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Random Movement and Orientation in Salmon Migration[1]

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Introduction

A substantial body of evidence, from the initial tagging experiments of GILBERT and RICH (1926) through recent extensive studies by the International North Pacific Fisheries Commission (Canada, Japan and the United States), demonstrates beyond reasonable doubt that many individuals of the five species of Pacific salmon (*Oncorhynchus*) and the steelhead trout *Salmo gairdneri*, hatched in a given stream return to the same area as adults for spawning after variable periods in the open sea. Reviews by HARTT (1960, 1962) and HASLER (1960) give some indication of the distribution pattern at sea by species as a result of tagging studies. The above-mentioned review authors also summarize specific data demonstrating that Pacific salmonid fishes may be found in feeding areas more than 1000 miles from their natal streams. Individuals tagged at sea in these feeding areas have successfully returned as breeding adults to their home streams.

It is the object of this paper to present a hypothesis which explains the observed migratory behaviour or 'homing' phenomenon by means of random searching combined with a low degree of orientation to an outside stimulus. This investigation is concerned exclusively with migration in the open sea and along the coast up to the vicinity of the natal stream and does not include migration in the streams. The role of olfaction, first postulated by HASLER and WISBY (1951), and later demonstrated by WISBY and HASLER (1954) in permitting recognition of a given stream when a fish is in its vicinity, is accepted. For the present purposes, a sea search is considered successful when the vicinity of the home stream is encountered because olfactory senses are considered effectively operative at this point and retention of fish in this area is assumed.

Although Pacific salmonid fishes are used as a primary source of empirical data for this paper, the hypothesis explicitly discussed may be applied to other migratory animals by a suitable choice of parameters. It may be seen from

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what follows that the hypothesis is generally compatible with the salmonid data at hand. It is appreciated that more field experimentation is needed in order to increase the statistical precision of the parameters used in the model. Subsequent computation with more comprehensive and/or precise data will allow further generalization or modification of the hypothesis presented herein. It seems appropriate at this time, however, to attempt a synthesis of available information into a mathematical model in order to understand better the migration phenomenon. Further elaboration of the numerical probability model described herein is in progress, and efforts are being made to consider the same problem from an analytical viewpoint.

Data and Assumptions

Data for the study have been compiled from diverse sources and are used to demonstrate the plausibility of the hypothesis by providing reasonable empirical values for the required parameters. In cases where no evidence to support assumptions is available, the more conservative assumption among reasonable alternatives has been chosen.

Orientation and step length

Evidence indicates that many species of fishes possess an innate mechanism for direction orientation. HARTT (1961, 1962) has recently indicated that the results of repeated purse seine sets suggest that salmon move in definite and consistent patterns in some areas at sea. A significantly higher return was achieved in sets with the seine open toward the west in the vicinity of the Aleutian Islands, however, an eastward movement in the Bering Sea was also shown. This suggests eastward orientation of some salmon on the high seas. It is presumed that these fish are destined for the Pacific coast of North America. A sun compass has been demonstrated for several species exclusive of salmon by HASLER, HORRALL, WISBY, and BRAEMER (1958), HASLER and SCHWASSMANN (1960), and SCHWASSMANN (1960). HASLER (1960) indicated that silver salmon possess a sun-compass mechanism. BRAEMER (1960) has shown for coho salmon, *O. kisutch*, that a compass direction can be maintained during the day as well as at night. Some conflicting evidence, however, is found concerning night movement of salmon. JOHNSON (1960) found from sonic tag tracking experiments that adult salmon either slow down or stop movement at night in the Columbia River. HASLER (1960) states that there have been direct observations of salmon movement at night in the sea, and night gill netting at sea for adult salmon is common practice.

Other guiding mechanisms in the open sea, such as water currents, have been postulated by BEVERTON and HOLT (1957). TAIT (1952) suggests that migration may be influenced by water temperature. The changing temperature and salinity structure over time in the north-east Pacific Ocean, as well as the irregular distribution of water masses and variable current patterns described by several authors (DODIMEAD, 1958; DODIMEAD and HOLLISTER, 1958; DOE, 1955; MISCHIMA and NISKIZAWA, 1955) do not appear to be continuously effective aids for orientation toward the Pacific coast of North America. The present model does not make provision for these effects of ocean currents and can, therefore, be considered a generalized model in the sense that it is not restricted to any specific geographic area because of current configurations peculiar to that area.

