

Mean free-path length theory of predator–prey interactions: Application to juvenile salmon migration

James J. Anderson^{a,*}, Eliezer Gurarie^a, Richard W. Zabel^b

^a School of Aquatic and Fishery Sciences, University of Washington, Box 358218, Seattle, WA 98195, USA

^b Northwest Fisheries Science Center, National Marine Fisheries Service,
National Oceanic and Atmospheric Administration, 2725 Montlake Blvd. East Seattle, WA 98112, USA

Received 3 February 2004; received in revised form 30 November 2004; accepted 10 January 2005

Available online 12 February 2005

Abstract

Ecological theory traditionally describes predator–prey interactions in terms of a law of mass action in which the prey mortality rate depends on the density of predators and prey. This simplifying assumption makes population-based models more tractable but ignores potentially important behaviors that characterize predator–prey dynamics. Here, we expand traditional predator–prey models by incorporating directed and random movements of both predators and prey. The model is based on theory originally developed to predict collision rates of molecules. The temporal and spatial dimensions of predators–prey encounters are determined by defining movement rules and the predator's field of vision. These biologically meaningful parameters can accommodate a broad range of behaviors within an analytically tractable framework suitable for population-based models. We apply the model to prey (juvenile salmon) migrating through a field of predators (piscivores) and find that traditional predator–prey models were not adequate to describe observations. Model parameters estimated from the survival of juvenile chinook salmon migrating through the Snake River in the northwestern United States are similar to estimates derived from independent approaches and data. For this system, we conclude that survival depends more on travel distance than travel time or migration velocity. Crown Copyright © 2004 Published by Elsevier B.V. All rights reserved.

Keywords: Predator–prey; Juvenile salmon; Migration; Survival; Mean free-path length

1. Introduction

The first predator–prey models (Lotka, 1925; Volterra, 1926), and nearly all subsequent predator–prey

models formulated in terms of differential equations, apply a law of mass action, which has its origins in chemical reaction theory first proposed by Waage and Guldberg (1864). In predator–prey models predation events are typically assumed analogous to the combining of molecules, such that in its simplest form the predation rate is equal to the product of predator and prey densities and a constant expressing a rate of interaction. The models have since evolved (Berryman,

* Corresponding author. Present address: Columbia Basin Research Puget Sound Plaza, 1325 4th Avenue, Ste 1820, Seattle, WA 98101-2509, USA. Tel.: +1 206 543 4772; fax: +1 206 616 7452.

E-mail address: jjm@cbr.washington.edu (J.J. Anderson).

1992), incorporating such refinements as predator satiation (Hollings, 1959), multi-predator and prey species (May, 1974), and dispersion and diffusion (Okubo and Levin, 2001). These improvements characterize the effective densities of predators and prey more realistically, but they ultimately use the Lotka–Volterra model mass action assumption. Models that go beyond the mass action assumption, e.g. ratio-dependent models (Arditi and Ginzburg, 1989) do not allow for variability in the behavior of predators and prey.

It has been noted that the spatial scales of interactions between organisms, sometimes referred to as the “ecological neighborhood,” is important in determining population dynamics and in particular predator–prey interactions (Addicott et al., 1987; Murdoch et al., 1992; Pascual and Levin, 1999; Hosseini, 2003). Within these local scales of interaction, the movements and distributions of predators and prey in response to each other can significantly complicate the interactions and are likely to invalidate many assumptions in simple predator–prey models (Lima, 2002). Peterson and DeAngelis (2000) address this issue by developing an individual-based model (IBM) of juvenile salmon migrating through a field of piscivores. Simulated pulses of fish move through a series of cells representing a stretch of river and within each cell there is some probability of encountering predators. The authors find that the estimated intensity of predation depends on the size of the cells (DeAngelis and Peterson, 2001). This result is useful in illustrating the importance of spatial effects and the effects of scale issues on a model. From a practical perspective, however, the appropriate cell size is not immediately evident and therefore the system dynamics depend on a free parameter with an uncertain ecological meaning. In general, IBMs can incorporate detailed behaviors and show great promise in exploring predator–prey reactions, but they are limited by difficulties in obtaining general results that can be scaled upward to the population level (Pascual and Levin, 1999; Murdoch et al., 1992).

