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DOES SCHOOLING BEHAVIOUR AFFECT ESTIMATES OF MOVEMENT PARAMETERS FROM TAGGING DATA

by

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Does Schooling Behavior Affect Estimates of Movement Parameters from Tagging Data?

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Introduction

Understanding tuna movement and estimating parameters of tuna movement is coming to be recognized as important in assessing the status of tuna stocks and for determining the degree of interaction between fisheries that harvest the tuna stocks (Kleiber, 1994). Tuna movement parameters and other parameters of tuna population dynamics have been estimated from tagging data (Hilborn 1990, Sibert and Fournier 1993, Kleiber and Hampton 1994). The numerical methods used in these studies all make the assumption that tagged fish are independent of each other when in fact it is known that tuna move in schools which maintain their integrity on the order of months (Bayliff 1988). Thus tagged tunas released in the same school are clearly not independent of each other in the early days following release, though they may become more independent as time goes on.

Kleiber and Hampton (1994) speculate that their estimation model might be indifferent to schooling behavior in terms of the parameter estimates, and that the goodness of fit would simply be poorer than would be expected with true independent (non-schooling) behavior. In other words, the parameter estimates may be unbiased by the fact that schooling occurs in nature but not in the model, even though the minimum value of the negative log likelihood is larger than it should be given the statistical structure of the model.

To check on that speculation, I have conducted a modeling experiment in which I created synthetic tagging data with and without schooling behavior imposed and with known parameter values of advection, diffusion, natural mortality and fishing mortality. I then used the same model to estimate the original model parameter values from both the schooling and non-schooling tag data.

Tagged Fish Dynamics Model

The basic model without schooling is a diffusion equation for a single, instantaneous release at a point in two dimensional space with uniform attrition throughout due to natural and fishing mortality and with a constantly increasing spatial offset due to advection. The probability density of capture, $P(x, y, t)$, at point x, y and time t for a single fish released at point x_0, y_0 at time $t = 0$ is calculated at all grid points of a spatio- temporal grid

consisting of 15 time steps and a 51 × 51 spatial array. An exact (analytical) solution for the independent case (no schooling) is obtained from the following formula:

$$p(x,y,t) = \frac{F}{4\pi Dt}\exp(-(F+M)t)\exp(-\frac{(x-x_0-ut)^2+(y-y_0-vt)^2}{4Dt}) \quad (1)$$

where F and M are the fishing and natural mortalities, u and v are the x and y components of advection velocity, and D is the diffusivity. The probability densities are assembled into a probablility space $\mathcal{P}_I(\beta) = \{p_i\}$ which is a function of the parameters $\beta = \{F, M, u, v, D\}$. The index i is organized to run in a ordered way through all the points in the spatio-temporal grid so that $p_i = p(x_i, y_i, t_i)$ for $i > 1$, and p_1 is defined by $p_1 = 1 - \sum_{i>1} p_i$. This implicitly integrates the probability densities assuming that the the grid spacings $(\Delta x, \Delta y, \Delta t)$ are all equal to 1 which in turn defines the spatial and temporal units of the model parameters in terms of the grid spacing.

I chose the following set of base values for the parameters $\beta_0 = \{F_0, M_0, u_0, v_0, D_0\}$:

$$\begin{aligned} F_0 &= .05 \text{ time}^{-1} \\ M_0 &= .15 \text{ time}^{-1} \\ u_0 &= 2.0 \text{ length time}^{-1} \\ v_0 &= 2.0 \text{ length time}^{-1} \\ D_0 &= 2.0 \text{ area time}^{-1} \end{aligned}$$

where the spatial and temporal units are the grid spacings. The resulting spatial distributions of probabilities after 1, 7, and 15 time steps are shown in figures 1-3. Figure 4 shows the distribution of return probability with time as well as the non-return probability.

A synthetic non-schooling tag data set with N releases and the base parameter set is produced first by randomly choosing N index values with replacement according to the probability space $\mathcal{P}_I(\beta_0)$. For this exercise, I set $N = 1000$. Because the choice of index values was made with replacement, a given value could be chosen more than once. The synthetic data set $\mathcal{R}_I(\beta_0)$ consists of the number of times that each index value (i.e. each of the grid points as well as the non-return case) was chosen. Any number of such synthetic data sets can be produced. There will be stochastic variation among them reflecting the statistical case of independent (non-schooling) fish.

The case for schooling fish was handled by randomly choosing a number of spatial grid points within a time level and reassigning all the probability within that time level equally among the chosen grid points. Grid point choice was made with replacement so that a grid point might get more than one share of probability. The chosen grid points represent schools. The number of grid points chosen varies linearly from 2 in the first time interval to 30 in the last time interval, thus mimicking exchange of tagged fish into untagged schools and resulting increasing independence with time. Figures 7-9 show one example of the chosen grid points at time steps 1, 7, and 15. Probability at unchosen grid points is set to zero. The resulting probability space for schooling $\mathcal{P}_S(\beta_0)$ has identical index structure

to $\mathcal{P}_I$, and the probability distribution with time is the same, but many of the grid points have zero probability. $\mathcal{P}_S(\beta_0)$ leads to a synthetic schooling data set $\mathcal{R}_S(\beta_0)$ in the same way that $\mathcal{P}_I(\beta_0)$ $\mathcal{R}_I(\beta_0)$. The only difference is that multiple examples of $\mathcal{R}_I(\beta_0)$ come from the same probability distribution whereas multiple examples of $\mathcal{R}_S(\beta_0)$ each involve two stochastic processes – one to produce $\mathcal{P}_S(\beta_0)$ and the next to produce $\mathcal{R}_S(\beta_0)$.

