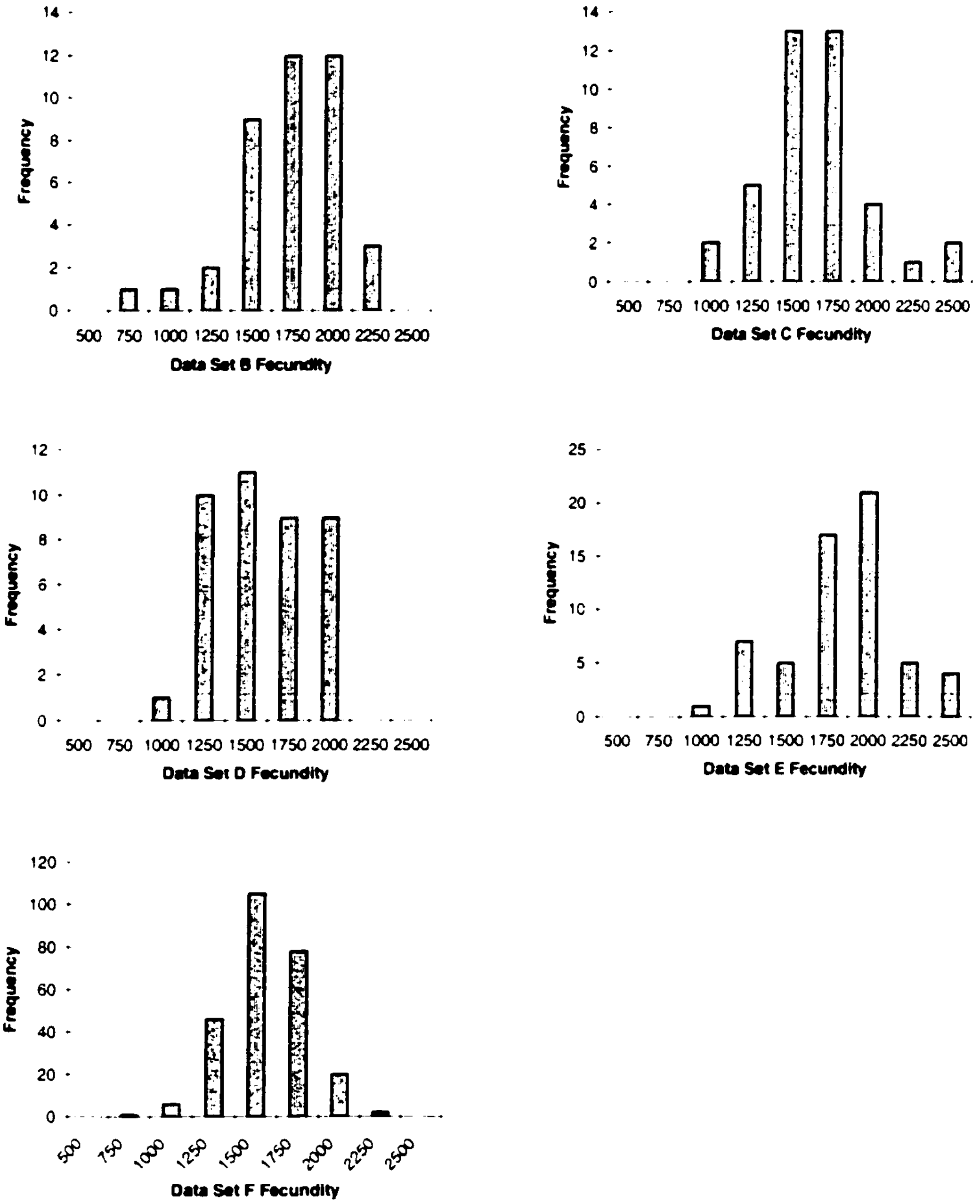
For each year, we calculated the mean observed survival for the fish within each dig-cluster, and calculated the squared coefficient of variation over all sites sampled for the year. In other words, we calculated averages and variances over sites that may have been affected by location within stream, effects of pollution or toxic effects of oil, and effects of fry density. If any of these effects were important, they should serve to inflate the coefficient of variation.

RESULTS

In the laboratory experiments, mean fecundity ranged from 1,437 to 1,713. These values may be biased slightly low because some egg shedding occured while potential breeders were held prior to full maturation. Plots of the distribution of dam-specific fecundity (Figure 4.1) did not appear to follow any common probability distribution.

A statistically detectable sire component of variation of freshwater life stage survival was found in four of the five data sets. Fisher's significance probability values that we considered "significant" ranged from 0.00001 to 0.022 (Table 4.1). Four of the five distributions of family-specific freshwater rearing survival (Figure 4.2) were left skewed, whereas one plot (Set C) was multimodal. The unusual pattern in Set C may have resulted from artificial spawning of some females before they were fully ripe, or this deviation from the other data sets may have resulted from the ordinary variability in survival patterns of cultured pink salmon.

Figure 4.1. Estimated distributions of fecundity of female pink salmon from five populations. In Data Sets B – E the fecundity of each sampled female was estimated by volumetric methods with counted subsamples. The data from Set F represents a hand count of each egg in 258 females.



Notably, the sample squared coefficients of variation ranged from 0.006 to 0.117 for fecundity and freshwater life stage survival (Table 4.1). In contrast, the squared coefficients of variation estimated, but not published by Geiger et al. (1997), for family-specific marine survival were 5.851, 0.438, 0.177, 1.902, and 0.751. When the histograms of the squared coefficients of variation from all data sets were plotted together, the variation of fecundity and freshwater survival cannot be distinguished from zero on a plot that spans the scale of variation of marine survival (Figure 4.3).

Figure 4.2. Distributions of freshwater survival in five laboratory-reared populations of pink salmon.