Celestial navigation, defined by Wallraff (1960) as a form of goal orientation in which no direct sensory contact with the goal itself or with known landmarks in its vicinity are used, has not been conclusively demonstrated in any animal to date (Wallraff, 1960). Celestial navigation as defined above implies that the direction of the goal is indirectly determined from other stimulus configurations of the environment. This form of goal orientation is not considered necessary in the hypothesis.

It is suggested that the postulated tendency to swim greater distances in the direction of 'home' by mature fish may be derived from the influence of the sun, and that this tendency is retained during the night. It will be assumed that any given fish may swim in any direction with equal probability at each turning point. It is also assumed that, at each turning point, the distance moved in any direction along a straight path is randomly determined within a selected range (0–20 miles). This randomly determined distance is multiplied by a direction sensitive factor which introduces a small and precisely defined bias toward the direction of the natal stream. Several different ranges were studied but the results presented herein are based on a range of zero to twenty miles. The geometry of the search pattern will be described in the discussion of the migration model.

Speed

Some indication of the average speed of migrating salmon is required. From an empirical formula presented by Bainbridge (1958), with coefficients of 3 and 4 beats per second for tailbeat frequencies and 30 inches (76 cm) for the average fish size, a calculated mean speed of about 3 miles per hour is obtained. These frequencies are the lowest values observed by Bainbridge. The above-mentioned formula provides an average speed of about twice the value of 1·5 miles per hour for adult salmon directly observed by Johnson (1960) in the Columbia River. It is conjectured that the swimming performance of adult salmon may be higher in salt water than in fresh water inasmuch as Groves (1954) indicates a higher performance of juvenile salmon in salt water than in fresh water. Osborne (1961) suggests that the actual performance of adults in fresh water exceeds the calculated performance and that salmon are efficient vehicles in energy transformations.

The calculated value of swimming speed exceeds the average velocities of salmon obtained by tag recapture data. However, it should be recognized that tag recapture data give minimal estimates because distance is computed as a straight line or a great circle distance. Values for the apparent rates of travel on the high seas have been computed from data presented by the International North Pacific Fisheries Commission (1958, 1959) and the Fishery Research Institute, University of Washington (1959). These range from 47 miles per day for pink salmon to 12 miles per day for chum salmon. It also appears from an analysis of the above-mentioned data as well as data given by Parker and Kirkness (1956) that swimming speed may be reduced when sexually mature salmon move in the vicinity of the coast or when they arrive in the vicinity of the home stream.

A value of 2·5 miles per hour is assumed to be a reasonable estimate of sustained cruising speed on the high seas. Inasmuch as reduction of swimming speed along the coast has been suggested, a value of 1·25 miles per hour is assumed for coastwise searching. Other values for swimming speed were also utilized and will be briefly considered. It is obvious, however, that, for a given level of endurance, a reduction of average search speed is equivalent to a proportional reduction in the amount of time available to a migrant for conducting the search.

Endurance

It is difficult to determine exactly how long salmon take to migrate from some distant area at sea to the home stream. The impulse to migrate by maturing salmon is presumed to be hormonal. That is, the hormone of the anterior part of the pituitary gland (the gonadotrophic hormone) ultimately exerts a strong enough effect on the nervous system to initiate the migratory instinct. Details of the histo-physiological and experimental studies involved in the hormonal theory are given by GERBILSKY (1958). Movement in the feeding area is assumed to be random prior to this gonadotrophic influence.

Migration by salmon is obviously associated with sexual maturity. A maximum endurance value of one year is evident because tagged sexually mature salmon are invariably recovered during the year of tagging (HARTT, 1960). Empirical values for endurance can also be obtained from tag recapture data. For example, HASLER (1960) describes the movement of a steelhead trout reported by the Oregon State Game Commission in which 143 days were involved in migration to the vicinity of Kodiak Island, Alaska (about 1200 miles) and 153 days were required for return to the home stream after recapture at sea. Data presented by the International North Pacific Fisheries Commission (1959) indicate that migration of immature pink salmon to the Kodiak Island feeding area takes about 175 days (spring to late autumn). From the energy expenditures of fish in motion reported by WINBERG (1960), it was estimated that a fish can swim up to 40 km (22 miles) at the expense of reducing its weight by 1%. Clearly salmon feed during migration as evidenced by successful troll fisheries along the Pacific coast of North America. Therefore, loss of weight is probably insignificant during this period. Thus endurance is probably not associated with energy reserves during migration at sea.

