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A QUANTITATIVE MEASURE OF MIGRATORY TIMING ILLUSTRATED
BY APPLICATION TO THE MANAGEMENT OF
COMMERCIAL SALMON FISHERIES

by

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fulfillment of the requirements
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A QUANTITATIVE MEASURE OF MIGRATORY TIMING
ILLUSTRATED BY APPLICATION TO THE MANAGEMENT
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UNIVERSITY OF WASHINGTON, PH.D., 1979

ABSTRACT: A quantitative measure of migratory timing is developed which, with minimum assumptions, can be used to estimate the timing of fish movements in rivers, streams, and lakes.

The measure, Relative Timing, is based on the assumption that fish move at different times in response to different environmental cues. Relative Timing is calculated by dividing the mean time of migration of each species by the mean time of migration of all species. The measure is shown to be independent of the number of species and to be able to distinguish between species with different migration times.

Relative Timing is applied to the management of commercial salmon fisheries. It is shown that the measure can be used to estimate the timing of fish movements in rivers, streams, and lakes. The measure is also shown to be able to distinguish between species with different migration times.

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CHAPTER 1. INTRODUCTION

The practice of assigning morphologically similar individuals a common name is probably as old as human language. As the disciplines of systematics and taxonomy developed, characteristics other than gross morphology such as chromosomes (karyotyping), blood constituents (sero-taxonomy) and behavior were all used to define physically discrete, temporally conservative assemblages of plants and animals for the purposes of study (Mayr 1970). Among migratory species the time distribution of abundance as viewed from a fixed reference point may be sufficiently distinct and conservative to serve as one criterion of classification.

Beyond the level of basic scientific curiosity, classificatory criteria such as the time distribution of abundance (migratory timing) have numerous practical applications. In the management of commercially exploited natural fish populations, for example, the identification of salmon races (also known as Mendelian populations or stocks) has long been recognized as essential (Thompson 1940). Indeed, the failure of early salmon fisheries management programs on the Karluk River, Alaska, and on the Columbia River, Washington-Oregon, can be explained by differential exploitation of the most abundant races with light or total protection of the less productive races (Thompson 1951). On the basis of a deterministic yield model (Ricker 1954) it has been shown mathematically that the maximum yield is obtained from a group of

salmon races of varying reproductive potential when each may be harvested separately (Ricker 1958; Paulik, Hourston and Larkin 1967).

Separate harvest or some approximation of separate harvest implies the ability to identify the races according to objective criteria such as migratory timing. Although migratory timing of adult sockeye salmon (Oncorhynchus nerka, Walbaum) has been routinely employed by the International Pacific Salmon Fisheries Commission, IPSFC, in commercial fisheries management for many years (see Henry 1961), apparent anomalies and unexplained interannual variation have prohibited its more than casual application in the harvest management of other Pacific salmon species (Oncorhynchus spp.) and other sockeye salmon fisheries. Before attempting to explain the anomalies and interannual variation through a general theory of migratory timing and associated phenomena which is the heart of this discussion, it is necessary to develop some background on migratory timing in diadromous salmonids and associated terminology since diadromous salmonids and particularly the anadromous Pacific salmons will be used to illustrate the development of the thesis.

Adult populations of diadromous salmonids such as Arctic char (Salvelinus alpinus, L.) (Mathisen and Berg 1968), sockeye salmon (Thompson 1945 and 1951; Royal 1953; Killick 1955; Narver 1963; Royce 1965; Dahlberg 1968), pink salmon (O. gorbuscha, Walbaum) (Sheridan 1962; Bevan and Lechner 1970) and king salmon (O. tshawytscha, Walbaum)

(Thompson 1951) exhibit migratory timing which is stable since it occurs during the same time period each year. On the west coast of the United States, fisheries biologists have assigned common names to commercially or recreationally important races of salmonids which reflect adult migratory timing: spring, summer and fall king salmon; early, normal, and late chum salmon (O. keta, Walbaum); summer and winter steelhead (Salmo gairdneri, Richardson). On the east coast of the United States the shad (Alosa sapidissima) makes its spawning run in the company of enthusiastic dipnetters who know when to expect the fish to appear. The list of fish species, diadromous, potadromous, and oceanadromous, which adhere to a predictable schedule of movement is a long one (Harden Jones 1968) and the terminology used in the discussion of migratory timing is by no means uniform.

As an illustration of the diversity of terms available to describe the time distribution of abundance for fishes, consider the salmonids. Migratory timing of adult abundance has been called: "time of adult migration," "time of passage" (Thompson 1945), "time of migration," "pattern of migration" (Thompson 1951), "timing of migration," "racial curve of availability" (Royal 1953), "arrival curve," "chronological order" (Killick 1955), "time-abundance curve," "time of occurrence" (Gilhouse 1960), "timing of entry," "timing of escapement," "timing of runs" (Sheridan 1962), "pattern of departure" (Bevan 1962), "dates of passage," "time of entry" (Narver 1963), "timing" (Paulik, Hourston and Larkin 1967), "entry," "pattern of entry," "entry pattern" (Dahlberg

1968), "time profile" (Lord 1973) and "recruitment curve" (Mobrand 1977). In the study of anadromous trout genetics, migratory timing is known as "time of return" (e.g., Garrison 1977; Peterson 1977). Part of the difference in choice of words among the preceding authors is due to the various spatial reference frames, marine, estuarine, freshwater, and hatchery, from which the authors were making observations.

A number of studies of migratory behavior in salmonids have not dealt with the numbers of fish per unit time but rather with the proportion or cumulative proportion of total abundance per unit time. Terms such as "daily percentage of the total" (Gilhousen 1960), "cumulative proportion of run" (Royce 1965; Rothschild and Balsiger 1971), "logistic time entry curve" (Mathisen and Berg 1968) and "time of entry" (Dahlberg 1968) are used to describe the same concept. All of the authors except Gilhousen modeled the cumulative proportion of total seasonal abundance as a two parameter inverted exponential function of time; $Y(t) = 1/(1 + \exp(-(a + bt)))$. This form of the logistic model was first employed within the context of migratory timing by Dr. G. J. Paulik in his population dynamics courses at the University of Washington. Gilhousen did not apply any deterministic function to his data but he noted, "The shape of the curve resembles but may differ significantly from the mathematically normal distribution". (p. 4). Although not related to general migratory behavior, hatchery studies of "spawning period" or "spawning date frequency" (Feldman 1974) are relevant to spawning migrations. The concept of date of spawning as a normally distributed random variable was employed by Feldman to

distinguish between the spawning behavior of two experimental populations of coho salmon.

The transition from describing migratory behavior in terms of numbers per unit time to modeling migratory behavior in terms of proportion of total abundance as a function of time is an important and crucial conceptual achievement. Migratory behavior is no longer measured with the dimension of fish or animals but it is now solely dimensioned in time.

Going one step further, consider that the proportion of the population associated with a time interval defines the probability of occurrence of that time interval. Stated less abstractly, "The probability of occurrence of any time unit during the migration is specified by the proportion of the population which occurs during the time unit as measured from a fixed location." Equivalently, a migration viewed from a fixed location is seen as the density function of the random variable time, T. Every migration is associated with a probability density function which will be referred to as its "time density." The term, migratory timing, will be reserved to refer to numbers per unit time.

The time density is defined with respect to a locale and to a single life history stage of a population whose abundance may be counted or estimated from that locale. If the population migrates at a constant rate between two locales, the time densities of the two locales will be identical. If the population maintains the same

schedule of migration from year to year, the annual time densities of a locale will be identical regardless of annual fluctuations in the total abundance of the population. Time densities may be discrete or continuous, depending ultimately on the magnitude of the time unit which is used in data acquisition.

By applying the concept of the time density to the migratory behavior of the diadromous salmonids which were previously discussed, the theory requires that the time density of a Mendelian population of salmon is a reliable quantitative classificatory criterion since the migratory timing is conserved across generations. It follows that any aggregate of Mendelian populations of the same species which exhibit conservative migratory timing and which share a common migratory path and direction may be characterized by the sum of their time densities.

Most generally, the migratory behavior of a Mendelian population of any species exhibiting a migratory timing which is conserved across generations may be characterized by its time density.

The importance of the existence of such a theory to the study and management of migratory species is manifold. The recognition that a probability density is associated with each annual time series of abundance (migratory timing) makes a large body of work from the discipline of mathematical statistics directly applicable to research and management. For example, any migration, conservative or not, may

be explicitly described in terms of the mean, variance, and p% confidence interval of the time density. This is a good deal more objective than using arbitrary measures of central tendency and dispersion such as peak abundance and "beginning" or "ending" date whose definition will vary from author to author.

For example, a vague statement such as, "In Bristol Bay, for example, the bulk of the fish in the entire complex of runs may come and go in less than 15 days." (Crutchfield and Pontecorvo 1969, p. 93) can be replaced by the specific assertion, "In Bristol Bay, for example, on the average 80% of the fish are available for harvest only during the time period, June 27-July 12." (Based on analysis presented in Chapter 5, Table 9).

In the case of anadromous fisheries harvest management of target stocks with conservative migratory timing, the p% confidence interval of the time density in the harvest area would define the management period in terms that can satisfy the rules of evidence of the legal system. A large fish packing firm which is concerned with the allocation of mobile processing units across salmon fisheries could use the various time densities to schedule the movement of the gear. (The data and analysis of Chapter 5 are presently being used by members of the industry for such purposes.)

Distribution and allocation of fishing effort across multiple races of salmon which simultaneously traverse the same fishing grounds

(mixed stock or cape fisheries) may be quantitatively specified through application of racial time densities to catch data or to projected catch data. In a related area, the time density of stock to be employed in a salmon hatchery program could be used in conjunction with the time densities of sympatric stocks to quantitatively evaluate potential harvest management conflicts before the hatchery program is initiated. Within hatcheries and hatchery-natural systems (see Chapter 2), the "time of return" is often evaluated as a distinguishing characteristic. The time density concept is well suited to quantifying differences in migratory timing between stocks or changes in migratory timing within a stock across generations.

Time densities of stocks of conservative migratory timing can be used to estimate the total abundance of the stocks before the end of the migration as will be illustrated in Chapter 6. If the accuracy of abundance forecasts can be improved at nominal cost, the benefits to the whole salmon fishing industry and particularly the benefits to the harvesters will be substantial (Mathews 1971).

By far, the most important application of the time density concept is to the development of a general theory of migratory behavior which can be quantitatively specified. As most carefully studied by Gilhousen (1960) for the sockeye races of the Fraser River, British Columbia, there is a substantial degree of unexplained interannual variation in migratory timing. As previously mentioned, the variation

is substantial enough to prohibit the application of a knowledge of the migratory timing to harvest management in most salmon fisheries. The lack of progress in explaining the causes of variability in migratory timing is due in part to the lack of a uniform measure of the migratory behavior which can be related to possible sources of variability (Sheridan 1962). Another obstacle is lack of data on possible sources of variability. With the general application and availability of time densities for migratory populations, the data base necessary to answer the questions of causes of interannual variation can be assembled.

Before proceeding to a consideration of the biological basis for conservative migratory timing, it is important to note that time, in and of itself, does not drive migratory behavior. At the present level of knowledge, time is a convenient quantity to study since it is a known covariate of physical factors which mediate growth and maturation. Maturation drives adult migratory timing in salmon as most recently demonstrated by Mobrand (1977) for coho salmon, O. kisutch, of Puget Sound, Washington state origin (see Chapter 2). Nishiyama (1977) has presented evidence relating differing rates of maturation among Bristol Bay sockeye salmon to differences in migratory timing. Brannon (1972) demonstrated that migratory behavior of fry from six races of sockeye salmon was induced by water current and that the behavior was controlled or mediated by a number of other factors (see Chapter 2). At some point in the future it may be possible to define "temperature densities" or "photoperiod densities" or a multivariate probability

density which might be termed a "migratory density." The recognition that time densities are constructed in lieu of migratory densities goes a long way toward explaining the interannual variability associated with time densities based on calendar dates since calendar time is not necessarily highly correlated with the physical factors that mediate migration.

The fact that migratory timing in adult salmon is not rigidly fixed to time as measured by calendar dates was illustrated by the success of Nobrand's (1977) stochastic model of the arrival of maturing salmon in the home estuaries. The parameter, t_0 , which fixes the location of the cumulative recruitment curve on the time axis is estimated within each season to which the model is applied. The stochastic properties of the maturation process are attributed in the present study to unmeasured heat and light regimes experienced by the maturing salmon. In the case of Bristol Bay sockeye salmon, for example, Burgner (1978) was able to explain more than 78% of the observed variability in the annual dates of the 50% point of the migration in terms of air temperature as recorded from land bases in close proximity to the migratory path.

CHAPTER 2. THE BIOLOGICAL BASIS OF CONSERVATIVE MIGRATORY TIMING.

The biological discipline which deals with the transmission of information between generations by gametic methods is genetics. Generally speaking, when a characteristic which cannot be learned or completely explained in terms of environmental stimuli is expressed in a population from one generation to the next, genetic transmission of the character is indicated. As pointed out in the Introduction, it would be misleading to assume that a race of Pacific salmon possesses genetic information which causes certain genotypes to pass a locale on one calendar date while other genotypes pass it on another. It is reasonable to assume, however, that a Mendelian population of Pacific salmon is adapted to a regime of temperature, light, and other physical and biotic factors which is unique to each of the series of environments linked by the life cycle of the population. Such a regime would vary seasonally, that is, with time. As W. F. Thompson aptly put it while speaking of the distinguishing characteristics of the races of Fraser River sockeye, "It is very hard to conceive that a characteristic time of adult migration is other than an inherited response; certainly it is not 'memory'" (1945, p. 20).

More recently Svardson (1970) studied various characteristics in the salmonid Coregonus spp. complex for use as genetic markers in the study of introgression. He found that the number of spawners as a

function of time was normally distributed about a characteristic date for some populations, but that the date of the center of the distribution could shift radically with unusual water temperatures. Svardson concluded that in the case of sympatric populations with widely separated spawning periods, e.g., widely separated spawning temperatures, that the spawning period would serve as the primary criterion to identify the species. Unfortunately for the purpose of the present discussion, Svardson chose a gill raker count as best suited for the purpose of a general genetic marker. Svardson's relation of spawning period to temperature in Coregonus spp. was preceded by a classic study of the same region (Fabricius 1950).

