

An advection–diffusion–reaction model for the estimation of fish movement parameters from tagging data, with application to skipjack tuna (*Katsuwonus pelamis*)

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Abstract: The mobility of fish populations is often ignored in population dynamics models. However, in many cases (with tunas being a prime example), movement and spatial heterogeneity may be striking features of the fish populations and their exploitation. We describe a general quantitative framework to estimate movement and mortality of fish populations from tagging data. Movement is represented by an advection–diffusion process, which is the population equivalent of individual movement based on a biased random walk. Finite difference approximations for solving the partial differential equation are provided. The model is parameterized by assuming that movement parameters are homogeneous within specified geographical regions and seasons, that fishing mortality is proportional to fishing effort, and that natural mortality is constant over area and time. All model parameters are estimated simultaneously by maximum likelihood. The method is illustrated by application to skipjack tuna (*Katsuwonus pelamis*) in the western Pacific Ocean. Skipjack movement is shown to be highly variable at both seasonal and interannual time scales. Comparison with the results of a spatially aggregated analysis of the same data reveals that the spatial model provides a much better fit to the data and, unlike the spatially aggregated model, enables estimation of the natural mortality rate free of the effects of movement within the model domain.

Résumé : La mobilité des populations de poisson est souvent ignorée dans les modèles de dynamique des populations. Cependant, dans de nombreux cas (celui des thons au premier chef), les déplacements et l'hétérogénéité spatiale peuvent être des caractéristiques marquantes des populations de poisson et de leur exploitation. Nous décrivons un cadre quantitatif général permettant d'estimer les déplacements et la mortalité des populations de poisson à partir de données de marquage. Les déplacements sont représentés par un processus d'advection et de diffusion, qui est, pour une population, l'équivalent des déplacements aléatoires biaisés d'un individu. Nous fournissons les approximations en différences finies nécessaires pour résoudre l'équation différentielle partielle. Nous avons paramétré le modèle en supposant que les paramètres des déplacements sont homogènes dans les régions et saisons spécifiées, que la mortalité par pêche est proportionnelle à l'effort de pêche et que la mortalité naturelle est constante dans l'espace et dans le temps. Tous les paramètres du modèle sont estimés simultanément selon le maximum de vraisemblance. Nous avons appliqué notre méthode à la bonite à ventre rayé (*Katsuwonus pelamis*) de l'ouest du Pacifique. Nous avons montré que les déplacements de ce poisson sont très variables d'une saison et d'une année à l'autre. La comparaison avec les résultats d'une analyse spatialement agrégée des mêmes données montre que le modèle spatial donne un bien meilleur ajustement aux données et, à la différence du modèle spatialement agrégé, permet d'estimer le taux de mortalité naturelle sans qu'interviennent les effets des déplacements dans le domaine du modèle.

[Traduit par la Rédaction]

Introduction

Although fish are mobile, the explicit effects of mobility on fisheries management policies are usually neglected. In

cases where fishing is distributed uniformly over the range of the exploited fish species, movement may not be relevant in models of population dynamics (Beverton and Holt 1957). For tunas, however, fishing is certainly not uniform and is often restricted to a fraction of the range of the exploited species. Therefore, neglecting movement may lead to errors in estimates of exploitation rates (Laloë 1989; Die et al. 1990).

Tuna movements have been the subject of many field studies that depend on a variety of tagging and tracking techniques (see review by Hunter et al. 1986), and extensive collections of tag release and recapture data are maintained by various organizations dedicated to the scientific analysis of tuna populations. These data have yielded important insights into the exploitation and population dynamics of tunas (e.g., Bayliff 1971; Kleiber et al. 1987).

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Quantitative analyses of tuna movement have been slower to develop, with treatment often confined to drawing arrows on maps to represent the long-range movement of a few tagged individuals. In fact, several general classes of models can be applied to the quantitative analysis of fish movement. Bulk transfer models, where exchange rates between large regions are characterized by transfer coefficients, were first outlined by Beverton and Holt (1957). Models of this type have been applied to yellowfin tuna (*Thunnus albacares*) in the eastern Pacific (Ishii 1979a, 1979b), to skipjack tuna (*Katsuwonus pelamis*) in the western Pacific (Sibert 1984; Hilborn 1990), and to southern bluefin tuna (*Thunnus maccoyii*) (Hampton 1991). In some cases, these models have closed-form solutions, are easily implemented in computer code, and have parameters that can be estimated statistically from tagging data. Although bulk transfer models can predict changes in population size in arbitrary regions, they cannot be used to predict the changes in population density at an arbitrary point within a region because they are not continuous in space.

Models based on diffusion concepts are continuous in both space and time. These models have a long history in animal ecology (Skellam 1951), and their potential application to fisheries population modeling dates back at least to Beverton and Holt (1957) and Jones (1959). Although the diffusion concept suggests that the population moves at random, it does not require that individual fish move randomly. The small-scale movements of individuals, which are surely nonrandom, may, in a large population, produce a net distribution that gives the appearance of being the result of random movements. Because purely diffusive movement will ultimately produce a uniform distribution of the population at equilibrium, other factors such as directional movement or spatial variability in recruitment, mortality, or population growth rate (Mullen 1989; MacCall 1990) are required to maintain persistent gradients in population density. Directional movements are easily incorporated into a diffusion model by introducing "advective" terms. Okubo (1980) presented an insightful derivation of the advection-diffusion equation as the limiting form of a biased random walk. Thus, the advection-diffusion model can be viewed as being equivalent to the individual-based modeling approach (Tyler and Rose 1994; Porch 1995) in the same sense that Eulerian and Lagrangian approaches are complementary views of fluid movement. Further discussion of the theoretical basis for the use of diffusion models in the analysis of fish movement is presented in Appendix A.

The application of advection-diffusion models to fish population dynamics has grown recently. MacCall (1990) developed an elegant theory relating movement, population growth, and habitat selection that, to a large extent, is based on an advection-diffusion model. Deriso et al. (1991) applied a Markovian transition matrix approach to estimating diffusion and advection parameters for eastern Pacific yellowfin tuna. Kleiber and Hampton (1994) applied an advection-diffusion model to the analysis of tagged skipjack tuna movements in relation to fish-aggregating devices.

The present paper extends previous work by providing a formal derivation of a general advection-diffusion-reaction model for the analysis of tagged fish movement. We provide a flexible means of parameterizing movement through

grouping of parameters by geographical regions and seasons and describe the maximum likelihood estimation of parameters from tagging data. We apply the model to the analysis of variability in skipjack tuna movement in the western Pacific Ocean, using tag release and recapture data from the 1977-1982 South Pacific Commission Skipjack Survey and Assessment Programme (SSAP) (Kearney 1982a, 1983). These results are contrasted with analysis of the same data using a spatially aggregated model.

The model

An advection-diffusion-reaction model is used to describe the movement and mortality of tagged skipjack tuna. Let \tilde{N}_{xytc} symbolize the density of tagged tunas (numbers of tagged fish per unit of surface area) at point (x,y) in the ocean at time t of tag release cohort c . The aggregate density of tagged tunas (or simply, tags) from all cohorts released up to time t is given by

$$(1) \quad N_{xyt} = \sum_{c=1}^{C_t} \tilde{N}_{xytc}.$$

Assuming that the tag cohorts move independently, the aggregate tag density satisfies the following partial differential equation:

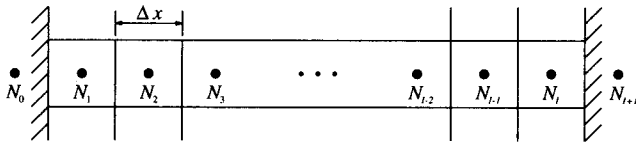
$$(2) \quad \frac{\partial N}{\partial t} = \frac{\partial}{\partial x} \left(D \frac{\partial N}{\partial x} \right) + \frac{\partial}{\partial y} \left(D \frac{\partial N}{\partial y} \right) - \frac{\partial}{\partial x} (uN) - \frac{\partial}{\partial y} (vN) - ZN.$$

Equation 2 partitions the local rate of change of tag density at point (x,y) into "dispersive" movements, "directed" movements, and mortality. The first two terms on the right-hand side of eq. 2 characterize dispersive movements in terms of a "diffusion" parameter D . The next two terms in eq. 2 characterize directed movements in terms of two "advection" parameters (u,v) that describe east-west (positive toward the east) and north-south (positive toward the north) movements. Note that the movement parameters u , v , and D may vary in space and time. The final term in eq. 2, the "reaction" term, describes the loss of tagged fish due to mortality from all sources. Since movement is explicit in this model, the mortality term does not include local losses due to emigration away from the fishing grounds.

