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Revisiting the Stock Concept in Pacific Salmon: Insights from Alaska and New Zealand

Introduction and Historical Perspective

Although systematists classify organisms by phylum, class, order, family, genus and species, it is widely appreciated that these are points along a continuum of genetic relatedness and evolutionary separation (Mayr 1982). This continuum extends to reproductively isolated breeding units within species, known to geneticists as demes and to most field biologists as populations. These populations may be spatially isolated from each other if they are on separate islands, mountaintops or in ponds. However, in many animals the isolation of populations is not a simple matter of geography and limited mobility but rather one of behavior. Many populations have broad, overlapping feeding distributions but segregate at the breeding season, each returning to the site where they were born. Among the most famous examples of this phenomenon are the anadromous fishes such as American shad (*Alosa sapidissima*) and salmon (*Oncorhynchus*, *Salmo* and *Salvelinus* spp.) (Quinn and Dittman 1992). These fishes are spawned in freshwater, migrate to sea to feed and grow, and then return to spawn, almost invariably in the same stream or lake where they were spawned.

Some astute scientists inferred the homing phenomenon in the 1800s from phenotypic differences in fish from different rivers. Milner (1876) noted "[t]he generally accepted fact in the habits of anadromous fishes that they are disposed to return to almost the exact locality where they passed their embryonic and earlier stages of growth... Observations of the shad brought to the large markets shows considerable difference in the physiognomy and general contour of those from different rivers. The suggestion is natural that they are distinct and separate colonies of the same species, and thus slight characteristics are perpetuated because they breed in-and-in and do not mix with those of other rivers." Others concluded from the isolated locations of salmon spawning groups that these must be fish returning to the location where they had been spawned. A report from the United States Commission on Fish and Fisheries (1876) stated, "This stream [near Elko, Nevada] is one of the many that form the headwaters of the Columbia River, and to this point, eighteen hundred miles from its mouth, the salt-water salmon come in myriads to spawn... From these facts we may infer that the instinct of location is probably sufficient to attract a colony of fishes as far inland as the headwaters of the longest

river, whenever their home has been once established there.”

Although homing is a fascinating phenomenon in its own right, the separation of the salmon species into more-or-less discrete populations is the key element in their management and conservation. The basis of this so-called stock concept is that salmon inhabiting different rivers experience different patterns of natural selection, owing to differences among rivers in abiotic factors such as flow regime, temperature and substrate, and biotic factors such as predators, competitors, prey and pathogens. These differences in selection result in salmon that differ in color, fat content, size, age, timing of migration, disease resistance, and many other phenotypic traits. Rivers may differ in the productivity of their salmon populations or their carrying capacity (Möbrant et al. 1997), thus the populations must be managed as separate entities to prevent over-fishing less productive populations when they intermingle with more productive ones. The connection between salmon homing, population-specific traits and conservation was the focus of a landmark symposium held in 1938 in Ottawa, Ontario, Canada (Moulton 1939). Several papers presented evidence for the population-specific traits of Atlantic and Pacific salmon (e.g., Rich 1939) and the published discussions make it absolutely clear that these scientists saw the close connection between homing, the stock concept, and salmon conservation.

The next major advance in the field of salmon population biology came with the publication of another symposium, also held in Canada, as part of the H. R. MacMillan Lectures in Fisheries at the University of British Columbia in Vancouver entitled “The Stock Concept in Pacific Salmon” (Simon and Larkin 1972). There were several interesting papers, but the volume is dominated by Ricker’s detailed review of information on salmon homing, the differences among populations in various phenotypic traits, and the general failure of transplanted salmon to thrive as well as local populations (Ricker 1972). This outstanding review of the early literature is still widely cited today and was the key publication in the field until 1981, when a special issue of the Canadian Journal of Fisheries and Aquatic Sciences published papers from the Stock Concept International Symposium, held in 1980 in Alliston, Ontario. The issue had papers on a vari-

ety of fishes, including sea lamprey (*Petromyzon marinus*), largemouth bass (*Micropterus salmoides*), and walleye (*Stizostedion vitreum*), but many were on salmonids, including very useful reviews on Canadian populations of Atlantic and Pacific salmon by Saunders (1981) and McDonald (1981), respectively. As with the previous symposia, the authors clearly drew the links between homing, stock-specific variation in phenotypic traits, and the conservation and management of populations. In the years that followed this symposium, many papers were published, documenting variation among salmon populations in a wide variety of adaptive traits. Taylor (1991) reviewed much of the literature and pointed out that in some cases of “local adaptation,” only phenotypic variation was documented. He argued that local adaptation implies not only phenotypic variation among populations in a given trait but also a genetic basis for the trait, and a demonstrated survival advantage associated with the trait.