For the purpose at hand, 175 days is postulated as the maximum length of time a given fish will search before dying or giving up. The choice of a time limit is arbitrary, and the assumption that all fish not reaching the vicinity of the natal stream within 175 days are lost or dead is artificial. This kind of constraint on the model, however, helps to insure that the results are more pessimistic than those which might actually occur in nature. Obviously, if a finite time limit were not imposed, all fish would ultimately reach home by random search alone!

Distance

A convenient summary of the distance from 'home' at which the various species of Pacific salmonids have been regularly captured is available from HASLER (1960), HARTT (1960), and the International North Pacific Fisheries Commission (1959). Data from these sources for the various species are listed below:—

Species		Distance in miles (Feeding area from natal stream)
Sockeye	*O. nerka*	1200
Pink	*O. gorbuscha*	1200
Chum	*O. keta*	1700
Chinook	*O. tshawytscha*	2500
Coho	*O. kisutch*	1200
Steelhead	*S. gairdneri*	1200

In this model, it was assumed that all hypothetical migrants began their Monte Carlo search from a point on the globe having the same value of latitude as the mouth of the home stream but longitudinally displaced 1200 miles to the west.

Random movement

It is assumed for this investigation that individual fish search independently. However, the results would not be altered substantially if the fish travelled in schools of limited size. A further assumption is that searching is random in the sense that a fish is not able to recognize a particular location at sea or on the coast (exclusive of home) even if it had been previously traversed.

Home stream and coast recognition

As stated previously, the olfactory senses of migrating salmon are presumed to be sufficiently acute to guide fish when they encounter the vicinity of the natal stream. A radius of 40 miles from the stream mouth is arbitrarily chosen as the area within which a successful search at sea is terminated. A small and practically insignificant handicap is imposed upon the fish at this point because the 40 mile radius does not extend into the sea. It applies only to the coast. Hence any individual whose search time expires when he is even one mile due west of home (not yet impingent upon the coast) is considered lost. This was done to facilitate programming the computer. Other radii of the same order of magnitude would not appreciably affect the computed return probability. Again, the chosen radius is considered a plausible figure for computations in this first approximation.

The coast in the migration model is idealized into a straight line of infinite length. This provides a pessimistic return probability when contrasted with the actual coastwise search which has finite bounds. It is assumed in the model that fish striking the idealized coast will remain in its vicinity. Parker and Kirkness (1956) have demonstrated for chinook salmon, *O. tshawytscha*, that coastwise migration occurs, and further that there is evidence to indicate some directional component in migration from north to south, inasmuch as tagged fish were invariably captured south of the release point.

In order to compare the model with a specific situation, we shall consider the migration of Pacific salmon to the Pacific coast of North America (for example, the Columbia River from a point 1200 miles to the west of the river mouth). It is assumed that completely random searching takes place when fish encounter the coast south of the natal stream and that random searching combined with one-half the directional component of movement experienced at sea takes place when fish strike the coast north of the home stream area. By this, it is meant that the effects produced by deviations from pure random search are only half as great in the northern coastal model as those produced in the open ocean search. As stated previously, search speed is reduced to one-half its value at sea when the coast is reached. This decrease in speed proportionately reduces the amount of search distance available to a fish for coastal searching because a finite time limit is assumed. The restrictions imposed by the model on coastwise searching are extremely severe. Random searching south of the 'home' area does not include a southern reflecting barrier, such as increased water temperature. Also, a random search combined with one-half the coefficient of directed versus undirected movement means that the randomly chosen step, if randomly determined to be in the direction of home, is augmented by only a small fraction of the step length. The rate of net movement toward home is, therefore, very small. An increase in the amount of directed movement toward home would significantly increase the calculated return probabilities. Conservative assumptions have again been applied to the model in this respect.

Migration Model and Results

Migration as defined in this investigation describes a behaviour which involves leaving a particular area (feeding grounds) by sexually maturing fish and the gaining of another defined area (the vicinity of the home stream), the two areas being separated by a considerable distance. This definition is compatible with GERKING's (1959) use of 'homing' which refers to the choice that a fish makes when returning to a place formerly occupied by that fish instead of going to other equally probable places. However, 'homing' generally refers to the return of animals which have been artificially displaced, and it is submitted that the distinction between artificial displacement and natural movement is sufficiently important to demand not only separate terminology but also separate assumptions regarding the mechanisms involved. The term migration as used in this investigation corresponds to WILKINSON's (1952) definition of anastrophic migration.

