Pacific Salmon Population Structure and Dynamics: 
A Perspective from Bristol Bay on Life History Variation 
across Spatial and Temporal Scales

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Abstract.—Pioneering scientists pointed out that conservation and management of salmon for human use and as a component of ecosystems depends on understanding their population structure. Many current controversies regarding exploitation rates, interceptions, and resuscitation of depleted populations hinge on issues of population structure. This paper examines the range of spatial scales over which salmon population structure can be defined, using Bristol Bay sockeye salmon *Oncorhynchus nerka* as the example. The region’s geology has created similar spawning habitats associated with different lakes, revealing the extent to which evolutionary processes repeat themselves. The life history patterns of the salmon reflect both genetic adaptations to their local environment, facilitated by homing to their natal site for spawning, and also the capability to respond to changing environmental conditions. This combination of variables may explain why similar environmental conditions result in different patterns of population dynamics among the lake systems, giving the Bristol Bay system as a whole more stability than is seen in any single lake. At still finer spatial scales, investigations show that sockeye salmon home not only to specific streams but even to habitat patches within a stream. Nevertheless, records of the presence of other salmon species, notably Chinook *O. tshawytscha*, chum *O. keta*, and pink salmon *O. gorbuscha*, seem to indicate more dynamic population structure, including straying and the possible establishment of new populations in streams where sockeye salmon are numerically dominant. The understanding of these patterns and processes stems largely from a well-conceived and persistent long term program of research and monitoring, and this provides lessons and cautions for research and management in systems where information is less extensive, such as in the Arctic-Yukon-Kuskokwim region.

Introduction

One of the seminal events in the conservation and management of salmon was a symposium, held in Ottawa, Canada in June 1938. The introduction to the volume (Moulton 1939) was written by A. G. Huntsman, who reviewed the mandate for the meeting in words that would seem all too appropriate today: “… alarm over decreases in the stocks of salmon” and “… the practical problem of getting sufficient salmon for food and for sport.” These scientists, working on both Atlantic and Pacific salmon, in Europe and North America, puzzled over many questions...
that are still not fully resolved, including open ocean movements and exploitation of mixed populations. Perhaps the most important paper was that by Willis H. Rich, who clearly outlined the requirements for rational management of salmon and other fishery resources (Rich 1939).

“(1) the extent to which the species is broken up into self-sustaining groups; (2) the fluctuations in the birth-death ratio of each independent group and for each life phase… and (3) the causes of these fluctuations, again for each independent group and for each life phase.” (p. 45).

Foreshadowing decades of research and hundreds of scientific papers to follow, Rich (1939) went on to point out the three main types of evidence pointing to the existence of independent populations: (1) differences in morphology, including body size, age at maturity, egg size, fat content, and scale patterns, (2) differences is population dynamics, cycles of abundance and other “statistical” differences, and (3) experimental evidence from tagging studies. He went on to describe the importance of understanding ocean migration patterns of salmon, interceptions by fleets in distant areas and along the migration route, and many other issues that are relevant to today’s salmon conservation.

The early-middle part of the 20th century also saw many important contributions to the study of population structure and dynamics in Canada (e.g., Clemens et al. 1939; see also reviews in Foerster 1968; Ricker 1972). With respect to salmon in Alaska, the landmark event was the formation of the Fisheries Research Institute (F.R.I.) at the University of Washington (Stickney 1989). W. F. Thompson, first director of F.R.I., reflected on the beginnings of the program and made clear that he and the other pioneers recognized the critical role of the discrete breeding populations in the overall management of the fisheries. He explicitly recognized that variation exists among breeding populations in average productivity, and also that variation occurs in productivity from year to year (Thompson 1962). The study of salmon population structure was advanced greatly in 1972 with the publication of a symposium volume, The Stock Concept in Pacific Salmon, edited by Raymond Simon and Peter Larkin. The volume was dominated by William Ricker’s monograph and this remains the most significant review of the subject (Ricker 1972). Since that time many discoveries have been made, including biochemical and molecular tools for distinguishing populations, and great number of symposia and scientific papers have been published on the subject, including several reviews (McDonald 1981; Scudder 1989; Taylor 1991: Quinn 1999).