In addition to the large and growing literature on population-specific variation in adaptive traits among wild salmon populations, the last few decades have seen rapid expansion of salmonid aquaculture. The successful culture of salmonids depended in part on the choice of suitable broodstock, and subsequent selective breeding for chosen traits. This requirement led to many experiments on the genetic control of traits of importance in culture such as fecundity and growth (e.g., Gjedrem 1983, Hershberger et al. 1990, Crandall and Gall 1993, Su et al. 1997, Jónasson et al. 1997). The general conclusion of these experiments is that there is a substantial genetic component to most of the traits, though of course there is a degree of environmental control as well. Finally, the 1970s and 1980s saw the development and use of molecular techniques to study the population genetics of fishes and especially salmon. These techniques initially used natural variation in the proportions of more or less selectively neutral polymorphic proteins to demonstrate reproductive isolation of salmon populations (see review by Utter 1991). More recently, variation in mitochondrial and nuclear DNA has also been used to study the population structure of salmon and other fishes (e.g., papers in the special issue of *Reviews of Fish Biology and Fisheries*, edited by Carvalho and Pitcher 1994).

Thus there have been three major lines of research into the subject of the “stock concept” or

evolution of salmon populations: natural variation in phenotypic traits, controlled or selective breeding, and variation in more selectively neutral molecular traits. As was pointed out in the 1994 American Fisheries Society symposium on "Evolution and the Aquatic Ecosystem" (Nielsen 1995, and notably Hard 1995), all are valid approaches and need to be integrated into a holistic view of salmon population structure, evolution and management (see also Utter et al. 1993, Grant et al. 1999). These lines of research, undertaken by scientists with diverse backgrounds and interests, form much of the scientific framework for the application of the U.S. Endangered Species Act to salmon populations (see discussions of this issue by Utter 1981; Waples 1991, 1995).

Taken as a whole, one can look at salmon populations from two perspectives. First, they have countless, genetically-based specializations for unique biotic and abiotic features of their environments. This perspective, bolstered by the general failure of anadromous salmonid transplants (Withler 1982, Fedorenko and Shepherd 1986, Harache 1992), sees salmon populations as tightly evolved for their natal systems, reinforced by nearly unerring homing behavior. The intermingling of populations may prevent management agencies from protecting the fine genetic structure but such structure exists. An alternative and perhaps complementary perspective (e.g., Quinn 1985, Wood 1995) is that since the post-glacial period, dispersal has been as much the hallmark of salmon population biology in the long run as homing. Following colonization of new habitat, subsequent homing isolates the nascent population. Natural selection and the high heritability of adaptive traits can lead to their rapid evolution. Differences in selectively neutral differences (e.g., molecular) traits may arise from founder effects at the time of colonization, or from drift over long periods of time.

Having presented this brief, and obviously selective, introduction to the subject of the stock concept in salmon, the purpose of this paper is to present studies supporting these two perspectives on the concept: fine-tuned adaptation or great capacity for evolutionary adaptation. The studies are drawn in large part from my own work, not because it is definitive but because it is familiar to me. It is not my objective to convince readers that either perspective is correct, but rather to emphasize the validity of both viewpoints.

What Constitutes a Population? Perspectives from Bristol Bay, Alaska Sockeye Salmon

The North American range of sockeye salmon (*Oncorhynchus nerka*) is primarily from the Columbia River to the Kuskokwim River in the Bering Sea (Burgner 1991). Early research by the International North Pacific Fisheries Commission revealed that Asian sockeye salmon (chiefly from the Kamchatka Peninsula and Russian coast of the Bering Sea) differed in marine distribution from North American conspecifics (French et al. 1976) and for some management purposes the continent of origin was the relevant scale for the "stock" (Figure 1, top; Harris 1987). However, data from tagging studies and analysis of naturally occurring parasites revealed that the distribution of sockeye salmon from the Bristol Bay region of southwest Alaska differed from those of other populations to the east and south (French et al. 1976). For example, the Fraser River complex of sockeye populations shows a different marine distribution (Figure 1, bottom), and also differs from Bristol Bay sockeye in survival rate patterns (Peterman et al. 1998).

