A Model for Predicting the Distribution of Albacore
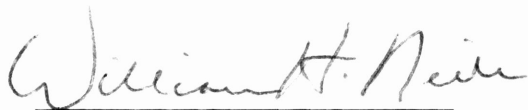Within Environmental Temperature Gradients

by

Kathryn Kulzer

Department of Wildlife and Fisheries Sciences

Submitted in Partial Fulfillment of the Requirements of the
University Undergraduate Fellows Program

1976 - 1977

Approved by:

William H. Neill

July 1977

ACKNOWLEDGEMENTS

ABSTRACT

The albacore, <u>Thunnus</u> <u>alalunga</u>, is a high seas pelagic tuna (Scombridae) whose distribution frequently seems governed by temperature. Tunas probably behaviorly thermoregulate using kineses. One method for explaining this process is a klinokinetic avoidance model. Actual telemetry data on albacore were analyzed and then used to construct such a model. Among the responses examined were instantaneous speed, angle of turn and temperature preference. A computer program was constructed to generate surface temperature isopleths using actual oceanographic data in the area of the tracked fish. Correlation analyses were performed on the data to determine the effect of the environment on fish movement. Two models were implemented: (1) a klinokinetic avoidance model and (2) a model using actual regression equations from the correlation analyses. The klinokinetic avoidance model proved to be the more successful of the two.

This paper follows the format and style of the Transactions of the American Fisheries Society.

INTRODUCTION

The idea of predicting the distribution of an animal by looking at the orientation mechanisms it employs, is a relatively new and untried area of research. It is an approach that could be vitally useful in understanding the ecology of organisms in both aquatic and terrestrial environments. The distribution of fishes is largely governed by their movements, which are affected by the structure of the environment, in the form of various stimuli. This paper looks at the factors affecting fish movement and orientation, with the goal of providing a model for predicting distribution. Tunas are logical subjects for such an effort, because the limits of their distributions frequently seem governed by a single environmental factor -- temperature (Blackburn, 1965).

The albacore, _Thunnus alalunga_, belongs to the teleost family Scombridae, which comprises the tunas and mackerals. Albacore occur circumglobally in temperate and subtropical waters. They are most intensively fished in the Pacific Ocean. Tagging studies indicate a single subpopulation in the North Pacific that migrates between the U.S. West coast commercial fishery and the Japanese longline and live-bait fisheries of the Western Pacific. The migratory routes encompass a broad region in the Pacific and vary among albacore age groups. In addition to supporting important commercial fisheries on both sides of the Pacific, the albacore is a highly prized game fish off the U.S. West coast.

Like the other tunas, the albacore is a schooling fish, although the schools are often somewhat loosely organized. Their diet consists of smaller fish (especially anchovies and sauries), cephalopods and crustaceans (Pinkas et al., 1971). For large predatory fish of the open seas, such as the tunas, the ability to swim fast is a distinct evolutionary

advantage. Many fast-moving prey species are available only to the swift-est of predators. Tunas are indeed physically well-adapted for fast swimming. They possess very streamlined, muscular bodies, with strong semilunate tails for efficient propulsion. Dorsal, anal and pectoral fins retract into grooves to further aid in the streamlining effect, and there are lateral keels present on the caudal peduncle which help produce a more laminar flow of water over the caudal fin. Tunas may maintain a speed of 10 body lengths per second and attain a burst speed of 20 body lengths per second (Stevens and Neill, in press). They are obligatory swimmers, in that they must swim continuously to maintain their position in the water column (many species don't have air-bladders at all, and that of the albacore and its congeners is only poorly developed) and to breathe. Tunas lack any mechanism to pump water over the gills. They practice ram-jet ventilation as means of aerating their gills (Brown and Muir, 1970). Their continuous forward motion keeps a flow of water rushing over the gills to oxygenate the blood via diffusion.

Tunas, being very active fishes, have exceptionally high metabolic rates -- 3 to 5 times those of typical fishes (Stevens and Neill, in press). The Scombrids and one family of sharks (Lamnidae) are unique among fishes in that they are warm-bodied. Most fishes have body temperatures that are within one degree of the water temperature. In contrast, tunas and lamnid sharks maintain an internal body temperature that is several degrees higher than the ambient water temperature (Carey et al., 1971). Elevated muscle temperature contributes to the greater power needed for fast swimming.

The elevated body temperatures of tunas and lamnid sharks are the result of both high metabolic rates and extraordinary modification of

their circulatory systems to form counter-current heat exchangers, which constitute effective barriers against rapid heat loss to the external environment. The essential component of the counter-current heat exchanger is a system of fine veins and arteries known as "retia mirable". The mass of venules and arterioles run parallel to each other, but with counter-current flow. While the blood is allowed to flow freely, heat diffuses from the metabolically warmed venous blood to the arterial blood, thus shunting heat back to the tissues instead of permitting it to be lost at the gills as in typical fishes (Carey et al., 1971).

Tunas' counter-current heat exchangers not only make them warm-bodied but also cause high thermal inertia; ie., core tissues of tunas have a high resistance to heat gain or loss. This creates a thermal lag in equilibration to changing ambient water temperatures. Neill, Chang and Dizon (1974) demonstrated that tunas' core tissues change temperature at only half the rate of other fishes in a similar gradient of environmental temperature. This inertia allows for a thermal buffer between the fish and the fluctuating environment.

Now, given a background on the thermal physiology of tunas, we can consider how they may respond to the thermal structure of their habitat so as to behaviorally regulate temperature. Tunas spend their lives in what is essentially an unbounded and unpredictable thermal environment. There are some notable exceptions to this generalization; eg., (1) the air-water and water-substrate interfaces are obvious boundaries and (2) the ocean's thermal structure is predictable to the extent that temperature tends to decrease from the surface downward and from the equator poleward. But, for tunas to efficiently regulate temperature in the horizontal plane, they must rely on other than predictive mechanisms, for the temperature-

latitude relation has high variance on scales of distance meaningful to tunas (meters to tens of kilometers).

The non-predictive mechanisms by which tunas orient in horizontal temperature gradients are probably kineses. These are "variations in generalized, undirected, random locomotory activity due to variations in intensity of stimulation" (Harden Jones, 1968). The basis for this assumption lies in the fact that temperature stimuli have no directional properties, but vary only in intensity. This precludes the use of most taxes (nonrandom, directed movements) as a means of orientation, the possible exception being situations in which the gradient is steep enough to allow simultaneous comparison of intensities along the length of the fish's body. Such steep gradients are unlikely in the horizontal plane of the open ocean except at the boundaries of ocean temperature fronts (Neill et al., 1974).

An orthokinesis refers to a change in the speed of locomotion, while a klinokinesis refers to a change in the frequency of turning or in the mean angle of turn. Temporal and/or spacial gradients of intensity, such as the temperature gradients of the open ocean, are very suitable fields for kinetic reactions (Harden Jones, 1968). Through simulation modeling of fish in unbounded one-dimensional temperature gradients, it has been demonstrated (Neill, 1976) that fish employing solely orthokinetic responses cannot achieve successful thermoregulation, and eventually (in most cases, quite rapidly) succumb to lethal temperature stress. In the same study, it was suggested that pure klinokinetic responses, although an improvement over orthokinesis, ultimately resulted in the same end. Neill, therefore, proposed a "klinokinetic avoidance" model to more accurately describe the behavior of fish in real-life temperature gradients.

This model suggests that for fishes to achieve efficient behavioral thermoregulation, it is sufficient that their rate of turning vary stochastically as a function of the interaction between two input variables, (1) kind and degree of current temperature stress and (2) recent experience with the rate of environmental temperature change (Figure 1). When either thermal stress or the rate of temperature change is minimal, fish orient randomly. But when the combination of the two input variables exceeds some threshold level (indicated by the inner set of curved lines in the large box, Figure 1), turning becomes biased. This bias leads to high probabilities of turning in worsening temperature conditions (TOO WARM, WARMING; TOO COOL, COOLING) and low probabilities of turning in improving conditions (TOO WARM, COOLING; TOO COOL, WARMING).

MATERIALS AND METHODS

In order to undertake successful simulation modeling, certain param-
eters of fish movement must be known. These parameters were estimated
from albacore telemetry data collected by the National Marine Fisheries
Service in waters off California (Laurs, Yuen, and Johnson, in press).
Individual fish were tracked by attaching an ultrasonic transmitter imme-
diately in front of the second dorsal fin. A hydrophone picked up the
signals, which were then fed into a receiver. The tracking vessel was
maintained on a heading of strongest signal attenuation and kept an esti-
mated 500 feet from the fish. Approximate hourly positions were taken on
each fish. The three fish used in this study, fish 4, 5 and 6, were
tracked for periods of 27.8, 41.4 and 50.0 hours respectively. In con-
junction with the actual tracking, extensive environmental data were col-
lected in the area of the telemetered fish. These included continuous
records of surface temperature, salinity and chlorophyll "a", and measure-
ments at selected stations of subsurface values for the above variables,
in addition to estimates of primary productivity (by ^{14}C methods) and
standing stocks of albacore food organisms.

The first step in the analysis was to determine the basic parameters
of movement of the tracked fish, utilizing the position data. For each
of the three fish, each successive position in the fish track was taken to
be the beginning of the next step; ie., the distance between each recorded
position was considered to be one step-length. It must be emphasized that
these are only apparent step-lengths, as dictated by the time interval be-
tween recorded positions, and do not indicate the precise turning of the
fish. This could only be accomplished by continuous monitoring. A com-
puter program was written to generate such information as distance between

fish positions (in meters), speed during each step, angle of turn at the beginning of each step, and time between recorded positions. A method for estimating the average instantaneous speed of the fish was then developed. The basic assumption was that apparent speed of the fish (straight-line distance / time between observations) was an exponential function of the time between paired observations on fish position, where each observation was paired with its 1st, 2nd, 3rd, 4th, 5th, and 6th successors. When apparent speed was regressed against time-interval, the speed value at the y-intercept (where time is theoretically equal to zero) estimated average instantaneous speed of the fish. Next, frequency histograms were constructed to survey the distribution of the angles of turn in each track. The angles were divided into ten-degree class intervals.

Attention was then turned to the supporting environmental data in the area of each tracked fish. These data were interpolated to estimate environmental parameters at each 1-km square center over the entire area from which oceanographic data were collected. This was done for four environmental variables -- surface temperature, chlorophyll "a", mixed layer depth, and depth of the 15°C isotherm. Contour maps for each of the four variables were produced for each of the three fish. The actual fish tracks could then be superimposed on these grids. Now, from each fish position, the available sampling environment could be reconstructed to arrive at an indication of environmental preference. This was done by comparing the value of the environmental variable chosen by the fish at the end of each step, as a function of what was available to the fish to choose from at the beginning of the step. At each fish position a circle was drawn, with radius equal to the next step-length. The available environmental values around the circle were then recorded, along with the

value in the direction the fish chose as the next step. From these data, the relationship used to give an indication of preference was (using temperature for example)

$$\frac{\% \text{ occurrence of fish in a temperature range}}{\% \text{ occurrence of the temperature range}}$$

In final preparation for implementation of the simulation model, the various parameters of movement (speed, angle of turn, etc.) were regressed against the environmental parameters to determine the effects of the environment on fish movement.