From what has been described in the data and assumptions, it is obvious that the analytic form of model necessary for the calculation of return probabilities could easily become involved with weighted or biassed random walks on a plane followed by two differently weighted random walk models along a straight line. A model of this nature would involve some complex calculations. For the purposes at hand, a numerical probability or Monte Carlo model of salmon migration has been devised. Monte Carlo methods have been applied to diverse problems with good results as indicated by MEYER (1956).

The pattern of steps (swim lengths) chosen for the migration model is described by a cardioid where:—

$$(1)\ R = P + Q\cos\theta$$
$$(2)\ R = P\,(1 + A\cos\theta),\ \text{where } A = Q/P$$

The variation of step vector, R, specified by the parametrics P and Q is direction sensitive because it is affected by the randomly chosen value of θ. Figure 1 illustrates a range of values of A, the coefficient of directed versus undirected movement. When $A = 0$, the search is completely random and the geometry of the search pattern is described by a circle (step vector is the same

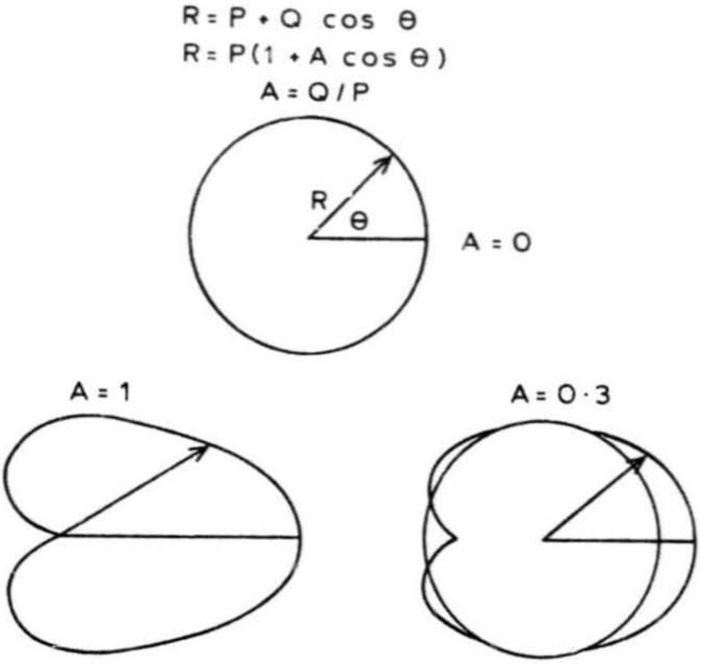

Figure 1. Various movement patterns illustrating ranges of '*A*' values. Swim length is proportional to the length of a vector drawn from the origin, O, to any point on the cardioid.

length in any direction). When $A = 1$, the typical cardioid is apparent. When $A = 0{\cdot}25$, as it was for most of the computations, the resulting cardioid is a very small departure from a pure circle (in Figure 1 a circle is superimposed upon the 0·3 cardioid for visual comparison). In this case, if we consider the circle in the figure as having a unit radius, the maximum step length varies from $-0{\cdot}7$ to $1{\cdot}3$. The length of a vector from the origin to any point on the cardioid is proportional to the distance a fish swims in each step of his random walk. The conservative '*A*' values which have been applied to this model represent very weak orienting influences (postulated as a sun compass).

Explicitly, the following input data have been used for the model. In all instances where units of measurement in miles are indicated, the specific unit is a nautical mile. Appropriate conversions of nautical miles to kilometres are indicated.

Speed (at sea)	variable
Speed (along coast)	one-half of speed at sea
Maximum endurance	175 days
Distance (feeding area to home stream)	1200 miles (2224 km)
A (directed versus undirected movement index)	variable
Radius of 'home' area	40 miles (74 km)
Maximum step (swim) length before turning	variable
Search mode along coast south of home	random
Search mode along coast north of home	A = (one-half of 'A' on high seas)

It is obvious that testing all possible combinations of the variables incremented over a reasonable range would be prohibitively time consuming in the model analysis. In spite of limited testing, certain generalizations appear evident.

