CHANGES IN SIZE AND AGE AT MATURITY OF COLUMBIA RIVER UPRIVER BRIGHT FALL CHINOOK SALMON (*ONCORHYNCHUS TSHAWYTSCHA*):

IMPLICATIONS FOR STOCK FITNESS, COMMERCIAL VALUE, AND MANAGEMENT

Technical Report 96-7

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August 30, 1996

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ABSTRACT

The average size and age of chinook salmon (*Oncorhynchus tshawytscha*) caught in commercial fisheries along the Pacific Coast of North America have decreased substantially in this century. These declines might be caused in part by changes in size and age at maturity within the stocks contributing to those fisheries. Upriver Brights (Brights), a stock of fall chinook salmon in the Columbia River, are one of those stocks. The purposes of this study were to (1) determine if average size and age at maturity of Brights have declined, (2) gain a better understanding of the factors that may contribute to such declines, and (3) describe potential consequences of these changes.

Data from in-river fisheries suggest that the average weight of mature Brights returning to the Columbia River has decreased approximately 2.7 kg since the 1910s, an average rate of about 45 $g \cdot yr^{-1}$ (0.1 $lb \cdot yr^{-1}$). Most of the potential biases in these data tend to make this estimate conservative. Insufficient data were available to describe changes in average age at maturity.

There are many potential causes for the decline in average size of mature Brights, including factors that affect very early life stages. Other researchers have determined that size at maturity appears to be highly influenced by inheritance, gender, and growth rate. I describe how maternal size can influence -- through time of spawning, choice of spawning site, and egg size -- the viability of the young, which carry the dam's genes for size. The size-related ability to produce viable offspring may have been changed by modifications in the environment. Very little is known about how changes in the natural environment for spawning, incubation, and rearing may have contributed to a decline in average size at maturity. Artificial propagation and rearing, such as at Priest Rapids Hatchery, seems to produce adult Brights that are smaller, younger, and more likely to be male than their natural counterparts. The net result is that the average hatchery fish may have only about 0.80 of the reproductive potential of the average natural fish. Changes in growth

conditions in the ocean probably did not contribute to the change in size, although the ocean fisheries of Southeast Alaska and British Columbia appear to select, in the genetic sense, against large size and old age in Brights.

Since 1978, in-river commercial fisheries have caught larger Brights and a higher proportion of females than are found in the escapement of the Priest Rapids Hatchery component of the stock, but the fisheries impact the two sexes differently by taking the <u>larger males</u> and the <u>smaller females</u>. The effect on the natural component may differ because of their apparently larger average size. I found no evidence that larger fish or more females were caught when 8-in. minimum restrictions were in effect on gillnet mesh size relative to periods when mesh size was not restricted. Impounding the mainstem during the last 50+ yr may have removed obstacles to migration (e.g., Celilo Falls) that selected for large size in Brights, but that hypothesis could not be tested.

The perseverance of larger and older phenotypes in the Bright stock suggests that countervailing selection --perhaps during spawning, incubation, and/or early rearing -- may have resisted the effects of a century of size- and age-selective fisheries. That resistance, however, may reduce the productivity of the stock.

Declines in average size and age at maturity can have undesirable consequences. Lower average size means less biomass landed and lower commercial value. Lower average fecundity and a diminished ability to reproduce in some environments are also expected. Loss of size and age classes may reduce the ability of the stock to adapt to environmental variations.

These results are relevant to several management practices. A holistic approach to fishery management issues is necessary to avoid erroneous conclusions based on narrow perspectives. Measuring reproductive potential of the catch and escapement would be superior to the conventional practice of simply counting numbers of fish. Many aspects of artificial propagation can be improved, including broodstock acquisition, mating regimes, and rearing practices. Stock abundance is a major factor in determining the effect of many management practices on the stock. In general, fisheries managers must be mindful that they manage very complex natural systems.

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PREFACE AND ACKNOWLEDGEMENTS

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INTRODUCTION

The Problem

Declines in Size and Age

The average size and age of chinook salmon (*Oncorhynchus tshawytscha*) caught in commercial fisheries along the Pacific Coast of North America have decreased substantially in this century. Troll-caught chinook salmon taken in British Columbia tagging studies of 1949-52 were dramatically smaller and younger than those taken in similar studies during the 1920s (Milne 1957). Between the 1926 and 1949 studies, the modal age of the catch decreased from 4 yr to 3 yr, and age classes 5 and 6 disappeared. At the same time the contribution of fish larger than 19 lb dropped from over 43% to less than 1%. The mean weight of chinook salmon taken in the lower Columbia River (Zone 1) gillnet fishery was significantly lower during 1951-60 than during 1918-40 for all four seasonal fisheries except spring (Pulford 1964). A significant decrease in size also occurred within the period 1951-61 for the same three seasons.

By 1975, catches of chinook salmon by the Washington coastal troll fisheries were markedly younger than during previous periods (Miller 1977). The contribution of age 3 fish to the commercial fishery increased for periods from 1950 to 1975, with concurrent declines in the contributions from older ages. Ages 2 and 3 contributed proportionately more to the sport fishery during 1970-75 than during the earlier period, 1964-69. A shift toward smaller lengths taken in both fisheries reflects the trend toward younger fish in the catch (Miller 1977, Fig. 9 and 10).

Fisheries in British Columbia and Southeast Alaska exhibit a similar trend (Ricker 1980). Average weights of chinook salmon in the British Columbia catch declined by nearly 33% between 1951 and 1975, approximately 0.22 $\mathrm{lb\cdot yr^{-1}}$. In the Southeast Alaska troll fishery, average weights decreased at a rate of 0.31 $\mathrm{lb\cdot yr^{-1}}$ from 1960 (17.6 lb) to 1974 (13.3 lb).

After a comprehensive review of size and age trends in chinook salmon catches of the Eastern Pacific Ocean, Ricker (1980) concluded that by 1975, average weights were no more than half of those recorded 50 yr earlier. Even the earliest size and age data that he examined do not represent populations untouched by harvest, as intensive fisheries had operated in some areas for decades prior to the 1920s. Because data from the period prior to heavy exploitation is lacking, the actual magnitudes of declines in size and age since that time may well exceed the estimates of Ricker (1980) and others.

Causes of Declines

Reasons for the declines in size and age of chinook salmon in the fisheries remain unknown, although hypotheses abound. Ricker (1980, 1981) proposed eight possible causes, including the fisheries themselves, environmental changes, and genetic changes. He focused on high exploitation rates by size- and age-selective fisheries as probable agents of genetic changes within and among stocks. Other researchers have supported the same hypothesis (Henry 1971; Van Hyning 1973; Schaffer and Elson 1975; Montgomery 1983; Hankin and McKelvey 1985), but there remains some doubt whether fisheries select with sufficient intensity to override natural forces (Healey 1986; Porter et al. 1986; Riddell 1986). The actual causes are so obscure, numerous, and complex that they will probably never be entirely unravelled.

Consequences of Declines

These trends have had obvious adverse impacts on the fisheries. With ceilings on number of fish harvested, fishery revenues are directly related to average weight of the fish caught. Still, the more important long-term potential consequences are less obvious.

Detrimental demographic changes in chinook salmon stocks may be associated with the trends observed in the fisheries. Many theorists argue that the loss of life history types, represented in part by adult size and age classes, may reduce the capacity of a population or species to evolve (Murphy 1968; Schaffer 1974; Helle 1981; Meffe 1986; Hirai 1987). In more immediate terms, if size and age distributions of a population represent adaptive traits (Healey 1986), then anthropogenic changes in those traits could reduce population fitness (Hershberger 1976a; Kapuscinski and Jacobson 1987). Smaller spawners tend to be less fecund (Rounsefell 1957; Mathews and Meekin 1971) and may be less well adapted for reproduction in the native environment (Ricker 1972; Schaffer and Elson 1975; van den Berghe and Gross 1984; Healey and Heard 1984). Less fit spawning populations, which produce fewer recruits, further diminish revenue opportunities in the fisheries.

Despite the great interest and debate regarding declines in size and age in the fisheries, the biology of the individual chinook salmon stocks forming the essential productive foundation of the fisheries has attracted little attention. Have average size and age declined in these stocks? If so, what are the causes and consequences? Examining the problem from a stock dynamics perspective might provide new insights.

Purposes and Overview

This study examined Columbia River upriver bright fall chinook salmon (Brights), a stock closely associated with the problem. Brights are of international interest, making substantial contributions to the ocean fisheries of Southeast Alaska and British

Columbia (Howell et al. 1985a; PSC 1988) and to Columbia River fisheries (ODFW and WDF 1990), in which size and age declines have been documented. The Bright stock was of critical concern during negotiations for the 1985 U.S.-Canada Pacific Salmon Treaty (PST)(Jensen 1986) and is now an indicator stock for monitoring exploitation and escapement during implementation of the PST (PSC 1988). Much production of this stock still occurs naturally (Norman 1984; sources cited in Dauble and Watson 1990), so maintenance of adaptations to the natural freshwater habitat is also important.

Study objectives were to:

1) Determine if average Bright size and age at maturity have declined.
2) Gain a better understanding of factors that cause changes in size and age at maturity of Brights.
3) Describe potential consequences of changes in size and age.

This report is structured around the three study objectives with some additional supporting chapters. Two supporting chapters, which immediately follow, describe the theoretical context of the problem and define the Bright stock. Then the objectives are addressed in turn. Applicable hypotheses, methods, results, discussion, and conclusions are included within appropriate chapters and sections. Concluding chapters describe management considerations and make an overall summary.

THEORETICAL CONTEXT

Evolutionary and related theories provide an essential context in which to consider the significance of changes in size and age at maturity of Brights. These theories will be briefly discussed, and a simple conceptual model of the life cycle will be used to apply theory to the problem.

Evolution, Life Histories, and Adaptive Capacity

Since Darwin (1968, from 1859 original) proposed his "theory of descent with modification", science has sought to better understand the processes of natural selection and evolution. Why do some organisms survive and reproduce while others do not? What traits confer greatest fitness in a given environment, and how must individuals, populations, and species adapt to maintain their fitness in variable environments?

The definition of fitness lies at the very heart of such questions (Stearns 1976). Fitness, according to Stearns (1976, p. 4), is "Something everyone understands but no one can define precisely," but he identifies "fit" organisms as "those better represented in future generations than their relatively unfit competitors." Falconer (1981, p. 301) limits fitness of an individual to "the contribution of genes that makes it to the next generation, or the number of its progeny represented in the next generation," but later (p. 303) he appropriately includes the "quality" of the offspring (F_1) as a component of fitness. Offspring "quality" is presumably their own fitness, which is measured by the number and fitness of their progeny (F_2), whose quality is in turn measured by the number and fitness of their own progeny (F_3), and so forth through subsequent generations (F_4...). Hence, the fitness of the original organism (P_1) depends not only on its relative contribution of offspring to the succeeding generation (F_1), but also on its contribution to the population innumerable generations into the future (F_n).

Such a concept of fitness, analogous to Endler's (1986) "durability" and virtually identical to Cooper's (1984) "expected time to extinction", precludes direct measurement because it is a function of uncertain future performances. Only when an organism dies without reproducing is its fitness known (it would have zero fitness). Therefore, fecundity, probability of survival to reproduce, the relative production of viable offspring, and the intrinsic rate of increase are among the commonly used surrogate (or "derived", Cooper [1984]) measures of fitness. These measures will be used as general approximations of fitness in this report. However, the all-important component of long-term persistence must not be forgotten.

A fit organism must adapt to a sequence of environments between conception and death, the pattern of such adaptive changes being known as the organism's life history (Lande 1982). Theorists, drawing heavily upon patterns of mortality and reproduction (for example, Schaffer 1974; Stearns 1976; Stearns and Crandall 1984), attempt to generalize about how life histories relate to the environments in which they occur (Warren and Liss 1980). Stearns (1976) provides an excellent review of life history theory and summarizes the optimum life history strategies that would theoretically be expected under certain environmental conditions.

Common life history patterns are generally presumed to be adaptive, the result of natural selection by prevailing environmental patterns. However, some theorists suggest that some life history traits may be nonadaptive phylogenetic residue (Gould and Lewontin 1979) or merely phenotypic responses to recent environmental changes (Nelson and Soule 1986). Also, mobile organisms have some ability to select their environments, so selection is not a simple unidirectional process from environment to organism. Both adaptive and nonadaptive life history traits no doubt exist, but because current knowledge rarely permits the two types to be differentiated, it seems prudent to assume that prevalent values of life history traits are to some degree adaptive. For example, if the most common age at maturity (a life history trait) is 4 yr (a value of that trait), then it is likely that maturing at age 4 has been adaptive, relative to maturing at other ages, in the present and past generations.

Environments are spatially and temporally variable to some degree; hence, no single life history type will be optimal in all locales or at all times. Indeed, there is a growing belief that diverse life history types are required for populations and species to adapt, evolve, and persist. This idea is not new; Darwin (1968, p. 163, from 1859 original) recognized the adaptiveness of intraspecific diversity. Recent support comes from theoretical and empirical work at the population and species levels (Van Valen 1965; den Boer 1968; Murphy 1968; Williams 1975; Warren and Liss 1980; Gross 1984; Meffe 1986; Hirai 1987). Although natural selection will favor one life history type (the optimum type) above all others in a particular environment, a population must maintain an array of types to retain its adaptive capacity (Thompson 1951, 1959; Warren and Liss 1980).

The population or species itself -- its abundance, mating habits, etc. -- is an environmental component in natural selection that is easily overlooked despite its possibly preeminent role in the evolution of life history patterns (or strategies, Gross 1987). Competition between closely related individuals or groups, such as for food or mating opportunities, may be a greater arbiter of fitness than physical or other biological environmental components (Darwin 1968, from 1859 original; Gross 1984). Sexual selection, discussed by Darwin (1968, from 1859 original) and Endler (1986), exemplifies interactive processes that can favor traits that might otherwise be maladaptive. Life history patterns must be interpreted in their social as well as their physical context.

To recapitulate: existing life history patterns reflect, at least in part, natural selection associated with certain environments. Intrapopulation and intraspecific interactions may be major fitness-determining components of the environment. Fitness is measured not merely by survival and short-term reproductive performance, but by adaptive capacity -- the ability to adapt and persist under environmental uncertainty. Adaptive capacity resides in life history and population diversity.

Relevance of Theory to the Study Problem

Differences in size and age at maturity represent some of the differences among life history types of chinook salmon. These differences may in turn represent adaptations to different environments (Warren and Liss 1980; Healey 1986; Nicholas and Hankin 1988).

The relationship between life history types and the sequential environments of anadromous chinook salmon life-cycles can be illustrated with a simple graphic model (Fig. 1). Consider the continuous sequence of environments as series of discrete events, with eachevent associated with a simplified developmental states: incubation, early rearing in fresh water, downstream migration, ocean rearing, spawning migration, and spawning. Within each developmental environment, limiting factors constrain chinook salmon to a window of opportunity that permits continued development. The relatively few fish that successfully negotiate all windows survive to reproduce, and the various patterns of their adaptations constitute successful life histories. To the extent that the adaptations are heritable (see p. 43, Heritability of Size and Age at Maturity), the successful life history types will be represented in the next generation. If the windows of opportunity are similar for the next generation, then those offspring inheriting previously successful adaptations will be favored, and selection for optimum life history types will continue.

Developmental environments influence size and age at maturity in at least four principal ways: (1) selecting optimal sizes and ages for spawning migration and spawning (direct selection), (2) selecting traits for other developmental environments that are correlated with size and age at maturity (indirect selection), (3) inducing purely phenotypic responses that do not change the relative fitnesses of size and age genotypes, and (4) reducing effective population size and thereby increasing the frequency of random genetic events.

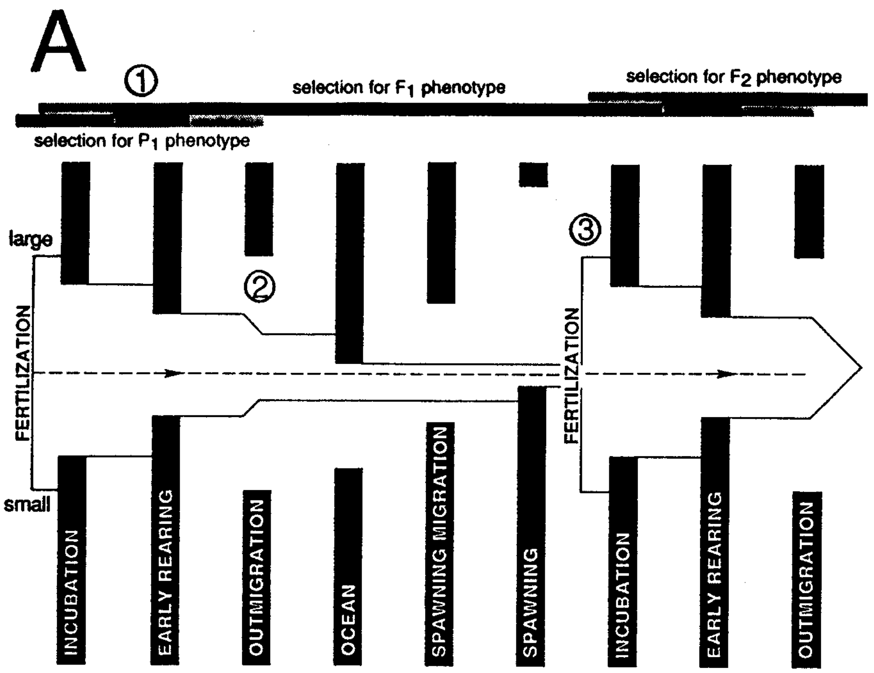

Figure 1. Selection by environmental "windows" and other possible reasons for change in size at maturity of Brights. Each generation begins at fertilization with the genetic potential for a range, from large to small, of sizes at maturity. As individuals of the generation develop, the various environments may select against particular sizes at maturity either directly -- as during the spawning migration and spawning, when the traits are expressed -- or indirectly by acting on correlated traits. Vertical bars represent simplified environments; vertical distance between the solid horizontal lines represents the range of potential sizes and, in some cases, numerical abundance of individuals. Dashed lines show range mid-points at relevant periods in the life cycle. Truncation selection is shown for simplicity, although environmental windows would not select so sharply on a quantitative trait like size at maturity. Note that selection may operate continually as the population flows from generation to generation, but the results are observable only during the spawning migrations and spawnings of each generation.

A. Because the size of the female parent greatly influences the phenotype of the progeny during their early life stages (see *Maternal Influences*, p. 50), selection on maternal size continues into the filial generation (1). The outmigration environment (2) may not be selective for adult size (hence the broad window), but a narrowing of the band represents a reduction in numbers due to high mortalities. At fertilization (3), genetic recombination regenerates a range of potential sizes at maturity, centered on the average parental size, in the next generation.

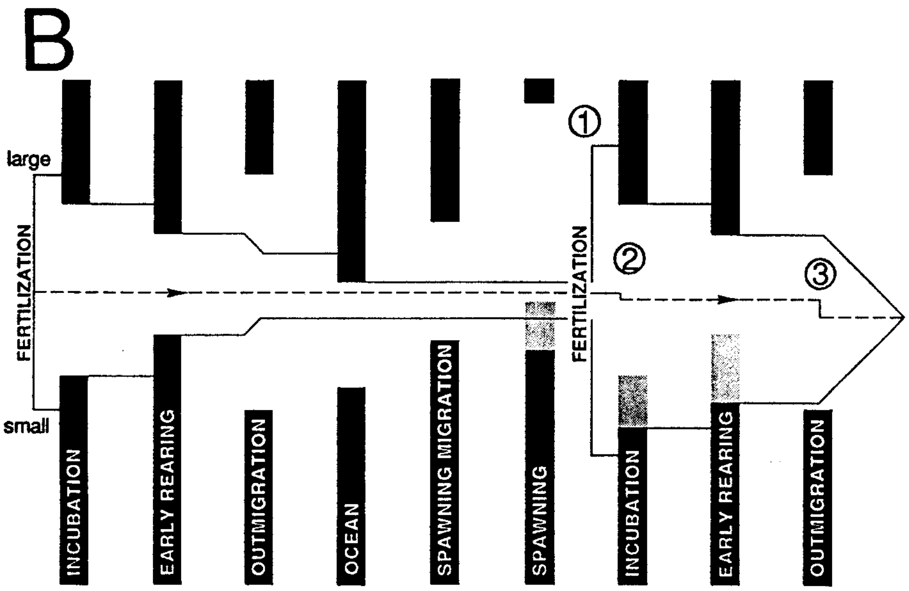

Figure 1. (continued)

B. Reduced size at maturity may result from relaxed selection against small size in some of the environments. In this example, selection is relaxed (shaded portion of bars) in the spawning, incubation, and early rearing environments, as might occur with artificial propagation. Because more adults spawn successfully, more embryos may result and represent a broader range of potential sizes at maturity (1). The reduction in selection at spawning causes a small decrease in the average potential size at maturity (2). Reductions in the selectivity of the incubation and early rearing environments could contribute to a further decrease in average size (3), if not counteracted in later environments.