Solution of the partial differential equation

Equation 2 is solved using a finite difference method on a regular grid with a spatial resolution of 60 nautical miles (Nmi), i.e., $\Delta x = \Delta y = 60$ (60 Nmi = 111.12 km), and a discrete time step. The numerical solution of eq. 2 is used in a numerical function minimization procedure to obtain estimates of model parameters. Therefore, the solution method must be fast because the partial differential equation (PDE) will be solved hundreds of time, and it must also be robust because function minimization algorithms may test parameter values that are not necessarily conducive to numerical stability. These two criteria are often conflicting. Speed is

Fig. 1. Cross section of a computational grid showing grid point labels and closed boundaries.



achieved by using large time and space steps, while stability is often achieved by using small time and space steps.

The finite difference approximation used for the time derivative is

$$(3) \quad \frac{\partial N}{\partial t} \Big|_{i,j}^{n+1} \approx \frac{N_{i,j}^{n+1} - N_{i,j}^n}{\Delta t}.$$

The subscripts i, j denote the spatial location of a grid point with position $(i\Delta x, j\Delta y)$; superscript n refers to time level $n\Delta t$.

Two schemes for the approximation of the first derivatives in the directed movement terms were considered: approximation by two-point “backward” differences, a scheme known as “upwind” or “upstream” differencing (Roache 1972; Press et al. 1988), and approximation by two-point centered-space differences.

Upwind differencing is very robust, but contributes numerical (i.e., nonbiological) diffusion to the solution field, which may confound estimation of the actual (i.e., biological) random movement parameter values for tagged tuna (O’Brien 1986). Upwind differencing of the directed movement terms at time level n takes the form

$$(4) \quad \frac{\partial uN}{\partial x} \Big|_{i,j}^n \approx \begin{cases} \frac{u_{i,j}N_{i,j}^n - u_{i-1,j}N_{i-1,j}^n}{\Delta x}, & u_{i,j} > 0 \\ \frac{u_{i+1,j}N_{i+1,j}^n - u_{i,j}N_{i,j}^n}{\Delta x}, & u_{i,j} < 0 \end{cases}$$

$$\frac{\partial vN}{\partial y} \Big|_{i,j}^n \approx \begin{cases} \frac{v_{i,j}N_{i,j}^n - v_{i,j-1}N_{i,j-1}^n}{\Delta y}, & v_{i,j} > 0 \\ \frac{v_{i,j+1}N_{i,j+1}^n - v_{i,j}N_{i,j}^n}{\Delta y}, & v_{i,j} < 0. \end{cases}$$

Centered-space differencing is a nondispersive alternative approximation to upwind differencing but introduces grid-scale oscillations into the solution field if advective terms are large relative to diffusive terms (Price et al. 1966; Roache 1972; Leonard 1979; Neuman 1981; Abbott and Basco 1989). In preliminary tests, such oscillations were large enough to cause negative values for tag density, and the parameter estimation procedure (see below) did not converge. All subsequent analysis was done using upwind differencing.

The second derivatives in the random movement terms are approximated using three-point finite differences as follows:

$$(5) \quad \frac{\partial}{\partial x} \left(D \frac{\partial N}{\partial x} \right) \Big|_{i,j}^n \approx N_{i-1,j}^n \frac{D_{i-1,j} + D_{i,j}}{2(\Delta x)^2} - N_{i,j}^n \frac{D_{i-1,j} + 2D_{i,j} + D_{i+1,j}}{2(\Delta x)^2} + N_{i+1,j}^n \frac{D_{i,j} + D_{i+1,j}}{2(\Delta x)^2}$$

$$\frac{\partial}{\partial y} \left(D \frac{\partial N}{\partial y} \right) \Big|_{i,j}^n \approx N_{i,j-1}^n \frac{D_{i,j} + D_{i,j-1}}{2(\Delta y)^2} - N_{i,j}^n \frac{D_{i,j-1} + 2D_{i,j} + D_{i,j+1}}{2(\Delta y)^2} + N_{i,j+1}^n \frac{D_{i,j+1} + D_{i,j}}{2(\Delta y)^2}.$$

Boundary conditions must be specified in order to solve the PDE. Closed boundaries occur naturally around islands and along continental coastlines. Either closed or open boundaries may be applied to the edges of the model region. Closed boundary conditions are appropriate where the model region encompasses a large proportion of the tagged fish distribution. For closed boundaries, a simple reflection condition on N and an impermeability condition on the normally directed component of movement are used. Thus:

$$(6) \quad \frac{\partial N}{\partial x} = 0 \quad \text{and} \quad u = 0$$

on eastern and western closed boundaries

$$\frac{\partial N}{\partial y} = 0 \quad \text{and} \quad v = 0$$

on northern and southern closed boundaries.

These conditions ensure that tagged tuna numbers are conserved in the model when both natural and fishing mortality are zero.

In the one-dimensional grid point lattice in Fig. 1, the reflection conditions on N at each boundary have the numerical counterparts in the x direction:

$$(7) \quad N_0 = N_1 \quad \text{and} \quad N_{I+1} = N_I$$

and guarantees tag conservation in the absence of mortality. A more complete discussion of boundary conditions can be found in Bills and Sibert (1997).

The obvious initial condition for N is

$$(8) \quad N_{xy0} = \begin{cases} \sum_c \tilde{N}_{x_c y_c 0c}, & \text{over all tag release sites} \\ 0, & \text{elsewhere} \end{cases}$$

where $\tilde{N}_{x_c y_c 0c}$ is the number of tagged skipjack released at point (x_c, y_c) at time 0 in tag cohort c . In the case of a cohort release s at a subsequent time t_s and at position (x_s, y_s) , the density of tags at that point is reassigned the sum of its present value and the cohort value, viz.:

$$(9) \quad N(x_s, y_s, t_s) \leftarrow N(x_s, y_s, t_s) + \tilde{N}(x_s, y_s, t_s).$$

The complete numerical approximation to the PDE is given by substituting finite difference approximations for the movement terms taken at appropriate time levels into the right-hand side of eq. 2. A combination of time levels $n + 1/2$ and $n + 1$ leads to the well-known alternating direction

Table 1. Values of bounds applied to parameter estimates and tag density in the penalty functions.

Parameter	Lower bound	Upper bound
M	0	0.5
Q_f	0	0.1
u	-1 500	1 500
v	-1 500	1 500
D	0	500 000
N_{ij}	0	None

implicit (ADI) method. This method is robust and converges to a solution unconditionally for all step sizes (Carnahan et al. 1969; Press et al. 1988).

Reparameterization

All of the solutions of the PDE described above require specification of each model parameter at every grid point. The 60×35 grid used in the present example requires values of each parameter u , v , D , and Z in eq. 2 to be specified at each time step at each of the 2100 grid points, a total of 8400 parameter values per time step. Direct estimation of so many parameters is impractical, and some means of reducing the number of parameters is required.