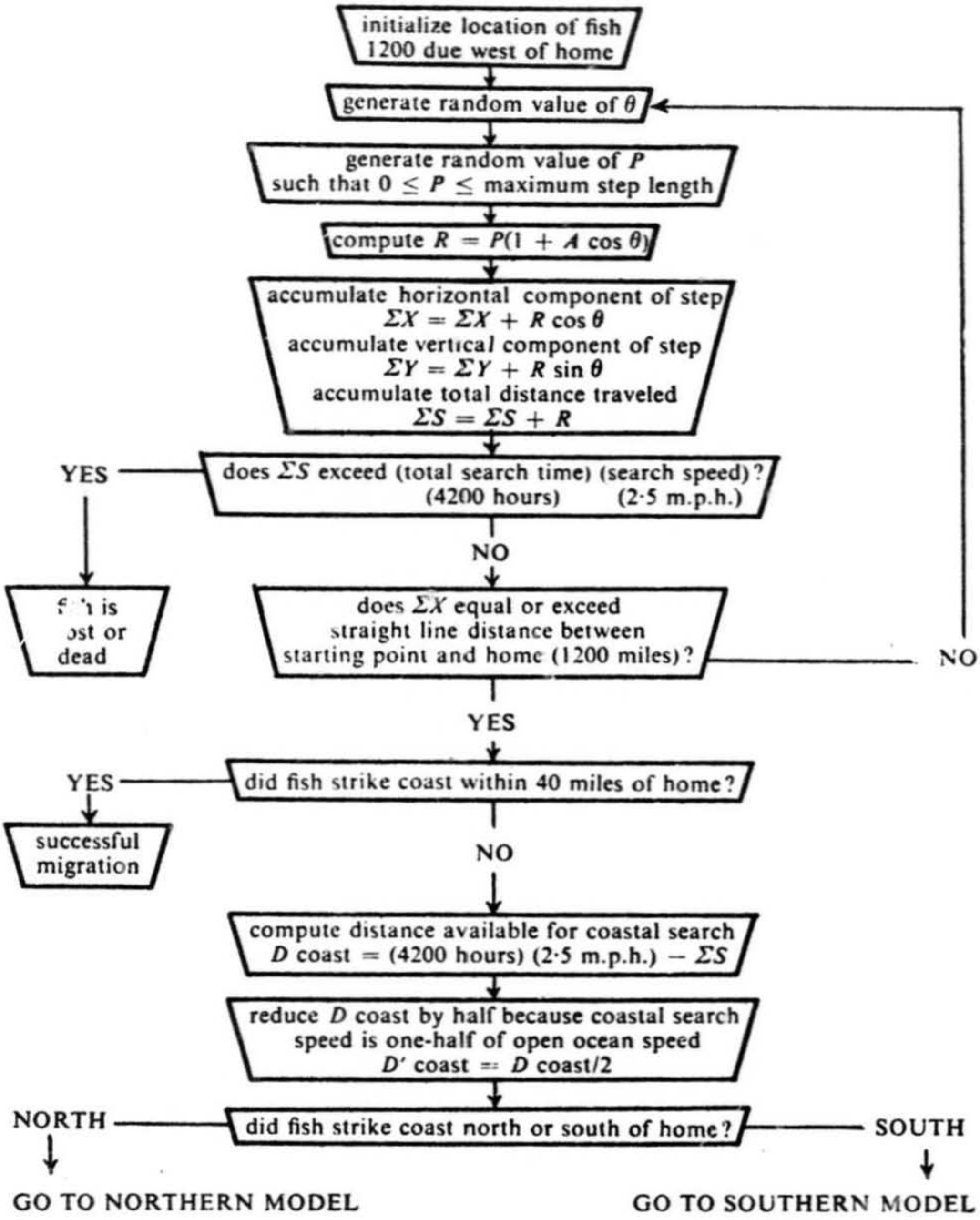

Figure 2. Programme logic for seach on open ocean.

A programme utilizing a random number generator and the above parameters was written for the IBM 709 Data Processing System. Figures 2, 3, and 4 show the flow diagrams for the three main sections of the computer programme. In the actual programme the number of individual migrants is specified and the values of the search parameters are accepted and stored. The simulation then proceeds by sending each migrant through the logical flow shown in the diagrams. The performance of each individual is produced as output by the computer, and, at the end of the run, a final statistical summary is produced.