Bristol Bay has some of the world's largest populations of sockeye salmon (Burgner 1991). These populations support important fisheries and have been the focus of much research, and in some contexts "Bristol Bay sockeye" is a meaningful stock or stock-complex. Despite the many lake systems tributary to Bristol Bay where adult sockeye salmon spawn, the adults generally return over a narrow time period (Burgner 1980). The populations also display coherent patterns of size at age and age at maturity (Rogers and Ruggerone 1993, Pyper et al. 1999), suggesting common responses to ocean temperature and density-related processes. Although for some purposes it is appropriate to speak of Bristol Bay sockeye, the management is based in districts at the mouths of the major river systems: Ugashik, Egegik, Naknek-Kvichak, Nushagak and Togiak, and to some extent these districts are functional stock units (Figure 2). As Minard and Meacham (1987) pointed out, this district-based management can lead to difficulties. For example, fishing in the Naknek-Kvichak district catches sockeye migrating to the myriad streams in the Naknek and Iliamna lake systems, and fishing in the Nushagak district intercepts fish with very different patterns

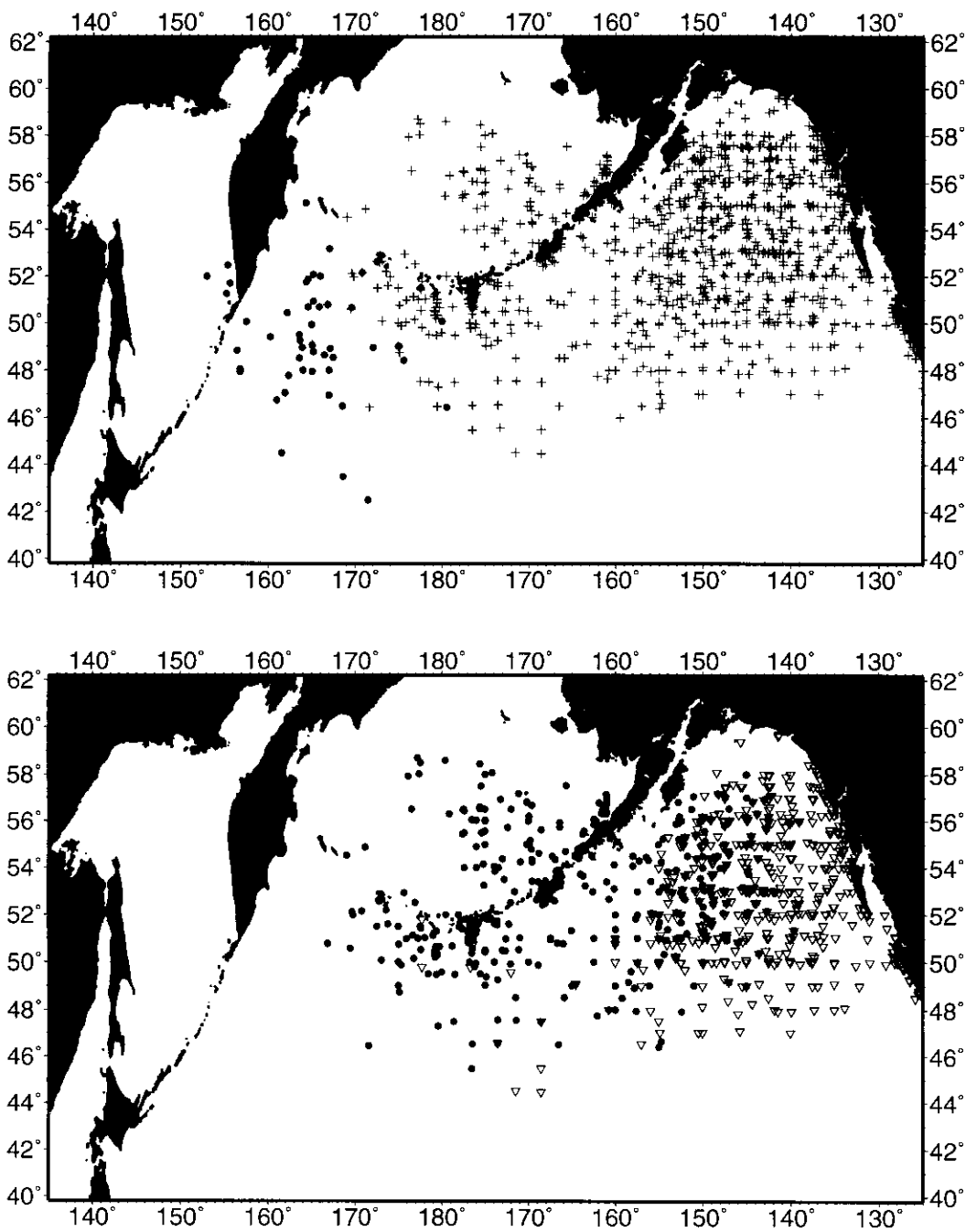


Figure 1. Locations at sea where sockeye salmon (immature and maturing) were tagged and subsequently recovered in coastal fisheries or spawning grounds. Top panel shows the distribution of sockeye recovered in Asia (solid circles) and North America (plus signs). Bottom panel shows the distribution of sockeye recovered in Bristol Bay (solid circles) and British Columbia (open triangles). Data should not be interpreted to indicate precise distributions or abundance, owing to uneven effort (source: North Pacific Anadromous Fish Commission data, map courtesy of Kerim Aydin, Fisheries Research Institute, School of Fisheries, University of Washington).