Fitting Model to Tag Data

Estimates of parameters are obtained from a set of tag data by minimizing the following multinomial negative log likelihood functions with respect to the parameters β:

$$\mathcal{L}_I(\mathcal{R}_I(\beta_0)|\mathcal{P}_I(\beta)) = \sum_i \mathcal{R}_I! - \log(N!) - \sum_i \mathcal{R}_I(\beta_0)\log(\mathcal{P}_I(\beta)) \tag{2}$$

for independent fish, and

$$\mathcal{L}_S(\mathcal{R}_S(\beta_0)|\mathcal{P}_I(\beta)) = \sum_i \mathcal{R}_S! - \log(N!) - \sum_i \mathcal{R}_S(\beta_0)\log(\mathcal{P}_I(\beta)) \tag{3}$$

for schooling fish. Note that the independent probability space $\mathcal{P}_I$ appears in both cases because the idea is to check how well a model, based on independence, functions as a parameter estimator when the fish are in fact schooling.

Results

Figure 8 shows the distributions of parameter estimates from 30 independent data sets (solid lines) and 30 schooling data sets (dashed lines). The precision of the estimates is less for schooling fish than independent fish, but there is little indication of bias from these 30 examples.

Figure 9 shows scatter plots of all pairs of parameter estimates for the independent case and the schooling case. In either case, the only appreciable correlation evident from the 30 examples is between natural mortality and fishing mortality.

Figure 10 shows the distributions of 200 negative log likelihoods calculated from independent fish ($\mathcal{L}_I(\mathcal{R}_I(\beta_0)|\mathcal{P}_I(\beta_0))$, the solid line) and schooling fish ($\mathcal{L}_S(\mathcal{R}_S(\beta_0)|\mathcal{P}_I(\beta_0))$, the dashed line). $\mathcal{L}_S$ tends to be larger than $\mathcal{L}_I$.

Conclusion

As Kleiber and Hampton (1994) speculated, when tag data from schooling fish are analyzed with a non-schooling model, the objective function (Negative log likelihood) tends to be larger (indicating poorer fit) than would be the case if the fish didn't school, but the minimum value of the objective function tends to occur at the correct parameter values. Thus the parameter estimates appear to be unbiased, but the goodness of fit of the model appears to be poorer than would be expected for non-schooling fish.

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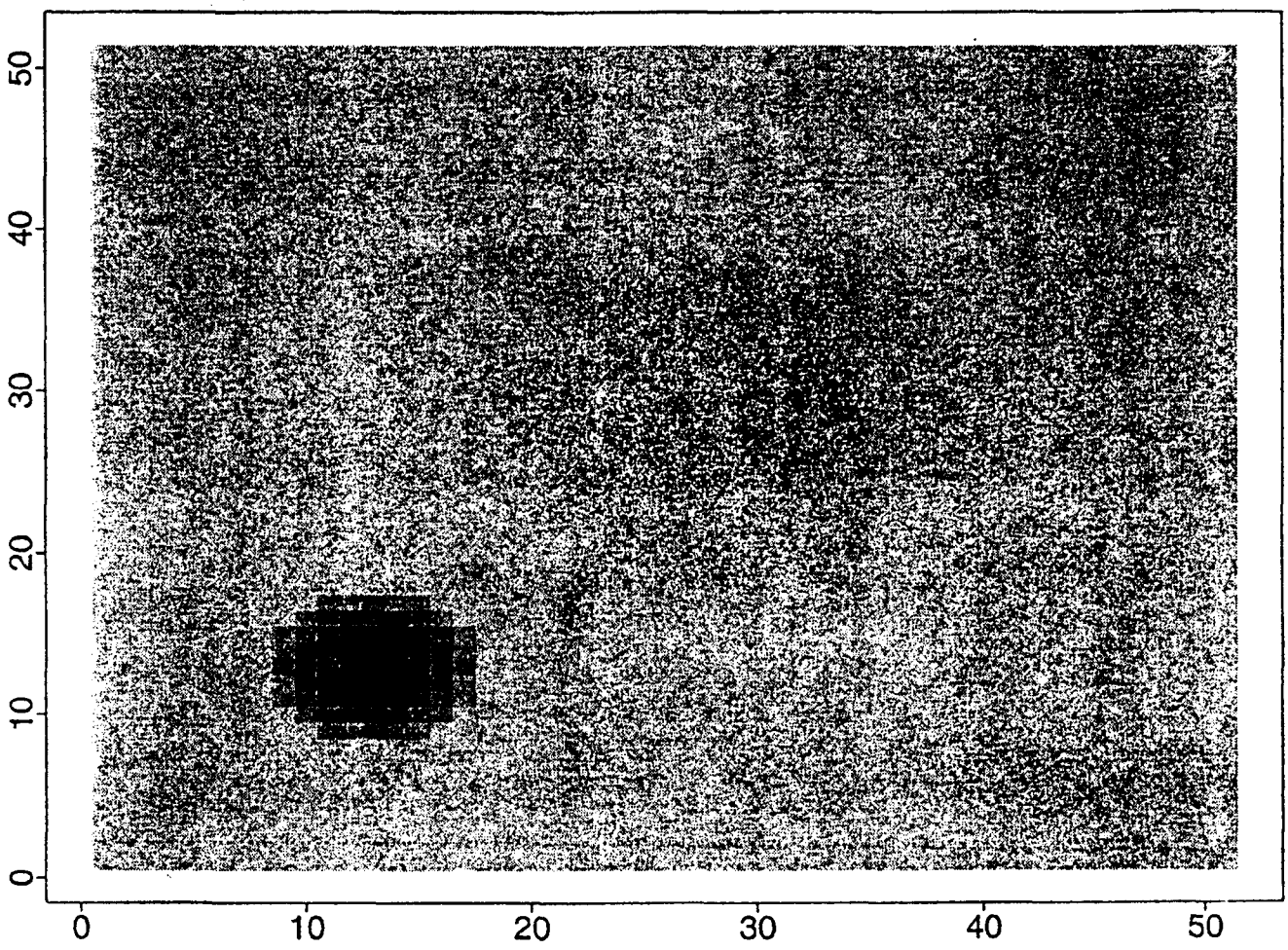