RESULTS AND DISCUSSION

Scatter plots designed to estimate instantaneous speed differed markedly among the three fish. Fish 4 fitted the exponential model relatively well (Figure 2). The fish 5 plot (Figure 3), however, included a cluster of points away from the general pattern of the data. These points resulted from the influence of a single, abnormally long step (540 minutes between consecutive observations). The plot for fish 6 (Figure 4) indicated high variance in the rate of turning and/or instantaneous speed. Looking at the plot for each fish, and mentally fitting regression lines to maximum values, I arrived at an **overall** estimate of 1.5 body lengths per second for instantaneous speed of all three fish. This figure is about 3 times the hydrodynamically dictated minimum swimming speed for 80-cm long albacore (Dotson, in press).

The distribution of the angles of turn during the track of fish 5 (Figure 6) indicates a relatively even spread from small to large angles, which could indicate random turning behavior. On the other hand, fish 4 (Figure 5) and fish 6 (Figure 7) show a predominance of smaller angles, which tends to indicate straighter paths. Figures 8, 9 and 10 show the 0.5-°C contours of surface temperature generated by the computerized interpolation procedure. The actual fish tracks are superimposed in each case. Fish 4 (Figure 8) made large turns, for the most part, and stayed in the same general area. Fish 5 and 6 (Figures 9 & 10) followed a less circuitous path and covered much greater distances, trending 161° and 224° (from east $= 0^\circ$), respectively. Note that none of the fish seemed to spend time in 15°C and colder water.

Using data from the complete 1-km square grids, temperature preference histograms were constructed. When a comparison of figures 11, 12 and

13 is made, it becomes apparent that the three fish were exposed to different temperature regimes. The environment through which fish 4 moved was relatively "flat", in a temperature-sense, with a maximum range of $<1\,^{\circ}$C. Fish 5 and 6 experienced a greater range of temperature and seemingly steeper gradients.

A stepwise regression procedure was implemented, using 4 dependent variables regressed against linear and logarithmic transformations of temperature variables, sine and cosine functions of time, and absolute deviation of the angle of the previous step from the trend line. The following 8 models were posed:

(1) $ADTHET = B_0 + B_1 TXL1 + B_2 TR + B_3 TXTR + B_4 ATHET + B_5 CTIME + B_6 STIME,$

(2) $LADTHET = B_0 + B_1 TXL1 + B_2 TR + B_3 TXTR + B_4 ATHET + B_5 CTIME + B_6 STIME,$

(3) $E = B_0 + B_1 TXL1 + B_2 TR + B_3 TXTR + B_4 ATHET + B_5 CTIME + B_6 STIME,$

(4) $LE = B_0 + B_1 TXL1 + B_2 TR + B_3 TXTR + B_4 ATHET + B_5 CTIME + B_6 STIME,$

(5) $ADTHET = B_0 + B_1 LATXL1 + B_2 LTR + B_3 LTXLTR + B_4 SLTXLTR + B_5 ATHET + B_6 CTIME + B_7 STIME,$

(6) $LADTHET = B_0 + B_1 LATXL1 + B_2 LTR + B_3 LTXLTR + B_4\ SLTXLTR + B_5 ATHET + B_6 CTIME + B_7 STIME,$

(7) $E = B_0 + B_1 LATXL1 + B_2 LTR + B_3 LTXLTR + B_4 SLTXLTR + B_5 ATHET + B_6 CTIME + B_7 STIME,$

(8) $LE = B_0 + B_1 LATXL1 + B_2 LTR + B_3 LTXLTR + B_4 SLTXLTR + B_5 ATHET + B_6 CTIME + B_7 STIME,$

where   ADTHET = absolute value of the angle of change at each step

LADTHET = ln (ADTHET)

E = eccentricity, which is apparent speed / instantaneous speed

LE = ln (E)

TXL1 = TB - TAL1, where TB is body core temperature and TAL1 is ambient temperature at the end of the previous step

LATXL1 = ln (|TXL1|)

$TR = TP - TAL1$, where TP is preferred temperature and TAL1 is as
defined above

$LTR = \ln(|TR|)$

$TXTR = (TXL1) \cdot (TR)$

$LTXLTR = LATXL1 \ (LTR)$

$SLTXLTR = (LTXLTR) \cdot (TX \cdot TR \ / \ |TX \cdot TR|)$

$ATHET$ = absolute deviation of angle of the previous step from the
trend angle (fish 4 trend angle is $30°$, fish 5 is $161°$ and
fish 6 is $224°$)

$CTIME = \cos((360/1440)(\text{time in minutes after midnight}))$

$STIME = \sin((360/1440)(\text{time in minutes after midnight}))$

The trend angle for each fish was calculated by finding the angle of the
line connecting the mean positions of the fish during the first and last
thirds of the track. The time variables were included in the regression
models to test for diel changes in behavior. Laurs et al. (in press) have
suggested that albacore tend to swim slightly slower at night. Larger
multiple correlation coefficients (R) were obtained with models involving
LADTHET than with models involving ADTHET, while those with E gave larger
R's than those with LE. For both LADTHET and E, the percent variance ex-
plained by regression was generally higher with models involving logarith-
mically transformed temperature variables. Therefore, models 6 and 7 were
judged best. For these models, Table 1 gives all variables significant
at probability less than 0.05.

When various values of preferred temperature were tried ($15°C$ - $20°C$
at $0.5°C$ intervals, $22°C$, $24°C$), $16.5°C$ emerged as the best estimate for
fish 5 and 6. The small range of temperature experienced by fish 4 pre-
cluded estimation of preferred temperature. The value of $16.5°C$ is fairly
consistent with the temperature preference histograms previously construc-
ted. It also lies within the temperature range that is judged optimum for
albacore fishing (Clemens and Craig, 1965). Next, chlorophyll information

was added to the best temperature models in an attempt to improve them.
The preferred chlorophyll level was taken to be 1.0 milligrams per cubic
meter. With LADTHET, temperature alone explained as much variance as
temperature and chlorophyll together. With E, the model was the same with
fish 4 and 6, and slightly better with fish 5. It was decided, on the
basis of the above analyses, that chlorophyll, at least in these instances
did not play an important role in determining fish movement.

The actual regression equations for ADTHET and E were then inserted
into the simulation model for fish 5 and 6 (the fish 4 regression analy-
sis of E was not significant for any temperature term, only time). The
resulting model was thus parameterized to the actual fish's movements as
closely as possible. More will be said about this after a general intro-
duction to the workings of the model.

The model itself simulates enviroregulatory movements of any number
of fish in a two-dimensional space as a biased random walk. It is based
on the theory that the probability distribution of the new direction taken
by the fish at the beginning of each step is in the form of an ellipse
directed along the fish's most probable path. The probability distribu-
tion depends on the eccentricity of the ellipse and stochastically dic-
tates the angle of turn of the fish. The eccentricity of the ellipse is
computed as the ratio of apparent speed to instantaneous speed, and ranges
from 0 (circle) to 1 (straight line). The actual angle is that angle, to
the nearest 1°, at which the cumulative probability density just exceeds
the value of a number between 0 and 1 randomly drawn from a rectangular
distribution. Figure 14 shows the relationship between E and the expected
absolute angle of deviation from the most probable path. An eccentricity
of 1 results in no deviation from the most probable path. At the other

end of the scale, eccentricity of 0 gives equal probability of absolute
deviations between $0°$ and $180°$, with an expected (average) deviation of
$90°$; at this limit, the path is therefore purely random.

One of the models tested (that which gave the best results) was the
klinokinetic avoidance model which is graphically represented in Fig-
ure 15. When the previous step of the fish resulted in an improvement of
thermal condition (TOO COOL, WARMING; TOO WARM, COOLING), eccentricity is
high and the probability of a turn is very low. As the fish nears its
preferendum, the probability of a turn increases somewhat, but eccentric-
ity still does not fall below .7. In the event of worsening conditions
(TOO COOL, COOLING; TOO WARM, WARMING), eccentricity goes to zero at some
threshold level, at which point the most probable path and thus the orien-
tation of the ellipse shifts $180°$ along the axis of the fish's previous
step; ie., the fish has essentially reversed direction, now with in-
creasing eccentricity. In worsening conditions past the threshold level,
eccentricity again increases. Figures 16 through 18 show the behavior of
the simulated fish in the three temperature gradients. The simulation
using the fish 4 track (Figure 16) resulted in much the same behavior as
the real fish; ie., essentially random behavior due to lack of strong
temperature input. The fish 5 simulation (Figure 17) did exeptionally
well, following a similar trend path to the real fish. The temperature
regime was such, that in the fish 6 simulation (Figure 18), the fish was
unable to break out of $15°C$ water, but was headed in the right direction.

Another model tested, with less successful results, involved the use
of the empirical equations for ADTHET and E, constructed for each fish
from the regression analysis. These were incorporated into the model to
parameterize it as close to the real fish as possible. This model was

implemented with fish 5 and 6 only, because no temperature term was significant for E with fish 4. A value for ADTHET was generated from the regression equation. If the resulting angle was less than $90°$, the next step was directed along the same path of the previous step. If the angle was greater than $90°$, the most probable direction of the step was made $180°$ from that of the previous step (the fish was made to reverse directions). Then an eccentricity value was calculated using the regression equation for E. Figures 19 and 20 show the results of this model. It is apparent that the fish did not perform as well as with the previous model.

The somewhat inconclusive results obtained from this study could be the result of several factors. First, it must be considered that the raw data used in the analyses had certain limitations and could only be manipulated up to a point. Of the three fish on which the study is based, each had distinctive characteristics and it was virtually impossible to determine "average" values for any of the parameters that would hold true for all three fish. In particular, the best regression model for each fish was different from that of the other fish. Also, the environmental temperature gradients that the actual fish were exposed to had a maximum range of $2.2°C$ (fish 6 track). It is very possible that the temperatures were not so extreme nor the gradients so steep as to elicit a strong thermoregulatory response from the fish. This is certainly the case with fish 4. Another factor that must always be taken into consideration with any experiment using live animals, is the possibility that the experiment is disrupting normal behavior and therefore, the results are suspect. For obvious reasons, tunas are particularly difficult subjects to observe in their natural surroundings. The data utilized in this study represent a major step in the methodology dealing with observation of tuna behavior.

Another far-reaching conclusion, but one that certainly deserves mention, is the possibility that the fish were regulating so successfully that they left no traces. A perfectly regulating fish will leave no evidence as to how he accomplishes the thermoregulatory process. The main limitation of the two-dimensional model designed to simulate the actual fish tracks was the lack of adequate input into the model of actual parameterized values from the real fish. It is hoped that future data, collected along similar lines, can be used to refine and better parameterize the model to provide for more accurate predictive capabilities.

LITERATURE CITED

Blackburn, M. 1965. Oceanography and the ecology of tunas. Oceanogr. Mar. Biol. Ann. Rev., 3: 299-322.

Brown, C. E., and B. S. Muir. 1970. Analysis of ram ventilation of fish gills with application to skipjack tuna (<u>Katsuwonus pelamis</u>). J. Fish. Res. Bd. Can., 27: 1637-1652.

Carey, F. G., J. M. Teal, J. W. Kanwisher, and K. D. Lawson. 1971. Warm-bodied fish. Am. Zool., 11: 135-143.

Clemens, H. B., and W. L. Craig. 1965. An analysis of California's albacore fishery. Calif. Dept. Fish Game, Fish Bull. 128: 125.

Dotson, R. C. In press. Minimum swimming speed of albacore, <u>Thunnus alalunga</u>. U. S. Fish. Bull.

Harden Jones, F. R. 1968. Fish migration. Edward Arnold (Publishers) Ltd. London. 325 p.

Laurs, R. M., H. S. H. Yuen, and J. H. Johnson. In press. Small-scale movements of albacore, <u>Thunnus alalunga</u>, in relation to ocean features as indicated by ultrasonic tracking and oceanographic sampling. U. S. Fish. Bull.