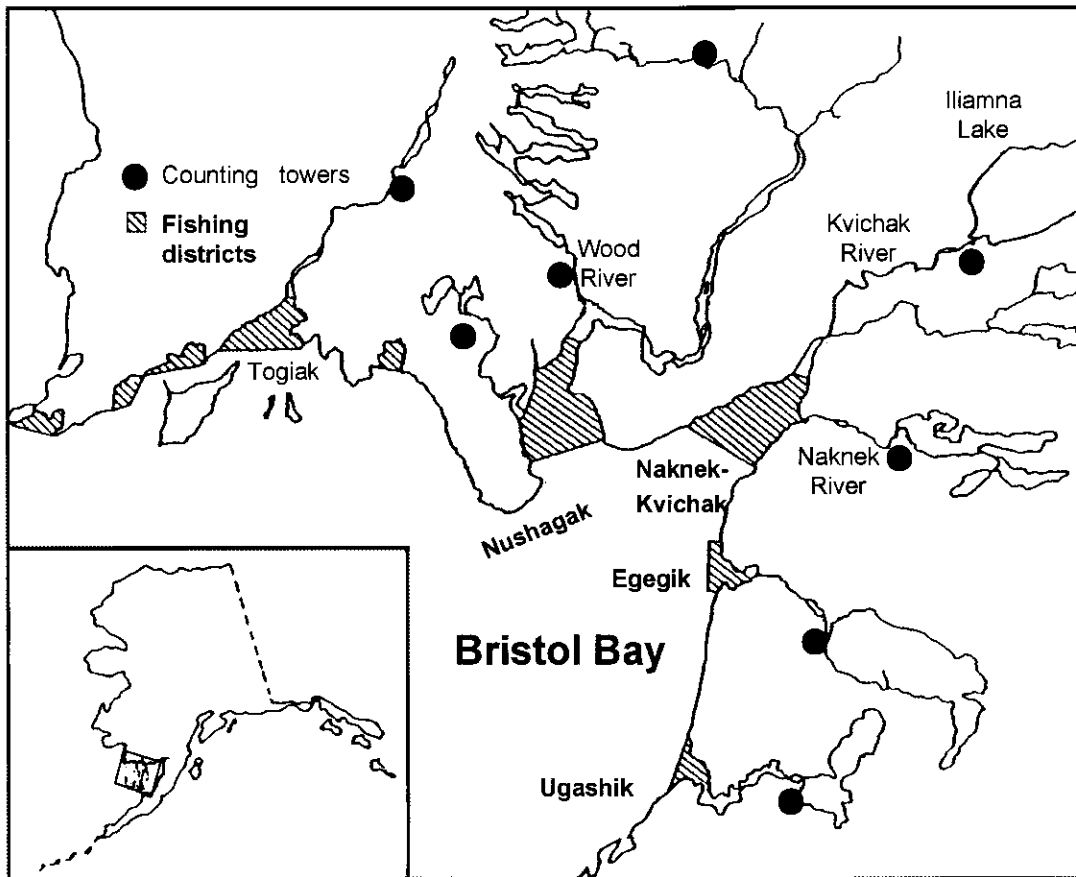


Figure 2. Map of Bristol Bay, Alaska, showing the fishing districts and locations of counting towers for sockeye salmon (modified from Minard and Meacham 1987).

of productivity and life history, going to discrete spawning sites in the Wood River, Nushagak, Nuyakuk and Igushik systems. There is always the danger of over-fishing one population while attempting to fully fish another. Efforts to avoid such management problems are complicated by the similar timing of the populations and the geographical proximity of their mouths. Counts of adult salmon migrating past towers such as the one at Igiugig on the Kvichak River provide in-season feedback for management (Minard and Meacham 1987) but still encompasses many spawning populations.

Even the fish migrating to a given river system may have very similar timing, as Smith (1964) and Jensen and Mathisen (1987) demonstrated for the Kvichak system. Sockeye tagged throughout the run were recovered at diverse spawning grounds

in tributaries and beaches of Iliamna Lake and Lake Clark. Thus from the viewpoint of commercial fisheries management, the Kvichak River is the smallest practical unit, even though it encompasses about 100 documented spawning sites (Figure 3) and two of the largest lakes in Alaska (Demory et al. 1964). The Wood River system includes about 50 spawning populations associated with a complex chain of lakes (Marriott 1964). Like the Kvichak River system, it is also managed as one unit though estimates are made of the abundance of adult sockeye salmon at most of the spawning sites.