Fig 1

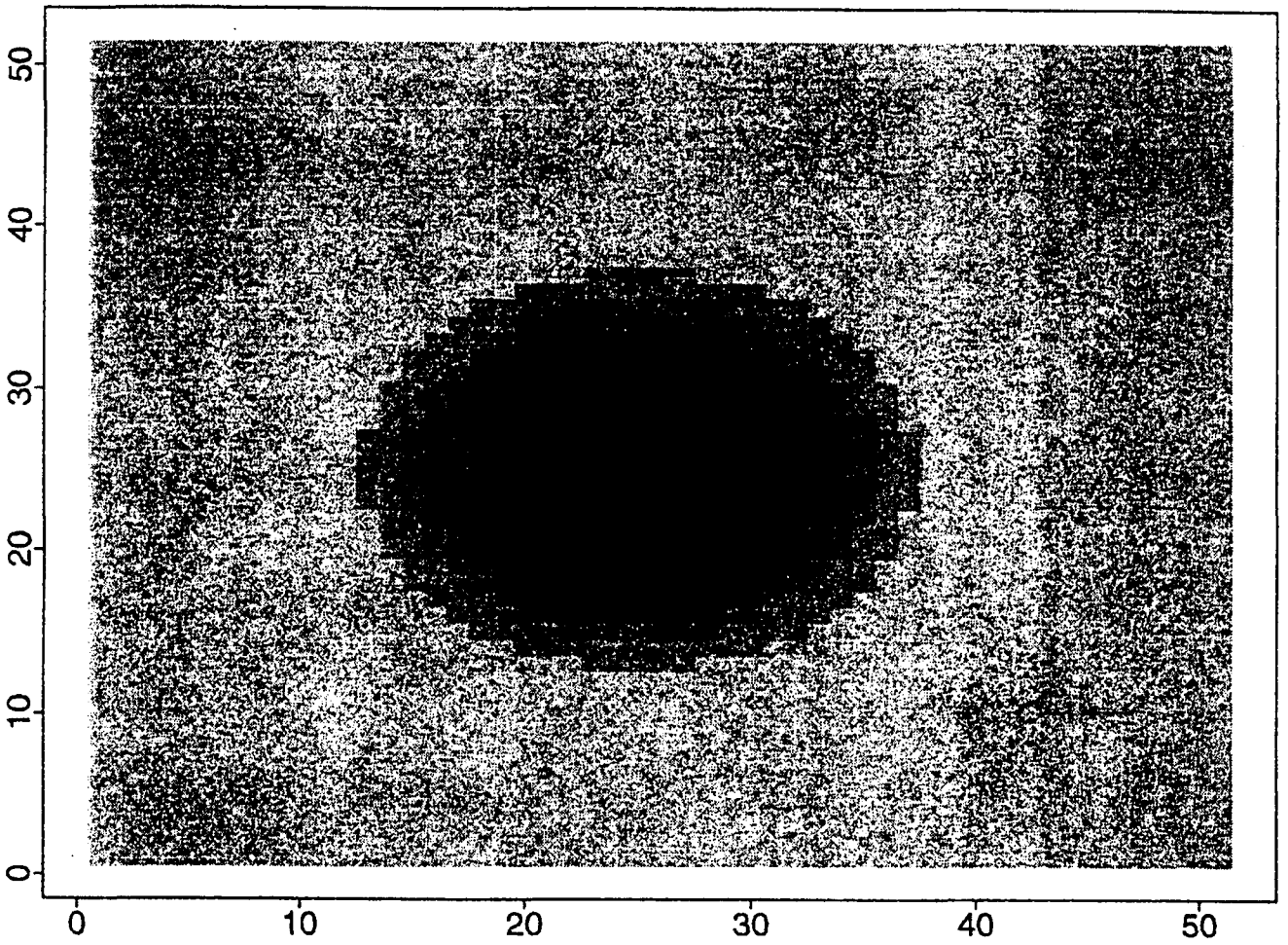
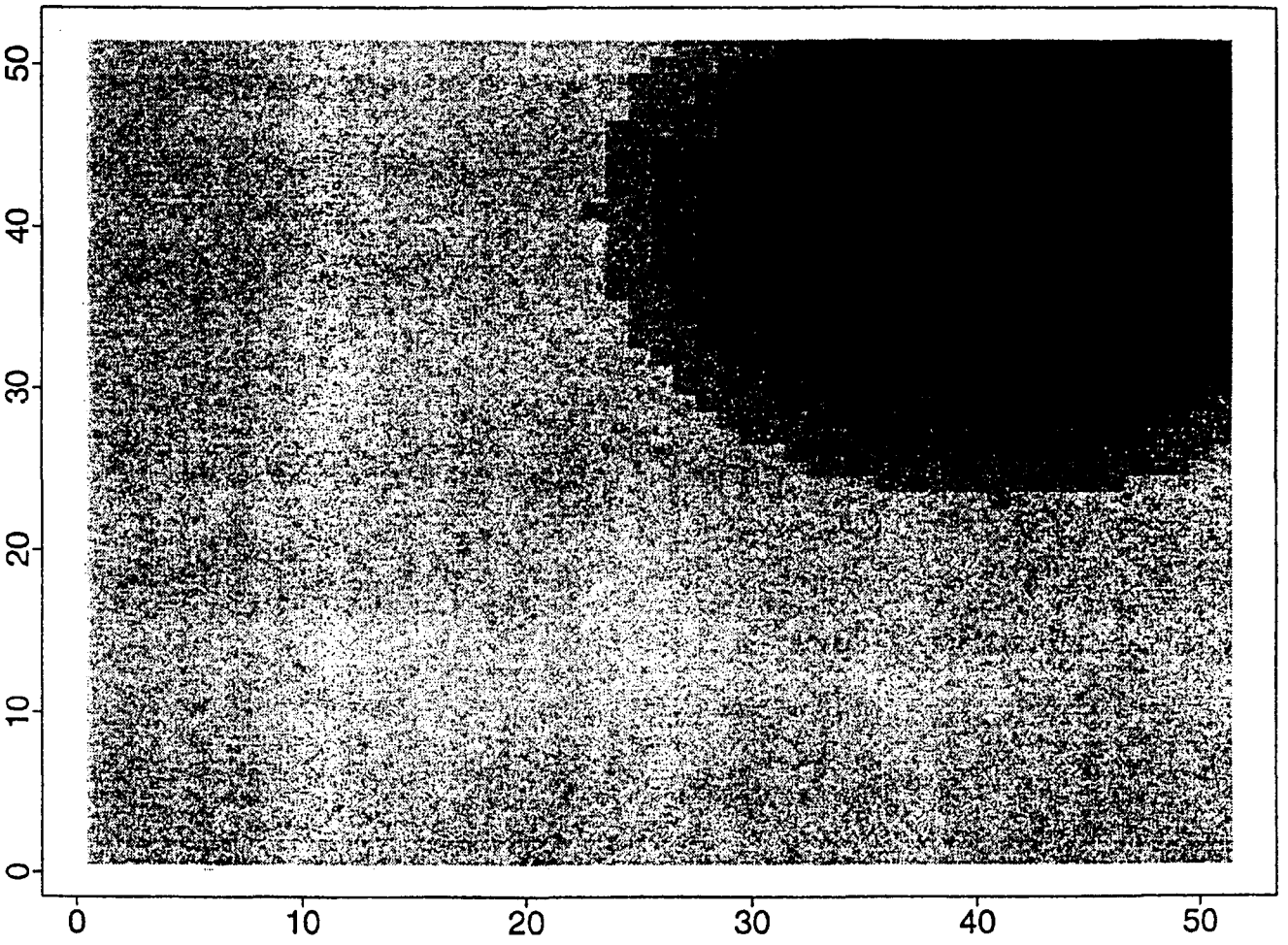