Tuna movement patterns are frequently represented by arrows on maps, often with months or seasons specified, to suggest the general trend of population movement at different times and places (e.g., see Kearney 1982b; Hunter et al. 1986). This point of view implies that fish movement may be time and site specific. Consistent with this possibility, "regions" are defined as subdivisions of the model domain over which the movement parameters u , v , and D are constant, and "seasons" are defined as periods of time during which the parameters within a region are constant. Let R_{ij} be a matrix that contains the region number for each model cell indexed by (i, j) and S^n be a vector that contains the season for each time step indexed by n . In other words, R_{ij} maps the model domain into specified regions and S^n maps calendar time to seasons. The model parameters are specified at each grid point by the following equations:

$$(10) \quad \begin{aligned} [u_{ij}^n] &= \mathbf{u}_{R_{ij} S^n} \\ [v_{ij}^n] &= \mathbf{v}_{R_{ij} S^n} \\ [D_{ij}^n] &= \mathbf{D}_{R_{ij} S^n} \end{aligned}$$

where \mathbf{u} , \mathbf{v} , and \mathbf{D} are matrices of parameters to be estimated. For a model with 10 regions and two seasons, \mathbf{u} , \mathbf{v} , and \mathbf{D} are 2×10 matrices, containing the 60 movement parameters required to specify values for \mathbf{u} , \mathbf{v} , and \mathbf{D} at the 2100 points in the model domain used in the present analysis. The matrices \mathbf{u} , \mathbf{v} , and \mathbf{D} are collectively referred to as movement "patterns" or "hypotheses" below.

Total mortality Z is separated into two components in a conventional manner by

$$(11) \quad Z_{ij}^n = M + \sum_f F_{ijf}^n$$

where F_{ijf}^n is the mortality due to fishing by fishing fleet f operating in computational element (i, j) during time step n and M is mortality due to other causes or "natural" mortality. Natural mortality is assumed to be constant at all places,

over the period of time that the tagged fish are at liberty. Fishing mortality is assumed to be a simple function of observed fishing effort:

$$(12) \quad F_{ijf}^n = Q_f \times E_{ijf}^n$$

where E_{ijf}^n is the observed fishing effort of fleet f operating in element (i, j) during time step n and Q_f is a fleet-specific proportionality constant or "catchability coefficient". This parameterization enables the specification of mortality at all grid points in terms of a small number of parameters of direct relevance to the dynamics of exploited populations.

Parameter estimation

The predicted number of skipjack tags returned during 1 month is given by

$$(13) \quad \hat{C}_{ijf}^n = \beta_f \frac{F_{ijf}^n}{Z_{ij}^n} (1 - e^{-Z_{ij}^n}) N_{ij}^n$$

where β_f is the reporting rate, i.e., the proportion of tags captured by fleet f returned with usable recapture information, and N_{ij}^n satisfies eq. 2 for time step n . For the example presented here, β_f is assumed to be 1.0 for all fleets.

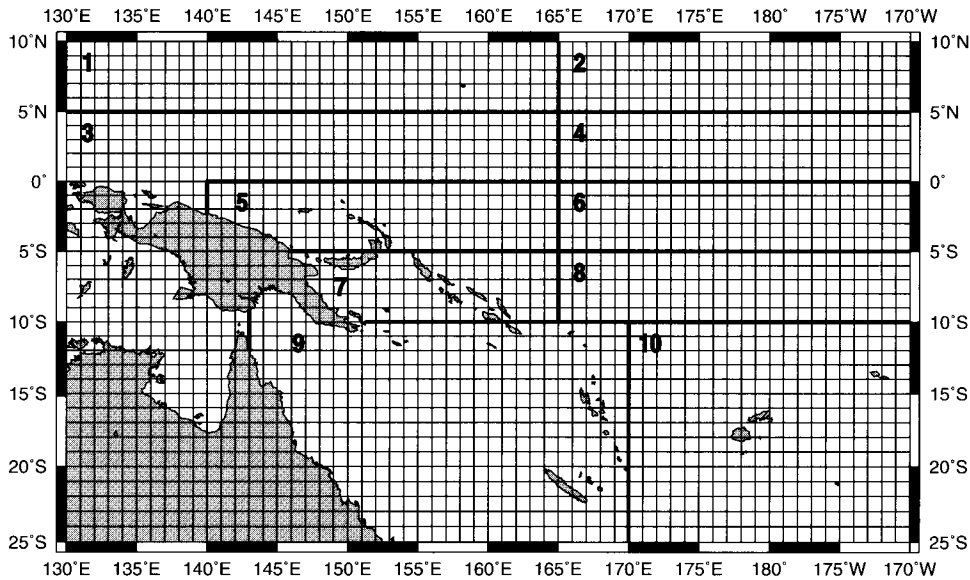
Observed numbers of tag returns, C_{ijf}^n , are related to predicted numbers of tag returns, \hat{C}_{ijf}^n , by a Poisson likelihood function:

$$(14) \quad L(\mathbf{u}, \mathbf{v}, \mathbf{D}, Q, M | C_{ijf}^n, E_{ijf}^n) = \prod_{ijf} \left[\frac{(\hat{C}_{ijf}^n)^{C_{ijf}^n} e^{-\hat{C}_{ijf}^n}}{C_{ijf}^n!} \right].$$

This function assumes that the predicted number of tag returns in each cell during 1 month is the expected value of a random variable with a Poisson distribution. This distribution is appropriate for an observation of a rare event such as the radioactive decay of an atom (Feller 1968) or the recapture and return of a tagged skipjack. Maximum likelihood parameter estimates are obtained by finding the values of the parameters that maximize eq. 14. The maximization is accomplished by minimizing the negative log of eq. 14 using a quasi-Newton numerical function minimizer, which, in turn, depends on the gradient of partial derivatives computed using adjoint functions (Griewank and Corliss 1991).

Additional information is provided to the function minimizer through the use of penalty functions (Bard 1974). These functions are continuous functions of the upper and lower bounds of the parameters and are interpreted as prior probability distribution functions added to the likelihood function. Penalty functions also restrict the minimization process to a region constrained by feasible parameter values. The net effect of the penalty functions is a more efficient minimization process. The values of the upper and lower bounds used in the penalty functions are given in Table 1. Certain combinations of parameter values will produce grid-scale oscillations in the solution of eq. 2. If these oscillations are large, the local tag density may take on negative values. A penalty function is therefore added to the likelihood function to prevent the function minimizer from seeking parameters that destabilize the numerical approximation of eq. 2. This penalty is equal to the sum of the squares of the local negative tag densities.

Fig. 2. Map of the southwest Pacific Ocean showing the location of the 10-region model area used for the skipjack tuna analysis.



Simulations have shown that parameter estimates for region \times season strata for which few tag returns were observed may be inaccurate (Sibert and Fournier 1994; Bills and Sibert 1997). The (spatial) gradients of the movement parameters are therefore constrained to be small by imposing a small penalty on the curvature of the movement field. That is, penalties are applied to $\frac{\partial^2 u}{\partial x^2}$, $\frac{\partial^2 v}{\partial y^2}$, $\frac{\partial^2 D}{\partial x^2}$, and $\frac{\partial^2 D}{\partial y^2}$. These

penalties help to ensure that estimates of movement parameters in regions with few tag returns will be similar to estimates in neighboring regions.

Estimates of the variance of the parameter estimates are computed from the Hessian matrix, \mathbf{H} , the elements of which are

$$(15) \quad H_{ij} = \frac{\partial^2(-\log L)}{\partial \theta_i \partial \theta_j}$$

where θ_i and θ_j are any two model parameters. The approximate covariance matrix, \mathbf{V} , is given by the inverse of the Hessian matrix $\mathbf{V} \approx \mathbf{H}^{-1}$ (Bard 1974). This procedure provides other useful information about the minimum attained by the function minimizer. If \mathbf{H} is not positive definite, the minimizer has found a saddle point or has not converged. Such a condition occurs when the minimum is not well determined by the data, as may occur when the likelihood function is dominated by constraints on parameter ranges or by various penalties.