The sockeye salmon ascending the Wood River tend to spawn in three major types of habitats: small streams, large rivers (flowing between lakes) and beaches. Rogers (1987) pointed out the great variation in age structure among these groups.

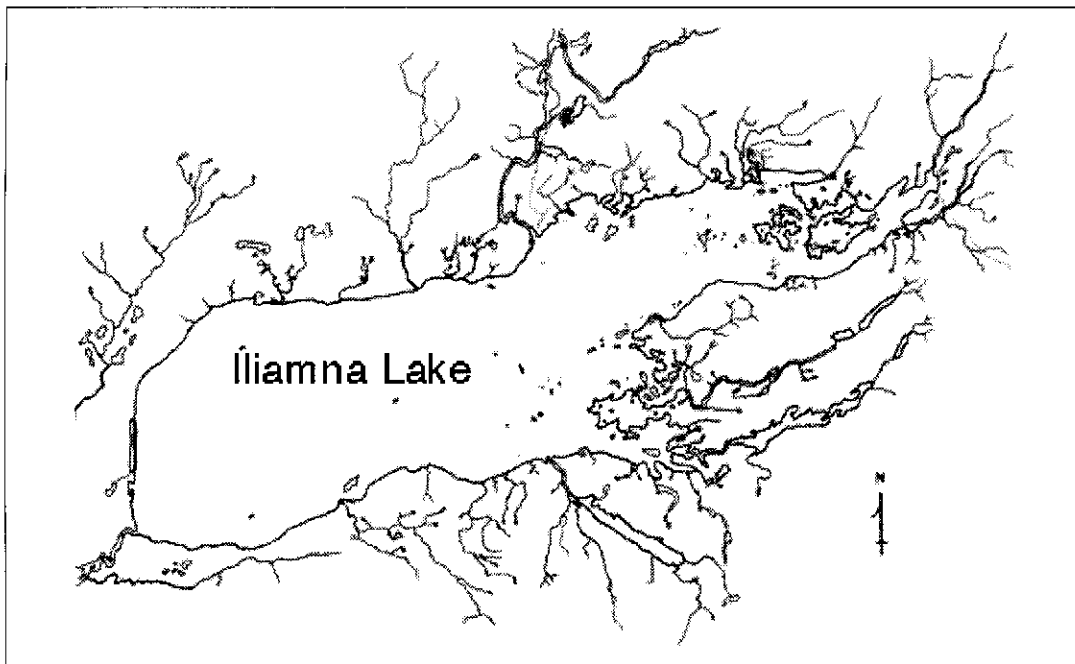


Figure 3. Map of Iliamna Lake, Alaska, showing some of the islands in the western part of the lake and the rivers that are used for spawning by sockeye salmon.

Notably, river spawners tend to spend three years at sea and so are larger than the creek spawners, which tend to return after two years at sea. The populations also differ in morphology, especially the development of the dorsal hump in males. Creek spawners are much less deep-bodied than river fish and the beach spawners are very deep-bodied (Bishop 1990, Wetzel 1993). The river and beach spawners in Iliamna Lake show parallel patterns of morphology (Blair et al. 1993) and these have been hypothesized (Blair et al. 1993, Quinn and Foote 1994) to result from the conflicting pressures of sexual selection (favoring deep bodies) and bear predation (Hanson 1992, Quinn and Kinnison, in press).

In Iliamna Lake, there are sockeye salmon spawning on beaches of low-lying islands, where the embryos incubate in water circulated by wind-driven surface currents. Only a few km away other females spawn on mainland beaches and spring-fed ponds supplied with upwelling water. The eggs deposited by females on the island beaches are exceptionally large whereas mainland beach and pond females have very small eggs, and these patterns of egg size match the size of the sub-

strate in which the embryos incubate (Quinn et al. 1995). There have been no tagging studies to explicitly demonstrate homing by sockeye salmon to discrete spawning sites but natural variation in otoliths strongly indicates that sockeye return to their natal incubation sites (Quinn et al. in press). This finding is consistent with molecular genetic variation among spawning sites within this and other lake systems (Varnavskaya et al. 1994).

