Population Field Theory with Applications to Tag Analysis and Fishery Modeling: the Empirical Green Function

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Salvadó, C.A.M. 1993. Population field theory with applications to tag analysis and fishery modeling: the empirical Green function. Can. J. Fish. Aquat. Sci. 50: 2491–2512.

A theoretical framework is proposed for analyzing fish movement and modeling the associated dynamics using tagging data. When tagged fish are released in an area small compared with the domain of the fish population and over a period short compared with the time they take to disperse throughout their domain, the pattern of movement approximates a point-source solution of the underlying population dynamics. A method of point sources (Green functions) is invoked for representing the solution of the tagged and untagged fish field equations (partial differential equations) in terms of integral equations. As an approximate representation of a tagging experiment, the Green function is interpreted as the probability density of survival and movement from point to point in space–time. The Green functions are constructed empirically using one parameter, catchability, as the ratio of population density of tagged fish divided by the number of tagged fish released. The number of tagging experiments necessary to characterize the population is dictated by the dependence of catchability on space–time. The moments of the Green function are used to calculate model parameters and lead to the identification of a closed form expression for the transition probability densities of the model assumed.

Un plan de travail théorique est proposé pour analyser les déplacements des poissons et modéliser la dynamique connexe au moyen de données de marquage. Lorsque des poissons marqués sont relâchés dans une zone de faibles dimensions par rapport au domaine occupée par la population de poissons et sur une courte période par rapport au temps de dispersion nécessaire dans leur domaine, le profil de déplacement correspond à peu près à une solution de source ponctuelle de la dynamique des populations sous-jacente. Une méthode de sources ponctuelles (fonction de Green) est retenue pour représenter la solution des équations de mouvement des poissons marqués et non marqués (équations aux dérivées partielles) en fonction d'équation intégrales. À titre de représentation approximative d'une expérience de marquage, la fonction de Green est interprétée comme la densité de probabilité de la survie et du déplacement d'un point à l'autre dans l'espace et dans le temps. Les fonctions de Green sont établies de façon empirique à l'aide d'un paramètre, la vulnérabilité, qui correspond au rapport entre la densité de population des poissons marqués divisée par le nombre de poissons marqués relâchés. Le nombre d'expériences de marquage nécessaires pour caractériser la population est dicté par la dépendance de la vulnérabilité à l'égard du temps et de l'espace. Les moments de la fonction de Green sont utilisés pour calculer les paramètres du modèle et permettent l'établissement d'une expression fermée des densités de la probabilité de transition du modèle hypothétique.

Received September 24, 1991
Accepted June 21, 1993
(JB232)

Reçu le 24 septembre 1991
Accepté le 21 juin 1993

1. Introduction

Considerable effort has been devoted to understanding animal movement patterns (Okubo 1980; Murray 1989). In particular, the study of fish movement patterns by the use of tagging experiments has been reviewed by Hilborn (1990), who discussed recent studies on the subject (Bayliff 1979; Ishii 1979; Sibert 1984; Hunter et al. 1986; Kleiber et al. 1987). These studies require the assumption of a model (a partial differential equation, or, in general, a field equation) parameterized in such ways so that it accommodates the movement of tagged fish and the catch and natural death rate densities. The model parameters are typically evaluated by means of the tagging data and such extreme value principles as maximum likelihood estimators.

A field equation is also employed in the empirical method discussed here. It is one of great generality that can be stated simply as the inhomogeneous advection–diffusion equation (Okubo 1980) with mortality for dilute populations with spatially and temporally varying coefficients. The empirical method that will be exposed in this work is a one-parameter model and is adequate for answering the question on fisheries interaction posed in Section 2. It is also the first step that would be taken to prepare the data for fitting a multiple parameter model.

In a typical tagging experiment, tagged fish are released over a time interval short in relation to the time they disperse throughout their domain and into an area small in relation to the domain of the population. Under these conditions, the release and recovery data from the experiment approximate a point-source solution of the field equations that represent the population dynamics of the fish. The method of solving inhomogeneous linear differential equations by use of their point-source solutions has been known for many years, and the subject is referred to as the method of Green functions (Feynman 1949; Courant and Hilbert 1953; Morse and Feshbach 1953; Bjorken and Drell

1964: Garabedian 1964; Feynman and Hibbs 1965; Byron and Fuller 1970; Gilbarg and Trudinger 1979). The Green function associated with a linear differential equation is the solution of the differential equation under the influence of a unit impulsive source at one point (i.e., a source of unit strength applied at one space–time point) and therefore is the point-source solution.

In general, if tagged fish were released at every space–time point, the subsequent recapture results would differ between points owing to uneven distributions of fishing effort in space–time. In addition, there may be other influences that affect the patterns of the point sources such as geographic (e.g., boundaries) and cyclic factors (e.g., seasonal, El Niño). Nevertheless, each of the release and recovery measures still represents a point-source solution of the field equations that describe the underlying fish dynamics and, therefore, in some manner must be approximately a Green function associated with the dynamics.

Apparently, Green functions have never been used in modeling tagged fish populations, the reason probably being that the use of the method of Green functions requires linearity, and fish population dynamics processes, such as recruitment, are thought to be nonlinear. By separating the linear and the nonlinear parts, and by considering the nonlinear portion as being part of the term that makes the field equation inhomogeneous, the method of Green functions becomes not only useful, but conceptually simple, in fish population modeling.

The following symbols are used:

$\mathcal{A}$ = domain of the population
$\mathbf{R}^2$ = infinite plane
$\partial\mathcal{A}$ = boundary of $\mathcal{A}$
$\mathbf{n}_\perp$ = unit vector normal to $\partial\mathcal{A}$ pointing outward
$\mathbf{R}$ = infinite line
$\partial\mathcal{A}_A$ = portion of $\partial\mathcal{A}$ on which population is absorbed
$\partial\mathcal{A}_R$ = portion of $\partial\mathcal{A}$ from which population is reflected
$\mathcal{A}_i$ = neighborhood of point $\mathbf{r}_i$ referred to as a cell
n = number of nonoverlapping cells defined in $\mathcal{A}$
$\mathbf{i}, \mathbf{j}$ = unit vectors respectively in the $+x$ and $+y$ directions
$\{O_i: i = 1, 2, \ldots\}$ = set whose members are $O_1, O_2 \ldots$
$\in$ = member of
$\subseteq$ = subset or equal to
$\cup$ = union
$<$ = less than
$>$ = greater than
$\ll$ = much less than
$\gg$ = much greater than
$\leq$ = less than or equal to
$\geq$ = greater than or equal to
$\sim$ = similar to, of the same order of magnitude
$\mathbf{r} = x\mathbf{i} + y\mathbf{j}$ = position vector $\in \mathcal{A}$
$r = \sqrt{\mathbf{r} \cdot \mathbf{r}}$ = magnitude of vector $\mathbf{r}$
$\mathbf{r}_T = x_T\mathbf{i} + y_T\mathbf{j}$ = location of tag release $\in \mathcal{A}$
t = time
a = age
t_T = time of tag release
$[t_i, t_f] = t_f - t_i$
$\mathcal{T}_I = [t_I, t]$
$\mathcal{T}_T = [t_T, t] \subseteq \mathcal{T}_I$
$\mathcal{T}_j = [t_j, t_{j+1}]$
$\mathcal{T}' = [t', t]$
$\mathcal{T}$ = interval of time of arbitrary length; a period
m = number of intervals of time $\mathcal{T}_j$ into which $\mathcal{T}_I$ is subdivided
$e(\mathbf{r},t)$ = fishing effort density field
$c_T(\mathbf{r},t)$ = tagged fish catch density rate field
$c(\mathbf{r},t)$ = untagged fish catch density rate field
$p_T(\mathbf{r},t)$ = tagged fish population density field
$p(\mathbf{r},t)$ = untagged fish population density field
dl = infinitesimal line element
$d^2\mathbf{r}$ = infinitesimal surface element = $dxdy$ in Cartesian coordinates
∇ = differential operator $\mathbf{i}\partial/\partial x + \mathbf{j}\partial/\partial y$
$\triangle = \nabla \cdot \nabla = \partial^2/\partial x^2 + \partial^2/\partial y^2$
$\mathbf{j}(\mathbf{r},t)$ = flux of p
$s(\mathbf{r},t)$ = source and/or sink density rate of field p
$d(\mathbf{r},t)$ = natural death density rate field
$m(\mathbf{r},t)$, $m(t)$ = natural death rate
$q(\mathbf{r},t)$ = catchability
$f(\mathbf{r},t)$ = fishing death rate field = $q(\mathbf{r},t)\, e(\mathbf{r},t)$
$z(\mathbf{r},t) = m(\mathbf{r},t) + f(\mathbf{r},t)$
$N_T(\mathbf{r}_T,t_T)$ = number of tagged fish released at space-time point $(\mathbf{r}_T,t_T)$
N_R = number of tagged fish recaptured in the interval of time $\mathcal{T}_T$
$\mathcal{L}_0$ = spatial differential operator dependent on f
$\mathcal{L}$ = spatial differential operator independent of f
$\mathcal{N}(\mathbf{r}',\sigma^2)$ = two-dimensional normal distribution centered at $\mathbf{r}' = x'\mathbf{i} + y'\mathbf{j}$ and variance σ^2
$\delta(\mathbf{r} - \mathbf{r}') = \delta(x - x')\delta(y - y')$ = two-dimensional Dirac delta function which can be represented as $\lim_{\sigma \to 0} \mathcal{N}(\mathbf{r}',\sigma^2)$
$g_0(\mathbf{r},t|\mathbf{r}',t')$ = effort-dependent Green function, which represents the probability density that a fish will survive the movement to point $\mathbf{r}$ from point $\mathbf{r}'$ in the interval of time $\mathcal{T}'$ when fishing takes place during that time interval
$g(\mathbf{r},t|\mathbf{r}',t')$ = effort-independent Green function, which represents the probability density that a fish will survive the movement to point $\mathbf{r}$ from point $\mathbf{r}'$ in the interval of time $\mathcal{T}'$ if no fishing takes place during that time interval
$r(\mathbf{r},t)$ = recruitment density rate field
$u_0(\mathbf{r},t)$ = population density due to recruitment = superposed recruitment density rate field with the effort-dependent Green function g_0
$u(\mathbf{r},t)$ = population density due to recruitment = superposed recruitment density rate field with the effort-independent Green function g
$h(t - t')$ = Heaviside step function which can be represented as $dh(t - t')/dt = \delta(t - t')$
$\mathbf{v}(\mathbf{r},t)$, $\mathbf{v}(t) = v_x\mathbf{i} + v_y\mathbf{j}$ = drift velocity
$k(\mathbf{r},t)$, $k(t)$ = diffusivity
$\mathcal{E} = \{e(\mathbf{r}_i,t_j) : i = 1, 2, \ldots, n;\ j = 1, 2, \ldots, m + 1\}$ = set of effort density measurements
$\mathcal{C} = \{c(\mathbf{r}_i,t_j) : i = 1, 2, \ldots, n; j = 1, 2, \ldots, m + 1\}$ = set of catch density rate measurements of untagged fish
$\mathcal{C}_T(\mathbf{r}_k,t_l) = \{c_T(\mathbf{r}_i,t_j) : i = 1, 2, \ldots, n; j = l, l + 1, \ldots, m + 1\}$ = set of catch density rate measurements of tagged fish released in cell $\mathcal{A}_k$ in the interval of time $\mathcal{T}_l$.
$\mathcal{C}_T = \{\mathcal{C}_T(\mathbf{r}_s,t_{l+s-1}) : s = 1, 2, \ldots, n\}$ = set of catch density rate measurement of tagged fish for n tagged fish releases in zones $\mathcal{A}_s$, correspondingly in the intervals of time $\mathcal{T}_{l+s-1}$ for $s = 1, 2, \ldots, n$.
$\mathcal{Q} = \{q(\mathbf{r}_s,t_{l+s-1}) : s = 1, 2, \ldots, n\}$ = set of catchabilities computed from tagging experiments in cells $\mathcal{A}_s$ correspondingly in the intervals of time $\mathcal{T}_{l+s-1}$ for $s = 1, 2, \ldots, n$
$\mathcal{R} = \{r(\mathbf{r}_i,t_j) : i = 1, 2, \ldots, n; j = l + n, l + n + 1, \ldots, m + 1\}$ =

set of recruitment density rates computed at $\mathcal{A}_i$ in the intervals of time $\mathcal{T}_j$ for $j = l + n, l + n + 1, \ldots, m$

$\mathcal{G}_0(\mathbf{r}_k,t_l) = \{g_0(\mathbf{r}_i,t_{l+s}|\mathbf{r}_k,t_l) : i = 1, 2, \ldots, n; s = 1, 2, \ldots, m - l + 1\}$ = set of values of the effort-dependent Green function computed from a release of tagged fish in cell $\mathcal{A}_k$ in the interval of time $\mathcal{T}_l$

$\mathcal{G}_0 = \{\mathcal{G}_0(\mathbf{r}_s,t_{l+s-1}) : s = 1, 2, \ldots, n\}$ = set of values of n Green functions from tagged fish releases in cells $\mathcal{A}_s$ correspondingly during the intervals of time $\mathcal{T}_s$ for $s = l, l + 1, \ldots, l + n - 1$

$\mathcal{G}_0^*(\mathcal{T}_j) = \{g(\mathbf{r}_i,t_{j+1}|\mathbf{r}_k,t_j) : i, k = 1, 2, \ldots, n\}$ = set of effort-dependent transition probability densities for the interval of time $\mathcal{T}_j$

$\mathcal{G}_0^* = \mathcal{G}_0^*(\mathcal{T}_{l+n}) \cup \mathcal{G}_0^*(\mathcal{T}_{l+n+1}) \cup \ldots \cup \mathcal{G}_0^*(\mathcal{T}_m) = \{g_0(\mathbf{r}_i,t_{j+1}|\mathbf{r}_k,t_j) : i, k = 1, 2, \ldots, n; j = l + n, l + n + 1, \ldots, m\}$ = set of effort-dependent transition probability densities in the intervals of time $\mathcal{T}_j$ for $j = l + n, l + n + 1, \ldots, m$

$\mathcal{G}^* = \{g(\mathbf{r}_i,t_{j+1}|\mathbf{r}_k,t_j) : i, k = 1, 2, \ldots, n; j = l + n, l + n + 1, \ldots, m\}$ = set of effort-independent transition probability densities in the intervals of time $\mathcal{T}_j$ for $j = l + n, l + n + 1, \ldots, m$

$$\langle f(\mathbf{r}) \rangle\ (t|\mathbf{r}',t') = \int_{\mathcal{A}} d^2\mathbf{r}\, f(\mathbf{r}) g(\mathbf{r},t|\mathbf{r}',t')$$

$$\langle f(\mathbf{r}_i) \rangle\ (t_{j+1}|\mathbf{r}_k,t_j) = \sum_{i=1}^{n} \mathcal{A}_i f(\mathbf{r}_i) g(\mathbf{r}_i,t_{j+1}|\mathbf{r}_k,t_j)$$

l.h.s., r.h.s. = left-hand side, right-hand side.

2. Problem Statement and Formulation

Assume that almost all of a fish population is contained in a domain $\mathcal{A} \in \mathbf{R}^2$. Although in reality, fish populations inhabit three-dimensional space, this work will deal with highly migratory species whose vertical movement is negligible compared with their horizontal motion. Such is the case, for example, of pelagic species of fish.

Assume also that the population is being exploited with effort density $e(\mathbf{r},t)$ over the time interval $\mathcal{T}_l = [t_l,t] = t - t_l$. During that time interval, a catch density rate $c(\mathbf{r},t)$ is realized. Because I wish to determine how an increased fishing effort in a portion of $\mathcal{A}$ will affect the catch density rate in another portion of $\mathcal{A}$, the movement patterns of the population must be determined. To this end, a tagging experiment with distinguishable tags is initiated at time $t_T \in \mathcal{T}_l$ which results in a tagged fish catch density rate $c_T(\mathbf{r},t)$ in the interval of time $\mathcal{T}_T = [t_T,t] \subseteq \mathcal{T}_l$. In addition, I wish to calculate the recruitment density rate $r(\mathbf{r},t)$ and estimate parameters assuming that the fish population is accurately modeled by a diffusive population that drifts.

I have previously considered the fisheries interaction problem formulated above making no use of differential equations by applying the principle of linear superposition (Salvadó 1994). Here, I will go about solving this problem by use of the Green functions associated with population field equations derived from the Rayleigh transport theorem (Okubo 1980). This theorem states that any population that is in motion and distributed in a space–time continuum must satisfy the relationship

$$(1)\quad \frac{\partial p(\mathbf{r},t)}{\partial t} + \nabla\cdot\mathbf{j}(\mathbf{r},t) = s(\mathbf{r},t)$$

where p is the population density, $\mathbf{j}$ is the flux of p (the amount of transport of population across a unit area in unit time), and s is the source (+) or sink (−) rate densities of p at space–time point $(\mathbf{r},t)$. The flux $\mathbf{j}$ will be assumed to be the result of an operation on the spatial distribution of p that results in a differential expression that is linear in p.

For a population whose movement and distribution in space–time are structured by age, the transport equation given in (1) must be modified. If $p(\mathbf{r},t,a)$ is the population density of individuals of age a at space–time point $(\mathbf{r},t)$, the transport equation is given by (Murray 1989)

$$(2)\quad \frac{\partial p(\mathbf{r},t,a)}{\partial t} + \frac{\partial p(\mathbf{r},t,a)}{\partial a} + \nabla\cdot\mathbf{j}(\mathbf{r},t,a) = s(\mathbf{r},t,a)\,.$$

However, because aging is at the same rate as the passing of time, transforming (2) with the set of transformations for $t > a$

$$t' = t$$
$$a' = t - a$$
$$\mathbf{r}' = \mathbf{r}$$

leads to the transport equation

$$(3)\quad \frac{\partial p(\mathbf{r}',t',t'-a')}{\partial t'} + \nabla'\cdot\mathbf{j}(\mathbf{r}',t',t'-a') = s(\mathbf{r}',t',t'-a')\,.$$

Equation (3) is of the same form as (1) except that the latter has fields with two arguments of time. It follows that the solutions of the age-dependent field equations can be inferred from those expressions corresponding to age-independence. Therefore, for simplicity, this exposition will be for the age-independent case.