Application to western Pacific skipjack tuna

Data sources and treatment

Skipjack tag releases within the model area (Fig. 2) during the period 1 October 1977 to 31 August 1980 were selected from the SSAP database. The selected data set comprised 94 430 releases and 5319 reported recaptures. Of these recaptures, 92 occurred outside the model area and were excluded from the analysis. The model considers tag

returns by the five main fishing fleets active in the area at the time: the Japan pole-and-line, Japan purse seine, Fiji pole-and-line, Papua New Guinea pole-and-line, and Solomon Islands pole-and-line fleets. Tag returns by other fleets (188 recaptures) were excluded from the analysis. Tag releases and returns were stratified by release "cohorts", each consisting of releases in a one-degree geographic area during a calendar month. Returns from each cohort were further stratified by one-degree area, calendar month, and recapture fleet. Recaptures that could not be so stratified (828 recaptures) because of missing or inaccurate data were also excluded from the analysis. The tag recapture period used in the model extended until 31 August 1983, which encompassed all observed tag recaptures. The final data set analyzed therefore consisted of 4211 returns, or 79% of the total reported recaptures. The rejection of recaptures from the analysis effectively contributes to nonreporting and therefore could be explicitly included in the analysis by adjustment of β_j in eq. 13. We have opted not to do so in the present analysis because the other sources of nonreporting cannot be quantified.

Fishing effort data, stratified by one-degree area, calendar month, and recapture fleet, for the period 1 October 1977 to 31 August 1993 were compiled from South Pacific Commission databases.

The model regions and computational grid are shown on the map in Fig. 2. The boundaries of the model domain were assumed to be closed. Representations of coastlines and islands at a resolution of one degree (about 60 Nmi) inevitably cause errors in the locations of fishing events (tag release, tag recapture, fishing) that occur within 60 Nmi of a shoreline. In some cases, fishing events may appear on land when mapped at one-degree resolution. Such events were arbitrarily shifted to an adjacent one-degree area. Tag releases, recaptures, and fishing effort positions that appeared on land at one-degree resolution were all shifted consistently.

Results

Interaction between the solution of the PDE and the function minimizer should be considered before the results of the

Fig. 3. Effects of time step size on the value of the negative log likelihood function at convergence (solid line, solid circles) and the number of evaluations of eq. 15 required for the function minimizer to converge (broken line, open circles).

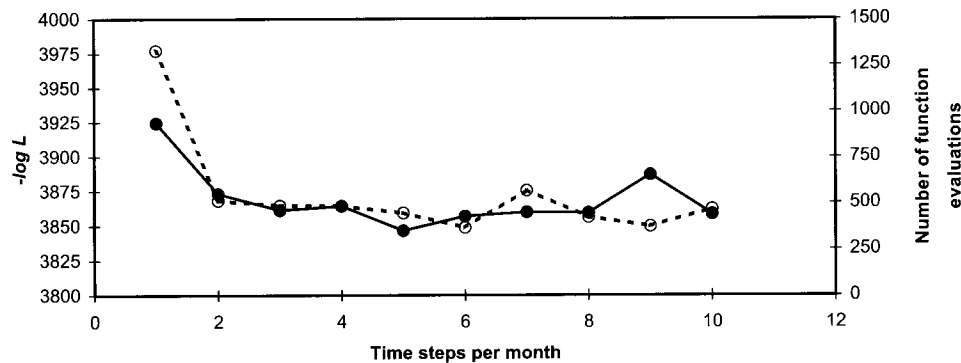
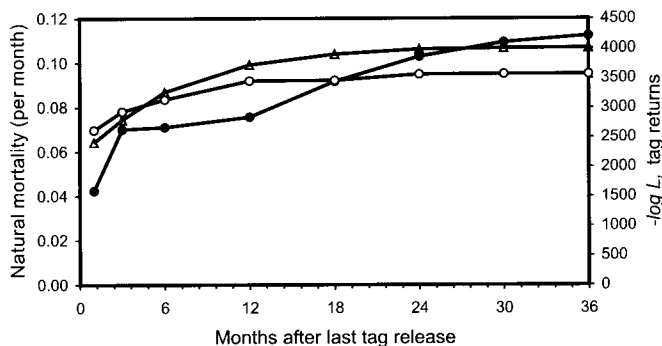


Fig. 4. Effect of length of recapture period (time since last tag release) on estimation of natural mortality rate (solid circles). Also shown is the value of the negative log likelihood function at convergence (triangles) and the predicted number of recaptures (open circles).



parameter estimation are presented. Solutions to eq. 2 using different approximations and different time steps are in effect different models from the standpoint of maximizing eq. 14. The effects of step size on the function minimization process are shown in Fig. 3 for the upwind approximation. Similar solutions were reached at most time steps. Six time steps per month is the method used unless otherwise noted.

The estimate of M is dependent on the time elapsed since the last release of tagged fish. Figure 4 shows the change in likelihood and change in the estimated value of M as the time since the last release is increased. It appears that it necessary to wait at least 2 years after all tags have been released before a reliable estimate of M can be obtained. A 36-month recapture period was routinely used for the results that follow.

Variability of movement was explored by comparing models with different numbers of "seasons". The single-season model with 10 regions (Fig. 2) has 36 estimated parameters: three movement parameters for each of the 10 regions, one catchability coefficient (Q_f) for each of the five fleets, and one natural mortality coefficient (M). All possible models with two seasons of 6-month duration were estimated. The two seasons per year models each have 66 parameters: three movement parameters for each of the 10 regions for each of the two seasons in addition to the six parameters for M and Q_f . Table 2 shows the values of the likelihood function for these models. The best fit is obtained for a model in which

the seasons start in March and September. Other two-season models are possible, but only those with seasons of 6-month duration were tested.

The best two-season model (model 2) can be compared with the single-season model. The single-season model has 36 estimated parameters with a negative log likelihood value of 4214.79. In contrast, the best two-season model has 66 estimated parameters with a negative log likelihood value of 4007.71. The significance of the improvement in fit of the two-season model over the one-season model can be tested using a likelihood ratio test (Brownlee 1965) in which twice the difference between the negative log likelihood for the two models is interpreted as a χ^2 variable with degrees of freedom equal to the difference in numbers of parameters estimated in the two models. In this case, the χ^2 value is 414.16 with 30 df, and the difference is significant with $P < 0.001$. A two-season hypothesis is therefore more consistent with the observed tag returns than is a single-season hypothesis.

The preceding process was extended to compare all possible models with four seasons of 3-month duration. These results are also presented in Table 2. The increase to four seasons produces a significant improvement in fit, with the best fit occurring for a seasonal pattern with seasons beginning in March, June, September, and December. The negative log likelihood decreases from 4007.71 (66) to 3854.56 (126) or $\chi^2(60) = 306.30$, again significant with $P < 0.001$.

Increasing the number of strata always increases the possibility that some strata will not contain any observations. Bills and Sibert (1997) showed that parameters for season \times region strata with low numbers of tag returns are not estimated accurately in simulations. Some of the strata in the four-season models had no observations, as indicated in Table 2. Therefore, no movement hypotheses with more than four seasons were tested.

Variability in movement was further tested by dividing the data into two periods spanning the early and late parts of the SSAP study. The tag release interval for the first period was October 1977 through December 1979 with recaptures through January 1980. The tag release interval for the second period was February 1980 through August 1980 with recaptures through August 1982. The M and Q_f were fixed at the estimates for the two-season model (see discussion on effects of the length of the recovery period on estimates of mortality). The results are presented in Table 3. The aggreg-

Table 2. Hypothesis tests for increasing the number of “seasons” per year.