For some purposes we might think of the sockeye salmon spawning on the beaches of Iliamna Lake as a population because they clearly share many attributes such as egg size, fecundity, age and length at maturity (Blair et al. 1993). However, is there finer structure to the populations? Experimental displacement of mature salmon (Blair and Quinn 1991) and surveys of spawning dates (Quinn et al. 1996a) provide circumstantial evidence that the fish using each island represent separate populations. Not only is there apparently fine population structure on spatial scales but there is evidence for temporal isolation as well. Even within a single beach on one island, a certain section is always occupied prior to nearby areas (Hendry et al. 1995). The high heritability of maturation

date (Smoker et al. 1998) means that there may be patterns of genetic structure over the course of the spawning season within a single site (McGregor et al. 1998). The fish that arrive early in the season not only seem to live longer in the stream than late-arriving fish but also display different patterns of energy allocation (Hendry et al. 1999).

These studies of Bristol Bay sockeye salmon reveal a series of scales at which we may view populations: North America, Bristol Bay, Naknek-Kvichak or Nushagak fishing districts, Kvichak River or Wood River tower counts, spawning habitat types (beaches, creeks and rivers), individual islands or creeks, and even temporal segments of the run at a given site. Some scales such as continent or region are too coarse to be meaningful as populations and others such as creeks or segments of the run to a creek are much too fine to be manageable. Nevertheless, studies on the finest scale are useful because they reveal the extraordinary suite of adaptations that natural populations can display as evolved and phenotypically plastic responses to environmental variation.

How Rapidly Can Populations Evolve? Perspectives from Chinook Salmon in New Zealand

The almost endless ways in which natural populations differ from each other, and the complex adaptations to the environment that these differences seem to demonstrate, raise the question of how rapidly these differences can evolve. Much of the present range of Pacific salmon was last glaciated about 10-15,000 years ago, and strays founded the present populations. Thus not only homing but also straying is an important component of the life history and evolution of salmon (Quinn 1985). The differences in gene frequencies that are observed among populations have presumably accumulated gradually through genetic drift but selective breeding studies reveal high heritabilities for important life history traits and imply that populations might evolve quite quickly, given sufficiently intense natural selection.

Transplanted populations provide opportunities for studying the early stages of adaptation to new environments. There are countless introduced freshwater populations of salmon, trout and char

worldwide but anadromous salmonids have proven very difficult to successfully transplant. This restriction is surprising because most population-specific differences seem to be adaptations for aspects of the freshwater environment (Taylor 1991) and one would think that marine life would be more generalized and so less problematical in new environments. Nevertheless, the transplant of chinook salmon from the Sacramento River (probably Battle Creek, Quinn et al. 1996b) to the Hakataramea River on the South Island of New Zealand (NZ) in the early 1900s was successful and the fish quickly colonized much of the suitable habitat and established self-sustaining populations in such large rivers as the Waimakariri, Rangitata and Rakaia (Figure 4), as well as smaller rivers.

Colonization must have been prevalent in the early years, given the rapidity with which the salmon distributed themselves, but present-day estimates indicate that the homing of NZ salmon is comparable to North American populations (Unwin and Quinn 1993). Examination of data collected over a period of years in several of the major chinook salmon rivers revealed differences in several of the life history traits commonly used to characterize chinook salmon populations in North America: freshwater life history type (yearling or subyearling migrants to sea), age at maturity, length at age, weight at length, fecundity, and the timing of return from the ocean and spawning (Quinn and Bloomberg 1992, Quinn and Unwin 1993). These differences indicated that the populations are now phenotypically different, though the extent to which these differences reflected only different rearing conditions could not be determined.

To determine whether chinook salmon have evolved into genetically distinct populations (in some sense of the word) during about 30 generations since the transplant (at a mean age of about 3), we initiated a large-scale controlled breeding and rearing experiment in 1994. The null hypothesis was that the fish from different rivers would not differ when reared under common conditions, implying that the differences in phenotypic traits observed in the earlier studies were environmentally induced. On the other hand, consistent differences between populations and genetic control (i.e., heritability) within populations would imply that the populations had already reached some level of genetic differentiation.