Rather than present another such review, the purpose of this paper is to use one geographical region, Bristol Bay in southwestern Alaska, to illustrate a number of salient points in the study of salmon population structure, including areas of continued uncertainty. This geographical area is best known for the large runs of sockeye salmon, Oncorhynchus nerka, but lessons can be learned from the other species as well. The premise of this paper is that three key themes pointed out by pioneering scientists working on salmon conservation are still of critical importance today: 1) the importance of geographical scale in organizing the dynamics and structure of salmon populations, and the fisheries that exploit them, 2) the interplay between genetic and environmental factors controlling phenotypic traits, including the role of fisheries, and 3) the nonstatic nature of salmon populations, in abundance and distribution. These three themes are briefly discussed, and then related to the challenges of managing and conserving salmon populations in the vast areas of the Arctic, Yukon, and Kuskokwim regions of Alaska. Finally, conclusions are drawn regarding the establishment and maintenance of long-term data sets, including the blessings and liabilities of such projects.
The Importance of Geography and Spatial Scales for Salmon Populations

The structure of salmon populations depends on three things: 1) the reproductive isolation of breeding populations that results from homing to the natal site, 2) the differences in regimes of natural and sexual selection that result from differences in biotic and abiotic factors among breeding and rearing areas used by a given population, and 3) the genetic basis for traits that affect the fitness of individuals in the environments that they use. The concepts of geography and spatial scale are thus important elements of all three factors contributing to population structure. The first reason for this importance stems from the homing behavior of salmon. In general, the salmon that survive to maturity return to their natal site to breed. The term “natal site” implies some spatial scale. For example, do sockeye salmon home to North America as opposed to Asia, to Bristol Bay as opposed to other regions of North America, to the Nushagak River as opposed to the other major river systems in Bristol Bay, to the Wood River as opposed to the upper Nushagak River itself or its tributaries, to Lake Nerka as opposed to another of the lakes in the Wood River system, to Hidden Lake Creek as opposed to one of the other creeks that flow into this lake, to Hidden Lake Creek itself or to beaches in Hidden Lake, at the headwaters of the creek, and to the specific site in the creek where they were spawned years earlier?

Information on the spatial scale of population structure comes from several sources, primarily studies of variation in selectively neutral genetic traits including polymorphic proteins and DNA microsatellites. In these studies, significant and consistent differences between salmon breeding at two sites can be taken as strong evidence of reproductive isolation but the failure to detect a difference does not mean that none exists. Early work revealed some genetic structure among populations breeding within the Iliamna Lake system, as with other lakes producing sockeye salmon (Varnavskaya et al. 1994), and data from Bristol Bay populations have contributed to the understanding of broad-scale genetic variation in sockeye salmon (Beacham et al. 2006). In many cases, sockeye salmon spawning in adjacent creeks can be distinguished using these selectively neutral traits, and creek spawning sockeye salmon may differ from nearby beach spawning conspecifics (Lin et al. 2008). Genetic divergence seems to result from a combination of variables: geographical distance, temporal isolation, and habitat differences. In general, sockeye salmon (and other species as well) are probably more likely to stray to a location near their natal site than to a distant one, and to a similar habitat (e.g., creek to creek, beach to beach) more than a different one. The likelihood that straying salmon will enter and successfully reproduce is also probably greater if conspecifics are present; thus, populations with distinctly different breeding dates are more isolated than those with more similar breeding dates. In addition, some populations have small effective population sizes (Habicht et al. 2004) and may be more genetically divergent than simple geographical distance, habitat, and timing might suggest (Ramstad et al. 2004), indicating possible past population bottlenecks.