	Starting month	–log <i>L</i>	Empty strata
Model 1. Single season (<i>n</i> = 36)		<u>4214.79</u>	
Model 2. Two seasons (<i>n</i> = 66)	1, 7	4056.46	
	2, 8	4020.03	
	3, 9	<u>4007.71</u>	
	4, 10	4059.42	
	5, 11	4092.81	
	6, 12	4100.96	
	7, 1	4019.84	
Model 4. Four seasons (<i>n</i> = 126)	1, 4, 7, 10	3886.39	2
	2, 5, 8, 11	3961.92	3
	3, 6, 9, 12	<u>3854.56</u>	1
	4, 7, 10, 1	3881.38	2

Note: The movement hypotheses are identified by the number of seasons per year (single, two, or four), number of parameters estimated (*n*), and the starting month of each season in the hypothesis. The underlined likelihood values indicate the best fit to the data within each model. The number of season × region strata with no reported recaptures is given for the four-season hypotheses. No empty strata occurred in the single- and two-season models.

Table 3. Hypothesis testing for dividing the SSAP tagging study into two periods.

	Model 2 Two seasons	Model 2A Period I	Model 2B Period II	Model 2C Aggregate
Cohorts	159	124	35	159
Tags released	94 430	64 186	30 244	94 430
Tags recaptured	4 211	2 495	1 716	4 211
–log <i>L</i>	4 007.71	1 726.49	1 767.67	<u>3 494.16</u>
Parameters	66	66	66	132
Empty strata	0	0	1	1

Note: “Aggregate” is the sum of periods I and II. The underlined likelihood value indicates the best fit to the data.

gate likelihood for the two periods is 3561.51 and the χ^2 value is 1027.10, a significant improvement in fit at $P < 0.001$. The hypothesis in which the seasonal movements vary among years is more consistent with the observed tag returns than is a hypothesis in which the same pattern of movement repeats each year.

Spatially resolved models predict both temporal and spatial distributions of tag recaptures. Figure 5 displays the aggregate distribution of observed and predicted tag returns from model 2 summed over the entire period of the analysis. Agreement is generally good, particularly for grid cells with large numbers of returns. Figure 6 shows the total observed and predicted returns from model 2 summed over the entire model domain plotted by calendar month. Sharp peaks in tag returns occur immediately following releases of large tag cohorts. These large numbers of returns are predicted fairly well by the model. Figure 7 shows observed and predicted

Table 4. Comparison of tropical (regions 1–8) and subtropical (regions 9 and 10) movement parameters for model 2 and division of the study into two periods.

Season	Region	<i>u</i>	<i>v</i>	\bar{D}
March–August (cool)	Tropical	120.9	99.6	7 504.3
	Subtropical	101.7	100.21	845.7
September– February (warm)	Tropical	132.6	50.5	24 376.5
	Subtropical	0.4	38.3	29.2

Note: |*u*| and |*v*| are the root mean squared averages of *u* and *v*, respectively, and \bar{D} is the arithmetic mean of the estimates of *D* over the indicated region.

returns summed over the entire model domain as a function of the time that the tagged fish were at liberty. Again, agreement in time of recapture between observed and predicted is good even for short times at liberty.

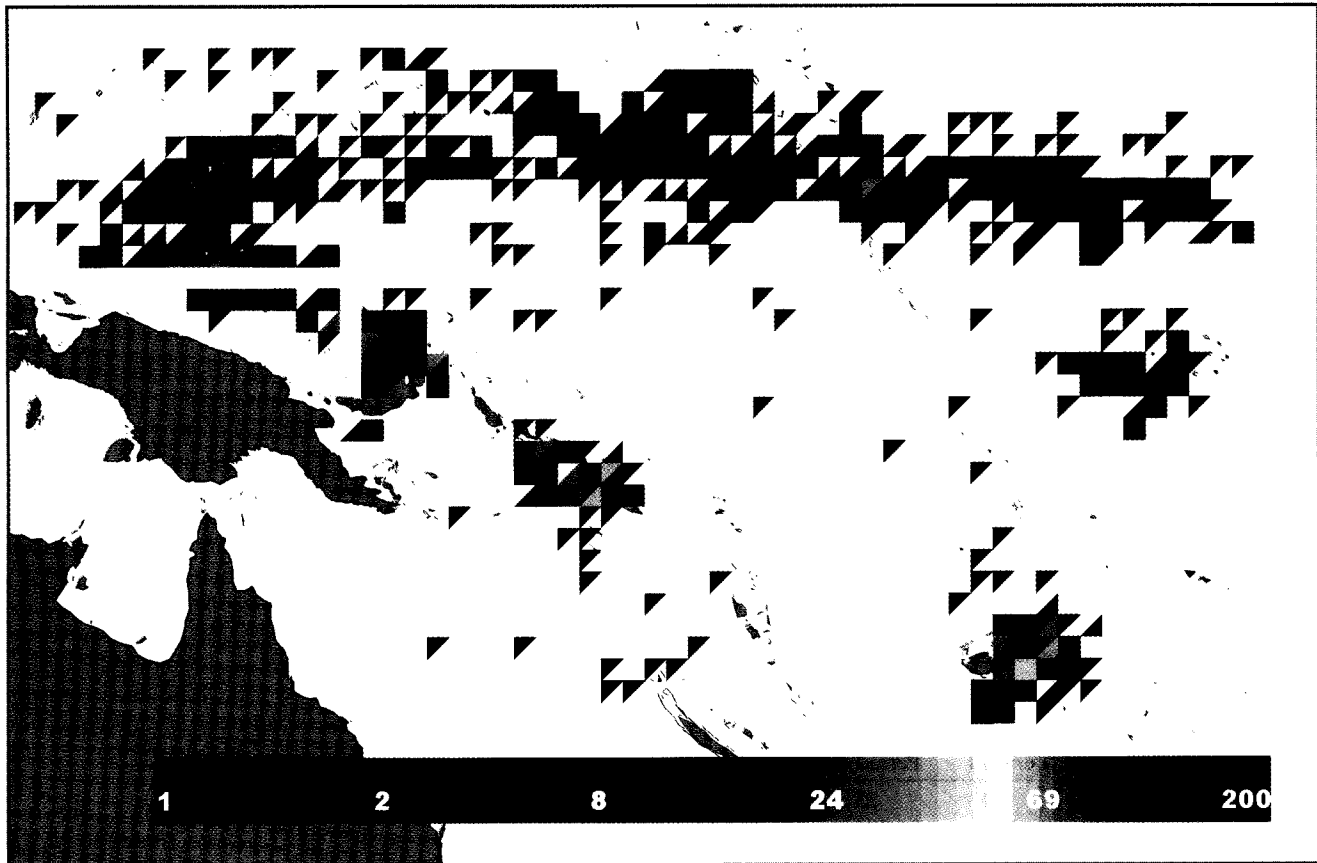
The estimated movement pattern for the two-season, 10-region model (model 2) shows considerable spatial variability in both directed and random components of movement, but with suggestions of large-scale spatial consistency (Fig. 8). There is consistent eastward and southward directed movement in regions 3, 5, 6, 7, and 8 during the September–February season. Directed movements in region 10 are northward in the March–August season and southward in the September–February season. Seasonal differences are more pronounced when the tropical (regions 1–8) and subtropical (regions 9 and 10) model regions are compared (Table 4). During the March–August period (the Southern Hemisphere cold season), the zonal and meridional components of directed movement are of about equal magnitude in both tropical and subtropical regions; diffusive movement is greater in tropical than in subtropical regions. In contrast, during the September–February period (the Southern Hemisphere warm season), the zonal component of directed movement is much greater than the meridional component in the tropical region, whereas the reverse is true in the subtropical region; diffusive movement is much greater in the tropical than in the subtropical region.

Estimates of all parameters and approximate coefficients of variation for the two-season fit (model 2) are tabulated in Appendix B for reference.