Fig. 2



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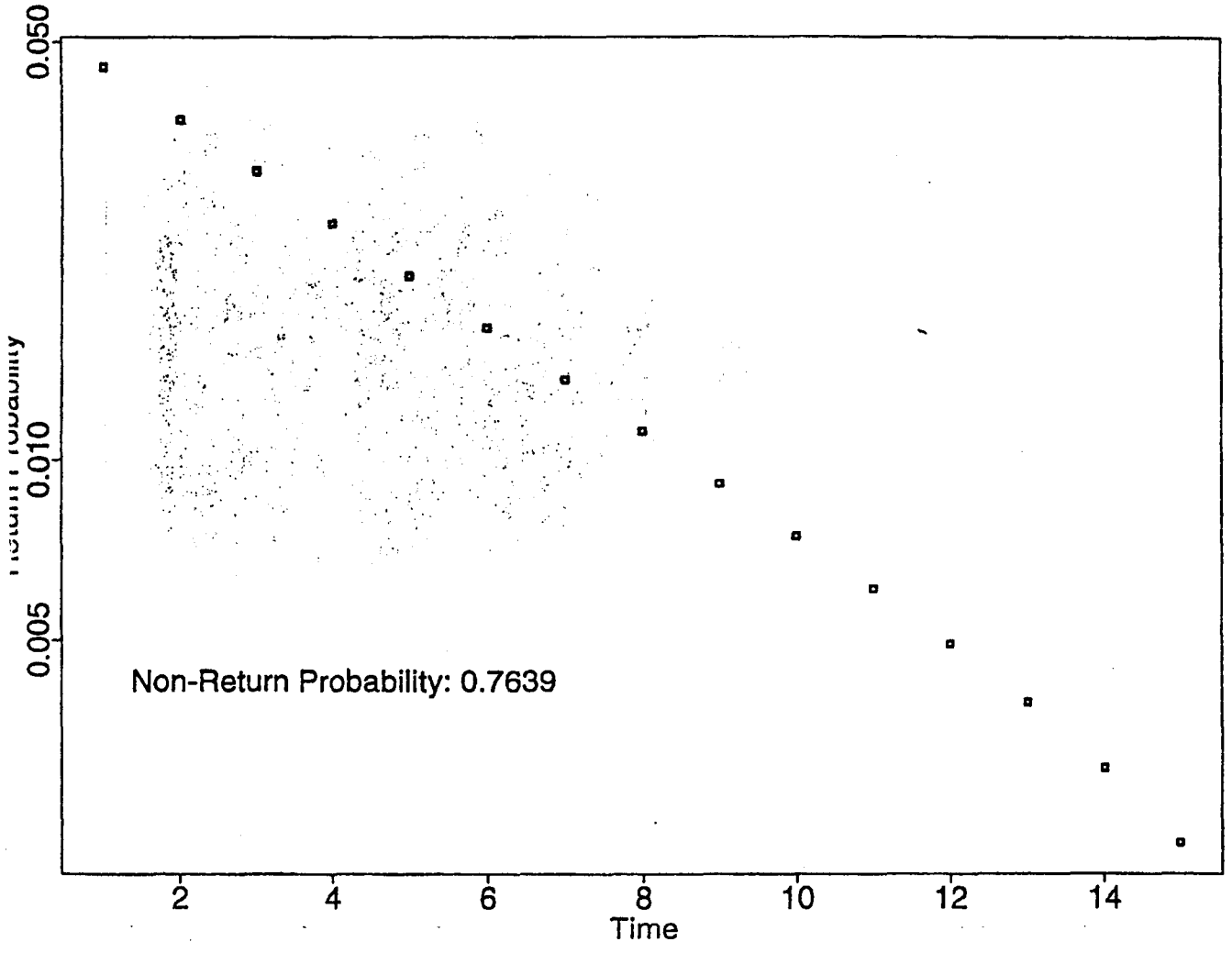

0.050
0.010
0.005
Non-Return Probability: 0.7639
2
4
6
8
10
12
14
Time

Fig. 4.