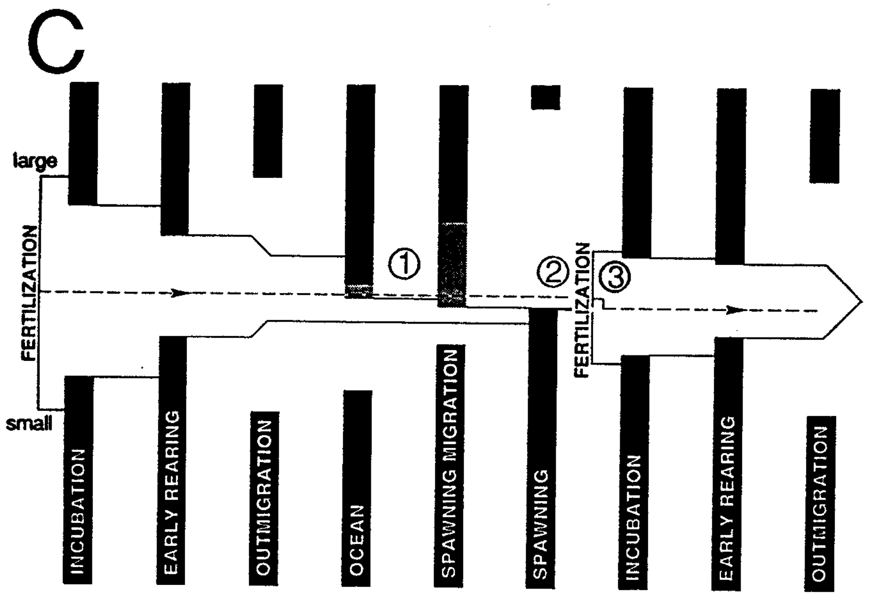

Figure 1. (continued)

C. Increased selection against large size (shaded portions of bars) could cause a reduction in size at maturity. Ocean and in-river fishing are examples of such selection in these environments (1). Selection against small size at spawning could counteract this change, but the combined result is a very small effective spawning population (2). Random genetic events may cause changes to any and all traits at low effective population sizes. The reduced reproductive ability of the escapement results in fewer offspring per spawner, although the average potential size at maturity in the next generation is little changed (3).

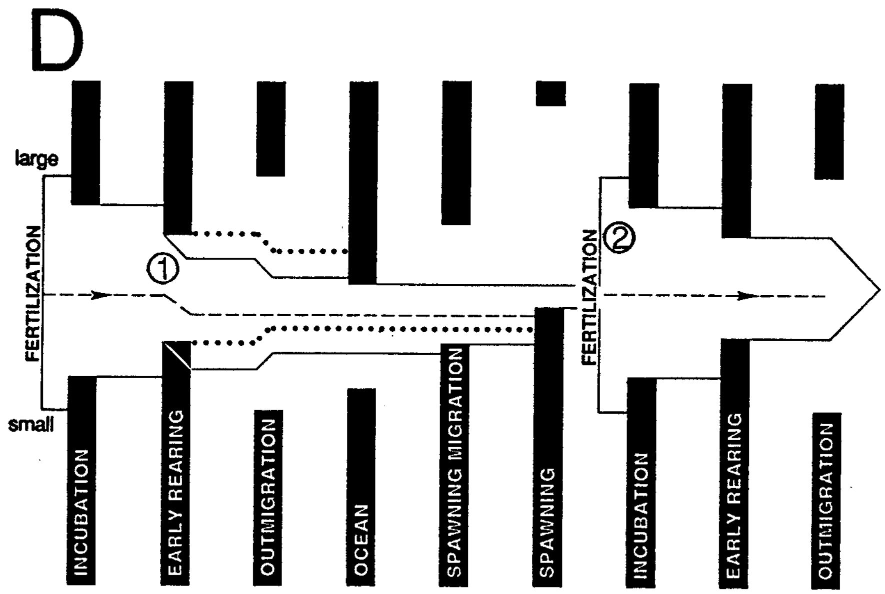

Figure 1. (continued)

D. Environmental conditions may alter the expression of the genetic potential. This example illustrates a shift to smaller potential average size at maturity caused by superior growth during early rearing (1). Dotted lines represent the range that would have been impacted by environmental windows had the shift not occurred. With the shift, fewer potentially large fish are selected out by the ocean environment, and more of the smaller and intermediate genotypes are selected out, because of their smaller phenotypes, during the spawning migration and spawning. The net result may be little change in the genetic potential for size at maturity in the next generation (2) or possibly a change favoring genotypes for larger size, due to the greater selection in the spawning migration and spawning environments.

Hypotheses relating the adaptiveness of size and age traits to migrational and spawning environments are common (for example, Hanson and Smith 1967; Schaffer and Elson 1975; Chebanov 1980; van den Berghe and Gross 1984; Hankin and McKelvey 1985; Healey 1986; Holtby and Healey 1986). However, prevalent values of these traits are not necessarily genetically programmed optima for migration and spawning (Miller 1957; Healey 1986; Nelson and Soule 1986). Size and age at maturity may be correlated with other heritable traits (e.g., growth rate) that are adaptive or maladaptive for other developmental environments. If so, size and age distributions in the spawning run may reflect compromises among heritable adaptations for several developmental environments (i.e., counteracting selection). In addition to selecting in favor of heritable size and age adaptations, environments could have only phenotypic effects on the traits, such as when superior growth conditions prompt anomalously early maturation (Riddell 1986). Random genetic events can disrupt adapted gene complexes during population bottlenecks when spawning numbers are severely restricted or mating patterns are distorted (Kapuscinski and Jacobson 1987).

Shifts in distributions of size and age at maturity can reflect environmental changes that are either beneficial or detrimental for the population. For example, relaxed selection against small size that results in smaller mean sizes can also promote increased survival and production (a benefit) if the relaxed selection is not counteracted in another environment (Fig. 1.B). In this case, reduction in size may lead to, and result from genetic adaptation to a modified environment (e.g., one in which smaller fish are preyed upon at a lower rate than formerly), a process necessary for the long-term survival of the population. Similarly, improved growth conditions may benefit survival while depressing mean age (and size) at maturity (Fig. 1.D). As an example of a detrimental environmental change that results in smaller average size, consider intensified selection against large size (e.g., in a fishery), which may result in counteracting selection that is strong enough to nearly extinguish the population (Fig. 1.C). Without some knowledge of the causes, or the associated changes in survival or production, the implications of shifts in size or age structure cannot be clearly interpreted as either beneficial or detrimental to the population. Generally, however, any reduction in the range of sizes and ages at maturity represents a loss of life history types, hence a reduction in adaptive capacity. Life history diversity confers adaptability under changing environmental conditions.

Observed values of size and age at maturity of chinook salmon are probably adaptive for the unique sequences of environments encountered during their life cycle. Changes in size and age at maturity probably reflect environmental changes, although the mechanisms are numerous and complex.

WHAT IS A BRIGHT?

A basic knowledge of the phylogenetic, geographic, and historical context of Brights is required to understand the significance of present life history patterns such as size and age at maturity. This chapter summarizes that context and defines the Bright stock.

The Bright Family Tree

Bright ancestors have demonstrated great adaptability. Adaptation to marine rearing environments, perhaps by a *Salmo*-like ancestor (Neave 1958; Hoar 1976; Miller and Brannon 1982; Smith and Stearley 1989; but see Thorpe 1982), allowed the development of anadromy and the eventual extension of spawning ranges into streams throughout the northern hemisphere. Pacific salmon (*Oncorhynchus* spp.) may have arisen in brackish waters from an ancestor resembling their recently reclassified congeners, Pacific trout (Neave 1958; Smith and Stearley 1987). Facultative anadromy and isolation by Pleistocene glaciation (Neave 1958; Allendorf and Thorgaard 1984), differing temperature regimes (Miller and Brannon 1982), and behavioral barriers (Neave 1958) have probably contributed to the radiation of at least eight species (Smith and Stearley 1987) and perhaps tens of thousands of stocks (Ricker 1972) within an evolutionarily brief time (Neave 1958).

Within its genus, *O. tshawytscha* is considered intermediate in evolutionary advancement (Neave 1958; Hoar 1976; Miller and Brannon 1982). It displays increased specialization for marine life (Wagner et al. 1969), considered an advanced trait (Neave 1958; Hoar 1976), but still retains vestiges of "primitive" facultative anadromy (Merrick 1984; Stokell 1955; Brown 1984) and iteroparity (Rich 1922; Gebhards 1960; Robertson 1957; see also possible evidence in Swartzell 1967). Such a diverse life history repertoire may have enabled the chinook salmon to colonize its broad native spawning range, which spanned from California's San Joaquin River (Fry 1961) around the North Pacific and Bering Sea to perhaps Hokkaido, Japan (O'Malley 1920), and to survive major habitat perturbations within its range.

In the Columbia River, where much of the indigenous fish fauna is euryhaline or anadromous, anadromy may have been an important adaptation for recolonizing habitat often disrupted by large-scale geologic events (Li et al. 1987). Aboriginal peoples on the Columbia used salmon at least as early as 10,000 yr ago (NPPC 1986), so salmonids may have inhabited the Columbia River Basin during the late Pleistocene when repeated failure of glacial dams unleashed the cataclysmic Bretz, or Spokane, Floods (McKee 1972; Allen et al. 1986). In more recent centuries the lower river was dammed by a massive landslide (ca. 1250 A.D.; Lawrence and Lawrence 1958) and thickened with ash from volcanic eruptions (Dawley et al. 1986). Chinook salmon stocks have had to remain adaptable to survive in the Columbia Basin.

Recent Historical Context

Dramatic geologic events did not prevent the Columbia River from becoming perhaps the world's greatest producer of chinook salmon (Ricker 1972), but overharvest and exploitation of other river resources by Euroamericans have greatly reduced the Columbia's salmonid populations (NPPC 1986). Predevelopment runs of 4.8 million to 9.2 million chinook salmon have dwindled to only 1.6 million in recent years (NPPC 1986, Table 6), of which probably fewer than half are produced naturally. Fisheries, river developments, and artificial propagation are major anthropogenic environmental disruptions that probably have induced changes in Bright life history patterns.

Fisheries

The salmon resources of the Columbia Basin have long sustained its human inhabitants. Aboriginal peoples may have harvested over one million Columbia River chinook salmon annually before diseases decimated the native human populations in the 1700s and early 1800s (NPPC 1986). Euroamericans began commercial exploitation as early as the 1820s and 1830s (Craig and Hacker 1940; Smith 1979), but not until after the onset of the canning industry in 1866 (Collins 1892) were the salmon runs heavily exploited. Large, bright, oil-rich spring- and summer-migrating chinook salmon were the foundation of the commercial fishery and processing industry (Smith 1895; Rich 1942; Thompson 1951). Only 17 yr after the inception of the canning industry (i.e., in 1883) at least 39 canneries (Craig and Hacker 1940; Smith 1979) were packing catches of approximately 2.3 million fish (over 40 million lb; Fig. 2; NPPC 1986). In addition to these enormous packs, many tons of chinook salmon were discarded when packing capacity was exceeded (Cobb 1911).

The unbridled exploitation in the lower river took its toll on the stocks. Chinook salmon of the spring and summer runs, although abundant in upper reaches of the Columbia and Snake Rivers during the 1870s, were scarce in the same areas by 1890 (Gilbert and Evermann 1895). By that time "the river was literally filled with devices for the capture of salmon," (Collins 1892, p. 221), and overfishing was generally acknowledged as fact (Smith 1895). However, increasing effort (Smith 1895) and increasing contributions from less desirable fall-run chinook salmon (Rich 1925; Fulton 1968) maintained relatively high but variable harvests through at least 1920 (Fig. 2) (Rich 1940b; Van Hyning 1973; Smith 1979). By 1919, the August (fall) run was "overwhelming in importance," (Thompson 1951 p. 24) and in the 1940s Brights and other fall-run chinook salmon were making the major contribution to in-river fisheries (Van Hyning 1973). Estimated harvest rates of fall chinook salmon in the "lower river" (probably the reach below the present site of Bonneville Dam) for 1928-54 range from 54% to 89% (excluding 37% during a fishermen's strike in 1952; Gangmark 1957). These estimates may be conservative (Van Hyning 1973).

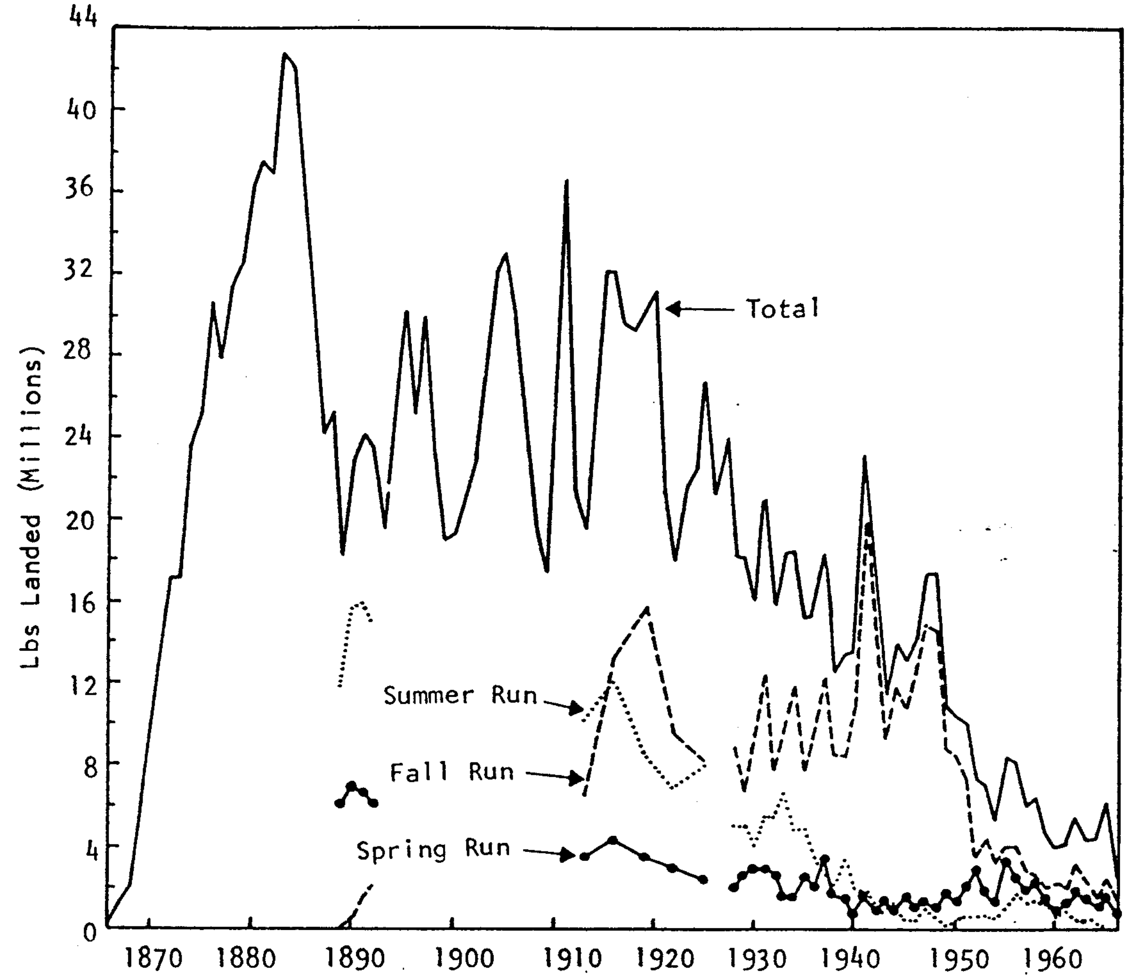

Figure 2. Chinook salmon landings, by run, in the Columbia River commercial fishery, 1866-1966. From Van Hyning (1973).

Sizeable harvests probably were also occurring outside the river; ocean fisheries as far north as Alaska take Brights and other Columbia River fall chinook salmon. The Southeast Alaska troll fishery, begun in 1905 (Cobb 1911) and with a peak chinook salmon catch of 17 million lb (approximately 0.9 million fish) in 1937 (Parker and Kirkness 1956), is known to harvest large numbers of Brights (Funk 1981; PSC 1988). The British Columbia troll fishery began before 1910 (Rounsefell and Kelez 1938) and as early as the 1920s was known to be taking many Columbia River fall chinook salmon (Williamson 1927). Net fisheries have been restricted to the inside waters of both the United States and Canada since the mid-1950s (Royce 1988), but they likewise catch Brights (Howell et al. 1985a; PSC 1988). Increased catches in the ocean fisheries between Oregon and British Columbia have been implicated in the reduced run sizes of fall chinook salmon of the late 1940s to the early 1960s in the Columbia River (Van Hyning 1973). Over 83% of the 1974-77 brood Brights that were harvested were taken in Southeast Alaska and British Columbia (Howell et al. 1985a, p. 411), and Brights may have been the principal support of commercial ocean fisheries in these areas in some more recent years (PSC 1988).

For most of a century, in-river and ocean fisheries have been harvesting Brights. Hence, the size and age distributions previously and presently observed in the stock may be in part an artifact of intensive and selective exploitation. During the same period the stock's freshwater habitat has been radically altered.

Development of the Columbia River

Since Euroamerican occupation of the Columbia River Basin, its water has been put to almost every conceivable use. Perhaps without exception those uses have promoted environmental changes to which salmon populations have had to adapt. Craig and Hacker (1940), Fulton (1968), and NPPC (1986) provide sobering reviews of the impacts that agriculture, logging, mining, nuclear reactors, and other developments have had on salmon habitat.

Dams probably have had the most profound influence on Brights. Over 140 hydroelectric, multipurpose hydroelectric, and irrigation dams exist in the basin (NPPC 1986). Beginning in 1931 with the completion of Rock Island Dam on the mid-Columbia, the mainstem spawning and rearing habitat of Brights has all but been eliminated by dams and reservoirs (Fulton 1968; NPPC 1986). Additionally, mainstem dams and reservoirs are known to delay adult and juvenile migrations (Schoning and Johnson 1956; Raymond 1969), trap sediments and reduce turbidity that once may have cloaked vulnerable migrating juvenile salmonids (Junge and Oakley 1966), harbor large populations of indigenous and exotic predators (Poe and Rieman 1988), kill substantial numbers of juveniles that pass dams (Schoeneman et al. 1961; review and annotated bibliography in Burchfield et al. 1986), and enable radical alteration of flows in unimpounded reaches (Becker 1985; Chapman et al. 1986). Li et al. (1987) provide additional examples of impacts.

Large storage reservoirs such as Lake Roosevelt behind Grand Coulee Dam have caused other environmental changes that, although subtle, may be serious. For example, Lake Roosevelt slightly increases and dampens the variability of river temperature and delays the annual temperature cycle by approximately 30 days (Jaske and Goebel 1967). If spawning, incubation, and early rearing success are dependent on a time-temperature match, the filling of Lake Roosevelt in 1941 would have substantially shifted the optimum spawning time for chinook salmon (e.g., Brights) in the mainstem waters downstream of Grand Coulee Dam. Present-day Brights may be descendents of individuals that were able to adapt during the last 50 yr to this temperature shift.

Like the fisheries, development of the Columbia River has changed the environmental windows of opportunity for spawning, incubation, and rearing, which may influence adaptive sizes and ages at maturity. Not only what we observe now, but also the earliest size and age data available, could have been influenced by these shifts. Another environmental change of great significance is the use of hatcheries to replace natural spawning and rearing habitat and mold the patterns of production to enhance fisheries.

Artificial Propagation

Artificial propagation has long been the management answer to overfishing and habitat destruction. It can affect Bright size and age at maturity through two principal means: 1) changing the species and stock composition in the runs in ways that alter the competitive environment and the prosecution of fisheries, and 2) subjecting the cultured stocks to different selective environments than would occur with natural production. (The latter is discussed in detail under Early Rearing, p. 50.)

The first hatchery in the Columbia River Basin was built in 1876 (Wahle and Smith 1979) or 1877 (Smith 1979) by a private firm on Oregon's Clackamas River, which joins the Willamette not far from its confluence with the Columbia. This hatchery was operated sporadically (1887 was the only year during the 1880s) and released only chinook salmon fry[1] (Wahle and Smith 1979), yet was credited with producing the increased run of 1890: "It is believed by those competent to judge that this [improved run] is directly traceable to artificial propagation at the hatchery on the Clackamas," (Collins 1892). By 1894 "practically unanimous" faith was being placed on artificial propagation to regenerate the fishery (Smith 1895 p. 241). Between 1895 and 1900 construction was completed or begun on at least seven additional salmon hatcheries on Columbia River tributaries, all emphasizing release of chinook salmon fry (Wahle and Smith 1979).

The Mitchell Act of 1938, intended to compensate for habitat destruction by water use projects in the Columbia River Basin, initiated the next major period of hatchery construction (Wahle and Smith 1979). Although upriver stocks suffered most from water use projects, all but one rearing pond (Ringold) of the 22 hatcheries and three major rearing ponds built with Mitchell Act funds since 1949 were sited on the mainstem or tributaries below McNary Dam (NPPC 1986). Of the 82 anadromous fish hatcheries and rearing ponds operated in the Columbia River Basin between 1960 and 1976, 49 (60%) were below McNary Dam and 28 (57%) of those 49 produced fall chinook salmon (fall chinook salmon were a minor group in 6 of the 28; Wahle and Smith 1979, data from Tables 14, 17, and 19). By the 1970s, hatcheries were producing over 70% of the fall chinook salmon outmigrants; hatchery releases of fall chinook salmon in the Columbia River approached 100 million juveniles by the early 1980s (Bottom et al. 1984; NPPC 1986). The resulting flood of mostly dark, or "tule",

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[1] Even with modern technology, unfed chinook salmon fry released from hatcheries are believed to survive at very low rates (sources cited in Miller et al. 1990 and Steward and Bjornn 1990).

race fall chinook salmon in the lower river has promoted overharvest of the natural upriver stocks (Brights), whose migration time coincides with that of the tules (NPPC 1986).

Spawning channels were employed in the 1960s and early 1970s to mitigate for destruction of Bright spawning habitat by mid-Columbia dams (those between Grand Coulee Dam and the confluence with the Snake River; Fig. 3). Designed to enhance survival in a seminatural spawning, incubation, and rearing environment, the facilities were plagued by high mortalities and poor returns (Chambers et al. 1963; Allen and Moser 1967, 1968; Allen and Meekin 1973). The concept was abandoned during the 1970s, and the facilities were converted to conventional tray incubation and raceway culture. Spawning channels were a laudable attempt to maintain a selectively natural freshwater environment and provide in-place and in-kind mitigation.