Neill, W. H. 1976. Mechanisms of behavioral thermoregulation in fishes, p. 156-169 <u>In</u> Report of a Workshop on the Impact of Thermal Power Plant Cooling Systems on Aquatic Environments, Vol. 2: Technical and Topical Papers. Electric Power Research Institute, Palo Alto, Calif. 94304.

Neill, W. H., R. K. C. Chang, and A. E. Dizon. 1976. Magnitude and ecological implications of thermal inertia in skipjack tuna, <u>Katsuwonus pelamis</u> (Linnaeus). Env. Biol. Fish., Vol. 1, pp. 61-80.

Pinkas, L., M. S. Oliphant, and I. L. K. Iverson. 1971. Food habits of albacore, bluefin tuna, and bonito in California waters. Calif. Dept. Fish Game, Fish Bull. 152: 11-46.

Stevens, E. D., and W. H. Neill. In press. Body-temperature relations of tunas, <u>In</u> Fish Physiology (W. S. Hoar and D. J. Randall, eds.), Vol. 7. Acad. Press, N. Y.

Figure 2. Plot of apparent swimming speed against the interval over which apparent speed was measured -- fish 4. See text for further information.
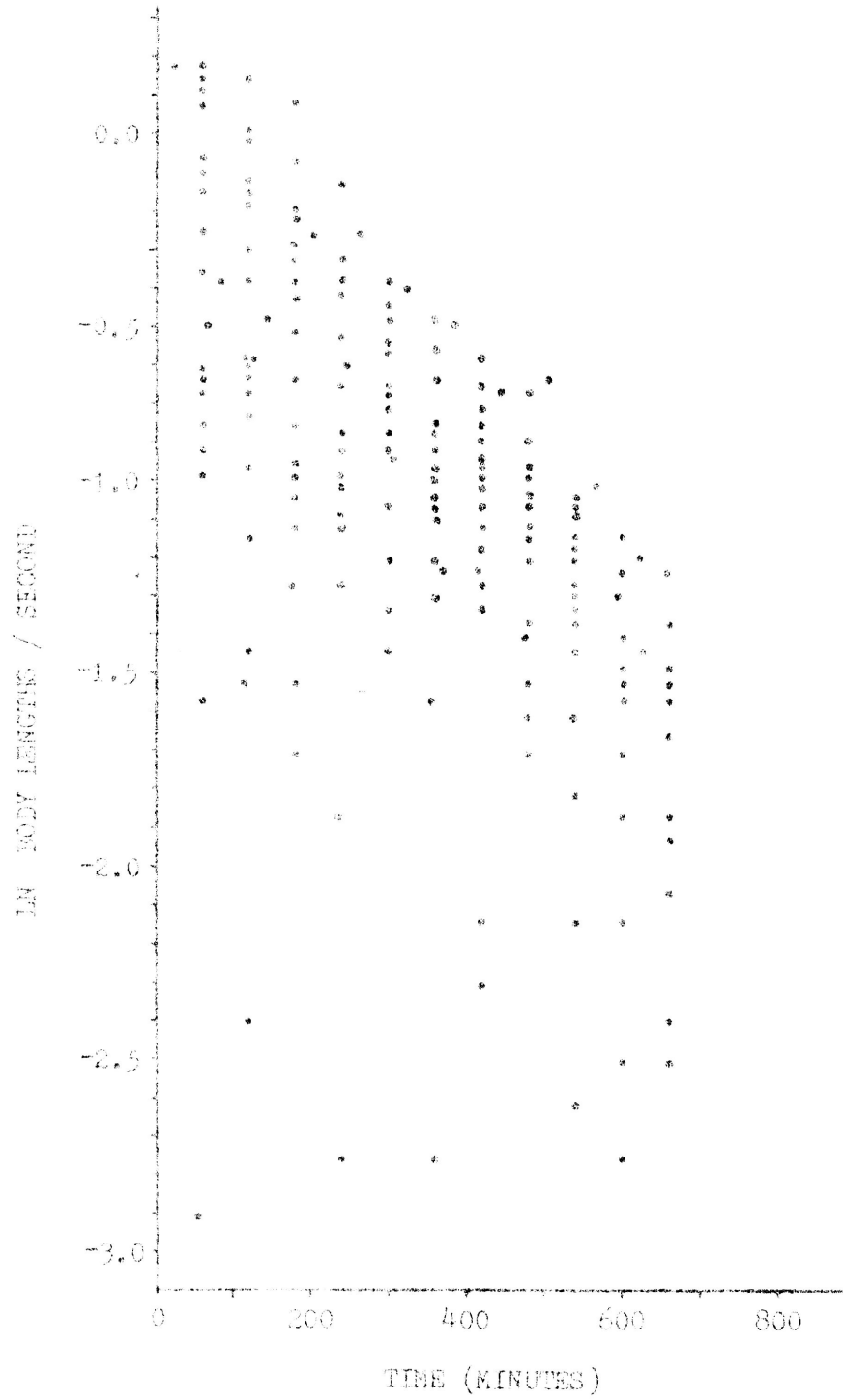
Figure 3. Plot of apparent swimming speed against the interval over which apparent speed was measured -- fish 5. See text for further information.
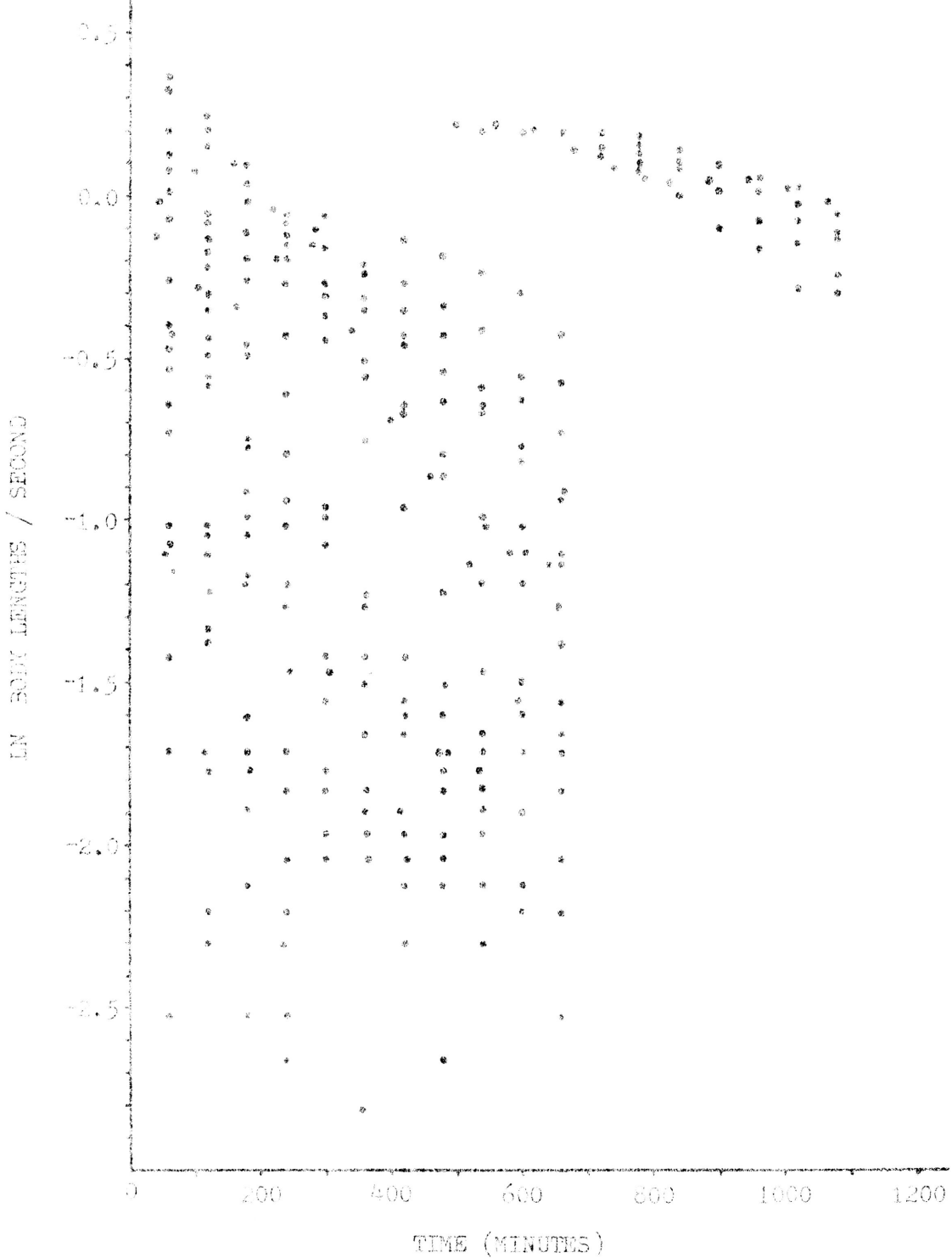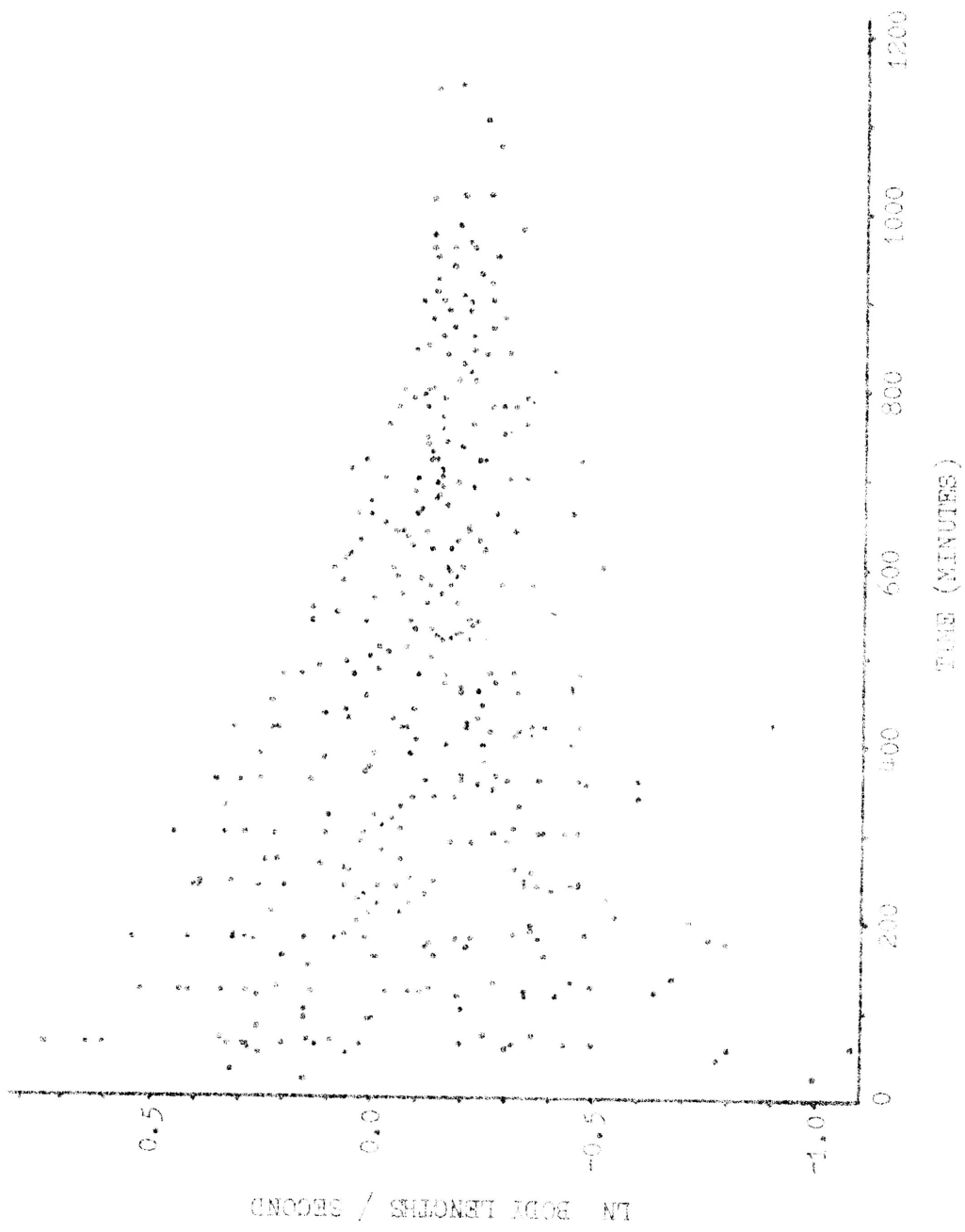
TIME (MINUTES)

Figure 4. Plot of apparent swimming speed against the interval over which apparent speed was measured -- fish 6. See text for further information.