On the basis of direct experimental evidence, Feldman (1974) concluded that the mean dates of spawning in two hatchery populations of coho salmon were conserved across generations. Furthermore, the conservation of mean spawning date was shown to be independent of changes in rearing temperatures for the two populations studied.

Recent genetic studies of anadromous trout (Salmo gairdneri, Richardson) in the northwestern United States lend credence to the interpretation of migratory timing as a genetically transmitted response to the unique set of physical factors which mediate maturation and reproduction for each Mendelian population (Allendorf 1975 and Thorgaard 1977). Working with proteins (Allendorf) and chromosomal number (Thorgaard) it was found that populations of steelhead at the same geo-

graphic locale which differed in migratory timing evolved independently in different geographic locales. These studies support the thesis that migratory timing of a Mendelian population of an anadromous salmonid species is not necessarily characteristic of an evolutionary line of development but migratory timing may well be an adaptive response to a complex of environmental parameters unique to each locale.

In a study of migratory behavior of sockeye salmon fry, Brannon (1972) identified both genetic and environmental components as active in the determination of migratory behavior among six races studied. Direct experimental evidence led Brannon to state, "In migrations of the Pacific salmon we are dealing with a basic genetic phenomenon which has the capacity to incorporate environmental information or learned responses to accomplish its purpose" (p. 123).

Among hatchery stocks, "time of return" is considered to be a legitimate object of selective breeding experiments (Garrison 1977) and the Oregon Department of Fish and Wildlife has used "time of return" as one characteristic in the evaluation of differences between hatchery and natural stocks (Peterson 1977).

The genetic basis for conservative migratory timing is implicit to the concept of time density since a time density is defined with respect to a geographic locale and to a life history stage of a Mendelian population or to an aggregate of Mendelian populations. The documentation of segregation of races of adult salmon according to

migratory timing is most complete for Fraser River sockeye (Killick 1955). Using tagging data, Killick found that the order in which the races entered the marine waters of the Strait of Juan de Fuca was preserved during migration to the spawning grounds which is a distance of over 600 miles for some of the races. Most importantly, the order in which the individuals arrived on the spawning grounds determined the order in which they spawned. Thus, the existence of a reproductive isolating mechanism which is dependent upon migratory timing has been rigorously demonstrated for one river system and one population. Henry (1961) used scale characteristics to identify the same races at various points in the migration and his findings verify the work of Killick. Gilhousen (1960) discusses the variability associated with migratory timing and migratory routes of Fraser River sockeye races and he offers analyses which point to physical factors, primarily heat and light, as contributors to the observed variability.

Thompson (1951) made repeated reference to the often observed inverse relation between the adult migratory timing of a race of salmon and the distance of the racial spawning grounds from marine water. In general, salmon races which must migrate the farthest distance to spawn within a watershed will be the first adult salmon of the year to enter the watershed. There are probable exceptions with the most notable being the Quinault River (Washington State) sockeye salmon.

The migratory timing of the Quinault sockeye is worth special consideration. As recently summarized by Johnson (1977) the sockeye enter the river between February and May of each year, as contrasted to the June to August range of river entry for other sockeye races at similar latitudes. Spawning does not occur until September and October although it is not known whether date of spawning is positively correlated with date of entry to the river.

The uniqueness of the migratory timing of adult sockeye salmon to the Quinault River indicates that the Quinault River may have been colonized from Lake Wenatchee stocks of the Columbia River system which had about the same migratory timing as presently seen at Quinault. In a documented instance of sockeye transplantation, Woodey (1966) found that the Baker River sockeye (tagit system, Washington) which were moved to the Lake Washington drainage in 1937 had maintained the same migratory timing from marine to freshwater as the parent stock even though the time of spawning had become later in the Cedar River of Lake Washington than was observed in the Baker River.

An attempt was made to relate migratory timing to spawning location for the sockeye of the Kvichak River, Alaska (Smith 1964). No consistent relation between migratory timing and spawning locale was apparent from the tagging data collected in 1957-1959. Unfortunately, the numbers escaping to the Kvichak during 1958 and 1959 were quite small; 534,785 and 680,000, respectively. It is possible that the

smaller races were present in such low numbers that the corresponding probability of tagging for an individual of a minor race made segregation on the spawning grounds difficult to determine. The escapement of 1957 was relatively large, 2,842,810, and a significant relation between spawning locale and migratory timing was demonstrated for one spawning area. The number of sockeye spawners entering the Kvichak is accurately determined by observation from counting towers on the river bank where observers take advantage of the high visibility afforded by the clear water near the outlet of Iliamna Lake.

Sheridan (1962) studied the segregation of pink salmon stocks in southeastern Alaska by migratory timing and he found, as other biologists earlier had determined for both pink and chum salmon of Prince William Sound, Alaska (Pacific Fisherman 1953), that the races bound for specific spawning locales were indeed separated to an extent by migratory timing. Sheridan's work is remarkable because he was able to define the relation between the temperature regime of the spawning grounds and the migratory timing in freshwater. It is also interesting to note that Sheridan felt his work was hampered for lack of a better measure of migratory timing. Again, there is clear evidence of a reproductive isolating mechanism in pink salmon which is dependent upon differences in migratory timing.

Royal (1953), Killick (1955), and others have pointed out that the coincidence of adult migratory timing with water temperature on the

spawning grounds is explained by the maximum tolerable temperature for adult survival and the minimum temperature at which gametes remain viable. In the Fraser River races most of the individuals of a race will arrive on the spawning grounds in time to spawn while the temperature is well within the range necessary for successful reproduction. But some individuals arrive early or late with respect to the temperature optimum of the locale and, as a consequence, the individuals in the tails of this temperature density are less successful at reproduction. These circumstances moved Killick to comment, ". . . whether or not true homogeneity does exist in such a population has never been determined but it is a well established fact, at least in certain cases, that the first and last migrants of a unit migration do not spawn as successfully as those from the peak" (1955, p.1).

Narver (1963) discussed the evidence for segregation of major races of Chignik, Alaska, sockeye according to adult migratory timing. For the major aggregates of races, Black Lake and Chignik Lake, the timing is sufficiently distinct to serve as the basis for the commercial fisheries management program now being conducted by the Alaska Department of Fish and Game. Later, Narver (1966) was able to demonstrate that the capacity of the races to produce adult returns in subsequent generations differed. Narver attributed the differential survival characteristics of the races to the differing extent with which each race is synchronized to physical conditions on the spawning grounds: ". . . time of maturation, in at least some stocks, is

controlled by a genetic code. The later spawning segment of a stock had poorer first year growth than did the earlier spawning segment; this reflected the difference in the time of emergence" (p. 292).

The home stream concept is at the heart of any argument regarding the existence of Mendelian populations of salmon within the mass of salmon which spawn in a watershed. It has been repeatedly demonstrated that most adult salmon return to spawn in the area within the watershed where their parents spawned (Hasler et al. 1978). A small percentage stray as consistently as the bulk of the salmon return to their natal streams. In the absence of straying genetic interchange between races of a population would be almost nonexistent to the detriment of small breeding populations. Thus the home stream concept requires that the spawners of any well defined locale are Mendelian populations. If the spawners are further reproductively segregated by differences in migratory timing, then each time segment within such a spawning locale would qualify as a Mendelian population.

While the literature record cannot possibly be complete for all races of all species of Pacific salmon, in the cases so far examined three important facts have been demonstrated: races of Pacific salmon as true Mendelian populations defined with respect to migratory timing do exist; the races of Pacific salmon may be characterized at some point in space by differences in migratory timing; and there are important differences between and within races in survival of offspring

which are related to migratory timing. These facts are reflected in the professional management of Pacific salmon (Thompson 1945; Royal 1953; Royce 1960; Paulik and Greenough 1967; and Larkin 1977) and they are not disputed by any authority or study at present.

Whether or not the adult migratory timing as reflected in racial time densities will be distinct enough to allow the commercial salmon manager to discriminate among the races in the process of harvesting in any given area will depend upon the nature of the fishing gear, the amount of fishing effort, and the budget of the management program for stock identification purposes, as well as upon the magnitudes of the differences between the means of the racial time densities and the variances of those time densities. But even if it is not practical to distinguish between races for the purposes of harvest management, the knowledge of the racial time densities is none the less important to fisheries management because of the need to know the composition of the spawning escapement in order to predict future production and in order to assess the relative impact of the fishery on the races.

The relevance of fisheries harvest management practices to a discussion of the genetic and biological basis of migratory timing should now be clear. Thompson (1951) was the first to point out that fisheries management practices can have substantial and often severe effects on the migratory timing of Pacific salmon populations through differential exploitation of the races. If the races which are elimi-

nated or decimated happen to be the most productive, the combined yield for the aggregate of races exploited by the fishery must decline.

Given the conservative migratory timing of Pacific salmon and given the ability of many salmon fisheries to harvest nearly all of the available fish, the practice of fixed annual fishing periods is definitely contraindicated.

Since the sources of variability in migratory timing are as yet poorly explained and since commercial fisheries can at times play havoc with the genetic composition of the races in any given area, direct measures of heritability (Ehrlich and Holm 1963) are not appropriate within the present context.

Studies of the heritability of migratory timing are appropriate whenever hatchery stocks of known genotype can be compared to native stocks of known genotype within the same watershed as suggested by the work of Thorgaard (1977). In studies of heritability (h^2) the total variance of a character, S_p^2 is partitioned into genetic, S_G^2 , and environmental, S_E^2 , components by comparison of a "natural" population to an inbred population which shares the same environment (or in the case of anadromous salmonids, the same series of environments). It is only valid to write $S_p^2 = S_E^2 + S_G^2$ if the environmental variance is independent of genotype. As previously discussed, the work of both Allendorf and Thorgaard indicates that the environmental variance in migratory timing may be independent of genotype.

As cited in the preceding developments of this Chapter, the observations which support migratory timing as a genetically transmitted character are:

- 1) migratory timing of many adult salmonid stocks is clustered about a mean or modal value with smaller numbers of individuals at the extremes of the time distribution of abundance;
- 2) selective breeding programs designed to change migratory timing of steelhead trout have been successful;
- 3) the ability to produce viable offspring has been related to migratory timing in the salmon stocks which have been critically studied.

The evidence is consistent with the theory that natural selection is acting to stabilize phenotypic frequencies of salmonid populations about an optimum migratory timing which maximizes fitness in the environment occupied by a given life history stage. The concept of stabilizing selection (Ehrlich and Holm 1963, p. 104; Falconer 1960, p. 338) is well known in the literature of genetics and an abundance of examples for other characters and species may be found there.

The heritability of migratory timing in salmonids has been emphasized in order to introduce evidence that migratory timing is conserved across generations and that it is a reliable characteristic of a race of salmon. It is contended that the apparently large interannual variation in migratory timing, as measured for a number of

species of salmonids, is a failure to distinguish and study two crucial factors.

First, migratory timing which is based on catch data from mixed stock areas will have a broader variability than that of any single geographic isolate represented in the catch data. Mixed stock migratory timing is a random variable in which the sum of random variables and the variances are additive. Even within geographic isolates there is evidence that migratory timing can be a reproductive isolating mechanism so that several Mendelian populations may spawn in a single locality.

Second, and most important, time does not drive migratory behavior. As previously mentioned in Chapter 1, time is used as a conveniently measured covariate of the physical factors (e.g., temperature) which mediate maturation and growth at various life history stages. Until the functional relations between migratory timing behavior and influential environmental factors can be specified, variability is inherent in the use of time. As will be shown, the inherent variability is not always an obstacle in practical applications of a quantitative measure of migratory timing.

In subsequent chapters the preceding contentions will be supported by theoretical and experimental developments. That any migration can be objectively described from a fixed reference frame will be developed in Chapter 3. For a population with conservative migratory timing, the estimation of abundance with a floating time scale will be

theoretically developed in Chapter 4.⁷⁷ Chapter 5 is an analysis of the migratory timing of a collection of sockeye salmon races for which an extensive and thorough data base has been developed. Chapter 5 also provides experimental validation for the theory of Chapter 3. Chapter 6 provides experimental verification of Chapter 4.

CHAPTER 3. MIGRATORY TIMING AS A PROBABILITY DENSITY

Discrete Case

In Chapter 1 the term, time density, was introduced to symbolize relative abundance as a function of time, while the companion term, migratory timing, was reserved to denote abundance of animals as a function of time. Recall that both such functions are defined within the context of a spatial reference frame on observations of a single life history stage of a Mendelian population or aggregate of Mendelian populations which is (are) moving in the same direction or toward the same point.

The choice of the term time density implies that migratory behavior will be modeled as a random variable which is defined over a sample space whose elements are measures of time. Practically speaking, migratory timing is an attribute of an individual of a population which can be measured and sampled. Thus migratory timing is seen as a frequency distribution of time and the time density is the probability density which can be constructed from the frequency distribution or developed from theoretical arguments (e.g., see Tables 8 and 9, Chapter 5).

To characterize the random variable, a calendar year is divided into ℓ many time intervals. Define a sample space, S , with elements (outcomes) which consist of all the ℓ time intervals of the calendar year. Associate the integer, 1, with the first time interval, the

integer, 2, with the second time interval, ..., and the integer ℓ with the last time interval.

Let T denote the real-valued function defined by the mapping of the integers 1, 2, ..., ℓ to the elements of S . T has range 1, 2, ..., ℓ and domain the elements of S . In order for the function T to be a random variable it is necessary to assign a probability measure to the elements of S . If some a priori hypothesis exists which specifies migratory behavior as a function of physical factors which are covariates of time (see Chapter 2) then probability measures can be assigned to the elements of S without sampling. In the absence of an a priori assignment of probability measures, an empirical approach is necessary.

Let t_i be a value within the range of T and define the arrival of an individual on the i -th time interval as an event with outcome, t_i . Recall that, by definition $t_i = 1, 2, \dots, \ell$. Let n_i be the number of events with outcome t_i and let n be the total number of events within the range of T . The empirical probability distribution of T is

$$f(t_i) = n_i/n$$

where $f(t_i)$ is the "time density" of T . Note that $f(t_i)$ assigns an empirical probability measure to each of the elements of S .