Artificial propagation has been embraced as the remedy for overharvest and habitat destruction, but its focus has been the expeditious enhancement of harvests, not the mitigation of damage to depleted stocks. Brights have not only adapted to environmental changes wrought by large-scale production of tule fall chinook salmon in downstream hatcheries, but are themselves increasingly being exposed to the hatchery environment. How hatchery practices influence size and age at maturity will be considered in later chapters; first let us define the Bright stock.

The Bright Stock

The term, "stock," has no explicit, universally accepted definition (see Howell et al. 1985a for discussion). In purest form, a stock is a population (or subpopulation, Nelson and Soule 1987), an interbreeding or potentially interbreeding group of individuals (Hershberger 1976a). In practice, a stock is a management unit of a species distinguished from other such units by differences that (1) are presumably based on genetic differences, (2) are readily

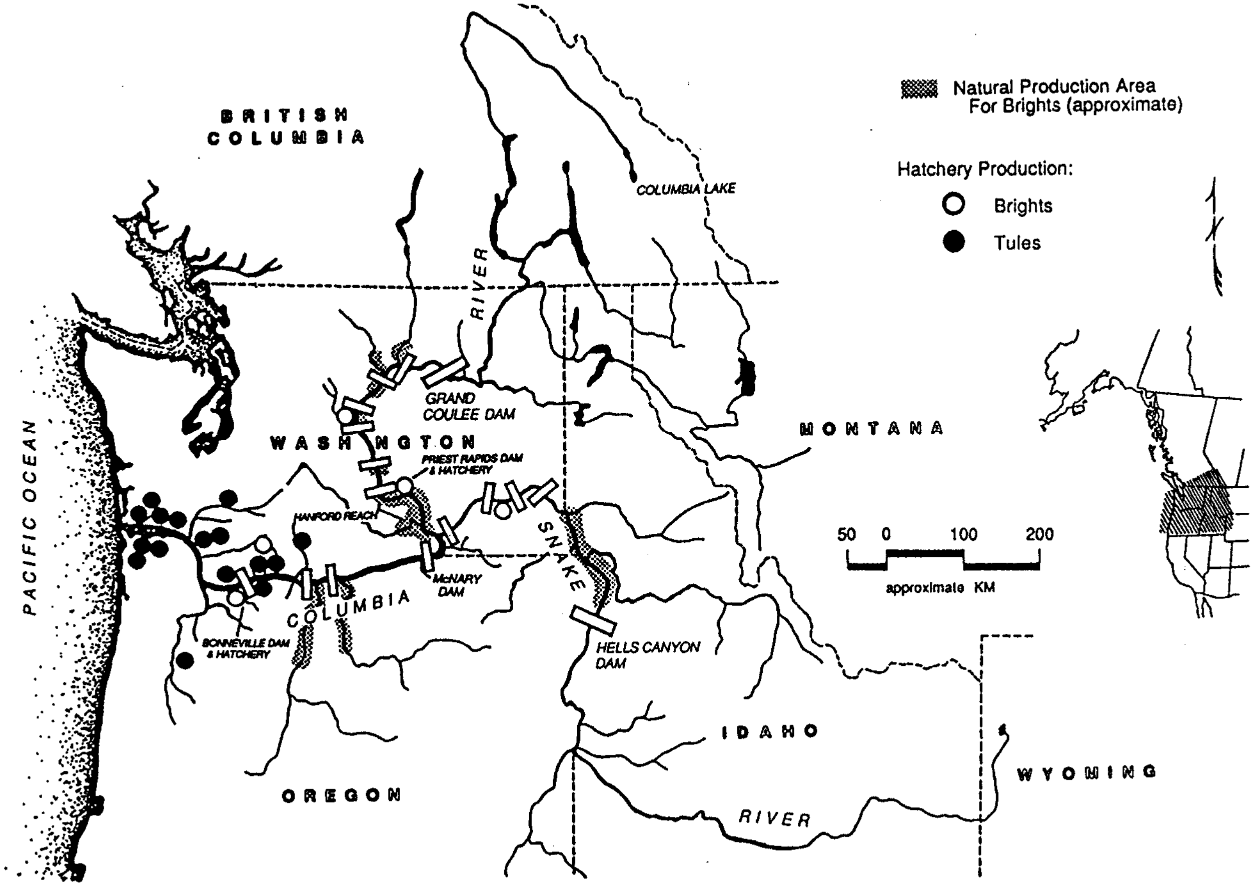

Figure 3. Present production areas of fall chinook salmon in the Columbia River Basin. Tule natural production not shown; use of some spawning areas by Brights was documented only during recent high escapements. Data from Howell et al. 1985a; Kohn 1988; Rogers et al. 1988; Heindl and Beaty 1989; and S. Hays., Chelan County Public Utility District, Wenatchee, WA, pers. comm. 1/89.

measurable, and (3) do not result in groupings that are impossible or unduly inconvenient to manage.

Brights are a heterogeneous group of fall-running chinook salmon that, along with their progenitors, have demonstrated their ability to adapt to severe anthropogenic environmental changes in the past 100+ yr. These human-caused changes are great enough to have created Brights as a relatively distinct stock, so early data on "Brights" must be used with care and proper qualification.

Brights are a fall-run stock, which under the current definition means that they pass Bonneville Dam on or after August 1. Columbia River fishery managers recognize four fall stocks, Lower River Wild, Lower River Hatchery, Bonneville Pool Hatchery, and Brights (Howell et al. 1985a). Bonneville Dam separates the lower and upper river stocks under this classification. Lower River Hatchery and Bonneville Pool Hatchery stocks are tules that return to the river when very ripe and spawn after little delay.

The spawning distribution of fall chinook salmon is a fragmented vestige of its former extent (Fig. 3 and 4). Natural Bright production has been replaced by production of tule fall chinook salmon in the lower river and Bonneville Pool, and to a lesser extent by Bright hatchery production in both lower and upper areas. Upper Columbia River wild Brights, depressed in the 1970s, were considered for listing as a threatened or endangered species under the Endangered Species Act (Horner and Bjornn 1979). However, the stock rebounded in the late 1980s, but is presently in decline (Fig. 5). Brights from all sources have contributed between approximately one-quarter and one-half of adult fall chinook salmon in the Columbia River since 1980 (Fig. 6).

The Bright stock is a complex unit (Howell et al. 1985a). The primary substock originates from natural (in the Hanford Reach) and hatchery (mostly Priest Rapids Hatchery) production between McNary and Priest Rapids Dam (Fig. 3). Several minor components include natural production in the Snake, Deschutes, and other tributary rivers above The Dalles Dam as well as hatchery production in the lower and upper river.

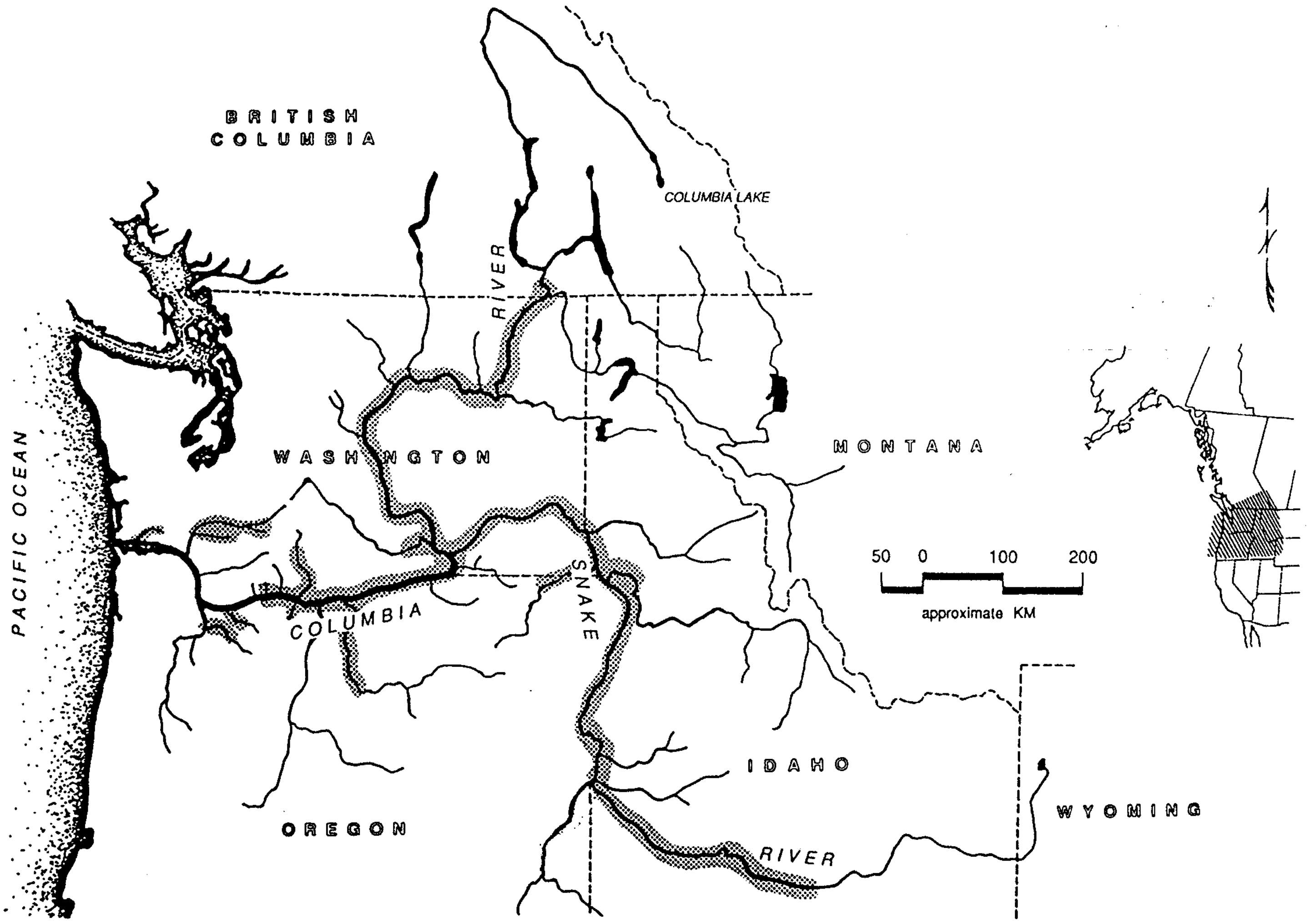

Figure 4. Estimated former extent of fall chinook salmon spawning in the Columbia River Basin (adapted from Fulton 1968).

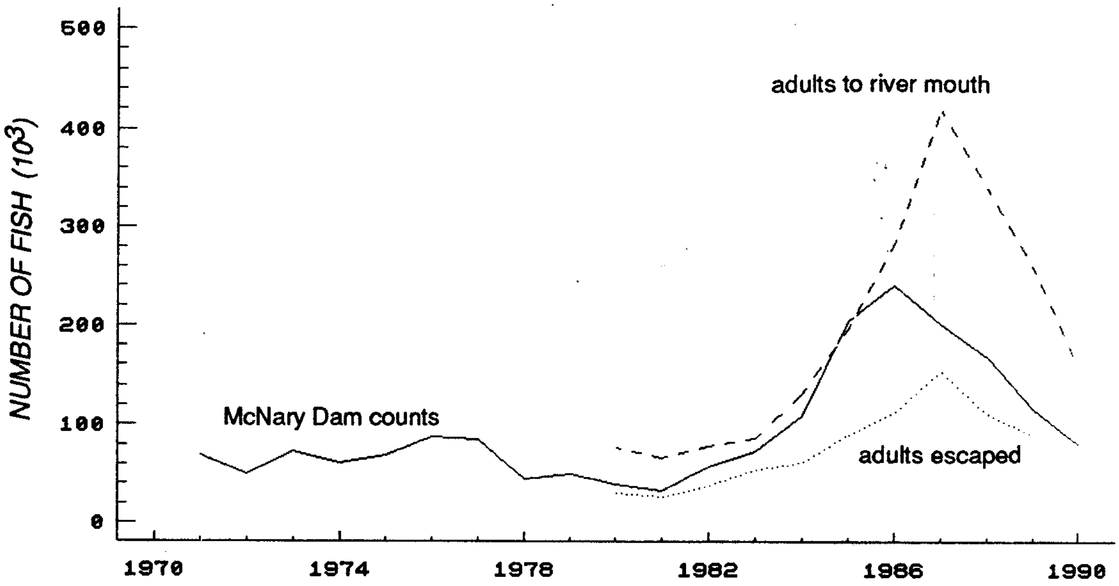

Figure 5. Bright run sizes and escapements. Counts of fall chinook (adults and jacks, combined) at McNary Dam from USACE (1989) and the Columbia River Inter-Tribal Fish Commission, Portland, OR (unpubl. data, B. P. Lumley). Estimated adult run size from ODFW and WDF (1990) (years 1980-89) and from Washington and Oregon Columbia River Staff (Dec. 5, 1990, memo to Columbia River and Ocean Salmon Managers, preliminary accountability of the 1990 return). Adult escapement estimates are from ODFW and WDF (1990).

Differences between subunits suggest that the present Bright stock comprises more than one population (Horner and Bjornn 1979; Utter et al. 1982, 1987; Seidel et al. 1988). Although Horner and Bjornn (1979) considered the stock to be relatively "pure" of exotic genetic material, it is quite likely that trapping Brights for hatchery brood stock at downstream dams and transferring eggs and juveniles around the Bright production area has been eroding the genetic differences between Bright populations and may be disrupting gene complexes that are adaptive for particular streams and areas.

This study examines the primary substock, which is produced naturally in the Hanford Reach and artificially at Priest Rapids

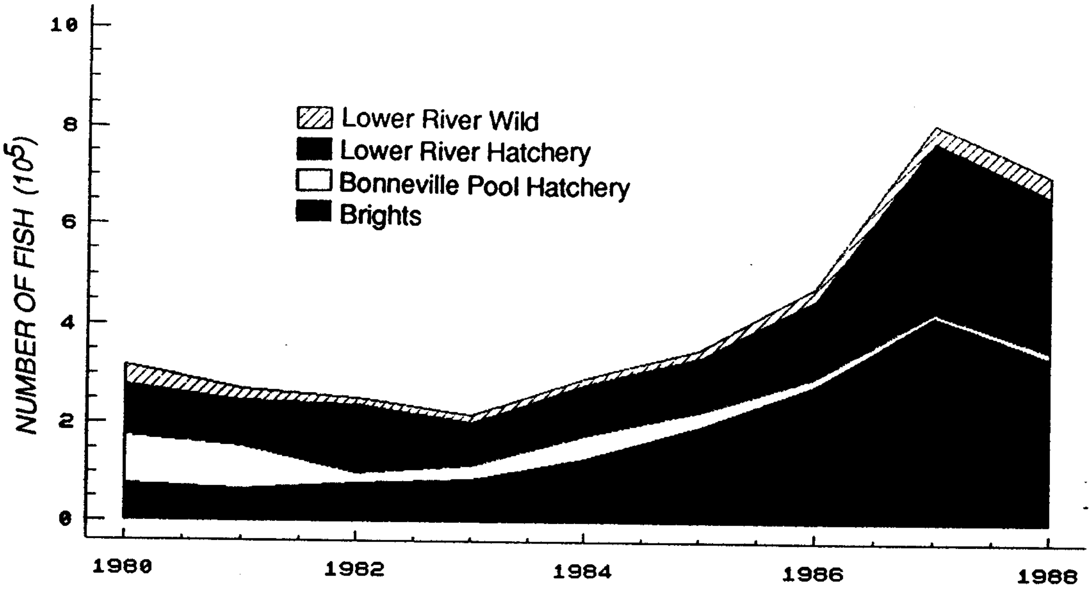

Figure 6. Estimated stock composition of the fall chinook salmon run (adults only) to the mouth of the Columbia River, 1980-88. From data in ODFW and WDF (1989).

Hatchery. Subsequently, "Brights" will refer to this substock unless noted otherwise.

Brights are probably different now than historically. Seufert (1980, p. 7) reports that:

> In the 1920s there were almost no Chinook salmon at The Dalles during the fall seasons that started on September 10. Some years there was not one single Chinook caught at The Dalles, and when any were taken at The Dalles it was a rarity. It was not until 1933 that the big fall Chinook run showed up on the Upper Columbia River. Why they came then, or from where, no one knows. Everyone was taken completely by surprise.

However, Delbert Frank, Sr. (Warm Springs, OR., pers. comm. 8/21/90), a tribal fisherman who began fishing at Celilo Falls in 1927, recalls a strong fall chinook salmon run coinciding with the coho salmon run even before 1933. Other tribal fishers who began fishing a few years later at Celilo say that their parents and other elder fishers never mentioned the sudden appearance of the fall run of chinook salmon at Celilo (Levi George, Sr. (deceased), and Wilferd Yallup, Toppenish, WA, pers. comm. 7/30/90). The presence of migrating adult chinook salmon at Kettle Falls (on the mainstem Columbia River just below the border with Canada) through November in the 1890s demonstrates the existence of an upriver, fall-spawning stock at that time (Gilbert and Evermann 1895). Brights spawn primarily in November, the latest of present chinook salmon stocks in the Columbia River. It may be that during the 1920s and early 1930s Brights were growing in numbers and emerging as a distinct stock.

Rather than discrete runs or stocks, the chinook salmon in the Columbia to some extent may have formerly composed a cline distributed through a relatively continuous spatial-temporal-thermal habitat spectrum (see Thompson 1951; Miller and Brannon 1982; Mullan 1987). Similarities between Brights and summer chinook salmon (Schreck et al. 1986), suggest that these two stocks may be essentially the same except for occupying slightly different positions on the spatial-temporal-thermal spectrum. Thompson (1951) suggested that the Bright stock, which is now relatively distinct, emerged from the late tail of the summer run that was protected for many years by an in-river fishery closure. Timing of the Bright run corresponded well with the time of this closure (Thompson 1951), which was August 10-September 10 in 1890 and reduced to August 25-September 10 by 1905 (Wendler 1966). Given the heritability of time of migration, it is probably no coincidence that a great majority of the fall run still passes Bonneville Dam during these days of late summer (Fig. 7). Habitat that was underseeded due to high exploitation rates on other stocks may have facilitated rapid growth of the Bright stock. The present identity of Brights appears to be at least partially a result of intensive and selective fisheries; habitat destruction, fragmentation, and modification; and stock management practices during the last century (Thompson 1951; Becker 1970; Watson 1970; Mullan 1987).

In summary, Columbia River chinook salmon descend from a very adaptable line. Brights have demonstrated their ability to adapt to

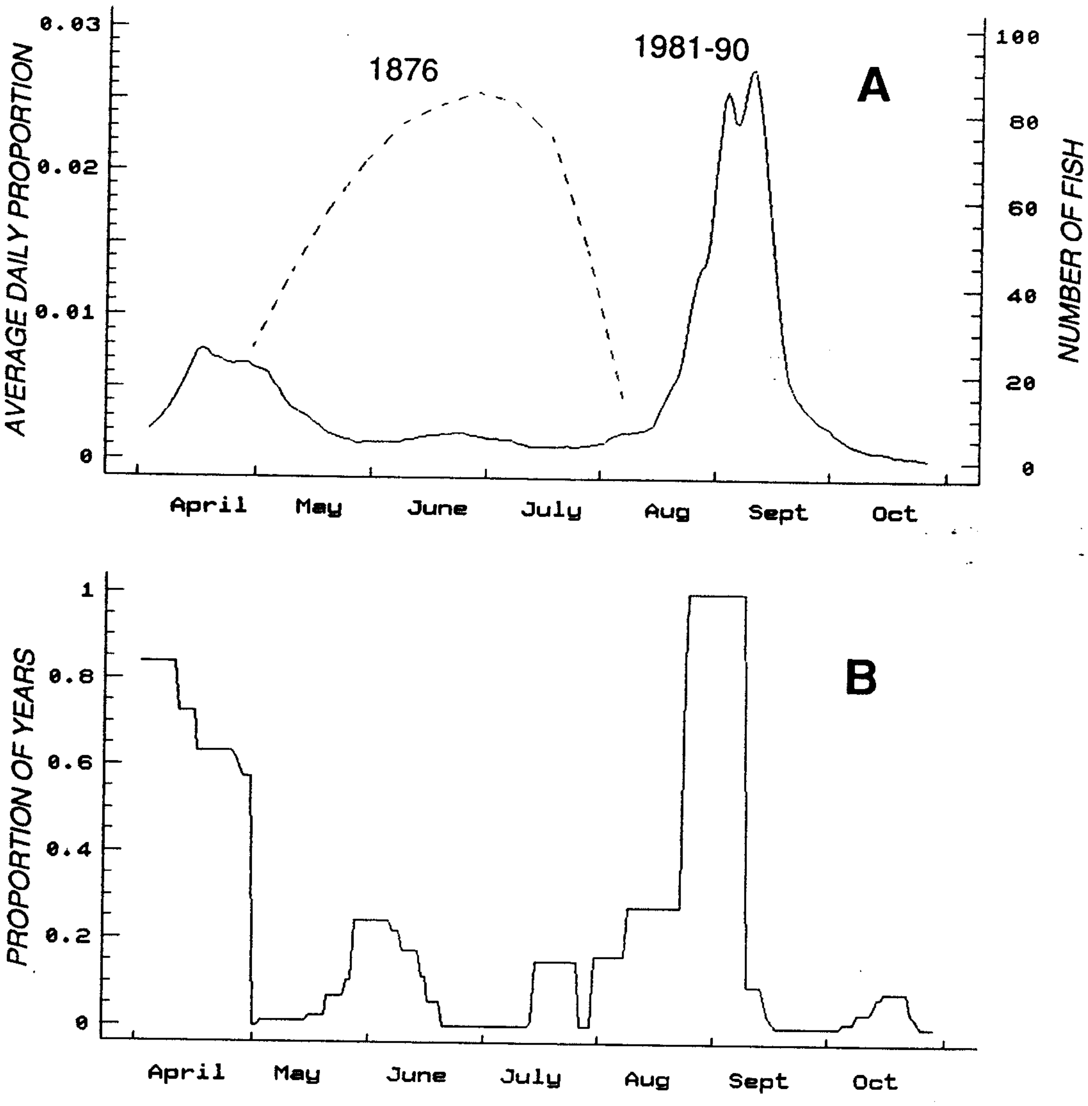

Figure 7. Comparison of recent and historical run timing of Columbia River chinook salmon (A) and historical closures of the in-river commercial fisheries (B).