Figure 5. Frequency distribution of changes in direction of apparent
steps -- fish 4. Angles during step-lengths between 55-65 min.
are indicated by —— , all others indicated by --- .

CHANGE IN DIRECTION (DEGREES)

NUMBER OF TURNS
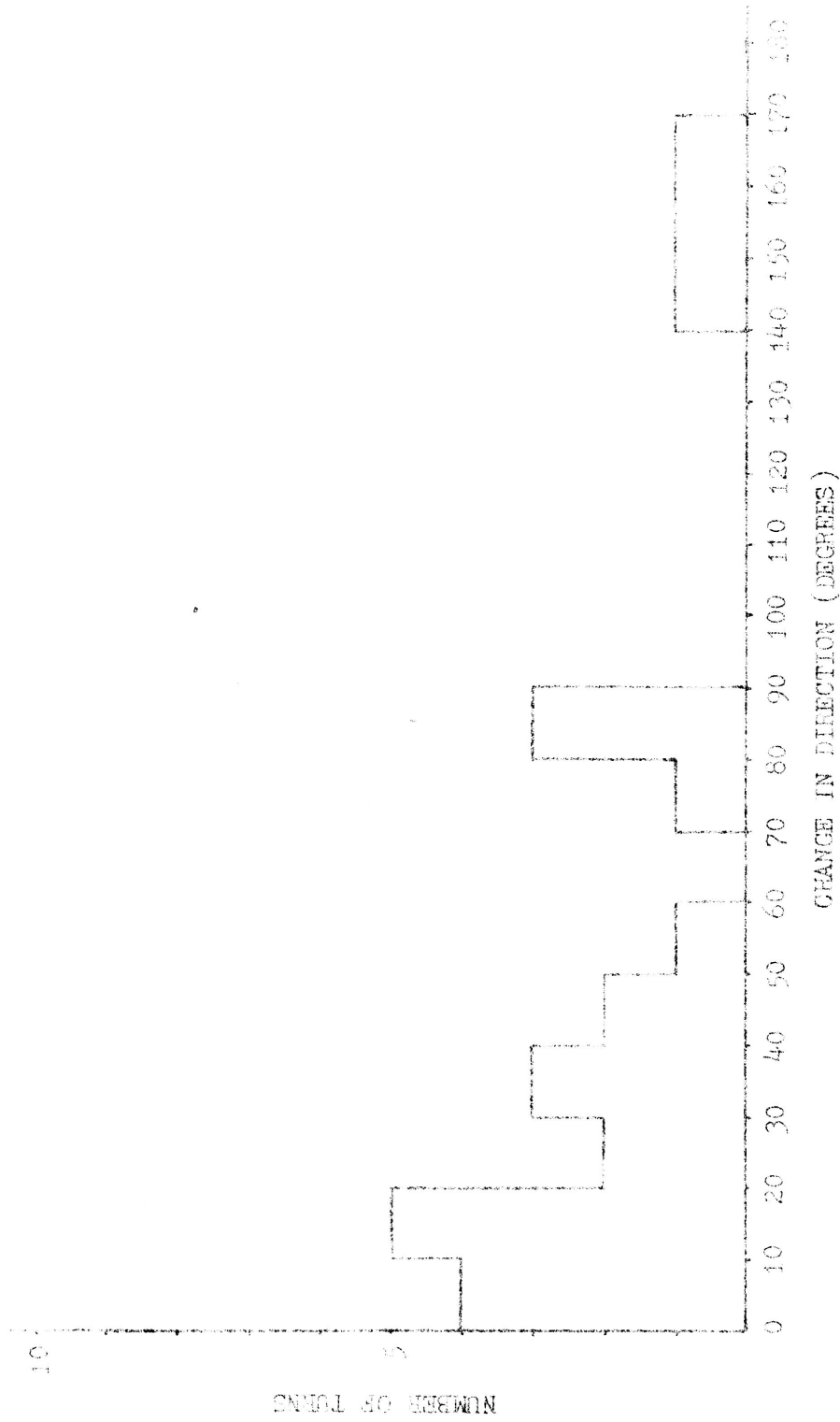
Figure 6. Frequency distribution of changes in direction of apparent
           steps -- fish 5. Angles during step-lengths between 55-65 min.
           are indicated by ── , all others indicated by --- .

CHANGE IN DIRECTION (DEGREES)

NUMBER OF TURNS
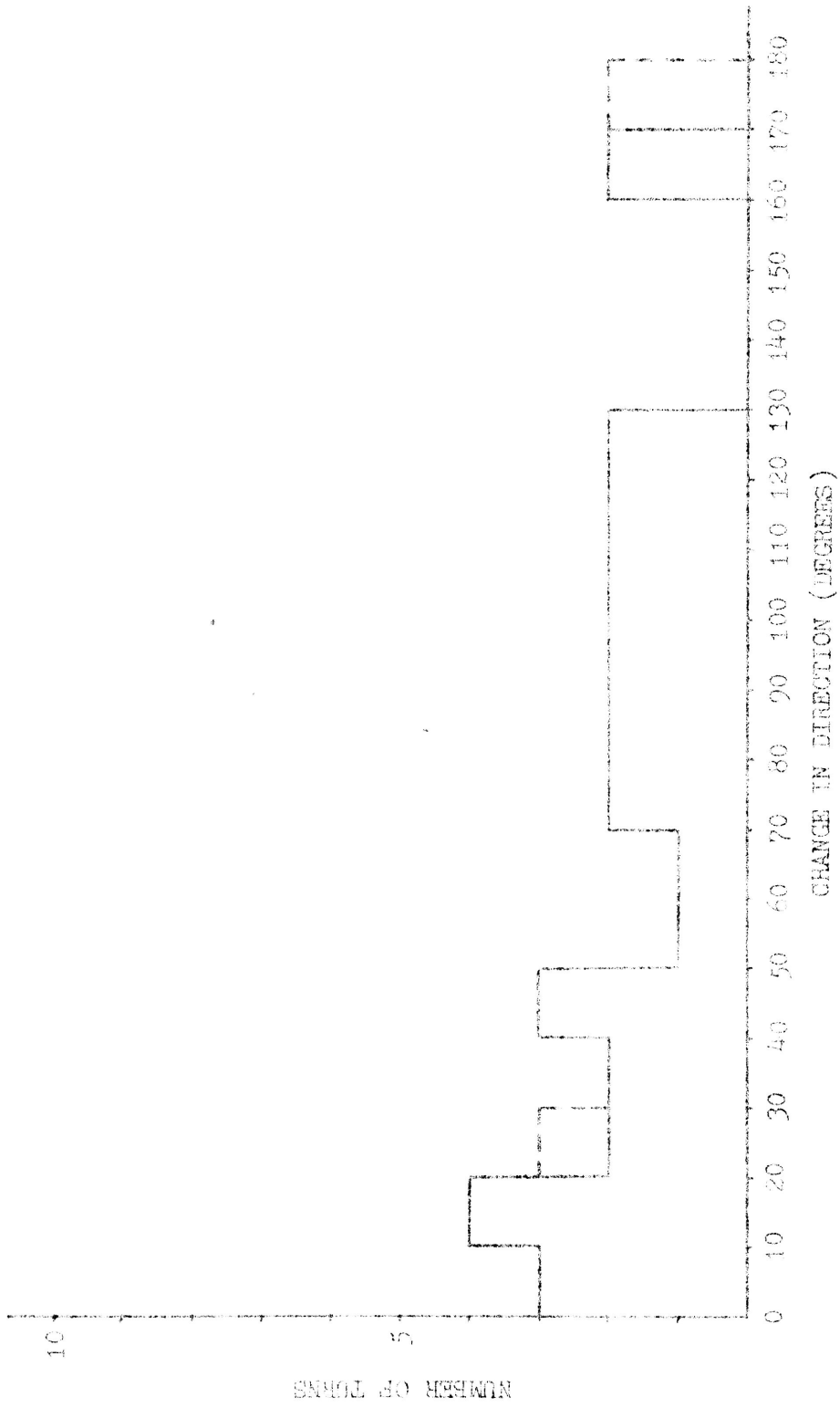
Figure 7. Frequency distribution of changes in direction of apparent
steps -- fish 6. Angles during step-lengths between 55-65 min.
are indicated by —— , all others indicated by --- .

CHANGE IN DIRECTION (DEGREES)