Discussion

Accurate finite difference approximation of the advective terms in eq. 2 is a well-known problem in numerical analysis. The upwind difference approximation introduces “numerical viscosity” into the solution that stabilizes the numerical solution, but may also introduce bias in the estimates of the diffusion coefficients, *D*. Low estimates of *D* are evident in some of the region × season strata shown in Fig. 8. Nevertheless, the model appears to give accurate predictions of both the temporal and spatial distribution of tag returns. This result and the results reported by Bills and Sibert (1997) show that introduction of numerical viscosity is probably not important as long as the parameter values estimated using the upwind approximation are used in prediction algorithms that also use upwind approximations. In this sense, the computer program (approximation method, time step, spatial resolution, and boundary conditions) rather than

Fig. 5. Spatial distribution of observed and predicted (model 2) skipjack tuna tag returns summed over time. Each one-degree area of the model region is divided into two triangles, the northwest triangle representing the observed and the southeast triangle representing the predicted tag returns. The color of the triangles represents the number of returns on a logarithmic scale. Two triangles forming a square of uniform color indicate close agreement between observed and predicted recaptures in a one-degree geographic area. Geographic boundaries are the same as in Fig. 2.



the PDE is the model. Discrepancies might occur if specific numerical values of the diffusion parameters were of interest. For example, if comparison of estimates of movement parameters between species or computation of movement parameters from environmental information were of interest, alternative approximations to the advective terms might be more appropriate. Less dispersive approximations are available in the numerical methods literature (e.g., Leonard 1979; Roe 1996), but they tend to be more difficult to implement and require more computational steps. These methods are currently under investigation for use in tuna movement analysis. In the meantime, O'Brien's (1986) criticism of the use of upwind differencing in fluid dynamics models suggests a potentially useful method to approximate the amount of numerical dispersion introduced by upwind differencing. A derivation of the correction is given in Appendix C, and "corrected" diffusion estimates based on it are included in Appendix B.

The model presented in this paper introduces a quantitative framework for expressing the movement of tagged fish and, perhaps more importantly, introduces means to objectively test alternative movement hypotheses. Statistically significant differences in skipjack movement patterns are detectable in the SSAP data, and movement appears to be highly variable in time and space. There is, however, some

degree of spatial consistency in the estimated patterns. The north-south movements noted in region 10 were previously noted in the context of exchange of fish between Fiji and New Zealand (Kearney 1982; Argue and Kearney 1983) and in the context of interaction between widely separated fisheries (Kleiber et al. 1984). Whether this particular movement represents a response to seasonal changes in habitat quality or to trophic and spawning taxes is a matter for speculation (Gauldie and Sharp 1996). Variability in movement on annual or longer time scales is not surprising given the likely response of tuna populations to environmental variation, such as that mediated by the El Niño – Southern Oscillation (Lehodey et al. 1997).

In general, agreement in both time and place of predicted and observed tag returns is excellent. Sporadic, isolated single returns are not well predicted, which should not be surprising. More importantly, the agreement between observed and predicted tag recaptures for short times at liberty in the aggregate attrition curve (Fig. 7) is very encouraging. This result represents a substantial improvement over previous analyses of these data using a spatially aggregated model in which the data for short periods at liberty were excluded from the analysis (Kleiber et al. 1987). Spatially aggregated models make the implicit assumption that tagged fish mix instantaneously through the population in a very large

Fig. 6. Observed (solid circles) and predicted (solid line) tag returns over the time course of the tagging study summed over the model area. The broken line indicates the predicted tag returns from the spatially aggregated model.

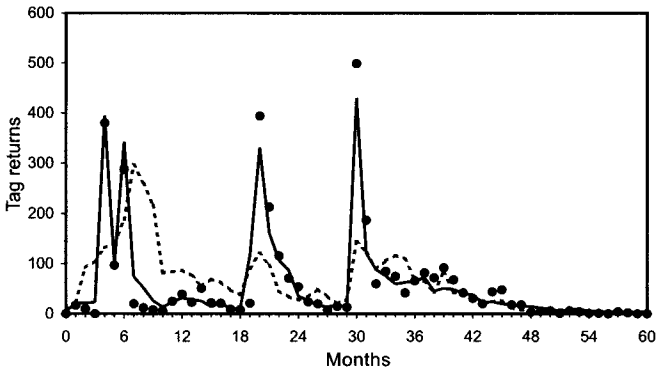


Fig. 7. Observed (solid circles) and predicted (solid line) tag returns over the life of each tag release cohort summed over the model area. The broken line indicates the predicted tag returns from the spatially aggregated model.

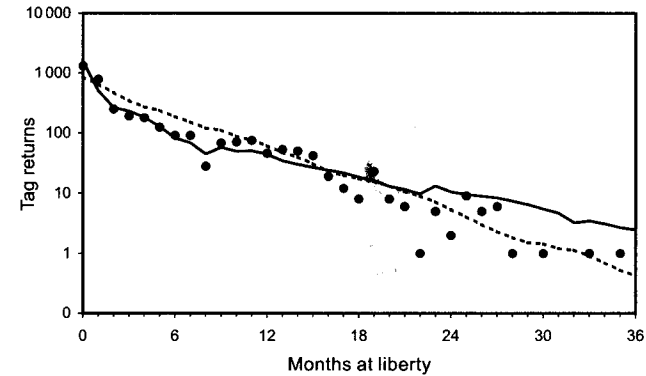
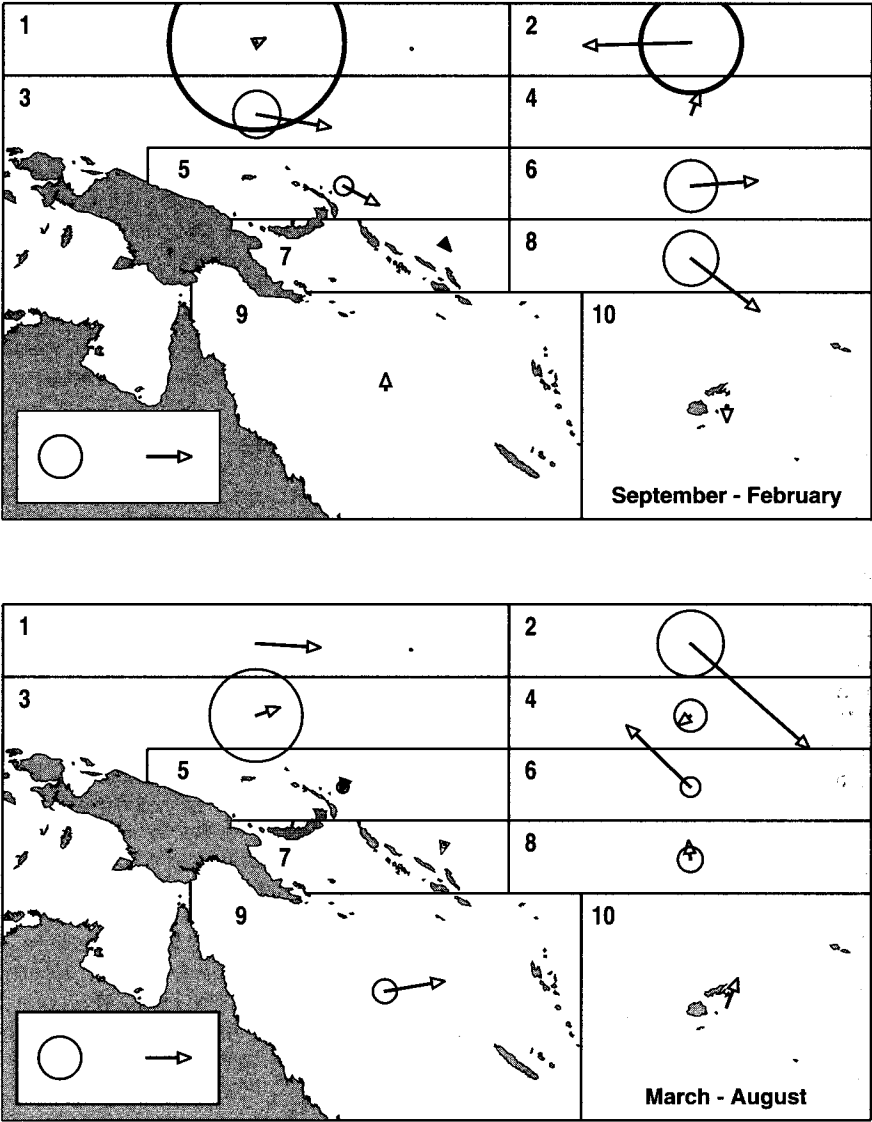