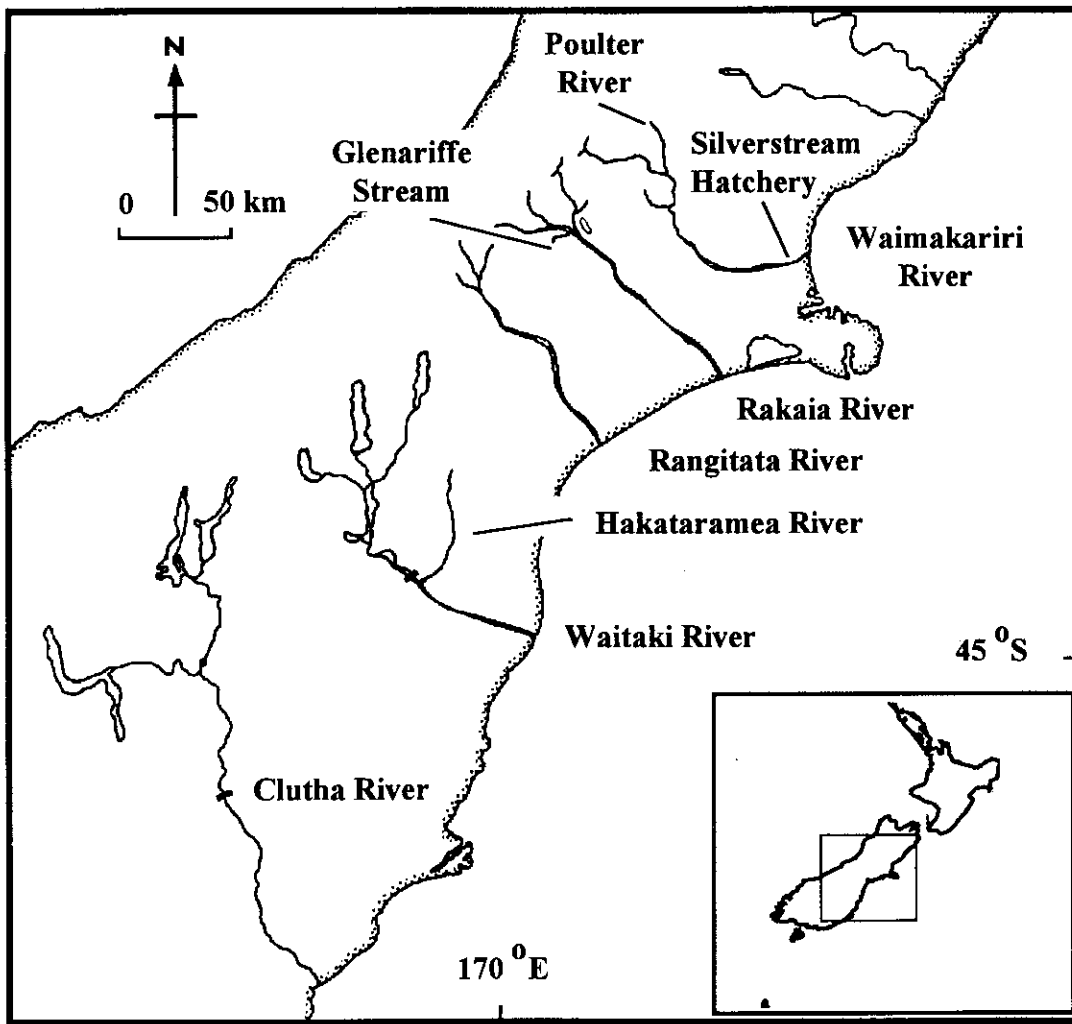


Figure 4. Map of the central South Island of New Zealand, showing the main chinook salmon rivers and locations of experimental facilities.

In 1994 and 1995, we sampled adult salmon from two populations that had shown phenotypic differences, the Hakataramea River and Glenariffe Stream, and recorded data on length, weight, age, morphology, egg size and fecundity. These phenotypic data were compared to data on fish from the current representatives of the ancestral Battle Creek, California population. We then spawned the NZ fish in a half-sibling mating design to allow us to estimate the genetic contribution to life history traits, and began a complex incubation and rearing experiment. We reared some families to maturity under common, controlled conditions in freshwater. In addition, we released

representatives from the families from two different hatcheries (Glenariffe and Silverstream). The use of two hatcheries provided some measure of insurance against poor year class survival at one site and also allowed us to compare the performance of fish returning to one hatchery near the coast (Silverstream) and one farther inland and at higher elevation (Glenariffe). In 1997, we initiated another controlled breeding experiment, this time with fish from Glenariffe Stream and the Poulter River, the latter chosen because the adults differ from Glenariffe Stream fish in spawning date and juvenile life history.

Our results show a mosaic of traits, some of which are apparently under strong environmental control and others have a clear genetic basis and differ between populations. The adult chinook salmon differ in morphology from Battle Creek, California fish, and also differ (though to a lesser extent) between the two New Zealand populations (Kinnison et al. 1998a). We are presently examining the data on the offspring from the experimental NZ parents and so are not sure yet how much of the variation has a genetic basis. We have evidence that the temperature-specific rate of embryonic development does not differ between populations, despite differences between the rivers in thermal regime (Kinnison et al. 1998b). Salmon populations adapt the timing of juvenile emergence primarily by differences in parental spawning date, which is strongly heritable (our unpublished data) rather than developmental rate.