NUMBER OF TURNS
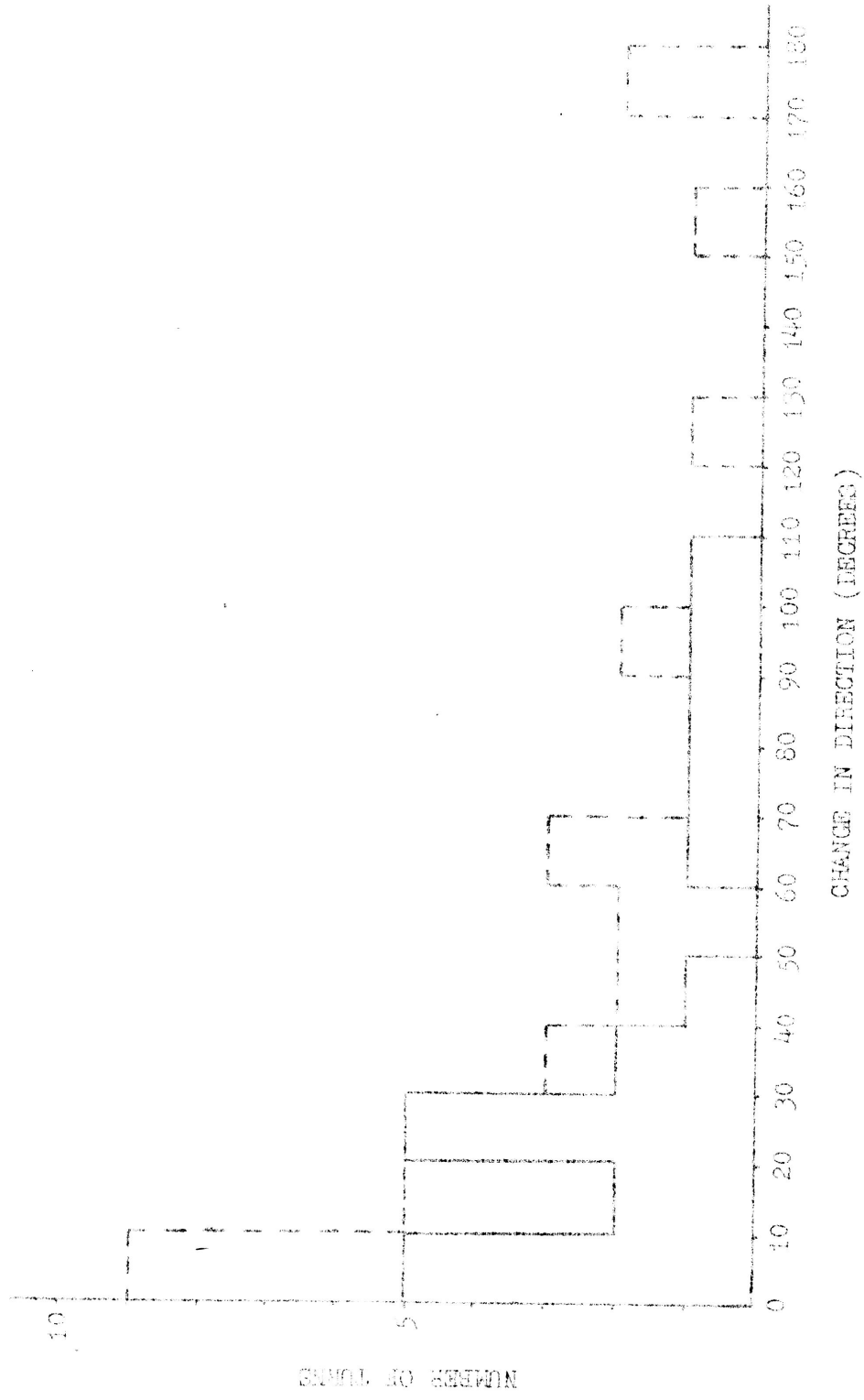
Figure 8. Surface-temperature isopleths with actual fish track superimposed -- fish 4. The kilometer values along the axes are distances from an arbitrary origin at 34°N.Lat. and 120°W.Long.
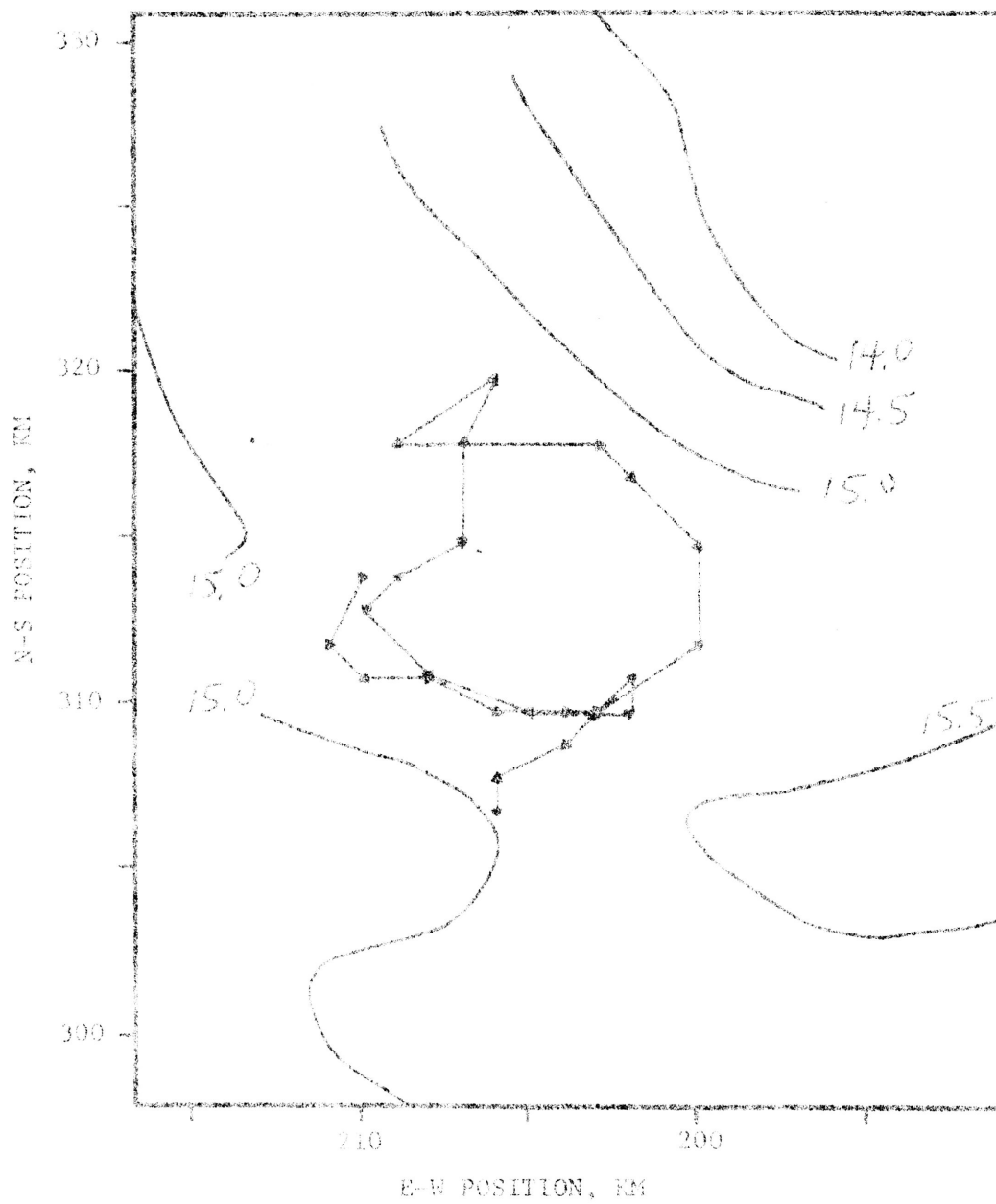
Figure 9. Surface-temperature isopleths with actual fish track superimposed -- fish 5. The kilometer values along the axes are distances from an arbitrary origin at $34°$N.Lat. and $120°$W.Long.
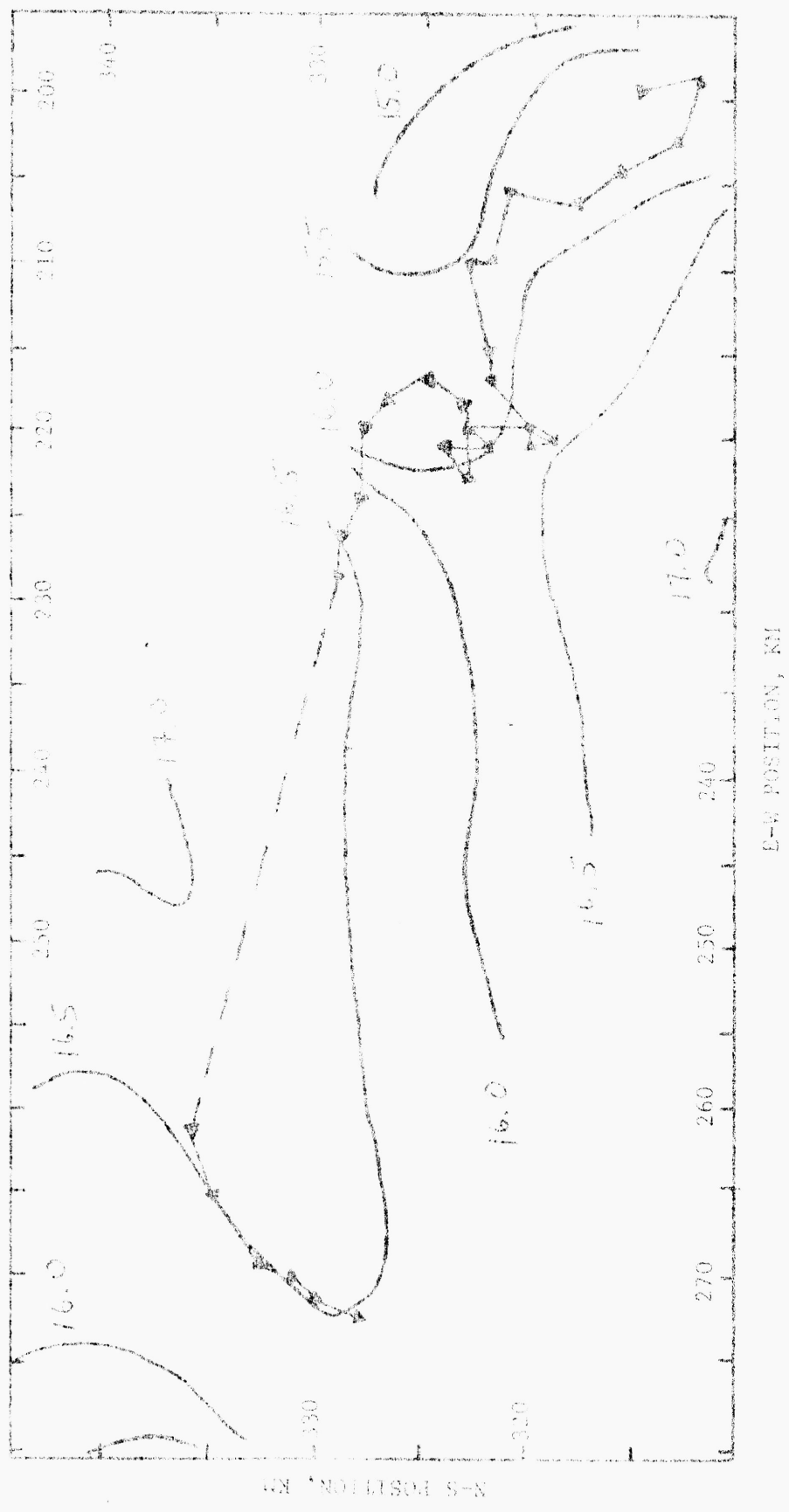
E-W POSITION, KM

N-S POSITION, KM

Figure 10. Surface-temperature isopleths with actual fish track superimposed -- fish 6. The kilometer values along the axes are distances from an arbitrary origin at $34°$N.Lat. and $120°$W.Long.
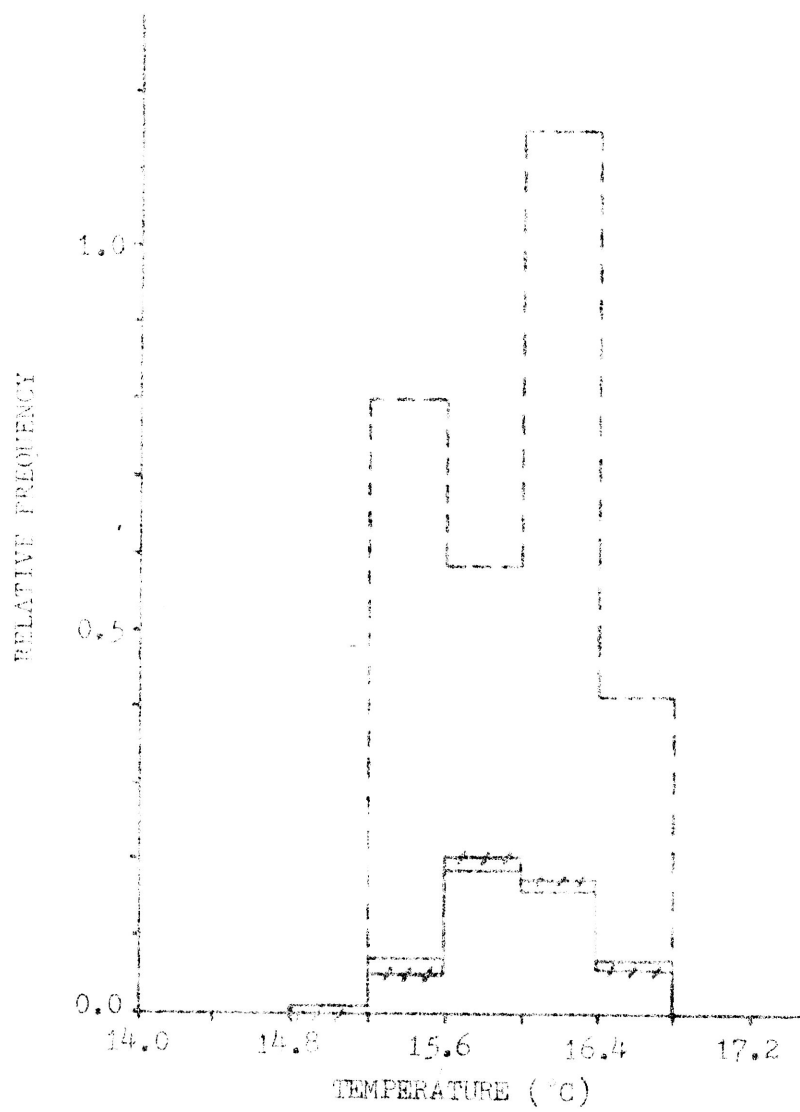
N-S POSITION, KM