It follows directly that the expected value of T , μ , may be estimated as

$$\bar{t} = \sum_{i=1}^{\lambda} t_i \cdot f(t_i) \quad [2]$$

and the variance of T , σ^2 , may be found as

$$s^2 = \sum_{i=1}^{\lambda} (t_i - \bar{t})^2 f(t_i) \quad [3]$$

Example: A year is divided into five time intervals, $t_i = 1, 2, \dots, 5$. A reference frame is selected such that all of the animals in a Mendelian population can be counted. The following results are obtained; 5 animals arrive on the second time interval, 10 on the third, 5 on the fourth, and none on the first or last time interval.

t_i	n_i	$f(t_i)$
1	0	0
2	5	0.25
3	10	0.50
4	5	0.25
5	0	0
$n=20$		

$$\bar{t} = (1)(0) + (2)(0.25) + (3)(0.50) + (4)(0.25) + (5)(0)$$

$$= 0.50 + 1.50 + 1.00$$

$$\bar{t} = 3.00$$

$$s^2 = (1-3)^2(0) + (2-3)^2(0.25) + (3-3)^2 + (0.50) + (4-3)^2(0.25)$$

$$+ (5-3)^2(0)$$

$$= 0 + 0.25 + 0 + 0.25 + 0$$

$$= 0.50$$

For multiple years of observations, say m many years, where the migratory behavior is considered to be an adaptive response of the population (see Chapter 2), we can specify T_1, T_2, \dots, T_m as random variables having a common distribution with means $\mu_1, \mu_2, \dots, \mu_m$ and variances, $\sigma^2_1, \sigma^2_2, \dots, \sigma^2_m$ where the mean of the j -th random variable, after [2], is estimated

$$\bar{t}_j = \sum_{i=1}^{\lambda} t_{ij} f(t_{ij}) \quad [4]$$

where t_{ij} is a value with the range of the random variable T_j and $f(t_{ij})$ is the probability that T_j assumes the value t_{ij} . The variance of the j -th random variable is estimated, after [3]

$$s_j^2 = \sum_{i=1}^{\lambda} (\bar{t}_{ij} - t_j)^2 f(t_{ij}) \quad [5]$$

To define $f(t_{ij})$ after [1] let n_{ij} be the number arriving in the i -th time interval in the j -th year and n_j be the total number arriving in all time intervals during the j -th year,

$$f(t_{ij}) = n_{ij}/n_j \quad [6]$$

In practice it may not be possible to distinguish between r many races as they pass the observation point. It should be recognized that the application of the procedures summarized by equations [1] - [6] are being applied to describe a random variable which is the sum of random variables defined with respect to each of the r races. The random variable which is being described in the j -th year (see [1] - [3]) is defined

$$Y_j = T_{1j} + T_{2j} + \dots + T_{rj}$$

$$k = 1, 2, \dots, r$$

The independence of the T_{kj} is required by the definition of a Mendelian population. Since the T_{kj} are independent random variables with moment generating functions $M_{T_{1j}}(x), M_{T_{2j}}(x), \dots, M_{T_{rj}}(x)$, the moment generating functions of the sum of the random variables $M_{Y_j}(x)$ is

$$\prod_{k=1}^r M_{T_{kj}}(x)$$

Thus, if the races cannot be distinguished from the observation post then it should be recognized that the time density applies to a random variable which is the sum of random variables.

The duration of the migration may be expressed as a probability statement concerning possible values assumed by the random variable, T . Given the mean, \bar{t} and the variance, var., the probability that T assumes a value less than $\bar{t} - k \sqrt{\text{var.}}$ or greater than $\bar{t} + k \sqrt{\text{var.}}$ is less than $1/k^2$ (Chebyshev's Inequality, Freund, 1962, p. 96). The length of the duration of the run which is to be specified depends on the magnitude of k (e.g., Chapter 5, Table 9).

If the population of the species in question is truly migratory then the time density function, $f(t_{ij})$ must be zero for one or more t_{ij} . In other words, if the individuals of the one life history stage can be counted as they pass one geographic point at all times of the year, then the species is not migratory. The counting locale must be

chosen with some prior knowledge of the biology of the species since $f(t_{ij})$ must have one or more nonzero values; trivial applications such as visual counting of polar bears from the grounds of the Washington Monument are disallowed. Furthermore, only one series of nonzero $f(t_{ij})$ is allowed for a year.

Consider the case of the migration where it is impossible to count the individuals, but some measure, c_{ij} , which is proportional to the abundance per unit time, n_{ij} , may be taken, $c_{ij} = a n_{ij}$; where a is a constant, $0 < a \leq 1$. The density function of the migratory timing will not be changed;

$$\begin{aligned} f(t_{ij}) &= a n_{ij} / \sum a n_{ij} \\ &= a n_{ij} / a \sum n_{ij} \\ f(t_{ij}) &= n_{ij} / \sum n_{ij} \end{aligned}$$

which is identical to the case where all of the individuals are counted, equation [6].

If the constant of proportionality, a , is the same for all years, \bar{t} and S^2 may be directly found as given above. If there is a different constant of proportionality for each year, a_1, a_2, \dots, a_m , the daily measure of abundance, c_{ij} , will have to be converted to absolute abundance $n_{ij} = c_{ij}/a_j$ before the computation of \bar{t} and S^2 is undertaken.

If the T_j are independent and uniformly bounded random variables with additive variances so that $Y_m = T_1 + T_2 + \dots + T_m$ will have an

infinite variance when $m \rightarrow +\infty$, the distribution of the standardized mean of the T_j will approach the standard normal distribution. The T_j must be uniformly bounded to meet the definition of migration employed here. The question of the independence of the T_j should be approached carefully. It has been argued that migratory timing is a genetically transmitted attribute of a Mendelian population. In a species with discrete or nearly discrete generations such as pink salmon the migratory timing of an unexploited race would theoretically meet the most stringent conditions for the application of the Central Limit Theorem to the standardized mean of the time densities: T_1, T_2, \dots, T_m are independent random variables which share the same distribution with mean, μ , and variance σ^2 , then as $m \rightarrow +\infty$, the limiting distribution of

$$Z = \frac{\bar{T}_j - \mu}{\sigma / \sqrt{m}}$$

approaches the standard normal distribution where Z is the standardized mean of the T_j . Note that the preceding is intended to develop the theoretical basis for application of the time density concept to migratory populations. The symbols, μ and σ^2 represent parametric quantities which should not be mistaken for estimates of the mean and variance.

Questions of the independence of the T_j for races of species with overlapping generations are more complex. By defining the probability

densities of the migrations in the time domain, it is recognized that only a gross measure of the maturation process is achieved (see Chapter 2). When other domains such as temperature are defined, it may be possible to address the question of independence in a straightforward manner. For the time being, it is assumed that each annual migration defines the probability density of the random variable T_j , unit time of the migration in year j . The random variables T_1, T_2, \dots, T_m are independent and uniformly bounded. It may or may not be the case that the T_j are identically distributed with a common mean and variance.

Summary, Discrete Case

Using the time density terminology it is possible to discuss a single migration or a sum of migrations at a specific locale in terms of the mean and variance of the time density. The probability of the occurrence of the migration during parts of the year may also be specified. Whether a single year is discussed or combined years are treated will depend on the similarity, or lack thereof, between the annual time densities.

In certain cases, again dependent on how conservative the time densities are across years, confidence limits for the mean of the time densities can be calculated by straightforward methods.

There is no need to assume anything about the form of the time density in order to apply the basic methods. More information can be

gained if assumptions regarding the form and the independence of the time densities can be verified. However, in terms of the predictive power of the time density concept for resource management, the form of the time density is irrelevant. The crucial feature is that the form of the time density is preserved from year to year. Examples are provided in the chapters demonstrating applications.

The Continuous Case

If the nature of the migration is continuous, the developments of the preceding section are applicable. The summation operator is replaced by an integral for a random variable, T_j , with continuous probability density, $f(t)$.

$$E(T_j) = \bar{t} = \int_0^{365} t \cdot f(t) dt \quad [7]$$

$$\text{var}(T_j) = s^2 = \int_0^{365} (t - \bar{t})^2 f(t) dt \quad [8]$$

where t is a value within the range of T_j .

The continuous models applied to the description of migratory behavior in the literature so far reviewed (see Chapter 1) are not always identified as probability densities. In particular, the inverted exponential model (see Mathisen and Berg 1968)

$$Y(t) = 1/(1 + \exp(-(a + bt))) \quad [9]$$

is a cumulative probability density if appropriate limits are placed on

the domain of Y . The first derivative,

$$Y' = b/(2 + \exp(a + bt) + \exp(-(a + bt))) \quad [10]$$

is symmetric about the mean, $-(a/b)$, and in application to the description of migratory behavior Y^l is analogous to the normal distribution, $N(t; -(a/b), 1/(4b^2\pi))$.

The choice of a function, $G(t)$, to describe the time density of a migration depends upon the degree of similarity of the observed time density to $G(t)$ and nothing else. Even though $Y(t)$ is the most commonly employed model, Y has no intrinsic biological significance. Any probability density function can be employed so long as the data support the contentions of the model.

The purpose of developing a rigorous concept of migratory behavior is to demonstrate that any migration can be described as a probability density regardless of the form of the migration. Reliance on statistics of the normal curve is frequently contrary to an understanding of the nature of the migration. Indeed, the methods employed in this chapter predate statistics of the normal curve by many years. Practical applications of time densities in resource management do not depend on the form of the time density, but on the interannual consistency of the time densities.

CHAPTER 4. ESTIMATION OF ABUNDANCE FROM TIME DENSITIES

When a cumulative time density, $Y(t)$, or a time density, $Y'(t)$, can be developed for a population at a locale, abundance estimation is theoretically quite a simple matter. Since $Y(t)$ specifies the expected proportion of the run to occur by day (time interval) of the run t , the cumulative counts as of time t are divided by $Y(t)$ to estimate the total abundance for the season.

$$\text{total abundance} = \frac{\text{total observed to date}}{\text{cumulative proportion expected to date}}$$

$$\text{or } N = R(t)/Y(t) \text{ where } R(t) = \sum_{i=1}^t r_i$$

and r_i is total abundance for time interval i .

In the management of commercial salmon fisheries, catch plus escapement by date has long been used as a subjective measure of total seasonal abundance. In the Bristol Bay, Alaska, sockeye salmon fishery, total abundance by July 4 is considered to be a good indicator of one half the total seasonal abundance since July 4 is the traditionally honored half way point in the season.

Walters and Buckingham (1975) investigated the preceding technique in a rigorous fashion and found it to be lacking since acceptable accuracy is not attained until $Y(t) \approx 0.6$, which is well beyond the time when the information is useful to managers of salmon populations. Walters and Buckingham give the following development (p. 114),

ADDITIONAL COMMENTS ON THE USE OF CUMULATIVE CATCHES

$$\hat{w}_t = R_t / P_t$$

$$\sigma_{w_t}^2 = \frac{R_t^2 \cdot \sigma_{P_t}^2}{P_t^4} \{1 + 2 \cdot 2\sigma_{P_t}^2 / P_t^2\}$$

where $\sigma_{w_t}^2$ = variance of the total run estimate for time t
in the season;

$\sigma_{P_t}^2$ = variance of the cumulative proportion

P_t = mean cumulative proportion at time t

R_t = cumulative catch plus escapement at time t

In application to salmon fisheries of the Skeena (British Columbia, Canada), the approach of Walters and Buckingham is presently considered less than adequate for management purposes (Walters, personal communication).

In order to make the time density approach more useful, there are two essential modifications to the preceding line of thought:

1. Catch plus escapement, R_t , is not a constant in fisheries management applications. Even under the best of circumstances it is only a good estimate.
2. Abundance estimation is a problem in the reconciliation of an observed, incoming time density to a theoretical time density. This is equivalent to stating that the form of the time densities will be

similar from year to year but the location of any given mean (\bar{t}_j) may be radically different from expectation.

Three cases will be discussed in the reconciliation of an observed time density to an expected time density; means and variances equal; means not equal, variances equal; neither means nor variances equal. The first two cases apply to a discussion of the work of Walters and Buckingham.

To approach consideration 1, means and variances equal, reverse the roles of R and P in the above. Assume that R is measured with error, and assume that P_t ($Y(t)$ in time density notation) is fixed as the best estimate of the cumulative proportion of total seasonal abundance at time t. Then the total abundance estimate, N is:

$$\hat{N}_t = \frac{\sum_{i=1}^t R_i^2}{\sum_{i=1}^t Y_i R_i} \quad \{2\}$$

which is found by setting the first derivative of the error function

$$\text{err} = \sum (Y_i - \hat{R}_i/N)^2$$

equal to zero and solving for \hat{N} .

Consideration 2, variances equal, means not equal, is met by requiring that err be a minimum over all reasonable lags, positive and negative, of the observed cumulative time series, R, with respect to the cumulative time series of expected proportions, Y. For

example, if k is one half the magnitude of the $(1 - \alpha)\%$ confidence interval for T , the appropriate minimization procedure is,

$$\min_{\Delta t} \left(\min_{\hat{N}} \left(\sum_i \left(\frac{Y_i - R_i}{\hat{N}} + \frac{\Delta t}{2} \right)^2 \right) \right)$$

where Δt assumes all values on the open interval $(-k, k)$ in increments of unit time. The analytic solution to the interior term for any Δt is given in [2].

If the variance is independent of the mean, and if the distribution is approximately symmetric with respect to the mean, when the means are equivalenced by the minimization procedure given above [3], the estimate, \hat{N}_t , will be incorrect for all values of time except t . In this case the only acceptable estimate is \hat{N}_t^* which is found at the inflection point of Y .

If the time density is not symmetric about the mean, the method of [3] will have to be combined with experience to determine at which point, t^* , \hat{N} becomes sufficient to the purposes of abundance estimation. For example, depending upon the shape of the probability density, t^* may correspond to the median or the mode.