A. Data for 1876 are daily catches of chinook salmon per gillnet boat delivering to a cannery in Astoria, OR, derived by smoothing (by eye) Figure 6 in Thompson (1951). Curve for 1981-90 is 5-d moving average of daily proportion of total annual counts of adults at Bonneville Dam (data from B. P. Lumley, Columbia River Inter-Tribal Fish Commission, Portland, OR).

B. Proportion of years from 1877 through 1963 when commercial salmon fishing in the Columbia River was closed by <u>both</u> Oregon and Washington on each day from April through October. Data adapted from Wendler (1966, Table 3 and Figure 4).

major environmental changes in the last 100+ yr, changes that may have caused Brights to emerge as a distinct, although heterogeneous, stock. Historical data must be carefully examined and qualified in the context of these changes in Brights and their environment before such data can be considered representative of this stock.

CHANGES IN BRIGHT SIZE AND AGE AT MATURITY

The first study objective, to determine if average Bright size and age at maturity have declined, will be addressed in this chapter. The null hypothesis is that mean size and age in the Bright spawning run are the same in recent as in earlier years.

Methods

Published and unpublished sources were searched for historical Bright size and age data. I found no data from the virgin stock (i.e., prior to ca. 1890), and references to average size dating from the period of accelerating fall chinook salmon harvests (1890-1920) are little more than anecdotal generalizations (Appendix A). Hence, the stock was probably heavily exploited (and perhaps altered) before size data were collected.

Catches in the in-river fisheries are the primary sources of size data. Season and location of the catch were used to identify data with a higher likelihood of representing Brights. Cannery records of deliveries from August trap catches near the river's mouth between 1918 and 1934 (Chapman 1940) provide early points, estimates from on-site sampling by biologists and fish purchase receipts ("fish tickets") for dipnet catches at Celilo Falls during or after mid-September between 1949 and 1956 provide intermediate points, and recent years (1980-86) are represented by fish ticket data from commercial gillnet catches in The Dalles and John Day pools (compiled from data in annual Washington Salmon Landings, Washington Department of Fisheries [WDF], Olympia, WA). All of these estimates are probably biased by gear selectivity, prior downstream removals by selective fisheries, or the presence of other stocks in the sample, but they are the most representative data that I could obtain. Data validity will be further considered in the discussion; used and unused data are described in Appendix A.

Recoveries in the in-river fisheries of binary coded wire tagged (CWT) Brights originating from Priest Rapids Hatchery and scale ages of samples from escapement areas are the basis of annual estimates of numbers of fish by age for Bright runs to the river in 1980-86 (unpublished data, J. DeVore, WDF, Columbia River Laboratory, Battle Ground, WA, pers. comm.). Although these estimates are made primarily for run forecasting and are not meant to be statistically defensible, they provide an approximation of age changes during recent years. Prior to 1980, one or more age classes lacked CWT individuals, and the estimates made by WDF of age composition in the run were based on numerous assumptions that render the estimates totally unsuitable for use here (L. LaVoy, Fisheries Biologist, WDF, Wenatchee, WA, pers. comm.). No earlier age data that would be even somewhat representative of the Bright runs were found.

The time series of data on average size (weight) was not continuous and, when plotted, separated (with the exception of one data point) into three groups of points. Each group was associated with a unique period in time, geographic area in the river, type of fishery (gear) sampled, and data source (Fig. 8 and Appendix A). I used the Mann-Whitney U-test to make pair-wise comparisons of differences in location of the three groups with respect to average weight (Sokal and Rohlf 1981; STSC, Inc. 1987), and simple linear regression (Model I of Sokal and Rohlf 1981) to roughly describe the rate of change in average weight. The software package, STATGRAPHICS 2.6, was used for all statistical procedures.

Mean ages were plotted for return years 1980-86 and brood years (cohorts) 1974-80. No tests for statistical significance tests were conducted on the recent age data because of the short time series and extraneous influences, which are discussed below.

Results

These data indicate that Brights taken by in-river fisheries have declined in average weight (Fig. 8). The center group (codes c, d, and e in Fig. 8) was not significantly different than either the early group (Z=-1.78, P=0.07) or the late group (Z=-1.45, P=0.15),

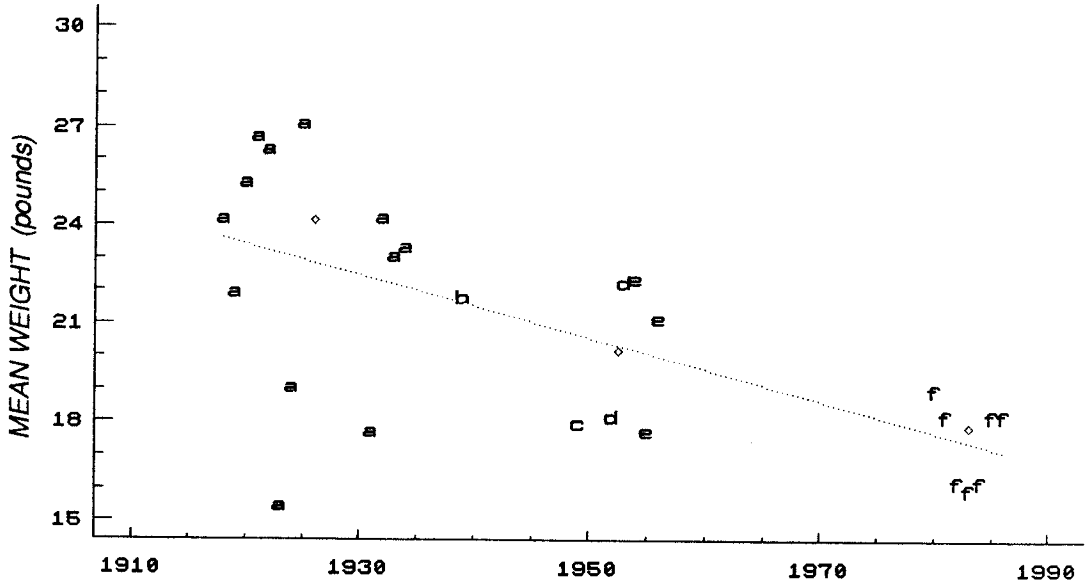

Figure 8. Trend in Bright mean weight, 1918-86. Data points form early (code *a*), middle (codes *c, d, e*), and late (code *f*) groups (code *b* not clearly part of any group), for which the weighted averages are shown (diamonds). The regression line (dotted; W = 206.4 - 0.0953Y, where W is the average weight (lb) and Y is the year) through all points shows approximate rate of change. Point values and sources are in Appendix A.

but the difference between the early and late groups was highly significant (Z=-2.58, P=0.01). The slope of the regression line suggested a rate of change (decline) in average weight of about 0.1 $lb \cdot yr^{-1}$ ($45\ g \cdot yr^{-1}$) for an overall loss of approximately 6.0 lb (2.7 kg) in average weight during the 68 yr between 1918 and 1986.

The mean age of Brights returning to the river declined rapidly (relative to rate of change in subsequent years) between 1980 and 1982, whence it remained relatively steady at approximately 3.1 yr through 1986 (Fig. 9). However, the mean age at return for broods (cohorts) shows an increasing trend over the 1974-80 brood year interval. The decline in the average age in the runs probably is a result of increased recruitment over a period of years (run size increased approximately five-fold between 1981 and 1986), which

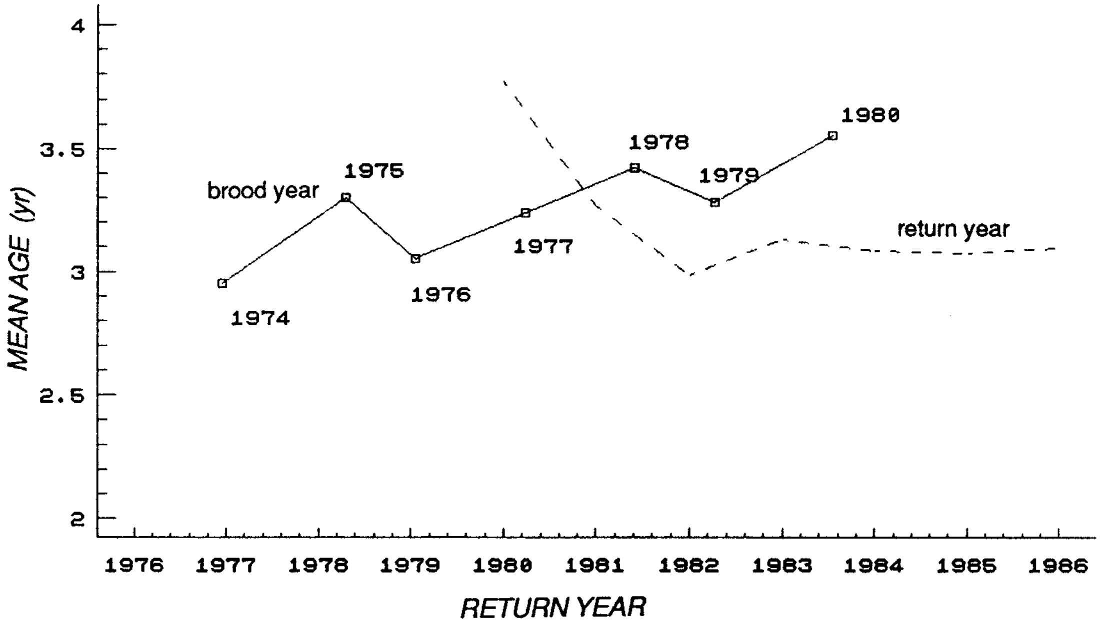

Figure 9. Mean ages of Brights by return year and brood year. Data points for brood years (shown beside points) are located, relative to the X axis, approximately when the 50th percentile of that brood returned to the river. Differing trends in standing crop (return year) and cohort (brood year) data are evident. Unpublished data from J. DeVore, Wash. Dep. Fish., Battle Ground, WA.

causes younger age classes to contribute larger proportions of the run. Thus, trends in mean age in return year data over short intervals may be more reflective of recruitment trends than of changes in the genetic or environmental factors directly influencing age at maturity of the stock. However, the preponderance of 2-yr-old jacks in recent years' runs may merit management attention (Fig. 10).

Discussion

The null hypothesis, that size and age of Brights in the spawning run was unchanged, could not be tested for age, but was tested and rejected for size (weight). This result is consistent with Ricker's (1980, 1981) hypothesis that declines in size and age of chinook salmon may be in part a result of changes within stocks,

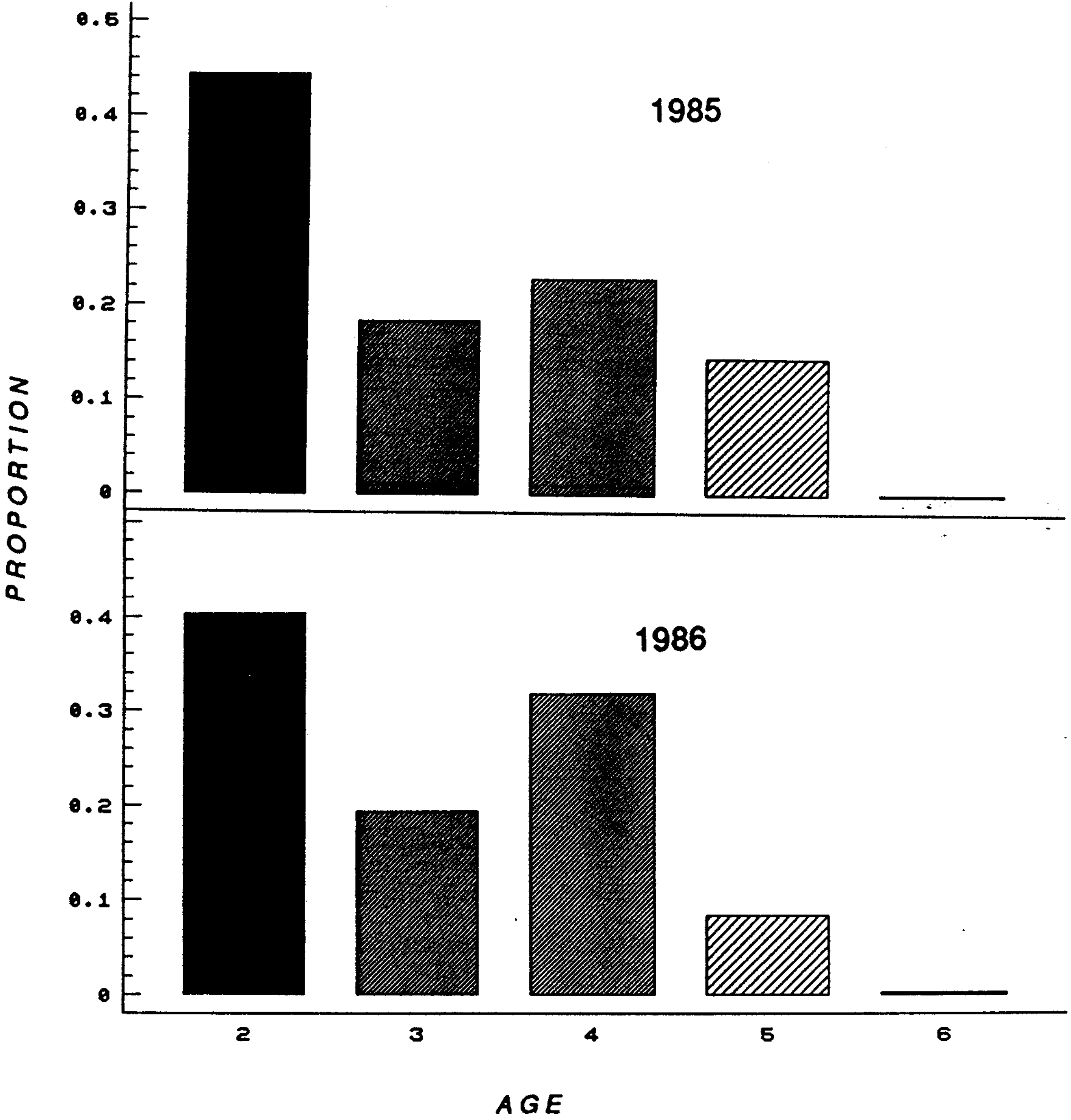

Figure 10. Estimated age composition of Brights returning to the mouth of the Columbia River in 1985 and 1986, years when run size was increasing (Fig. 5). A very high proportion of jacks (age 2) is common between the two years, which have similar age compositions overall. The high relative abundance of jacks in 1985 did not presage an increase in the relative abundance of age 3 fish in 1986. Unpublished data provided by J. DeVore, Wash. Dep. Fish, Battle Ground, WA.

rather than being a result solely of a relative loss of stocks producing the largest fish. However, the rate of decline estimated here is only about one-half and one-third of those estimated for the ocean fisheries in British Columbia and Southeast Alaska, respectively (Ricker 1980, 1981). Certain questions about the reliability of the data used in this analysis must be addressed to demonstrate that the noted decline probably reflects a real trend.

Size

A fundamental concern is the former identity or nature of the Bright stock and how well the data represent the stock. The distinctiveness of Brights was apparently first recognized by fisheries managers in the late 1940s when the Celilo Falls Indian dipnet fishery was closely examined. It became apparent then that the fall fishery took almost exclusively Brights, as opposed to tules originating in Bonneville Pool and the lower river. Some of the earliest samples used for this analysis may have been from portions of the late summer run, a likely precursor of Brights, or from the Bright stock as it was emerging to fill a fishery-created niche (discussed earlier). Size changes between the precursors and present-day Brights would still be of interest here.

The samples used for this analysis probably included unknown proportions of stocks other than Brights, particularly in samples from the lower river. However, between 1918 and 1934, lower river hatcheries (including those presently located on Bonneville Pool) were probably not yet contributing substantially to the tule runs (suggested in Wahle and Smith 1979). Also, it was not until the 1930s that Brights began to suffer habitat loss due to dam construction, so potential contribution of Brights to the fisheries prior to that time was probably unabridged. Brights, or their precursors, may have composed a major part of lower river catches of fall chinook salmon during fall seasons between 1918 and 1934. It is unlikely that the chinook salmon of other stocks that may be included in the samples were sufficiently numerous and consistently large enough to cause a significant upward bias.

It is reasonable to assume that nearly all fall chinook salmon taken at Celilo Falls or above The Dalles Dam during most years since 1933 were Brights. The seines just downstream of Celilo caught some tules, but the dipnets at the falls rarely took them (Schoning et al. 1951; F. Cramer, pers. comm., 11/88), suggesting that Celilo Falls may have been the approximate upstream limit for the ripe tules. Inundation of Celilo Falls in March of 1957 (Cramer 1974) may be responsible for the large numbers of tules noted as far upstream as the Priest Rapids Spawning Channel from 1957 through the early 1960s (Meekin 1967a; Allen and Meekin 1973). No data from this period have been used in this analysis. The samples from Celilo Falls and the pools of The Dalles and John Day dams used for this analysis were probably almost exclusively Brights.

The sizes of fish in the samples are also a function of the size-selectivity of the capture gear, and the intensity and selectivity of downstream fisheries. The trap-caught fish measured by Chapman (1940) included 2-yr-old jacks and were probably more representative of the run than the significantly larger (by approximately 4.5 lb [2.0 kg], on average) than fish taken by gillnets at the same time (August) in the same lower river area. Water depth in trap areas may have had some influence on the size of fish available to the traps (e.g., larger fish may have avoided the traps by migrating in mid-channel) and removal of larger fish by gillnetters downstream of the traps may have reduced the average size of the trap-caught fish. In both cases the potential biases, most of which would reduce the average size in these early data, would probably make the present analysis and conclusion more conservative. The earliest size estimate from Celilo Falls (1939, point "b" in Fig. 8) further suggests that the lower river trap catches do not overestimate Bright size for the 1918-34 period.

The lower river gillnet fishery probably substantially reduced the average size of fish available to upstream fisheries (Rich 1940a, 1942; Gangmark 1957); hence, the Celilo Falls samples may be biased downward. Dipnet catches at the falls, however, averaged 2.5 lb (1.1 kg) heavier than seine catches immediately downstream in mid-September, 1949 (Schoning et al. 1951). It is not known which gear is more representative, but dipnet catch data are far more available and are not likely to overestimate size in the run as a whole (considering that the lower river fishery removed larger fish). Bias in this intermediate group of data points (from Celilo) would not distort the apparent amount of total size decrease during the 1918-86 interval. Change over the entire period is reflected primarily in the difference between the early and late estimates of average size.

The gillnet catches in The Dalles and John Day pools, 1980-86, may be slightly biased upward. The size-selectivity of gillnets in this fishery during these years is discussed in a later chapter. Again, the effect of this potential bias is to make the analysis and conclusion more conservative.

The variability of size estimates is surprisingly large in the earliest group of points (the "a"s of Fig. 8). Changes in average size between years is often opposite for the trap-caught and gillnet-caught fish (Chapman 1940, Table 3), suggesting that the average weights in one or both fisheries do not consistently reflect average weights in the run. The low point of the cluster (15.5 lb [7.0 kg] in 1923) corresponds with a relatively very small sample (232 fish, only about 5% of the average number sampled in all 12 yr of the group), but its inclusion merely makes the analysis more conservative. There is no apparent explanation for the high variability in the earliest group of points.

Only the Celilo Falls dipnet catch (points "c," "d," and "e," in Fig. 8) was sampled by trained technicians, otherwise the data were recorded by fish buyers. There would be little incentive for the cannery to falsify their own records (source of points "a"), and there is no reason to believe that measurement errors by the buyers would be biased. WDF considers the pounds and numbers of fish reported on fish tickets during recent years to be reasonably accurate (D. Ward, Research Analyst, WDF, Olympia, WA, pers. comm.

1/89). The data used here are probably an unbiased, although not necessarily accurate, representation of the catch.

The 68-yr span represented by the size data (approximately 17 generations for Brights) is probably sufficient to avoid the effects of strong recruitment trends and cyclic dominance. Such effects are believed responsible for the opposing trends of brood year (cohort) and return year (standing crop) mean ages for recent years.

Age

The lack of reliable historical age data precluded an examination of long-term trends in Bright mean age. Approximations of recent age compositions in the run showed opposite trends when return year (standing crop) and brood year (cohort) data were compared, illustrating a potential danger in drawing conclusions from short series of standing crop data. Van Hyning (1973) found greater variability in age of Columbia River fall chinook salmon using standing crop analysis as opposed to cohort analysis. Although size and age at maturity may change independently through evolutionary time, the two are closely related. Over the course of a few generations a decrease in mean age may have been associated with the observed decrease in mean size.

Conclusion

A decrease in average weight of Brights has probably occurred since the 1910s. Although Brights as we now know them may be a relatively recent development, the data used in the analysis are probably representative of the stock or its precursors. The data are probably biased, but the biases so far identified would tend to make the conclusion more conservative.

Some consequences of declining size and age were noted in the introduction and will be described further in a later chapter. The next chapter describes possible causes of the decline.