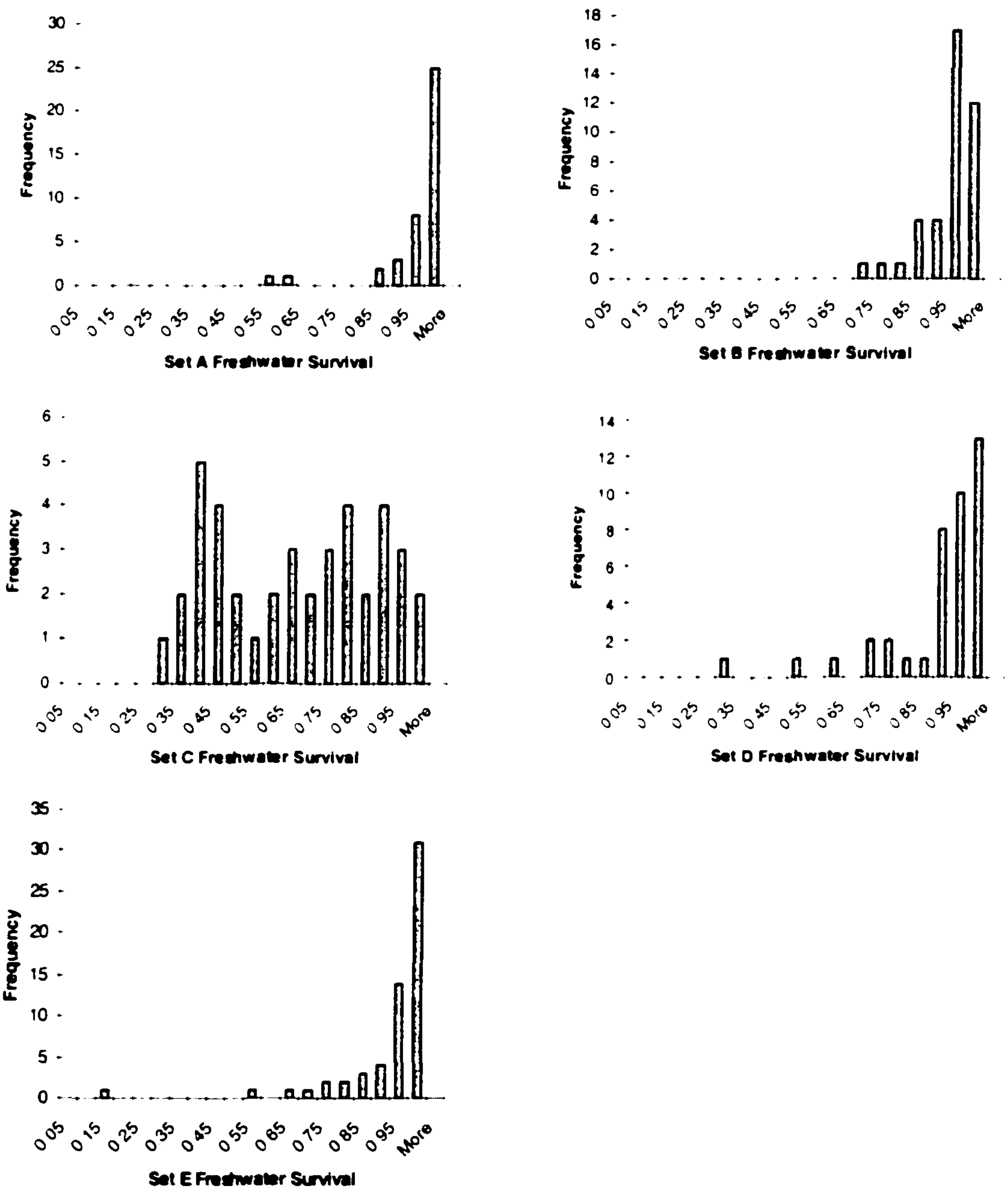


Figure 4.3. Squared coefficients of variation (G(•) = variance(•)/mean^2(•)) of fecundity (max. value 0.047) and freshwater rearing survival (max. value 0.118) of five laboratory-reared populations of pink salmon, together with five estimates of the squared coefficients of variation of marine survival. Missing are values for egg retention. The sum of the coefficients of variations from all four sources is approximately proportional to the variance of family size. The variation of survival in the marine lifestage dominates the estimates we have, although the egg loss source of variation could be as high or higher.

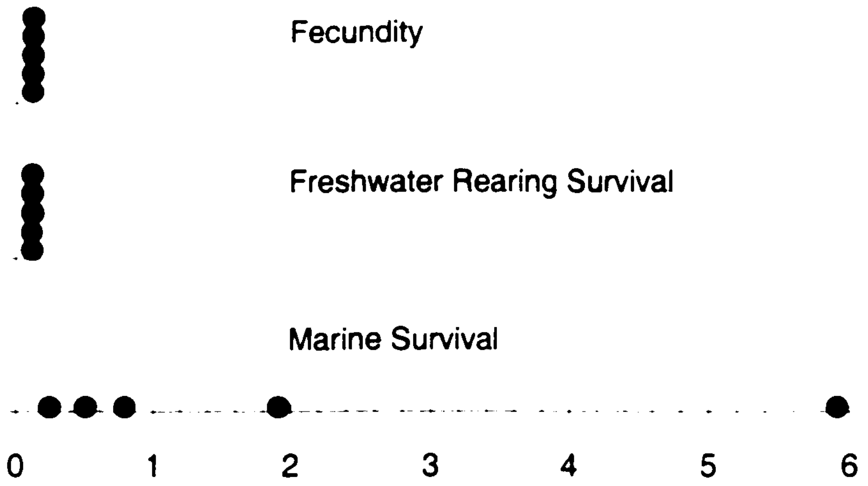


Table 4.1. Estimates of pink salmon fecundity, squared coefficients of variation (G(•) = variance(•)/mean^2(•)) of fecundity for five populations of pink salmon, and average family-specific freshwater survival and squared coefficients of variation of family-specific freshwater survival in five populations of laboratory-reared pink salmon. The breeding designs allowed for an estimate of a sire effect in the logit-transformed survival. A sire significance level (*P*-value) less than 0.1 was taken as evidence of a genetic component to freshwater survival

Data Set	Mean Fecundity f	Squared Coefficient of Variation $G(f)$	Mean Freshwater Survival q	Squared Coefficient of Variation of freshwater survival $G(q)$	Sire Effect *P*-value
A	na	na	0.929512	0.011042	0.0001
B	1625	0.045	0.908703	0.006271	0.0037
C	1526	0.047	0.637691	0.117618	0.0024
D	1488	0.033	0.863994	0.029359	0.2791
E	1713	0.036	0.901886	0.024828	0.0218
F	1439	0.027	na	na	

Of the eggs retained within the redds in the Prince William Sound field study, the mean proportions of live eggs for an entire year were 0.868, 0.754, and 0.694 for 1989, 1990, 1991, respectively. The average survival for fry that were retained within the redd was above 0.699, 0.570, and 0.589, respectively. While some fry may have died and then decomposed or been scavenged, in this cold environment it is unlikely that decomposition caused much measurement error. Of eggs that had remained within redds until the time of observation, the squared coefficients of variation for survival were 0.014, 0.060, 0.092, respectively for the three years – similar to our laboratory results for freshwater survival among families. The squared coefficients of variation of fry survival were 0.223, 0.432, and 0.318, respectively.

DISCUSSION

Biologists have realized for a long time that a small fraction of the total potential egg deposition of salmon survives all life stages from deposition to emergence from the spawning gravel. Bailey (1969) assumed less than 25%, and Heard (1991), in his review of the literature on pink salmon life history, speculated that this value "commonly reaches 10%-20%, and at times as low as about 1%." In the wild populations we studied, it appears that mortality in the freshwater lifestage resulted primarily from superimposition of redds by sequential spawners (McNeil 1964; Fukushima et al 1998), washout and scouring by high streamflow, and retention of eggs within the mother. Heard (1991) reported that egg retention may be in part density dependent, and may range from less than 1% to over 40% of potential egg deposition, or aggregate fecundity. In one year at Auke Creek, Alaska, 30% - 70% of females retained more than 500 eggs (about one fourth of potential fecundity) at death, a proportion that varied directly with migration date and stream temperature (Fukushima and Smoker 1997). Clearly, because of streamflow events, superimposition, or other random catastrophes, a large part of the variability of family size is a result of a loss of all or nearly all of some families.