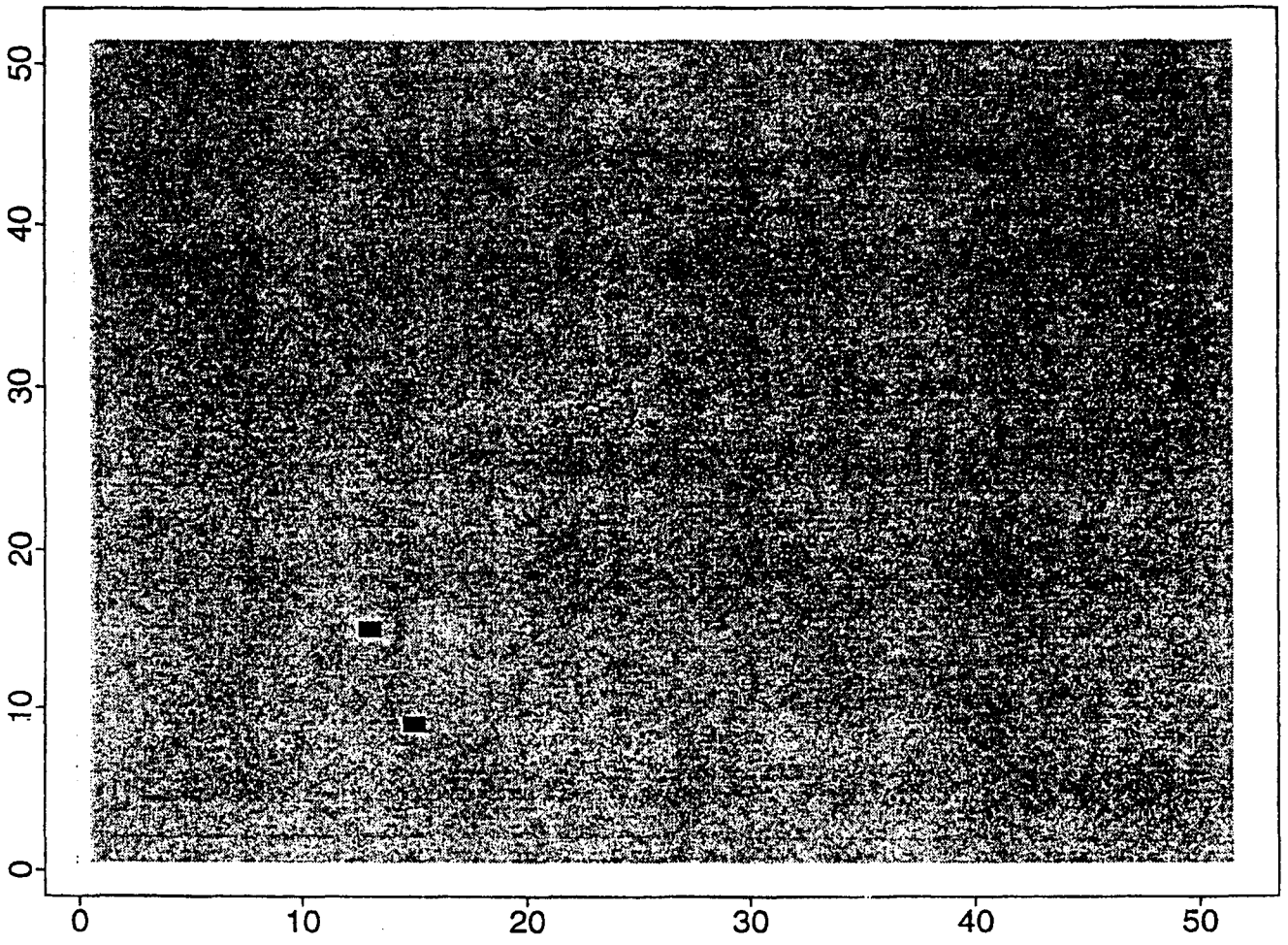


Fig. 5.