CAUSES OF SIZE AND AGE CHANGES

Introduction

The study's second objective was to gain a better understanding of factors that cause changes in size and age at maturity of Brights. Ricker (1980) ventured beyond a mere description of size and age trends of chinook salmon and proposed eight possible causes for the declines. His orientation was on mixed stock fisheries, and he emphasized the role that those fisheries could have in causing changes in size and age in the stocks, changes that probably have a genetic basis. The orientation of the present study, however, was on a single stock, and knowledge of the history and life cycle of the Bright stock facilitates a more detailed examination of factors that may have contributed to declines in its mean size and age at maturity.

A conceptual tool, which I call The Causal Sphere, is useful for understanding the network of factors that may influence size and age. Another tool, a mathematical model, is useful because it permits explicit treatment of individual factors, their interactions, and the magnitude of their influences on size and age. However, this model demands data that are usually not available or realistically obtainable. These two models are the first of several preliminary concepts and topics in this introduction that will lay the groundwork for considering the potential causes themselves.

The Causal Sphere

Earlier in this paper I used a conceptual model of simplified developmental environments and windows of opportunity to illustrate selection of life history types (Fig. 1). The sequence of developmental environments during the Bright life cycle is a natural organizational framework for examining potential causes for life history changes. Each environment, itself a collection of selective factors, may be thought of as an influence or contributing cause of the observed size and age of spawners (Fig. 11). In addition to the environments, other factors such as the genome and recruitment trends are probably influential causes. These primary causes form a shell around the observed performance. Each environment or other cause is directly affected by a host of other factors (which may be viewed as secondary causes of size and age performances), each of which itself is a result of still other factors (tertiary causes), and so forth *ad infinitum*. For example, the Bright juvenile environment, a potential primary cause of adult size and age, could be affected by operation of the hydroelectric system (secondary cause), which is influenced by (among many other things) markets for electrical power (tertiary cause), etc. The result is a multilayered sphere of potential causes surrounding the observed stock performance.

The causes are neither discrete nor independent, but are an interwoven network. For example, environmental causes can, through selection, cause changes in not only the spawning run of the immediate generation (a phenotypic response), but also in the genome affecting size and age in subsequent generations (a genetic response). Large-scale climatic changes have the potential to affect all causes directly or indirectly, perhaps triggering a chain of cumulative or counteracting effects on size and age.

The Causal Sphere model draws heavily on the contextualistic world view (Pepper 1970), which considers empirical events as unique, ever-changing expressions of their settings (contexts). An event's context is a dynamic, never-ending fabric of processes and other events that cannot be unravelled. Strands of the fabric -- specific processes, relationships, and events -- can, however, be raised in relief and explored to a limited degree. Insight into how human actions and other environmental factors influence life history traits might be obtained thereby.

An alternative, more mechanistic (Pepper 1970) world view might couch the same problem of identifying causes of life history phenomena as a mathematical model whose terms must be experimentally defined. Such a model for predicting or explaining size or age at heritability (h^2) of about 0.30 for chinook salmon age at maturity from Donaldson's work (presented in Ricker 1972, Table XII). Heritability of age at maturity in Chinook salmon was estimated at 0.37-0.48 based on a one-generation study at Oregon Department of Fish and Wildlife's (ODFW) Elk River Hatchery (T. Downey, ODFW, Springfield, OR, pers. comm., 4/88). Heritability for age at maturity has been estimated at 0.39-0.49 for Atlantic salmon (*Salmo salar*) and 0.21-0.26 for rainbow trout (*O. mykiss*; Gjedrem 1985).

Such relatively high estimates of heritability, considering that size and age are closely associated with "fitness" components (e.g., fecundity; see CONSEQUENCES OF CHANGES IN SIZE AND AGE, p. 155), are inconsistent with the expectations of genetic and life history theory (Falconer 1981; Riddell 1986). Heritabilities are difficult to measure precisely (Falconer 1981) and may be easily biased toward overestimation (Gjerde 1986); hence, the estimates above may be exaggerated. However, complex interactions among selective factors, high correlations between traits, and/or spatial-temporal environmental variability may also favor retention of genetic additivity for size and age. Regardless of theoretical considerations, the heritability of size and age at maturity of chinook salmon appears, on the surface, to be well established. However, measuring heritability of these traits may not be as straightforward as some investigators may believe.

Numerous known and potential correlations between traits confound interpretation of breeding study results. Age at maturity, size at maturity, growth rate, egg size, fecundity, spawning behavior, egg and fry survival, fry size, and fry growth rate have all been shown, directly or indirectly, to be interrelated (Fig. 12). Even ocean distribution is known to be genetically influenced (Nicholas and Hankin 1988) and could conceivably differ within stocks based on genetic characters that are correlated with one or more of the traits listed above. Most of these traits are easily measured; however, other traits that are unknown or immeasurable could also be related and influential. Because of these complex correlations, we cannot be certain which genetic traits were inherited by the

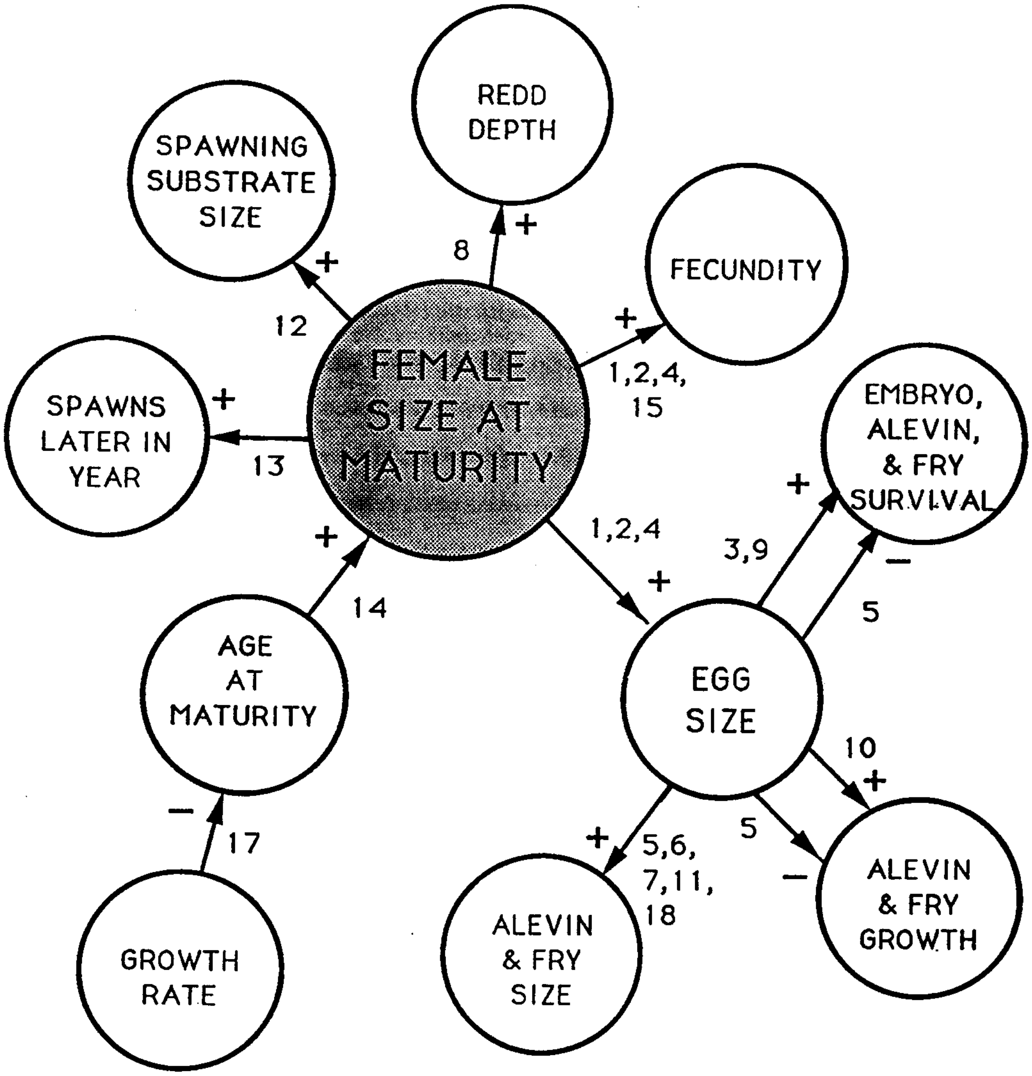

Figure 12. Some traits directly or indirectly correlated with female size at maturity. Pluses and minuses represent the nature of the correlations; numbers are reference sources:

1 Rich 1925
2 Rounsefell 1957
3 Bagenal 1969
4 Mathews and Meekin 1971
5 Fowler 1972
6 Iwamoto et al. 1984
7 Thorpe et al. 1984
8 van den Berghe and Gross 1984
9 Hardy 1985
10 Gjerde 1986 (review)
11 Smoker 1986
12 Chapman 1988 (hypothesized)
13 This study (Fig. 14)
14 This study (Fig. 13)
15 Hankin and McKelvey 1985
16 Weatherley and Gill 1987
17 see citations in "Growth and Age at Maturity" (p. 59)
18 Thorpe et al. 1984

reducing the fitness of Brights that would be larger or older at maturity.

Relationship Between Size and Age at Maturity

Size and age at maturity are directly related (Fig. 13), but only one of the two traits may be the basis for selection by a given factor or may be important for particular concerns. For example, size is the selected trait in fisheries with minimum size limits (e.g., commercial troll; given that some nonretained sublegal-sized fish survive to spawn), size-selective gears (e.g., gillnets), and/or methods of operation that impose differential selection based on size (e.g., effort concentrated in rearing areas with high incidence of small fish). Adult size may also be selected by conditions during upstream migration, spawning, and egg incubation, among others. Because size is so closely related to fitness components, maintenance of certain size classes may be essential for stock productivity.

Age is the trait selected by at least two factors, natural mortality and fisheries in rearing areas. In both cases the longer the fish waits to mature, the more mortality to which it is subjected. These factors select for younger age at maturity.

Both size and age are considered in this study because they are so closely related. When evaluating potentially selective factors, however, one or the other trait will usually be examined. Generally, size will be considered the more important, because the trend observed was in average size. This trend could reflect a similar trend in average age, however.

General Methodology

Starting with the embryo in the incubation and early rearing environment, the succession of developmental environments encountered during the Bright life-cycle were examined for factors that could be responsible for declining size at maturity. The literature was

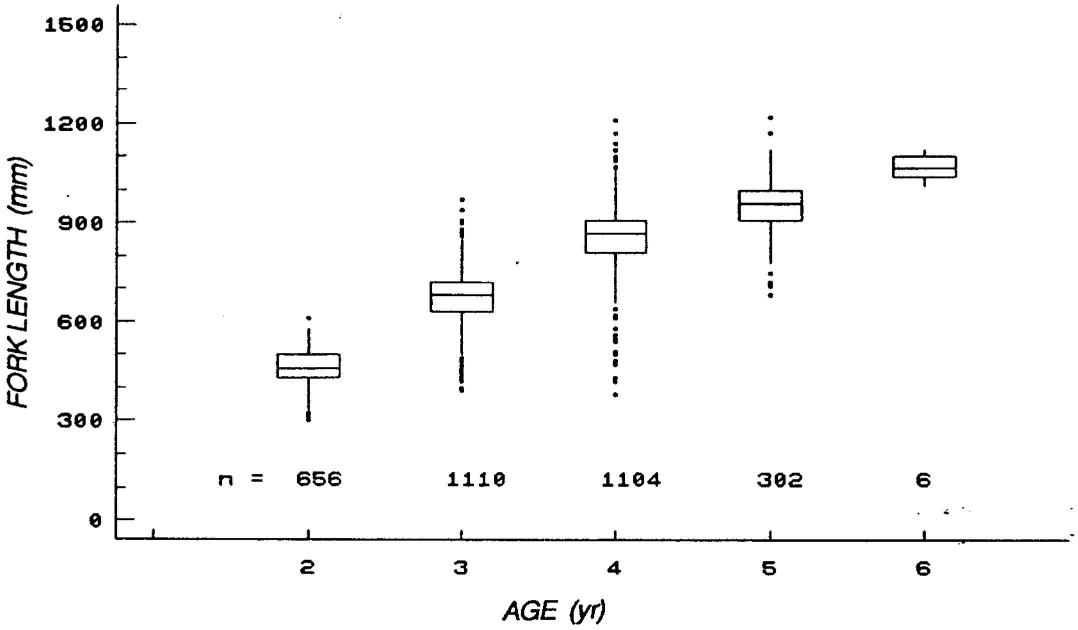

Figure 13. Box-and-whisker plot of length at age of Bright spawners, both sexes combined. Whiskers extend only to points within 1.5 times the interquartile range (STSC, Inc., 1987). Lengths of coded wire tagged Brights sampled in the escapements to Priest Rapids Hatchery and natural spawning areas in 1978-87 are combined. (Data from S. Markey, WDF, Olympia, WA.)

reviewed and data, when available, were collected for a more substantive analysis. Specific hypotheses, methods, results, discussion and conclusions are presented in the sections for each developmental environment:

1) Early Rearing
2) Outmigration
3) Ocean
4) Spawning Migration
5) Spawning

A concluding discussion melds findings from the five sections into a summary of potential causes of the declines.

Early Rearing

Factors at work during even the earliest period of life can influence the age at which individual Brights mature and the mean size and age in the stock. This association has not been widely acknowledged, so it is not surprising that relatively little effort has been applied to defining it. Defining this association is the purpose of this section, which emphasizes "maternal influences" and environmental factors affecting growth and selecting for traits that are correlated with adult size and age.

Maternal Influences

Early in life -- as embryos, alevins, and fry -- the young fish are still greatly under maternal influence; the progeny phenotype (e.g., egg and alevin size) is determined in large part by the dam's phenotype (e.g., body size; Fig. 12). "Maternal influences" are not the same as "maternal effects", a term used to describe mother-offspring similarities that are not based directly on genetic traits (Falconer 1981). Instead, maternal influences are important here insofar as they affect the viability of the progeny (due to size-related spawning success or egg size, for example), but not necessarily their phenotype for a particular maternal trait (e.g., size at maturity).

For example, if a large female is able to spawn in a more favorable location or if her larger eggs are more likely to survive, then her progeny should be relatively more abundant in some later developmental stages than those of a small female spawner. To the extent that size and age at maturity are inherited from the mother, the more viable progeny of the large spawner should also be somewhat larger, contributing to an overall greater mean size at maturity in their generation. However, the fact that the progeny inherited genes for large size is separate from the fact that their mother's size may have enhanced their probability of survival. In this case, maternal size (phenotype) influences the relative abundance of her offspring, and, if her size at maturity is directly or indirectly heritable (genotype), may also have a bearing on their size at maturity.

Three maternal influences -- spawning time, spawning site, and egg size -- were examined. If these influences are correlated with spawner size or age, and if they are related to fitness differences in the offspring, then they may influence size and/or age at maturity of Brights. Size, rather than age, is the principal trait of interest. The null hypotheses are that the influences are unrelated to spawner size and to fitness differences in the offspring.

Spawning Time Cushing (1975, 1981, 1982) argues for the importance of a spatial-temporal match between reproduction of marine fishes and the production of food for the larvae. Similar "time-windows" models have been used to describe evolution of life histories in Pacific salmon (Thompson 1959; Becker 1970; Miller and Brannon 1982), which are reflected in Mullan (1987) and the environmental "windows of opportunity" model of this paper. Spawning time may be critical not just to match windows in the spawning environment, but to match the subsequent developmental stages of the offspring with time windows in their environments.

Data from known Bright female spawners at Priest Rapids Hatchery during 1979-87 (see Appendix C for CWT codes used) were examined for a relationship between spawning time (week of year) and female size (fork length [FL]). Data were obtained from the WDF CWT recovery database in Olympia, WA. (S. Markey). Recoveries of CWTs in weeks prior to 42 (mid-October), assumed to be unspawned fish that were disposed of as surplus (G. Osborne, WDF, Manager, Rocky Reach Hatchery, pers. comm.), were not used in the analysis. Recoveries during later weeks were assumed to fairly approximate the time that spawning would have occurred in nature. No data were found to test for a relationship between time of spawning and progeny fitness.

On average, females spawning earlier in the season were larger than those spawning later for the years examined (Fig. 14). The

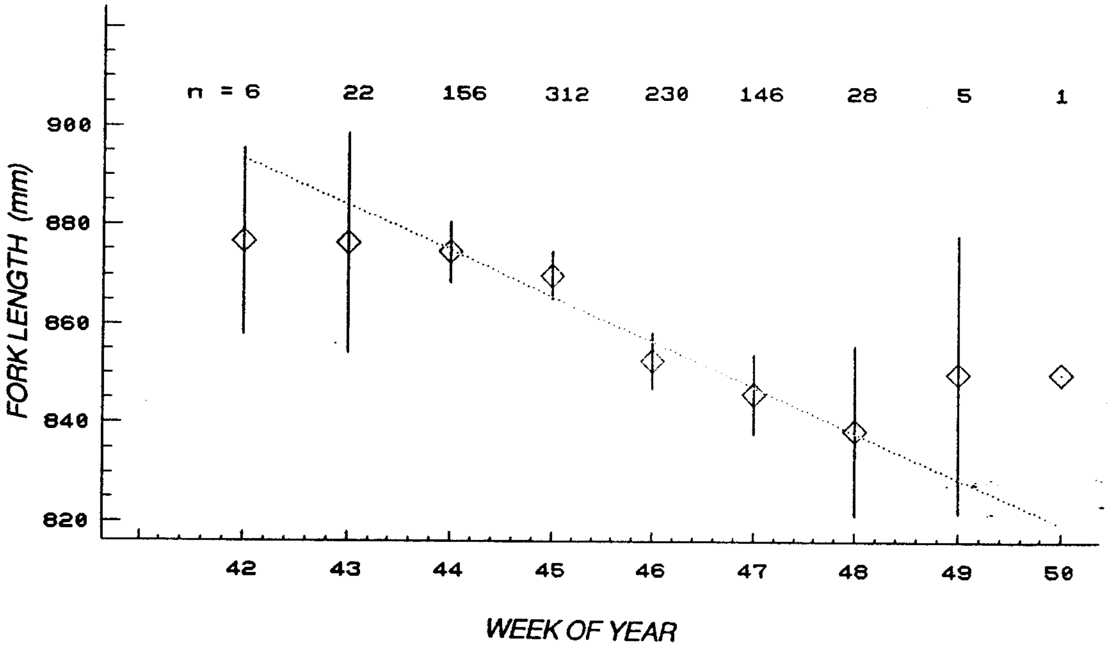

Figure 14. Trend in size of Bright females by week of spawning. Week of tag recovery at Priest Rapids Hatchery in 1979-87, combined, of Brights coded wire tagged as juveniles at the hatchery, is assumed to represent actual time of ripening and spawning. Mean length and SE are shown for each week. Recoveries prior to week 42 were omitted because they are believed to be from fish disposed of as surplus; hence, the date of tag recovery would not reflect time of spawning. Trend line is from simple regression: 1281.2 - 9.231W, where W is week of year when spawned, $n = 906$, $t = -3.85$, $P < 0.001$, and $r^2 = 0.02$. (Data from S. Markey, WDF, Olympia, WA.)

slope of the linear regression of female length on week is negative and highly significant ($P < 0.001$). Female mean length for all years combined declined by 9.2 mm per week, or a total of approximately 74 mm for the 8-wk range spanned by the data. Eliminating the few data points for weeks 42, 49, and 50 increased the rate of decline in the slope and its statistical significance. This decline in size during the spawning season has been noticed, but not measured, by personnel at Priest Rapids Hatchery (G. Osborne, WDF, Manager, Rocky Reach Hatchery, pers. comm.). Extremely weak and nonsignificant correlations among year, annual average size, and annual average week of spawning indicate that this trend toward smaller spawners in later weeks is not strictly a result of trends across years.

Whether time of spawning within the season confers any fitness advantages on the progeny of early-spawning large females or late-spawning small females is not yet known. Differential development times for eggs of large and small females (e.g., Smoker 1986) may make the different spawning times adaptive for placing the fry within the time windows of opportunity for their environments. If the thermal shift caused by completion of Grand Coulee Dam in 1941 (Jaske and Goebel 1967) necessitated a shift to a later time of spawning, then older (larger) fish with longer generation times may be slower in adapting. There is evidence (see *In-river Fisheries*, p. 110) that Bright run timing is becoming later, particularly for smaller fish. If those later-spawning females were also smaller, then small size would have been relatively more fit since 1941 (assuming that early season water temperatures have been adversely high since then), and the increased fitness of small females could have contributed to the observed long-term decline in size and age. Other reasons may also account for or contribute to this trend, such as artifacts of hatchery rearing or broodstock holding, smaller females taking longer to reach the spawning grounds, etc.

Spawning Site Fewer embryos or alevins will survive if, due to her size, the maternal spawner is unable to obtain or effectively use a favorable spawning site. Sites are definable in terms of depth of the water, flow velocity, substrate characteristics, and depth within the substrate. There are few data and little information available to relate spawner size to site characteristics and site characteristics to progeny viability. Therefore, this discussion will be largely hypothetical.

If dominance were a function of size, and if certain sites were favorable for females of many sizes, then smaller females could be forced to spawn in poorer habitat. Winter low flows and temperatures in the mid-Columbia where Brights spawn may have favored spawning in deep water rather than along the shallow stream margins where redd dewatering and freezing could inflict high embryo and alevin mortality (Chapman et al. 1986). On Vernita Bar, a heavily used Bright spawning area just below Priest Rapids Dam, spawning begins in deeper locations and progresses into shallower areas, suggesting that the shallower areas are perceived to be less favorable (Chapman et al. 1986). Alternatively, the deep-to-shallow spawning progression could reflect the progression of increasingly smaller spawners occupying habitat to which they are better suited. Poor visibility has prevented divers from observing potential differences in size between deepwater and shallow-water spawners (G. Swan, National Marine Fisheries Service, Pasco, WA, pers. comm.; D. Chapman, Don Chapman Consultants inc., Boise, ID, pers. comm., 1/89).