Geiger et al. (1997) estimated the squared coefficient of variation of marine survival among families to be on the order of 0.1 to 10 in the marine environment, where pink salmon may occupy a variety of habitats and subsist on a variety of prey (also reviewed in Heard 1991). The squared coefficients of variation of familial freshwater survival and fecundity were estimated to be on the order of 0.01 in our studies of both wild and laboratory-reared pink salmon. Therefore, even though we detected a nonzero heritability of freshwater survival, variation in this trait, as compared to other life history stanzas, seemed to negligibly affect variation in family size and effective population size.

Falconer (1952) introduced the idea of "character states" to convey the idea that quantitative characters expressed in different environments can be considered genetically correlated states, each of which is expressed in only one environment. We might think of freshwater survival this way, in which case survival in our laboratory studies would be expected to be only partially correlated with freshwater survival of salmon in the wild – but the degree of correlation would be unknown. Although the egg and fry-dig data from Prince William Sound are not family-specific, these observations seem to confirm and reinforce our interpretation that the approximate magnitude of the coefficients of variation we observed in laboratory experiments of freshwater survival are similar to coefficients of variation that occur in natural populations.

Many authors have stressed the effects of water flow, redd superimposition, and density dependence on egg loss in pink salmon (Neave and Wickett 1953, Wickett 1958, McNeil 1964, Fukushima et al. 1998). I did not consider the effects of density, and our measurements from wild populations are measurements on highly exploited, managed populations, where stream-densities were held to an intermediate level – probably somewhat below a level that would generate maximum recruitment. If density were to increase in a spawning area, it would lead to increases in family-specific mortality and overall average mortality because of egg loss from redd superimposition, increased embryo mortality from mechanical shock, competition among females for spawning areas, increased egg retention, and so on (Heard 1991). Even though it is probably impossible to generalize – even about gross trends in variation of family size – without somehow taking density into account or referring to a particular fishery management regime, our conclusions provide one view of these trends at moderate to low density.

We used functions of survival and fecundity as the response variables and used the genetic concept of the "sire effect" to detect a genetic source of variation above background levels in the laboratory populations. Detecting a statistical "sire effect" is equivalent to demonstrating a nonzero heritability, in the narrow sense, of a trait. Heritability in the narrow sense is the ratio of the additive genetic variation of a phenotype, to the total variation of the phenotype (from genetic and environmental causes; Falconer 1989). Heritability can only be estimated, and has theoretical meaning only in the context of a particular environment, and can only be discussed within the context of a given level of environmental variation. We considered survival a quantitative trait, and used our experiment to test for a nonzero heritability of freshwater survival. Based on first principles, the null hypothesis of zero heritability for freshwater survival is not reasonable, but as far as we know, no one has previously reported detecting a nonzero heritability in freshwater survival. While our laboratory environment is unquestionably unlike most natural environments, a natural environment would be an unsuitable study situation because strong environmental variation would make small to intermediate values of heritability in survival undetectable. Additionally, large gene-by-environment effects (Hebert et al 1998) would make estimates from any particular environment hard to generalize.

Finally, we consider the variance effective population size (e.g., Falconer 1989),

$$N_e = \frac{(N_{t-1} - 1)\bar{k}}{R_k + 1} \ .$$

where R_k is the index of variability ($R_k = v(k)/\bar{k}$, with

$$v(k) = \sum_i \frac{(k_i - \bar{k})^2}{n-1}$$, and n the number of families).

Then for the populations we studied, assuming that $R_k \approx V(k)/E(k)$, so that for $\bar{k} \approx E(k)$, and for $G(f)$ and $G(q) << 1$, (recall that f denotes fecundity and q denotes freshwater survival)

$$\frac{N_e}{N} \approx \frac{E(k)}{\frac{V(k)}{E(k)}+1} \approx \frac{1}{\frac{V(k)}{E(k)^2}+\frac{1}{E(k)}} \approx \frac{1}{G(r)+G(s)+\frac{1}{E(k)}}.$$

Assuming that $G(s)$ (s denotes marine survival) is approximately 1 [(the order of magnitude observed by Geiger et al. (1997)], and $E(k)$ is at the replacement level of 2, the ratio of effective population size to number of breeders might be expected to be crudely approximated in the populations we studied by $[1.5 + G(r)]^{-1}$. Then for an N_e-to-N ratio less than ½ (see Nunney 1995), this would mean that $G(r)$ (egg deposition and retention in the redd) would be less than one half – implying that mortality mechanisms in the marine environment predominate in the control of the effective population size and variation in family size. Alternatively, assuming a value of 1/10 for the N_e-to-N ratio, and making the same assumptions about other values, we find that $G(r) >> G(s)$ – suggesting that it is entirely plausible for family-specific variation in egg loss to have the greatest effect on effective population size and variation in family size.

In summary, family-specific egg retention, freshwater survival, or marine survival could influence variation in family size and effective population size in pink salmon. Considering variation in density, local summer freshwater warming, local winter cooling and snowfall, early marine conditions, and so forth, it does not appear that one source consistently controls variation in family size. Indeed each of these factors varies annually and intra-annually, and the effect on variation in family size must vary also. However, egg loss mortality and marine mortality appear to be responsible for most variation in family size in the managed populations of pink salmon we have examined, in which density has not been allowed to vary to extremes.

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Don't give them any more than what they want.

— Comment attributed to a former Alaska Department of Fish and Game commissioner, giving advice on how to manage seine fisheries

CHAPTER 5 – RECOMMENDATIONS TO MANAGEMENT

At the Alaskan Salmon Workshop on ocean-climate change held in Anchorage in 1999, Prof. Tom Royer made the point that oceanographers began the last century trying to describe the average ocean, but they didn't make any progress until they started studying why things vary. It turns out that many fields of science advanced in the 1900s by moving from a focus on averages, to looking at why things vary – especially the fields of statistics and genetics. R.A. Fisher (1970) made a similar point:

> The conception of statistics as the study of variation is the natural outcome of viewing the subject as the study of populations... To speak of statistics as the study of variation also serves to emphasize the contrast between the aims of modern statisticians and their predecessors. For until comparatively recent times, the vast majority of workers in this field appear to have had no other aim than to ascertain aggregate, or average values. Variation itself was not an object of study, but was recognized rather as a troublesome circumstance which detracted from the value of the average.

The previous three chapters of this dissertation are organized into a look at average life history benchmarks, a beginning of the study of variation in family size by looking at variation in the marine life stage, and then a chapter that takes on the question of why family size varies.

Why does variation in family size matter? Average family size is directly related to population size and population increases in any sexually reproducing species. In other words, the total population size is equivalent to the average family size, given the number of families in the previous generation. It is the variation between individuals within a population that allows some individuals to survive epizootic events, extreme environmental swings, and any number of the random hardships that kill some organisms, while others live; without this variation, a population in an unstable environment will decline and fail to recover. Individuals vary either from non-genetic causes or because of partial genetic control of (heritable) traits. Evolution can only act when there is both variation among individuals, and when there is an underlying genetic basis for the variation. Variation in family size is one way to observe and describe this selection, but in populations of wild animals, variation in family size over time indicates that that the favored genetic types are changing with the random environment.