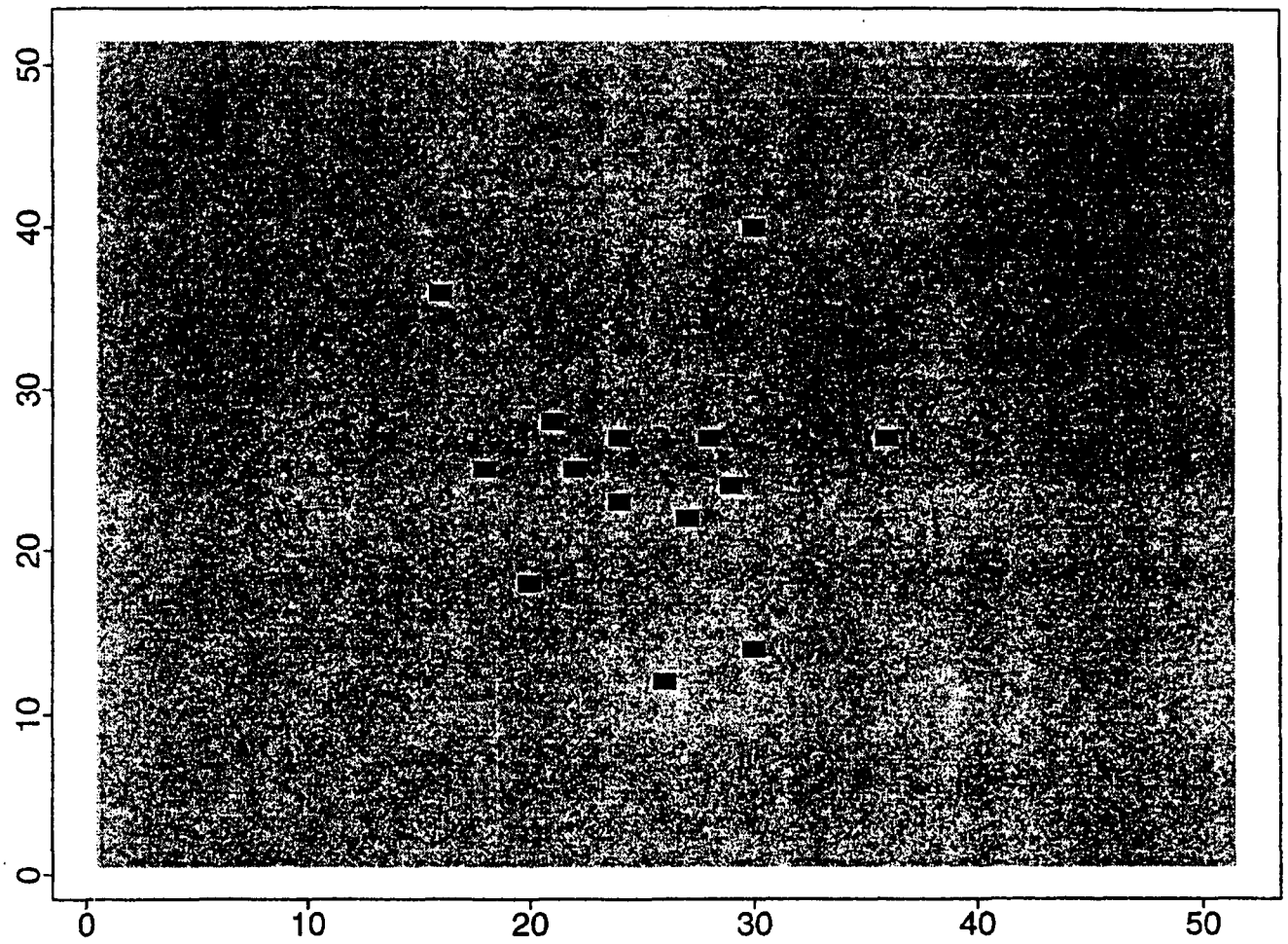
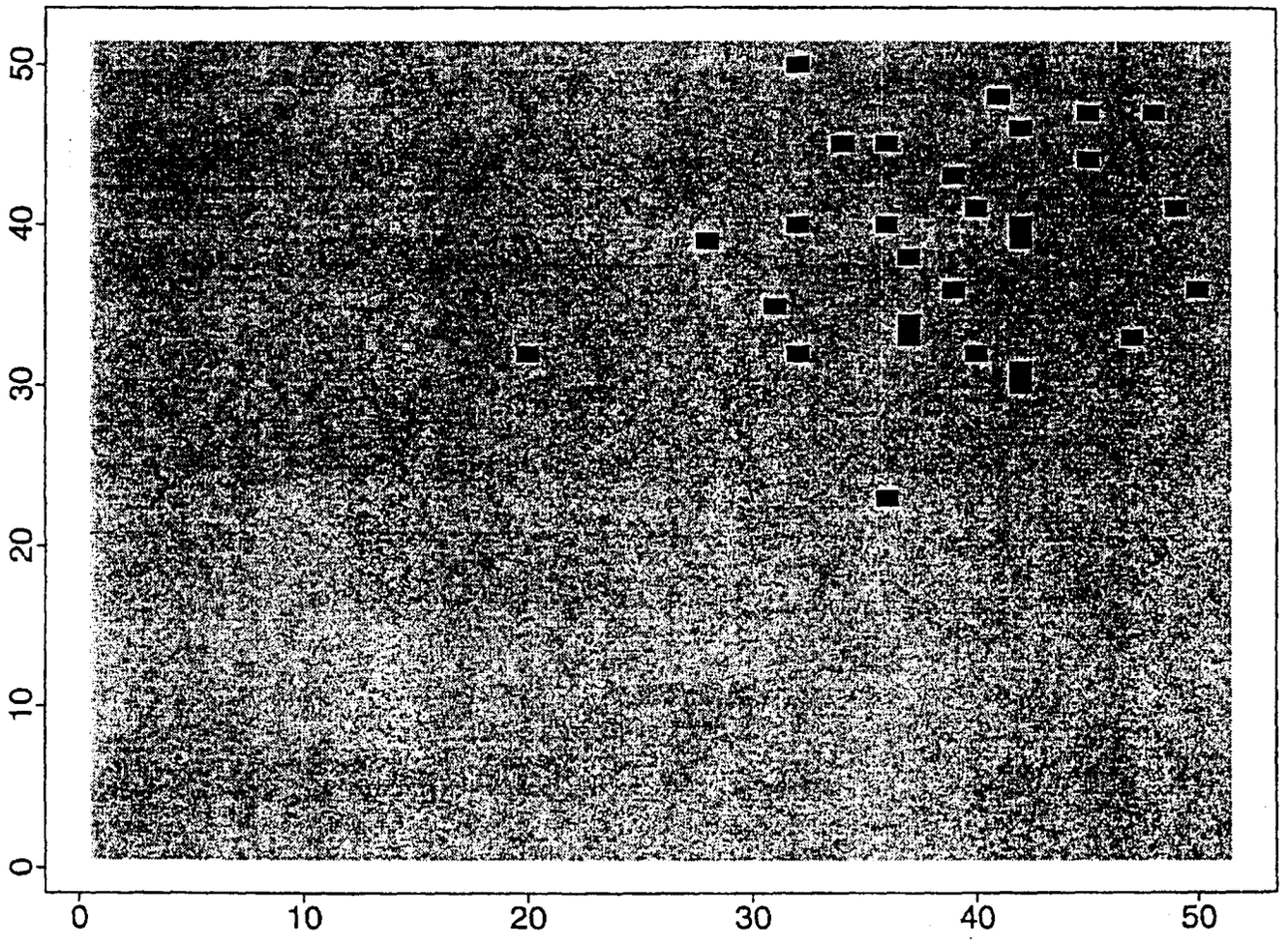


Fig. 6.