Only in recent years have redds in shallow areas of Vernita Bar received some protection from adverse flows. Regulation of the Columbia River has moderated the cold temperatures (Jaske and Goebel 1967) and low flows of winter, but has greatly increased weekly and daily flow fluctuations (up to 4.5 m in 24 h; Chapman et al. 1986) due to variable demand for hydroelectricity (Fig. 15). Massive egg and fry mortalities have been attributed to extreme short-term flow reductions (Bauersfeld 1978). Flow restrictions have been imposed at Priest Rapids Dam to discourage spawning at high elevations on Vernita Bar and to protect redds from dewatering (FERC 1988). These restrictions should improve the survival chances of eggs and alevins in shallow-water redds, regardless of maternal size.

Not only are the relative sizes of deepwater and shallow-water Bright spawners unknown, but it is also not known how primitive conditions and recent decades of regulated variable flows may have selected against the progeny of shallow-water spawners. I can only say that, despite the variability, regulated flows in recent decades may have selected less harshly against the margin spawners, which may have been the less dominant and later-spawning smaller fish. Hence, the fitness costs of being a small female spawner may have declined with changes in the spawning environment, hence contributing to the

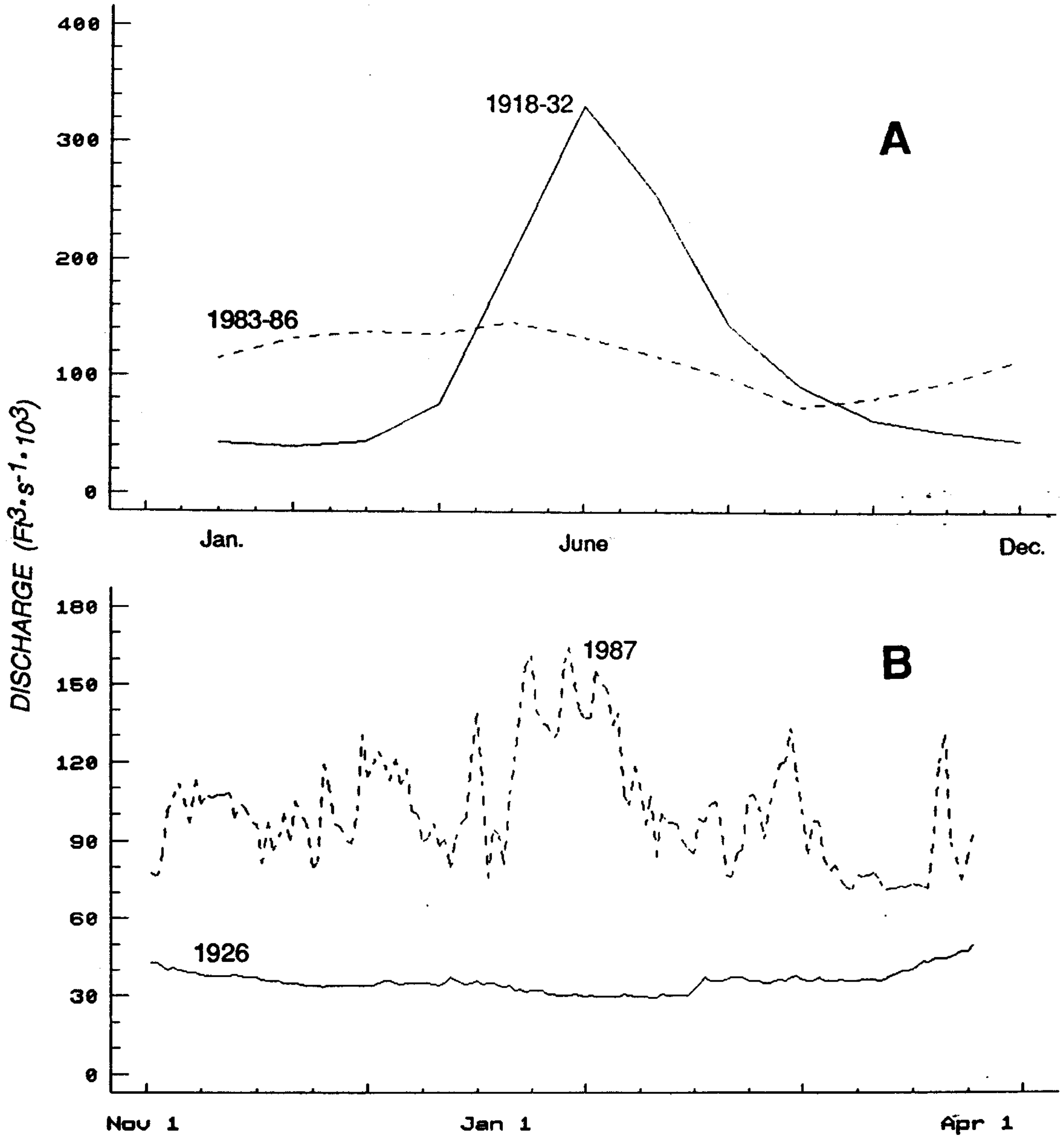

Figure 15. Historical and recent flow patterns in the Hanford Reach immediately below Priest Rapids Dam. (A) Monthly average flows for the early period (averaged for calendar years 1918-32, except 1925-26; solid line) show a distinct peak in June with minimum flows in winter. Presently (1983-86; dashed line), storage reservoirs allow a leveling and reshaping of the hydrograph with higher flows during winter when local demand for hydroelectricity is greater. (B) Similar short-term flow shaping to meet power demand has caused dramatic day-to-day and even hour-to-hour variations in river level during intragravel development of Bright embryos and fry (e.g., in 1987), compared to the relatively constant short-term flows of predevelopment years (e.g., in 1926). (Data from USGS, Portland, OR and Pasco, WA for gage station 12472800.)

Agreement is lacking on the effects of egg size on survival, but some of the disagreement may be attributable to species, stock, and methodological differences among the studies. Probably without exception the studies were conducted under controlled hatchery conditions, so there must be some question whether relative survivals of small and large eggs, and the fry that issue from them, would be similar in the natural environments. Large eggs may require higher dissolved oxygen concentrations (McNeil 1965), and shorter development times (Smoker 1986). However, the times and sites at which the different-sized females spawn could compensate for the differing requirements of their larval young. The ability to fast during the first feeding stage (Bagenal 1969) would likely be an advantage for large fry in a natural environment, but such an advantage would not be evident in studies providing regular and liberal feedings. Fry size can be an advantage for avoiding predators (Taylor and McPhail 1985), although at least one study, perhaps because of an inadequate study design, found that it was not (Fresh and Schroder 1987). In nature, large fry may be better able to establish and hold territories than fry that are smaller but faster growing (Thorpe et al. 1984).

The correlation between female size and egg size is clear, but the relation between egg size and fitness in the young is not, particularly for natural incubation and rearing environments. Although potential advantages of egg size offer a tantalizing hypothetical solution to riddles about chinook salmon life histories (e.g., Hankin and McKelvey 1985), those advantages are far from being proved. I can only conclude that progeny may enjoy fitness advantages due to egg (and, therefore, maternal) size.

Maternal Influences Summary Maternal influences form a phenotypic bridge between parent and offspring generations. The bridge in this case is the role played by size of the female spawner in determining how many of her young survive to adulthood. Female size is associated with egg size, spawning time, and perhaps with spawning site chosen. Egg size is the only maternal influence, that

I am aware of, that has been investigated for potential fitness effects on the progeny. Large eggs produce initially larger fry, but beyond that little is known about whether egg size is adaptive for particular environments.

Changes in spawner density, temperature regime, flow variations, and other factors in the Bright spawning environment may have contributed to the observed decline in size by modifying the expression of maternal influences. For example, if small females were more likely to spawn in shallow margin areas and the penalty for doing so was lessened by a moderation of flow variability during incubation, more small fish could be expected in later generations as a consequence.

Growth and Age at Maturity

Growth rate is an essential element in determining the life histories of salmon and other diadromous fishes (Gross 1987). It is among the very few early life performances that has a demonstrated association with size and age at maturity. Unlike maternal influences, which do not directly affect size and age at maturity of individual fish, growth rate can affect both the age (and hence size) at which individuals mature, as well as their relative viability. This section will consider the influence of juvenile growth rate on age at maturity of individuals; the next section will discuss how growth helps determine which individuals contribute to the spawning population.

Although heredity is a known factor in determining growth rate (Alm 1959; Donaldson and Menasveta 1961; Ricker 1972; Naevdal 1983), it is the environmental factors that are of interest here. Might different growth conditions in the freshwater environment have contributed to the observed decline in mean size and age? Here I will present evidence that juvenile growth rate is associated with age at maturity; later I will discuss changes in the early rearing environment of Brights that could influence growth rate and contribute to the decline.

There is considerable evidence that growth rate during early life and age at maturity are closely associated. As might be expected, the effects of juvenile growth on age at maturity are most apparent in the youngest age classes of mature fish. In Atlantic salmon, precocious parr are among the fastest growing of their age class up until the onset of maturation (Glebe and Saunders 1986). A significant increase in the percentage of mature age 1+ Arctic char (*Salvelinus alpinus*) was associated with intensified feeding in all of the several life history types studied by Nordeng (1983). Male rainbow trout maturing at 1 yr of age were approximately 15% heavier than the average weight of siblings in one study (Gall 1985). Coho salmon released from hatcheries at large size return more jacks (2-yr-old males that mature in the same year as their release) relative to adults (mature after one ocean winter) (Lorz 1971; Johnson 1970; Bilton et al. 1982). Alm (1959) provides further examples of growth effects on age at maturity in his excellent review; Wallis (1968) and Lorz (1971) also provide good reviews for anadromous Pacific salmon and trout.

This inverse relationship between juvenile growth rate and age at maturity has also been noted in Columbia River chinook salmon. Average lengths of groups of mature fry (age 0+) found at various locations in the Columbia River Basin ranged from 16% to 23% larger than the average lengths of sympatric immature specimens (Rich 1922). Returns of extraordinary numbers of spring chinook salmon "minijacks" (same life history as a coho salmon jack) to WDF's Cowlitz Hatchery were attributed to releases of unusually large smolts (Paul Peterson, Manager, Cowlitz Hatchery, pers. comm.; see also Mullan 1987, p. 89).

Size is obviously a function of both growth rate and time. In the examples used here, size differences between groups within a study reflect differences in growth over an approximately equal time period.

There are apparent exceptions and some noteworthy considerations bearing on the general rule that early maturity is associated with rapid juvenile growth. Iwamoto et al. (1984) found an inverse, but nonsignificant, relationship between size and early maturation (as jacks) among full-sib groups of coho salmon involved in a breeding study comparing jack and adult sires. This finding opposes those of the studies previously mentioned. Alm (1959) cites comparisons between populations of fish wherein the slower-growing population matured at an earlier age, but he rightly points out that genetic differences are probably the cause. Populations develop genetically based life histories in response to unique growth, mortality, and fertility patterns in the population and its environments (Stearns and Crandall 1984). The coho salmon exception noted above (Iwamoto et al. 1984) could be explained by differences in growth being too small to override genetic control of maturation within the jack- and adult-sired groups. Environmental influence on the age at maturity of individual fish is probably limited to modifying the expression of genetic potential.

Most of the studies above document increases in the relative abundance of the youngest age classes associated with rapid juvenile growth, but there is little evidence that the distribution of the older classes of mature anadromous salmonids is related to freshwater growth. The later a Bright is likely to mature based on its inheritance (Brights can probably mature at ages 1-7, although ages 2-6 are the most common), the less sensitive its age at maturity probably is to growth during early (freshwater) rearing. Thus, the genetic potential for later maturity buffers the effects of between-year variations in growth potential in the early rearing environment on size and numbers of fish in the runs of subsequent years. Growth during later life stages continues to be influential in determining age at maturity, but this topic will be reserved for later discussion.

The association between growth rate and age at maturity is almost certain, but whether improved growth causes early maturity is less so. Gjedrem (1985) and Gjerde 1986) caution that maturation may in fact cause increased growth (rather than *vice versa*), or that both growth and maturation may be stimulated by sex hormones. However, the former hypothesis is not consistent with other findings, and the latter is not necessarily relevant for the immediate problem. Onset of maturation actually retards, at least momentarily, the growth rate of the faster growing, early maturing individuals (review in Alm 1959; Gall 1985; Thorpe 1986). Hence, the immediate process of gametogenesis (maturation) does not improve growth. Steroid hormones are indeed known to influence growth rate in fish (Lorz 1971; McBride and Fagerlund 1973; Weatherley and Gill 1987; but see Sower et al. 1983). However, of principal importance here is that environmental factors promoting growth (e.g., better feeding conditions, Nordeng 1983; warm winter temperatures, Dirin-Khalturin 1982) are also likely to promote earlier maturity; how the effects of the environmental factors are mediated is of lesser concern.

In an evolutionary sense, early maturity is adaptive for quickly colonizing and fully exploiting favorable habitats. Rapid growth can shorten the generation time (and increase survival, as will be seen in the next section), thereby favoring population growth until carrying capacity is reached (Larkin 1981). By the same association, an older age distribution might be expected when population densities are high and growth is relatively poor. For Brights and other Columbia River anadromous salmonids, a maturity schedule that is sensitive to growth conditions would be an asset for recolonizing habitats frequently disrupted by major geologic events (Li et al. 1987).

Hatcheries, which are increasingly used for production of Brights and other anadromous salmonids in the Columbia River, are rearing habitats where juvenile growth conditions are nearly always favorable. The implication of such favorable growth for Bright age at maturity may now be apparent, but a later section will investigate the relation in detail.

Unfortunately, the effects of changing growth conditions on age at maturity may not be distinguishable from the effects of other causes, particularly genetic changes due to selection. Fisheries (or other factors) may promote reduced age and size at maturity by reducing densities during life stages when growth is density dependent (Miller 1956; Riddell 1986; Thorpe 1986), or by selecting for early maturity and/or slower growth genotypes (Schaffer and Elson

1975; Ricker 1980, 1981), or both. A changing genome due to selective fisheries is certainly the more threatening scenario, because the process and its effects are largely irreversible (Ricker 1980). Therefore, as long as the effects of the two causes remain indistinguishable, prudence requires that the growth hypothesis not be simplistically embraced to the exclusion of the genetic hypothesis. Human activities could cause severe and relatively immutable changes in the life histories of important species if resource managers mistakenly believed that the changes were merely easily reversed phenotypic responses.

To summarize, growth conditions for juvenile Brights can influence age at maturity of individual fish, particularly those genetically predisposed to early maturity. Improved freshwater growth conditions in the natural and hatchery habitats may contribute to reduced size and age in the Bright run. How growth conditions can also affect the survival of individuals that might mature at different ages will now be considered.

Growth and Survival to Maturity

"The little fish that feeds well, grows well, swims quickly, evades predators and feeds better than ever" (Cushing 1975 p. 241).

That size confers survival advantages to fish, particularly in their early developmental stages, is virtually axiomatic (for example, Cushing 1975, 1981; Ricker 1976; Wooster 1983; Weatherley and Gill 1987). Might changes in freshwater growth conditions or size-selective mortality factors favor survival of faster- or slower-growing individuals? If so, could mean size and age at maturity be affected?

This section presents evidence supporting the association between size and survival, and discusses how environmental factors, by influencing growth rate, can also influence mean size and age in the spawning run. The emphasis is on how environmental factors determine which fish survive to mature, those that will be older or younger, not on how the factors influence the age at maturity of individual fish.

Numerous studies have provided evidence that associate growth rate and survival to maturity. Hatchery time and size at release studies with Pacific salmon (e.g., review by Wallis 1968; Johnson 1970; Lorz 1971; Allen and Meekin 1973; Reisenbichler et al. 1981; Bilton et al. 1982) have firmly established the relationship between larger size at release and better survival to return. Maximizing size at release, within certain time constraints, is now a norm for some culturists (Seidel et al. undated). In the Columbia River, a greater portion of the smaller juvenile chinook salmon are apparently lost during the time it takes to migrate from the release point to the estuary (Dawley et al. 1986; Zaugg et al. 1986). Better survival has also been associated with larger smolt size within and among natural stocks of sockeye salmon (Ricker 1976; West and Larkin 1987). Scale growth comparisons in natural chinook salmon stocks confirm that juveniles with better growth and larger size at outmigration are more likely to survive to adulthood (Reimers 1973; Nicholas and Hankin 1988). Juvenile chum salmon with wider scale circulus spacing (i.e., the faster-growing individuals) apparently have had superior survival in nearshore rearing areas (Healey 1982). As the chum salmon grew, particularly through the 45-55 mm length range, size-selective mortality appeared to intensify, suggesting perhaps a change of predators concurrent with migration into more open pelagic habitat.

There is at least one exception to the wealth of evidence for an association between growth rate (expressed as size at a given time) and survival. Holtby and Healey (1986) found that smolt size (based on scale measurements) was "not consistently an important factor in marine survival," (p. 1956) for coho salmon from Carnation Creek (Vancouver Island, British Columbia, Canada) that smolted during 1971-82. Possible explanations for this contrary observation were not offered, nor are any immediately apparent.

Predation is the most commonly postulated cause of size-selective mortality. Aquaria tests with pink salmon and chum salmon fry prey demonstrated that small size is a predation handicap that can be outgrown (Parker 1971). Size-related swimming speed may be the critical factor in avoiding predation (Taylor and McPhail 1985). Smaller juveniles may also be more vulnerable to parasites (West and Larkin 1987).

The available evidence supports the hypothesis that rapid growth is associated with higher survival. Growth is a self-reinforcing process, the greater the growth, the greater the opportunity to continue growing (Larkin et al. 1956; Cushing 1975, 1981). If size-selective mortalities consistently favor rapid growth, then they probably also favor early maturity. Hence, any factor that increases the selection against slow growth (e.g., intensified predation) could contribute to declines in size and age at maturity. However, because slow growth (and older age at maturity) can provide fitness advantages in other developmental stages (e.g., older, larger adults with superior spawning ability), genotypes for slow growth/late maturity and rapid growth/early maturity may exist in balance in a population (Gross 1987). Selection favoring rapid growth in some environments may be counteracted during other stages of development (Healey 1986).

The ability of growth to influence both age at maturity and survival to maturity is a cornerstone principle for considering the natural and artificial early rearing environments of Brights.

Hanford Reach Environment

Described as "remnant habitat" (Becker 1985), the 94-km Hanford Reach is the last free-flowing stretch of the Columbia River between Bonneville Dam and Canada (Fig. 3). This area, the primary source of natural Bright production (Norman 1984; Howell et al. 1985a), is not pristine, however. The U.S. Atomic Energy Commission Hanford Nuclear Reservation, which contains or borders most of the Hanford Reach, has both changed and preserved Bright rearing habitat since the early 1940s. Since Grand Coulee Dam was closed in 1941, the hydroelectric power system has altered Hanford Reach flows to meet its needs, largely irrespective of impacts on Bright production. Becker (1985) provides a good description of the Hanford Reach environment.

This section examines the incubation and early rearing environment in the Hanford Reach to determine if changes in temperature, flows, and other environmental factors may have contributed to declines in size and age in the Bright runs. How some of these factors may contribute to changes in the relative fitness of small or large female spawners was described in the earlier section on maternal influences. How these factors relate to growth of juvenile Brights, which is closely associated with their size and age at maturity, was of interest for this part of the study.

The Hanford Reach gravels receive the fertilized Bright ova beginning in mid-late October (peak in early-mid-November) (Howell et al. 1985a) as the water temperature declines below 15°C (Fig. 16). This is similar to the generalization by Chambers (1956) that fall chinook salmon in the Columbia River Basin spawned when temperatures dropped below 13.3°C (56°F). The current temperature cycle, with a January-March low of approximately 4°C and an August-September peak of approximately 18°C, is later and less variable than before Grand Coulee Dam was closed (Jaske and Goebel 1967).

The temperature regime may favor later spawning in the Hanford Reach. During the 1960s as many as nine (in 1964) nuclear reactors were discharging thermal effluents into the Hanford Reach (Coutant 1969) and probably increasing the temperature of the Columbia River. During that time Olson et al. (1970) found that Bright eggs subjected to the warmest experimental temperatures (at increments above Hanford Reach ambient) had abnormally high mortalities just before hatching, with survivors suffering further exceptional mortalities much later at the critical first-feeding stage. The researchers did not identify a temperature tolerance ceiling, although their results (their Fig. 1, 7, 13, and 19) suggest 15°C (59°F) as the approximate limit (see also EPA 1971). Even this upper limit may be too high for best embryo viability (Combs and Burrows 1957; EPA 1971). Bright eggs spawned early in the season may be less viable because of exposure to higher water temperatures.