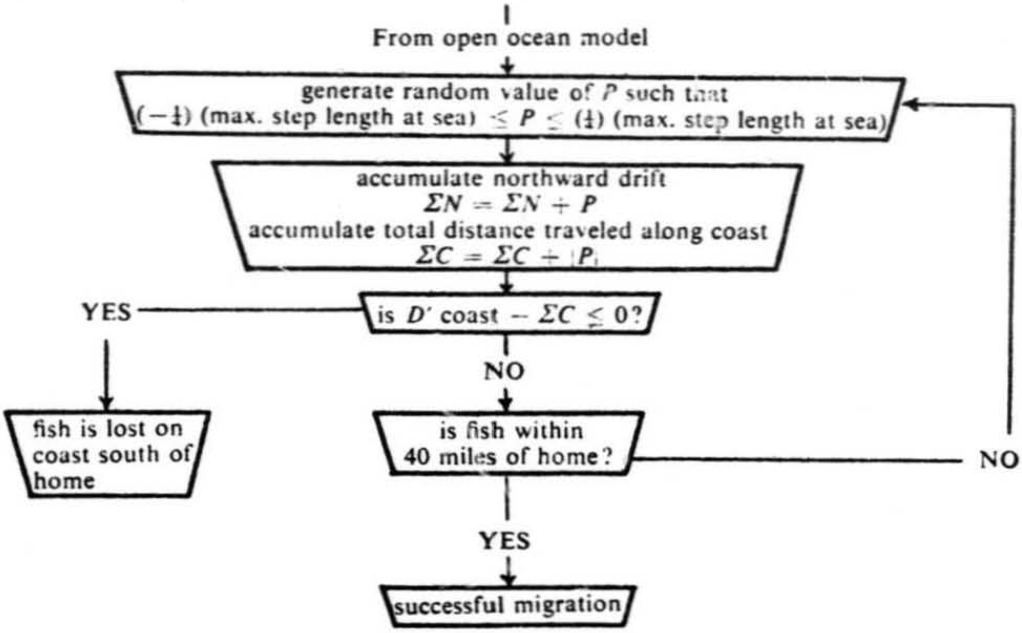

Figure 3. Programme logic for search along southern coast.

Reference to Figure 2 will show how the programme was designed to allow each hypothetical migratory fish to choose an azimuthal direction of travel from a point at sea 1200 miles west of the coast. The angle between the randomly chosen direction and the east-west axis is entered in the parametric form of the cardioid to produce the step vector: $R = P + Q \cos \theta$. This process is repeated until: (a) the allotted search time for the fish expires, or (b) the accumulated eastward movement exceeds the specified straight line distance between the starting point and the north-south absorbing barrier, the coast line. If the second possibility actually occurs, the simulation continues in a one dimensional random walk along the coast. This coastal searching continues until the allotted search time is completely used or until the animal arrives within the specified home region. Reference to Figure 3 will show that searching is purely random on the coast south of home. In Figure 4, one can see how a homeward bias equal to one half 'A' is applied in the northern coastal model.

A series of computer runs were made to get some indication of the return probability as a function of the magnitude of A, the coefficient of directed versus undirected movement. From Table 1 it is clear that return probability increases significantly with relatively small changes in 'A' holding other parameters constant. From this table it is also evident that a return probability of 0·08 was achieved with a value of 0·20 for 'A'. This value is very close to the average of a 10% recovery rate for mature salmon tagged on the high seas as reported by HARTT (1960). Tag returns up to 22% have been reported for mature red salmon (Report of Operations . . . 1958, Fisheries Research Institute, University of Washington). An 'A' value of 0·3 gives a return probability of 0·37 which considerably exceeds the observed return of tagged salmon. This value of 'A' still does not demand precise orientation on the part of the fish. The values of the other parameters in Table 1 are considered to be conservative. Small sample size accounts for the apparent anomaly in return probability for 'A' values of 0·15 and 1·0.