E-W POSITION, KM
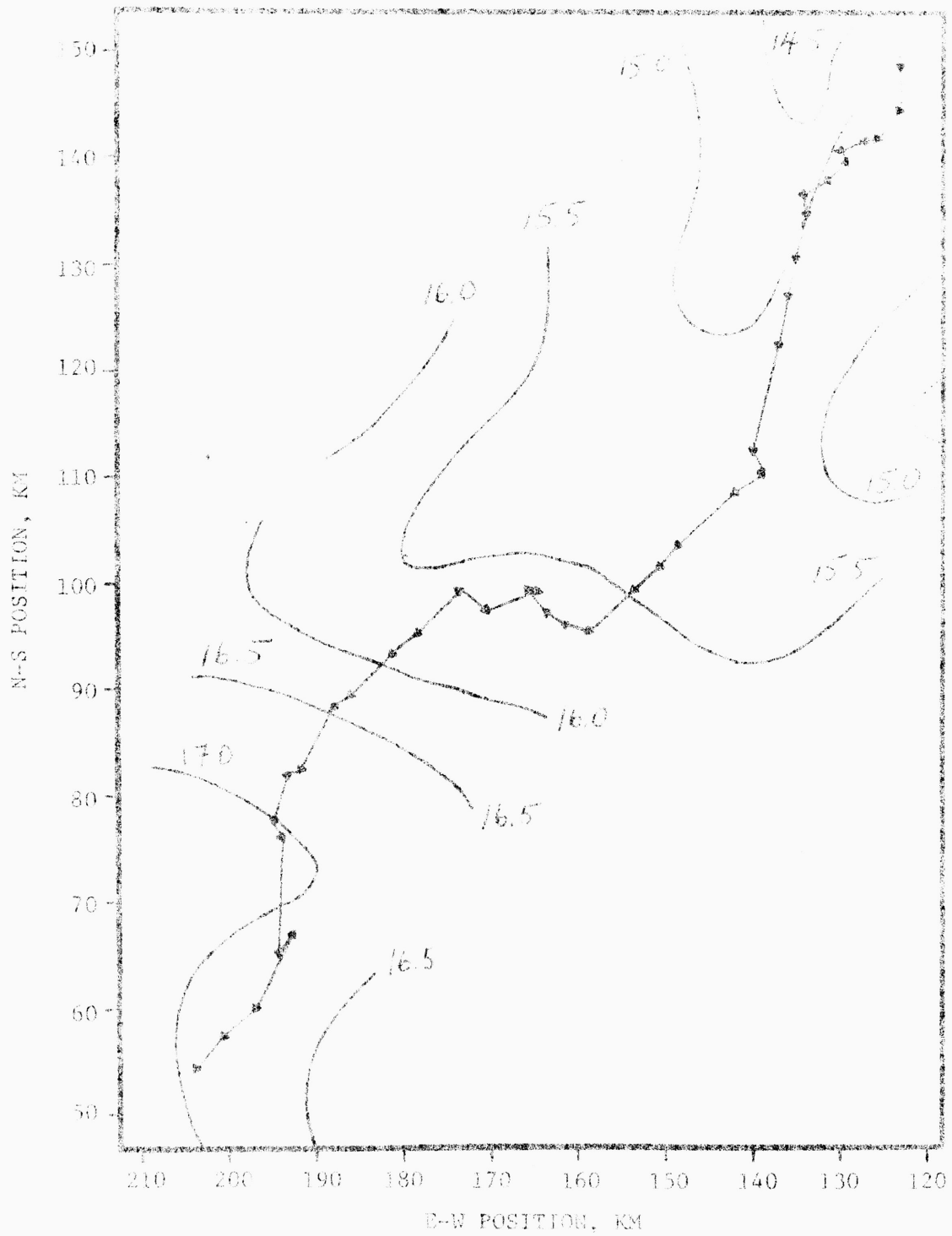
Figure 11. Frequency distributions of sea surface temperature in the neighborhood (see text) of the tracked fish (E, ——), sea surface temperatures at the observed fish positions (F, ✚✚), and the ratios of the occurrence of the tracked fish at a particular temperature to the availability of that temperature (F/E, ---) -- fish 4.
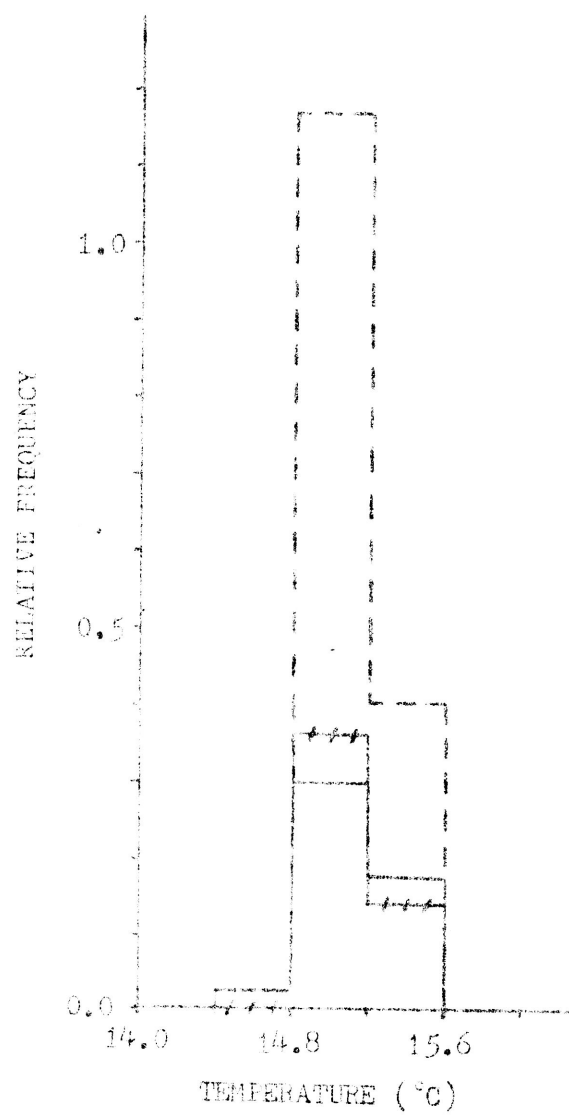
TEMPERATURE (°C)

Figure 12. Frequency distributions of sea surface temperature in the
neighborhood (see text) of the tracked fish (E, ——), sea sur-
face temperatures at the observed fish positions (F, ✚✚), and
the ratios of the occurrence of the tracked fish at a partic-
ular temperature to the availability of that temperature (F/E,
---) -- fish 5.

Figure 13. Frequency distributions of sea surface temperature in the
neighborhood (see text) of the tracked fish (E, ——), sea sur-
face temperatures at the observed fish positions (F, ┼┼), and
the ratios of the occurrence of the tracked fish at a partic-
ular temperature to the availability of that temperature (F/E,
---) -- fish 6.
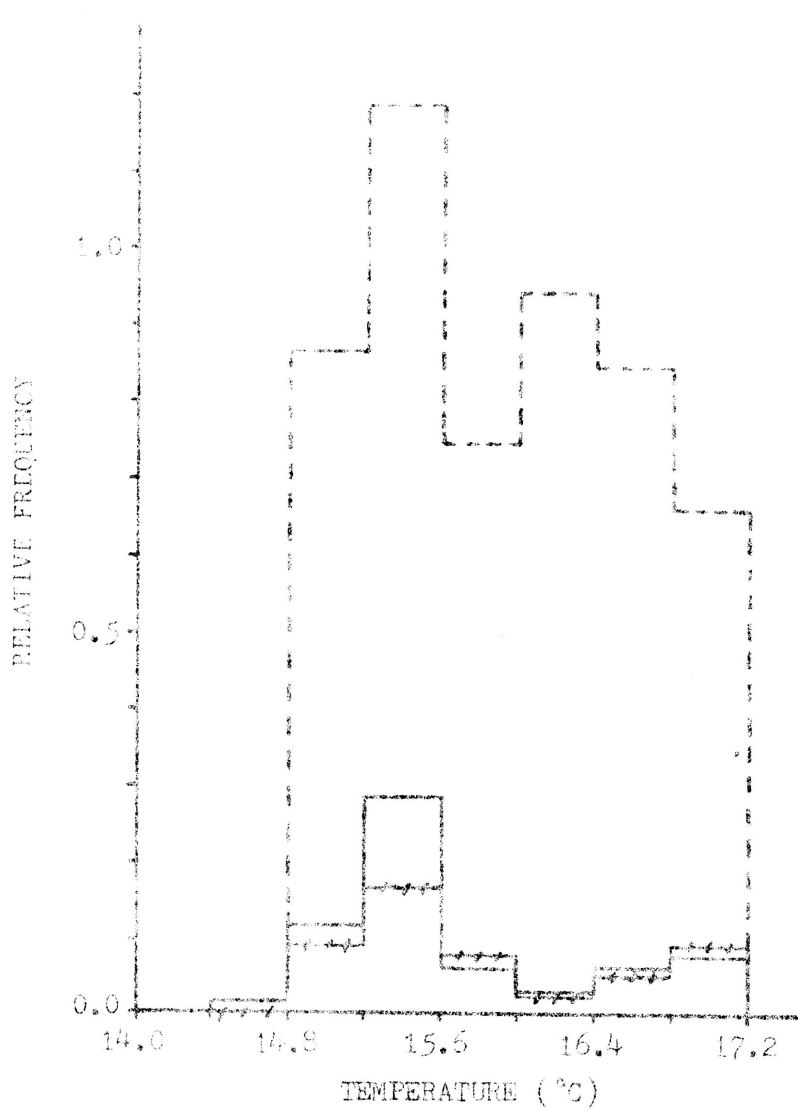
Figure 14.   Expected value of the absolute deviation, in degrees, from
             the most probable swimming direction as a function of path
             eccentricity (= apparent speed/instantaneous speed), under
             the assumption of an elliptical probability distribution of
             turning.
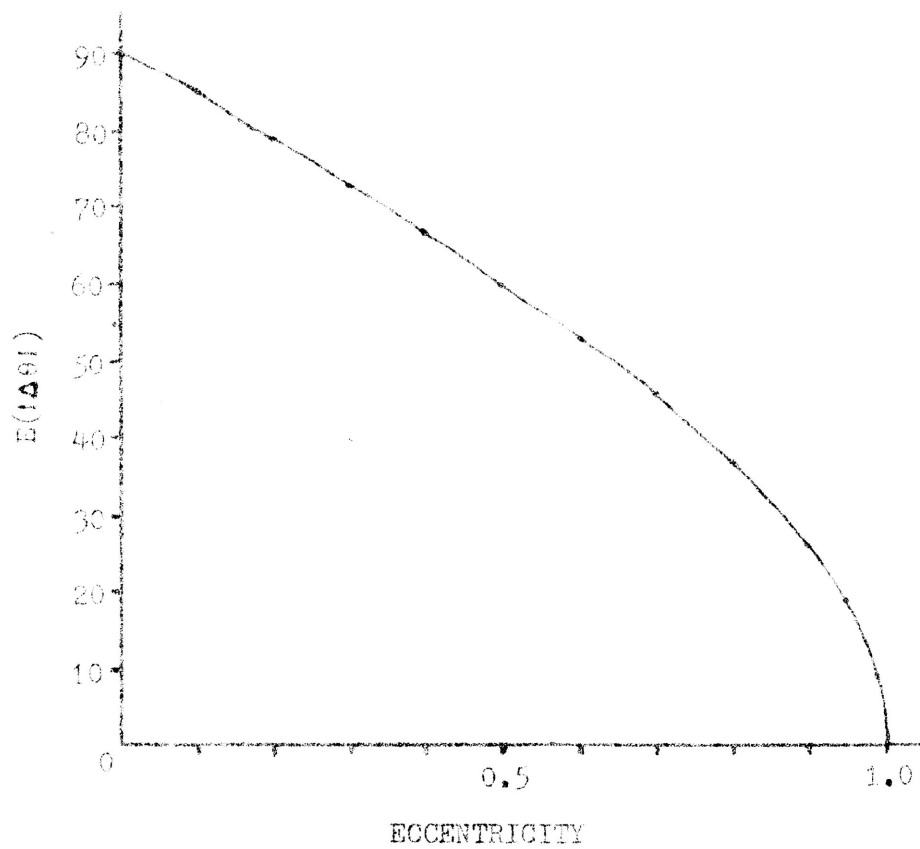
Figure 15. A klinokinetic avoidance model for two-dimensional movements
of thermoregulating albacore. TR = (ambient temperature) –
(preferred temperature), where preferred temperature is
assumed to be 16.5°C. TX = (fish core temperature) – (ambient
temperature), where fish core temperature is calculated by
exponentially lagging ambient temperature (see Neill et al.,
1976). The curves are isopleths of eccentricity. Eccentricity
is 0.7 for TR = 0 or TX = 0; eccentricity is not permitted to
exceed 0.95. Under conditions of substantially worsening
thermal conditions (hatched areas), the most probable direction
of travel is 180° from that during the previous step; other-
wise, the most probable direction of travel is the same as
that during the previous step.