The theory of gene diversity analysis (Nei 1973, Chakraborty and Leimar 1987) was developed to partition genetic variability into within and among subpopulation components. However, this theory is based on a somewhat artificial analysis of easily measured single-allele or simple multi-allele collections of traits. In wild salmon populations, from the human perspective, the most important trait is survival; what matters as far as stock productivity and evolution is how individuals differ in ways that affect survival.

In this final chapter, I will take a look at the guiding paradigm of Alaska's salmon management, the Ricker theory of stock and recruitment, in terms of Prince William Sound pink salmon. Even without bringing a great deal of understanding of pink salmon biology into the discussion, I take a look at alternative hypothesizes for recruitment to show why the view of recruitment should be expanded and approached with much more open mindedness. Next, I will review the results of Chapters 2 – 4, and try and draw my conclusions about the under-appreciated role of variation in the marine environment into some lessons for managers. Finally, I wish to return to the history of salmon management, which we reviewed in the first chapter, and reflect on the outlook for sustainability of Alaska's salmon resource.

An Example Of The Danger of Relying On A Single Model

The Alaska Department of Fish and Game's new Escapement Goal Policy states that "whenever the department wishes to establish a new [escapement goal] or modify and existing [escapement goal], a scientific analysis with supporting data must be prepared." Again, such an analysis is almost always synonymous with a "Ricker analysis" (Ricker 1975, Hilborn and Walters 1992, Quinn and Deriso 1999), or a similar "stock-recruit analysis," confined within some expanding perimeter of statistical options.

Writing about the effect of environmental factors and stock-recruit analysis, Walters and Collie (1988) state, "... feedback policies for dealing with unpredictable variation can be constructed without knowing the causes of the variation. *Once the statistical properties of the variation are specified* the same policy will be optimal no matter what the cause (emphasis added)." But, specifying the "statistical properties of variation" greatly begs the question. Making strong, untested assumptions about the statistical properties of variation are equivalent to simply making strong assumptions about the stock-recruit relationship (Schnute 1991). Assuming a simple, well-understood pattern of variation has a strong effect on what features of the data appear to be the stock-recruit relationship – even when they are not.

Consider the idea of stock-size contrast from the "adaptive management" literature (e.g., Walters 1986). Adaptive management proponents have argued that in order to increase certainty about the true underlying stock-recruit relationship, managers should intentionally manage to increase the variation in stock size. That way, there will be more observations at the low end of the stock, the middle, and the high end of the stock; any statistical relationship between stock and recruitment will be easier to estimate with regression or statistical curve fitting algorithms (Draper and Smith 1981). This idea has come up over and over recently in discussions about actual escapement ranges in Alaska. It just seems to be a matter of common sense that managers should increase contrast in the data, because to fit a statistical regression, it is always better to have higher contrast than low contrast (Figure 5.1).

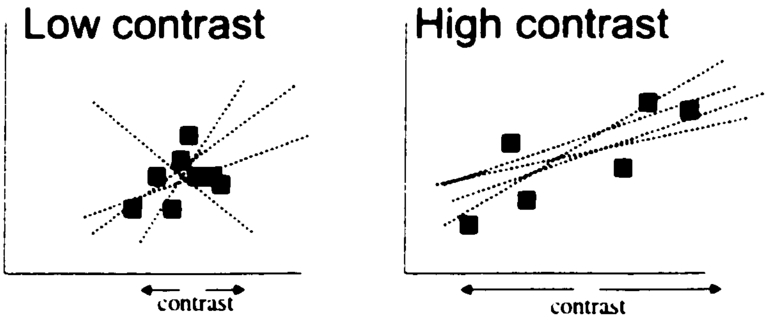

Figure 5.1. Hypothetical data and hypothetical fits of regression lines, showing how higher contrast leads to less ambiguous fits.

In salmon management, this has been translated into the practical advice as follows: allow escapement below the escapement goal during years of low recruitment, and allow escapement above the escapement goal in years of high recruitment. Many people have already noted this pattern occurs in Alaskan salmon fisheries because of the nature of management error, even when managers are not trying to increase contrast in the data, but are managing for fixed escapement goals (Eggers 1993, Geiger 1994, Schmidt et al. 1997).

However, a problem that should be obvious arises when (1) stock and recruit data points "cluster" because of step-environmental changes, persistent changes in predator or prey populations, etc., and (2) management error is correlated with recruitment (either by serendipity or because of the belief that this will create more contrast). When management error and recruitment are correlated, low values of stock tend to be paired with low values of recruitment in the near future, and high values of stock tend to occur during periods of high values of recruitment. Figure 5.2 shows recruits per spawner for Prince William Sound pink salmon prior to the *Exxon Valdez* oil spill, and prior to the influence of large hatcheries. Note that recruitment seems to change level every six or seven years in Prince William Sound, but these changes are much less pronounced for Kodiak.

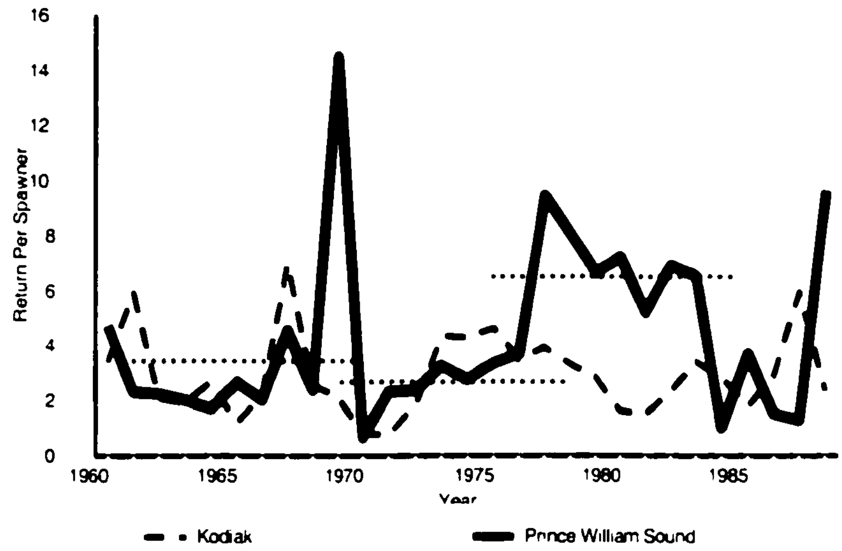

Figure 5.2. Pre-oil spill, and pre-hatchery returns per spawner for Prince William Sound and Kodiak pink salmon.

An analysis of Prince William Sound pink salmon data shows that underharvest (relative to a point escapement goal) does correspond to high recruitment events, and overharvest does correspond to low recruitment events (Geiger 1994). Because *low recruitment causes low stock size* – just the opposite of the theory, which states stock size causes recruitment – it is possible for the data to fit very well to an entirely incorrect model.