A population density is said to be conserved if the source and/or sink term s in Eq. (1) vanishes, but in the general treatment here, population density may be nonconservative. With $d(\mathbf{r},t)$ as the natural death density rate, and $r(\mathbf{r},t)$ as the recruitment density rate, $s(\mathbf{r},t)$ is generally given by

$$s(\mathbf{r},t) = r(\mathbf{r},t) - [d(\mathbf{r},t) + c(\mathbf{r},t)]\,.$$

The biomass volume of fish populations is small in comparison with the volume of water they inhabit and, therefore, I shall assume that the population is dilute. As a consequence of this assumption, I can make some linear approximations. Because the catch density rate must be a function of population density (i.e., there can be no catch if there are no fish), expanding $c(p)$ in a Taylor series about $p = 0$ up to the linear term yields $c(p) = fp$ ($c(0) = 0$ necessarily), where $f = [\partial c(p)/\partial p]_{p=0}$ is the death rate due to fishing. Because f must be a function of effort density (i.e., there can be no fishing death if there is no fishing), expanding $f(e)$ in a Taylor series about $e = 0$ up to the linear term yields $f(e) = qe$ ($f(0) = 0$ necessarily), where $q = [\partial^2 c(p,e)/\partial p \partial e]_{p=e=0}$ is the catchability. Therefore, for low population and effort densities, one can assume the model for catch density rate to be

$$(4)\quad c(\mathbf{r},t) = f(\mathbf{r},t)\,p(\mathbf{r},t) = q(\mathbf{r},t)\,e(\mathbf{r},t)\,p(\mathbf{r},t)\,.$$

Similarly, the natural death density rate d must be a function of population density. Therefore, with m the natural death rate (i.e., natural mortality) and $d(p)$ expanded in a Taylor series about $p = 0$ up to the linear term (where $d(0) = 0$ necessarily), at low population density the model for natural death density rate can

be assumed to be

$$(5)\quad d(\mathbf{r},t) = m(\mathbf{r},t)\,p(\mathbf{r},t)\,.$$

In the method of analyzing the dynamics of populations in space–time that follows, it is not necessary to invoke a particular model for the source term corresponding to recruitment density rate. However, as I shall show, it is possible to determine empirically the recruitment density rate once the population density due to recruitment is calculated.

I shall further assume that the population drifts with velocity $\mathbf{v}(\mathbf{r},t)$. The population is also assumed to disperse diffusively with diffusivity $k(\mathbf{r},t)$. Then, consistent with the assumption of linearity due to diluteness used in the formulation of the catch density rate and natural death density rate, the flux of the population density is

$$(6)\quad \mathbf{j}(\mathbf{r},t) = [\mathbf{v}(\mathbf{r},t) - k(\mathbf{r},t)\nabla]\,p(\mathbf{r},t)\,.$$

Therefore, the field equation the population density is assumed to satisfy is

$$(7)\quad \left[\frac{\partial}{\partial t} + \mathcal{L}_0\right] p(\mathbf{r},t) = r(\mathbf{r},t)$$

in the spatial domain $\mathbf{r} \in \mathcal{A}$, where $\mathcal{L}_0$ is a differential operator that operates only on the spatial distribution of $p(\mathbf{r},t)$ and is given by

$$(8)\quad \mathcal{L}_0 = b_0(\mathbf{r},t) + \mathbf{b}_1(\mathbf{r},t)\cdot\nabla + b_2(\mathbf{r},t)\,\Delta$$

where

$$\nabla = \mathbf{i}\frac{\partial}{\partial x} + \mathbf{j}\frac{\partial}{\partial y}$$

$$\Delta = \nabla\cdot\nabla = \frac{\partial^2}{\partial x^2} + \frac{\partial^2}{\partial y^2}$$

$$(9)\quad b_0(\mathbf{r},t) = z(\mathbf{r},t) + \nabla\cdot\mathbf{v}(\mathbf{r},t)$$

$$\mathbf{b}_1(\mathbf{r},t) = \mathbf{v}(\mathbf{r},t) - \nabla\,k(\mathbf{r},t)$$

$$b_2(\mathbf{r},t) = -k(\mathbf{r},t)$$

and $z(\mathbf{r},t) = m(\mathbf{r},t) + f(\mathbf{r},t)$. The restrictions on the parameters of the field equation are that $\int_{t_\tau}^{t} d\tau z(\mathbf{r},\tau) \geq 0$, $\int_{t_\tau}^{t} d\tau k(\mathbf{r},\tau) \geq 0$, and that $\nabla\cdot\mathbf{v}(\mathbf{r},t)$ and $\Delta k(\mathbf{r},t)$ exist. For $b_0(\mathbf{r},t) = r(\mathbf{r},t) = 0$, field equation (7) is a Fokker–Planck equation used in the study of stochastic processes where probability is conserved (Gardiner 1990). In the general treatment of this work, $b_0(\mathbf{r},t) \neq 0$ and $r(\mathbf{r},t) \neq 0$. Because these terms represent sources and/or sinks of population, probability will not be conserved.

The domain of the population is finite, so I must discuss the boundary $\partial\mathcal{A}$ of $\mathcal{A}$. For the purposes of this paper the boundary $\partial\mathcal{A}$ is defined as the line at the edge of $\mathcal{A}$ (i.e., $\partial\mathcal{A} \subset \mathcal{A}$) beyond which the population is unlikely to inhabit due to unfavorable physicobiological conditions. In general, fish populations have two types of boundaries: well-defined ones delineating, for example, the water–land interface and fuzzy ones demarcating, for example, lines beyond which if a member of the population strays is likely to perish due to unfavorable environmental conditions. It can be shown (Appendix A) that with a prescribed population density at an initial time (initial condition) the solution of (7) is unique and "simply" represented when $p(\mathbf{r},t)$ or the component normal to $\partial\mathcal{A}$ of $\nabla p(\mathbf{r},t)$ vanish on $\partial\mathcal{A}$. By "simple" representation of the solution, I mean that the Green function associated with (7) is a simple function of measurable quantities, a concept that will become evident when I discuss the solutions. However, the required simplicity does lead to physicobiological pertinent boundaries of fish population domains.

Consider the first boundary condition

$$(10)\quad p(\mathbf{r},t) = 0$$

for $\mathbf{r} \in \partial\mathcal{A}$. The drift $\mathbf{v}(\mathbf{r},t)$ could be the motion of the medium, relative to a fixed coordinate system, that the population is riding or fighting. The diffusivity $k(\mathbf{r},t)$ is ultimately an environmental variable that could be negatively correlated with the amount of food encountered by the population at space–time point $(\mathbf{r},t)$. Low food availability in a region of the population domain would mean that the random motion of a foraging fish population in that region could increase and, according to (7), would be "pushed" in the opposite direction in which $k(\mathbf{r},t)$ changes the fastest towards a region of lower k. As I shall later show in an example, an increased diffusivity at a particular space–time point results in a decrease of the population density at that point. Although the natural death rate $m(\mathbf{r},t)$ has limits imposed by evolution, it is dependent also on environmental factors such as food availability and probability of encounters with predators. A high value for $m(\mathbf{r},t)$ could mean low food availability and/or high probability of encounter with a predator at space–time point $(\mathbf{r},t)$. Therefore, the boundary condition (10) would be a good model of a "fuzzy" population boundary preceded by regions of increasing diffusivity and/or natural death rate. A boundary on which (10) holds is aptly known as the perfectly absorbing boundary (Okubo 1980; Gardiner 1990). In the mathematical literature, this boundary condition is known as homogeneous Dirichlet conditions.

A second boundary condition mentioned above that leads to unique simple solutions of (7) (together with an initial condition) is formulated by considering the integral over $\mathcal{A}$ of equation (1) and applying the Divergence Theorem (Courant and Hilbert 1953) to the term containing the divergence of $\mathbf{j}(\mathbf{r},t)$. Letting $\mathbf{n}_\perp$ be the unit vector normal to $\partial\mathcal{A}$ pointing outward, then

$$\int_{\mathcal{A}} d^2\mathbf{r}\frac{\partial p(\mathbf{r},t)}{\partial t} = \int_{\mathcal{A}} d^2\mathbf{r}s(\mathbf{r},t) - \oint_{\partial\mathcal{A}} dl\,\mathbf{n}_\perp\cdot\mathbf{j}(\mathbf{r},t)\,.$$

This states that the change in population density over time is due to the sinks and sources of population in $\mathcal{A}$ and the flux of $p(\mathbf{r},t)$ across $\partial\mathcal{A}$. However, because $\mathcal{A}$ is the domain of the population, the flux of p across $\partial\mathcal{A}$ must vanish and the change in population density is due to the sources and sinks. Therefore,

$$\mathbf{n}_\perp\cdot\mathbf{j}(\mathbf{r},t) = 0$$

for $\mathbf{r} \in \partial\mathcal{A}$. Using (6), it can be written as

$$\mathbf{n}_\perp \cdot \nabla p(\mathbf{r},t) = \frac{\mathbf{n}_\perp \cdot \mathbf{v}(\mathbf{r},t)}{k(\mathbf{r},t)} p(\mathbf{r},t)$$

in the domain $\mathbf{r} \in \partial\mathcal{A}$. Furthermore, because $\mathcal{A}$ is the domain of the population the vanishing of the flux must be due to the inability of any member of the population to cross $\partial\mathcal{A}$. Therefore, the component of the drift velocity normal to $\partial\mathcal{A}$ must also vanish (i.e., $\mathbf{n}_\perp \cdot \mathbf{v}(\mathbf{r},t) = 0$ for $\mathbf{r} \in \partial\mathcal{A}$) and the boundary condition reduces to

$$(11) \quad \mathbf{n}_\perp \cdot \nabla p(\mathbf{r},t) = 0$$

for $\mathbf{r} \in \partial\mathcal{A}$. A boundary on which (11) holds is aptly known as the perfectly reflecting boundary (Okubo 1980; Gardiner 1990). In the mathematical literature, this boundary condition is known as homogeneous Neumann conditions. This boundary condition is appropriate for the ocean–land boundary.

I shall assume throughout this work that the boundary of the domain of the population is composed of segments or portions which are perfectly absorbing and the remainder perfectly reflecting. If $\partial\mathcal{A}_A$ is the total of the absorbing segments, and $\partial\mathcal{A}_R$ is the total of the reflecting segments, then $\partial\mathcal{A} = \partial\mathcal{A}_A + \partial\mathcal{A}_R$. The solution of the field equation (7), with a prescribed initial condition, satisfying the mixed boundary conditions is unique (Appendix A).

Using this formulation, I shall show that data from a tagging experiment properly performed may be used to construct an approximate representation of a Green function. I shall, therefore, develop an empirical technique to construct Green functions using tagged fish catch and effort data and use these results for a fishery interaction problem and the calculation of model parameters.

3. Problem Solution

In this section, I will develop the Green function as an approximate representation of a tagging experiment, list its properties, and use it to represent the tagged and untagged fish population densities. For an intuitive approach to the developments in this section which makes no use of differential equations, see Salvadó (1994).

3.1. Effort-Dependent Green Function

In this subsection, I formulate and find representations of the solutions for the tagged and untagged portion of the population in terms of a point-source solution that is dependent on the death rate due to fishing. I shall also show how the point-source solutions are constructed from the fields c_T and e. Although these are correct solutions to model the population field at one level of fishing effort, unless $m(\mathbf{r},t) \gg f(\mathbf{r},t)$, they are not of much use for the case of considering the interaction between different cells (for the time being defined as a small subset of $\mathcal{A}$) of the domain of the population at various levels of effort.

3.1.1. Tagged fish dynamics

Consider a tagging experiment in which N_T tagged fish are released in an area small compared with $\mathcal{A}$ about position $\mathbf{r}_T$ beginning at time $t_T \in \mathcal{T}_f$. The duration of the tagged fish release is short conpared with $\mathcal{T}_T$, where $t \gg t_T$. I shall index the number of tagged fish, location, and initial time of release by writing $N_T(\mathbf{r}_T,t_T)$.

Let $\mathcal{L}_0$ be a linear differential operator which contains the terms of the field equation that describe the natural and fishing death rates and the spatial dynamics. Consistent with (7) and the general fish population problem formulated in Section 2, the tagged fish population density $p_T(\mathbf{r},t)$ must satisfy a field equation of the form

$$(12) \quad \left[\frac{\partial}{\partial t} + \mathcal{L}_0\right] p_T(\mathbf{r},t) = 0$$

in the space–time domain $\mathbf{r} \in \mathcal{A}$, $t \geq t_T$.

The initial condition of the tagged fish release process will be approximated as if the release is at one point (i.e., at $\mathbf{r} = \mathbf{r}_T$) and instantaneous (i.e., at $t = t_T$): an approximate representation of the initial condition of the population density of tagged fish is

$$(13) \quad p_T(\mathbf{r},t_T) = N_T(\mathbf{r},t_T)\, \delta(\mathbf{r} - \mathbf{r}_T)$$

in the space domain $\mathbf{r} \in \mathcal{A}$ and where δ is a two-dimensional Dirac delta function (Lighthill 1964; Butkov 1968). The discretization of space–time will relax the condition of an instantaneous release at a point of all the tagged fish.

The boundary $\partial\mathcal{A} = \partial\mathcal{A}_A + \partial\mathcal{A}_R$ is assumed composed of segments on which it is absorbing ($\partial\mathcal{A}_A$) and those on which it is reflecting ($\partial\mathcal{A}_R$). Therefore, $p_T(\mathbf{r},t)$ satisfies

$$(14) \quad p_T(\mathbf{r},t) = 0$$

on the space–time domain $\mathbf{r} \in \partial\mathcal{A}_A$, $t \geq t_T$, and

$$(15) \quad \mathbf{n}_\perp \cdot \nabla p_T(\mathbf{r},t) = 0$$

in the space–time domain $\mathbf{r} \in \partial\mathcal{A}_R$, $t \geq t_T$.

I seek the solution of (12) that satisfies conditions (13), (14), and (15). To this end, I consider the Green function that is associated with (12) for a source space–time point at $(\mathbf{r}',t')$. With respect to the receiver space–time coordinates $(\mathbf{r},t)$, the Green function associated with (12) satisfies (Appendix A)

$$(16) \quad \left[\frac{\partial}{\partial t} + \mathcal{L}_0\right] g_0(\mathbf{r},t|\mathbf{r}',t') = \delta(\mathbf{r}-\mathbf{r}')\, \delta(t-t')$$

in the domain $\mathbf{r} \in \mathcal{A}$, a causality condition

$$(17) \quad g_0(\mathbf{r},t|\mathbf{r}',t') = 0 \text{ if } t < t'$$

in the domain $\mathbf{r} \in \mathcal{A}$, and boundary conditions

$$g_0(\mathbf{r},t|\mathbf{r}',t') = 0$$

for $\mathbf{r} \in \partial\mathcal{A}_A$ and

$$\mathbf{n}_\perp \cdot \nabla g_0(\mathbf{r},t|\mathbf{r}',t') = 0$$

for $\mathbf{r} \in \partial\mathcal{A}_R$.

The solution that satisfies (12), (13), (14), and (15) is given by (Appendix A)

$$(18) \quad p_T(\mathbf{r},t) = g_0(\mathbf{r},t|\mathbf{r}_T,t_T)\, N_T(\mathbf{r}_T,t_T)\,.$$

As an example, if $\mathcal{L}_0$ is given by

$$\mathcal{L}_0 = z(t) + \mathbf{v}(t) \cdot \nabla - k(t) \Delta , \quad (19)$$

then the solution of (16) in an unbounded domain that satisfies the causality condition (17) and boundary condition

$$\lim_{r \to \infty} g_0(\mathbf{r},t|\mathbf{r}',t') = 0$$

where $r = \sqrt{\mathbf{r} \cdot \mathbf{r}}$ for a source at $(\mathbf{r}_T,t_T)$ is

$$g_0(\mathbf{r},t|\mathbf{r}_T,t_T) = \exp\left[-\int_{\mathcal{T}_T} d\tau z(\tau) \right] \times \mathcal{N}\left(\mathbf{r}_T + \int_{\mathcal{T}_T} d\tau \mathbf{v}(\tau), \sigma^2\right) h(t - t_T) , \quad (20)$$

$\mathcal{N}(\mathbf{r}_T,\sigma^2)$ is the normal distribution centered at $\mathbf{r}_T$ with variance σ^2 given by

$$\sigma^2(t, t_T) = 2 \int_{T_T} d\tau k(\tau) , \quad (21)$$

and $h(t - t_T)$ is the Heaviside step function defined as

$$h(t - t_T) = \begin{cases} 0 \text{ if } t < t_T \\ 1 \text{ if } t \geq t_T . \end{cases}$$

As can be appreciated the amplitude of (20) decreases when m and/or k increase. It is initially (i.e., at $t = t_T$) a normal distribution centered at $\mathbf{r} = \mathbf{r}_T$ with vanishing variance (i.e., a Dirac delta function). For $t < t_T$ the distribution vanishes, while for $t > t_T$ the distribution spreads at a rate that depends on the diffusion coefficient k, and the mean drifts at a rate determined by the drift velocity $\mathbf{v}$. While the distribution $\mathcal{N}$ is normalized for all $t \geq t_T$, the distribution g_0 does not conserve probability. Because $z(t) = m(t) + f(t) > 0$, the exponential function or survivability coefficient (Ricker 1975) leading $\mathcal{N}$ in (20) decreases with increasing time from an initial value of unity. I shall show that these properties of g_0 are general properties of the point-source solutions associated with (19). To see this, I solve for g_0 from (18). With the use of (4), I can express g_0 as a function of the measured fields e and c_T as

$$g_0(\mathbf{r},t|\mathbf{r}_T,t_T) = \frac{p_T(\mathbf{r},t)}{N_T(\mathbf{r}_T,t_T)} = \frac{c_T(\mathbf{r},t)}{q(\mathbf{r},t)\, e(\mathbf{r},t)\, N_T(\mathbf{r}_T,t_T)} . \quad (22)$$

Because I know the number N_T of tagged fish released at space–time point $(\mathbf{r}_T,t_T)$, and I have $c_T(\mathbf{r},t)$ and $e(\mathbf{r},t)$ in the interval of time $\mathcal{T}_T$, I can construct empirically the Green function $g_0(\mathbf{r},t|\mathbf{r}_T,t_T)$ in the interval of time $\mathcal{T}_T$ if I have $q(\mathbf{r},t)$.