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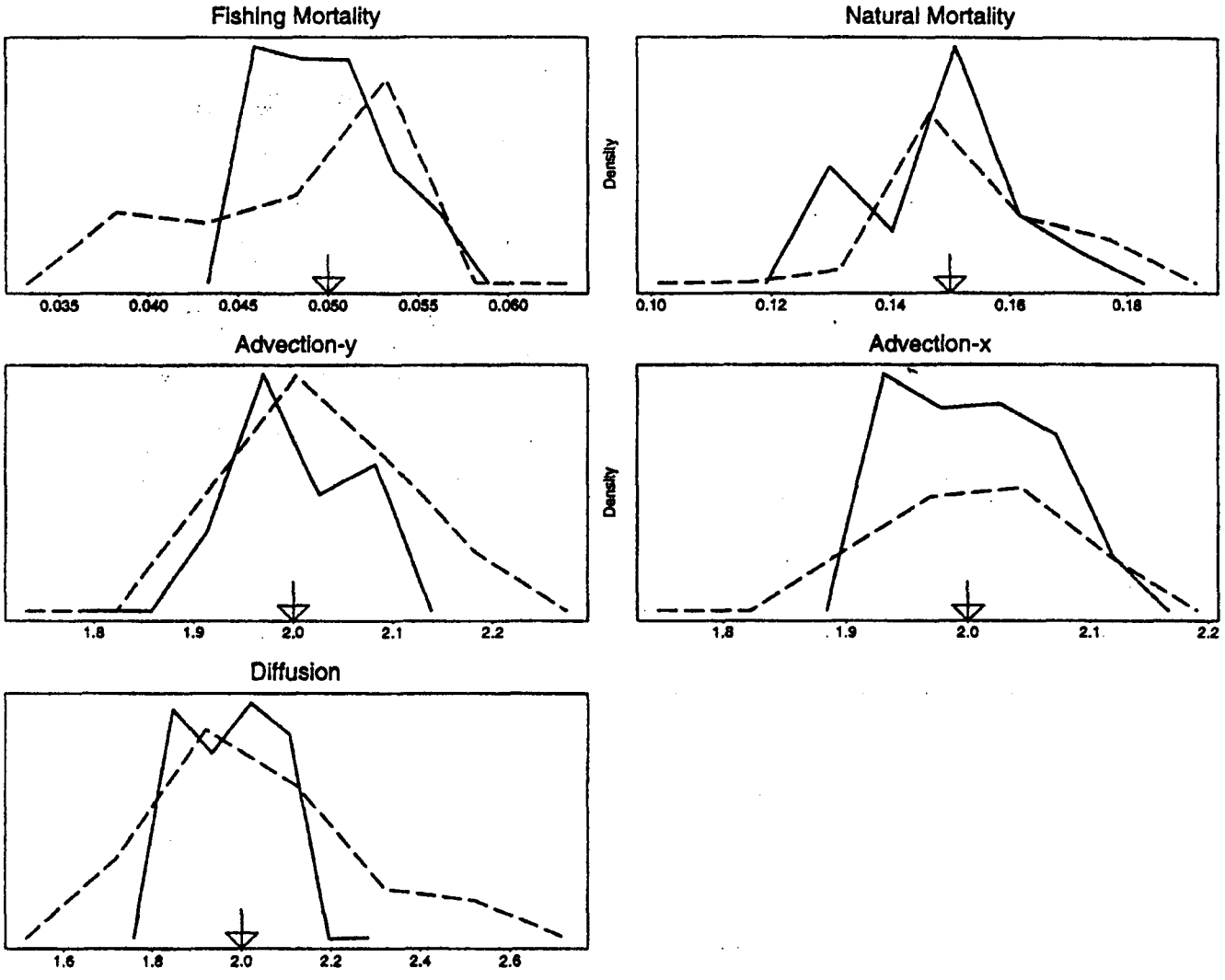
Fishing Mortality
0.035
0.040
0.045
0.050
0.055
0.060
Natural Mortality
0.10
0.12
0.14
0.16
0.18
Density
Advection-y
1.8
1.9
2.0
2.1
2.2
Advection-x
1.8
1.9
2.0
2.1
2.2
Density
Diffusion
1.6
1.8
2.0
2.2
2.4
2.6