The preceding development relies on the conservative nature of the migratory behavior to be studied. If the time densities are radically different from year to year, abundance estimation by means of the time

density approach may not be possible. This is equivalent to stating that if the residual variance about $\bar{Y}(t)$ is so large that $\bar{Y}(t)$ may not be regarded as a constant then the analysis is not to be undertaken.

What "so large" may mean is a subjective choice of the investigator as in the choice of an acceptable α error level in any study.

In the case of large interannual variation in the mean and/or variance of the time densities, it may be possible to remove all or most of the interannual variation by the introduction of independent variables on which the mean and variance may depend (e.g., Burgner 1978, Nishiyama 1977; see Ch. 6).

CHAPTER 5. MIGRATORY TIMING OF BRISTOL BAY SOCKEYE SALMON

Bristol Bay sockeye salmon serve to illustrate the application of the time density concept to aid management of an anadromous fishery. Extensive records on catch and spawning escapement in a form amenable to analysis are complete for major Bristol Bay tributaries to 1955 and for most other tributaries to 1957 (Knudsen, Poe, and Mathisen 1972).

Methods

In order to construct the time densities summarized in Tables 1-6, two assumptions were necessary before the basic methods of Chapter 3 could be applied. Whenever a catch reporting period extended across more than one calendar date, catch was distributed to each calendar date on the basis of the hours fished on that date. For example, a catch of 1,000 fish during the period 1800, 7/15 - 0600, 7/16 would be apportioned as 500 fish caught on 7/15 and 500 fish caught on 7/16. Since the reference frame necessary for harvest management is the fishing district, counts from the escapement enumeration towers (see Chapter 2) which are taken at locations upriver from the fishing districts had to be referred to the date on which the escaping fish passed the estuaries of the fishing districts. Average transit times from estuary to counting tower, in days, were used to refer each daily escapement count to the date of estuarine passage (Royce 1965). For example, an escapement of 1,000 fish recorded at Wood River tower on 6/30 adds 1000 fish to the abundance figure for the fishing district on 6/27.

While neither assumption is perfectly correct (see Bevan 1962), violation of either assumption is not critical to the analysis. In the case of catch apportionment, extended fishing periods which span several calendar dates are usually restricted to early and late in the migration, periods of low abundance. In years of exceptionally high abundance (1960, 1965, 1970, 1975), extended fishing periods do occur in the middle of the migration but, at peak abundance, harvest is evenly paced by the processing capacity of the canning industry which is constant within a year.

Rate of migration undoubtedly behaves as a random variable but, as documented in a recently completed study (McBride 1978, unpublished), the variance in migratory rate from estuary to counting tower is small. Also, small variability in migratory rate between marine and estuarine locales has been found to be relatively constant for Bristol Bay sockeye salmon (see Chapter 6, Table 13).

Calendar dates from June 15-July 31 are coded as integers from 1-47. This is the time period when records on catch and escapement are usually available, and a slight truncation of the time densities is a consequence of this choice of dates. The truncation is of no practical significance; far less than 5% of the migration can be expected to occur outside the chosen time interval (see Table 7).

Results

The annual time densities of the individual Bristol Bay fishing districts (Tables 2-5) and the combined fishing districts (Table 1) are noteworthy in several respects. The interannual variation in the mean of the time densities is small and the means are normally distributed about the grand mean of all annual observations. For example, the distribution of means in Table 1 is $N(20.02, 5.230)$. As would be expected in the case of a normally distributed random variable, the magnitude of the variance is independent of the magnitude of the mean.

An example of the working form of a time density is given in Table 6. The values assumed by the random variable, day of the run, coded for ease of computation, are in column, DAY. The calendar dates which correspond to the coded dates are in column 1. The frequency (col. 2) and cumulative frequency (col. 3) of each value of the attribute are tabulated along with the probability of occurrence (col. 4) and cumulative probability of occurrence (col. 5). The mean and variance are computed after [4] and [5] in Chapter 3, respectively. N refers to the total number of days of observation and the sample size is the last entry in column 3 divided by the last entry in column 5. Note that the density function (Table 6) is nearly identical to $N(20.74, 35.99)$.

Table 1. Yearly time density statistics; discrete observations
for combined Bristol Bay fishing districts, red salmon.

YEAR	MEAN	DATE	VARIANCE
1957*	22.26 +	7/07	30.36
1958*	20.38 +	7/04	30.48
1959	22.26 +	7/06	35.52
1960	22.56 +	7/07	28.92
1961	18.69 -	7/03	30.48
1962	19.37 -	7/03	29.67
1963	20.33 +	7/04	30.19
1964	21.51 +	7/06	26.71
1965	21.29 +	7/06	41.67
1966	19.91 -	7/04	19.33
1967	15.65 -	6/29	38.67
1968	16.50 -	7/01	26.64
1969	18.91 -	7/03	25.38
1970	18.62 -	7/03	28.07
1971	25.15 +	7/09	28.99
1972	19.19 -	7/03	20.16
1973	19.80 -	7/04	32.88
1974	17.11 -	7/01	24.41
1975	20.94 +	7/05	29.31

\bar{x} ; 20.02

s; 2.283

n; 19

95% confidence interval about \bar{x} ; 18.92-21.12

Assuming $N(20.02, 5.230)$ 95% of
values fall between 15.54 - 24.49

*Nushagak District partially excluded.

Table 2. Yearly time density statistics; discrete observations
for the Naknek-Kvichak fishing district, red salmon.

YEAR	MEAN	DATE	VARIANCE
1957	22.09 +	7/06	28.26
1958	20.82 +	7/05	22.44
1959	22.65 +	7/07	31.84
1960	22.42 +	7/06	28.29
1961	18.12 -	7/02	25.67
1962	18.69 -	7/03	29.39
1963	18.99 -	7/03	26.92
1964	21.07 +	7/05	22.15
1965	21.32 +	7/05	41.56
1966	19.23 -	7/04	15.36
1967	15.50 -	6/29	41.13
1968	16.39 -	6/30	25.62
1969	18.74 -	7/03	26.59
1970	18.29 -	7/02	28.32
1971	24.63 +	7/09	29.83
1972	18.49 -	7/02	17.51
1973	19.37 -	7/03	30.16
1974	16.25 -	6/30	22.52
1975	20.31 +	7/04	30.78

\bar{x} ; 19.65

s; 2.374

n; 19

95% confidence interval about \bar{x} ; 18.51 - 20.79

Assuming $N(19.65, 5.634)$ 95% of values fall between
15.00 - 24.30

Table 3. Yearly time density statistics; discrete observations for the Nushagak fishing district, red salmon.

YEAR	MEAN	DATE	VARIANCE
1959	21.52 +	7/05	39.54
1960	21.87 +	7/06	40.24
1961	20.96 -	7/05	36.68
1962	21.18 -	7/05	26.16
1963	20.47 -	7/05	27.94
1964	21.97 +	7/06	29.61
1965	21.70 +	7/06	32.34
1966	22.08 +	7/06	21.30
1967	17.35 -	7/01	30.36
1968	17.43 -	7/01	30.72
1969	20.48 -	7/04	19.16
1970	21.23 -	7/05	16.14
1971	27.02 +	7/11	24.36
1972	22.85 +	7/07	15.94
1973	21.17 -	7/05	33.80
1974	18.87 -	7/03	24.75
1975	23.96 +	7/08	13.06

\bar{x} ; 21.30

s; 2.261

n; 17

95% confidence interval for \bar{x} ; 20.14 - 22.46

Assuming $N(21.3, 5.112)$ 95% of values fall between
16.87 - 25.73

Table 4. Yearly time density statistics; discrete observations for the Egegik fishing district, red salmon.

YEAR	MEAN	DATE	VARIANCE
1957	21.86 +	7/06	32.58
1958	18.84 -	7/03	25.11
1959	22.48 +	7/06	33.30
1960	22.43 +	7/06	28.87
1961	18.89 -	7/03	38.22
1962	18.15 -	7/03	25.74
1963	20.98 +	7/05	32.43
1964	20.50 +	7/04	26.79
1965	19.50 +	7/04	31.60
1966	18.98 -	7/03	19.67
1967	14.16 -	6/28	26.76
1968	15.01 -	6/29	17.19
1969	18.18 -	7/02	20.53
1970	17.99 -	7/02	23.92
1971	23.96 +	7/08	29.13
1972	18.09 -	7/02	17.18
1973	18.35 -	7/02	30.52
1974	17.44 -	7/01	23.10
1975	21.14 +	7/05	20.57

\bar{x} ; 19.31

s; 2.483

n; 19

95% confidence interval \bar{x} ; 18.11 - 20.51

Assuming $N(19.31, 6.163)$ 95% of values fall between
14.44 - 24.18

Table 5. Yearly time density statistics; discrete observations
for Ugashik fishing district, red salmon.

YEAR	MEAN	DATE	VARIANCE
1957	25.20 +	7/09	35.28
1958	19.97 -	7/04	34.11
1959	23.70 +	7/08	36.59
1960	24.67 +	7/09	17.54
1961	23.42 +	7/07	27.81
1962	22.58 -	7/07	26.71
1963	23.64 -	7/08	24.65
1964	24.25 +	7/08	29.24
1965	25.51 +	7/10	35.71
1966	23.32 +	7/07	20.58
1967	18.24 -	7/02	53.10
1968	19.73 -	7/04	43.29
1969	21.28 -	7/05	11.70
1970	23.16 +	7/07	21.54
1971	26.92 +	7/11	18.42
1972	21.51 -	7/06	18.00
1973	22.64 -	7/07	26.96
1974	20.93 -	7/05	6.08
1975	26.13 +	7/10	13.81

\bar{x} ; 22.99

s; 2.287

n; 19

95% confidence interval about \bar{x} ; 21.89 - 24.09

Assuming N(22.99, 5.231) 95% of values fall between
18.51 - 27.47

Table 6. Estimated total run size as observed in the fishing districts, 1956-1975. (1) Month and day, (2) Daily numbers, (3) Cumulative numbers, (4) Daily proportion, (5) Cumulative proportion. Red salmon, Bristol Bay, Alaska.

DAY	(1)	(2)	(3)	(4)	(5)
	***	*****	*****	*****	*****
1	615	28501	28501	.0001	.0001
2	616	34811	63312	.0001	.0002
3	617	79143	142455	.0002	.0004
4	618	125163	267618	.0004	.0008
5	619	374903	642521	.0011	.0019
6	620	731537	1374058	.0022	.0041
7	621	1245439	2619497	.0038	.0079
8	622	1725191	4344688	.0052	.0131
9	623	2704462	7049150	.0082	.0213
10	624	4396368	11445518	.0133	.0345
11	625	6493332	17938850	.0196	.0541
12	626	7148167	25087017	.0216	.0756
13	627	10362973	35449990	.0312	.1069
14	628	13263052	48713042	.0400	.1469
15	629	14258041	62971083	.0430	.1999
16	630	17635406	80606489	.0532	.2430
17	701	20970792	101577281	.0632	.3063
18	702	22809806	124387087	.0688	.3751
19	703	22632224	147019311	.0682	.4433
20	704	22928469	169947780	.0691	.5124
21	705	20218199	190165979	.0610	.5734
22	706	20022629	210188608	.0604	.6338
23	707	17094461	227283069	.0515	.6853
24	708	17986470	245269539	.0542	.7396
25	709	14622475	259892014	.0441	.7836
26	710	14380967	274272981	.0434	.8270
27	711	12472078	286745059	.0376	.8646
28	712	10369043	297114102	.0313	.8959
29	713	8893702	306007804	.0268	.9227
30	714	5903471	311911275	.0178	.9405
31	715	4533094	316444369	.0137	.9542
32	716	3966327	320410696	.0120	.9661
33	717	3749372	324160068	.0113	.9774
34	718	2395698	326555766	.0072	.9846
35	719	1939971	328495737	.0058	.9905
36	720	934591	329430328	.0028	.9933
37	721	704323	330134651	.0021	.9954
38	722	523732	330658383	.0016	.9970
39	723	374101	331032484	.0011	.9981
40	724	390124	331422608	.0012	.9993
41	725	126645	331549253	.0004	.9997
42	726	54499	331603752	.0002	.9999
43	727	31315	331635067	.0001	1.0000

MEAN, 20.74

VARIANCE, 35.99

N, 47

Discussion

The choice of Bristol Bay sockeye salmon to demonstrate time density analysis is both fortunate and unfortunate. The time densities for the sockeye populations of the Bristol Bay tributaries from which the data of Tables 1-6 are derived are essentially normal probability densities. It is not surprising that the district time densities, as sums of the river time densities, are also normal probability densities. This is unfortunate because the flexibility of time density analysis with respect to the form of the migratory timing timing of a target population is not well illustrated (see Chapter 3). The choice is fortunate because the Bristol Bay sockeye time densities are consistent across years and thus lend themselves to the estimation of abundance as illustrated in Chapter 6.

As argued in Chapters 2 and 3, the preceding analysis demonstrates that the migratory timing of an assemblage of salmon populations can be described as a random variable in time and the analysis also demonstrates that, in the case of Bristol Bay sockeye salmon, the mean of the time densities is conserved across generations in the face of fishing pressure and environmental variability. For the combined fishing districts, the means of the annual time densities have a range of only 10 days over a 19-year period (Table 1). During the same time period (1957-1975) the range in annual observed adult abundance was 47.5 million fish. Although the variances are similar in most cases, there are occasional wide fluctuations (e.g., 1965, 1966, Table 1).

The sample sizes for testing equality of variances are the total annual adult abundances which number in the millions each year. With nineteen groups and such large sample sizes the critical value of the F_{max} distribution, $F_{max} .01[19,00]$, is equal to unity, so the variances may be compared directly. On the basis of a direct comparison, the variances of Table 1 are clearly heteroscedastic. The same conclusion would be reached using any other test of equality of variances (e.g., Bartlett's).

In examining the variances of the individual fishing districts which represent fewer Mendelian populations than the combined fishing districts, the same results were obtained; the mean of the time densities varies little while the variances are obviously unequal. The practical consequences of such a pattern is that, while determining the sources of variability in the mean of the time densities is important, determining the sources of variability for the variance is much more critical in the case of Bristol Bay.