The Green function g_0 has a series of properties that can be inferred. The first of these properties will allow the estimation of $q(\mathbf{r},t)$ as follows.

A. Initial — Assuming tagged fish disperse at a finite rate, initially they must be present at the point of release only. Therefore, for a source space-time point at $(\mathbf{r}_T,t_T)$, g_0 must satisfy

$$g_0(\mathbf{r},t_T|\mathbf{r}_T,t_T) = \delta(\mathbf{r} - \mathbf{r}_T) .$$

Analytically this can be deduced by dividing through (13) by the number of tagged fish released. Therefore, multiplying expression (22) by $q(\mathbf{r},t)$ and integrating over the spatial domain and application of the initial property of g_0 for $t \to t_T$ yields

$$q(\mathbf{r}_T,t_T) = \frac{1}{N_T(\mathbf{r}_T,t_T)} \int_{\mathcal{A}} d^2\mathbf{r} \frac{c_T(\mathbf{r},t_T)}{e(\mathbf{r},t_T)} . \quad (23)$$

Dimensional analysis of (23) reveals that q has the dimensions of area × time^{-1}. The dependence of its value on spatiotemporal location will ultimately dictate in how many cells and intervals of time must tagged fish be released in order to characterize the pattern of fish movement within $\mathcal{A}$. The empirical construction of $g_0(\mathbf{r},t_T|r',t')$ requires knowledge of $q(\mathbf{r},t)$ for all $\mathbf{r} \in \mathcal{A}$ and all $t \in \mathcal{T}_T$. The calculation of q by (23) requires that it be done at the space–time point of the tagged fish release. It follows, therefore, that to construct $q(\mathbf{r},t)$ for all $\mathbf{r} \in \mathcal{A}$ and all $t \in \mathcal{T}_T$ in principle requires performing nondenumerably infinite tagging experiments if q depends strongly on $(\mathbf{r},t)$. However, as will be discussed later, discretization and weak dependence of q on $(\mathbf{r},t)$ will allow some approximations.

The accurate estimation of q using (23) requires that the loss of tagged fish due to natural mortality during the time of release be negligible. It is, therefore, important to release the tagged fish in as short a time as possible. If $[t_T, t_{T+\delta}]$ is the interval of time over which the tagged fish are released, the required condition of small loss of tagged fish due to natural death rate during the time of release will be fullfilled if $m(\mathbf{r},t_T) \ll 1/[t_T,t_{T+\delta}]$. Other properties of g_0 are as follows.

B. Dimensional — Dimensional analysis of (22) reveals that g_0 is a density. That is, g_0 has the dimensions of area^{-1}.

C. Causal — Because tagged fish can exist in their domain only if they are present at an equal or earlier time, for a source time t_T, g_0 must satisfy

$$g_0(\mathbf{r},t|\mathbf{r}_T,t_T) = 0 \text{ for } t < t_T .$$

D. Normalization — As a consequence of the initial property,

$$\int_{\mathcal{A}} d^2\mathbf{r}\, g_0(\mathbf{r},t_T|\mathbf{r}_T,t_T) = 1 .$$

E. Probabilistic — Because the number of tagged fish recaptured cannot be greater than those released, for $t \geq t_T$,

$$0 \leq g_0(\mathbf{r},t|\mathbf{r}_T,t_T) \leq \delta(\mathbf{r} - \mathbf{r}_T)$$

and therefore,

$$0 \leq \int_{\mathcal{A}} d^2\mathbf{r}\, g_0(\mathbf{r},t|\mathbf{r}_T,t_T) \leq 1 .$$

Hence, $g_0(\mathbf{r},t|\mathbf{r}_T,t_T)$ can be regarded as the probability density of a tagged fish surviving the movement to position $\mathbf{r}$ from $\mathbf{r}_T$ during the interval of time $\mathcal{T}_T$ when fishing takes place in that interval of time. Assuming that the recaptured tagged fish are not rereleased, I will call g_0 the effort-dependent Green function.

F. Nonconservation of probability — Because tagged fish are being removed from their domain by natural and fishing deaths,

in general it must be true that for $t > t_T$,

$$\int_{\mathcal{A}} d^2\mathbf{r}\, g_0(\mathbf{r},t|\mathbf{r}_T,t_T) < 1 .$$

In order to derive the property of linear superposition of Green functions, consider the solution (18) which I will write as

$$(24)\quad p_T(\mathbf{r}',t') = g_0(\mathbf{r}',t'|\mathbf{r}_T,t_T)\, N_T(\mathbf{r}_T,t_T) .$$

Suppose I wanted to use the final condition $p_T(\mathbf{r}',t')$ of (24) as the initial condition of a tagged population problem. The population density must then satisfy field equation (12) and initial condition

$$p_T(\mathbf{r}',t') = \frac{c_T(\mathbf{r}',t')}{q(\mathbf{r}',t')\, e(\mathbf{r}',t')}$$

for $\mathbf{r}' \in \mathcal{A}$ (or some other estimate at $(\mathbf{r}',t')$ of p_T) and boundary conditions (14) and (15). The solution is given by (Appendix A)

$$(25)\quad p_T(\mathbf{r},t) = \int_{\mathcal{A}} d^2\mathbf{r}'\, g_0(\mathbf{r},t|\mathbf{r}',t')\, p_T(\mathbf{r}',t') .$$

Dividing (25) by $N_T(\mathbf{r}_T,t_T)$ and using the definition of g_0 given by (22) leads to the following property.

G. Linear superposition of probability densities — The probability density satisfies

$$(26)\quad g_0(\mathbf{r},t|\mathbf{r}_T,t_T) = \int_{\mathcal{A}} d^2\mathbf{r}'\, g_0(\mathbf{r},t|\mathbf{r}',t')\, g_0(\mathbf{r}',t'|\mathbf{r}_T,t_T) .$$

Another important property of g_0 is its periodicity.

H. Periodicity — A Green function is said to be periodic in time, of period $\mathcal{T}$, if $\mathcal{T}$ is a constant such that

$$g(\mathbf{r},t|\mathbf{r}',t') = g(\mathbf{r},t+\mathcal{T}|\mathbf{r}',t'+\mathcal{T})$$

(Tolstov 1962). A spatial periodicity can also be defined.

3.1.2. Untagged fish dynamics

Consistent with (7) and the general fishery problem formulated in the foregoing section, I would like to find expressions for the population density of the untagged portion in the interval of time $\mathcal{T}_I$. However, because the empirical Green function is constructed for $t \geq t_T \geq t_I$, in general it is not possible to define empirically the population density in the interval of time $t_I \leq t \leq t_T$ from a tagging campaign initiated at time t_T. Therefore, I shall pose the problem for the untagged portion of the population in the interval of time $\mathcal{T}_T$.

The population density of untagged fish $p(\mathbf{r},t)$ obeys the field equation

$$(27)\quad \left[\frac{\partial}{\partial t} + \mathcal{L}_0\right] p(\mathbf{r},t) = r(\mathbf{r},t)$$

in the space–time domain $\mathbf{r} \in \mathcal{A}$, $t \geq t_T$ subject to initial condition

$$(28)\quad p(\mathbf{r},t_T) = p_{\text{in}}(\mathbf{r}) = \frac{c(\mathbf{r},t_T)}{q(\mathbf{r},t_T)\, e(\mathbf{r},t_T)}$$

in the domain $\mathbf{r} \in \mathcal{A}$ (or some other estimate at $(\mathbf{r},t_T)$ of p) and boundary conditions

$$(29)\quad p(\mathbf{r},t) = 0$$

in the domain $\mathbf{r} \in \partial\mathcal{A}_A$, $t \geq t_T$ and

$$(30)\quad \mathbf{n}_\perp \cdot \nabla p(\mathbf{r},t) = 0$$

in the domain $\mathbf{r} \in \partial\mathcal{A}_R$, $t \geq t_T$.

Because the differential operators for the tagged and untagged portions of the fish population are identical, even though their inhomogeneous term and initial conditions differ, this means that the movement and survivability of tagged and untagged fish are linked through the equality of their Green functions. In practice, this is true only if sufficient numbers of tagged fish are released so that g_0 constructed as indicated by (22) approximately represents the average movement and survivability of the total fish population.

The solution that satisfies (27), (28), (29), and (30) is (Appendix A)

$$(31)\quad p(\mathbf{r},t) = \int_{\mathcal{A}} d^2\mathbf{r}'\, g_0(\mathbf{r},t|\mathbf{r}',t_T)\, p_{\text{in}}(\mathbf{r}') + u_0(\mathbf{r},t)$$

where the field $u_0(\mathbf{r},t)$ is the contribution to the population density due to recruitment and is given by

$$(32)\quad u_0(\mathbf{r},t) = \int_{\mathcal{T}_T} dt' \int_{\mathcal{A}} d^2\mathbf{r}'\, g_0(\mathbf{r},t|\mathbf{r}',t')\, r(\mathbf{r}',t') .$$

Multiplying (31) by the fishing death rate $f(\mathbf{r},t)$ yields the expression for the catch density rate:

$$(33)\quad c(\mathbf{r},t) = f(\mathbf{r},t)\left[\int_{\mathcal{A}} d^2\mathbf{r}'\, g_0(\mathbf{r},t|\mathbf{r}',t_T)\, p_{\text{in}}(\mathbf{r}') + u_0(\mathbf{r},t)\right]$$

The contribution to the population density due to recruitment at the level of exploitation at which the empirical probability density g_0 was constructed can be computed by use of (33). Solving for u_0, I have

$$(34)\quad u_0(\mathbf{r},t) = \frac{c(\mathbf{r},t)}{f(\mathbf{r},t)} - \int_{\mathcal{A}} d^2\mathbf{r}'\, g_0(\mathbf{r},t|\mathbf{r}',t_T)\, p_{\text{in}}(\mathbf{r}') .$$

Because in the interval of time $\mathcal{T}_T$, I know $f(\mathbf{r},t)$ and the resulting $c(\mathbf{r},t)$, (34) can be used to calculate $u_0(\mathbf{r},t)$ at the level of effort for which $g_0(\mathbf{r},t|\mathbf{r}',t_T)$ was constructed. However, in general, I cannot use equation (33) to compute the catch density rate at a new level of effort unless I perform another tagging experiment at the desired level. The survivability embedded in g_0 depends on the level of exploitation during the recapture of the tagged fish. Therefore, although these equations using g_0 are valid for modeling the movement and distribution of a fish population, they are in general useful only at the level of effort for which g_0 was constructed. In general, no other case can be rigourously considered. In Section 4, I shall show that if the natural death rate is much greater than that due to fishing, the equations derived in this section can be used for a fisheries interaction study. However, in order to be able to consider the general fisheries interaction problem formulated in Section 2 without having to perform tagging experiments for all the levels of effort that wish

to be considered, I need to reformulate the problem so that the solutions for the population density are in terms of a Green function that is effort independent.

3.2. Effort-Independent Green Function

In this subsection, I shall find the solutions for the population density for tagged and untagged fish in terms of a Green function that is effort independent. I shall also show how to construct the effort-independent Green function from knowledge of the effort-dependent one. This new Green function satisfies, other than the fact that it is independent of fishing death rate, properties identical to those of g_0.

3.2.1. Tagged fish dynamics

Consider again a tagging experiment in which N_T tagged fish are released in an area small compared with $\mathcal{A}$ about position $\mathbf{r}_T$ beginning at time $t_T \in \mathcal{T}_I$ with a duration short compared with $\mathcal{T}_T$ where $t \gg t_T$. Here again, I shall index the number of tagged fish, location, and initial time of release by writing $N_T(\mathbf{r}_T,t_T)$. However, in this case, I shall pose the problem with a differential operator that is independent of the fishing death rate, and I shall pass on to the inhomogeneous part of the field equation the responsibility for embedding into the solution for the population density the information of catch density rate.

Let $\mathcal{L}$ be a linear differential operator which contains the terms of (7) that describe the natural death rate and the spatial dynamics. In terms of operator $\mathcal{L}_0$, operator $\mathcal{L}$ is given by

$$\mathcal{L} = \mathcal{L}_0 - f(\mathbf{r},t) .$$

Consistent with (7) and the general fishery problem formulated in Section 2, the tagged fish population density must therefore satisfy a field equation of the form

$$(35)\quad \left[\frac{\partial}{\partial t} + \mathcal{L}\right] p_T(\mathbf{r},t) = -c_T(\mathbf{r},t)$$

in the space–time domain $\mathbf{r} \in \mathcal{A}$, $t \geq t_T$, subject to initial condition (13) and boundary conditions (14) and (15). The tagged fish catch density rate is now the inhomogeneous term of the field equation. It is a negative contribution because it is a sink of population. The solution that satisfies (35), (13), (14), and (15) is given by (Appendix A)

$$(36)\quad p_T(\mathbf{r},t) = g(\mathbf{r},t|\mathbf{r}_T,t_T)\, N_T(\mathbf{r}_T,t_T) - \int_{\mathcal{T}_T} dt' \int_{\mathcal{A}} d^2\mathbf{r}'\, g(\mathbf{r},t|\mathbf{r}',t')\, c_T(\mathbf{r}',t') .$$

I need to determine how the effort-independent Green function is related to g_0. On dividing equation (36) by N_T and using the definition of g_0 given by (22), the relation between the effort-dependent and effort-independent Green functions becomes

$$(37)\quad g(\mathbf{r},t|\mathbf{r}_T,t_T) = g_0(\mathbf{r},t|\mathbf{r}_T,t_T) + \frac{1}{N_T(\mathbf{r}_T,t_T)} \int_{\mathcal{T}_T} dt' \int_{\mathcal{A}} d^2\mathbf{r}'\, g(\mathbf{r},t|\mathbf{r}',t')\, c_T(\mathbf{r}',t')$$

which is an integral equation where $g(\mathbf{r},t|\mathbf{r}',t')$ is the unknown. The exact solution to integral equation (37) is given by the Neumann series (Courant and Hilbert 1953; Byron and Fuller 1970)

$$(38)\quad g(\mathbf{r},t|\mathbf{r}_T,t_T) = \sum_{i=0}^{\infty} g_i(\mathbf{r},t|\mathbf{r}_T,t_T)$$

where

$$(39)\quad g_i(\mathbf{r},t|\mathbf{r}_T,t_T) = \frac{1}{N_T(\mathbf{r}_T,t_T)} \int_{\mathcal{T}_T} dt' \times \int_{\mathcal{A}} d^2\mathbf{r}'\, g_{i-1}(\mathbf{r},t|\mathbf{r}',t')\, c_T(\mathbf{r}',t')$$

for $i = 1, 2, \ldots$. The series (38) converges over an arbitrary interval of time whenever the number of tagged fish recaptured is less than the total number of tagged fish available at the beginning of the interval (Appendix B), and therefore, it converges uniformly to the solution under that condition (Byron and Fuller 1970).

To discuss some approximations, consider the total number of tagged fish recaptured in the interval of time $\mathcal{T}_T$:

$$N_R(t) = \int_{\mathcal{T}_T} dt' \int_{\mathcal{A}} d^2\mathbf{r}'\, c_T(\mathbf{r}',t') .$$

If $N_R < N_T$ but $N_R \nsim N_T$, the approximation

$$g(\mathbf{r},t|\mathbf{r}_T,t_T) \approx g_0(\mathbf{r},t|\mathbf{r}_T,t_T) + g_1(\mathbf{r},t|\mathbf{r}_T,t_T) \approx g_0(\mathbf{r},t|\mathbf{r}_T,t_T) + \frac{1}{N_T(\mathbf{r}_T,t_T)} \int_{\mathcal{T}_T} dt' \times \int_{\mathcal{A}} d^2\mathbf{r}'\, g_0(\mathbf{r},t|\mathbf{r}',t')\, c_T(\mathbf{r}',t')$$

can be used. However, if $N_R \ll N_T$, which implies $m(\mathbf{r},t) \gg f(\mathbf{r},t)$, then the approximation

$$g(\mathbf{r},t|\mathbf{r}_T,t_T) \approx g_0(\mathbf{r},t|\mathbf{r}_T,t_T)$$

is adequate. In a practical computational sense, the expansion is stopped at the term whose contribution is negligible.

The properties of g can be determined with the help of (37). It satisfies all the properties of g_0 listed in Subsection (3.1.1.). However, because g does not have fishing death rate included, the survivability associated with it must be in general of larger magnitude than that of g_0 except initially. It therefore satisfies

$$g(\mathbf{r},t|\mathbf{r}_T,t_T) \geq g_0(\mathbf{r},t|\mathbf{r}_T,t_T)$$

where the equality holds for $t = t_T$. Therefore, $g(\mathbf{r},t|\mathbf{r}_T,t_T)$ can be regarded as the probability density of a tagged fish surviving the movement to position $\mathbf{r}$ from $\mathbf{r}_T$ during the interval of time $\mathcal{T}_T$ in the absence of fishing during that interval of time. I will therefore call g the effort-independent Green function.