In addition to biochemical and molecular evidence of isolation of populations breeding in nearby areas, variation in phenotypic traits under some degree of genetic control provides further evidence that populations are discrete, and adapted to local conditions. Early stream catalogs (Demory et al. 1964; Marriott 1964) noted differences in the timing of salmon spawning in different habitats that we continue to observe. In general, creeks are occupied early in the season and large rivers (draining lakes) and beaches are occupied late in the season, often for more protracted peri-
ods. These differences in timing are, in general, adaptations to the regimes of temperature that the embryos will experience so that they emerge in time to take advantage of feeding opportunities the following spring, though some evidence exists that not all populations emerge synchronously in a lake (Abrey 2005). Experimental evidence from several sources indicates that the date of breeding by salmonids is under strong genetic control (Smoker et al. 1998; Quinn et al. 2000; Sato et al. 2000) so these differences likely reflect genetic adaptations of populations to local conditions. The spawning sockeye salmon in different areas also differ markedly in age at maturity, length at age, body morphology, and egg size (Rogers 1987; Blair et al. 1993; Quinn et al. 1995; Quinn et al. 2001), apparently reflecting the balancing forces of natural and sexual selection. The various lines of evidence indicate that salmon populations are organized into discrete breeding units, with more or less gene flow among them as a function of proximity, habitat similarity, and temporal overlap. In general, phenotypic diversity reflects primarily contemporary selection and so similar habitats in distant locations often give rise to similar phenotypes, whereas genotypic diversity reflects a combination of ancient colonization events that took place long ago, and contemporary gene flow from successful reproduction by strays. For example, male sockeye salmon spawning on lake beaches are typically deep-bodied, and their shape is similar to that of sockeye salmon using similar habitats in a different lake (Quinn et al. 2001). Little gene flow occurs between lakes and it is inferred that the exaggerated male shape evolved independently in each lake.

The question often arises, “What is the spatial unit to which salmon home?” In many cases one might safely conclude that it is the river, and that each female then must select a redd site based on habitat suitability and competition with other females. However, a recent marking experiment indicated that sockeye salmon planted as eyed eggs in the gravel of a small spring-fed pond homed back there as adults rather than to the rest of the small stream below or above the pond (Quinn et al. 2006). The ability of sockeye salmon to home to specific locations within a small stream only partially addresses the question of the spatial scale of homing. In other cases, habitat complexes are used to varying extents among years. Iliamna Lake has many low-lying islands, primarily in the eastern end of the lake, used for spawning by sockeye salmon (Kerns and Donaldson 1968). Sockeye salmon spawn on discrete beach sites on the islands (Leonetti 1997), separated by generally similar but apparently less suitable habitat. Individuals (males as well as females) seldom move between beach sites, even to other sites nearby, once they have begun breeding at a given location (Hendry et al. 1995). The embryos incubate in a matrix of coarse gravel and rocks, in lake water circulated by wind-driven surface currents (Leonetti 1997), and sites not used seem to have finer substrate and poorer water circulation than those used, or are so exposed to storms that the gravel is not stable.

Are the sockeye salmon spawning on all the islands of Iliamna Lake one population, is each island a population, or is each beach on each island a population? The absence of site-specific water sources would seem to present special challenges for homing. Reciprocal transfers of adults from one island to another revealed some tendency to return to the site where the fish were first caught; however, less than what was shown by sockeye from a nearby creek (Blair and Quinn 1991). Aerial surveys of adult salmon revealed that the levels of abundance of sockeye salmon on the beaches are highly correlated among years (Stewart et al. 2003a). This coherence might suggest that they represent one population, but this result might also be explained by the fact that common environmental conditions such as ice cover and lake level
would affect all the beaches synchronously, even if they were entirely independent breeding units. Finally, analysis of detailed age composition data provided evidence that the populations were independent, at least to some extent, even though selectively neutral genetic markers could not discriminate them (Stewart et al. 2003b). Thus, the structure of these populations remains ambiguous, and evidence exists for both homing to specific locations and for the exercise of spawning habitat choice by the salmon. These may be examples of metapopulations (Hanski 1999; Schtickzelle and Quinn 2007) that can persist as a whole because there is sufficient asynchrony in the extinction and re-colonization events experienced by the populations using the discrete breeding sites. Alternatively, these may be better termed “messy populations” that expand and contract over habitats of unequal quality, using some regions only when density is greatest, and persisting at the core, high quality areas.