Additional Applications

Bristol Bay Fishing Periods

A practical application of the time density approach will further illustrate the utility of having an objective measure of migratory timing. Working from the combined time density data (Table 6), consider the problem of designing a management period during which various proportions of the migration could be given the protection of

fishing regulations. Since the combined time density can be appropriately modeled $N(20.74, 35.99)$, the values assumed by day of the run could be converted to standard deviation units, and proportions of the run by date could be read from a table of areas under the normal curve. This approach is illustrated in Table 7.

But if no appropriate model was available, the mean and variance could be taken as the best estimates of the corresponding parametric quantities for the distribution of the discrete random variable, day of the run. By applying the method of Chebyshev's Inequality (Chapter 3) time periods in which no less than a specified percentage of the run would occur could be designed (see Table 7).

Finally, without making any assumptions at all, percentage points of the migration (Table 6), read from column 5, can be converted to management dates by reading the corresponding entry from column 1 (See Table 7).

Note that the management periods developed by methods 2 and 3 are about the same. Chebyshev's Inequality, in this case, yields incontrovertably true probability statements, but the management periods are quite conservative.

Table 7. Management time periods designed to control harvest of different percentages of the Bristol Bay sockeye salmon by three methods.

Expected percentage under control is greater than	Period				
	Mo.	Begin Day	End Mo.	Day	
50	ch ¹	6	26	7	13
	N ²	7	1	7	9
	TD ³	6	30	7	8
60	ch	6	25	7	14
	N	6	30	7	10
	TD	6	29	7	9
70	ch	6	24	7	16
	N	6	29	7	11
	TD	6	28	7	10
80	ch	6	21	7	18
	N	6	27	7	12
	TD	6	26	7	12
90	ch	6	16	7	24
	N	6	25	7	15
	TD	6	24	7	14
95	ch	6	9	8	1
	N	6	23	7	16
	TD	6	23	7	17

1. Method of Chebyshev's Inequality.

2. N(20.74, 35.99).

3. Time density of combined fishing districts.

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The Weaver Creek Hatchery

As summarized in the environmental impact statement for the Weaver Creek Salmon hatchery (State Environmental Policy Act, Washington Department of Fisheries, Olympia, unpublished) for the Skokomish River

System (Mason Co., Washington), an analysis of the "starting" and "ending" dates (bar graphs, Fig. 1) of the migration of a proposed hatchery chum salmon stock (Oncorhynchus keta, W., Hoodsport) revealed an apparent conflict with the migratory timing of the indigenous chum salmon stock. The one dimensional bar graphs available for comparison of the native and hatchery stocks showed an overlap of about 10 days in the migratory timing of the two stocks.

The Skokomish Tribe, a treaty Indian government with a reservation adjacent to the river, objected vehemently to any destruction or displacement of the native stock which could result from harvest of the anticipated large hatchery migration while the native migration was occurring in the same waters. Battle lines formed around the draft environmental impact statement, as biologists exchanged conflicting opinions and a flock of attorneys circled overhead. Many tens of thousands of dollars were consumed in the dispute which centered around the allegedly conflicting migratory timings of the natural and hatchery chum stocks.

After abandoning the bar graphs, a time density analysis showed that the battle was probably fought for nothing. The time density approach was indicated because harvest of the proposed hatchery stock (Hoodsport), as reared at an existing hatchery, had been occurring intensively in waters adjacent to the Skokomish System since 1972 with no apparent impact on the catch or escapement of the native stock. As demonstrated in Fig. 1, while the effective domains of the two time

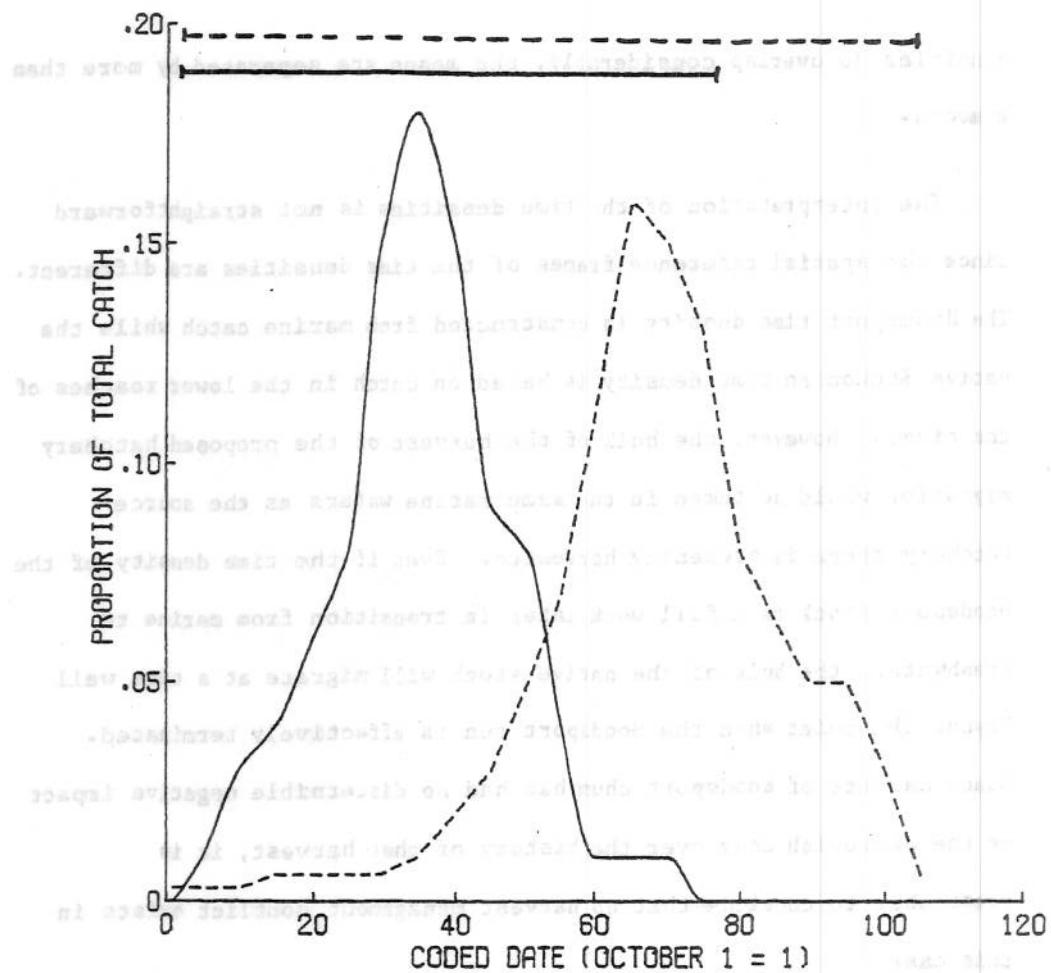


Fig. 1. Hoodsport area marine chum salmon catch as proportion of total catch, 1973-1977 (solid line) compared to Skokomish River chum salmon catch as a proportion of total catch, 1960-1970 (dashed line). Bar graphs above curves show overlap in duration of migrations. Unpublished data, Point No Point Treaty Council, Kingston, WA. and Washington Department of Fisheries, Olympia, WA.

densities do overlap considerably, the means are separated by more than a month.

The interpretation of the time densities is not straightforward since the spatial reference frames of the time densities are different. The Hoodsport time density is constructed from marine catch while the native Skokomish time density is based on catch in the lower reaches of the river. However, the bulk of the harvest of the proposed hatchery migration would be taken in the same marine waters as the source hatchery stock is presently harvested. Even if the time density of the Hoodsport stock is a full week later in transition from marine to freshwater, the bulk of the native stock will migrate at a time well beyond the point when the Hoodsport run is effectively terminated. Since harvest of Hoodsport chum has had no discernible negative impact on the Skokomish chum over the history of that harvest, it is reasonable to conclude that no harvest management conflict exists in this case.

Introgression may or may not be a proper object of investigation in this case. Skokomish chum are not presently recognized as taxonomically distinct from Hoodsport chum although there is substantial circumstantial evidence that such is the case. Based upon what is now known about the conservation of migratory timing in transplanted salmon stocks (e.g., Woodey 1966; Ricker 1972) it is reasonable to conclude that the migratory timing of the Hoodsport x Skokomish stocks will ultimately be bent to conform to the conditions

of the watershed if, indeed, these crosses possess the capability of making such an adaptive response at all. In any event, the spawning dates of these populations appear to be widely separated enough to make the probability of such crosses very small.

17

to the second and following seasons would probably not be
CHAPTER 6. ESTIMATION OF THE ABUNDANCE OF ADULT SOCKEYE
SALMON IN BRISTOL BAY, ALASKA.

Background

The abundance estimation techniques outlined in Chapter 4 represent the minimum information necessary to estimate abundance from a conservative time density of known form. A good deal of knowledge has been presumed available for the construction and use of the requisite time density when, in practice, little information may be available to the manager of the commercial salmon fishery until the adult migration is long over. Even if the information on catch and escapement could be assembled, the technique does not promise to deliver accuracy until sixty or, at best, fifty percent of the migration is over. Given the handicaps outlined above, it would appear that the use of time density abundance estimation has little to offer in a practical sense. The appearance is, of course, very far from the truth.

The abundance estimation procedures to be presented are direct adaptations of time density theory and a simple catch model, well known in population biology, to the solution of a practical fisheries management problem during the course of a major salmon fishery over a two year period. No panacea for the ills of anadromous fisheries management will be found here; only a crude particular solution to a general problem is offered. But the method of approach to problem

solving used here may yet yield a general solution of interest to all forms of commercial fisheries management.

The general procedure is best visualized in terms of a flow chart (Fig. 2). An estimate from initial observation, \hat{N}_1 , is tested against a later count of the same quantity, N_2 , which is known without error. If the initial estimate is found to be lacking in terms of the second, the estimation procedure is corrected and the process starts over until the estimation procedure is perfected. Once perfected, the estimation procedure can be applied to any series of observations with predictable results. This sort of dynamic estimation procedure is directly analogous to aiming an artillery barrage by means of a forward observer. The first round is fired at a theoretical angle (average performance). The observer reports the area of impact (predicted \hat{N}_1) relative to the target (observed N_2). The angle is corrected and the process repeated until the target is hit.

In theory, a number of estimates of an attribute of the same population can be chained to increase the accuracy of the estimation procedure. The process is known in engineering sciences as the "Kalman filter function" (Kalman 1960). In the following experiments, \hat{N}_1 , will be made at a locale called Port Moller and N_2 will come from the fishing districts of Bristol Bay.

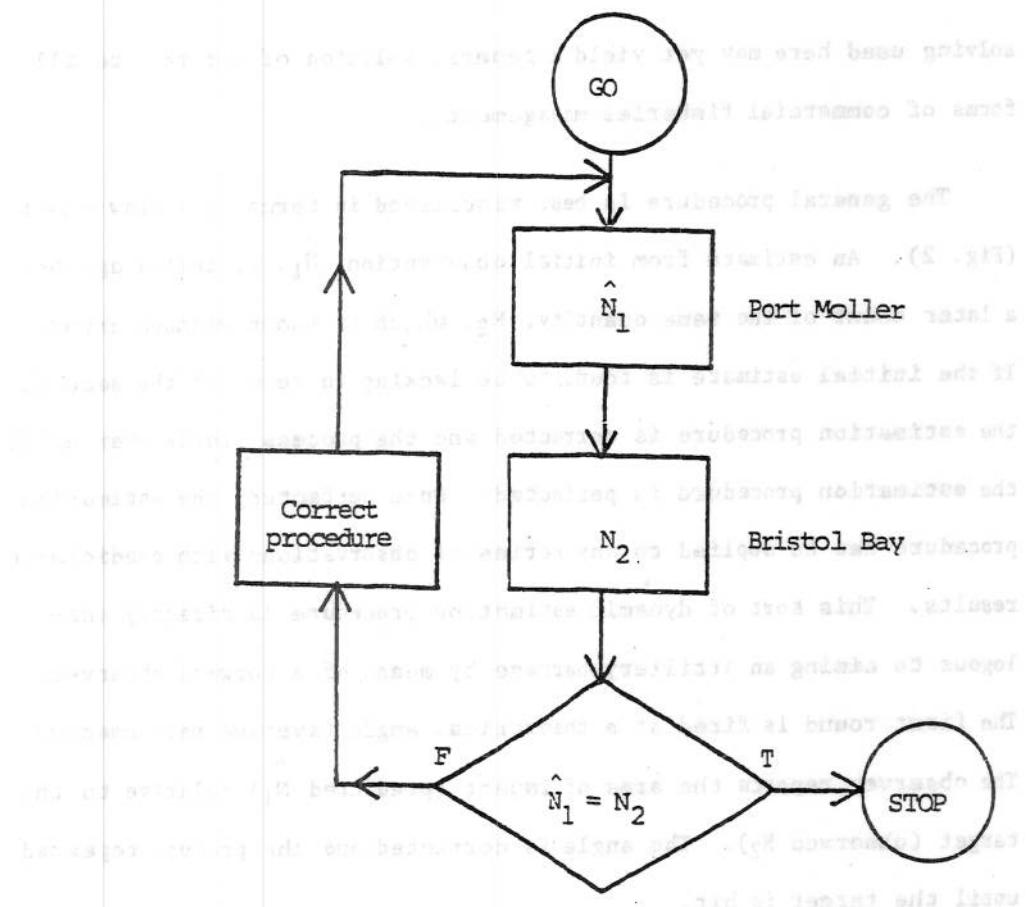


Fig. 2. A schematic of an estimation procedure as a feedback control system.

Abundance Estimation: The Port Moller Program.

Since the time density approach lacks timely accuracy as applied to observations from within a fishery, the alternative strategy is to collect observations from a reference frame which precedes the commercial fishery in time. If the migration proceeds from the new reference frame to the fishery at a constant rate, the time density will be the same as constructed at either locale. Observations at the new locale may be counts of abundance per unit time or observations which are proportional to total abundance.