On multiplying (36) by the fishing death rate, the tagged fish catch density rate is the solution of integral equation

$$c_T(\mathbf{r},t) = f(\mathbf{r},t)\left[g(\mathbf{r},t|\mathbf{r}_T,t_T)\, N_T(\mathbf{r}_T,t_T) - \int_{\mathcal{T}_T} dt' \int_{\mathcal{A}} d^2r'\, g(\mathbf{r},t|\mathbf{r}',t')\, c_T(\mathbf{r}',t')\right].$$

3.2.2. Untagged fish dynamics

Consistent with (7), the general fishery problem formulated in Section (2) and the fact that the empirical Green function is known only for $t \geq t_T$, the population density of untagged fish must obey a field equation

$$(40)\quad \left[\frac{\partial}{\partial t} + \mathcal{L}\right] p(\mathbf{r},t) = -c(\mathbf{r},t) + r(\mathbf{r},t)$$

in the space–time domain $\mathbf{r} \in \mathcal{A}$, $t \geq t_T$, and the conditions (28), (29), and (30). The solution is

$$(41)\quad p(\mathbf{r},t) = \int_{\mathcal{A}} d^2\mathbf{r}'\, g(\mathbf{r},t|\mathbf{r}',t_I)\, p_{in}(\mathbf{r}') + u(\mathbf{r},t) - \int_{\mathcal{T}_T} dt' \int_{\mathcal{A}} d^2\mathbf{r}'\, g(\mathbf{r},t|\mathbf{r}',t')\, c(\mathbf{r}',t')$$

where

$$(42)\quad u(\mathbf{r},t) = \int_{\mathcal{T}_T} dt' \int_{\mathcal{A}} d^2\mathbf{r}'\, g(\mathbf{r},t|\mathbf{r}',t')\, r(\mathbf{r}',t')$$

represents the contribution to the population density attributable to recruitment.

The untagged fish catch density rate is the solution of

$$(43)\quad c(\mathbf{r},t) = f(\mathbf{r},t)\left[\int_{\mathcal{A}} d^2\mathbf{r}'\, g(\mathbf{r},t|\mathbf{r}',t_T)\, p_{in}(\mathbf{r}') + u(\mathbf{r},t)\right] - f(\mathbf{r},t) \int_{\mathcal{T}_T} dt' \int_{\mathcal{A}} d^2\mathbf{r}'\, g(\mathbf{r},t|\mathbf{r}',t')\, c(\mathbf{r}',t') .$$

Because the catch density rate is known for the level of effort employed during the time interval $\mathcal{T}_T$, then (43) can be applied to those data to determine empirically the field u using

$$(44)\quad u(\mathbf{r},t) = \frac{c(\mathbf{r},t)}{f(\mathbf{r},t)} - \int_{\mathcal{A}} d^2\mathbf{r}'\, g(\mathbf{r},t|\mathbf{r}',t_T)\, p_{in}(\mathbf{r}') + \int_{\mathcal{T}_T} dt' \int_{\mathcal{A}} d^2\mathbf{r}'\, g(\mathbf{r},t|\mathbf{r}',t')\, c(\mathbf{r}',t') .$$

Assuming that the recruitment does not change significantly at other levels of effort, catch density rate c can then be computed for differing effort densities e because (43) is valid for any level of effort as opposed to equation (33), which applies only to the measure of effort for which the effort-dependent Green function was constructed.

4. Example: Skipjack Tuna Fishery in the Eastern Tropical Atlantic

The following example shows how a subset of the type of fishery models considered in Section 3 can be reduced to a simple calculation whenever the effort density is sufficiently low. The fishery of interest is the skipjack tuna (*Katsuwonus pelamis*) fishery in the five cells of the eastern tropical Atlantic (ETA) indicated in Fig. 1. As a politically interesting question, A. Fonteneau (C.R.O.D.T., B.P. 2241, Dakar, Senegal) asks in a personal communication what effect the doubling of effort in one cell might have on the catches from the other four.

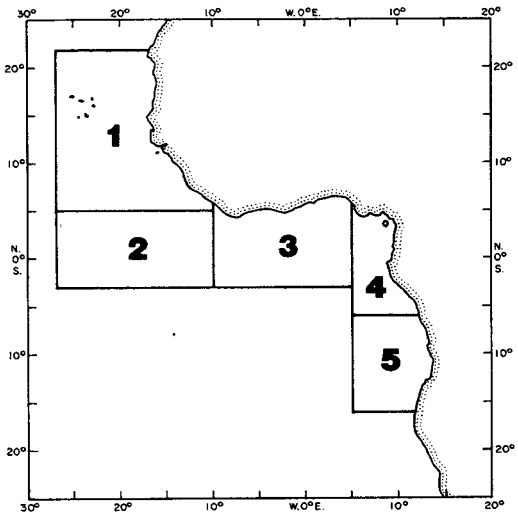

FIG. 1. Eastern tropical Atlantic (ETA) geographic cells: 1, Senegal; 2, Liberia; 3, Ghana; 4, Cape Lopez; 5, Angola.

The data required for the analysis consist solely of the mark and recapture measures from the International Skipjack Year Program, conducted over a 3-yr period by the International Commission for the Conservation of Atlantic Tunas (Symons et al. 1986). Although the corresponding catch and effort densities are also given in Symons et al. (1986), the only information needed here is the reported 5% tag return, together with the assumptions that almost all of the tagged fish survived the trauma of tagging and that almost all of the recaptured tags were reported. As I will show, the fishing effort expended during the experiment was sufficiently low to permit me to regard the dynamic catch density rate as approximately a linear function of effort density.

In the most extreme case, all of the $N_R = 5 \times 10^{-2} N_T$ recovered tags could have been taken in just one of the five cells over a single time interval corresponding to the space–time point $(\mathbf{r}_R, t_R)$ for $t_R \geq t_T$. Accordingly, the catch density rate of the tagged fish would then be $c_T(\mathbf{r},t) = N_R \delta(\mathbf{r} - \mathbf{r}_R)\delta(t - t_R)$. Therefore, on substituting those values in (37) and integrating, I can conclude that the difference between the effort-independent and effort-dependent Green functions is no greater than

$$g(\mathbf{r},t|\mathbf{r}_T,t_T) - g_0(\mathbf{r},t|\mathbf{r}_T,t_T) = 5 \times 10^{-2}\, g(\mathbf{r},t|\mathbf{r}_R,t_R) .$$

Because $5 \times 10^{-2} \ll 1$, $g \approx g_0$, which in turn implies that the natural death rate is much greater than the fishing death rate. In that limit, (33) becomes

$$c(\mathbf{r},t) \approx f(\mathbf{r},t)\left[\int_{\mathrm{ETA}} d^2\mathbf{r}'\, g(\mathbf{r},t|\mathbf{r}',t_T)\, p_{in}(\mathbf{r}') + u(\mathbf{r},t)\right].$$

The catch density rate, under the condition of low fishing death rate in relation to the natural death rate, is approximately a linear function of effort density. Had the tag return been double its reported value, the approximation of catch as a linear function of effort would still hold because $N_R/N_T = 0.1$ is an order of

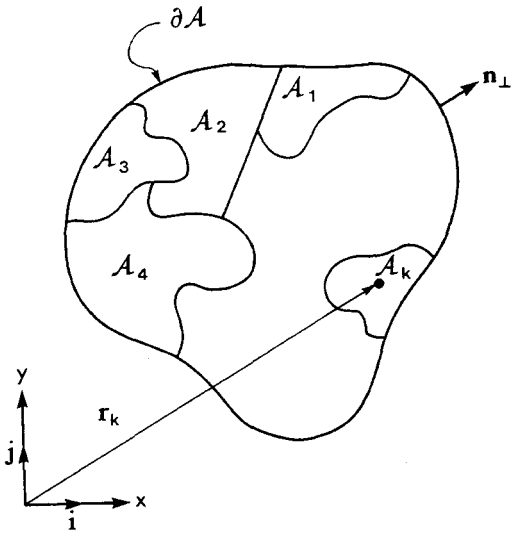

FIG. 2. Domain $\mathcal{A}$ of the population is divided into n nonoverlapping cells. The vector $\mathbf{n}_\perp$ is the unit vector normal to the boundary $\partial\mathcal{A}$ of the domain pointing outward.

magnitude smaller than 1. Should the recruitment density rate not change sigificantly, doubling the effort would have the effect of approximately doubling the catch. Thus, in answer to the Fonteneau question, if the effort in one or more of the five cells were doubled, the catch from the remaining cells would remain approximately constant.

5. Discretization of the Fields

Should the fishing death rate approach or exceed the natural death rate, the field equations of Section 3 must be treated in much more detail to address the general fishery problem outlined in Section 2. A numerical solution is proposed in this section.

With reference to Fig. 2, the individual cells of area $\mathcal{A}_i$ of the domain $\mathcal{A}$, where $i = 1, 2, \ldots, n$, are such that

$$\mathcal{A} = \sum_{i=1}^{n} \mathcal{A}_i$$

(i.e., no overlap of cells), and $\{\mathbf{r}_i \in \mathcal{A}_i : i = 1, 2, \ldots, n\}$. Here, cell $\mathcal{A}_i$ is defined as a neighborhood around point (or nuclei) $\mathbf{r}_i$. A cell is defined about every data collection nucleus. An economic zone can be composed of more than one cell. The closed time interval $\mathcal{T}_T = [t_T, t] = [t_l, t_{m+1}]$, where $l \geq 1$ and the equality holds only if $\mathcal{T}_T = \mathcal{T}_l$. The m time intervals $\{\mathcal{T}_j = t_{j+1} - t_j : j = 1, 2, \ldots, m\}$ are such that

$$\mathcal{T}_l = \sum_{j=1}^{m} \mathcal{T}_j = [t_l, t_{m+1}] .$$

The value of a field ϕ within cell $\mathcal{A}_i$ in the interval of time $\mathcal{T}_j = [t_j, t_{j+1}]$ will be written $\phi(\mathbf{r}_i, t_j)$. Henceforth, $(\mathbf{r}_i, t_j)$ is interchangeable with $(\mathcal{A}_i, \mathcal{T}_j)$.

I will assume that N_T number of tagged fish are released in cell $\mathcal{A}_k$ at time t_l. The following discrete fields are available for the analysis: $\mathcal{C} = [e(\mathbf{r}_i, t_j) : i = 1, 2, \ldots, n; j = 1, 2, \ldots, m+1\}$, $\mathcal{C} = \{c(\mathbf{r}_i, t_j) : i = 1, 2, \ldots, n; j = 1, 2, \ldots, m+1\}$, and $\mathcal{C}_T(\mathbf{r}_k, t_l) = \{c_T(\mathbf{r}_i, t_j) : i = 1, 2, \ldots, n; j = l, l+1, \ldots, m+1\}$. These are, respectively, the measurements of effort density, the untagged fish catch density rate, and tagged fish catch density rate for the release of tagged fish in cell $\mathcal{A}_k$ at time t_l. It will soon become evident that at the very least there should be as many tagging experiments as there are cells in the domain, one per cell.

As I showed in Section 3, I first need to evaluate the catchability in order to construct the effort-dependent Green function. The discrete version of (23) is

$$(45)\quad q(\mathbf{r}_i, t_s) = \frac{1}{N_T(\mathbf{r}_i, t_s)} \sum_{i=1}^{n} \mathcal{A}_i \frac{c_T(\mathbf{r}_i, t_s)}{e(\mathbf{r}_i, t_s)} .$$

However, by its very definition, I can calculate only one value of q from every tagging experiment. If the tagged fish release is only at $(\mathbf{r}_k, t_l)$, then I can only calculate $q(\mathbf{r}_k, t_l)$. So in the case of the single tagging experiment, I am left with the necessity of assuming q constant throughout space–time.

The discrete version of (22) for g_0 for a tagged fish release at $(\mathbf{r}_k, t_l)$ is

$$(46)\quad g_0(\mathbf{r}_i, t_j | \mathbf{r}_k, t_l) = \frac{c_T(\mathbf{r}_i, t_j)}{q(\mathbf{r}_i, t_j)\, e(\mathbf{r}_i, t_j)\, N(\mathbf{r}_k, t_l)} .$$

If only the one tagging experiment has been performed, then, as mentioned above, it is necessary to assume $q(\mathbf{r}_i, t_j) = q(\mathbf{r}_k, t_l) =$ constant for $i = 1, 2, \ldots, n$ and $j = l, l+1, \ldots, m+1$. Thus, using the set $\mathcal{C}_T$ of a single tagging experiment and set $\mathcal{C}$, I can construct an approximate g_0. The set of values calculated for g_0 for a release of fish at $(\mathbf{r}_k, t_l)$ will be called the set $\mathcal{G}_0(\mathbf{r}_k, t_l) = \{g_0(\mathbf{r}_i, t_{l+s} | \mathbf{r}_k, t_l) : i = 1, 2, \ldots, n; s = 1, 2, \ldots, m-l+1\}$. To describe the elements of $\mathcal{G}_0(\mathbf{r}_k, t_l)$, it is helpful to use the Kroenecker delta function:

$$\delta_{ik} = \begin{cases} 1 & \text{if } i = k \\ 0 & \text{otherwise} . \end{cases}$$

Then

$$g_0(\mathbf{r}_i, t_j | \mathbf{r}_k, t_l) = \begin{cases} 0 & \text{for } t_j < t_l \\ \delta_{ik} / \mathcal{A}_k & \text{for } t_j = t_l \end{cases}$$

and

$$g_0(\mathbf{r}_i, t_j | \mathbf{r}_k, t_l) \leq \delta_{ik} / \mathcal{A}_k \quad \text{for } t_j > t_i .$$

As a consequence of this last property, for $t_j \geq t_l$:

$$0 \leq \sum_{i=1}^{n} \mathcal{A}_i\, g_0(\mathbf{r}_i, t_j | \mathbf{r}_k, t_l) \leq 1 .$$

The discrete version of (37) is given by

$$g(\mathbf{r}_i,t_{j+1}|\mathbf{r}_k,t_l) \approx g_0(\mathbf{r}_i,t_{j+1}|\mathbf{r}_k,t_l) + \frac{1}{N_T(\mathbf{r}_k,t_l)} \times \sum_{s=1}^{f\le m} \mathcal{T}_s \sum_{v=1}^{n} \mathcal{A}_v\, g(\mathbf{r}_i,t_{j+1}|\mathbf{r}_v,t_s)\, c_T(\mathbf{r}_v,t_s)\,.$$

Therefore, for an arbitrary single interval of time, say $\mathcal{T}_j$, the relationship between g and g_0 is

$$(47)\quad g(\mathbf{r}_i,t_{j+1}|\mathbf{r}_w,t_j) \approx g_0(\mathbf{r}_i,t_{j+1}|\mathbf{r}_w,t_j) + \frac{\mathcal{T}_j}{N_T(\mathbf{r}_w,t_j|\mathbf{r}_k,t_l)} \times \sum_{v=1}^{n} \mathcal{A}_v\, g(\mathbf{r}_i,t_{j+1}|\mathbf{r}_v,t_j)\, c_T(\mathbf{r}_v,t_j)$$

where $N(\mathbf{r}_w,t_j|\mathbf{r}_k, t_l)$ is the number of tagged fish at $(\mathbf{r}_w,t_j)$ from a release conducted at $(\mathbf{r}_k,t_l)$. From (18), this is

$$N_T(\mathbf{r}_w,t_j|\mathbf{r}_k,t_l) = \mathcal{A}_w\, p_T(\mathbf{r}_w,t_j) = \mathcal{A}_w\, g_0(\mathbf{r}_w,t_j|\mathbf{r}_k,t_l)\, N_T(\mathbf{r}_k,t_l)\,.$$

The exact solution of (47) is given by the series

$$(48)\quad g(\mathbf{r}_i,t_{j+1}|\mathbf{r}_w,t_j) = \sum_{r=0}^{\infty} g_r(\mathbf{r}_i,t_{j+1}|\mathbf{r}_w,t_j)$$

and

$$g_r(\mathbf{r}_i,t_{j+1}|\mathbf{r}_w,t_j) \approx \frac{\mathcal{T}_j}{N_T(\mathbf{r}_w,t_j|\mathbf{r}_k,t_l)} \sum_{v=1}^{n} \mathcal{A}_v\, g_{r-1}(\mathbf{r}_i,t_{j+1}|\mathbf{r}_v,t_j)\, c_T(\mathbf{r}_v,t_j)$$

for $r = 1, 2, \ldots$. For cases where $m \ll f$, that is, if the number of tagged fish recaptured in the interval of time $\mathcal{T}_j$ is

$$N_R(t_{j+1}) \approx \mathcal{T}_j \sum_{i=1}^{n} \mathcal{A}_i\, c_T(\mathbf{r}_i,t_j)\,,$$

the approximation

$$g(\mathbf{r}_i,t_{j+1}|\mathbf{r}_w,t_j) \approx g_0(\mathbf{r}_i,t_{j+1}|\mathbf{r}_w,t_j) + \frac{\mathcal{T}_j}{N_T(\mathbf{r}_w,t_j|\mathbf{r}_k,t_l)} \times \sum_{v=1}^{n} \mathcal{A}_v\, g_0(\mathbf{r}_i,t_{j+1}|\mathbf{r}_v,t_j)\, c_T(\mathbf{r}_v,t_j)$$

will give accurate results if $N_R < N_T$ but $N_R \nsim N_T$. As I mentioned in Section 3, if $N_R \ll N_T$, implying that natural death rate is much greater than that due to fishing, then the approximation $g(\mathbf{r}_i,t_{j+1}|\mathbf{r}_w,t_j) \approx g_0\,(\mathbf{r}_i,t_{j+1}|\mathbf{r}_w,t_j)$ is adequate. However, in general, one can proceed by expanding and stop the expansion with the term whose contribution is negligible.

Either the exact or approximate solution for g requires the knowledge of the transition probability density elements $\mathcal{G}_0^* = \{g_0(\mathbf{r}_i,t_{j+1}|\mathbf{r}_v,t_j) : i, v = 1, 2, \ldots, n;\ j = l, l+1, \ldots, m\}$. For tagged fish releases starting in the interval of time $\mathcal{T}_l$ the empirical construction of g_0 by (46) yields only $\mathcal{G}_0(\mathbf{r}_k,t_l)$. So it is necessary to calculate the transition probability density elements. This will be done with the property of superposition of probability densities (Property G in Section 3).