Management of the fisheries takes place at the scale of the district or subdistrict (e.g., Nushagak District and the Wood River), and only limited subsistence and personal use fisheries take place on specific creeks (e.g., Yako Creek in the Wood River system). This conflict between the scale of management and fishing, and the scale of population structure creates the possibility for over-exploitation of certain populations of salmon, or salmon using certain habitat types, especially if they differ in size and timing. Abundant evidence exist that salmon from different populations and habitat types vary in age at maturity, size at age, and morphology, and gillnets are notably size-selective forms of fishing gear, so a high potential for differential exploitation exists (Kendall and Quinn, in press). In general, it seems as though the populations within a system migrate synchronously (Jensen and Mathisen 1987; Rowse 1985), though recent work in the Wood River system indicates that this may not be entirely true (Doctor 2008).

Exploitation can be heavier on late than early-arriving fish, if escapement goals have been met (Quinn et al. 2007), and so there may be selection on run timing as well as size. Larger, older salmon tend to migrate and spawn earlier than smaller ones (Quinn et al. in press), further complicating the possible regimes of selection from fishing. As long as a generous escapement goal to the system as a whole is met, the productivity of populations at low densities may allow them to rebound from a brief period of heavy fishing. However, the possible chronic effects of long-term excessive and selective fishing should not be ignored.

The Genetic and Environmental Effects on Life History Traits

Salmon, like all fish, are a product of both nature and nurture. However, their phenotypic traits are not the result of two independent factors (genetic and environmental) but also the differences among populations in the interaction between these factors. Two examples, the transition from lake-rearing juveniles to seaward migrating smolts, and the transition from ocean-rearing adults to home-ward migrating mature adults, illustrate this point. Before delving into this fundamental concept, it is important to note that full documentation of age composition patterns in a given population requires a great deal of data. For several reasons, samples must be collected in a consistent manner over many years to accurately characterize the overall patterns and the variation in age composition and size at age for a population. First, many species have multiple ages at maturity, so at a minimum one entire generation of data would be needed to encompass all possible ages. This aspect is especially important for species with variation in freshwater and marine ages, and sockeye are the most variable species of all Pacific salmon (Healey 1986;
Healey 1987). Second, the environment modulates the proportions of these ages that occur in any given brood year (detailed below), so even complete sampling of an entire brood cycle may not be sufficient. One might be tempted to sample in one year and not worry about these sources of variation but broods vary so much in strength that a highly unrepresentative result might be obtained. Finally, it is difficult to obtain a random sample of fish differing in size (hence age) because the small fish may be systematically underrepresented in the samples from spawning grounds (Zhou 2002). In this kind of work, the temptation is to consider individual salmon sampled for age (based on examination of otoliths or scales) as the unit of replication, or perhaps the numbers of calendar years, but the number of brood cycles may be a more appropriate unit of replication. This fact is sobering for those just beginning to sample a population, especially if it has a long lifespan or complex age structure.