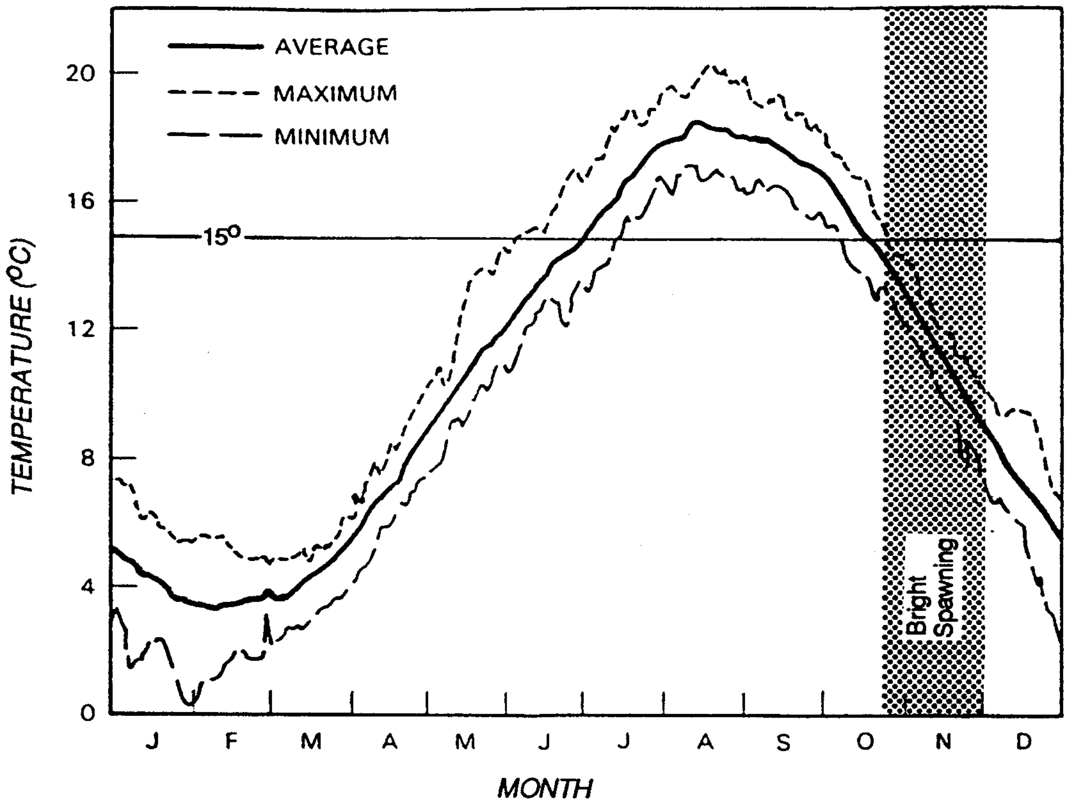

Figure 16. Period of Bright spawning in relation to water temperatures at Priest Rapids Dam. Onset of spawning corresponds with temperatures declining below about 15°C (horizontal line). Modified from Becker 1985; used with permission.

The filling of Lake Roosevelt behind Grand Coulee Dam has probably shifted the thermal window of opportunity in the Bright incubation environment. Before 1941, the Hanford Reach temperature may have fallen below the 15°C ceiling a month earlier than it presently does (mid-October; Fig. 16; Jaske and Goebel 1967). Although time of Bright egg deposition prior to 1941 is not known, it was probably earlier than at present, because temperatures declined to acceptable levels earlier in the season. Minimum winter water temperatures also are probably higher since 1941 (Jaske and Goebel 1967), which would shorten incubation time and might improve survival to, and size at hatch (Combs and Burrows 1957; Olson et al. 1970; Beacham and Murray 1987).

Bright fry 35-40 mm (FL) long emerge from the gravel as early as March (Mains and Smith 1964; Becker 1973), and fry of this size may still be found in June (Norman 1987). The earliest emergents are apparently able to find food items, although the rapid increase in numbers of fry in shoreline feeding areas in April corresponds with a minimum in the average dry weight of stomach contents (Becker 1973). Insects -- mostly Chironomidae (midges) and a few other floating, drifting, or free-swimming autochthonous aquatic insects -- compose approximately 95% of the juvenile Bright diet (Becker 1973).

Water temperature becomes most favorable for growth in May, but during June it ascends beyond the optimum range (Fig. 17). Fish lengths are most variable during June and July (Becker 1973), when both 33-mm emergent-sized fry and 90-mm fingerlings may be present (Norman 1987). This range of sizes undoubtedly reflects broad differences in emergence timing and growth. Early emergence and rapid growth might favor survival and better growth during the relatively short May-June period of optimum growth temperatures, but adaptiveness of emergence timing has apparently not been studied.

At least one attempt has been made to estimate growth of Bright juveniles in the Hanford Reach. Norman (1987) estimated growth of approximately 0.99 mm/day based on differences between average lengths of wild coded-wire-tagged fry released in early June and recaptured in early July. Although such changes in average lengths are frequently used as growth estimates (e.g., Reimers and Loeffel 1967; Becker 1973; Reimers 1973), they probably reflect size-selective sampling methods, mortality, and emigration as well as fish growth. Good estimates of juvenile Bright growth or Hanford Reach growth conditions are lacking.

Bright juveniles are transients; "populations" in a given area are always in flux. Daily flow variations that disrupt territorial behavior, minimal shoreline habitat relative to discharge volume, and dispersed food availability may contribute to the continuous

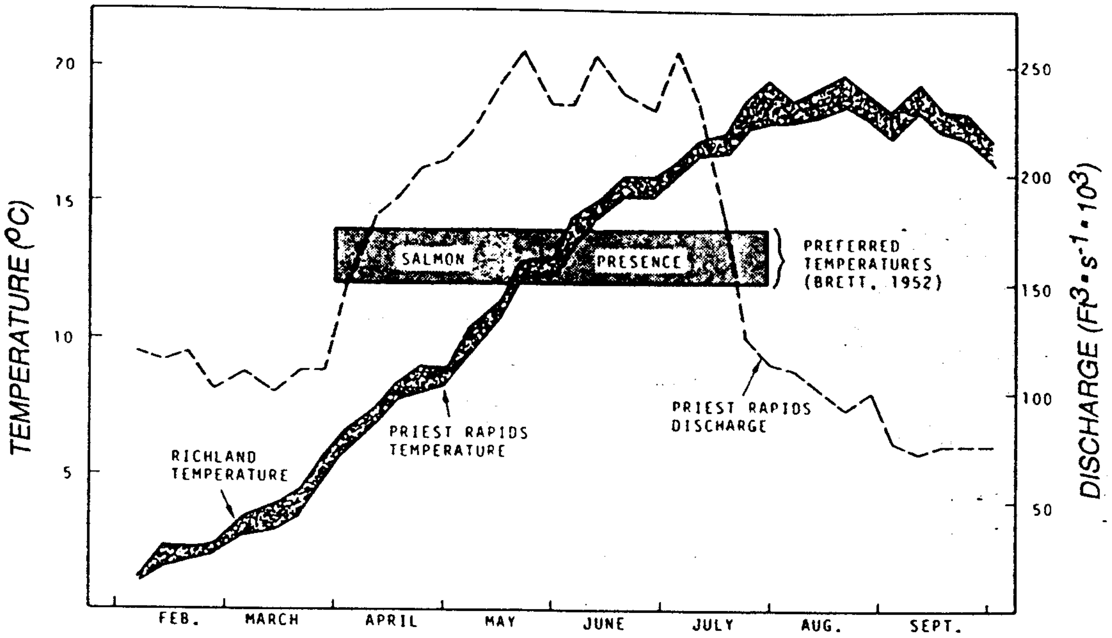

Figure 17. Columbia River temperature and flow in the vicinity of the Hanford Reach during 1969 in relation to the presence of juvenile Brights and the preferred temperatures of juvenile fall chinook salmon. Becker (1973), Fig. 2; used with permission of the author.

downstream movement of young Brights (Becker 1973). Whether movement is size related is not known. Outmigration, which generally occurs a few months after emergence during the first year of life, is considered in a later section.

As previously discussed, the larger the juveniles at time of outmigration, the better their chances for survival, continued growth, and early maturity. Juvenile size is a function of emergence time and size, growth rate, and duration of growth. Temperature, flows, and other environmental factors influencing these determinants of size have changed due to developments in the 1940s and since. Unfortunately, the limited information available provides little basis for conclusions about effects of these environmental changes on juvenile growth and size and age at maturity.

One thing is certain, too little is known about the mechanisms and potential for Bright production in the Hanford Reach. When a 1986 spawning escapement of nearly twice the management escapement goal produces "a large healthy 1987 presmolt wild fall chinook rearing population in the Hanford reach," (Norman 1987, p. 15), the rationale for the escapement goal must be questioned; it may be too low. Others have also challenged the basis for the escapement goal (Rogers and Hilborn 1988).

Priest Rapids Hatchery Environment

Introduction Hatchery practices can directly influence size and age at maturity in the propagated stocks in at least two principal ways, through mating procedures and rearing practices. Bright broodstock acquisition and spawning practices at Priest Rapids Hatchery are addressed in a later section; rearing practices are of interest here. Does the rearing environment at Priest Rapids Hatchery contribute to lower size and age at maturity? I tested the null hypothesis that Brights produced by Priest Rapids Hatchery mature at the same age as those produced naturally in the Hanford Reach.

Releasing large smolts has become a norm for Columbia River hatcheries that raise anadromous Pacific salmon (Wallis 1968; Seidel et al. undated). As discussed previously, this practice achieves a higher survival rate, but can also lead to undesirably early maturity. Still, survival rate (regardless of sex composition and size at return) apparently continues to be the favored measure of hatchery performance (Seidel et al. undated, 1988).

Priest Rapids Hatchery began operation as a spawning channel in 1963 to mitigate for Bright spawning habitat lost when Priest Rapids and Wanapum dams were constructed. Designed to accommodate 2,500 pairs of spawners in a 6000-ft (1969 m) long channel, the facility was beset by high mortalities and low adult returns during its first decade (Allen and Meekin 1973). Artificial spawning and incubation began in 1972, and since 1978 the spawning channel has been used exclusively for conventional raceway rearing (M. Dell, Public Utility District No. 2 of Grant County, WA, pers. comm., 8/88).

Since the spawning channel concept was abandoned, Priest Rapids Hatchery has released Bright juveniles that are much larger than the naturally produced Brights residing at the same time in the Hanford Reach. Allen and Meekin (1973) recommend release of fingerlings at approximately 80 mm (about $75 \cdot lb^{-1}$), and others have recommended rearing to a size of $40 \cdot lb^{-1}$ (Kaczynski and Moos 1979). Fingerling releases since 1978 have generally been at sizes of $50\text{-}100 \cdot lb^{-1}$ (unpubl. data provided by M. Dell, Public Utility District No. 2 of Grant County, WA), and those released in 1987 (June 6-18) averaged $60\text{-}74 \cdot lb^{-1}$ and 82-90 mm long (unpubl. data provided by G. Osborne, WDF, Manager, Rocky Reach Hatchery)[3]. This contrasts with naturally produced fingerlings seined from the Hanford Reach on June 9, 1987, which averaged only 57.0 mm in length (Norman 1987).

Incubation in 11.7°C (53°F) well water at Priest Rapids Hatchery accelerates embryonic development, permitting a longer period of feeding and growth prior to release. Fry hatch in December and are ponded (when feeding starts) from the last week of January through the third week of February. Ponded fry have in the past enjoyed 10°C (50°F) environments and rations of ≤4% of body weight per day while the unemerged and perhaps unhatched natural fry are exposed to the 4°C winter waters of the Hanford Reach. As the hatchery fry grow, Columbia River water at ambient temperature supplants the well water. Growth is regulated through temperature and diet to attain 100,000-120,000 lb of total production for mid-June release (Paul Pedersen, Manager, Priest Rapids Hatchery, pers. comm.). Can this prolonged period of favorable growth, which results in such large size at release, cause the fish to mature earlier?

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[3] Length at release for Brights from Priest Rapids Hatchery reported by Howell et al. (1985a; 100-130 mm) and cited by Mullan (1987) appears to be inconsistently high for the reported number of fish per pound (60-100) and the data available from other sources.

Methods Mean ages, lengths, and sex compositions (percent female) of known hatchery-produced spawners were compared, for return years 1980-87, with spawners presumably produced naturally in the Hanford Reach. Recoveries of Priest Rapids Hatchery CWT codes (Appendix C) in the Hanford Reach spawning ground surveys, at Priest Rapids Hatchery, and in spawning ground surveys above Priest Rapids Dam represented fish of Priest Rapids Hatchery origin (unpubl. data provided by S. Markey, WDF, Olympia, WA). Over 95% of the CWT recoveries were from Priest Rapids Hatchery.

Bright fingerlings produced naturally in the Hanford Reach have been coded wire tagged only since 1987 (1986 brood, first returns as jacks in 1988; Norman 1987), so natural fish could not be positively identified during the return years examined. Biological samples taken during spawning ground surveys in the Hanford Reach by personnel from WDF's Columbia River Laboratory, Battle Ground, WA, were used, with some modification, to represent naturally produced fish. For the 1985-87 returns, spawners bearing CWT codes from any hatchery were eliminated from the data set. Because most of the coded wire tagged fish were from representative tag groups in a larger release (i.e., only a fraction of the release group was tagged), enough fish of the same sex, age, and length (as each CWT-bearing fish) were also eliminated to account for untagged fish in the hatchery release that could be expected in the spawning ground survey samples. For 1985-87, less than 5% of the records were eliminated as known hatchery (coded wire tagged) or as being representative of untagged hatchery fish.

Not all hatchery-produced fish could be identified and eliminated, but this failure only makes observed differences more conservative. In many years, substantial proportions (approximately 80% for 1983-85 releases) of the hatchery Bright releases in and above the Hanford Reach were not represented by CWT groups (Coleman and Rasch 1981; Castoldi and Rasch 1982; Castoldi 1983; Hill 1984; Kirby 1985; Abrahamson 1986; PMFC 1988). Additionally, spawning ground survey data for 1980-84 -- obtained largely in computerized form from the National Marine Fisheries Service, Portland, OR (R.

Vreeland) -- did not identify tagged fish, so no hatchery fish were eliminated from the data for 1980-84. Hence, data from spawning ground surveys that were used to represent natural fish in all years contained an unknown, but probably minor proportion of hatchery-produced fish. In 1979-82, as many as 8% to 33% of the spawners on Vernita Bar (a heavily used spawning area near Priest Rapids Hatchery) and elsewhere in the Hanford Reach may have originated in hatcheries (Chapman et al. 1983 cited in Becker 1985; other sources cited in Dauble and Watson 1990). Norman (1984) estimated that only 8.7% of the fish spawning naturally in the entire Hanford Reach in 1983 were of Priest Rapids Hatchery origin. The effect of this "contamination" would be to reduce the apparent differences between the two groups and make resulting conclusions more conservative.

Scale samples taken from Bright carcasses during the spawning ground surveys were analyzed by WDF personnel to determine age. Only records for which an age was recorded were included in these analyses.

No statistical tests of significance were attempted between hatchery and natural groups within each year, because of potentially large biases in the data. For example, returns of Priest Rapids Hatchery fish in a given year are of five age classes (2-6), and the distribution among the classes is a function of at least three extraneous factors in addition to the inherent age distribution:

1) numbers of tags released for each of the several broods represented in the run,
2) fingerling-to-adult survival for the broods, and
3) proportion of, and selection criteria for Priest Rapids Hatchery brood stock trapped at Priest Rapids Dam (large fish and females are generally selected). (This selection also represents a potential bias, which will be discussed later.)

Differences in these factors among broods and return years can affect the real and apparent age distributions of returning hatchery fish. Similarly, differences in production and survival of broods distort expression of the inherent age distribution for natural fish.

Numbers of tags released for the hatchery broods are known and corrections could be made for the differences in numbers of tags among releases, but differences in natural production, survival of both groups, and broodstock selection during dam trapping are not known. These biases, which influence values (i.e., mean age, mean length, and percent female) for the two groups, may act independently and could be sufficiently large to render tests of significance for single year comparisons meaningless.

Annual means of length and age for each sex, as well as percent female for all years (1980-87) were evaluated with the sign test for the null hypothesis that the values for hatchery and natural fish were equal. Generally, the mean values within a treatment and among years are sufficiently independent that the outcomes between treatments within years are not influenced by the results of prior years. Graphical comparisons were made using ratios of mean length-at-age to illuminate potential differences in growth and maturity patterns.

<u>Results</u> For the years 1980 through 1987 the returning hatchery fish were shorter, were younger, and had a lower percentage of females in nearly all years (Table 1 and Appendix D). The differences were generally, but not consistently, less for females (higher ratios in Appendix D) than for males. Only for male length (both for all ages and ages 3-6 comparisons) and percent female (all ages) were differences sufficiently consistent among years to be statistically significant (sign test; $P \leq 0.01$). Including jacks (all ages) or excluding jacks (ages 3-6) made little difference in the outcomes (Table 1).

There are no striking patterns in the ratios of mean length at age, although negative slopes are common (Fig. 18). Negative slopes indicate that hatchery fish become smaller, relative to their natural counterparts, with increasing age. Any potential size (growth) advantage associated with hatchery rearing, which <u>is not</u> clearly demonstrated in Fig. 18, is expressed more in younger age classes.

Table 1. Summary of length, age, and sex composition of hatchery and natural spawners returning in 1980-87. Means and percent female are unweighted averages of the eight annual observations. Probabilities (P) are from the sign test (two-tailed, cumulative for observed distribution plus more extreme distributions), which compared hatchery and natural values for each year to test the H_o that the overall hatchery value = overall natural value. ** = significant at $P \leq 0.01$. Detailed data are in Appendix D.

		Mean		No. of Years (of 8) when Mean is Greater for:		
		Hatchery	Natural	Hatchery	Natural	P
<u>All Ages</u>						
Males:	Length (mm)	700	748	0	8	0.008 **
	Age (yr)	3.21	3.36	1	7	0.07
Females:	Length (mm)	858	888	2	6	0.29
	Age (yr)	4.05	4.24	2	6	0.29
Percent Female:		40.8	49.8	0	8	0.008 **
<u>Ages 3-6</u>						
Males:	Length (mm)	764	823	0	8	0.008 **
	Age (yr)	3.52	3.70	1	7	0.07
Females:	Length (mm)	858	890	2	6	0.29
	Age (yr)	4.05	4.25	2	6	0.29
Percent Female:		46.6	55.4	1	7	0.07

Such a trend is expected under the hypotheses that favorable early growth hastens maturity and that this effect is expressed most clearly in individuals genetically predisposed to early maturity.

The results of the comparisons of mean age, mean length, and percent female are consistent among themselves. As would be expected, earlier maturity in the hatchery group is associated with lower mean lengths and lower percentages of females (males prevail at ages 2 and 3 and may be more "elastic" in their age at maturity).

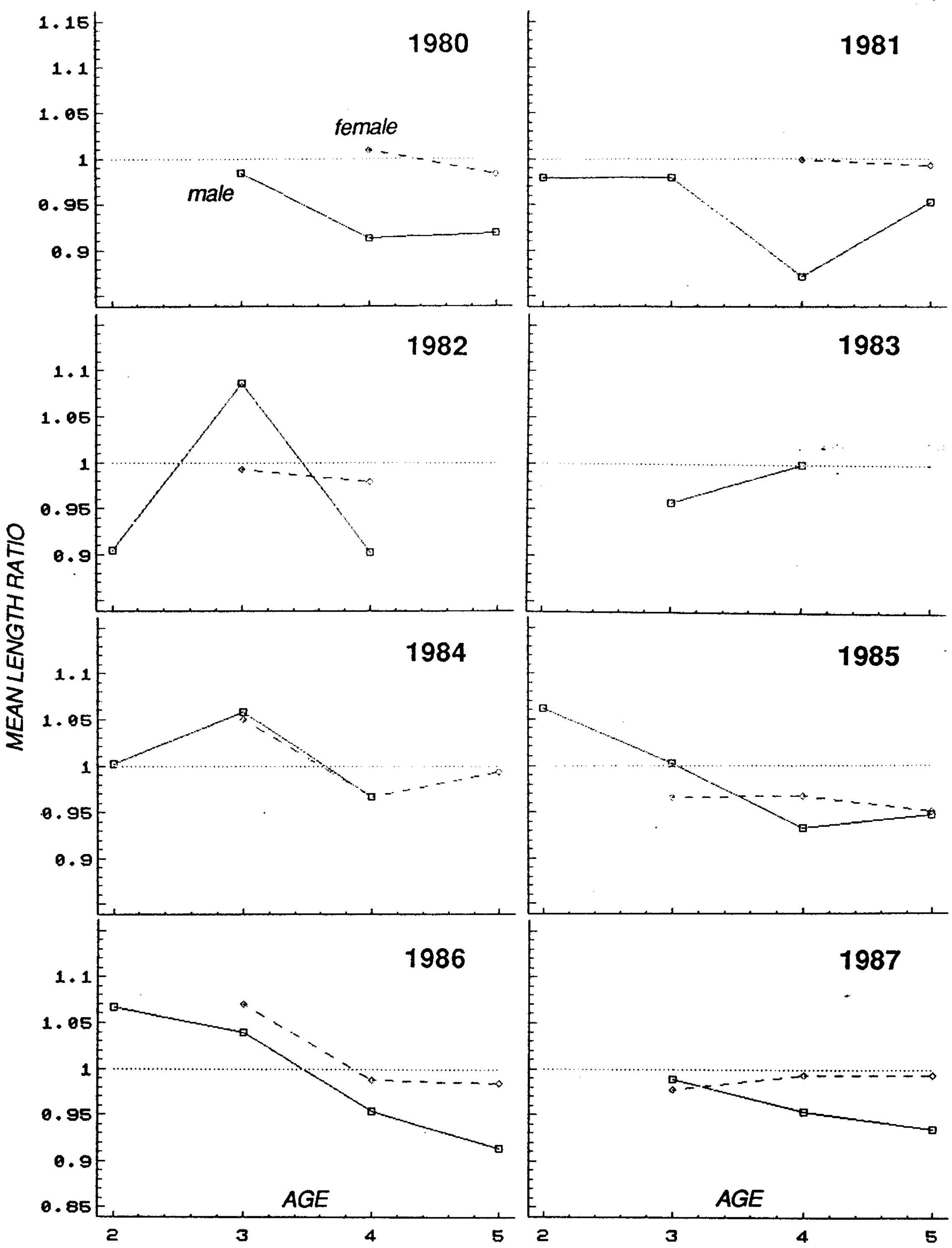

Figure 18. Ratios of mean length at age of Bright hatchery and natural spawners returning in years 1980-87. Ratios are derived by dividing hatchery mean length by natural mean length; hence, values less than unity (horizontal dotted line) indicate the hatchery value is the lesser. See Appendix D and text for data details.