The discrete version of the superposition property of probability densities for consecutive time intervals is given by

$$(49)\quad g_0(\mathbf{r}_i,t_{l+2}|\mathbf{r}_k,t_l) \approx \sum_{v=1}^{n} \mathcal{A}_v\, g_0(\mathbf{r}_i,t_{l+2}|\mathbf{r}_v,t_{l+1})\, g_0(\mathbf{r}_v,t_{l+1}|\mathbf{r}_k,t_l)\,.$$

In order to define a completely determined system of equations for the transition probability densities $\mathcal{G}_0^*(\mathcal{T}_{l+1}) = \{g_0(\mathbf{r}_i,t_{l+2}|\mathbf{r}_v,t_{l+1}) : i, v = 1, 2, \ldots, n\}$ from the information of a single tagging experiment, it is necessary to assume that the Green function is spatially translationally invariant. That is, it is necessary to assume that no matter where the tagged fish are released, the results are identical. However, the concept of translational invariance of the Green function is incompatible with the presence of boundaries, for the results of a tagged fish release away from the boundaries, for example, will be different from the results if the release were close to a boundary. Furthermore, fishing effort is not uniform throughout $\mathcal{A}$. Thus, one cannot possibly define a completely determined system of equations for the transition probability densities $\mathcal{G}_0^*(\mathcal{T}_{l+1})$ from the information of a single tagging experiment if the population has a bounded domain or there is an inhomogeneous distribution of fishing death rate. Investigation of (49) leads to the conclusion that at least n tagging experiments are necessary to perform, one per cell, to define a completely determined system of equations. As can be appreciated in (49), if n simultaneous tagged fish releases were done, one per cell, the data at the initial interval of time and all subsequent intervals define completely determined systems of n equations. However, it is not necessary to perform the tagged fish releases simultaneously. To see this, it is best to consider an example.

For simplicity, I will suppose that the release at time t_l is in cell $\mathcal{A}_1$, the release at time t_{l+1} is in cell $\mathcal{A}_2, \ldots$, and the release at time t_{l+n-1} is in cell $\mathcal{A}_n$. To determine the complete set of transition probability densities for an interval of time, it is necessary that there be as many tagging experiments as there are cells in the domain, one per cell, but it is sufficient that there be only one experiment per interval of time. Some or all can be done simultaneously. With the catch data of each experiment, because I have assumed distinguishable tags, one has the set of sets $\mathcal{C}_T = \{\mathcal{C}_T(\mathbf{r}_s,t_{l+s-1}) : s = 1, 2, \ldots, n\}$, that is, the set of catch density rates of the n tagging experiments. Use of $\mathcal{E}$ and $\mathcal{C}_T$ in equation (45) will yield a set of computed catchabilities given by $\mathcal{Q} = \{q(\mathbf{r}_s,t_{l+s-1}) : s = 1, 2, \ldots, n\}$. I can use these to compute a set of discrete Green functions $\mathcal{G}_0 = \{\mathcal{G}_0(\mathbf{r}_s,t_{l+s-1}) : s = 1, 2, \ldots, n\}$ as indicated by (46). However, the catchability of the ith cell at time t_j should be used for the computation of terms of all n Green functions evaluated in the ith cell (i.e., receiver point $\mathbf{r}_i$) at time t_j.

Assuming the tagged fish live longer than $[t_l,t_{l+n}]$, the second transition when there is data from all n tagging experiments is during interval of time $\mathcal{T}_{l+n}$. I am arbitrarily using the transitions at $\mathcal{T}_{l+n}$ rather than those at $\mathcal{T}_{l+n-1}$ for the sake of uniformity of notation in the analysis that follows. From (49), for the release of tagged fish in $\mathcal{A}_1$:

$$g_0(\mathbf{r}_i,t_{l+n+1}|\mathbf{r}_1,t_l) \approx \sum_{v=1}^{n} \mathcal{A}_v\, g_0(\mathbf{r}_i,t_{l+n+1}|\mathbf{r}_v,t_{l+n})\, g_0(\mathbf{r}_v,t_{l+n}|\mathbf{r}_1,t_l)\,.$$

For the release of tagged fish in $\mathcal{A}_2$:

$$g_0(\mathbf{r}_i,t_{l+n+1}|\mathbf{r}_2,t_{l+1}) \approx \sum_{v=1}^{n} \mathcal{A}_v\, g_0(\mathbf{r}_i,t_{l+n+1}|\mathbf{r}_v,t_{l+n})\, g_0(\mathbf{r}_v,t_{l+n}|\mathbf{r}_2,t_{l+1})$$

$$\vdots$$

and finally, for the release of tagged fish in $\mathcal{A}_n$:

$$g_0(\mathbf{r}_i,t_{l+n+1}|\mathbf{r}_n,t_{l+n-1}) \approx \sum_{v=1}^{n} \mathcal{A}_v g_0(\mathbf{r}_i,t_{l+n+1}|\mathbf{r}_v,t_{l+n})\, g_0(\mathbf{r}_v,t_{l+n}|\mathbf{r}_n,t_{l+n-1})\,.$$

This is a system of equations of the form

$$(50)\quad \mathbf{d}_s = \sum_{v=1}^{n} \mathcal{P}_{sv}\, \mathbf{m}_v \text{ for } s = 1, 2, \ldots, n\,.$$

In this equation, identify by comparison with (49)

$$\mathbf{d} = \begin{pmatrix} g_0(\mathbf{r}_i,t_{l+n+1}|\mathbf{r}_1,t_l) \\ g_0(\mathbf{r}_i,t_{l+n+1}|\mathbf{r}_2,t_{l+1}) \\ \cdot \\ g_0(\mathbf{r}_i,t_{l+n+1}|\mathbf{r}_n,t_{l+n-1}) \end{pmatrix}$$

as the data vector,

$$\mathcal{P} = \begin{pmatrix} \mathcal{A}_1 g_0(\mathbf{r}_1,t_{l+n}|\mathbf{r}_1,t_l) & \mathcal{A}_2 g_0(\mathbf{r}_2,t_{l+n}|\mathbf{r}_1,t_l) & \cdot & \mathcal{A}_n g_0(\mathbf{r}_n,t_{l+n}|\mathbf{r}_1,t_l) \\ \mathcal{A}_1 g_0(\mathbf{r}_1,t_{l+n}|\mathbf{r}_2,t_{l+1}) & \mathcal{A}_2 g_0(\mathbf{r}_2,t_{l+n}|\mathbf{r}_2,t_{l+1}) & \cdot & \mathcal{A}_n g_0(\mathbf{r}_n,t_{l+n}|\mathbf{r}_2,t_{l+1}) \\ \cdot & \cdot & \cdot & \cdot \\ \mathcal{A}_1 g_0(\mathbf{r}_1,t_{l+n}|\mathbf{r}_n,t_{l+n-1}) & \mathcal{A}_2 g_0(\mathbf{r}_2,t_{l+n}|\mathbf{r}_n,t_{l+n-1}) & \cdot & \mathcal{A}_n g_0(\mathbf{r}_n,t_{l+n}|\mathbf{r}_n,t_{l+n-1}) \end{pmatrix}$$

as the $n \times n$ matrix of coefficients, and

$$\mathbf{m} = \begin{pmatrix} g_0(\mathbf{r}_i,t_{l+n+1}|\mathbf{r}_1,t_{l+n}) \\ g_0(\mathbf{r}_i,t_{l+n+1}|\mathbf{r}_2,t_{l+n}) \\ \cdot \\ g_0(\mathbf{r}_i,t_{l+n+1}|\mathbf{r}_n,t_{l+n}) \end{pmatrix}$$

as the model vector. Solving this system of equations for $i = 1, 2, \ldots, n$ gives the set $\mathcal{G}_0^*(\mathcal{T}_{l+n}) = \{g_0(\mathbf{r}_i,t_{l+n+1}|\mathbf{r}_v,t_{l+n}) : i, v = 1, 2, \ldots, n\}$. Following the previous procedure for the next time step (i.e., $\mathcal{T}_{l+n+1}$), solve (50) with

$$\mathbf{d} = \begin{pmatrix} g_0(\mathbf{r}_i,t_{l+n+2}|\mathbf{r}_1,t_l) \\ g_0(\mathbf{r}_i,t_{l+n+2}|\mathbf{r}_2,t_{l+1}) \\ \cdot \\ g_0(\mathbf{r}_i,t_{l+n+2}|\mathbf{r}_n,t_{l+n-1}) \end{pmatrix}$$

as the data vector,

$$\mathcal{P} = \begin{pmatrix} \mathcal{A}_1 g_0(\mathbf{r}_1,t_{l+n+1}|\mathbf{r}_1,t_l) & \mathcal{A}_2 g_0(\mathbf{r}_2,t_{l+n+1}|\mathbf{r}_1,t_l) & \cdot & \mathcal{A}_n g_0(\mathbf{r}_n,t_{l+n+1}|\mathbf{r}_1,t_l) \\ \mathcal{A}_1 g_0(\mathbf{r}_1,t_{l+n+1}|\mathbf{r}_2,t_{l+1}) & \mathcal{A}_2 g_0(\mathbf{r}_2,t_{l+n+1}|\mathbf{r}_2,t_{l+1}) & \cdot & \mathcal{A}_n g_0(\mathbf{r}_n,t_{l+n+1}|\mathbf{r}_2,t_{l+1}) \\ \cdot & \cdot & \cdot & \cdot \\ \mathcal{A}_1 g_0(\mathbf{r}_1,t_{l+n+1}|\mathbf{r}_n,t_{l-n-1}) & \mathcal{A}_2 g_0(\mathbf{r}_2,t_{l+n+1}|\mathbf{r}_n,t_{l+n-1}) & \cdot & \mathcal{A}_n g_0(\mathbf{r}_n,t_{l+n+1}|\mathbf{r}_n,t_{l+n-1}) \end{pmatrix}$$

as the matrix of coefficients, and

$$\mathbf{m} = \begin{pmatrix} g_0(\mathbf{r}_i,t_{l+n+2}|\mathbf{r}_1,t_{l+n+1}) \\ g_0(\mathbf{r}_i,t_{l+n+2}|\mathbf{r}_2,t_{l+n+1}) \\ \cdot \\ g_0(\mathbf{r}_i,t_{l+n+2}|\mathbf{r}_n,t_{l+n+1}) \end{pmatrix}$$

as the model vector. Its solution for $i = 1, 2, \ldots, n$ will yield the set $\mathcal{G}_0^*(\mathcal{T}_{l+n+1}) = \{g_0(\mathbf{r}_i,t_{l+n+2}|\mathbf{r}_v,t_{l+n+1}) : i, v = 1, 2, \ldots, n\}$. Proceeding successively to the last system of equations, which in the interval of time $\mathcal{T}_m$, are given by

$$\mathbf{d} = \begin{pmatrix} g_0(\mathbf{r}_i,t_{m+1}|\mathbf{r}_1,t_l) \\ g_0(\mathbf{r}_i,t_{m+1}|\mathbf{r}_2,t_{l+1}) \\ \cdot \\ g_0(\mathbf{r}_i,t_{m+1}|\mathbf{r}_n,t_{l+n-1}) \end{pmatrix}$$

as the data vector,

$$\mathcal{P} = \begin{pmatrix} \mathcal{A}_1 g_0(\mathbf{r}_1,t_m|\mathbf{r}_1,t_l) & \mathcal{A}_2 g_0(\mathbf{r}_2,t_m|\mathbf{r}_1,t_l) & \cdot & \mathcal{A}_n g_0(\mathbf{r}_n,t_m|\mathbf{r}_1,t_l) \\ \mathcal{A}_1 g_0(\mathbf{r}_1,t_m|\mathbf{r}_2,t_{l+1}) & \mathcal{A}_2 g_0(\mathbf{r}_2,t_m|\mathbf{r}_2,t_{l+1}) & \cdot & \mathcal{A}_n g_0(\mathbf{r}_n,t_m|\mathbf{r}_2,t_{l+1}) \\ \cdot & \cdot & \cdot & \cdot \\ \mathcal{A}_1 g_0(\mathbf{r}_1,t_m|\mathbf{r}_n,t_{l+n-1}) & \mathcal{A}_2 g_0(\mathbf{r}_2,t_m|\mathbf{r}_n,t_{l+n-1}) & \cdot & \mathcal{A}_n g_0(\mathbf{r}_n,t_m|\mathbf{r}_n,t_{l+n-1}) \end{pmatrix}$$

as the matrix of coefficients, and

$$\mathbf{m} = \begin{pmatrix} g_0(\mathbf{r}_i,t_{m+1}|\mathbf{r}_1,t_m) \\ g_0(\mathbf{r}_i,t_{m+1}|\mathbf{r}_2,t_m) \\ \cdot \\ g_0(\mathbf{r}_i,t_{m+1}|\mathbf{r}_n,t_m) \end{pmatrix}$$

as the model vector. Solving these for $i = 1, 2, \ldots, n$ will yield the set $\mathcal{G}_0^*(\mathcal{T}_m) = \{g_0(\mathbf{r}_i,t_{m+1}|\mathbf{r}_v,t_m) : i, v = 1, 2, \ldots, n\}$. Any number of numerical techniques can be used to solve (49), or the integral equations of Section 3 for those cases in which an analytical model is chosen (Franklin 1970; Tikhonov and Arsenin 1977; Lavrentev et al. 1986; Parker 1990; Wahba 1990; Press et al. 1992). For noisy data characteristic of fisheries, stable solutions resulting from the inversion of the above systems of equations will have the effect of smoothing the solutions at the expense of resolution. In the end of this process of solving these $m - l - n$ systems of n equations, I will have constructed the set $\mathcal{G}_0^* = \mathcal{G}_0^*(\mathcal{T}_{l+n}) \cup \mathcal{G}_0^*(\mathcal{T}_{l+n+1}) \cup \ldots \cup \mathcal{G}_0^*(\mathcal{T}_m) = \{\mathcal{G}_0^*(\mathcal{T}_j) : j = l + n, l + n + 1, \ldots, m\} = \{g_0(\mathbf{r}_i, t_{j+1}|\mathbf{r}_v, t_j) : i, v = 1, 2, \ldots, n;\ = l + n, l + n + 1, \ldots, m\}$ necessary to generate the set $\mathcal{G}^* = \{g(\mathbf{r}_i,t_{j+1}|\mathbf{r}_v,t_j) : i, v = 1, 2, \ldots, n; j = l + n, l + n + 1, \ldots, m\}$ of effort-independent transition probability densities by use of (48).

If the population exhibits periodic behavior of period $\mathcal{T} < t_{m+1} - t_{l+n}$, then some of the transitions will be repeated because

$$g_0(\mathbf{r}_i,t_{j+1}|\mathbf{r}_v,t_j) = g_0(\mathbf{r}_i,t_{j+1} + \mathcal{T}\,|\mathbf{r}_v,t_j + \mathcal{T}) .$$

It is desirable that tagged fish persist in their domain as long as possible but at least for two periods. This means that, in general, some transitions will have more than one value, one for each period that the tagged fish persist in their domain and there is catch of tagged fish. Due to statistical fluctuations, they will be generally unequal and can be averaged.

Natural periods, such as seasonal, are at best approximate. Due to the inherently stochastic nature of fish movement, the approximate repetition of their seasonal movement may be advanced or retarded. However, the transition probability densities may help decide the duration of a period by the consistent lack or peaks of a subset of $\mathcal{G}^*$, the set of effort-independent transition probability densities. For the estimation of periods the set $\mathcal{G}_0^*$ should not be used because some of the periodic nature of its subsets could be due to seasonal application of fishing effort.

Once the set $\mathcal{G}^*$ of effort-independent transition probability density elements for the fish dynamics are determined, they can be used to determine the contribution to the population density due to recruitment. The discrete version of (44) for a single time interval is

$$(51)\quad u(\mathbf{r}_i,t_{j+1}) \approx \frac{c(\mathbf{r}_i,t_{j+1})}{q(\mathbf{r}_i,t_{j+1})\, e(\mathbf{r}_i,t_{j+1})} - \sum_{v=1}^{n} \mathcal{A}_v g(\mathbf{r}_i,t_{j+1}|\mathbf{r}_v,t_j) \times \left[\frac{1}{f(\mathbf{r}_v,t_j)} - \mathcal{T}_j\right] c(\mathbf{r}_v,t_j) .$$

Because I have sets $\mathcal{C}$, $\mathcal{Q}$, $\mathcal{E}$, and $\mathcal{G}^*$, I can compute with (51) the set $\mathcal{U} = \{u(\mathbf{r}_i,t_{j+1}) : i = 1, 2, \ldots, n; j = l + n, l + n + 1, \ldots, m\}$. To compute the catch density rate $\mathcal{C}' = \{c'(\mathbf{r}_i,t_{j+1}) : i = 1, 2, \ldots, n; j = l + n, l + n + 1, \ldots, m\}$ at a new level of effort density $\mathcal{E}' = \{e'(\mathbf{r}_i, t_{j+1}) : i = 1, 2, \ldots, n; j = l + n, l + n + 1, \ldots, m\}$, the population density at the different level of effort density can be computed with the discretized version of (41) which for a single interval of time $\mathcal{T}_j$ is given by

$$(52)\quad p'(\mathbf{r}_i,t_{j+1}) \approx \sum_{v=1}^{n} \mathcal{A}_v g(\mathbf{r}_i,t_{j+1}|\mathbf{r}_v,t_j)\,[1 - \mathcal{T}_j\, q(\mathbf{r}_v,t_j) \times e'(\mathbf{r}_v,t_j)]\, p(\mathbf{r}_v,t_j) + u(\mathbf{r}_i,t_{j+1})$$

and is applied recursively for $j = l + n, l + n + 1, \ldots, m$. In (52), one assumes that the recruitment density rate does not change significantly at the new level of effort. The catch density rate $\mathcal{C}'$ at the different level of effort density $\mathcal{E}'$ is computed by multiplying the result of (52) by $q(\mathbf{r}_i,t_{j+1})e'(\mathbf{r}_i,t_{j+1})$.