The alternative reference frame was established for Bristol Bay in 1967. The Alaska Department of Fish and Game (ADF&G) established a gillnet sampling program along a transect line (Fig. 3) which was designed in accordance with the results of many years of tagging studies (Straty 1969) by the federal government (Paulus 1973, unpublished).

By the end of operations at Port Moller in 1975, ADF&G and its federal predecessors had established that nearly all of the sockeye salmon in the Port Moller area were: 1) vulnerable to the sample gear, 2) available for harvest at some point along the transect line, and 3) of Bristol Bay origin.

Abundance estimation from the Port Moller program had limited predictive power prior to 1976 since the total abundance estimate was

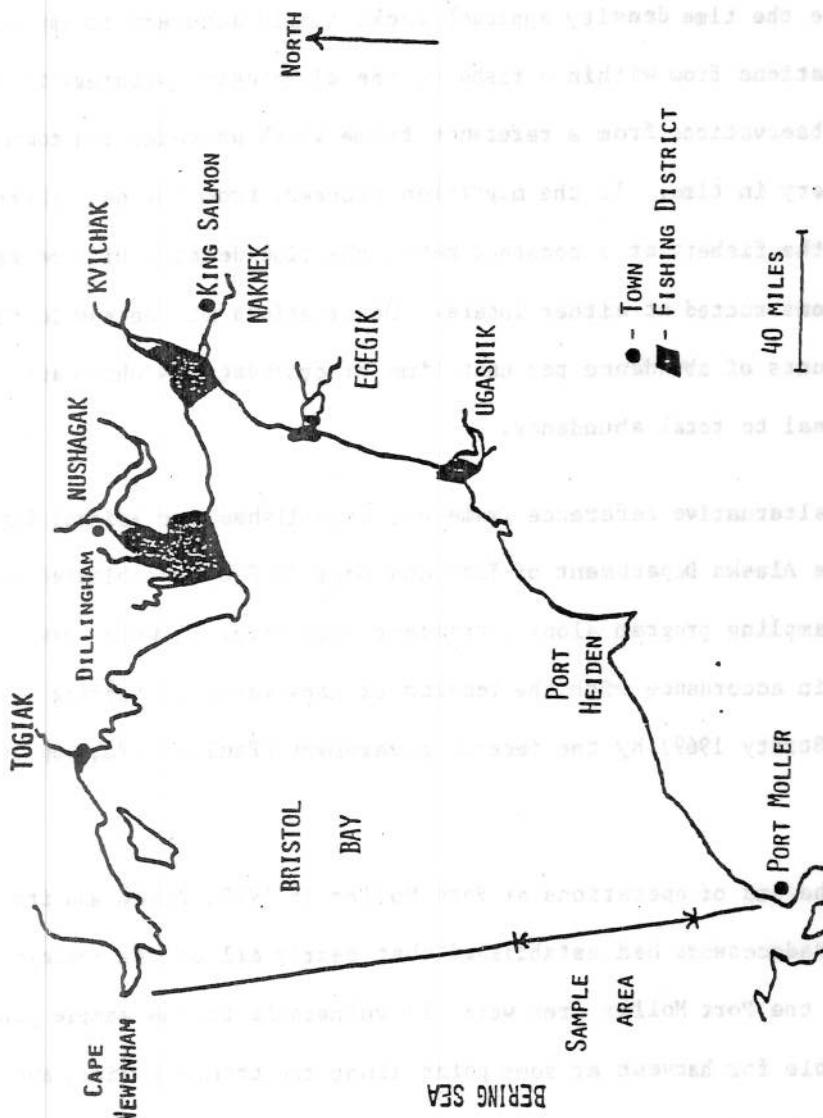


Fig. 3. The Port Moller transect line as established by the Commercial Fisheries Division of the Alaska Department of Fish and Game.

made at the end of operations as a sum of daily abundance estimates. Daily abundance estimates had not been projected into Bristol Bay daily estimates.

Development of Methods

Total abundance estimation assumes that total annual catch-per-unit-effort (CPUE), C/f , number caught/100 fathoms/hour, is proportional to total annual abundance, N ,

$$\frac{C}{f} = qN \quad [1]$$

The estimate, \hat{C} , is found by applying the method of Chapter 4 to the estimated cumulative time density constructed from Port Moller CPUE of 1975, Table 8. In 1976, the estimated time density was $\hat{Y}(t) = 1/(1 + \exp(-(-5.6911 + 0.37071t)))$ where the parameters were estimated by linear regression. The 1977 estimated cumulative time density was $\hat{Y}(t) = 1/(1 + \exp(-(-5.452 + 0.3067t)))$ where the parameters were estimated by nonlinear least squares regression using, again, only the data from the 1975 Port Moller program.

Initial catchability, \hat{q}_0 , was found from 1975 data as $\hat{q}_0 = \hat{C}/\hat{N} = 1274/24,100,000$ where 1274 is the total Port Moller CPUE and 24,100,000 is the total inshore return of sockeye salmon to Bristol Bay.

Since the gillnet sample gear is size selective, adjustments to \hat{q} were made during the season as $q_t = c_t/r_{t+\Delta t} = \text{cumulative sample CPUE}$

Table 8. Port Moller sample catch data, 1975. (1) month, day;
 (2) daily number of sockeye caught/100 fathoms/hour
 (CPUE); (3) cumulative daily CPUE; (4) cumulative daily
 CPUE as proportion of total yearly cpue.

(1)	(2)	(3)	(4)
613	1.0	1.0	.001
614	2.9	3.9	.003
615	4.7	8.6	.007
616	5.7	14.3	.011
617	22.5	36.8	.029
618	37.7	74.5	.058
619	11.2	85.7	.067
620	8.6	94.3	.074
621	17.6	111.9	.088
622	27.6	139.5	.110
623	37.6	177.1	.139
624	47.6	224.7	.176
625	57.6	282.3	.221
626	60.0	342.3	.269
627	261.7	604.0	.474
628	60.0*	664.0	.521
629	60.0*	724.0	.568
630	60.0*	784.0	.615
701	62.3	846.3	.664
702	60.5	906.8	.711
703	112.5	1019.3	.800
704	57.4	1076.7	.845
705	99.9	1176.6	.923
706	33.1	1209.7	.949
707	18.0	1227.7	.963
708	47.0	1274.7	1.000

* Interpolation, Alaska Department of Fish and Game. Missing CPUE = CPUE of 626

on day t divided by the cumulative observed inshore returns Δt days later. The choice of Δt was made graphically in 1976 and most of 1977 in a manner analogous to [3] of Chapter 4.

The first attempt to define $q(\bar{W})$ (1977) was based on the catchability in two years of widely differing average weights (1973; 7.1 lbs and 1975; 5.5 lbs) in which the catchabilities, after [1], were $1/7000$ and $1/18917$, respectively. The line, $1/q(\bar{W}) = -3583.3(\bar{W}) + 38982.6$ was constructed from the two data points, since number of inshore returns for each catch/100 fathoms/hour ($1/q$) is a convenient mode of expression for management purposes. This expression is convenient but it is based on limited data and on a quantity, average weight of inshore returns, which is not known during the course of the season. Alternatively, the relation, $q(\bar{W}_t)N_t = C_t$ [2], was developed from a linear regression of average Port Moller sample catch weights on the inverse of catchability;

Year	$(1/q)$	$(\bar{W}, \text{ lbs.})$
1975	18714.6	5.6
1976	14385.2	6.1
1977	8067.2	7.2

$$r_{xy} = -0.99 ; S_{xy} = -4358.39$$

$$y = -6505.07x + 54704.3 \quad [2A]$$

(Data prior to 1975 must be used with caution since the program was experimental and changes in gear and vessel type were made.)

Relation [2], where \bar{W} is computed from sample catch weights, is flawed in direct proportion to the true variance of the population for the attribute, W . Also, $1/q$ for both 1976 and 1977 is too low due to short sampling seasons at Port Moller. While $q(\bar{W})$ is replaced later in the season by $q_t = c_t/r_t + \Delta t$, the relation [2A] or its predecessor is better than making no correction to q_0 at all.

Daily abundance estimation is based on the same principle as total abundance estimation:

$$q(\bar{W}_t) \hat{n}_t = c'_t$$

$$\text{or } \hat{q}_t \hat{n}_t = c'_t \quad [3]$$

where n_t is abundance in the transect area on day t and c'_t is the daily total cpue. The estimated daily abundance in the fishing districts, \hat{r}'_t , is a direct mapping of \hat{n}_t by the rule,

$$\hat{n}_t = \hat{r}'_t + \Delta t \quad [4]$$

where Δt is the average transit time for sockeye salmon between Port Moller and Bristol Bay.

During the course of the season, the determination of Δt and q are intimately related. As is the case with q , Δt may be adequately

described by an average value within a season, although average transit time varies from year to year. If sample cpue is proportional to total abundance and if the individuals all travel at approximately a constant rate, even if q and Δt are incorrectly estimated, the values of the time series, \hat{r}_t' will parallel the values of the time series, R_t' , catch plus escapement on day t .

Returning to an approach analogous to the determination of N in Chapter 4, assuming that the R_t' are measured without error, define the error function

$$\text{err}_t = \sum (r_i - R_i)^2 = \sum (c_t/q - R_i)^2 \quad [5]$$

where r , c , and R are the cumulative forms of r' , c' , and R' . Take the first derivative of err with respect to q , set it equal to zero and solve for q ,

$$\hat{q}_t = \frac{\sum r_i^2 / \sum r_i R_i}{t} \quad [6]$$

The migration time, Δt , is found as the positive time shift necessary to minimize the error function

$$\text{err}_t = \sum (r_i - R_{i+\Delta t})^2$$

where a reasonable maximum Δt in the case of Bristol Bay is about 9 days.

Results

The 1976 season was characterized by a clearly bimodal time density with an unusually late mean, July 10 (Tables 9 and 10). The $\hat{q}_0 = 1/18917$ was replaced by $\hat{q}_5 = 1/16500$ with a $\Delta t = 8$. The "final" date estimate for management purposes, t_f , was July 2. $\hat{N}_{tf} = 11.3$ million for an actual return of 11.4 million. The progress of N_t is plotted in Figure 4 (Table 10). Although the observed time density was bimodal, the fit of c_t/C to $\hat{Y}(t)$ (parameters estimated by linear regression) was adequate to support retaining the model (Fig. 5). $\hat{q}_{tf} = q_5$ was less than q_0 because each fish was about 1/2 pound heavier than its 1975 counterpart, on the average. Even so, the change in catchability was fairly quickly detected and corrected so that the daily abundance estimates were reasonably accurate (Figure 6).

The 1977 season exhibited a nearly average Bristol Bay time density with a mean of July 5, although the time density was attenuated to the right of the mean (Table 11). The major abnormality was the size of the fish, 7.1 lb as a Bay wide average. It was apparent soon after the start of sampling that $\hat{q}_0 = 1/16,500$ (1976) was much too small. A $q(\bar{W}) = 1/8235$ was used after sample day 3 (June 14) to estimate daily inshore abundance. Catchability as a function of inshore returns fluctuated widely but $\hat{q}_{15} = 1/10,100$ was used from June 26-July 4 for total abundance estimation with $\Delta t=7$. The wide fluctuation in catchability was noted in time to produce reasonably

Table 9. Port Moller sample catch data, 1976. (1) month, day;
 (2) daily number of sockeye caught/100 fathoms/hour
 (cpue); (3) cumulative daily cpue; (4) cumulative cpue
 as proportion of total estimated cpue; (5) $Y(t) =$
 $1/(1 + \exp(-(-5.6911 + 0.37071t)))$; (6) t.

(1)	(2)	(3)	(4)	(5)	(6)
613	1.9	1.9	.00323	.00336	1
614	2.8	4.7	.00799	.00486	2
615	3.0	7.7	.01309	.00704	3
616	1.5	9.2	.01564	.01016	4
617	0.0	9.2	.01564	.01465	5
618	1.5	10.7	.01819	.02109	6
619	16.3	27.0	.04591	.03027	7
620	3.9	30.9	.05255	.04326	8
621	26.7	57.6	.09795	.06148	9
622	10.0	67.6	.11496	.08669	10
623	21.4	89.0	.15136	.12089	11
624	23.4	112.4	.19115	.16612	12
625	18.8	131.2	.22312	.22398	13
626	33.1	164.3	.27942	.29486	14
627	19.2	183.5	.31207	.37726	15
628	31.7	215.2	.36598	.46742	16
629	111.6	326.8	.55578	.55977	17
630	57.5	384.3	.65357	.64815	18
701	28.1	412.4	.70136	.72743	19
702	18.6	431.0	.73299	.79451	20
703	21.5	452.5	.76955	.84852	21
704	48.9	501.4	.85280	.89029	22
705	62.5	563.9	.95913	.92161	23

Table 10. 1976 abundance estimation program, Bristol Bay sockeye salmon. (1) predicted total annual abundance (millions); (2) predicted cumulative daily abundance moved ahead 8 days; (3) observed cumulative daily abundance.

MO/DAY	(1)	(2)	(3)*
627		0.4x	0.1
628	10.8	0.6x	0.4
629	13.2	1.0x	0.8
630	13.0	1.2x	0.9
701	12.2	1.6	1.3
702	11.3	2.0	1.9
703	10.8	2.5	2.8
704	11.2	3.0	2.8
705	12.0	3.8	3.8
706		4.2	4.4
707		6.5	6.1
708		7.4	6.4
709		8.1	6.4
710		8.6	7.0
711		9.0	7.7
712		10.1	9.2
713		11.0	10.6

* Preliminary figures, Alaska Department of Fish and Game, King Salmon, Alaska.

x Back calculation, not prediction.

Table 11. Port Moller sample catch data, 1977.
 (1) month, day; (2) daily number of
 sockeye caught/100 fathoms/hour (CPUE);
 (3) cumulative daily CPUE; (4) cumu-
 lative CPUE as proportion of total es-
 timated CPUE; (5) $Y(t) = 1/(1 + \exp(-(-5.452 + 0.3067t)))$.