The problem of understanding the role of local scales of interaction on population dynamics can be approached by identifying individual level behaviors that are important for determining population dynamics and incorporating these behaviors into population models. Gerritsen and Strickler, 1977 developed a spatially explicit model of predator–prey encounter rates in terms of relative velocities and densities of zooplankton and

their prey. Here, we consider this problem from a perspective somewhat similar to Gerritsen and Strickler’s model, henceforth labeled GS, in which we define an interaction length scale in terms of fundamental behaviors of the interacting species. Because we are primarily interested in the survival of migrating prey, we pay particular attention to the interaction between directed and random components of movement.

Our approach is motivated by the “mean free-path” theory, which lies at the foundations of kinetic theory as conceived by Maxwell and Boltzmann in the late nineteenth century. In the kinematic theory of gases, the collision rate between molecules depends not only on the relative magnitude of velocities but also on the degree of randomness they exhibit. An emergent property is the mean free-path length between molecular collisions (Feynman et al., 1963). We apply this theory to predator and prey populations by describing their movements in terms of both directed and random components. This allows us to distinguish predator tactics such as “cruising search” and “sit-and-wait” (Hart, 1997). As free-path length theory characterizes the mean features of a gas in terms of the small-scale properties of molecules, the theory applied to animals characterizes large-scale predator–prey dynamics in terms of the small-scale interactions of the predators and prey.

To demonstrate the practical capabilities of a mean free-path length theory (MFL), we apply the model to data on the mortality of juvenile salmon migrating through the Snake River. During their seaward migration, millions of juvenile salmon are consumed by indigenous and non-indigenous predators (Ward et al., 1995). This predation is one of several factors that determine the dynamics of salmon populations in the Columbia River Basin (NRC, 1996). Understanding the details of the predator–prey interactions is therefore of practical as well as theoretical interest. We utilize an extensive data set where several hundred thousand spring chinook salmon (*Oncorhynchus tshawytscha*) were tagged and released at several hatcheries in the Snake River Basin (Fig. 1). After a migration ranging from approximately 100 to 800 km, the fish were detected at a downstream site and mortality for each release group was estimated. We test the results of the MFL model, by comparing the fitted model coefficients to independently estimated values.

Finally, we note that the GS model, which described interactions among zooplankton in explicit spheri-