Numerous studies have documented the variation among sockeye salmon populations in average size of smolts (Quinn 2005); thus, the “decision” to initiate seaward migration is not triggered by a species-specific size threshold but rather each population must have evolved its own threshold. In some lakes (e.g., the Wood River system), the vast majority of sockeye salmon smolt after one full year in freshwater whereas in the Ugashik system, the age-1 smolts are similar in size (implying roughly comparable growth rates) but only about half migrate at age-1. In the Egegik River system the age-1 smolts are even larger than those in the other systems but a smaller fraction migrates after one year in the lake than in the Ugashik River system (Quinn 2005). The “decision” to migrate at a young age should be associated with lakes in which mortality risk is high and growth in the second year would be low, or a second year of growth in the lake provides little advantage in marine survival. Despite this general theory, little if any systematic research has demonstrated the specific costs and benefits of smolt age from system to system. Within a given lake, the proportion of sockeye salmon that leave after a single year, rather than two, depends on growth during the first year; when the fish are large at the end of the first growing season, a larger proportion leave than is observed in years when growth is slower (Koenings and Burkett 1987; Rich et al., in press). Growth variation among years is primarily controlled by temperature and competition, and the relative importance of these two variables varies among lakes. For example, in Lake Aleknagik, the more important factor is competition (Schindler et al. 2005b), whereas in Iliamna Lake, temperature exerts the stronger influence, despite the great variation in number of returning adults (Rich et al., in press).

Mirroring the patterns in smolts, many studies have revealed that size-at-age and age-at-maturity vary among populations, at many spatial scales and for many salmon species, including Chinook salmon *O. tshawytscha* (Roni and Quinn 1995), chum salmon *O. keta* (Beacham and Murray 1987), coho salmon *O. kisutch* (Weitkamp et al. 1995), sockeye salmon (Rogers 1987; Blair et al. 1993; Healey et al. 2000), and steelhead *O. mykiss* (Busby et al. 1996). This variation in age and size is controlled by environmental and genetic processes. Growing conditions at sea are affected by competition and temperature (e.g., Pyper and Peterman 1999; Pyper et al. 1999). Bristol Bay sockeye salmon are so numerous that they have generally been viewed as their own prime competitor but evidence indicates that competition with Asian pink salmon *O. gorbuscha* may also affect them (Ruggerone et al. 2005). In general, the accelerated growing conditions (or large size at seawater entry) are associated with earlier age at maturation (Quinn et al. in press).

The genetic basis for age-at-maturity in salmonids has been shown by experiments on
various species, often with the goal of understanding the genetic basis of early male maturity (i.e., jacks) or increasing size at maturity: Chinook salmon (Hard et al. 1985; Hankin et al. 1993; Heath et al. 1994), steelhead (anadromous rainbow trout) (Tipping 1991), and coho salmon (Iwamoto et al. 1984; Appleby et al. 2003). Natural selection from a variety of processes results in variation among populations experiencing common or at least similar growing conditions. For example, sockeye salmon populations that rear in the same lake prior to seaward migration, have access to the same feeding grounds at sea, and return at the same time of year can vary dramatically in age-at-maturity and size-at-age. In the Wood River system, sockeye salmon from large rivers are older, longer for their age, and heavier for their length than those from small streams (Quinn and Buck 2001; Quinn et al. 2001; Rogers 1987). Intense, size-selective predation from bears selects against large, old fish in small streams, sexual selection favors large fish when predation pressure is reduced, and use of large rivers for breeding also seems to favor large fish (Quinn et al. 2001). At a proximate level, it is unclear whether these differences in growth rate at sea result from variation among populations in their feeding distribution (though all have access to the same areas), feeding behavior (e.g., diet, vertical distribution or diel movements), or growth physiology. Perhaps more intriguing than the simple variation in size achieved at sea among populations is the fact that the adults of some populations (e.g., Hansen Creek in Lake Aleknagik) are not only younger and but also smaller for their age than other populations nearby such as Bear Creek (Quinn 2005). This difference implies that it is not merely the growth rate at sea that varies but the relationship between growth and maturity; otherwise, the population with fast-growing fish would compensate by maturing at an earlier age and thus be similar in overall average size at maturity. Thus, at both transition periods (from freshwater to sea, and back again to spawn), population-specific “set-points” or norms of reaction control the relationship between fish size or growth rate and the probability of making the transition. Consequently, different populations may grow at the same rate and yet show different maturation patterns.