Growth rates differed slightly between Hakataramea River and Glenariffe Stream fish (Kinnison et al. 1998c) but the Poulter River fish grew much slower than Glenariffe Stream fish under common conditions (our unpublished data). This difference is particularly interesting because the Poulter River fish tend to spend a full year in freshwater prior to seaward migration whereas Glenariffe Stream fish rear in warmer water and typically migrate to sea in their first year of life (Unwin and Glova 1997). We infer that the fundamental environmental basis for growth differences between populations is becoming reinforced by a genetic difference as well. Smaller fish are less tolerant of seawater than larger fish (Kinnison et al. 1998c) and also have lower survival rates at sea (unpublished data) so there will be continued selection for fish in slow-growth environments to remain for a full year before going to sea – the life history pattern referred to as stream-type (see Teel et al. 1999 for insights into the evolutionary basis of stream-type and ocean-type life histories in North America).

Survival at sea was not only correlated with smolt size but there were also family-level differences independent of size, suggesting some genetic basis for survival. Survival is not a trait in itself but a consequence of many traits including growth, seawater tolerance, predator avoidance, etc. Perhaps most exciting was our finding that the two populations (Glenariffe and Hakataramea) showed similar survival rates when

released from a site which was home to neither population (Silverstream) but that Glenariffe fish had a significantly higher survival rate than Hakataramea River fish when released from Glenariffe Stream. This "home site advantage" implies that some form of adaptation for the natal site has taken place that affects survival. Of the fish that survived and returned to the hatcheries, there is little evidence of inter-population differences in size at age, but we have detected consistent differences between populations in the timing of return and maturation, and also in female reproductive traits such as egg size. The energetic demands of upriver migration also seem to affect egg size, so the phenotypic traits seen in wild fish reflect the interplay between genetic and environmental controls. The genetic differences between populations in phenotypic (possibly adaptive) traits contrasts with the low level of variation among populations found using molecular markers within NZ, though the NZ fish differed from the Sacramento River fish (Quinn et al. 1996b). Further studies, using DNA microsatellites, are ongoing but it seems that selection has worked quickly on life history traits and drift may lead to differences, albeit small, in more neutral traits.

One additional finding, though not explicitly a goal of the study, was that many male chinook salmon held in freshwater became sexually mature at one year of age. This is not unprecedented, either in New Zealand or in the native range, but what was surprising was that they survived spawning and lived to spawn again, not only at age two but in some cases a third time at age three (Unwin et al. 1999). This illustrates that some aspects of salmon life histories, which we view as fixed, such as semelparity (i.e., death after reproduction), may actually be flexible but reveal only one pattern under normal environmental conditions. Another example of this phenomenon of apparently fixed traits that change in new environments is the age at maturity of pink salmon. Almost without exception they are two years old at maturity in their natural range but they have been reported to mature from ages 1-4 in the Great Lakes (Kwain 1987).

Conclusions

The population biology, genetics and conservation of fishes and salmon in particular is an exceptionally vital area of research, as revealed

by the diversity of papers in the American Fisheries Society symposium edited by Nielsen (1995), the set of papers in a special section of the journal *Conservation Biology* (Hedgecock et al. 1994), and the contributions of many scientists to a wide variety of other publications. I have tried to present two perspectives on the subject. In North America, we see stocks or populations defined over a range of scales, depending on the management goal and the tools of the scientists. We can observe differences in phenotype and often also genotype at spatial scales that may be too small for all be the most draconian fisheries management to actively protect. These myriad specializations are clearly critical to the health of salmon populations. In many cases there are obvious adaptive advantages to the traits, and failure of the vast majority of salmon introductions within and outside the natural range of the species also testifies to the importance of local adaptations.

How, then do we interpret the evidence from New Zealand that salmon can apparently evolve quite quickly? Does this mean that all we need to conserve are a few generic salmon stocks and we can use them to replenish any habitat from which salmon are lost? Or does their rapid evolution demonstrate how critical the local adaptations are to the fitness of individual salmon and the productivity of populations? The scientists and policy makers wrestling with the application of the U.S. Endangered Species Act to "distinct population segments" have a very difficult job, weighing the various attributes that define populations (Utter 1981, Waples 1991, 1995). They must rely on different kinds of data, including molecular markers, life history traits, and geology (e.g., Myers et al. 1998) to define the "evolutionarily signifi-

cant units" that society will try and protect, and must deal with criticisms of the ESU concept (e.g., Pennock and Dimmick 1998). My own view is that there are some populations with unique attributes and we should strive to protect them but for the most part we need to give salmon access to healthy, diverse physical habitats and allow those habitats to be filled (or over-filled) with the full community of salmonid species native to the region. The salmon can take it from there.

Acknowledgements

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