(1)	(2)	(3)	(4)	(5)
612	5.1	5.1	.001	.001
613	11.8	16.9	.017	.012
614	2.6*	19.5	.019	.016
615	6.4*	25.9	.025	.021
616	10.1	36.0	.035	.028
617	26.2	62.2	.061	.037
618	20.6	82.8	.082	.050
619	39.1	121.9	.120	.066
620	54.3	176.2	.174	.087
621	26.5	202.7	.200	.114
622	59.4	262.1	.258	.148
623	55.1	317.2	.312	.190
624	56.9	374.1	.368	.240
625	49.7	423.8	.417	.299
626	70.3	494.1	.487	.366
627	87.7A	581.8	.573	.438
628	71.4A	653.2	.643	.512
629	65.0A	718.2	.707	.586
630	57.0A	775.2	.764	.656
701	48.4A	823.6	.811	.720
702	39.8A	863.4	.851	.776
703	19.5	882.9	.870	.824

* Interpolation $t_n = (t_{n-1} + t_{n+2})/2$.

A Interpolation $t_u = Y(t_n) \times \hat{C}$.

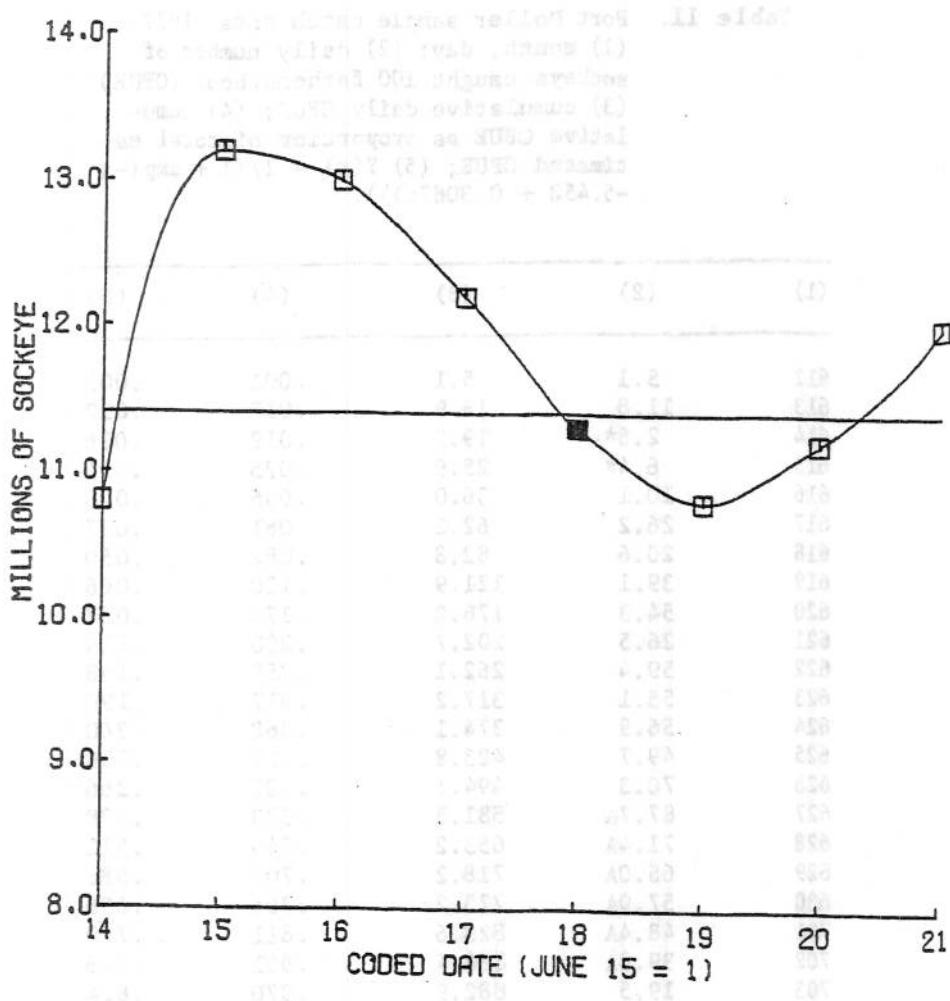
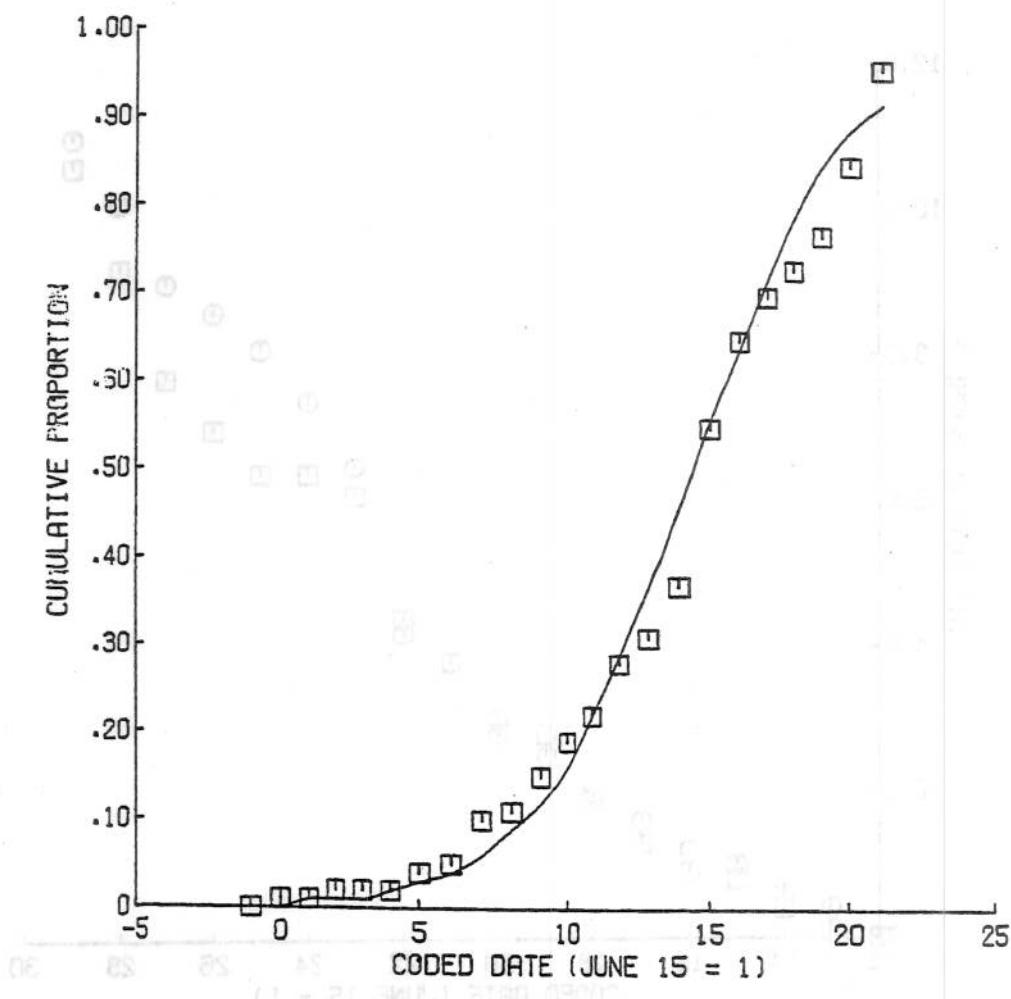


Fig. 4. Estimated total annual abundance (blocks) by date, 1976.
 Solid block locates estimate used for management purposes.
 Center line is actual total abundance.



□ TIME VERSUS OBS 23 VALUES
 TIME VERSUS EXP 23 VALUES

Fig. 5. Comparison of expected cumulative proportion of total abundance (line) to estimated cumulative proportion of total abundance (squares). Fit of estimate to expected based on estimate of total sample catch on July 2, 1976.

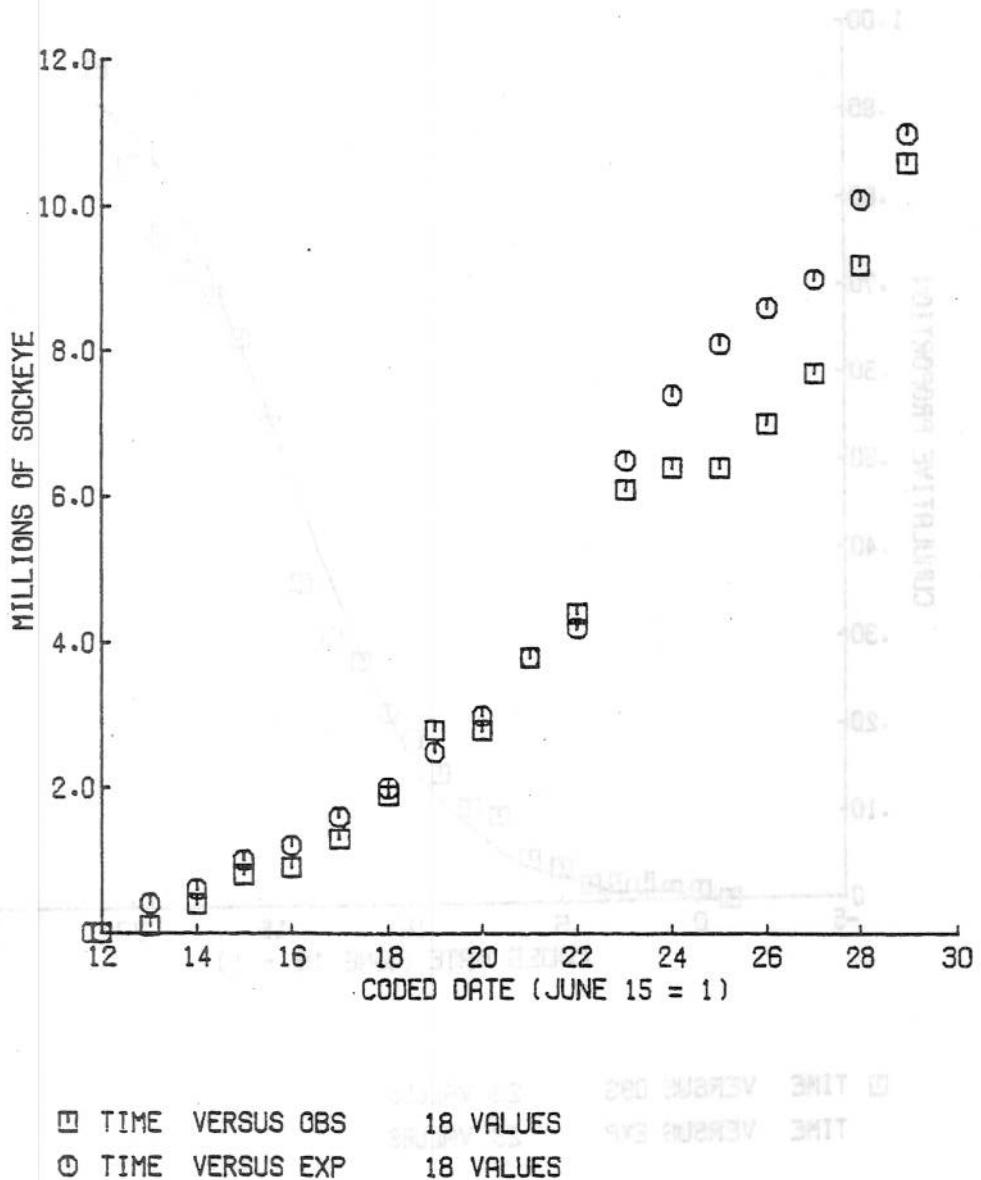


Fig. 6. Observed cumulative daily abundance in the fishing districts (squares) compared to estimated cumulative daily abundance in the Port Moller area moved ahead 8 days (octagons), 1976 season.

Table 12. 1977 abundance estimation program, Bristol Bay sockeye salmon. All figures given in millions of fish. (1) predicted total annual abundance; (2) predicted cumulative daily abundance; (3) observed cumulative daily abundance.

MO/DAY	(1)	(2)	(3)*
620	9.1	0.1	0.1
621	9.4	0.2	0.1
622	9.9	0.2	0.3
623	9.6	0.3	0.5
624	8.7	0.5	0.7
625	9.2	0.7	0.9
626	10.5	1.0	1.5
627	10.5A	1.5	-
628	10.5A	1.7	-
629	10.5A	2.2	-
630	10.5A	2.6	-
701	10.5A	3.1	3.1
702	10.5A	3.5	-
703	10.5A	4.2	-
704	8.36	4.9	4.2
705		5.5	-
706		6.0	5.6
707		6.5	-
708		6.9	-
709		7.2	-
710		7.4	7.0

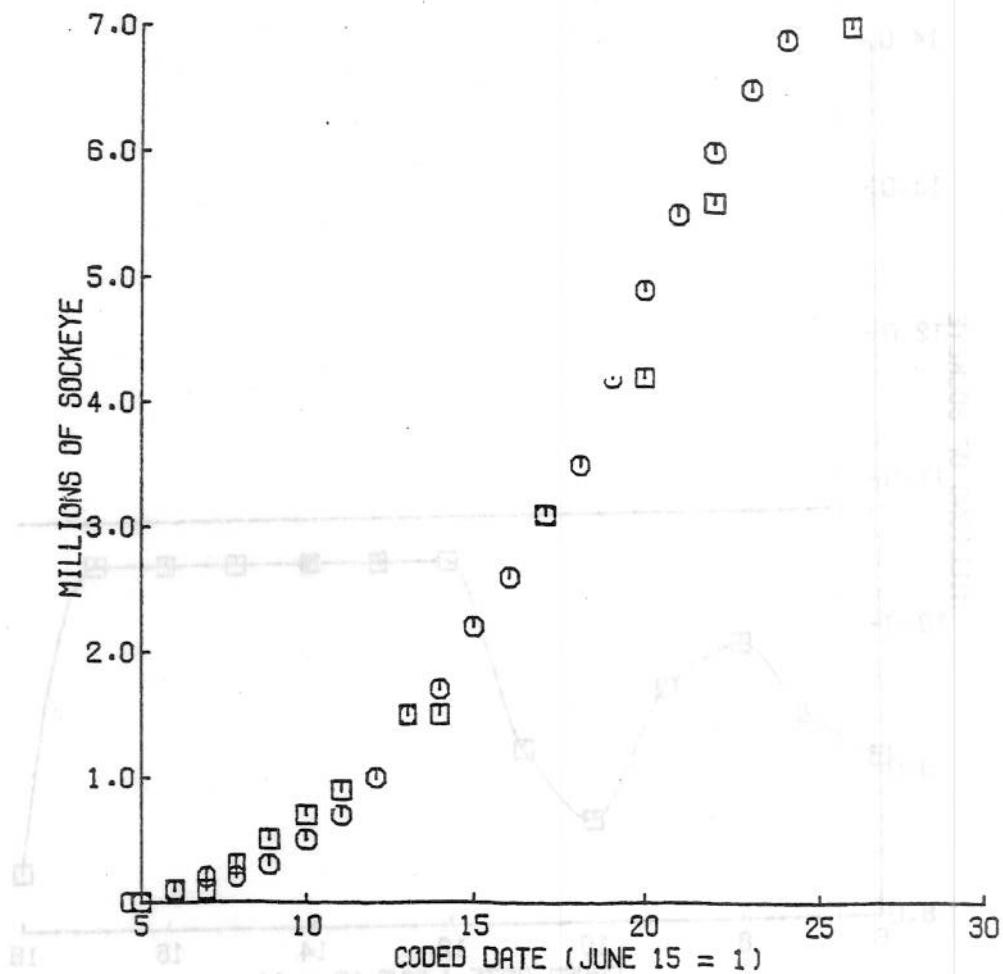
* Preliminary figure, Alaska Department of Fish and Game, King Salmon, Alaska.
 - Figure not available during season.
 A Sampling program not operational.

accurate daily abundance estimates (Fig. 7). The sampling program was effectively eliminated from June 27 onward so the total abundance estimate did not change thereafter (Fig. 8) until a last fit of projected inshore returns to observed yielded a $\hat{q} = 1/8035$. The $N_{tf} = 10.5$ million occurred on June 28 (July 5- Δt) as compared to an actual return of 10.9 million. The fit of c_t/C to $Y(t)$ (Table 12, Fig. 9) was quite good.