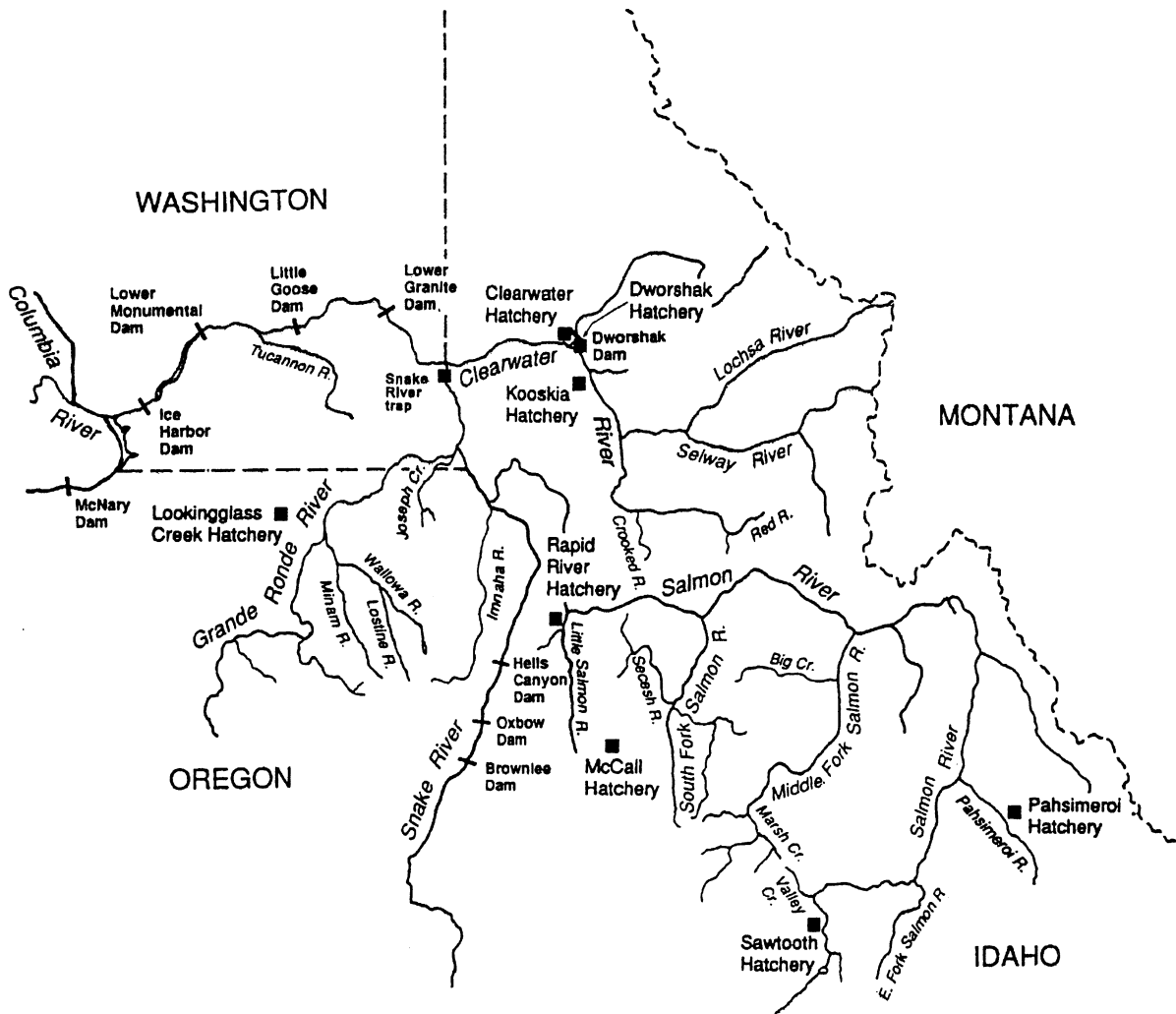


Fig. 1. Map showing Snake River tributaries and the hatcheries from which fish were released for survival studies.

cal coordinates, yields similar dynamics to the MFL model. This conclusion corroborates a result obtained by Evans (1989).

2. Model of predator–prey interactions

The assumptions of the model are as follows: (1) a prey can be described as a point in space that takes a path with mean velocity \mathbf{U} and random component \mathbf{u}^* ; (2) predators are likewise points with mean velocity \mathbf{V} and random component \mathbf{v}^* . The directed components of velocity have magnitudes U and V ; (3) predators are

randomly distributed with a uniform probability distribution in space with density ρ ; (4) the scale of the predator–prey encounter volume is described by a constant cross-sectional area of interaction α . A predation event, which eliminates the prey, occurs when a predator and prey are within a distance $r = \sqrt{\alpha/\pi}$.