To summarize the previous example, the following steps must be taken to solve the fisheries interaction problem:

1. Using the set of tagged fish catch density rates of n tagging experiments ($\mathcal{C}_T$) and the set of effort density measurements ($\mathcal{E}$), the set of catchabilities ($\mathcal{Q}$) is constructed by use of (45). There will be one catchability associated with each cell and interval of time where tagged fish are released. If only one tagging experiment is conducted in each cell, then one is forced to assume that the value of each catchability in each cell is time independent.

2. Using the sets $\mathcal{C}_T$, $\mathcal{E}$, and $\mathcal{Q}$, the set of discrete Green functions ($\mathcal{G}_0$) for the n tagging experiments is constructed by use of (46).

3. The set of effort-dependent transition probability densities ($\mathcal{G}_0^*$) is constructed by application of $\mathcal{G}_0$ to (49).

4. The set of effort-independent transition probability densities ($\mathcal{G}^*$) is constructed by application of $\mathcal{G}_0^*$ to (48).

5. With the set of catch density rates of untagged fish ($\mathcal{C}$) and sets $\mathcal{Q}$, $\mathcal{E}$, and $\mathcal{G}^*$, the set of population densities due to recruitment $\mathcal{U}$ is constructed by applying (51).

6. Assuming a new level of effort given by the set $\mathcal{E}' \neq \mathcal{E}$, the resulting catch $\mathcal{C}'$ is computed using $\mathcal{E}'$, $\mathcal{Q}$, and $\mathcal{U}$ in (52) and multiplying the population densities $p'(\mathbf{r}_i,t_{j+1})$ by $f(\mathbf{r}_i,t_{j+1}) = q(\mathbf{r}_i,t_{j+1})e'(\mathbf{r}_i,t_{j+1})$.

The recruitment density rate $\mathcal{R} = \{r(\mathbf{r}_i,t_j) : i = 1, 2, \ldots, n; j = l + n, l + n + 1, \ldots, m\}$ is computed by inversion of the system by inversion of the system of equations

$$u(\mathbf{r}_i,t_{j+1}) \approx \mathcal{T}_j \sum_{\nu=1}^{n} \mathcal{A}_\nu g(\mathbf{r}_i,t_{j+1}|\mathbf{r}_\nu,t_j)\, r(\mathbf{r}_\nu,t_j)\,,$$

which is the discretized field $u(\mathbf{r},t)$ given in (42) for a single time interval $\mathcal{T}_j$. For this system of equations, identify in (50)

$$\mathbf{d} = \begin{pmatrix} u(\mathbf{r}_1,t_{j+1}) \\ u(\mathbf{r}_2,t_{j+1}) \\ \cdot \\ u(\mathbf{r}_n,t_{j+1}) \end{pmatrix}$$

as the data vector,

$$\mathcal{P} = \mathcal{T}_j \begin{pmatrix} \mathcal{A}_1 g(\mathbf{r}_1,t_{j+1}|\mathbf{r}_1,t_j) & \mathcal{A}_2 g(\mathbf{r}_1,t_{j+1}|\mathbf{r}_2,t_j) & \cdot & \mathcal{A}_n g(\mathbf{r}_1,t_{j+1}|\mathbf{r}_n,t_j) \\ \mathcal{A}_1 g(\mathbf{r}_2,t_{j+1}|\mathbf{r}_1,t_j) & \mathcal{A}_2 g(\mathbf{r}_2,t_{j+1}|\mathbf{r}_2,t_j) & \cdot & \mathcal{A}_n g(\mathbf{r}_2,t_{j+1}|\mathbf{r}_n,t_j) \\ \cdot & \cdot & \cdot & \cdot \\ \mathcal{A}_1 g(\mathbf{r}_n,t_{j+1}|\mathbf{r}_1,t_j) & \mathcal{A}_2 g(\mathbf{r}_n,t_{j+1}|\mathbf{r}_2,t_j) & \cdot & \mathcal{A}_n g(\mathbf{r}_n,t_{j+1}|\mathbf{r}_n,t_j) \end{pmatrix}$$

as the $n \times n$ matrix of coefficients, and

$$\mathbf{m} = \begin{pmatrix} r(\mathbf{r}_1,t_j) \\ r(\mathbf{r}_2,t_j) \\ \cdot \\ r(\mathbf{r}_n,t_j) \end{pmatrix}$$

as the model vector. The system of equations must be solved for the $j = l + n, l + n + 1, \ldots, m$ time intervals. However, in order to be able to accurately resolve the population density due to recruitment from the population at large by use of (51), it is essential that the Green function also be a measure of the survivability and movement of the untagged portion of the population. As has been discussed before, this condition is true only if sufficient numbers of tagged fish are released.

Once the recruitment density rate is resolved from the above inversions, I am free to interpret it as a nonlinear function of population density. The same result is achieved by inverting for the recruitment density rate using the corresponding algebraic equations that involve the effort-dependent Green function.

6. Estimation of the Field Equation Coefficients

In this section, I will show how to calculate the coefficients of the field equation using tagged fish data. This method is a modification of an analytical technique that is used to construct solutions of stochastic differential equations from Fokker–Planck equations (Okubo 1980; Zwillinger 1989) by the use of moments. The modification developed here will lead to the identification of a closed-form expression for the transition probability densities for small intervals of time. I will show that because the moment method is unable to resolve the divergence of the drift velocity and the Laplacian of the diffusivity, I am left with two alternative models that do equally well interpreting the data.

I assume that I have resolved a smooth set $\mathcal{G}^*$ of the effort-independent transition probability density elements. However, this analysis can also be done with $\mathcal{G}_0^*$. The Green function of the dynamics the population follows is given by

$$(53)\quad \left[\frac{\partial}{\partial t} + \mathcal{L}\right] g(\mathbf{r},t|\mathbf{r}',t') = \delta(\mathbf{r} - \mathbf{r}')\,\delta(t - t')$$

in the space–time domain $\mathbf{r} \in \mathcal{A}$, where operator $\mathcal{L}$ is

$$\mathcal{L} = b_0(\mathbf{r},t) + \mathbf{b}_1(\mathbf{r},t) \cdot \nabla + b_2(\mathbf{r},t)\,\Delta$$

subject to causality condition

$$g(\mathbf{r},t|\mathbf{r}',t') = 0 \text{ if } t < t'$$

and boundary conditions

$$g(\mathbf{r},t|\mathbf{r}',t') = 0$$

for $\mathbf{r} \in \partial\mathcal{A}_A$ and

$$\mathbf{n}_\perp \cdot \nabla g(\mathbf{r},t|\mathbf{r}',t') = 0$$

for $\mathbf{r} \in \partial\mathcal{A}_R$. The only difference between this field equation and (7) is that here, $b_0(\mathbf{r},t) = m(\mathbf{r},t) + \nabla \cdot \mathbf{v}(\mathbf{r},t)$.

The even moments of g are found by multiplying (53) by r^{2N} and integrating over space $\mathcal{A}$ in the interval of time $\mathcal{T}_{-\infty} = [-\infty,t]$. Once these integrations are performed, space–time discretization of the resulting equation for a single interval of time and invoking the initial property of g, for a source in cell $\mathcal{A}_i$ in the interval of time $\mathcal{T}_j$, leads to the equation for the $2N$th moment of g (Appendix C) given by

$$(54)\quad r_k^{2N} m(\mathbf{r}_k,t_j) - 2Nr_k^{2N-2}\,\mathbf{r}_k\cdot\mathbf{v}(\mathbf{r}_k,t_j) - 4N^2 r_k^{2N-2}k(\mathbf{r}_k,t_j) - 2Nr_k^{2N-2}\mathbf{r}_k\cdot\nabla_k k(\mathbf{r}_k,t_j) = \frac{1}{\mathcal{T}_j}\left[r_k^{2N} - \langle r_i^{2N}\rangle(t_{j+1}|\mathbf{r}_k,t_j)\right]$$

for $\mathbf{r}_k \notin \partial\mathcal{A}$, where

$$\langle r_i^{2N}\rangle(t_{j+1}|\mathbf{r}_k,t_j) = \sum_{i=1}^{n} \mathcal{A}_i\, r_i^{2N}\, g(\mathbf{r}_i,t_{j+1}|\mathbf{r}_k,t_j)\,.$$

The odd moments are calculated by going through the same process after multiplication of the field equation for g by $r^{2N}\mathbf{r}$. The result is (Appendix C)

$$(55)\quad r_k^{2N}\mathbf{r}_k m(\mathbf{r}_k,t_j) - r_k^{2N}\mathbf{v}(\mathbf{r}_k,t_j) - 2Nr_k^{2N-2}\mathbf{r}_k[\mathbf{r}_k\cdot\mathbf{v}(\mathbf{r}_k,t_j)] - 4N(N+1)\,r_k^{2N-2}\mathbf{r}_k\,k(\mathbf{r}_k,t_j)$$
$$- r_k^{2N}\nabla_k k(\mathbf{r}_k,t_j) - 2Nr_k^{2N-2}\mathbf{r}_k[\mathbf{r}_k\cdot\nabla_k k(\mathbf{r}_k,t_j)] = \frac{1}{\mathcal{T}_j}\left[r_k^{2N}\mathbf{r}_k - \langle r_i^{2N}\mathbf{r}_i\rangle(t_{j+1}|\mathbf{r}_k,t_j)\right]$$

for $\mathbf{r}_k \notin \partial\mathcal{A}$, where

$$\langle r_i^{2N}\,\mathbf{r}_i\rangle(t_{j+1}|\mathbf{r}_k,t_j) = \sum_{i=1}^{n} \mathcal{A}_i\, r_i^{2N}\mathbf{r}_i\, g(\mathbf{r}_i,t_{j+1}|\mathbf{r}_k,t_j)\,.$$

Because data are collected only at the points that are interior to $\mathcal{A}$, I will consider only those source points $\mathbf{r}_k \notin \partial\mathcal{A}$. For points $\mathbf{r}_k \notin \partial\mathcal{A}$, corrections are necessary (Appendix C). However, for the purposes of this work, they are unnecessary.

With the moments of the transition probability densities for a single interval of time $\mathcal{T}_j$, it is not possible to estimate the values of $\nabla_k\cdot\mathbf{v}(\mathbf{r}_k,t_j)$ and $\triangle_k k(\mathbf{r}_k,t_j)$ in cell $\mathcal{A}_k$. As can be appreciated in (54) and (55), the even- and odd-moment equations are independent of these parameters. For the remaining parameters, $\{m(\mathbf{r}_k,t_j), \mathbf{v}(\mathbf{r}_k,t_j), k(\mathbf{r}_k,t_j), \nabla_k k(\mathbf{r}_k,t_j)\}$, there are restrictions to their resolvablility. To see this, construct from the moment equations (54) and (55) a completely determined system of linear equations. Because the even-moment equations are scalar and the odd moments generate two component vector equations, it is only necessary to compute up to the third order moment. It leads to a system of linear algebraic equations

$$\mathbf{d}_s = \sum_{v=1}^{6} \mathcal{P}_{sv}\,\mathbf{m}_v \quad s = 1, 2, \ldots, 6$$

with

$$\mathbf{d} = \frac{1}{\mathcal{T}_j}\begin{pmatrix} 1 - \langle 1\rangle(t_{j+1}|\mathbf{r}_k,t_j) \\ x_k - \langle x_i\rangle(t_{j+1}|\mathbf{r}_k,t_j) \\ y_k - \langle y_i\rangle(t_{j+1}|\mathbf{r}_k,t_j) \\ r_k^2 - \langle r_i^2\rangle(t_{j+1}|\mathbf{r}_k,t_j) \\ r_k^2 x_k - \langle r_i^2 x_i\rangle(t_{j+1}|\mathbf{r}_k,t_j) \\ r_k^2 y_k - \langle r_i^2 y_i\rangle(t_{j+1}|\mathbf{r}_k,t_j) \end{pmatrix}$$

as the data vector

$$\mathbf{m} = \begin{pmatrix} m(\mathbf{r}_k,t_j) \\ v_x(\mathbf{r}_k,t_j) \\ v_y(\mathbf{r}_k,t_j) \\ k(\mathbf{r}_k,t_j) \\ \partial k(\mathbf{r}_k,t_j)/\partial x_k \\ \partial k(\mathbf{r}_k,t_j)/\partial y_k \end{pmatrix}$$

as the model vector, and

$$\mathcal{P} = \begin{pmatrix} 1 & 0 & 0 & 0 & 0 & 0 \\ x_k & -1 & 0 & 0 & -1 & 0 \\ y_k & 0 & -1 & 0 & 0 & -1 \\ r_k^2 & -2x_k & -2y_k & -4 & -2x_k & -2y_k \\ r_k^2 x_k & -r_k^2 - 2x_k^2 & -2x_k y_k & -8x & -r_k^2 - 2x_k^2 & -2\,x_k y_k \\ r_k^2 y_k & -2x_k y_k & -r_k^2 - 2y_k^2 & -8y & -2x_k y_k & -r_k^2 - 2y_k^2 \end{pmatrix}$$

as the matrix of coefficients. The matrix of coefficients $\mathcal{P}$ has $det\mathcal{P} = 0$. Therefore, the equations are not linearly independent. Keeping natural death rate and diffusion, there are two alternatives regarding the fields $\mathbf{v}$ and $\nabla_k k$ within cell $\mathcal{A}_k$ during the interval of time $\mathcal{T}_j$: either $\mathbf{v}(\mathbf{r}_k, t_j)$ is constant and $\nabla_k k(\mathbf{r}_k,t_j) = 0$ or $\mathbf{v}(\mathbf{r}_k,t_j) = 0$ and $\nabla_k k(\mathbf{r}_k,t_j)$ is constant. In either case, it is only necessary to consider up to the second moment to define a completely determined system of equations. The matrix of

coefficients given by

$$\mathcal{P} = \begin{pmatrix} 1 & 0 & 0 & 0 \\ x_k & -1 & 0 & 0 \\ y_k & 0 & -1 & 0 \\ r_k^2 & -2x_k & -2y_k & -4 \end{pmatrix},$$

which has a determinant given by $det\mathcal{P} = -4$, and the data vector given by

$$\mathbf{d} = \frac{1}{\mathcal{T}_j} \begin{pmatrix} 1 - \langle 1 \rangle (t_{j+1}|\mathbf{r}_k,t_j) \\ x_k - \langle x_i \rangle (t_{j+1}|\mathbf{r}_k,t_j) \\ y_k - \langle y_i \rangle (t_{j+1}|\mathbf{r}_k,t_j) \\ r_k^2 - \langle r_i^2 \rangle (t_{j+1}|\mathbf{r}_k,t_j) \end{pmatrix}$$

are sufficient to define uniquely

$$\mathbf{m} = \begin{pmatrix} m(\mathbf{r}_k,t_j) \\ v_x(\mathbf{r}_k,t_j) \\ v_y(\mathbf{r}_k,t_j) \\ k(\mathbf{r}_k,t_j) \end{pmatrix}$$

in the first alternative or

$$\mathbf{m} = \begin{pmatrix} m(\mathbf{r}_k,t_j) \\ \partial k(\mathbf{r}_k,t_j)/\partial x_k \\ \partial k(\mathbf{r}_k,t_j)/\partial y_k \\ k(\mathbf{r}_k,t_j) \end{pmatrix}$$

in the second alternative. Because the moment method cannot resolve the derivatives $\nabla_k \cdot \mathbf{v}(\mathbf{r}_k,t_j)$ and $\Delta_k k(\mathbf{r}_k,t_j)$, either of the alternatives above will interpret the data equally well. In other words, because the divergence of $\mathbf{v}$ and the Laplacian of k are unresolvable by the moment method, the inverse will interpret the data equally well if $\mathbf{v} = b(t_j)$ and $k = a(t_j)$ or $\mathbf{v} = 0$ and $k = a(t_j) - b(t_j)\mathbf{r}_k/2$. This does not mean that the entire domain of the population has $\{m,\mathbf{v},k\}$ or $\{m,\nabla_k,k\}$ that are independent of position. It means that within each cell of the domain, each, in principle, arbitrarily small, the resolved coefficients $\{m,\mathbf{v},k\}$ or $\{m,\nabla_k k\}$ are constant within an interval of time.

The solution to the system of equations for the case of the first alternative is

$$m(\mathbf{r}_k,t_j) = \frac{1}{\mathcal{T}_j}\left[1 - \langle 1 \rangle (t_{j+1}|\mathbf{r}_k,t_j)\right]$$

$$\mathbf{v}(\mathbf{r}_k,t_j) = \frac{1}{\mathcal{T}_j}\left[\langle \mathbf{r}_i \rangle (t_{j+1}|\mathbf{r}_k,t_j) - \mathbf{r}_k \langle 1 \rangle (t_{j+1}|\mathbf{r}_k,t_j)\right]$$

$$k(\mathbf{r}_k,t_j) = \frac{1}{4\,\mathcal{T}_j}\left[\langle r_i^2 \rangle (t_{j+1}|\mathbf{r}_k,t_j) - 2\mathbf{r}_k \cdot \langle \mathbf{r}_i \rangle (t_{j+1}|\mathbf{r}_k,t_j) + r_k^2 \langle 1 \rangle (t_{j+1}|\mathbf{r}_k,t_j)\right].$$

These are the same results, linearized in $\mathcal{T}_j$, that the discrete transition probability density

$$(56)\quad g(\mathbf{r}_i,t_{j+1}|\mathbf{r}_k,t_j) = \exp\left[-\mathcal{T}_j\, m(\mathbf{r}_k,t_j)\right] \mathcal{N}\left(\mathbf{r}_k + \mathcal{T}_j\, \mathbf{v}(\mathbf{r}_k,t_j),\sigma^2\right)$$

where

$$\sigma^2 = 2\,\mathcal{T}_j\, k(\mathbf{r}_k,t_j)$$

(see equation (20)) yields for the unbounded domain when its coefficients are calculated using moments. In fact, (56) yields the moments of g of any order in the interval of time $\mathcal{T}_j$, but those derived here (Appendix C) are linearized in $\mathcal{T}_j$ due to the discretization of the field equation necessary for the derivation. The fact that the moment equations of this section are correct for either the unbounded domain, or the domains bounded by absorbing and/or reflecting boundaries if $\mathbf{r}_k \notin \partial\mathcal{A}$ (Appendix C), leads to the expectation that the closed-form transition probability (56) is also correct for the bounded domain of this work. Because $\mathcal{T}_j$ is small, the transition probability densities are very nearly Dirac delta functions, so for points $\mathbf{r}_i$ not near $\mathbf{r}_k$ the distributions are nearly vanishing.