Fig. 8

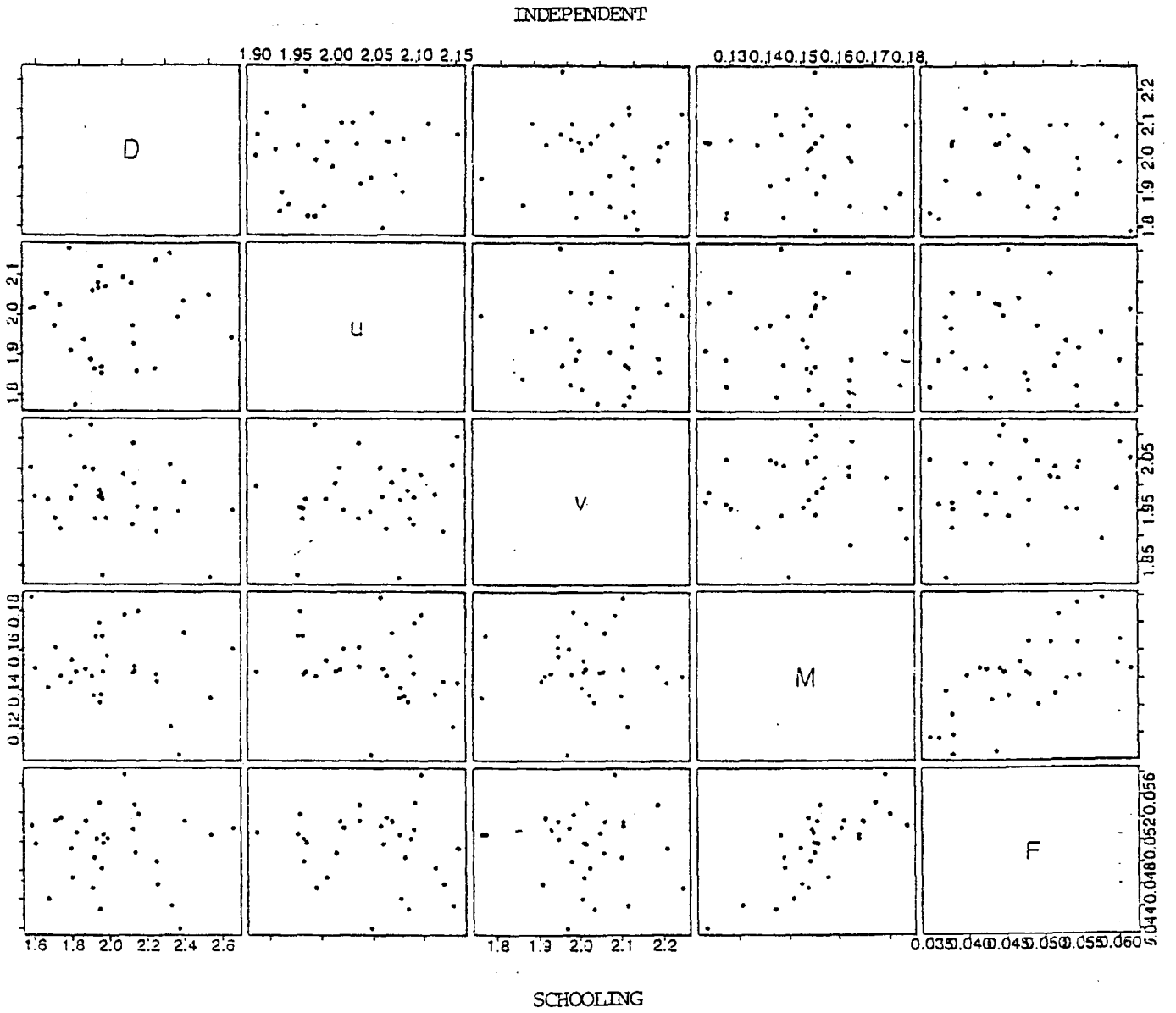

Fig. 9.

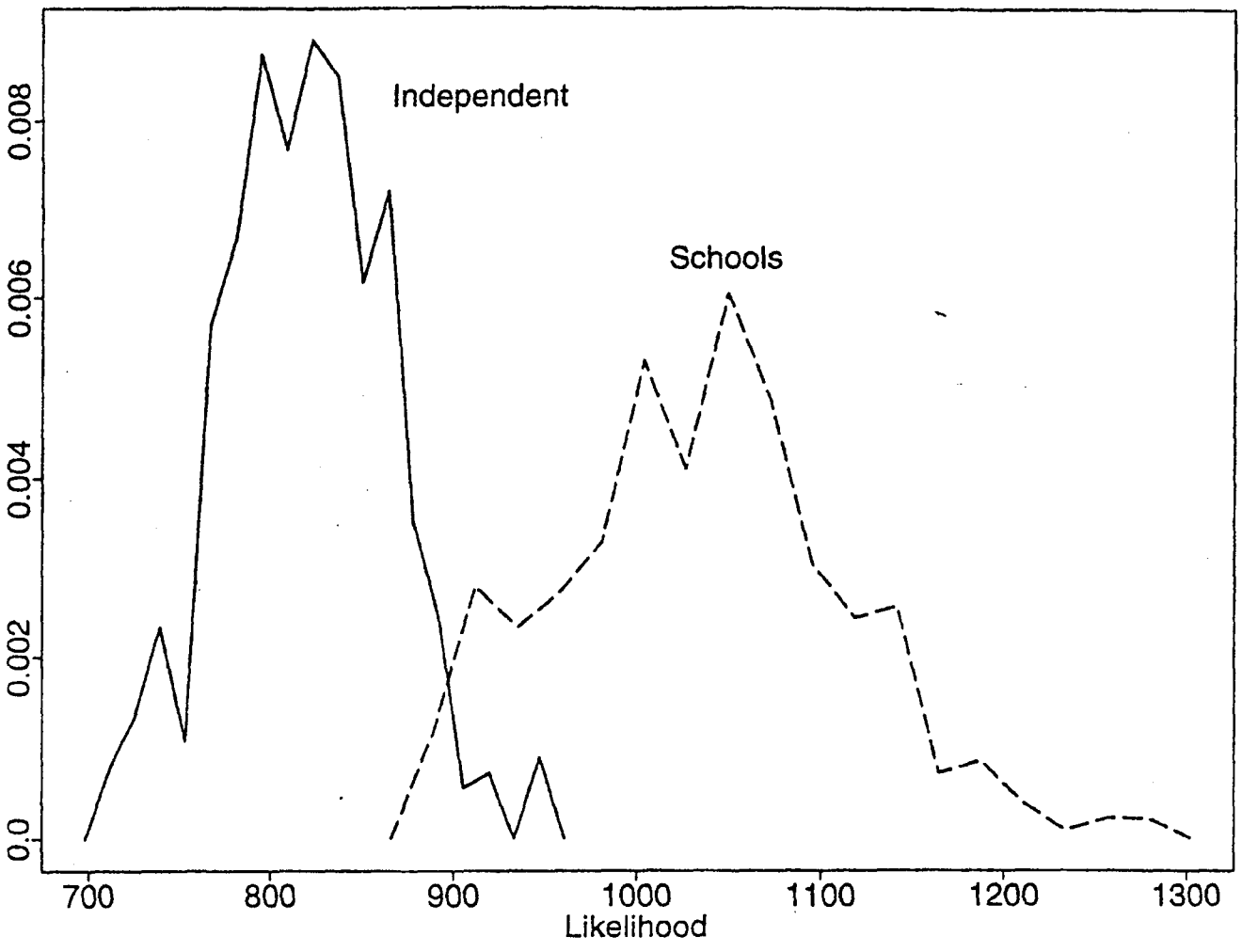
Independent
Schools
0.0
0.002
0.004
0.006
0.008
700
800
900
1000
1100
1200
1300
Likelihood

Fig. 10.