Over an ensemble of prey and predator–prey interactions, the average time between encounters is τ and the probability of a single encounter follows a Poisson distribution such that

$$\begin{aligned} &\text{probability of predator encounter in time} \\ &= \exp(-t/\tau) \end{aligned} \quad (1)$$

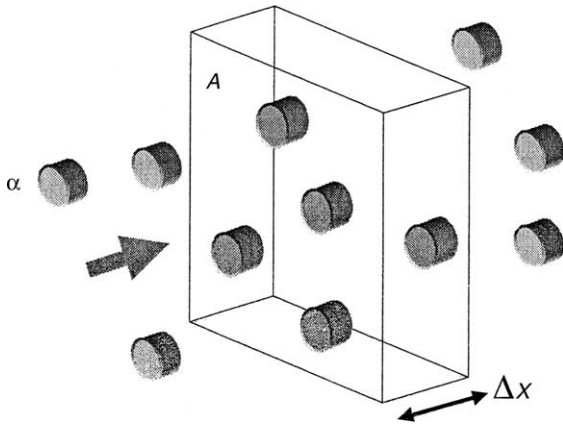


Fig. 2. Illustration of a prey (arrow) moving a distance Δx through a unit area A , of predator habitat. Predators (cylinders) have a cross-sectional area α . The probability of encountering a predator while traveling Δx is equal to the fraction of the unit area covered by predators.

where t is the total exposure time. This is also an expression of the survival over time. To derive an expression for τ , first define the chance a prey encounters a predator in traveling a short distance as

$$\text{probability of predator encounter in distance} = \frac{\Delta x}{\lambda} \quad (2)$$

where λ is the prey's path length and Δx is the small distance in the direction the prey travels.

Similar to the mean free-path length in molecular collisions (Feynman et al., 1963), the chance of encounter can also be expressed in terms of the fraction of a unit encounter area occupied by predators. Consider a plane of unit area, $A_{\text{unit}} = 1$, that is perpendicular to the relative average movement between the prey and its predators (Fig. 2). Over a short distance of its path Δx , the prey sweeps out a small volume $A_{\text{unit}} \Delta x$. This volume contains n predators where $n = \rho A_{\text{unit}} \Delta x$. The area of the plane covered by predators is $A_{\text{predator}} = \alpha n = \alpha \rho A_{\text{unit}} \Delta x$ where α is the encounter area of a predator–prey interaction. The encounter area can be expressed in terms of the encounter distance, r , at which a predation event occurs, so $\alpha = \pi r^2$. The chance of encountering a predator traveling the small distance Δx is equivalent to the area occupied by the predators divided by the unit area of the plane, which is simply

$$\text{probability of predator encounter in } \Delta x = \pi r^2 \rho \Delta x \quad (3)$$

Equating Eqs. (2) and (3) the path length is

$$\lambda = \frac{1}{\rho \pi r^2} \quad (4)$$

The encounter time, or mean time between encounters, and path length are related by w , which is the magnitude of the relative speed of the prey with respect to the predators. Thus, $\lambda = w \tau$ and the characteristic encounter time is

$$\tau = \frac{1}{\rho \pi r^2 w} \quad (5)$$

The relative speed, which we designate the encounter speed, is expressed as a root-mean-square (rms) speed between the predator and prey as

$$w = \sqrt{E[(\mathbf{v} - \mathbf{u})^2]} \quad (6)$$

Next, represent prey and predator velocity vectors in terms of their average and random parts as

$$\mathbf{u} = \mathbf{U} + \mathbf{u}^* \text{ and } \mathbf{v} = \mathbf{V} + \mathbf{v}^* \quad (7)$$

where \mathbf{U} and \mathbf{V} are the mean prey and predator velocity vectors and \mathbf{u}^* and \mathbf{v}^* are the associated random or fluctuating velocity vectors about the mean vectors. This decomposition into mean and random parts is commonly used in kinematic studies and in hydrodynamics (Sverdrup et al., 1942). By our definition, the random components are uncorrelated and have zero means, and so the expected value of the square of the difference between the velocity vectors is

$$\begin{aligned} E[(\mathbf{v} - \mathbf{u})^2] &= E[\mathbf{U}^2] - E[2\mathbf{UV}] + E[\mathbf{V}^2] \\ &\quad + E[\mathbf{u}^{*2}] + E[\mathbf{v}^{*2}] \end{aligned} \quad (8)$$