TN

TOO COOL,
WARMING

TOO COOL,
COOLING

.95

2

1

.7

.95

0

-.2   -.1   .7   .7   .1   .2   TX

0

.7

.95

-1

TOO WARM,
WARMING

-2
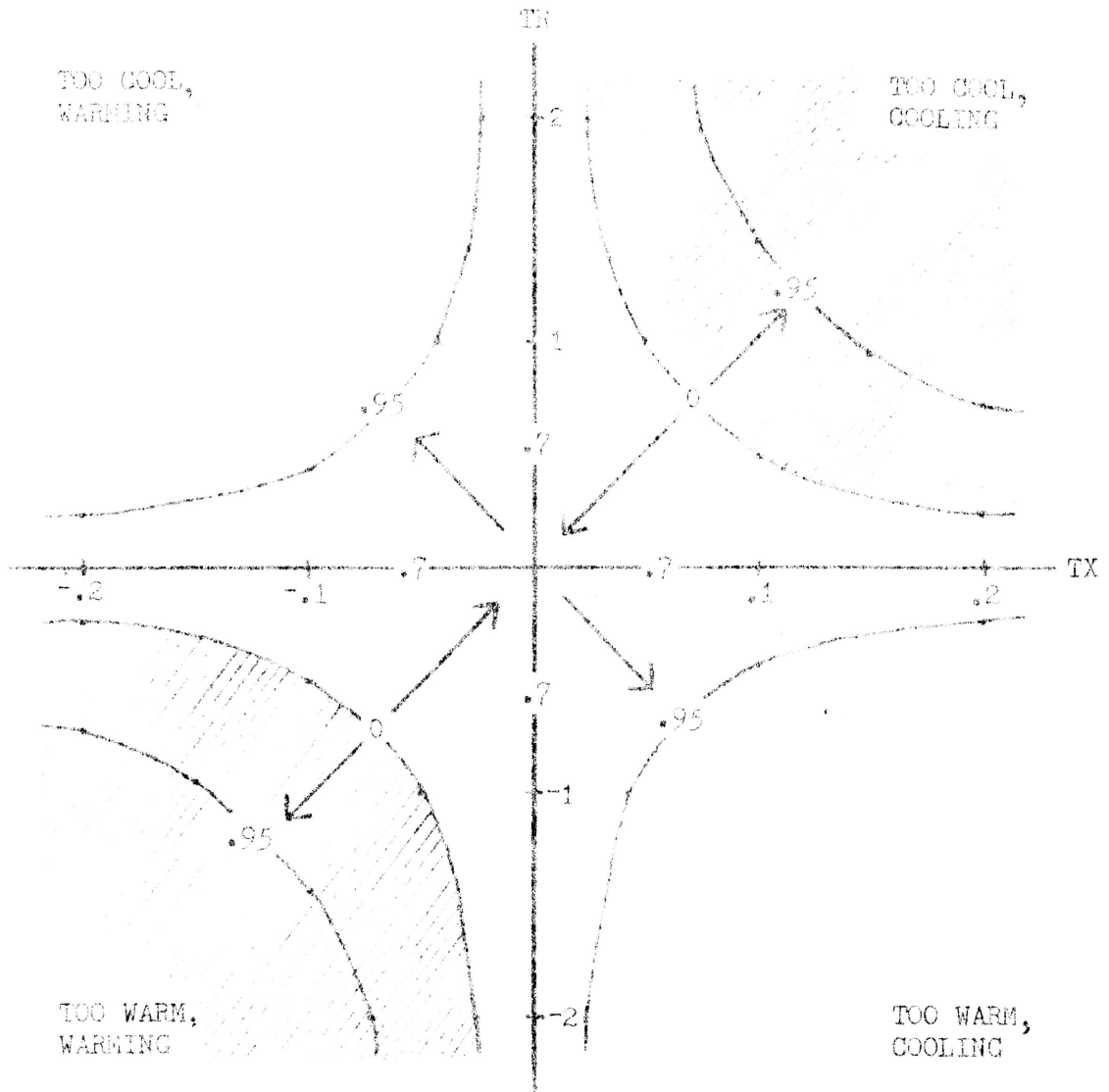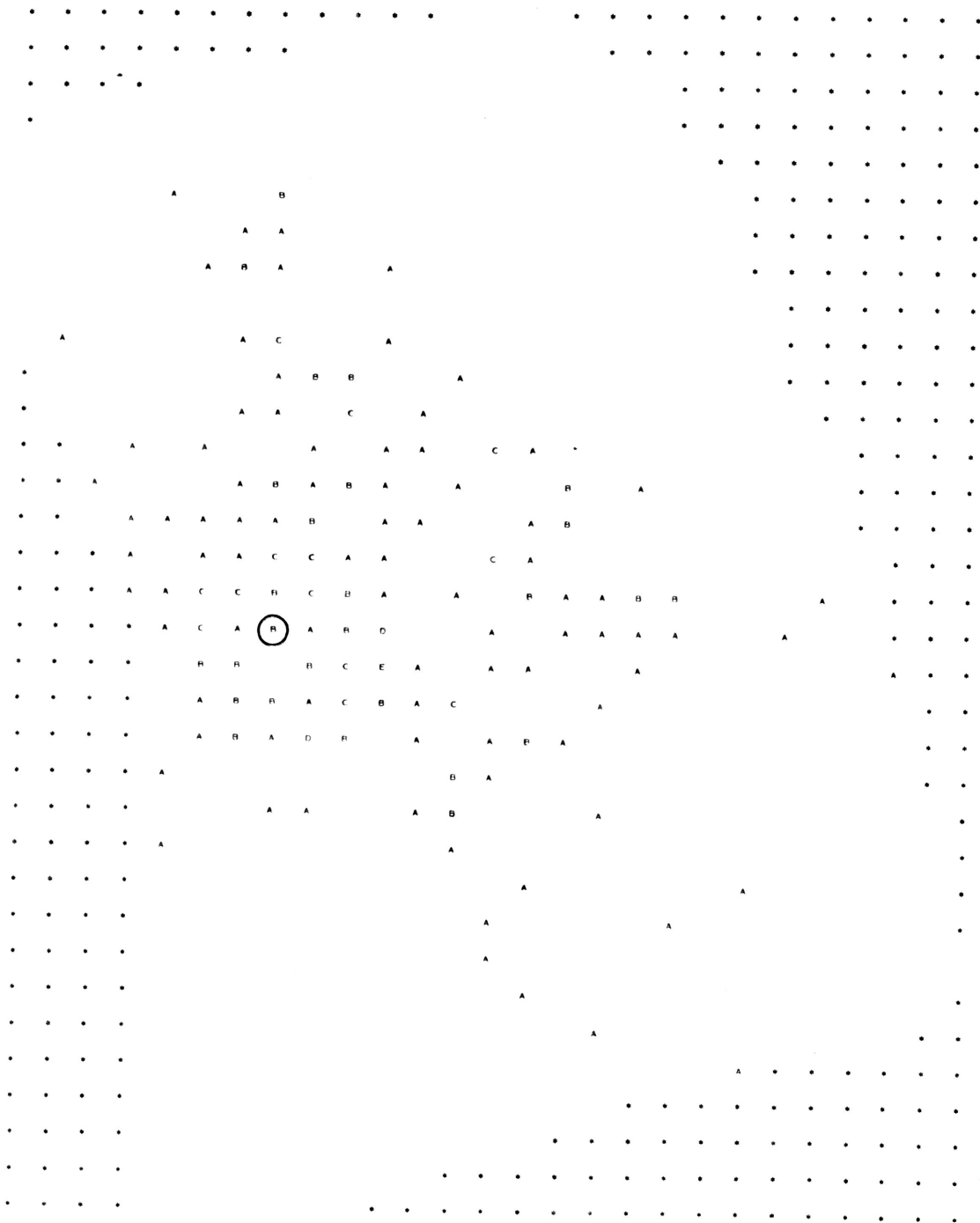
TOO WARM,
COOLING

Figure 16.   Simulated distribution of 20 hypothetical fish using a
             klinokinetic avoidance model -- fish 4. Each letter corre-
             sponds to the number of times a fish occupied a particular
             1-km square (A=1, B=2, etc.). The point of fish "release"
             is circled. Each fish made 60-min steps until it either left
             the tracking area (bounded by asterisks) or exceeded the time
             limit set by the real fish track.