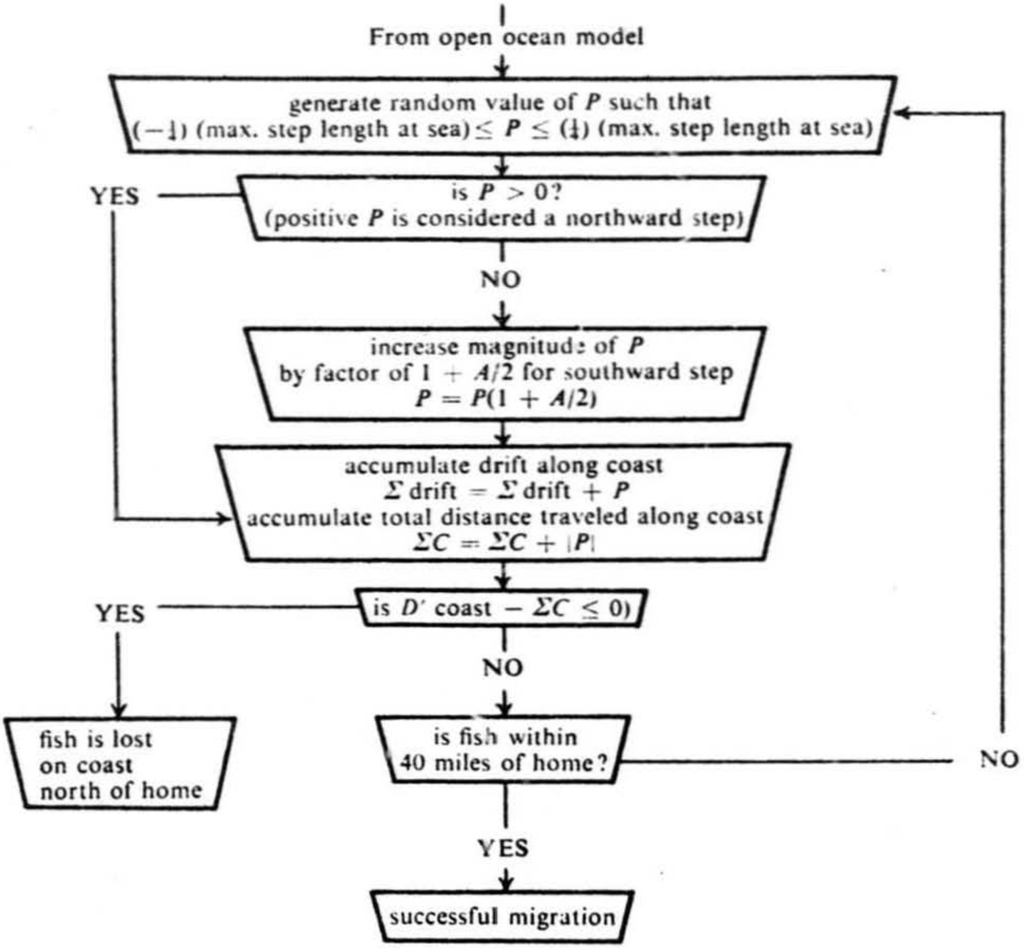

Figure 4. Programme logic for search along northern coast.

It is evident that tag returns provide a biassed estimate (low) of actual returns of salmon because of immediate tagging mortality and incomplete tag reporting. Both of these sources of error are probably variable according to the species and tagging conditions. Natural mortality is unknown for the period of migration in the sea. Inasmuch as there is at present no way to estimate these losses, a coefficient of directed versus undirected movement corresponding to a significantly higher return than is actually observed is considered most realistic. The 'A' value of 0·3 is taken to be the best approximation of orientation requirements.

It can be argued that a very high degree of orientation which is not coupled with random searching would actually result in no returns if the fish were subject to even a small drift with water movements. Thus the simplest assumptions regarding orientation also appear to be most logical. It should also be reemphasized that these calculations are based on a conservative model as indicated by the data and assumptions.

The results of the simulated migrations were programmed to permit detailed analysis of the outcome of each individual hypothetical fish. Oscilloscope traces showing the actual paths of four hypothetical fishes have been published (SAILA and SHAPPY, 1962). These details are not considered important except

Table 1

Return probability as a function of the coefficient of directed versus undirected movement. Other parameters are as indicated below:

'*A*' value	Return probability	Number of hypothetical fish
0	0	100
0·1	0	10
0·15	0·40	10
0·20	0·08	100
0·25	0·22	100
0·30	0·37	100
0·50	0·70	10
1·0	0·60	10

Speed (at sea)	2·5 m.p.h. (4·6 km/hr)
Speed (along coast)	1·25 m.p.h. (2·3 km/hr)
Maximum endurance	175 days
Distance	1200 miles (2224 km)
Radius of 'home' area	40 miles (74 km)
Maximum step length	20 miles (37 km)
Search mode along coast south of 'home'	random
Search mode along coast north of 'home'	'*A*' = one-half of '*A*' above

Table 2

Return probability as a function of searching speed. Other parameters are as indicated below:

Searching speed (miles per hr and km per hr)	Return probability	Number of hypothetical fish
5 (9·3)	0·60	100
4 (7·4)	0·54	100
3 (5·6)	0·36	100
2·5 (4·6)	0·22	100