The rms encounter speed defined by Eq. (6) reduces to

$$w = \sqrt{W^2 + \omega^2} \quad (9)$$

where the squared mean encounter speed is

$$W^2 = V^2 + U^2 - 2UV \cos \theta \quad (10)$$

where V and U are the magnitudes of vectors \mathbf{V} and \mathbf{U} , respectively, θ the angle between the mean paths of the predator and prey, and the mean squared random

encounter speed is described in terms of the variances of \mathbf{v}^* and \mathbf{u}^* as

$$\omega^2 = E[v^{*2}] + E[u^{*2}] \quad (11)$$

Note that ω^2 is the sum of the variances of the random parts of the predator and prey speeds and it admits any distribution for the random velocities as long as the mean values are zero.

Using Eq. (9) in Eq. (5) to define τ in Eq. (1), the probability of a prey encountering a predator over time, which is also equivalent to the prey survival, S , over time, is

$$S = \exp\left(-\frac{t}{\lambda}\sqrt{W^2 + \omega^2}\right) \quad (12)$$

From Eq. (12) we can express the rate of predation in the form of traditional predator–prey terminology. Noting $\rho = P/H$ where P is the predator population in the habitat of volume H , then the rate of mortality expressed in a Lotka–Volterra type predator–prey equation is

$$\frac{dS}{dt} = -\frac{\pi r^2}{H}\sqrt{W^2 + \omega^2}PS \quad (13)$$

Noting the predator's encounter area, πr^2 , has a dimension of area/predator, the combined terms, $\pi r^2\sqrt{W^2 + \omega^2}/H$, has as dimension of t^{-1} predator $^{-1}$ and is thus equivalent to the time constant in a Lotka–Volterra type predator–prey equation. However, here the rate term is specified in terms of the predator's ecological neighborhood through the encounter length scale r , and the predator–prey mean and random encounter speeds, W and ω . With visual predators, r should depend on the range of visibility in the environment, the sensory ability of the predators, and the near field probability of a predator's chance of capturing a prey. The encounter speeds characterize the probabilities of predator–prey encounters over space and time.

The model, in the form of Eq. (12) or Eq. (13) has characteristics not found in a formulation in which the rate coefficient is simply a constant. For example, because the predation rate depends on the mean and random speeds of the predator and prey, the predator's foraging rate is explicitly coupled to its energy expenditure, and so the optimal foraging strategy for the predator may depend on the character of the prey's speed. This issue was explored by Gerritsen (1984) for

the case of random free-swimming aquatic animals. In addition, prey survival over time and space depends on the relative motions of predators and prey. Some special cases illustrating the effect of behaviors on the survival equation are discussed below.

2.1. Special cases of prey survival

The general MFL model can be further simplified to a number of cases in which the predators and prey have different mean and random motions that are germane to ecological situations.

If prey migrate through a corridor or field of resident predators, then by definition the predator mean speed is zero ($V = 0$), and by definition of the prey's migration behavior, its mean speed, is simply its average migration velocity U . Then the average prey migration time t , distance x , and velocity are related by $x = Ut$, and Eq. (12) simplifies to

$$S = \exp\left(-\frac{1}{\lambda}\sqrt{x^2 + \omega^2 t^2}\right) \quad (14)$$

Eq. (14) will be referred to as the *XT model* because survival depends on both the distance traveled and the travel time. The relative importance of migration distance and time on prey survival depends on the random encounter velocity ω . The length scale λ is a measure of distance between predator–prey encounters and from Eq. (4) it depends on the encounter length scale and the predator density as

$$\lambda = \frac{1}{\pi r^2 \rho} \quad (15)$$

Whereas, the x term in the equation could equally be replaced with Ut , the dependence on x is appropriate for characterizing the survival of animals as they migrate over fixed distances. In this case, the importance of migration velocity, i.e. travel time over a fixed distance, in determining the prey's survival depends on the magnitude of the random encounter speed relative to the average migration velocity. To illustrate the importance of migration velocity, we rewrite Eq. (14) as

$$S = \exp\left(-\frac{x}{\lambda}\sqrt{1 + \left(\frac{\omega}{U}\right)^2}\right) \quad (16)$$

and plot S vs. U/ω for migration over an arbitrary distance $x = \lambda$ (Fig. 3). The result is a hockey stick like