To be concrete, suppose that in Prince William Sound there are three "environmental states," which can be represented as stock-recruit curves, and that the environment switches states *at a random unpredictable time every several years* (Figure 5.3

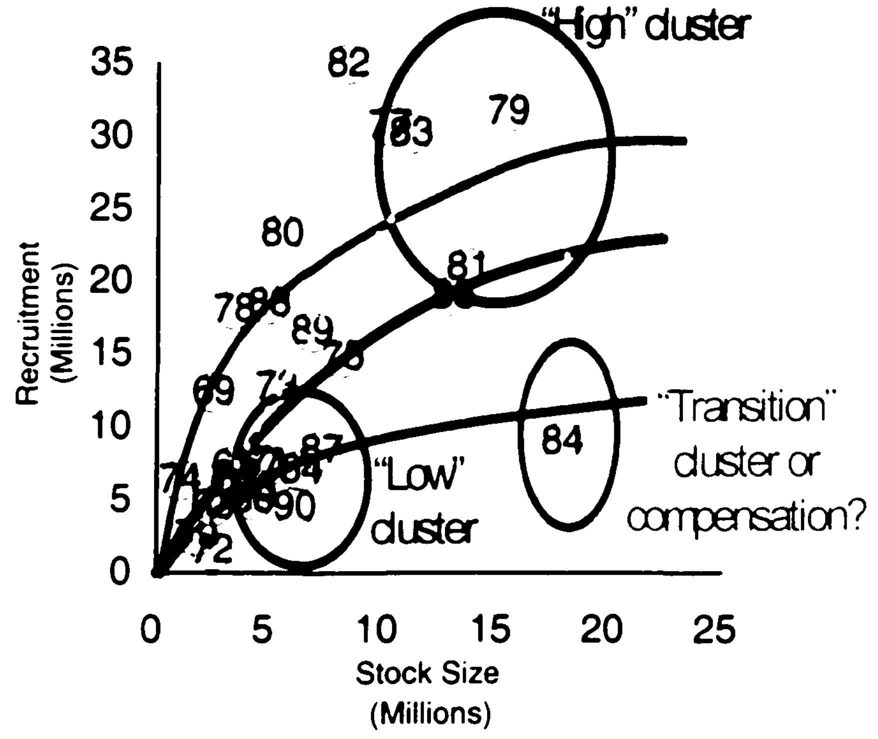

Figure 5.3. Stock-recruit data (provided by Sam Sharr, formerly of ADF&G Cordova, Alaska) from Prince William Sound Pink salmon with three hypothetical stock-recruit relationships, corresponding to hypothetical "environmental states," shown by the solid "stock-recruit" lines. During periods of persistent high or low recruitment, observations tend to fall into clusters. These clusters tend to form a spurious dome-shaped stock-recruit function (dotted line). The 1984 brood year, labeled "84," has traditionally been seen by managers as clear evidence of strong compensation mortality. However, this could also be a cluster formed by switching from a period of high productivity to low productivity.

Because the environmental states persist, the lowest stock-recruit curve is over-sampled at the low end of the stock size range (denoted "low clusters"); the high stock recruit curve is over-sampled at the high end of the stock size range (denoted "high clusters"), and in 1984 when the environment switched from "high" to "low" a single-point cluster occurred in a unique region. When the data is examined with a stock-recruit analysis, the relationship appears highly dome shaped, and considerably understates the stock's *average* yield potential at low stock sizes, and overstates the *average* yield potential at high stock sizes, and greatly misstates the stock's average response to very high stock sizes.

This "adaptive management" idea of increasing certainty about stock-recruit relationships pairing low escapement with low recruitment years and visa versa, can lead to poor predictions about how the stock will respond when the environment switches between "states." In these cases, conventional statistical measures, such as R^2, will provide incorrect guidance and lead to false confidence about model effectiveness.

The fact that analysts often get R^2 values near 0.8 or even 0.9 in Ricker-analysis relationships between the logarithm of the ratio of recruitment to stock size regressed on the stock size (e.g., Clark 1995, and many other examples) tends to reinforce the idea that stock size is a strong predictor of future recruitment. But the ability to forecast salmon production into the future has never been reliable, and stock size has not been an effective predictor of future salmon recruitment. Quinn and Marshall (1989) pointed out forecasts of Alaska salmon "have not been accurate." Geiger and McNair (2000) cite over 30 years of salmon forecast in Alaska, describing forecasts that have generally been based on stock and recruitment relationships; a review of those documents supports Quinn and Marshall's conclusion.

Caution about stock-recruit analysis with a cycling environment is found in the stock-recruit literature, and others have described similar situations with stock-recruit analysis (Botsford 1986, Collie and Walters 1988, Walters and Parma 1996, and elsewhere). Actual data sets from Alaska do seem to demonstrate an interaction of management error and persistent changes in recruitment level that produced spurious stock-recruit relationships using a conventional analysis, and show the under-appreciated role of high-frequency climate change in recruitment control.

A Ricker analysis of this Prince William Sound data will not necessarily lead to poor management, even if that analysis is based on a misreading of the situation, and even if the model incorrectly predicts the stock's future behavior. A Ricker analysis of this Prince William Sound stock-recruit data would lead to essentially status quo management, which seemed to be successful. Although there are certainly some controversies about what level of escapement is appropriate in several areas, I do not know of even one example in Alaska where a Ricker analysis has clearly led to a serious overharvest, or a serious loss of potential yield. The real danger from relying so strongly on a model of salmon recruitment that is very simplified, unsupported, and so strikingly unquestioned, is that managers can't ever gain any new understanding or insight, because all possible outcomes seem to support the single explanation for recruitment.

Unfortunately, if salmon production were to drop in 2002, salmon managers are not in a substantially better position to explain to the public what happened than they were when production dropped in the early 1970s. The 1997 El Niño event was widely reported on in the popular literature. So when salmon production dropped quickly in Western Alaska in the late 1990s, managers tentatively pointed to El Niño in public meetings and on radio interviews, even though there was no evidence that the effects of the 1997 El Niño had reached waters that Western Alaskan salmon would have encountered. Western Alaskan salmon managers continued to point to El Niño for several years when productivity did not return, because they really had no other way of looking at the problem. Indeed "El Niño" came to be a kind of shorthand for "we don't know why" in the jargon of salmon management of Western Alaska. It is hard to imagine that salmon managers are in much better position today than they were in 1970 to make sensible recommendations beyond simply reducing harvest rate for how to respond to a large-scale drop in salmon production, when their whole view of salmon recruitment is based on a model that predicts recruitment will immediately return to the long-term average once escapement has been controlled.