Fig. 8. Estimated movement pattern for model 2. The length of the arrows is proportional to the resultant directed movement component (u, v), and the areas of the circles are proportional to the random movement component (D). The arrow in the legend inset represents directed movement of 100 Nmi-month⁻¹; the circle represents random movement of 3000 Nmi²-month⁻¹. Geographic coordinates are the same as in Fig. 2.



and undefined area. The model presented here makes the assumption that mixing of tags occurs within a single computational element of 60×60 Nmi, a much weaker assumption.

We fitted a model similar to that of Kleiber et al. (1987) to the same data used in the present analysis, obtaining estimates of m and q_f as the spatially aggregated analogs of natural mortality and catchability coefficients. This six-parameter model has a negative log likelihood function value of 5023.04. The likelihood ratio comparison with model 2 is 2030.66 with 60 df, significant with $P < 0.001$. The predicted tag returns from the aggregated model are also shown in Figs. 6 and 7 and demonstrate clearly the lack of fit at short times at liberty.

The spatially resolved estimate of natural mortality is about one half of the analogous estimate from the spatially aggregated model. The usual interpretation of "natural" mortality includes losses from the tag population that cannot be attributed to the recapture of tagged fish. Therefore, M is like fishing mortality for a fishing fleet that never reports catches. This distinction is important because the catchability coefficients, Q_f , are closely related to the predicted recaptures, whereas M is a "residual" mortality related to tagged fish that were never recaptured or were recaptured outside the model domain. In the spatially resolved model, the model domain is precisely defined, and movement of tagged fish within the model domain is explicitly parameterized. In a spatially aggregated model, the model domain is not well defined, and emigration of tagged fish from the fishing grounds could be a major component of natural mortality. The extent to which such movement is explicitly captured by the spatially resolved model depends on the size of the model domain in relation to the distribution of the tagged population and whether closed or open boundaries are specified. In the present analysis, using open boundaries or increasing the size of the model domain had little effect on the estimate of M , indicating that emigration from the model domain is probably not a major component of the estimated M .

Estimates of skipjack natural mortality from spatially aggregated analyses are known to be size dependent, with highest mortality at smallest and largest sizes (South Pacific Commission 1996). However, since most of the fish tagged by the SSAP were greater than 40 cm fork length, the assumption of constant M is justified for most of the period at liberty. The overestimation of recaptures at times at liberty greater than 18 months (Fig. 7) could be attributed to increasing natural mortality for these older fish. Age- or size-structured versions of the diffusion model are possible, requiring solutions of eq. 2 for each age or size cohort. Such models are probably feasible with the current generation of personal computers.

Interpretations of the estimates of M and Q_f are complicated by nonreporting of tag recaptures. Our analysis assumes complete reporting; failure of this assumption would tend to cause overestimates of M and underestimates of Q_f . If the numerical values of these parameters are of interest, accurate estimates of tag-reporting rates are required (Hampton 1997).

Tuna populations often span entire ocean basins. They are not uniformly distributed within their range, and the fisher-

ies that exploit them are also not uniformly distributed. Inclusion of movement in assessment models for such widely distributed and mobile resources would seem essential. The diffusion equation appears to be well suited to describe the dynamics of tag movement, and using modern computer hardware and efficient estimation algorithms, it is possible to estimate movement parameters from tagging data. The diffusion equation may thus be a useful framework for quantitatively considering spatial heterogeneity when devising precautionary policies for "management...of highly migratory fish stocks in their entirety" (Lévy and Schram 1996, emphasis added).

Work is in progress to improve the approximation of the directed movement terms and to apply the model to other large-scale tagging data, including data for other species. Future work will be directed to inclusion of size-related natural mortality and selectivity, environmentally mediated movement (Bertignac et al. 1999), and estimation of movement in circumstances where extensive tagging data are not available.

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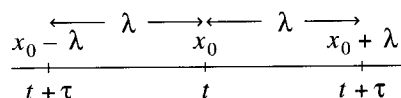
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Appendix A. Applicability of diffusion models to fish movement

The applicability of diffusion models to fisheries in general and to skipjack tuna in particular has been criticized recently (Gauldie and Sharp 1996). These criticisms are based on common misconceptions about diffusion models. We present some general material that we hope will clarify diffusion models and correct some erroneous interpretations. The following presentation is based loosely on material presented by Okubo (1980) and Feller (1966, 1968). Readers requiring more detail and complete mathematical derivations are referred to these references.

The diffusion equation can be derived from the concept of a simple random walk in which an animal is assumed to move a constant small distance, λ , in a constant small interval of time, τ , as shown schematically below in one dimension:



At time 0, the animal is at position x_0 and can move either to the right with probability P_1 or to the left with probability P_2 . At time $t + \tau$, the animal is at position $x_0 + \lambda$ with probability P_1 or at position $x_0 - \lambda$ with probability P_2 . The difference in probability of moving to the left or to the right is $\epsilon = P_1 - P_2$, or bias.

Okubo (1980) showed that

$$(A1) \quad \lim_{\lambda, \tau, \epsilon \rightarrow 0} \epsilon (\lambda/\tau) = u \quad \lim_{\lambda, \tau \rightarrow 0} \lambda (\lambda/\tau) = \frac{D}{2}$$

and that the rate of change in density of animals at a point can be expressed as

$$(A2) \quad \frac{\partial N}{\partial t} = -u \frac{\partial N}{\partial x} + \frac{D}{2} \frac{\partial^2 N}{\partial x^2}.$$

This equation is the special case of eq. 2 in one dimension without mortality and gradients in u and D . The quantity λ/τ has the dimensions of speed. The constant movement implied by this quantity is characteristic of obligate swimmers such as tunas, and the presence of such a quantity in the derivation of the diffusion equation argues strongly for its applicability to skipjack. There is no direction implied by λ/τ . Direction is given to movement by the bias, ϵ . Thus, it is possible for the directed movement term, u , to be zero without implying that the animals are immobile. Rather, $u = 0$ because there is no preferred direction to their movements. The quantity λ/τ also appears in the diffusion parameter D and can be interpreted as a "characteristic speed" parameter.

The model presented in this paper implicitly interprets ϵ and λ , and hence u and D , to be determined by time and place (i.e., season and region) as might be appropriate for an animal with well-defined seasonal migratory pathways. In principal, it is equally possible to parameterize ϵ and λ in terms of gradients in environmental variables such as sea surface temperature, depth of the oxycline, or forage (Bertignac et al. 1999). The result would be a model in which all movement is determined by features of the environment.

The diffusion equation is closely related to the normal probability distribution. Feller (1968) showed that if the probability of observing an animal at point x at time t is given as a normal probability density function

$$(A3) \quad p(t, x) = \frac{1}{\sqrt{2\pi Dt}} e^{-\frac{1}{2} \frac{(x-ut)^2}{Dt}}$$

the function p uniquely satisfies eq. A2. In other words, if animals are dispersing according to eq. A2, after a period of time t , their mean position will be given by ut and the variance of their position will be Dt . Thus, u can be considered to be the average rate of displacement (which may be zero) and D a measure of the rate at which the variance of the displacement increases with time, or spreading rate (Feller 1966).