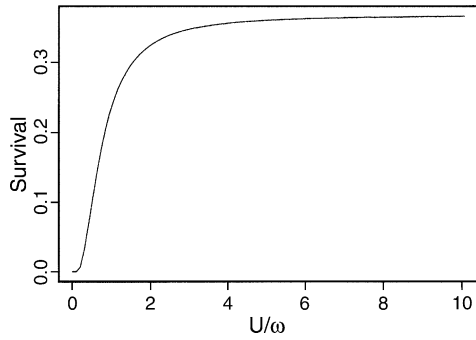


Fig. 3. XT model survival vs. average migration velocity U , divided by the random component of the velocity ω .

survival response versus prey migration rate expressed in terms of the random velocity relative to the directed velocity. The break, at which survival becomes proportional to migration velocity, occurs when the migration velocity drops below the random encounter velocity, i.e. $\omega/U \geq 1$.

If the prey migration is rapid, so the predators are essentially stationary relative to the prey's migration velocity, then $U^2 \sim W^2 \gg \omega^2$. In this case, prey that move with different average migration velocities experience the same survival probability over a fixed migration distance even though their migration times may be different over the distance. Under these conditions, the asymptotic form of prey survival depends on distance as

$$S = \exp\left(-\frac{x}{\lambda}\right) \quad (17)$$

Eq. (17) will be referred to as the *gauntlet model* and over a fixed migration distance survival is independent of the prey's velocity. Although the average travel time is related to survival through the average velocity, the equation $S = \exp(-Ut/\lambda)$ is not a suitable description of survival in a gauntlet model since both velocity and travel time are required to characterize survival and their product is simply the migration length x . In this case, survival simply decreases exponentially with distance traveled and is independent of the amount of time it takes to travel the distance.

If predators and prey are both mobile and resident within the habitat, then $W=0$ and we obtain a traditional *exposure model*

$$S = \exp\left(-\frac{\omega}{\lambda}t\right) \quad (18)$$

Note the survival over time depends on the predation length scale characterized by λ , and the intensity of the predator–prey interactions as characterized by ω . In this case, survival declines exponentially with exposure time t .

In these special cases, the specific rate of prey mortality, defined $(1/S) dS/dt = f(\bullet)/\lambda$, depends on the reciprocal of the predator length scale λ and a rate function $f(\bullet)$ that characterizes the rate of predator–prey encounters. The length scale depends on the number of predators in the habitat and the predator–prey encounter distance r . The encounter rate function characterizes the rate at which predators and prey interact, which in turn depends on their behaviors. In the gauntlet model, each prey encounters an individual predator at most once while in the exposure model multiple encounters are possible.

2.2. Comparison with the Gerritsen–Strickler model

The Gerritsen and Strickler (1977) predator–prey encounter model for zooplankton is similar to the MFL model in that both characterize a relative speed between predators and prey and describe predation in terms of an encounter distance. Here, we illustrate the similarity between the GS model and Eq. (18) and corroborate a result obtained by Evans (1989).

The GS model assumes uniform distributions of predator and prey moving randomly in a three-dimensional field. The model characterizes the frequency of interaction using a spherical polar coordinate reference frame. The predator and prey have swimming velocities v and u , respectively and their relative speed is

$$w = \sqrt{u^2 + v^2 - 2uv \cos \theta} \quad (19)$$

where θ is the angle of prey relative to the angle of the vector v of the predator's motion. Assuming the prey and predators are randomly distributed, the encounter rate of a prey to predators in the GS model is

$$\frac{1}{S} \frac{dS}{dt} = \frac{\pi r^2 \rho}{6} \frac{(\bar{u} + \bar{v})^3 - |\bar{u} - \bar{v}|^3}{\bar{u} \cdot \bar{v}} \quad (20)$$

where \bar{u} and \bar{v} are the mean speeds of the predator and prey populations. The equivalent encounter rate in the