Maximum endurance	175 days
Distance	1200 miles (2224 km)
Radius of 'home' area	40 miles (74 km)
Maximum step length	20 miles (37 km)
Search mode along coast south of 'home'	random
Search mode along coast north of 'home'	$A = 0{\cdot}125$
Coefficient of directed versus undirected movement, *A*, on high seas	0·25

to point out some generalizations observed when '*A*' was assigned values of 0·20, 0·25, and 0·30. (1) About twice as many fish found 'home' from the north than from the south in coastwise searching. As, however, about twice as many fish made contact with the coast to the north of 'home' than to the south of 'home', it appears that the superimposed directional component in the northern coastal model is not strong enough to increase noticeably the probability of successful search for fishes striking the coast north of home. The restrictions on the directional element of coastwise searching were previously stated, and its ineffectiveness is apparent. (2) The number of hypothetical fish lost at sea from this model is about 40%. Of the remaining 60%, approximately two-thirds are lost in the coastal search. (3) About 7% of the hypothetical fishes arrive home directly with no coastwise searching.

Table 3

Return probability as a function of maximum step length. Other parameters are as indicated below:

Maximum step length (miles and km)	Return probability	Number of hypothetical fish
100 (185)	0·13	100
75 (139)	0·24	100
50 (93)	0·24	100
40 (74)	0·29	100
30 (56)	0·13	100

Speed (at sea)	2·5 m.p.h. (4·6 km/hr)
Speed (along coast)	1·25 m.p.h. (2·3 km/hr)
Maximum endurance	175 days
Distance	1200 miles (2224 km)
Radius of 'home' area	40 miles (74 km)
Search mode along coast south of 'home'	random
Search mode along coast north of 'home'	$A = 0{\cdot}125$
Coefficient of directed versus undirected movement, A, on high seas	0·25

Results were obtained from several computer runs by varying the speed of the fish but holding other parameters constant. It should be remembered that coastwise search speed is reduced to one-half its value shown in column 1 of Table 2. It is evident from the results shown in Table 2 that there is an increase in return probability with increasing speed. The reason for this has been previously stated.

Similar runs were made in an effort to determine the relationship between return probability and maximum step length. As stated previously, step lengths were randomly determined within an arbitrary range. The figures listed in column 1 of Table 3 are the maximum values for the specified range. It is evident that the average step length randomly chosen between 0 and the maximum is about one-half the maximum value. The return probabilities achieved in Table 3 suggest a complex relationship between the maximum step length and return probability. It is submitted that this may be due to the nature of the numerical probability model. However, precise empirical information on the movement of individual fish on the high seas by sonic tracking or other methods is highly desirable at this point.

Acknowledgement

Part of the computations required in this study were performed at the Computation Center, Massachusetts Institute of Technology, Cambridge, Massachusetts.

Summary

A numerical probability model (Monte Carlo method) of the migration of salmonid fishes was developed. Empirical values for the model parameters available from published literature were utilized to demonstrate the plausibility of the model as an explanation for migration in the sea, and to provide a quantitative indication of the degree of orientation required to provide a high return probability. Specifically, a random number generator in a high speed digital computer was used to allow a hypothetical migratory fish to choose an

azimuthal direction of travel. The angle between the randomly chosen direction and the east-west axis was entered into the parametric form of a cardioid to produce a 'step vector' as follows: $R = P + Q \cos \theta$. This was repeated until (a) the allotted search time for the animal expired, or (b) the accumulated east-west displacement exceeded the specified straight line distance between the starting point and a north-south barrier (the coast). A small strip of coast was designated as 'home'. If an individual reached the coast, the cardioid model was dropped and the random walk continued along the coast until the remaining search time was completely used or the animal arrived 'home'. A return probability of 37% (significantly higher than observed returns based on tag recoveries) was achieved with a model utilizing random movement combined with only a small amount of orientation. It was concluded that neither navigation nor precise orientation was necessary to explain the large scale migration of salmon to the vicinity of their natal streams from distant feeding areas.

It is submitted that construction and manipulation of a mathematical model is helpful in achieving a better understanding of any phenomenon. The model discussed above is admittedly an oversimplification of a complex biological phenomenon. However, because of the paucity of empirical data regarding the migrant's endurance and the unknown nature of the frequency distribution of lengths of step vectors, a more complex set of assumptions does not appear to be justified. Nevertheless, the results indicated by this model do not suggest the necessity of navigational ability or even precise directional orientation on the part of migrating salmonid fishes. We await the firm foundation of diverse biological data to support or modify our hypothesis.

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