Simple diffusion models are not very interesting without augmentation. If $u = 0$ in eq. A2, the equilibrium condition is achieved when all horizontal gradients in population density vanish, i.e., no spatial heterogeneity, $\partial N/\partial x = 0$. This case is, of course, the "heat equation" used to describe the distribution of heat in a uniform plate. Various authors who have used diffusion models to describe spatial heterogeneity have introduced additional structure into the diffusion framework. For instance, MacCall (1990) introduced spatially variable logistic population growth and linked the advective parameter u to the instantaneous growth rate. Similarly, Mullen (1989) also introduced spatially variable logistic population growth, but linked the diffusive parameter to local carrying capacity.

Spatial heterogeneity can also be achieved using a diffusion model in which there are spatial gradients in the advective terms, i.e., $\partial u/\partial x \neq 0$. Such variability can be introduced explicitly as in eq. 2 with the term $(\partial/\partial x)(uN)$. Alternatively, the diffusive term can be expressed as $(\partial^2/\partial x^2)(DN)$, which introduces "implicit" advection equal to $\partial D/\partial x$ (which has the same units as velocity). This parameterization may be preferable in some situations (Okubo 1980) but limits the amount of advection that can be expressed by the model.

The diffusion model presented in eq. 2 is one of a large class of models that can be applied to the analysis of spatial variation in ecology and fisheries. Other models can be derived by making alternative assumptions about the underlying process,

e.g., random walks where the step size is not uniform (Schlesinger and Klafter 1985) or correlated (Okubo 1980). The challenge for fisheries is not whether the diffusion framework is suitable, but rather to explicitly include population movement and spatial structure in stock assessment models. Diffusion models are one class of models that appear to work.

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Appendix B. Numerical values of all estimated model parameters with coefficients of variation

Table B1. Estimates and coefficients of variation (CV) of natural mortality, M , and catchability coefficients, Q_f , for the best two-season \times 6-month model (2).

	Estimate	CV	Estimate from aggregated model
M (month ⁻¹)	0.11	0.013	0.20
Q_f of fleet			
Pole-and-line, Papua New Guinea	0.00041	0.0016	0.0000052
Pole-and-line, Solomon Islands	0.00040	0.0025	0.00000029
Pole-and-line, Fiji	0.0046	0.0040	0.0000080
Pole-and-line, Japan	0.00083	0.0058	0.000000094
Purse seine, Japan	0.0057	0.018	0.0000032

Table B2. Estimated movement parameters with approximate coefficients of variation given in parentheses.

Season	Region	Tag returns	u (Nmi·day ⁻¹)	v (Nmi·day ⁻¹)	D (Nmi ² ·month ⁻¹)	$D + \tilde{D}$ (Nmi ² ·month ⁻¹)
1	1	30	4.9 (0.021)	-0.30 (0.0013)	0.047 (0.021)	4 600 (0.020)
	2	2	8.9 (0.057)	-7.9 (0.043)	17 000 (0.23)	32 000 (0.11)
	3	73	1.8 (0.017)	0.64 (0.0057)	34 000 (0.093)	36 000 (0.087)
	4	238	-1.0 (0.0074)	-0.75 (0.0030)	4 100 (0.027)	5 700 (0.019)
	5	779	-0.14 (0.0010)	-0.41 (0.0012)	510 (0.0026)	999 (0.0015)
	6	3	-4.8 (0.027)	4.7 (0.017)	1 600 (0.079)	10 000 (0.018)
	7	285	-0.20 (0.0010)	-0.70 (0.0016)	110 (0.0095)	920 (0.0020)
	8	2	-0.14 (0.0065)	1.4 (0.0097)	2 400 (0.042)	3 900 (0.025)
	9	2	4.5 (0.0067)	0.78 (0.0023)	2 400 (0.013)	7 100 (0.0051)
	10	1309	0.87 (0.0011)	2.2 (0.0016)	8.5×10^{-5} (0.0087)	2 800 (0.0012)
2	1	114	0.68 (0.021)	0.34 (0.018)	120 000 (0.012)	120 000 (0.012)
	2	47	-8.1 (0.031)	-0.22 (0.0085)	40 000 (0.12)	47 000 (0.10)
	3	125	5.6 (0.020)	-0.989 (0.0069)	8 900 (0.048)	15 000 (0.028)
	4	251	0.67 (0.0059)	1.7 (0.0039)	3.0 (0.055)	2 200 (0.0031)
	5	137	2.7 (0.0048)	-1.5 (0.0047)	1 400 (0.015)	5 200 (0.0043)
	6	35	5.0 (0.033)	0.40 (0.0070)	11 000 (0.10)	16 000 (0.074)
	7	259	0.49 (0.0016)	-0.56 (0.0019)	41 (0.017)	990 (0.0016)
	8	11	5.1 (0.036)	-4.0 (0.016)	12 000 (0.0540)	20 000 (0.035)
	9	20	0.017 (0.0082)	1.3 (0.0037)	2.9×10^{-3} (0.034)	1 200 (0.0036)
	10	490	0.0021 (0.0016)	-1.2 (0.0014)	58 (0.0088)	1 200 (0.0015)

Note: $D + \tilde{D}$ is the "corrected" estimate of total diffusive movement based on the derivation presented in Appendix C.

Appendix C. Approximating numerical dispersion

O'Brien's (1986) criticism of the use of upwind differencing in fluid dynamics simulations suggests a potentially useful method to approximate the amount of numerical dispersion introduced by upwind differencing. It is necessary to assume that there are no spatial gradients in the movement parameters to apply this correction, i.e., to assume that $\frac{\partial u}{\partial x} = \frac{\partial v}{\partial y} = \frac{\partial D}{\partial x} = \frac{\partial D}{\partial y} = 0$. Under these assumptions the upwind difference approximation, eq. 4, of the directed movement

term for $u_{ij} > 0$ is

$$(C1) \quad u_{ij} \frac{\partial N}{\partial x} \approx u_{ij} \frac{N_i - N_{i-1}}{\Delta x} = 2u_{ij} \frac{N_i - N_{i-1}}{2\Delta x}.$$

Adding a very particular zero, the approximation becomes

$$(C2) \quad u_{ij} \frac{\partial N}{\partial x} \approx 2u_{ij} \frac{N_i - N_{i-1}}{2\Delta x} + 2u_{ij} \frac{N_{i+1} - N_i}{2\Delta x}$$

which upon rearrangement yields

$$(C3) \quad u_{ij} \frac{\partial N}{\partial x} \approx u_{ij} \left(\frac{\Delta x}{2} \right) \frac{N_{i-1} - 2N_i + N_{i+1}}{(\Delta x)^2} + u_{ij} \frac{N_{i+1} - N_{i-1}}{2\Delta x}.$$

The right-hand term in eq. C3 is the centered-space approximation of the directed movement term, appropriate when $\frac{\partial u}{\partial x} = 0$.

The left-hand term is a finite difference approximation for a second partial derivative in the x direction used for the random movement term appropriate when $\frac{\partial D}{\partial x} = 0$. The numerical dispersion introduced by upwind differencing is approximately

$u_{ij} \left(\frac{\Delta x}{2} \right)$ for $u_{ij} > 0$. Similar derivations apply for $u_{ij} < 0$ as well as for the terms involving v_{ij} . The approximate amount of numerical dispersion is thus

$$(C4) \quad \tilde{D} = \frac{1}{2} (\Delta x |u| + \Delta y |v|).$$

Equation C4 approximates the bias introduced into the estimates of the random movement parameter by the use of upwind differencing in areas of the model domain where gradients in the movement parameters (u , v , D) are small, such as the interior parts of regions.