Lessons from Chapters 2 – 4 and Genetics in Salmon Management

Pacific salmon are exceptional top-level pelagic ocean predators, which breed in freshwater and spawn only once in their life. Salmonid species have fewer and larger eggs than most other teleost fishes (Elgar 1990, Marshall et al. 1997). Their embryonic development is extended in time and emergence seems to be strongly linked to food availability. Even within the genus *Oncorhynchus*, there is quite a bit of variability among life history strategies. Some species, such as sockeye or coho salmon, may have extended lacustrine or river residence. Pink and chum salmon have the least dependence on the freshwater lifestage, and usually migrate directly into the marine environment following emergence, with minimal freshwater residence. Chinook, chum, coho, and sockeye salmon have multiple age classes, which extend the effective population size, and hedge the population against year-class failure (Felsenstein 1971, Waples 1990). Coho salmon are strongly territorial as juveniles, and like chinook and sockeye salmon, they have a specialized freshwater life history strategy (Sandercock 1991). Although the previous three chapters deal almost exclusively with pink salmon, the basic management of all species is very similar, and the basic needs for sustainability are exactly the same: salmon habitat must be maintained and managed, human-induced mortality must be controlled, and managers must balance yield with the need for an adequate spawning stock sizes to sustain the run.

Pink salmon were used in the studies described in Chapters 2 - 4, because of their ease of study. Pink salmon have the least dependence on the freshwater environment of any of the five species of Pacific salmon in Alaska, and they virtually all return in a single age class; both features that make observations about variability in separate lifestages easer to find and interpret, and features that make conclusions about effective population size less cluttered. However, the simplicity of observing pink salmon complicates generalizing conclusions about the role of variation in Pacific salmon.

Salmon in Alaska show a large variety of patterns of behavior and adaptation. Most pink salmon populations in Alaska are found in short, coastal streams in Southeast Alaska, Prince William Sound, and Kodiak. Fall chum salmon migrate far up the Yukon River to spawn, but some coastal summer chum salmon stocks spawn within a short distance from salt water. Many lakes in Alaska have two or more runs of phenotypically distinct sockeye salmon, which have adapted to spawn in different habitats within the same lake system. So, variation on a very broad scale is both obvious and seemingly necessary for salmon to thrive in so many different habitats. That is, it is not hard to convince skeptics that stocks that are very visibly and obviously well adapted to a particular habitat need to be maintained to protect the productivity of that habitat. But the necessity of variation within a population, and that variation itself, is much harder to observe and describe and to convince the public of its importance.

The biology of Pacific salmon within the ocean is poorly understood, but because of the nearness to land the near-shore stage is the best studied of the oceanic phase. Referring to pink salmon, Heard (1991) wrote:

> Newly formed schools may move quickly from natal stream area or remain to feed along shorelines up to several weeks. That timing and pattern of seaward dispersal is influenced by many factors, including general size and location of the spawning stream, characteristics of the adjacent shoreline and marine basin topography, extent of tidal fluctuations and associated current patterns, physiological and behavioral changes with growth, and possibly, different genetic characteristics of individual stocks.

Heard's assessment leads to the conclusion that the phenotypes involved in early marine survival or mortality are probably often related to behavioral characteristics controlling early-marine growth and dispersal. The conventional view in salmon biology, dating back to the work of Parker (1962a, 1962b), is that the majority of marine mortality takes place in the very early marine lifestage, and this time is often thought of as a "critical period" for establishing the total size of the future return. Survival was formerly thought to be dependent on the juvenile salmon's ability to grow rapidly to leave the size class of preferred prey of the salmon's principal predators.

More recent work in Prince William Sound gives the impression that the situation is more complex than that, with both the preferred size class and the principal predators changing from year to year, depending on the availability of alternative prey, and the constantly changing size of predator populations (Cooney et al. 2001). As part of that same series of studies, Willette et al. (2001) reported on pink salmon losses to alternative predators – related to what they called the "prey switching hypothesis," and the "size-refuge hypothesis." They reported that, "Two facultative planktivourous fishes, Pacific herring (*Clupea pallasi*) and walleye pollock (*Theragra chalcogramma*), probably consumed the most juvenile pink salmon each year, although other gadids were also important." They went to say, "Our size-refuge hypothesis was supported by data indicating that size- and growth-dependent vulnerabilities of salmon to predators were a function of predator and prey sizes and the timing of the predation events." So again, the phenotypes that are affecting early marine mortality appear to be those related to dispersal and growth. But based on the new work from Prince William Sound, it appears that the favored phenotypes are changing as a function of predator abundance, the distribution of the ratios of predators, and the sizes of predators – and these controlling attributes of predators are constantly changing.

The first lesson to take from the previous chapters has to do with the role of variation among individuals in a population in relation to a variable marine environment. As previously mentioned several times, managers in Alaska have tended to look to the freshwater environment to explain variation in salmon recruitment, especially in the case of pink salmon, which have the most variable and unpredictable yield in the Alaskan commercial salmon fishery (Quinn and Marshall 1989). Mangers looking for evidence of the relative stability of the marine environment sometimes cite high R^2 statistics from Ricker analyses. Studies looking directly at partitioning survival estimates into lifestages have not been fashionable in Alaska. In careful studies of the survival of managed coho salmon in Southeast Alaska – a species with strong dependence on the freshwater lifestage – Shaul (1998) concluded that the marine environment contributed 27.0%, 48.4%, 39.2%, 73.0%, 51.6%, and 60.8% to the overall estimates of survival in the populations he examined; his overall estimate of the average percentage of variation in adult abundance due to marine survival was 61.8%. Evolution operates on traits that vary if there is a genetic basis for this variation. We saw in Chapter 3 that marine survival had more genetically based variation than freshwater survival in pink salmon, and this emphasizes the importance of the unobservable, unobvious variation.

Salmon managers and scientists should now know from experience, and from the previously cited developing body of knowledge from the atmospheric sciences and oceanography, that the ocean changes states at random, unpredictable times (see Chapter

1 for a discussion of this), and salmon productivity is strongly tied to these environmental states. These changes have tended to confuse management, because managers have tended to think of recruitment only in terms of stock size, and possibly weather phenomena they could sense in the terrestrial world. The results in Chapters 3 and 4 and Shaul (1997) support the hypothesis that salmon populations have evolved to be prepared for moderate change and instability in the marine environment, and that genetic variation in traits that affect survival in the marine environment are important for conservation or for an exploitable potential yield.

The second lesson to take from the previous chapters has to do with the ratio of effective population size to census size. We saw in Chapter 3 that family-specific variation of survival in the marine environment alone might be enough to reduce the effective population size to between, maybe, 30 to 80% of the census population size of pink salmon with populations that are stable or increasing. The situation is much more complex in other species of Pacific salmon, because variation in the freshwater environment is undoubtedly more important, and because the presence of multiple age classes expands the effective population size and makes its calculation or estimation more complex (Waples 1990). We saw that Simon et al. (1986) generated results with hatchery-produced coho salmon that were very near the results with pink salmon in Chapter 3 – not surprisingly, as coho salmon have a relatively limited distribution over ocean-age at return. Hedrick et al. (2000) examined the effective population size of captive and endangered hatchery-produced winter-run chinook salmon, and estimated an effective population size slightly larger than the census population in one year, and an effective population size half of the census population size in another year. The Hedrick et al. data set is hard to draw general conclusions from, because these fish were bred using a protocol to keep the effective population size high; and they interpreted their results as evidence of the success of that protocol. Waples (1990) shows how the presence of multiple age classes in chinook salmon extends their effective population sizes. Considering everything we have learned by examination of effective population size in Pacific salmon, the direct measurements do not conflict with Nunney's (1995) conjecture that effective population size should be near half of the census stock size, and rarely less than 25% for pink salmon with their single age class. For other species, additional family-specific variation in the freshwater environment should tend to reduce the ratio of effective population size to census population size, but the extended age classes at return should tend to inflate this ratio.