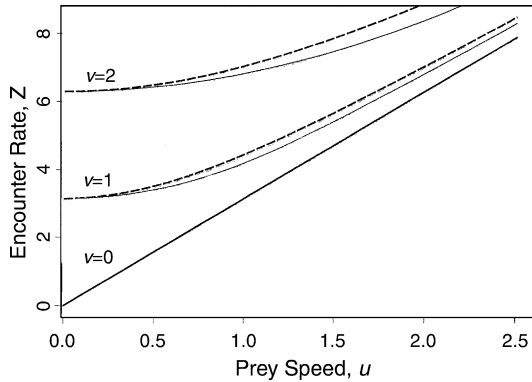


Fig. 4. Comparison of encounter rate of predators by prey as function of prey and predator speeds for the GS model (—) and the MFL model (---).

MFL model is

$$\frac{1}{S} \frac{dS}{dt} = \pi r^2 \rho \sqrt{E(u^{*2}) + E(v^{*2})} \quad (21)$$

Note that the mean speeds in the GS model are equivalent to the rms speeds in the MFL model such that $\bar{u} = \sqrt{E(u^{*2})} = u_{\text{rms}}$. Thus, the formulations of the encounter rate by the Eq. (20) for the GS model and (21) for the MFL model are different. Furthermore, in the GS formulation the mean speeds are deterministic, while in the MFL model speeds have probability distributions with intensities characterized by the rms speeds. The encounter rates for the case with probability distributions in the animals' speeds were numerically calculated by Gerritsen and Stricker. On average, Eq. (20) underestimates the encounter rates by about 1–10% depending on the distributions assumed for the predator and prey speeds. However, even though the formulations are different, their characteristics are virtually identical. This is illustrated in Fig. 4, which compares the encounter rates of the two equations for differing predator and prey speeds. Note that in the deterministic form of the GS model, encounter rates are between 0 and 5% lower than the rates of the MFL model. This is the same level of under prediction that Gerritsen and Strickler determined when comparing the deterministic speeds form of the GS model to a numerical form in which the predator and prey speeds were normally distributed.

We conclude that the MFL model is a simpler expression than the GS model and that it provides a close fit to the deterministic form of the GS model. The

MFL model agrees even more closely with the numerical form of the GS model using randomly distributed predator and prey speeds.

In a brief discussion of the GS model, Evans (1989) simplifies the GS relative encounter rates and includes a turbulent term that is functionally equivalent to the random velocities with the important distinction of being for both predator and prey. He concludes that the values obtained for encounter rates differ from the GS model by no more than 6%, corroborating the result obtained above.

3. A case study with migrating juvenile salmon

We apply the model to data on the survival of juvenile salmon during their seaward migration. Each year during their migration through the Snake and Columbia Rivers and their tributaries, predators consumed millions of juvenile salmonids (Rieman et al., 1991). The major piscivores are the native northern pikeminnow (*Ptychocheilus oregonensis*) and three non-indigenous species—smallmouth bass (*Micropterus dolomieu*), walleye (*Stizostedion vitreum*) and channel catfish (*Ictalurus punctatus*) (Poe et al., 1991). In addition, birds consume migrating juvenile fish. Notably predation by the Caspian tern (*Sterna caspia*) has increased over the past decade as a result of a substantial increase in its population (Roby et al., 1998).

These predators are generalists that feed seasonally and may employ different tactics so our application of the model to the survival data reflects a mixture of different foraging strategies by predators. However, the model is flexible and accommodates a variety of behaviors. Ultimately, the fact that we know the fate of thousands of prey after migrating past a field of predators yields a rich data set for our analysis.