Finally, transforming (56) with the transformation $m(\mathbf{r}_k,t_j) \rightarrow m(\mathbf{r}_k,t_j) + f(\mathbf{r}_k,t_j)$ yields the closed-form expression for the effort-dependent transition probability densities. These results, coupled with the discrete equations of Section 5, simplify considerably numerical analysis and simulations for an interval of time of arbitrary length. This method should be applicable to problems whose field equation has a Green function with a probabilistic interpretation: Fokker–Planck equations, but more generally, any linear field equation with at most a first-order time derivative but spatial derivatives of arbitrary order. As can be seen by comparing (20) with (56), it is only necessary to find the Green function associated with the field equation that is invariant under space–time translations, and then expressions for small intervals of time for the discrete transition probability densities associated with the corresponding field equation that is not invariant under space–time translations are constructed by inspection. In general, it is only possible to construct exact closed-form expressions for the transition probability densities if the differential operator has spacial derivatives no higher than fourth order.

7. Summary

When members of a population are released in an area small compared with their domain and over an interval of time short compared with the length of time they take to disperse throughout their domain, the pattern of movement approximates a point-source solution (or Green function) of the underlying population dynamics. The Green functions, one for each release, can be empirically determined with the mark and recapture data of tagged members of the population with distinguishable tags. The assumed field equations for the population dynamics were inverted to represent the solution in terms of integral equations for the tagged and untagged portions of the population.

Because for a fish population it is necessary to use catch per unit effort of tagged fish to construct the Green functions empirically, the resulting point-source solutions are effort dependent and, therefore, not practical for a fishery interaction problem where it is desired to determine the catch resulting from a different level of effort, the field equations were reformulated such that the term containing effort was redefined as an inhomo-

geneous term of the field equation. This leads to a method of constructing the effort-independent Green function from knowledge of the effort-dependent one.

Discretization of the integral equations was achieved by defining non overlapping cells of arbitrary shape in the neighborhood of each point where data were collected. The integral equations of the theory, upon discretization, result as systems of coupled algebraic equations which for a single interval of time coincide with a Markovian formulation of the exchange of members of the population between the cells of the discretized space.

For every tagging experiment, it is possible to calculate only one catchability at the cell and time of release. However, to be able to determine approximately a complete effort-independent Green function from knowledge of the effort-dependent one in a bounded population domain, it is required that there be as many tagging experiments as there are cells defined in the domain.

The Green functions were interpreted as the tagged fish probability density of surviving movement to the receiver space–time coordinates from the release coordinates. If sufficiently large numbers of tagged fish are released, then the tagged fish dynamics are representative of the population. Both the effort-dependent and effort-independent Green fuctions can be decomposed into transition probability densities for a single interval of time. The transition probability densities can be used to determine the recruitment density rate which, once resolved, can be freely interpreted as a nonlinear function of the population density. The moments of the transition probability densities lead to the evaluation of model parameters and the identification of the closed-form transition probability densities.

Acknowledgements

Fruitful conversations were held with Alain Fonteneau, Nancy Lo, and Patrick Tomlinson. I also wish to thank Salah Baouendi, Richard Deriso, Hector Echavarría, and Linda Rothschild for discussions, commentaries, and suggestions. Ian Fletcher and Geneva Simmons provided valuable editorial suggestions. David Fournier, Don Ludwig, and Marc Mangel, who reviewed the original manuscript, provided valuable editorial and technical commentaries. In particular, Pierre Kleiber's support of the research, constant availability for discussions while in residence at the SWFSC, and asking of pertinent questions that influenced the research are very gratefully acknowledged.

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Appendix A. Representation Theorem for the Population Density

The purpose of this appendix is to derive an integral representation for the population density. I will show that if on the boundary of the population domain the population density satisfies either homogeneous Dirichlet or Neumann conditions, the integral representation for the solution does not contain a boundary integral. The proof is not intended to be rigorous, but follows mathematical procedures well established and elucidated in the literature (Courant and Hilbert 1953; Morse and Feshbach 1953; Garabedian 1964; Gilbarg and Trudinger 1979).

Let the domain of the population $\mathcal{A} \in \mathbf{R}^2$ be bounded by $\partial\mathcal{A} \in \mathbf{R}$. Let $\mathbf{r} = x\mathbf{i} + y\mathbf{j} \in \mathcal{A}$ be the receiver or measuring point with respect to an arbitrarily chosen fixed coordinate system where $\mathbf{i}$ and $\mathbf{j}$ are, respectively, the unit vectors pointing in the $+x$ and $+y$ directions. Let time t be the receiver time. At time t_i, there is an initial population whose subsequent dynamics I wish to model. I assume that the dynamics of the population are correctly given by (7):

$$\text{(A1)}\quad \left[\frac{\partial}{\partial t} + \mathcal{L}_0\right] p(\mathbf{r},t) = r(\mathbf{r},t)$$

where

$$\text{(A2)}\quad \mathcal{L}_0\, p(\mathbf{r},t) = b_0(\mathbf{r},t)\, p(\mathbf{r},t) + \mathbf{b}_1(\mathbf{r},t)\cdot \nabla p(\mathbf{r},t) + b_2(\mathbf{r},t)\, \Delta\, p(\mathbf{r},t)\,.$$

In equation (A2) the coefficients $\{b_0,\mathbf{b}_1,b_2\}$ are related to the coefficients $\{z,\mathbf{v},k\}$ by

$$b_0(\mathbf{r},t) = z(\mathbf{r},t) + \nabla\cdot\mathbf{v}(\mathbf{r},t)$$

$$\text{(A3)}\quad \mathbf{b}_1(\mathbf{r},t) = \mathbf{v}(\mathbf{r},t) - \nabla k(\mathbf{r},t)$$

$$b_2(\mathbf{r},t) = -k(\mathbf{r},t)$$

where the derivatives $\nabla\cdot\mathbf{v}(\mathbf{r},t)$ and $\Delta k(\mathbf{r},t)$ are finite.

The general problem for the population density can be formulated as follows: the population density $p(\mathbf{r},t)$ satisfies the inhomogeneous field equation (A1) in the space–time domain $\mathbf{r}\in\mathcal{A}$, $t\geq t_I$, subject to initial condition

$$\text{(A4)}\quad p(\mathbf{r},t_I) = p_{in}(\mathbf{r})$$

in the domain $\mathbf{r}\in\mathcal{A}$. I wish to determine boundary conditions that can be imposed on $\partial\mathcal{A}$ that leads to a unique representation of the solution for $p(\mathbf{r},t)$.

Defining $\mathbf{r}' = x'\mathbf{i} + y'\mathbf{j} \in \mathcal{A}$ as the source point and t' as the source time, the Green function $g_0(\mathbf{r},t|\mathbf{r}',t')$ that is associated with field equation (A1) satisfies field equation

$$\text{(A5)}\quad \left[\frac{\partial}{\partial t} + \mathcal{L}_0\right] g_0(\mathbf{r},t|\mathbf{r}',t') = \delta(\mathbf{r}-\mathbf{r}')\,\delta(t-t')$$

in the domain $\mathbf{r}\in\mathcal{A}$ and the causality condition

$$g_0(\mathbf{r},t|\mathbf{r}',t') = 0 \text{ if } t < t'$$

in the domain $\mathbf{r}\in\mathcal{A}$. The key to constructing an integral representation of the solution of an initial-boundary value problem for a field is the ability to construct a bilinear function of the field and a Green function associated with it. Because the differential operator associated with field equation (A5) is not self-adjoint, I must consider the adjoint field equation

$$\text{(A6)}\quad \left[-\frac{\partial}{\partial t} + \mathcal{L}_0^*\right] g_0^*(\mathbf{r},t|\mathbf{r}'',t'') = \delta(\mathbf{r}-\mathbf{r}'')\,\delta(t-t'')$$

in the domain $\mathbf{r}\in\mathcal{A}$, where

$$\mathcal{L}_0^*\, g_0^*(\mathbf{r},t|\mathbf{r}'',t'') = b_0(\mathbf{r},t)\, g_0^*(\mathbf{r},t|\mathbf{r}'',t'') - \nabla\cdot[\mathbf{b}_1(\mathbf{r},t)\, g_0^*(\mathbf{r},t|\mathbf{r}'',t'')] + \Delta[\mathbf{b}_2(\mathbf{r},t)\, g_0^*(\mathbf{r},t|\mathbf{r}'',t'')]$$

subject to the causality condition

$$g_0^*(\mathbf{r},t|\mathbf{r}'',t'') = 0 \text{ if } t > t'.$$

By definition of the field equation that $g_0^*(\mathbf{r},t|\mathbf{r}',t')$ satisfies, it is the function adjoint to Green function $g_0(\mathbf{r},t|\mathbf{r}',t')$.

Multiplying field equation (A5) by $g_0^*(\mathbf{r},t|\mathbf{r}'',t'')$ and (A6) by $g_0(\mathbf{r},t|\mathbf{r}',t')$, subtracting the former resulting equation from the latter resulting equation, and integrating over the interval of time $[-\infty,\infty]$ and over $\mathcal{A}$ leads, by application of the Divergence Theorem, to

$$g_0^*(\mathbf{r}',t'|\mathbf{r}'',t'') - g_0(\mathbf{r}'',t''|\mathbf{r}',t') = \int_{t'}^{t''} dt \oint_{\partial\mathcal{A}} dl\, \mathbf{n}_\perp\cdot\mathbf{P}[g_0^*(\mathbf{r},t|\mathbf{r}'',t'')|g_0(\mathbf{r},t|\mathbf{r}',t')]\,.$$

The bilinear function $\mathbf{P}[g_0^*(\mathbf{r},t|\mathbf{r}'',t'')|g_0(\mathbf{r},t|\mathbf{r}',t')]$ is given by

$$\text{(A7)}\quad \mathbf{P}[g_0^*(\mathbf{r},t|\mathbf{r}'',t'')|g_0(\mathbf{r},t|\mathbf{r}',t')] = -g_0(\mathbf{r},t|\mathbf{r}',t')\,\mathbf{b}_1(\mathbf{r},t) \times g_0^*(\mathbf{r},t|\mathbf{r}'',t'') + g_0(\mathbf{r},t|\mathbf{r}',t')\,\nabla[b_2(\mathbf{r},t)\, g_0^*(\mathbf{r},t|\mathbf{r}'',t'')] - b_2(\mathbf{r},t)\, g_0^*(\mathbf{r},t|\mathbf{r}'',t'')\,\nabla g_0(\mathbf{r},t|\mathbf{r}',t') + \mathbf{C}$$

where $\mathbf{C}$ is an arbitrary constant. In order that between g_0 and its adjoint g_0^* there be the simple reciprocity relation

$$\text{(A8)}\quad g_0^*(\mathbf{r}',t'|\mathbf{r}'',t'') = g_0(\mathbf{r}'',t''|\mathbf{r}',t')\,,$$

it is sufficient that

$$\text{(A9)}\quad \mathbf{n}_\perp\cdot\mathbf{P}[g_0^*(\mathbf{r},t|\mathbf{r}'',t'')|g_0(\mathbf{r},t|\mathbf{r}',t')] = 0\,.$$

However, because I also demand uniqueness of the solution, it must vanish in such a way that the conditions imposed that lead to (A9) specify the behavior of both g and its adjoint. Not doing so leads to a solution that is not unique. For example, specifying that $g_0(\mathbf{r},t|\mathbf{r}',t')$ satisfy homogeneous Cauchy conditions (i.e., $g_0(\mathbf{r},t|\mathbf{r}',t') = 0$ and $\mathbf{n}_\perp\cdot\nabla g_0(\mathbf{r},t|\mathbf{r}',t') = 0$ for $\mathbf{r}\in\partial\mathcal{A}$ satisfies (A9) but leaves $g_0^*(\mathbf{r},t|\mathbf{r}'',t'')$ arbitrary. However, the boundary conditions

$$\text{(A10)}\quad g_0(\mathbf{r},t|\mathbf{r}',t') = 0$$

and

$$\text{(A11)}\quad g_0^*(\mathbf{r},t|\mathbf{r}',t') = 0$$

or, if $\mathbf{n}_\perp\cdot\mathbf{v}(\mathbf{r},t) = 0$

$$\text{(A12)}\quad \mathbf{n}_\perp\cdot\nabla g_0(\mathbf{r},t|\mathbf{r}',t') = 0$$

and

$$\text{(A13)}\quad \mathbf{n}_\perp\cdot\nabla g_0^*(\mathbf{r},t|\mathbf{r}',t') = 0$$

for $\mathbf{r} \in \partial\mathcal{A}$ result in g_0 and g_0^* uniquely specified, and such that the reciprocity relation (A8) holds

Now, as a consequence of (A8), $g_0(\mathbf{r},t|\mathbf{r}',t')$ satisfies the field equation

$$\left[-\frac{\partial}{\partial t'} + \mathcal{L}_0'^*\right] g_0(\mathbf{r},t|\mathbf{r}',t') = \delta(\mathbf{r} - \mathbf{r}')\,\delta(t - t')$$

in the domain $\mathbf{r}' \in \mathcal{A}$, where $\mathcal{L}_0'^*$ is operator $\mathcal{L}_0^*$ under the change of variables $(\mathbf{r},t) \rightarrow (\mathbf{r}',t')$. Therefore, the representation of the solution that satisfies field equation (A1) and initial conditions (A4) is given by

$$\text{(A14)}\quad p(\mathbf{r},t) = \int_{\mathcal{A}} d^2\mathbf{r}'\, g_0(\mathbf{r},t|\mathbf{r}',t_T)\, p_{in}(\mathbf{r}') + \int_{\mathcal{T}_t} dt' \int_{\mathcal{A}} d^2\mathbf{r}'\, g_0(\mathbf{r},t|\mathbf{r}',t')\, r(\mathbf{r}',t') + \int_{\mathcal{T}_t} dt' \oint_{\partial\mathcal{A}} dl'\, \mathbf{n}_\perp \cdot \mathbf{P}[g_0(\mathbf{r},t|\mathbf{r}',t'),p(\mathbf{r}',t')]$$

where the integral with respect to time is in the domain $\mathcal{T}_t$ by virtue of the initial condition and causality. In (A14) the bilinear function $\mathbf{P}[g_0(\mathbf{r},t|\mathbf{r}',t'),p(\mathbf{r}',t')]$ is given by

$$\text{(A15)}\quad \mathbf{P}[g_0(\mathbf{r},t|\mathbf{r}',t'),p(\mathbf{r}',t')] = -p(\mathbf{r}',t')\mathbf{b}_1(\mathbf{r}',t') \times g_0(\mathbf{r},t|\mathbf{r}',t') + p(\mathbf{r}',t')\,\nabla'[b_2(\mathbf{r}',t')\, g_0(\mathbf{r},t|\mathbf{r}',t')] - b_2(\mathbf{r}',t')\, g_0(\mathbf{r},t|\mathbf{r}',t')\,\nabla' p(\mathbf{r}',t') + \mathbf{C}$$

where $\mathbf{C}$ is an arbitrary constant. Furthermore, because (A8) holds due to boundary conditions (A10) and (A11) or (A12) and (A13), it follows that $g_0(\mathbf{r},t|\mathbf{r}',t')$ satisfies boundary condition

$$\text{(A16)}\quad g_0(\mathbf{r},t|\mathbf{r}',t') = 0$$

or

$$\text{(A17)}\quad \mathbf{n}_\perp \cdot \nabla' g_0(\mathbf{r},t|\mathbf{r}',t') = 0$$

for $\mathbf{r}' \in \partial\mathcal{A}$, and therefore,

$$\text{(A18)}\quad p(\mathbf{r},t) = \int_{\mathcal{A}} d^2\mathbf{r}'\, g_0(\mathbf{r},t|\mathbf{r}',t_T)\, p_{in}(\mathbf{r}') + \int_{\mathcal{T}_t} dt' \int_{\mathcal{A}} d^2\mathbf{r}'\, g_0(\mathbf{r},t|\mathbf{r}',t')\, r(\mathbf{r}',t')$$

is a unique solution of (A1) subject to initial condition (A4) and homogeneous Dirichlet boundary conditions

$$\text{(A19)}\quad p(\mathbf{r},t) = 0$$

or homogeneous Neumann conditions

$$\text{(A20)}\quad \mathbf{n}_\perp \cdot \nabla p(\mathbf{r},t) = 0$$

in the domain $\mathbf{r} \in \partial\mathcal{A}$.

Assume now that the boundary of $\mathcal{A}$ is composed of segments, denoted $\partial\mathcal{A}_A$, on which homogeneous Dirichlet conditions are satisfied, and the remainder of $\partial\mathcal{A}$, denoted $\partial\mathcal{A}_R$, on which the homogeneous Neumann conditions (A20) are satisfied. Proceeding in the same manner as above, the following conclusion can be made: (A18) uniquely satisfies field equation (A1), initial condition (A4), and boundary conditions

$$p(\mathbf{r},t) = 0$$

for $\mathbf{r} \in \partial\mathcal{A}_A$ and

$$\mathbf{n}_\perp \cdot \nabla p(\mathbf{r},t) = 0$$

for $\mathbf{r} \in \partial\,\mathcal{A}_R$ if $\mathbf{n}_\perp \cdot \mathbf{v}(\mathbf{r},t) = 0$.