The Non-Static Nature of Salmon Populations

The use of the word “population” implies something with a degree of permanence—perhaps not as much as a “species,” but not exactly a will o’ the wisp either. However, it is important to remember that the great majority of Pacific salmon populations were established since the last glacial period. This period ended ca. 10,000 years ago in some areas but in others, notably Glacier Bay, Alaska, it has been much more recent. Work in Glacier Bay has revealed how rapidly salmon and other fishes can colonize new habitat (Milner and Bailey 1989; Milner et al. 2000), and this is a reminder that salmon populations are not at all static. Thus, each year a small (but ecologically significant) number of maturing salmon do not home but rather stray and spawn in nonnatal waters (Quinn 1993; Hendry et al. 2004). Despite the importance of this phenomenon, neither the prevalence of straying in wild populations nor the underlying mechanisms are known in any detail. In most cases, strays cannot be readily distinguished from conspecifics that homed. In sockeye salmon, natural variation in parasite prevalence among lakes (Quinn et al. 1987) provides evidence of straying but only at this rather coarse spatial scale. Species such as pink and chum salmon that do not acquire extensive and distinct collections of parasites will not be readily distinguished in this manner. Natural variation in thermal regime experienced by the embryos incubat-
ing in different sites can induce detectable differences in otolith banding patterns, and these differences can also suggest (but not really demonstrate) straying (Quinn et al. 1999). Natural variation in chemistry among basins can also be used to identify fish (Ingram and Weber 1999; Kennedy et al. 2002; Wells et al. 2003) but this will not be useful in all situations. Thus, the discreteness of existing populations is controlled by balance between isolation and homogenization, though the precise levels are difficult to determine in wild populations and few estimates exist. The homing by the great majority of the salmon and the different regimes of selection tend to isolate the populations but straying and the gene flow that results if the strays reproduce successfully tend to homogenize them. In the case of Bristol Bay sockeye salmon, populations can be phenotypically similar but genetically different, and vice versa, indicating complex patterns of selection and gene flow. These populations are not static but rather represent the products of ongoing evolutionary processes.

In some cases, a salmon is observed in a river where the species have not been seen before, or where it does not occur regularly. For example, the observation of Chinook salmon in the Mackenzie River was worthy of note (McLeod and O’Neil 1983), as was the observation of a chum salmon much farther up the Fraser River than they normally occur (Welch and Till 1996). Recently, Pacific salmon have been documented in rivers draining into the Arctic Ocean (Babaluk et al. 2000; Stephenson 2006). It is difficult to know whether the incidence of salmon in this region has actually increased, or whether the distributions and behavior of the fish are unchanged but the tendency to observe and report them has increased. Given the recent warming conditions in many areas of Alaska, it is plausible that salmon might stray into new areas but at present the evidence seems to be equivocal.

The overwhelming numerical dominance of sockeye salmon in Bristol Bay presents an interesting opportunity to examine issues of straying and colonization. The staff in the Fisheries Research Institute at the University of Washington have conducted foot surveys of about two dozen creeks in the Wood River system annually to count sockeye salmon since the late 1940s. Beginning in about 1968, the survey forms were changed and records were kept of Pacific salmon species other than sockeye salmon. Coho salmon tend to spawn much later than sockeye species other than sockeye salmon. Coho salmon tend to spawn much later than sockeye salmon and the other species of salmon other than sockeye salmon are so scarce. Indeed, the high densities of sockeye salmon and the abundance of suitable gravel (Quinn et al. 1995) suggest that many of the streams are exceptionally good spawning sites. Like sockeye salmon, juvenile pink and chum salmon migrate downstream after emerging from the gravel, so any features of the stream’s habitat should affect all juveniles similarly. Despite the apparent suitability of the streams, species of salmon other than sockeye are unusual. Some streams have been surveyed for over 40 years and no salmon other than sockeye salmon have ever been seen, whereas in other streams the annual incidence of nonsockeye ranges up to about 50%. In general, the other species are least often observed in the smallest streams (in terms of width and depth), even though these streams often support high densities of sockeye salmon. The absence of Chinook and chum salmon from small streams is not surprising because they are larger than the sockeye salmon. However, it is less obvious why the pink salmon are in the large and not in the
small streams because they are smaller than the sockeye salmon.