Finally, after reviewing the material in the previous chapters, can variability of family size be used as a new way to communicate about genetic ideas, such as effective population size, and affect important decisions in salmon management? Currently genetic ideas are not used to their full potential in the salmon management decision process, whether deciding about escapement goals, enhancement, or habitat alteration. To some extent, this is because fishery genetics education has failed to reach many of the people that go into fishery management, and certainly failed to reach most influential members of the general public. Although there are definite exceptions, many senior managers within the Alaska Department of Fish and Game that do have advanced training in genetics have often studied the agricultural model that applies to the breeding of captive animals in controlled environments. When combined with the fisheries bias towards seeing the ocean as a stable, unchanging environment, the need for genetic variation has been under-appreciated in salmon management in Alaska and elsewhere.

At least in Alaska, general genetic principles can be seen to have affected large policy statements about management. For example, the State of Alaska has a genetics policy (ADFG 1985). However, the field of genetics has probably not had the same effect on decisions about enhancement or habitat alteration as say, the field of fish pathology. Fishery managers, regulators of enhancement, and influential members of the public see genetics as abstract and confusing, and a field that rarely has concrete advice based on broad consensus within the field.

Often genetic advice is simply excluded from important decisions about salmon management because genetics does not offer a simple calculus, or economics, to examine tradeoffs. In other words, managers have simply been puzzled about how to use genetic advice in the process of making unavoidable decisions with potential losses of costs associated with each decision option. Consider for a moment the advice that genetic variation must be preserved. Industrial fishing, undoubtedly reduces overall genetic variation, as does the natural ecological process of forest succession, as does unavoidable climate change, as does many forms of development. If the advice is, allow nothing that will reduce genetic variation, that impractical advice will just not be considered. This advice simply does not fit the need, which is to make tradeoffs.

Is the point of all of this that managers need a new, more complex recruitment model – perhaps a model like the Ricker model, but one that incorporates effective population size and other genetics concepts? I think the answer is no. First, there are just too many principles and too much specific technological knowledge to produce a workable, robust model: principles from genetics, limnology, economics, ecology, and technical knowledge economics, other social sciences, and on and on. Adding a lot of complexity and a lot of parameters to the model, especially parameters describing factors that are not well studied will just erode the robustness of the model, and result in a loss of model precision.

Moreover, management has goals that are much bigger than simply controlling harvest rate in the short term. Unfortunately, some of these goals are in conflict. One of management's most important goals is to maintain public confidence in its ability to study and understand the dynamics of the resource. The public is looking to managers to help ensure that the resource will last far into the future. The goal of sustaining the resource in the long term is very different than simple management tasks, like choosing among escapement goals. This is especially true when managers are faced with the issues of enhancement, alternate habitat uses, or other tradeoffs. In other word, managers are faced with a complex world, complex set of challenges, yet they have been looking for guidance from very simple models. I believe this may be what Larkin (1988) meant when he stated, " Present management, albeit moderately successful, is characterized by reaction and a special jargon of stained glass language."

Any action that can change the phenotypic distribution within an animal population can reduce the genetic variation the population may need in the future for both yield and for sustainability. Fishing activities can and do change size, age of maturity, geographic distribution, timing, and other characters related to fitness (Conover and Munch 2002). Managers don't need just more and more inputs into the models they use to justify their actions. Managers clearly need a better overall understanding of the consequences of a large variety of actions, and they need a better calculus for explaining tradeoffs to the public and themselves. It seems that the best that we can hope for, at present, is that managers try to draw on a wider range of technical knowledge from a variety of fields, and managers focus on the possible consequences that flow from such things as enhancement or climate change if their models are wrong. It seems the most important need for future research is work that moves towards a calculus that helps show the specific effects on, costs to, and tradeoffs involving genetic resources, as a consequence of various actions.

In the mean time, the larger conclusions from Chapters 2 through 4 are that sustainability and yield are dependent on moderate or large stock sizes, and that genetic variability is important – again, ideas that don't give managers any specific or concrete operational guidance in a specific situation, where management is asked to make tradeoffs. But even these larger conclusions are often hard to communicate to the general public – especially when the conclusions are supported by unintuitive technical terms and estimates of highly specialized genetic parameters. The concept of variation in family size may be a better way to try and communicate with the general public about a number of deeper genetic concepts like effective population size, heritability, selection, and fitness. In other words, by explaining that some families have higher survival, greater yield, and a greater contribution to future runs, and that the preferred families are unpredictable – an idea that appeals to common sense – the link between genetic variation and production and sustainability might be easer to bring to a decision.

As we saw in the third and forth chapters, even when family size varies for purely random reasons, variation in family size controls the amount of genetic variation a population can hold. In the case of Pacific salmon, this genetic variation, together with a changing environment, are the sources of population increases and the production surplus to what the population needs to sustain itself. Although these results do not help salmon managers find exact escapement levels for particular situations or systems, these results supply more justification for the principles that stock sizes need to be maintained at high levels, all genetic components of the runs should be maintained, and that removals from the population need to be balanced with the number of animals that must be returned to the population for it to be sustained – principles that are already well established. However, these results also show a more important principle – one that is not well established, but should be – that instability and variation are important features of the recruitment process, so loss of genetic variation has a concrete cost.

Effectiveness of Management and Implications for Policies

An obvious question is how should the results of previous chapters affect the policies of the Alaska Department of Fish and Game? The Alaska Department of Fish and Game already has probably the most extensive, complete, and well thought out policies to protect wild salmon of any management agency in the world. For example, the ADF&G genetic policy (ADFG 1985) restricts movement of fish, and places boundaries on hatcheries and enhancement activities. Recently, the Alaska Department of Fish and Game and the Alaskan Board of Fisheries standardized and formalized some long-standing principles and procedures, and jointly prepared a policy on sustainable salmon fisheries, and the Board formally placed the policy into regulation in November, 2000 (5 AAC 39.222). The *Policy for the Management of Sustainable Salmon Fisheries* directs the Department of Fish and Game to require assessments necessary for sustainable management of existing fisheries and wild stocks (section c.3.J). In the coming years, these assessments should take a more standardized form, and they should be produced on a predictable three-year cycle. The policy requires the Department to protect wild stocks and fisheries on them from adverse impacts from artificial propagation and enhancement efforts (section c.1.D); to develop and to review periodically management objectives in harvest management plans, strategies, guiding principles, and policies for hatchery production (section c.3.B); and to document potential impacts and gather other information needed to assure sustainable management of wild stocks (section c.3.K). Moreover, the policy requires the burden of proof to be placed on the proposers of activities that "...pose a risk or hazard to salmon habitat or production" (section c.5.A.v). The policy outlines procedures for the establishment of an escapement goal – expressed as a range – and defines a *sustainable escapement threshold* as a value that triggers a procedure for classifying the stock as a stock of concern, when management allows this threshold to be crossed.