Appendix B. Convergence Condition of the Neumann Expansion

Here, I shall show that the expansion given in (38) converges if the number of tagged fish recovered during an interval of time is less than the number of tagged fish available at the beginning of the interval. To see this, consider the perturbation expansion given in (38):

$$\text{(B1)}\quad g(\mathbf{r},t|\mathbf{r}_T,t_T) = \sum_{i=0}^{\infty} g_i(\mathbf{r},t|\mathbf{r}_T,t_T)$$

where

$$g_i(\mathbf{r},t|\mathbf{r}_T,t_T) = \frac{1}{N_T(\mathbf{r}_T,t_T)} \int_{\mathcal{T}_T} dt' \int_{\mathcal{A}} d^2\mathbf{r}'\, g_{i-1}(\mathbf{r},t|\mathbf{r}',t')\, c_T(\mathbf{r}',t')$$

for $i = 1, 2, \ldots$. Presume now that the maximum number of tagged fish recaptured at any one time is N_M. Then, I can state the following:

$$c_T(\mathbf{r}',t') \le \frac{N_R}{\mathcal{A}\mathcal{T}_T^2}$$

where $N_R \le N_M\mathcal{T}_T$ is the number of tagged fish recovered in the interval of time $\mathcal{T}_T$. It follows from the probabilistic property of g_0 (Property E in Section 3) that there exists a constant $0 \le C \le 1$ such that

$$\int_{\mathcal{T}_T} dt' \int_{\mathcal{A}} d^2r'\, g_0(\mathbf{r},t|\mathbf{r}',t') \le C\mathcal{T}_T.$$

By making use of the first inequality, the iteration relation can be written

$$g_i(\mathbf{r},t|\mathbf{r}_T,t_T) \le \left(\frac{N_R}{N_T(\mathbf{r}_T,t_T)\mathcal{A}}\right)\frac{1}{\mathcal{T}_T^2} \times \int_{\mathcal{T}_T} dt' \int_{\mathcal{A}} d^2\mathbf{r}'\, g_{i-1}(\mathbf{r},t|\mathbf{r}',t')$$

for $i = 1, 2, \ldots$, and from which I can compute all terms of the iteration:

$$g_1(\mathbf{r},t|\mathbf{r}_T,t_T) \le \left(\frac{C}{\mathcal{A}\,\mathcal{T}_T}\right)\left(\frac{N_R}{N_T(\mathbf{r}_T,t_T)}\right)$$

$$g_2(\mathbf{r},t|\mathbf{r}_T,t_T) \le \left(\frac{C}{\mathcal{A}\,\mathcal{T}_T}\right)\left(\frac{N_R}{N_T(\mathbf{r}_T,t_T)}\right)^2$$

$$g_N(\mathbf{r},t|\mathbf{r}_T,t_T) \le \left(\frac{C}{\mathcal{A}\,\mathcal{T}_T}\right)\left(\frac{N_R}{N_T(\mathbf{r}_T,t_T)}\right)^N$$

Performing the ratio test

$$\lim_{N\to\infty}\left|\frac{g_{N+1}(\mathbf{r},t|\mathbf{r}_T,t_T)}{g_N(\mathbf{r},t|\mathbf{r}_T,t_T)}\right| = \frac{N_R}{N_T(\mathbf{r}_T,t_T)},$$

which is less than 1 if the number of tagged fish recovered is less than the number of tagged fish released, and therefore, the series converges under that condition.

Appendix C. Moment Equations of the Green Function

In this appendix, I will find expressions for determining the coefficients of the population field equation by computing the moments of the Green function. I will also show that the inverse problem of determining the coefficients of the field equation in every cell at every interval of time, from the moments of the Green function, leads to nonuniqueness. For source points not on $\partial\mathcal{A}$, the moment equations are correct for either the infinite domain or the domains bounded by a perfectly absorbing and/or perfectly reflecting boundaries. For source points on $\partial\mathcal{A}$, corrections are necessary.

I consider a linear differential operator

$$\mathcal{L} = b_0(\mathbf{r},t) + \mathbf{b}_1(\mathbf{r},t)\cdot\nabla + b_2(\mathbf{r},t)\,\Delta$$

where the coefficients

$$b_0(\mathbf{r},t) = m(\mathbf{r},t) + \nabla\cdot\mathbf{v}(\mathbf{r},t)$$

(C1) $$\mathbf{b}_1(\mathbf{r},t) = \mathbf{v}(\mathbf{r},t) - \nabla k(\mathbf{r},t)$$

$$b_2(\mathbf{r},t) = -k(\mathbf{r},t).$$

The derivatives $\nabla\cdot\mathbf{v}(\mathbf{r},t)$ and $\Delta k(\mathbf{r},t)$ are assumed to exist. The effort-independent Green function $g(\mathbf{r},t|\mathbf{r}',t')$ satisfies the field equation

(C2) $$\left[\frac{\partial}{\partial t} + \mathcal{L}\right] g(\mathbf{r},t|\mathbf{r}',t') = \delta(\mathbf{r}-\mathbf{r}')\delta(t-t')$$

in the space domain $\mathbf{r}\in\mathcal{A}$, subject to the causal condition

$$g(\mathbf{r},t|\mathbf{r}',t') = 0 \text{ if } t < t'.$$

The boundary of the domain $\mathcal{A}$ is $\partial\mathcal{A} = \partial\mathcal{A}_A + \partial\mathcal{A}_R$. In terms of the measuring space–time point $(\mathbf{r},t)$, the boundary conditions satisfied by $g(\mathbf{r},t|\mathbf{r}',t')$ are (Appendix A)

$$g(\mathbf{r},t|\mathbf{r}',t') = 0$$

in the spatial domain $\mathbf{r}\in\partial\mathcal{A}_A$ and

$$\mathbf{n}_\perp\cdot\nabla\, g(\mathbf{r},t|\mathbf{r}',t') = 0$$

in the spatial domain $\mathbf{r}\in\partial\mathcal{A}_R$ and where $\mathbf{n}_\perp$ is the unit vector normal to $\partial\mathcal{A}$ pointing outward.

To compute the even moments of g, multiply (C2) by the scalar r^{2N} and integrate over domain $\mathcal{A}$ in the interval of time $\mathcal{T}_{-\infty} = [-\infty,t]$. Explicit integration with respect to time can only be performed on the term that contains the time derivative of g:

$$\int_{\mathcal{T}_{-\infty}} d\tau \int_{\mathcal{A}} d^2\mathbf{r}\, r^{2N}\,\frac{\partial g(\mathbf{r},\tau|\mathbf{r}',t')}{\partial\tau} = \int_{\mathcal{A}} d^2\mathbf{r}\, r^{2N}\, g(\mathbf{r},t|\mathbf{r}',t')$$

where I am allowed to change the order of integration by Fubinis' Theorem because the integrand is absolutely integrable (Royden 1968). I then have

$$\int_{\mathcal{T}_{\infty}} d\tau \int_{\mathcal{A}} d^2\mathbf{r}\, r^{2N}\,\mathcal{L}g(\mathbf{r},\tau|\mathbf{r}',t') = r'^{2N} - \langle r^{2N}\rangle(t|\mathbf{r}',t')$$

where

$$\langle r^{2N}\rangle(t|\mathbf{r}',t') = \int_{\mathcal{A}} d^2\mathbf{r}\, r^{2N} g(\mathbf{r},t|\mathbf{r}',t').$$

For the spatial integration in the l.h.s., I apply partial integration and the Divergence Theorem to those terms containing the gradient and the Laplacian of g. For the term containing the gradient of g, this results in

$$\int_{\mathcal{A}} d^2\mathbf{r}\, r^{2N}\mathbf{b}_1(\mathbf{r},t)\cdot\nabla\, g(\mathbf{r},t\,|\,\mathbf{r}',t') = \oint_{\partial\mathcal{A}} dl\, r^{2N}\,\mathbf{n}_\perp\cdot\mathbf{b}_1(\mathbf{r},t)\, g(\mathbf{r},t\,|\,\mathbf{r}',t') - \int_{\mathcal{A}} d^2\mathbf{r}\,\nabla\cdot[r^{2N}\mathbf{b}_1(\mathbf{r},t)]\, g(\mathbf{r},t\,|\,\mathbf{r}',t')$$

while for the term with the Laplacian of g, the same procedure generates

$$\int_{\mathcal{A}} d^2\mathbf{r}\, r^{2N} b_2(\mathbf{r},t)\,\Delta\, g(\mathbf{r},t|\mathbf{r}',t') = \oint_{\partial\mathcal{A}} dl\, r^{2N}\, b_2(\mathbf{r},t)\mathbf{n}_\perp\cdot\nabla g(\mathbf{r},t|\mathbf{r}',t') - \oint_{\partial\mathcal{A}} dl\,\mathbf{n}_\perp\cdot\nabla\,[r^{2N}\, b_2(\mathbf{r},t)]\, g(\mathbf{r},t|\mathbf{r}',t') + \int_{\mathcal{A}} d^2\mathbf{r}\,\Delta\,[r^{2N}\, b_2(\mathbf{r},t)]\, g(\mathbf{r},t|\mathbf{r}',t').$$

The boundary integrals are used to satisfy the boundary conditions. After doing so, I am left with

$$\int_{\mathcal{T}_{-\infty}} d\tau \int_{\mathcal{A}} d^2\mathbf{r}\, E(\mathbf{r},\tau)\, g(\mathbf{r},\tau|\mathbf{r}',t') + \int_{\mathcal{T}_{-\infty}} d\tau\, C_E(\tau|\mathbf{r}',t') = r'^{2N} - \langle r^{2N}\rangle(t|\mathbf{r}',t')$$

where

$$E(\mathbf{r},\tau) = r^{2N} b_0(\mathbf{r},\tau) - \nabla \cdot [r^{2N} \mathbf{b}_1(\mathbf{r},\tau)] + \triangle [r^2 b_2(\mathbf{r},\tau)]$$

$$C_E(\tau|\mathbf{r}',t') = \begin{cases} -\oint_{\partial\mathcal{A}} dl\, r^{2N} k(\mathbf{r},t)\, \mathbf{n}_\perp \cdot \nabla\, g(\mathbf{r},\tau|\mathbf{r}',t') & \text{for } \partial\mathcal{A}_A \\ +\oint_{\partial\mathcal{A}} dl\, \mathbf{n}_\perp \cdot (\nabla r^{2N})\, k(\mathbf{r},t) g(\mathbf{r},\tau|\mathbf{r}',t') & \text{for } \partial\mathcal{A}_R\,. \end{cases}$$

Discretizing time in these expressions for a single interval of time for a source time t_j, I have

$$\left[\int_{\mathcal{A}} d^2\mathbf{r}\, E(\mathbf{r},t_j) g(\mathbf{r},t_j|\mathbf{r}',t_j) + C_E(t_j|\mathbf{r}',t_j)\right] = \frac{1}{\mathcal{T}_j}\left[r'^{2N} - \langle r^{2N}\rangle(t_{j+1}|\mathbf{r}',t_j)\right]$$

where

$$\langle r^{2N}\rangle(t_{j+1}|\mathbf{r}',t_j) = \int_{\mathcal{A}} d^2\mathbf{r}\, r^{2N} g(\mathbf{r},t_{j+1}|\mathbf{r}',t_j)\,.$$

As can be appreciated, the integrals on the l.h.s. of the expression have $g(\mathbf{r},t_j|\mathbf{r}',t_j)$ in the integrand. Making use of the initial property of g:

$$g(\mathbf{r},t_j|\mathbf{r}',t_j) = \delta(\mathbf{r}-\mathbf{r}')\,.$$

Integrating with the reminder that $\partial\mathcal{A} \subset \mathcal{A}$, I can conclude

$$E(\mathbf{r}',t_j) = r'^{2N} b_0(\mathbf{r}',t_j) - \nabla' \cdot \left[r'^{2N} \mathbf{b}_1(\mathbf{r}',t_j)\right] + \nabla'\left[r'^{2N} \mathbf{b}_2(\mathbf{r}',t_j)\right]$$

by use of the properties of the gradient of Dirac delta functions (Lighthill 1964; Butkov 1968) and the assumption that $\partial\mathcal{A}$ is piecewise smooth:

$$C_E(\mathbf{r}',t_j) = C_E(t_j|\mathbf{r}',t_j) = \begin{cases} 0 & \text{if } \mathbf{r}' \notin \partial\mathcal{A} \\ \nabla' \cdot [\boldsymbol{n}_\perp \mathbf{r}'^{2N} k(\mathbf{r}',t_j)] & \text{if } \mathbf{r}' \in \partial\mathcal{A}_{\mathcal{A}} \\ \boldsymbol{n}_\perp \cdot (\nabla' r'^{2N}) k(\mathbf{r}',t_j) & \text{if } \mathbf{r}' \in \partial\mathcal{A}_{\mathcal{R}}\,. \end{cases}$$

Evidently, $E(\mathbf{r}',t_j)$ is correct for points in $\mathcal{A}$ regardless of the boundaries. Therefore, it is also correct for the boundless domain. Henceforth, I shall ignore the terms with the source at the boundary of the domain because data are seldomly collected there.

Using the identities

$$\nabla' \cdot \mathbf{r}' = 2\,,$$

and

which is a consequence of $\mathcal{A} \in \mathbf{R}^2$,

$$\nabla' \mathbf{r}'^{2N} = 2N r'^{2N-2} \mathbf{r}'\,,$$

and

$$\nabla' \cdot (r'^{2N-2} \mathbf{r}') = 2N r'^{N-2}$$

to expand $E(\mathbf{r}',t_j)$ leads to the expression

$$E(\mathbf{r}',t_j) = r'^{2N} b_0(\mathbf{r}',t_j) - 2N r'^{2N-2}[\mathbf{r}' \cdot \mathbf{b}_1(\mathbf{r}',t_j)] - r'^{2N} \nabla' \cdot \mathbf{b}_1(\mathbf{r}',t_j) + 4N^2 r'^{2N-2} b_2[\mathbf{r}',t_j)] + 4N r'^{2N-2}[\mathbf{r}' \cdot \nabla' b_2(\mathbf{r}',t_j)] + r_k'^{2N} \triangle' b_2(\mathbf{r}',t_j)\,.$$

Discretizing space with $\mathbf{r}_k$ as the source point and $\mathbf{r}_i$ as the receiver point, and substituting for $\{b_0,\mathbf{b}_1,b_2\}$ their expressions in terms of $\{m,\mathbf{v},k\}$, yields

$$E(\mathbf{r}_k,t_j) = r_k^{2N} m(\mathbf{r}_k,t_j) - 2N r_k^{2N-2}[\mathbf{r}_k \cdot \mathbf{v}(\mathbf{r}_k,t_j)] - 4N^2 r_k^{2N-2} k(\mathbf{r}_k,t_j) - 2N r_k^{2N-2}[\mathbf{r}_k \cdot \nabla_k k(\mathbf{r}_k,t_j)]$$

where I am using the notation

$$\nabla_i k(\mathbf{r}_i,t_j) = [\nabla k(\mathbf{r},t_j)]_{\mathbf{r}=\mathbf{r}_i}\,.$$

The scalar equations for the even moments of the Green function for source points $\mathbf{r}_k \notin \partial\mathcal{A}$ are then

$$E(\mathbf{r}_k,t_j) = \frac{1}{\mathcal{T}_j}[r_k^{2N} - \langle r_i^{2N}\rangle(t_{j+1}|\mathbf{r}_k,t_j)]$$

and where

$$\langle r_i^{2N}\rangle(t_{j+1}|\mathbf{r}_k,t_j)] = \sum_{i=1}^{n} \mathcal{A}_i r_i^{2N} g(\mathbf{r}_i,t_{j+1}|\,\mathbf{r}_k,t_j)\,.$$

With these, I can generate the zeroth ($N = 0$), second ($N = 1$), . . ., moments of the Green function.

To derive the odd-moments equation, I can initially multiply the field equation for the Green function by $r^{2N}\mathbf{r}$ and perform

analogous operations using the algebra and calculus of dyads. This leads to the vector $\boldsymbol{O}(\mathbf{r}_k,t_j)$ analogous to the scalar $E(\mathbf{r}_k,t_j)$ given by

$$\boldsymbol{O}(\mathbf{r}_k,t_j) = r_k^{2N}\mathbf{r}_k m(\mathbf{r}_k,t_j) - r_k^{2N}\mathbf{v}(\mathbf{r}_k,t_j) - 2Nr_k^{2N-2}\mathbf{r}_k[\mathbf{r}_k \cdot \mathbf{v}(\mathbf{r}_k,t_j)]$$
$$-4N(N+1)r_k^{2N-2}\mathbf{r}_k k(\mathbf{r}_k,t_j) - r_k^{2N}\nabla_k k(\mathbf{r}_k,t_j)$$
$$-2Nr_k^{2N-2}\mathbf{r}_k[\mathbf{r}_k \cdot \nabla_k k(\mathbf{r}_k,t_j)]$$

for $\mathbf{r}_k \notin \partial\mathcal{A}$. The vector equations for the odd moments of the Green function are then

$$\boldsymbol{O}(\mathbf{r}_k,t_j) = \frac{1}{\mathcal{T}_j}[r_k^{2N}\mathbf{r}_k - \langle r_i^{2N}\mathbf{r}_i \rangle (t_{j+1}|\mathbf{r}_k,t_j)]$$

where

$$\langle r_i^{2N}\mathbf{r}_i \rangle (t_{j+1}|\mathbf{r}_k,t_j) = \sum_{i=1}^{n} \mathcal{A}r_i^{2N}\mathbf{r}_i g(\mathbf{r}_i,t_{j+1}|\mathbf{r}_k,t_j) .$$

With these, I can generate the first ($N = 0$) , third ($N = 1$), . . ., moments of the Green function.