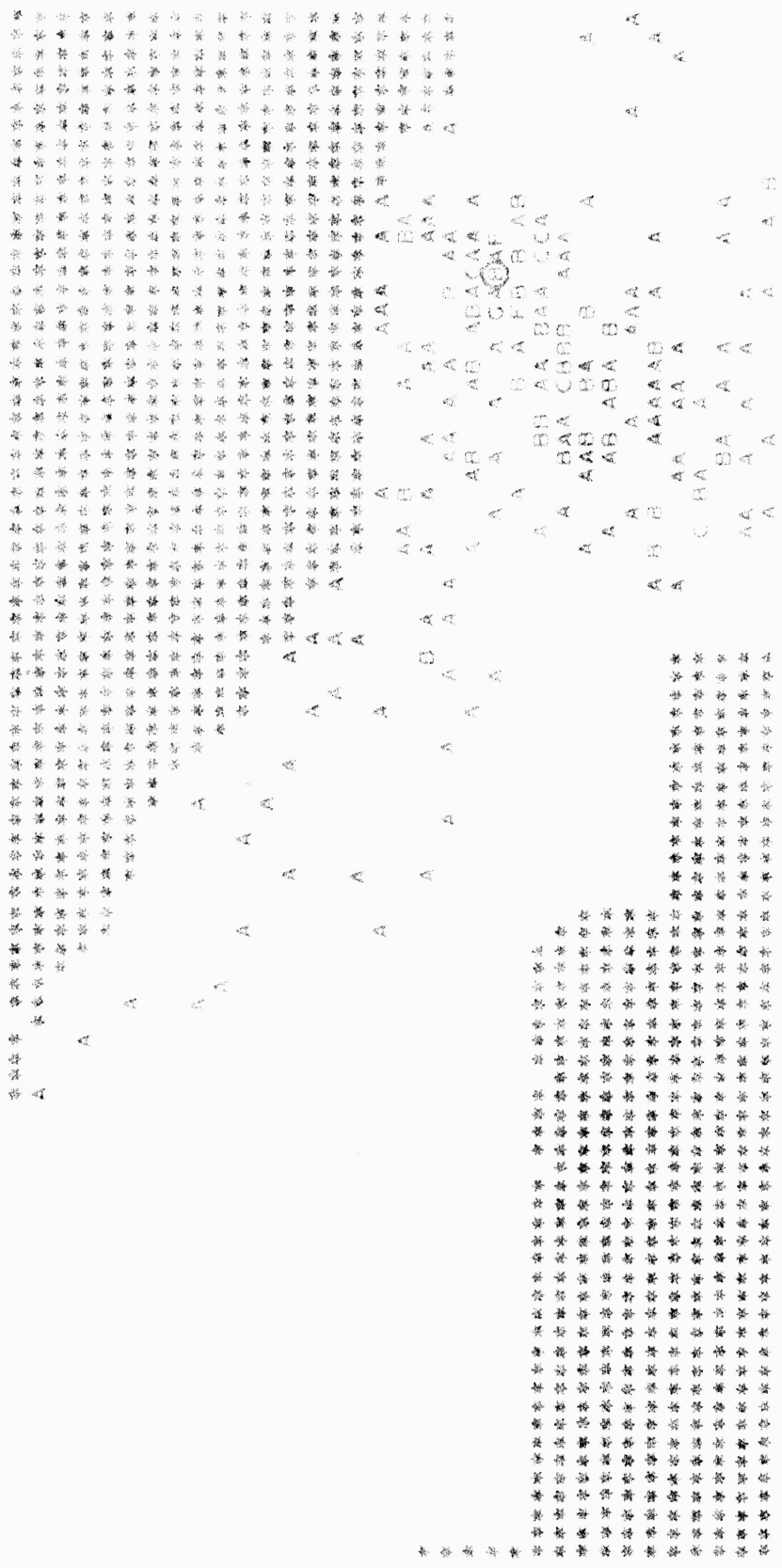SEAMAP   4--SIMULATED FISH DISTRIBUTION
331N.217W

Figure 17. Simulated distribution of 20 hypothetical fish using a
klinokinetic avoidance model -- fish 5. Each letter corre-
sponds to the number of times a fish occupied a particular
1-km square (A=1, B=2, etc.). The point of fish "release" is
circled. Each fish made 60-min steps until it either left the
tracking area (bounded by asterisks) or exceeded the time
limit set by the real fish track.

SEAMAP   C---SIMULATED FISH DISTRIBUTION

3,43N,290W

Figure 18.   Simulated distribution of 20 hypothetical fish using a
              klinokinetic avoidance model -- fish 6. Each letter corre-
              sponds to the number of times a fish occupied a particular
              1-km square (A=1, B=2, etc.). The point of fish "release"
              is circled. Each fish made 60-min steps until it either left
              the tracking area (bounded by asterisks) or exceeded the time
              limit set by the real fish track.
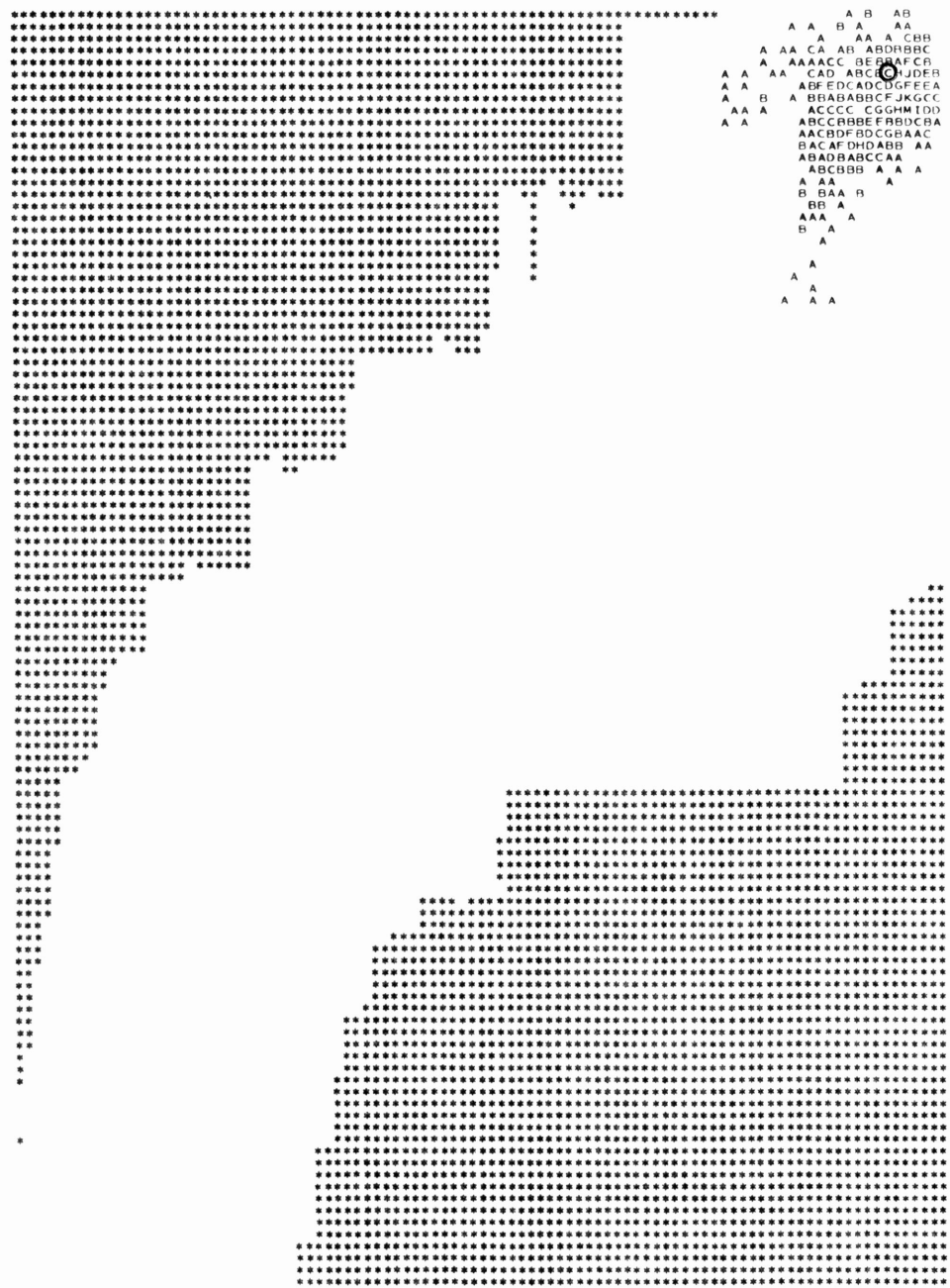
SEAMAP   6--SIMULATED FISH DISTRIBUTION

153N,214W

Figure 19. Simulated distribution of 20 hypothetical fish using a model
developed from regression analysis of the actual tracking
data -- fish 5. Each letter corresponds to the number of
times a fish occupied a particular 1-km square (A=1, B=2, etc.)
The point of fish "release" is circled. Each fish made 60-min
steps until it either left the tracking area (bounded by
asterisks) or exceeded the time limit set by the real fish
track.

SCAMAP   SIMULATED FISH DISTRIBUTION

34°N, 28°W

Figure 20. Simulated distribution of 20 hypothetical fish using a model developed from regression analysis of the actual tracking data -- fish 6. Each letter corresponds to the number of times a fish occupied a particular 1-km square (A=1, B=2, etc.). The point of fish "release" is circled. Each fish made 60-min steps until it either left the tracking area (bounded by asterisks) or exceeded the time limit set by the real fish track).

SEAMAP   6--SIMULATED FISH DISTRIBUTION

153N,214W

```
                                              A  B   AB
                                          A A   B  A   AA
                                           A    AA  A  CBB
                                        A AA CA  AB  ABDRBBC
                                        A  AAAACC  BEBBAFCB
                                 A  A  AA  CAD  ABCECHJDEB
                                       ABFEDCADCDGFEEA
                                 A   B  A BBABABBCFJKGCC
                                   AA A   ACCCC CGGHMIDD
                                         ABCCBBBEFBBDCBA
                                         AACBDFBDCGBAAC
                                         BACAFDHDABB AA
                                         ABADBABCCAA
                                          ABCBBB  A A
                                         A  AA      A
                                         B  BAA  B
                                          BB  A
                                         AAA   A
                                          B   A
                                              A
                                          A
                                        A
                                        A  A  A
```

Table 1. Summary statistics from regression analyses of LADTHET = ln (absolute angle of turn) and E = eccentricity against temperature, trend, and time variables. Numbers opposite the independent variable are regression coefficients; a blank indicates no significant ($p \leq 0.05$, except as indicated) contribution of that variable; a (+ or -) indicates the sign of an independent variable's coefficient that approached significance. See text for definition of variables.

LADTHET   E

FISH	4	5	6	ALL	4	5	6	ALL
R^2	0.43	0.46	0.16	0.11	0.41	0.26	0.31	0.17
Pr (F'>F)	0.0005	0.0004	0.0427	0.0288	0.0041	0.0105	0.0013	0.0019
ERROR df	22	29	35	90	21	30	35	90
INTERCEPT	5.3375	4.8810	4.1928	4.6651	0.3690	0.3489	0.4947	0.4206
LATXL1				0.1947				
LTR	2.4080	1.3379			(+)			0.1046
LTXLTR		0.0888	-0.1920	0.0390*		0.0148	0.0494	0.0507
SLTXLTR			-0.0107**			(-)	-0.0632	-0.0295
ATHET	(-)	(-)	-0.0063					(-)
STIME				0.4170	0.1231			
CTIME		0.9587			-0.1003	-0.1482		-0.0728

* P = 0.4   ** P = 0.11