Under the Policy, three levels of concern are defined, which the Department will use in the future to describe stock status. A *yield concern* is defined to be a chronic inability, despite specific actions, to meet "expected yield," which is essentially the lower end of the yield that had been observed in the recent past. This is the least serious level of concern. A *management concern* is defined to be the chronic inability, despite specific actions, to maintain escapement within the stated escapement goal range. The most serious classification is a *conservation concern*, defined to be the chronic inability, despite specific actions, to maintain escapement above the *sustainable escapement threshold*.

These policies are an attempt to formalize the management behavior that led to such high yields when the environment was favorable in the late 1980s and the 1990s, and the behavior that protected salmon stocks when the environment was unfavorable in the 1970s. The real test of management is what it does when runs decline. As mentioned several times previously, beginning in the late 1990's, returns of many Western Alaska stocks fell dramatically. Management (ADF&G and especially the Board of Fisheries) responded by essentially eliminating commercial fishing and drastically reducing subsistence and sport fishing in the affected areas. These disruptive fishery closures were in an area with few other economic opportunities, yet there was strong public support for these closures because of the high value Western Alaskans place on future runs.

However, it is not hard to find cases where the Alaska Department has simply ignored policies when there was strong public pressure to do so. A good example of this would be the continual overharvest of wild pink salmon in Prince William Sound in the early 1990s. Geiger et al. (1992) stated,

> In 1992, the smallest number of even-year wild pink salmon spawned since statehood. In spite of this shortfall, fishermen harvested nearly 75% of the wild run. To put these numbers in perspective, managers closed the directed pink salmon fishery in 1972 and 1974 for conservation reasons – yet in these years more wild spawners were observed in the streams of Prince William Sound.

This pattern of overharvest continued, even while Alaska Department of Fish and Game officials were publicly stating that they would not allow this to happen. Geiger (1994) explains how escapements to the northwestern Prince William Sound began to fall, as production from Prince William Sound's large pink salmon hatcheries came on line. Templin et al. (1996) shows that these northwestern stocks were being harvested with excessive harvest rates in large hatchery fisheries. It is probably the case that uncontrolled harvest of wild stocks in northwestern Prince William Sound caused a far bigger loss of adult wild-stock salmon than the *Exxon Valdez* oil spill. The escapement situation, both in terms of actual escapement numbers and the distribution of the escapement, have improved, and one would like to think this is because of an intentional correction of management to bring their actions in line with the policy. However, it is more likely that this is simply the result of the drastic drop in the price of pink salmon, which has simply reduced the competitiveness of the fishing in western Prince William Sound.

Part of the strength of management comes from the public's trust that the managers understand the resource. Management cannot take painful and disruptive actions unless the public trusts that managers understand the dynamics of the resource and that managers are working in the resource consumer's best interests. Lichatowich's (1999) history of the failed salmon management in the Pacific Northwest is a study of management that is unable and unwilling to question its assumptions, and unable to adapt to failure and improve.

The Outlook for Sustainability

Both the Pacific Northwest and Alaskan salmon management has over 100 years of experience managing large fisheries and the salmon and habitat that support them. At the seventh Alaskan Salmon Workshop in Anchorage, Jeff Cederholm from the Washington Department of Natural Resources warned Alaskan managers that they were failing to learn the lessons of management of the Pacific Northwest. As he described his interpretation of these lessons, which involved maintaining high levels of marine derived nutrient levels in streams, it occurred to me that few people understand the history of either the Pacific Northwest or Alaska, and that that there is a lot more to sustainability than very specialized technical knowledge – whether it is knowledge of marine derived nitrogen, variation of family size, or mathematical descriptions of the recruitment process.

In the sense that commercial harvests in Alaska increased by a factor of 10 from 1974 to 1995, the management has been successful, and management's policies have worked. But just as it would be misguided for Alaskan salmon managers to try and take all the credit for increases in production, which we now know are partially the result of favorable environmental conditions of the 1980s and 1990s, it would be even more misguided to give all the credit to managers for forming effective management policies and actions. Managers have been able to take effective and painful actions when they have had broad public support, and they have been thwarted when they lost public trust, or otherwise lost public support. We saw in Prince William Sound, that simply having a strong policy to maintain wild stock escapement was meaningless without strong public support for that policy. At other times, managers took actions to increase run sizes and took concrete steps to protect wild stocks – and this was possible because of broad public support for strong fishery and habitat management, and a strong and loud public lobby for effective management policies.

The single most important lesson from the failed management of the Pacific Northwest is that when salmon lost their value to the residents of the region, management could not function effectively. Salmon was a foundation of the economy of the Pacific Northwest a few hundred years ago, but as NRC (1996) observed: "The Euro-American settlers that migrated to the region in large numbers after 1800 were farmers." The NRC report goes on to document how salmon were less valuable to the industrial economy of the Pacific Northwest than the agricultural activities, the logging, and the many other activities that a strong fishery management would have interfered with. Alternatively, the salmon resource has remained every bit as important in the economy of Alaska as it did before the Euro-Americans arrived in the 1800s. At the peak of the resource's ex-vessel value, in the late 1980s, the seafood harvesting industry was the largest private-sector employer in the Alaskan economy, both in terms of income and employment (Jeff Hartman, Alaska Department of Fish and Game, personal communication).

The most important lesson about sustainability from the last 50 years is that salmon must have enough value to support a well-organized, politically powerful lobby for conservation. At the time of statehood for Alaska, the two important goals for fishery management were to take control of the biological management of the runs, and equally as importantly, to broadly distribute the economic benefits of the resource.

In looking to the future, I suspect that two factors will affect the long-term status of Pacific salmon in Alaska more than any others. The first is the ocean-climate change, which is essentially unpredictable at this time. But even so, for over 40 years the Alaskan public has encouraged their managers to respond to unfavorable environmental conditions by controlling harvest rates and protecting habitat. The more important factor in the biological health of salmon is the economics of the salmon trade, and the value that Alaskans place on salmon. The commercial value of salmon in the Alaskan economy has fallen dramatically to less than a third of its nominal ex-vessel value in the since the late 1980s (Geiger and McNair 2001). The value of salmon for subsistence and in the sport fishery has probably increased quite a bit, although this is a much harder thing to measure on a similar scale. If the loss of commercial value of salmon does not reverse, it will remain to be seen how society will trade the need to protect genetic variation and large, sustainable salmon populations against pressures pushing towards development, urbanization of salmon habitat, and benefits that come from habitat alteration. Currently, the most important conservation genetics issue in Alaska maybe the loss of a strong, healthy, well-funded salmon industry that places a high economic value on the future existence of Pacific salmon.

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