Clearly, much remains to be learned about the habitat use and segregation among salmon species in the Bristol Bay area. More fundamentally, the processes determining the distribution patterns of salmon species are poorly known, and it is hard to see how management can succeed without a better understanding of why certain species are in one river but not another, and why their densities and productivities vary so much. The differences in basic habitat requirements (e.g., gravel size, water temperature, dissolved oxygen, stream gradient, habitat complexity, presence or absence of an estuary) of salmon species are not sufficient to explain the vagaries in their distributions. The great number of unsuccessful efforts to transplant salmon and establish new populations within their native range (Withler 1982) suggests that if a stream is suitable for a given species it probably already contains it, and if the species is absent there is probably a good (though often not obvious) reason for its absence. Thus, we are left with a paradox; the distributions of species exhibit elements of rigidity and also elements of plasticity, and the rules underlying these patterns are not clear.

**Application of these Concepts to the Conservation of Salmon in the Arctic, Yukon, and Kuskokwim Systems**

**The importance of long term records**

One might well ask, what is the relevance of work on sockeye salmon in the lake-studded Bristol Bay region to those interested in Chinook and chum salmon in the more northerly areas of Alaska? Marked differences exist in the physical attributes of the systems, the nature of the fisheries, the mix of species, the management concerns, and the available data. However, several lessons from the research in Bristol Bay may help those working elsewhere. The first lesson is the value of long-term research and monitoring. Much that we have learned about Bristol Bay sockeye salmon and their ecosystems stems from the long-term data collected by our program and by the Alaska Department of Fish and Game (Baker et al. 2009, this volume). However, most of the methods used to characterize the populations in the Bristol Bay systems are simple, requiring persistence and dedication more than specialized skills. In species with simpler freshwater life history patterns (e.g., pink, chum, and Chinook salmon), it should be possible to obtain important and meaningful data to help define population structure by such phenotypic traits as age composition, size-at-age, fecundity and egg size, and spawning date. I recommend that the mantra for long-term research projects be “sufficient but sustainable.” Projects need to collect enough data at enough different spatial scales and levels of ecological organization to be meaningful, yet not so much that they cannot be sustained. Costly projects of short duration are much less desirable (though often more appealing to funding sources) than ones with more modest budgets that are stable over long periods of time.

Importantly, data collected on the fish must be linked to relevant ecological information. The pioneers of the Fisheries Research Institute did not use terms like “global warming” and “climate change” but they measured important physical variables such as the date of ice-out each year, solar radiation, lake level, and water temperature. I had the pleasure of hearing the late Donald Rogers describe how knowledge developed in the Wood River system that he came to know so intimately. He said that initially the staff were unsure what to measure and so they made decisions based on the principles of ecology: physical and biotic factors affecting growth and survival of the target species, and elements of com-
munity structure that might also be important. At first, he said, many discoveries were made, as new streams were explored and new things were learned about the biology of the various species, and the ecological processes. This exciting early period was followed by years when it seemed as though they were just putting another “dot on the graph” in terms of annual average fry size, date of ice-out, peak zooplankton density, and so forth. At this point it would have been easy to stop, assuming that everything interesting had already been learned, or to cut back radically on the scope of sampling. However, the biologists were persistent as well as insightful. The records initially showed a lot of variation but later, when viewed over many decades, they slowly revealed the warming trend and shift in salmon productivity that eventually became so obvious and were seen at even broader scales (Beamish and Bouillon 1993; Mantua et al. 1997; Hilborn et al. 2003; Pyper et al. 2005). The early Fisheries Research Institute scientists also did not use the term biodiversity but they had the foresight to monitor not just the sockeye salmon but also the zooplankton and emerging aquatic insects, and they counted and measured the other fish species such as threespine stickleback *Gasterosteus aculeatus*, nine-spine stickleback *Pungitius pungitius*, pond smelt *Hypomesus olidus*, and least cisco *Coregonus sardinella* that were caught in beach seines and tow nets deployed to sample juvenile sockeye salmon. This holistic view of fisheries science can be critical, especially when it is not initially clear which players and processes will be the most important. In summary, one should first choose the variables to measure wisely, and then sample both consistently and persistently over the long haul.