The lower proportion of females and their smaller size in the returns of hatchery fish indicate that hatchery fish probably have lower reproductive potential on a per-fish basis (both sexes and all ages) than the returning natural fish. This can be coarsely quantified using a fecundity-length regression and a ratio of percent female. The equation,

$$F = 9.853L - 3484$$

where F is fecundity and L is FL (mm), was derived for Bright spawners in 1983, 1985, and 1986 from the egg bank at Bonneville Hatchery (unpubl. data provided by D. Hankin, Humboldt State University, Arcata, CA). The coefficients in this equation are within the broad range of coefficients calculated for Bright spawners at McNary, Priest Rapids, and Rocky Reach spawning channels (Mathews and Meekin 1971). Estimated fecundities were calculated for all hatchery and natural females in the samples. The average estimated fecundity (all years and all ages combined) of hatchery females, because of their generally smaller size, was 96% of that estimated for natural females (Appendix Table D.6). The proportion of females in the returning hatchery fish was only 82% (40.8/49.8, from Table 1) that of the returning natural fish. Hence, the reproductive potential of the hatchery fish sampled in the escapement was only about 79% (0.96 · 0.82 · 100) as great as the natural fish sampled. Most of this difference is a result of the lesser proportion of females in the hatchery samples.

<u>Discussion</u> This analysis suggests that Brights produced and coded wire tagged at Priest Rapids Hatchery and returning during 1980-87 were younger, smaller, and more likely to be male than their natural counterparts from the Hanford Reach. Therefore, the average hatchery fish in the escapement may not be the equal of a natural fish in reproductive potential. This does not take into account potential differences in spawning success and viability of progeny. Although it could not be shown statistically that Brights from Priest Rapids Hatchery mature earlier than their natural counterparts,

statistically significant differences were found in lengths of males, and sex composition, and females were proportionately fewer among escaping hatchery fish than among natural fish. Potential sources of bias exist that could have influenced, positively or negatively, the differences found in these results.

Aging of Bright scales tends to be biased slightly downward (Roler et al. 1984; LeFleur and Roler 1985), perhaps due to resorption of the scale margins and resulting loss of annuli. Such bias could cause the mean estimated ages of the presumed natural fish used in this analysis to be lower than means of true ages. The true differences between mean ages of the two groups may therefore be greater than indicated here. Ages of hatchery fish are determined from CWT codes and are not likely to be biased, although the age composition in a given year may be biased for other reasons.

Carcasses sampled on the spawning ground surveys may not be accurately sexed, although the net effect of misidentifying the sex of the fish on differences in reproductive potential, as calculated here, is probably negligible. Fish of smaller sizes, whose external morphology differs little or not at all between sexes, may be the greatest source of error. For example, in 1984, 44 (8.5%) of the 516 2-yr-olds sampled were identified as females, but in the subsequent 3 yr none of the 422 total 2-yr-olds were identified as females. Currently, the proportion of 2-yr-old females is assumed to be negligible (even 3-yr-old females are few), and all jack-size carcasses are automatically designated as male (personal observation). This assumption, which is probably correct, apparently did not prevail during 1984, and it is likely that most or all of the 44 2-yr-olds reported as female were actually males. This probable misclassification would cause the 1984 natural female mean age and length to be too low, those of males to be too high, and the percent female to be too high. The 2-yr-old "females" in 1984 also reduced the estimated fecundity of the natural females (Appendix Table D.6). The small overall effect of this misidentification is to make the differences appear smaller than they actually are.

It may not be accurate to assume that hatchery and natural females have the same length-fecundity relationship. Rapid freshwater development, as would occur in a hatchery environment, has been associated with higher fecundity (but smaller egg size) at a given body size in Atlantic salmon (Thorpe et al. 1984). A similar phenomenon may occur in Brights.

Potentially serious and unrecognized biases may be associated with the two different sources of the data. Samples of returning hatchery fish came overwhelmingly from Priest Rapids Hatchery itself, either from spawners voluntarily entering the discharge stream (hereafter, "volunteers") or from brood stock trapped at Priest Rapids Dam (hereafter, "conscripts") just upstream from the hatchery.

Conscripts are intentionally unrepresentative of the run; hatchery personnel selected the larger fish, and the proportion of brood stock obtained by this method (Fig. 19) and the selection criteria often vary from year to year (Allen and Meekin 1973; Bruce Ault, WDF, Soleduck Hatchery, pers. comm.). An upward bias in mean age of the hatchery fish could be expected, depending on how much of the brood stock was obtained from the dam trap and how intense the selection was during the 8-yr period. This potential bias would make the differences appear smaller than they really are.

The volunteers to Priest Rapids Hatchery, which contributed substantially to the data set of hatchery-produced fish, may be smaller and younger on average than the population of returning hatchery fish. The hatchery discharge stream, which flows through an excavated ditch from the end of the former spawning channel to the Columbia River, is shallow and miniscule compared to the river channel. It is possible that large spawners may prefer to remain in the deep, broad mainstem. Large fish (> 20 lb) are believed to avoid using shallow overflow entrances to fishways (Bell 1986). Jacks were especially prevalent among the Bright volunteers at the McNary Spawning Channel discharge stream (Meekin and Harris undated, 1967), suggesting a greater attraction to smaller fish. Jacks have also been abundant among the volunteers to Priest Rapids Hatchery (Fig. 20), but it is not known whether their proportions are exceptional

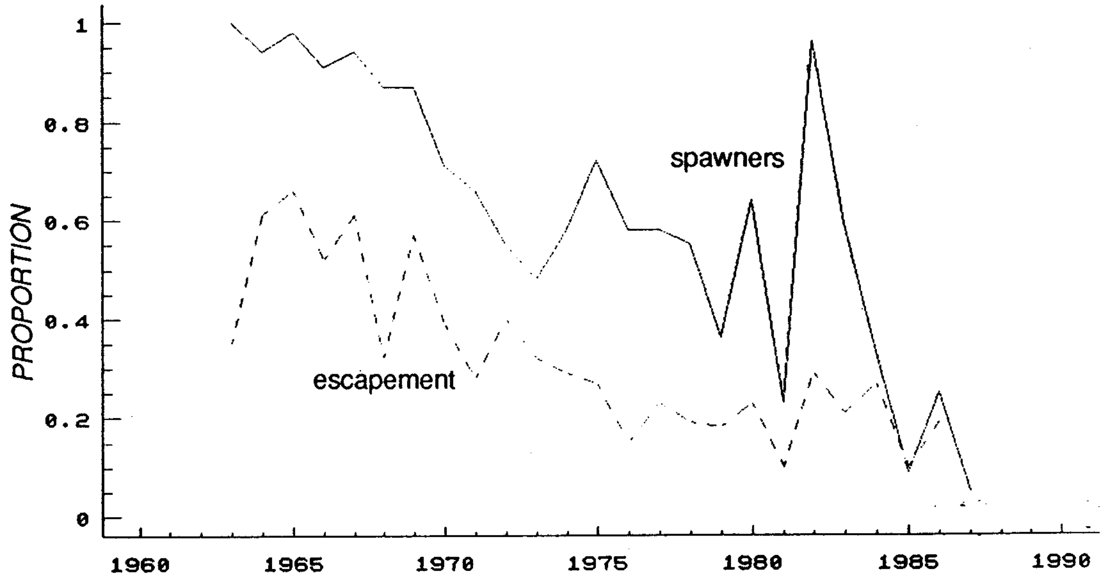

Figure 19. Proportion of adult brood stock for Priest Rapids Hatchery that was trapped at Priest Rapids Dam (solid line) and the proportion of adult Brights passing Priest Rapids Dam that was removed for use as brood stock at the hatchery (dashed line). Data provided by M. Dell, Public Utility District No. 2 of Grant County, Ephrata, WA.

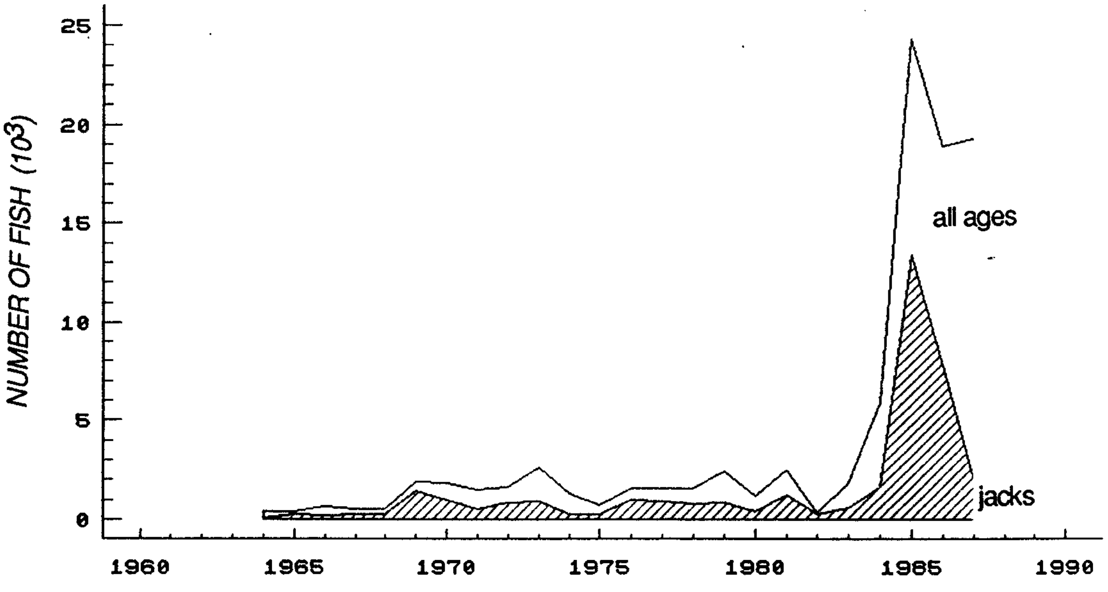

Figure 20. Numbers of jacks and Brights of all ages that voluntarily entered the Priest Rapids Spawning Channel trap, 1964-87. Data provided by M. Dell, Public Utility District No. 2 of Grant County, Ephrata, WA.

relative to the entire run of hatchery fish. Insufficient numbers of tagged fish have been recovered from the Hanford Reach to test for differences between those that remain in the river to spawn and those that voluntarily return to the hatchery. Biases in size and/or sex associated with volunteers to the hatchery, if real, would cause the differences noted here to be exaggerations; they would also cause data collected from volunteers at Priest Rapids Hatchery to be unrepresentative of the run.

Likewise, carcasses sampled on the spawning ground surveys may not be totally representative of the Brights spawning naturally in the Hanford Reach. Factors associated with size and sex may influence which carcasses are washed ashore, come to rest in shallow waters, or otherwise become available to sampling. Of the estimated numbers of spawners in the Hanford Reach in 1983-87, less than 6% were encountered during spawning ground surveys (from estimates and data in Roler et al. 1984; LeFleur and Roler 1985; Roler and LeFleur 1986; Roler 1987, 1988). Can it be assumed that those 6% or less found along the shorelines have the same size and sex compositions as the remaining 94+% that are caught-up on submerged boulders and debris (Swan et al. 1988) or are otherwise unavailable to samplers? Perhaps not.

Oregon Department of Fish and Wildlife (ODFW) studies on fall chinook salmon in the small coastal Salmon River suggest that in some years males and the smaller fish of both sexes are recovered at lower rates by the spawning ground surveys than they occur in the run (Boechler and Jacobs 1987; unpubl. data provided by S. Jacobs, ODFW, Corvallis, OR). Differences in postreproductive behavior between the sexes and removal of small carcasses by scavengers have been hypothesized as possible reasons. Although the results from the Salmon River cannot be extrapolated to the Hanford Reach, we also cannot assume that Hanford Reach samples are always good indicators of the naturally spawning Bright population. A majority of spawning in the Hanford Reach may occur in very deep water (Swan 1989), and it is questionable whether the fish that spawn there are adequately represented in the spawning ground samples. Males and small fish may be under (or over) represented in the spawning ground survey data, possibly contributing to (or detracting from) the apparent differences between hatchery and natural fish.

Considering the potential biases, the apparent reproductive inferiority of hatchery-produced fish can be interpreted in two ways: (1) as a real difference, meaning hatchery fish have substantially lower reproductive potential and are not representative of the run as a whole (including natural fish), or (2) as a spurious result of sampling biases, meaning that one or both sources of escapement data (CWT recoveries and spawning ground surveys) may be biased. Both interpretations may be correct in part, and neither can be ruled out. However, available evidence suggests that something about hatchery rearing, probably favorable growth conditions, tends to reduce age at maturity and contribute to a high proportion of males in the returns. Atlantic salmon are expected to develop more rapidly and mature earlier when exposed to practices similar to those used at Priest Rapids Hatchery (Ritter et al. 1986; Saunders 1986; Thorpe 1986). For chinook salmon, age-specific maturation probabilities are believed by some to be strongly influenced by hatchery rearing and release practices (Hankin and Healey 1986). It is reasonable to suspect that rearing practices at Priest Rapids Hatchery contributed to real differences in age (and size) at maturity that were manifest in the comparison with natural spawners.

Changes in age at maturity caused by hatchery rearing practices (e.g., rapid early growth) are probably phenotypic and do not necessarily lead to genetic changes in the stock (Fig. 1.D; see also *Growth and Age at Maturity*, p. 59). However, there is one relatively obvious way that hatchery practices can indirectly result in genetic selection for size and age. Hatchery stocks that have higher lifetime survival can support higher harvest rates in fisheries. Survival benefits obtained in the spawning, incubation, and early rearing stages can be passed on to fisheries as higher harvest rates. If those fisheries are selective, then the increased harvest rate made possible by hatchery operations can intensify selection in the fishery. Selection intensity is a function of degree of selection and proportion of the population impacted by selection (Appendix B; see also Role of Stock Abundance, p. 173).

<u>Summary and Conclusion</u> This section examined the Priest Rapids Hatchery environment to determine if incubation and juvenile rearing practices could have contributed to declining size in the run. Conditions at Priest Rapids Hatchery are favorable for rapid development and growth; size at release has been greater than the concurrent size of natural fingerlings in the Hanford Reach. Good growth conditions are known to hasten maturity (Alm 1959; Wallis 1968; Lorz 1971; and other sources cited in *Growth and Age at Maturity*, p. 59).

Known hatchery Brights in the 1980-87 escapements were generally younger, smaller, and less likely to be female than presumedly natural Brights sampled during spawning ground surveys. The differences are probably real, at least in part, meaning that returning hatchery fish may have lower reproductive potential than their natural counterparts (0.79 was the calculated ratio of reproductive values, with all ages and years combined). Known and potential biases in the data could have influenced, positively or negatively, the apparent differences. Such biases, if real, would make escapement data from these two sources unsuitable for many analyses. In either respect, it appears that CWT recoveries from Priest Rapids Hatchery are not representative of the natural spawners and hence the Bright run as a whole.

I conclude that rearing practices at Priest Rapids Hatchery probably contribute to reduced size at maturity in Brights produced at the facility. The sex composition of the returning hatchery fish also appears to be influenced. Increased hatchery production and a greater emphasis on large size at release during the last three decades has very likely contributed in an unknown degree to the observed declines in age and size at maturity in the run as a whole. Brights, even now managed principally as a hatchery stock (Rogers and Hilborn 1988), can be expected to show a greater tendency toward early maturity as artificial propagation contributes greater portions

Outmigration

Formerly a free-flowing conduit for outmigrating Brights, the mainstem Columbia River between the Hanford Reach and Bonneville Dam is now a chain of four dams and reservoirs. Turbine-caused mortalities are estimated at 10-30% per dam (NPPC 1987), and total passage mortalities may be 35-51% per dam/reservoir project (based on 6-18% survival of juveniles released at Ringold Ponds relative to juveniles transported to below Bonneville Dam in 1968-69; Dawley et al. 1986). Ameliorating the large dam- and reservoir-related mortalities to juvenile outmigrants is probably the most pressing and controversial problem facing fishery managers on the Columbia. I examined these mortalities to determine how, if at all, they might be selective for traits related to size and age in the adult run. Good relevant information is scant; hence, this coverage will be brief and largely conjectural.

The outmigration pathway is a virtual gauntlet of dams and reservoirs. Downstream movement of newly emerged fry in the Hanford Reach has been known to begin in March and peak in April, with larger fingerlings outmigrating at least into July (Edson 1957; Mains and Smith 1964). In recent years, Brights and other subyearling chinook salmon outmigrants have passed McNary Dam, the nearest downstream project (Fig. 3), during relatively short periods principally during June and July, with smaller numbers passing during late summer and fall months (Karr and DeHart 1986; DeHart and Karr 1987, 1988) (Fig. 21). The present contracted migration period may be the result of selective forces imposed by in-river developments.

Turbines and predators are important causes of outmigrant mortalities associated with dams and reservoirs. Since 1972, the mainstem dams have had the generating capacity to pass essentially all of the Columbia's flow (and outmigrating Brights) through turbines (Park 1985). At least one study has suggested that turbine mortality may be a function of fish size (Cramer and Oligher 1964),

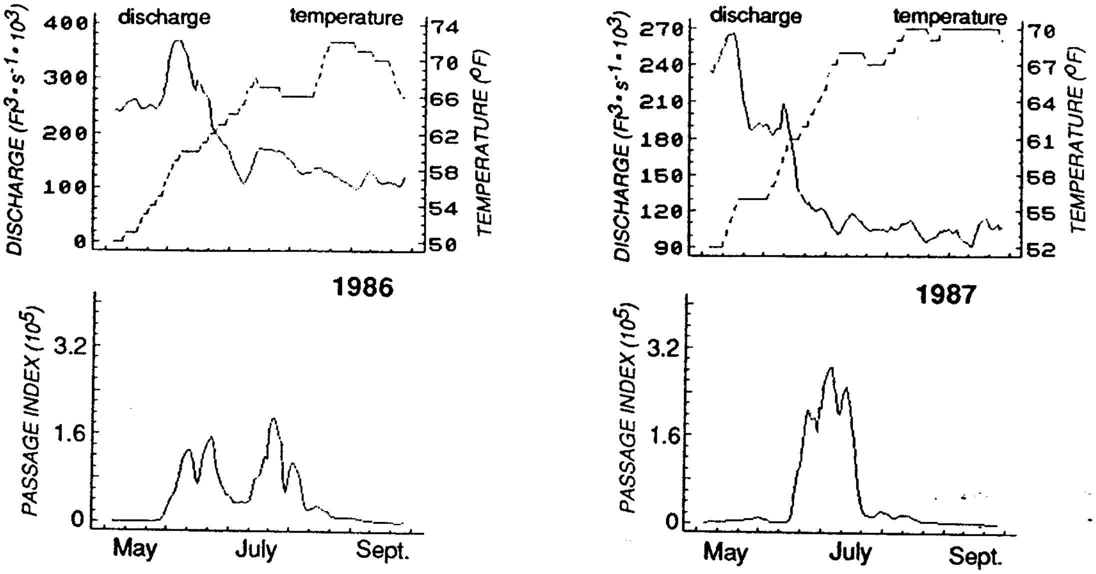

Figure 21. Passage of outmigrating subyearling chinook salmon (mostly Brights) at McNary Dam in association with discharge (river flow) and water temperatures, 1986 and 1987. All points represent 7-d moving averages. The passage index is assumed by some to be proportional to the number of juveniles passing the dam (DeHart and Karr 1988). Data from the Fish Passage Center, Portland, OR.

but differential mortality over the size range of outmigrating Brights is not likely to be great. McNary Dam's highly regarded mechanical bypass system (NPPC 1987) is estimated to divert less than 50% of subyearling chinook salmon around turbines under the best conditions (0.65 maximum theoretical fish guiding efficiency times 0.75 submersible travelling screen effectiveness, Brege et al. 1988, pp. 17-19). At McNary Dam, fish that are not guided must negotiate the lower three dams and reservoirs, as well. Brights collected in the bypass system at McNary Dam are usually transported by truck and barge past the downstream dams and released below Bonneville Dam. High temperatures associated with low flows during the latter part of the subyearling outmigration apparently contribute to the poor bypass efficiency at McNary Dam (Brege et al. 1988) and to direct mortalities (Koski et al. 1988).

Flows are controlled by the U.S. Army Corps of Engineers, although the tribes and fishery agencies may request a small volume of water (known as the Water Budget) to assist the passage of spring migrants between 15 April and 15 June (DeHart and Karr 1989). Because most Brights migrate later, in the summer, very few benefit from the Water Budget, and most suffer from it because of energy storage accounts that reduce flows in the summer to compensate for Water Budget use in the spring (DeHart and Karr 1989, 1990). Low flows increase the time required for smolts to pass through the reservoirs (DeHart and Karr 1990), thereby increasing exposure to predators.

Increased predation by northern squawfish (*Ptychocheilus oregonensis*) and other predators on subyearling migrants passing McNary Dam is associated with increased temperatures and reduced flows during July and August (Vigg et al. 1988; Rieman et al. 1988). Dam passage mortalities and predation appear to select for earlier Bright outmigration. But, earlier (smaller) outmigrants may be vulnerable to a greater size range of predators (Poe et al. 1988), so predation may also select for larger size at outmigration. (Recall that predation is the favored hypothesis to explain the association between juvenile growth and survival.) Predation by mainstem reservoir fishes provides a plausible explanation for the relative paucity of young, early migrants and the contracted period of subyearling passage at McNary Dam (Koski et al. 1988). If predation and/or other factors in the outmigration environment select for early migration at large size, then they select for rapid growth. Rapidly growing juveniles also are more likely to mature early.

In addition to harboring hundreds of thousands of predatory fish (Beamesderfer and Rieman 1988), the mainstem reservoirs may also be rearing environments for small Brights (Miller and Sims 1984; Becker 1985; Rondorf et al. 1990). Whether reservoirs represent better growing environments than the free-flowing stretches they replaced is certainly open to debate, as is the net benefit (perhaps negative) to the population of reservoir rearing when predation rates are high. Like other size-selective factors, intense predation may