Discussion

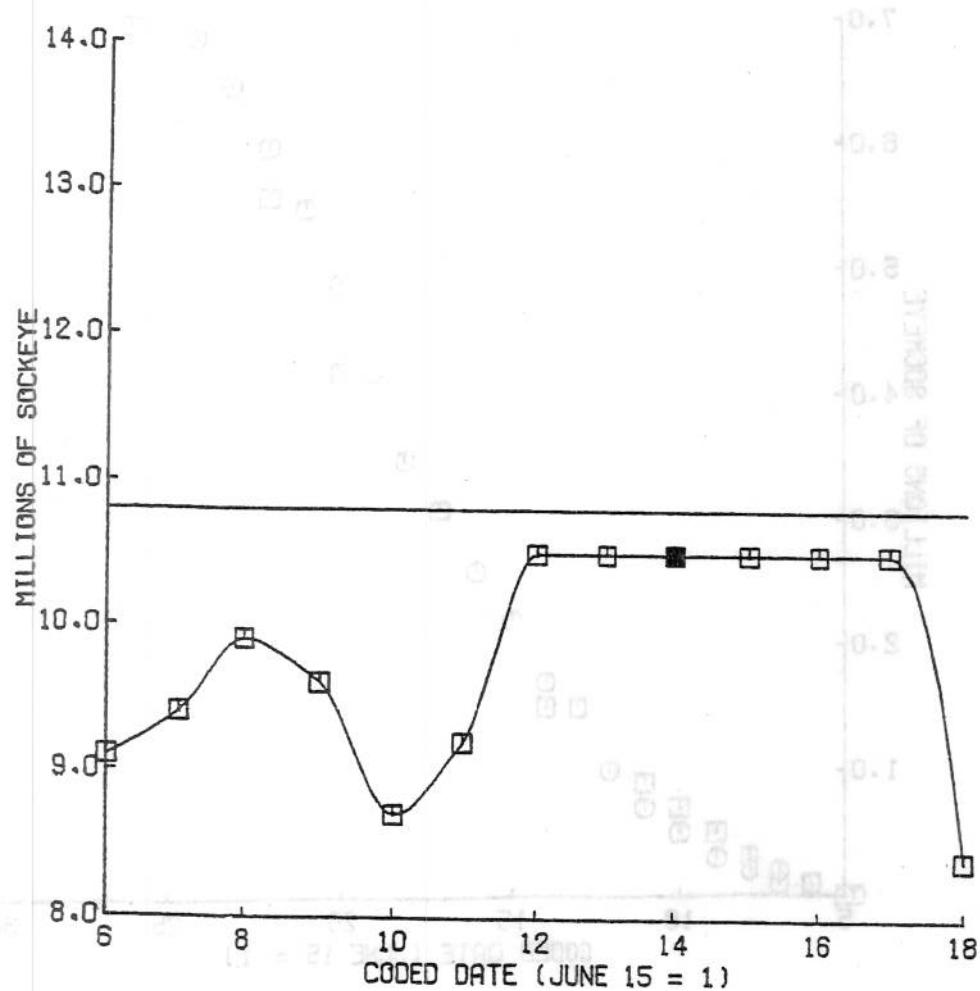
In spite of the bimodal time density, 1976 was a good year to start the abundance estimation program due to the small variation in catchability during the season and the excellent sampling weather. The fish were quite uniform in size and the approximation of q by an average was adequate.

Even though the time density of 1977 was nearly as expected, it was a far more difficult year for estimation of abundance than 1976. Poor weather was a constant problem after June 26 and in the first few days of sampling. But by far the worst problem was the large size of the fish and the high variability in the size of the fish. Unfortunately, the severity of the problem of estimating catchability in 1977 was initially badly underestimated. Daily sample catch weights, although recorded, were not routinely reported during 1977. The decision to use a single $q(\bar{W})$ for daily abundance estimation was a gamble based on the presumption that the average weight of the fish



□ TIME VERSUS OBS 22 VALUES
 ○ TIME VERSUS EXP 22 VALUES

Fig. 7. Cumulative observed daily abundance in the fishing districts (squares) compared to predicted cumulative daily abundance in the Port Moller area moved ahead 7 days (octagons), 1977 season.



TIME VERSUS OBS 14 VALUES
 □ TIME VERSUS EXP 14 VALUES

Fig. 8. Predicted total annual abundance by date, 1977. Solid block shows final estimate effective for management purposes. Center line is actual total abundance.

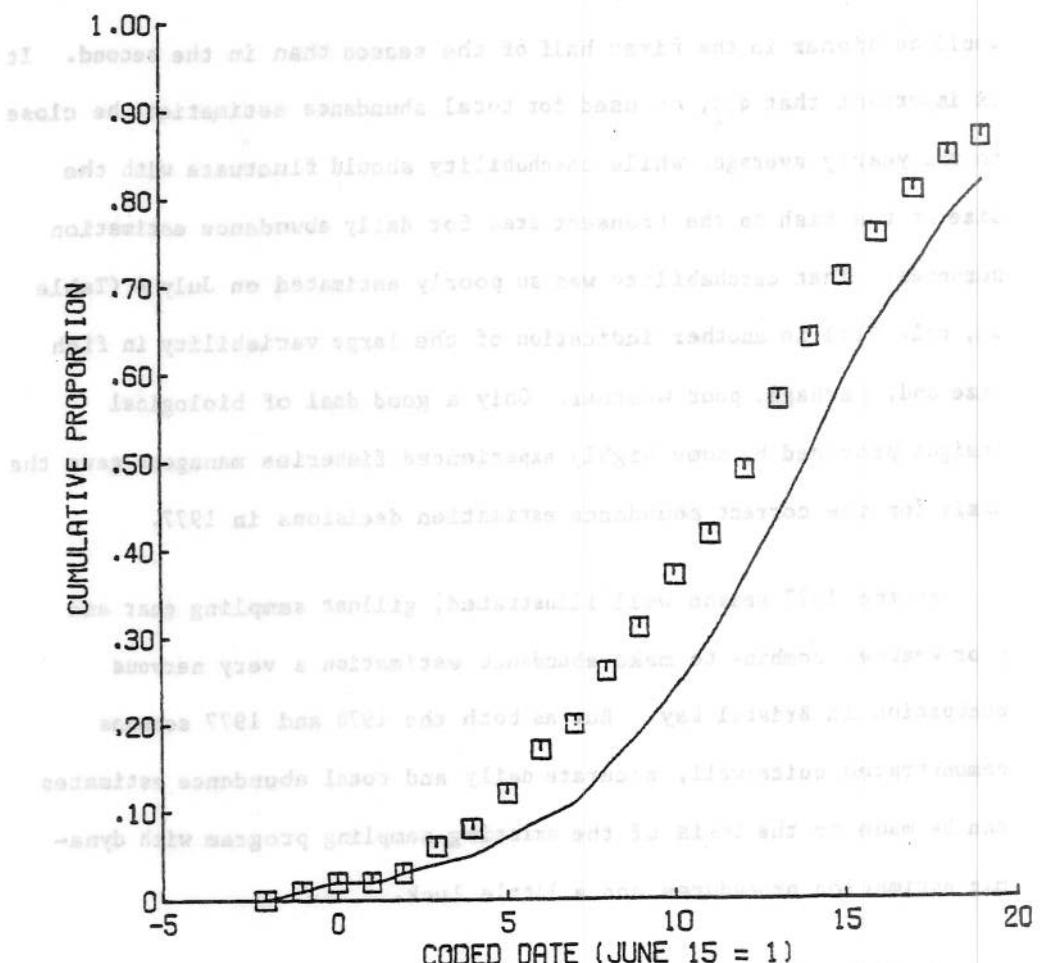


Fig. 9. Cumulative expected proportion of total test catch at Port Moller (line) compared to estimated cumulative proportion of test catch (squares) based on total sample catch estimate of June 26, 1977.

would be higher in the first half of the season than in the second. It is important that q_{tf} , as used for total abundance estimation, be close to the yearly average, while catchability should fluctuate with the size of the fish in the transect area for daily abundance estimation purposes. That catchability was so poorly estimated on July 4 (Table 11, col. (1)) is another indication of the large variability in fish size and, perhaps, poor weather. Only a good deal of biological insight provided by some highly experienced fisheries managers gave the basis for the correct abundance estimation decisions in 1977.

As the 1977 season well illustrated, gillnet sampling gear and poor weather combine to make abundance estimation a very nervous occupation in Bristol Bay. But as both the 1976 and 1977 seasons demonstrated quite well, accurate daily and total abundance estimates can be made on the basis of the existing sampling program with dynamic estimation procedures and a little luck.

To remove the element of chance as best as presently possible, the experience gained in 1976 and 1977 was developed into a set of rules which were coded into a computer program known as AAFMS, the Automated Anadromous Fisheries Management System. The AAFMS was applied in Bristol Bay in the 1978 season. Unfortunately, the weather again was a negative factor, and not enough samples were collected to give the program a meaningful test. In lieu of an actual field application, the program was applied in simulation to past Port Moller sample data in

years in which the average weight of the sample catch was recorded.

The data of Table 13 show that the program is more accurate than long range forecasts, whose average absolute error is about 50%, in all years except 1973. The year 1973 may be discounted since the Port Moller crew leader's logbook (unpublished) tells of rotten decks, rotten nets, personnel problems and much more, best forgotten.

In recent work, Burgner (in press) was able to explain as much as 78% of the variability in date of the 50% point of the migration in the fishing districts in terms of air temperature from land bases near the migratory path. Burgner's work, as well as that of Nishiyama (1977), hold promise that the mean and variance of an annual time density could be forecast before the start of operations at Port Moller. If such was the case, accuracy comparable to that of 1976 (about 1-2% error) would be the rule rather than the exception.

The AAFMS is not a final product but the beginning of a stronger rational basis for fisheries management in Bristol Bay. Left unsolved are the problems of the true nature of the catchability function, the influence of temperature and other physical factors on rate of migration and mean and variance of the time density as well as the problems of the estimation of abundance by river system and abundance estimation for species other than sockeye, such as chum and pink salmon. Perhaps future generations of AAFMS will be good enough that the presumptuous title of the program can be forgiven.

Table 13. Estimated total annual abundance from the Port Moller program as simulated for years in which average weight of the sample catch was recorded. Estimates in millions of fish.

	Year			1971	1973	1975
N	15.8	2.4	24.1	15.8	2.4	24.1
Δt_f (days)	4	9	6	4	9	6
Mo/day of estimate	\hat{N} ; $q = \bar{f}(\bar{W})$			\hat{N} ; $q = \bar{f}(R)$		
625	34.9(121) ¹	7.4(208)+	25.0(4)	-	4.2(75)+	21.0(13)
626	36.7(132)	6.7(179)	24.3(1)	74.8(373)	3.7(54)	28.1(17)
627	34.4(118)	6.2(158)	28.3(17)	92.2(483)	4.7(96)	43.4(80)
628	30.5(93)	5.9(146)	28.8(20)	22.5(42)	4.7(96)	39.3(63)
629	26.9(70)	5.6(133)	28.3(17)+	32.2(104)	4.2(75)	39.1(62)+
630	23.5(49)	5.2(117)	27.4(14)*	18.8(19)	4.4(83)	28.7(19)*
701	20.7(31)	4.9(104)*	26.4(9)	17.6(11)	4.2(75)*	29.7(23)
702	18.3(16)	4.6(92)	25.6(6)	16.9(7)	4.5(87)	36.3(51)
703	16.3(3)	4.3(79)	25.1(4)	17.1(8)	4.9(104)	23.5(2)
704	14.6(8)	4.1(71)	24.7(2)	14.3(9)	4.5(87)	23.6(2)
705	13.5(15)*+	4.0(67)	24.6(2)	16.9(7)*+	4.6(92)	26.0(8)
706	12.8(19)	-	24.4(1)	18.3(16)	-	28.2(17)

¹ absolute percent error; $|(\text{observed}-\text{expected})/\text{observed}| \times 100$.

* date on which estimated cumulative proportion of run greater than or equal 0.5.

+ mean of inshore time density - final time lag, Δt_f .

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