On the other hand, it must be acknowledged that long-term research has drawbacks. First, it tends to limit the focus to that site, especially as infrastructure (cabins, boats, etc.) and data build up. The system being studied is well known, but is it representative? One is less likely to notice changes in other places, and indeed the basic ecology (species composition, key biotic and abiotic factors, etc.) of the long-term site may differ from other sites, even ones nearby. Second, maintaining long-term data sets can be a lot of work, both in terms of collecting appropriate data in the field and also the less obvious but absolutely essential task of database management. The Fisheries Research Institute program predated computers, and data entry and storage spanned the eras of pencil and paper, punch cards, magnetic tapes, 5¼ inch and 3½ inch “floppy” disks, zip drives, “flash” drives, and so forth. Third, it can be difficult to maintain financial support for long-term projects. They may seem less innovative than new projects, and the continuous need to demonstrate the timeliness of the long-term project can be tedious. Finally, frustration inevitably occurs when we realize what data we should have been collecting all along but did not. Do we start now, or is it too late? How long will funding continue?

**The importance of diversity, and learning from the past**

In addition to the importance of long-term data, including a range of biotic and abiotic variables, the research program on sockeye salmon in Bristol Bay has shown that salmon production can come from a range of different habitats, and that patterns of productivity can vary dramatically from one time period to another (Hilborn et al. 2003). Districts (notably the Naknek-Kvichak) that largely supported the fisheries during some periods of the 20th century recently came under stricter regulatory protection from the fishery whereas others (e.g., Egegik and Nushagak) have returned exceptional numbers of adults per spawner. Even within the Naknek-Kvichak district, the production has shifted in recent years as the Kvichak has barely replaced itself while the
Alagnak River system has seen extraordinary levels of sockeye salmon abundance (Clark 2005). Shifts have also occurred within the Iliamna Lake system in terms of the spawning habitats (creeks, rivers, mainland beach and island beaches) that produce most of the salmon. Thus, conservation (and research) should not focus merely on the systems that are presently large or productive, as apparently minor contributors may be dominant in the future. It may seem pointless to sample a stream with few or no salmon, or one dominated by a species that is not presently valued. However, one of the key lessons from Bristol Bay is that things change, and a “snapshot” in any one year may not be representative. Donald Rogers remarked once that after working in Bristol Bay for more than 40 years he was still waiting for an average year. Each year had some unusual features and often unusual combinations of features (migration timing, fish size, temperatures, precipitation, strike by the fishermen, changes in management, etc.).

The variation in production (of salmon and also lower trophic levels) not only spans the recent decades but the prehistoric period was also characterized by large variation, as inferred from several paleolimnological studies (Finney et al. 2002; Finney et al. 2000; Schindler et al. 2005a; Schindler et al. 2006). Perhaps more important than the mere variation in salmon runs inferred from these samples is the conclusion that the total runs of salmon in the past were no larger than those seen during the past century. Optimistic humans tend to view good times as normal and bad times as aberrant but the runs of salmon in parts of Alaska in the late 20th century have been unusually high, when viewed over the longer period of record. Thus, a final lesson from Bristol Bay is that the fishing community and their managers should plan on changes and surprises, some pleasant, and some otherwise. However, the likelihood of surprises in the future does not mean that we should not investigate and plan. Quite the contrary—future uncertainty makes it all the more important that we initiate and maintain well planned research and monitoring to detect the kinds of changes that will affect our ecosystems and human communities (Beamish and Sweeting 2009, this volume).

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