We use mark recapture studies conducted on Snake River system. Between 1993 and 2003, 287 tagged groups of spring chinook were released from 17 hatcheries located in the tributaries of the Snake River Basin (Fig. 1). The fish, tagged with passive integrated transponders (PIT) (Prentice et al., 1990), were released from locations in the Snake River tributaries ranging from 31 to 772 km upstream of the detection site at Lower Granite Dam. Release sample sizes ranged from 6 to 51,196 fish with a median release size of 796 fish. Fish were released between days of

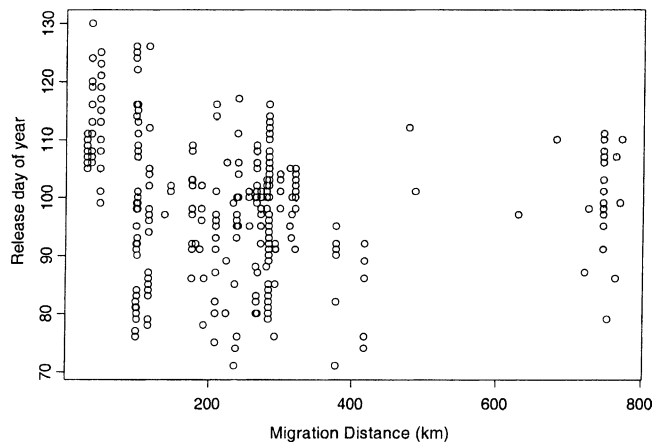


Fig. 5. Tag group release day of year vs. distance of migration to Lower Granite Dam.

the year 71 through 130 and, in general, fish released further upstream tended to be released earlier (Fig. 5). Survivals to Lower Granite Dam were estimated with the multiple-recapture model for single-release groups (Muir et al., 2001).

The relationship between log survival and the migration travel time was variable from one year to the next (Fig. 6). Individually, only 1996–1998, 2001 and 2002 exhibited significant ($p < 0.01$) linear regressions of $\log(S)$ versus t , which were weighted by the standard error of S . Correlations were typically low with only 1993 and 1995 exhibiting $r^2 > 0.5$. No relationship between log survival and travel time was evident for all

years combined ($r^2 = 0.08$, $p < 0.0001$). A stronger and consistent relationship was evident between log survival and migration distance (Fig. 7). Weighted regressions of $\log(S)$ versus x were significant ($p < 0.005$) for all years except 1997. The r^2 correlations were above 0.7 for 6 of the 10 years and the regression of all years combined was very significant ($r^2 = 0.65$, $p < 0.0001$). Migration velocities increased with release site distance from Lower Granite Dam. An unweighted linear regression gave u (cm/s) = $1.4 + 0.026x$ (km) ($r^2 = 0.70$, $p < 0.0001$). However, there was no relationship between release day and migration velocity ($r^2 = 0.03$, $p < 0.0019$).

Table 1

Regressions coefficients for Eq. (22) coefficients for spring chinook hatchery releases and migration to Lower Granite Dam over the years 1993–2003

Year	n	r^2	a ($\times 10^{-6}$ km $^{-2}$)		b ($\times 10^{-5}$ day $^{-2}$)	
			Estimate	S.E.	Estimate	S.E.
1993	17	0.94	3.11	0.34	−3.21	13.78
1994	38	0.97	4.76	0.21	6.22	11.79
1995	43	0.80	7.25	1.00	24.35	28.08
1996	15	0.97	7.96	0.44	−18.04	4.60
1997	12	0.68	1.56	1.46	20.66	9.28
1998	15	0.88	1.32	0.27	9.45	3.70
1999	22	0.54	1.19	0.40	4.76	2.85
2000	43	0.60	1.34	0.39	6.73	2.39
2001	26	0.81	1.93	0.43	6.21	2.27
2002	26	0.86	5.19	0.87	−2.97	5.43
2003	25	0.78	6.91	1.00	0.20	5.07
All years	287	0.65	4.85	0.25	−1.85	2.12

“ n ” is the number of release groups.

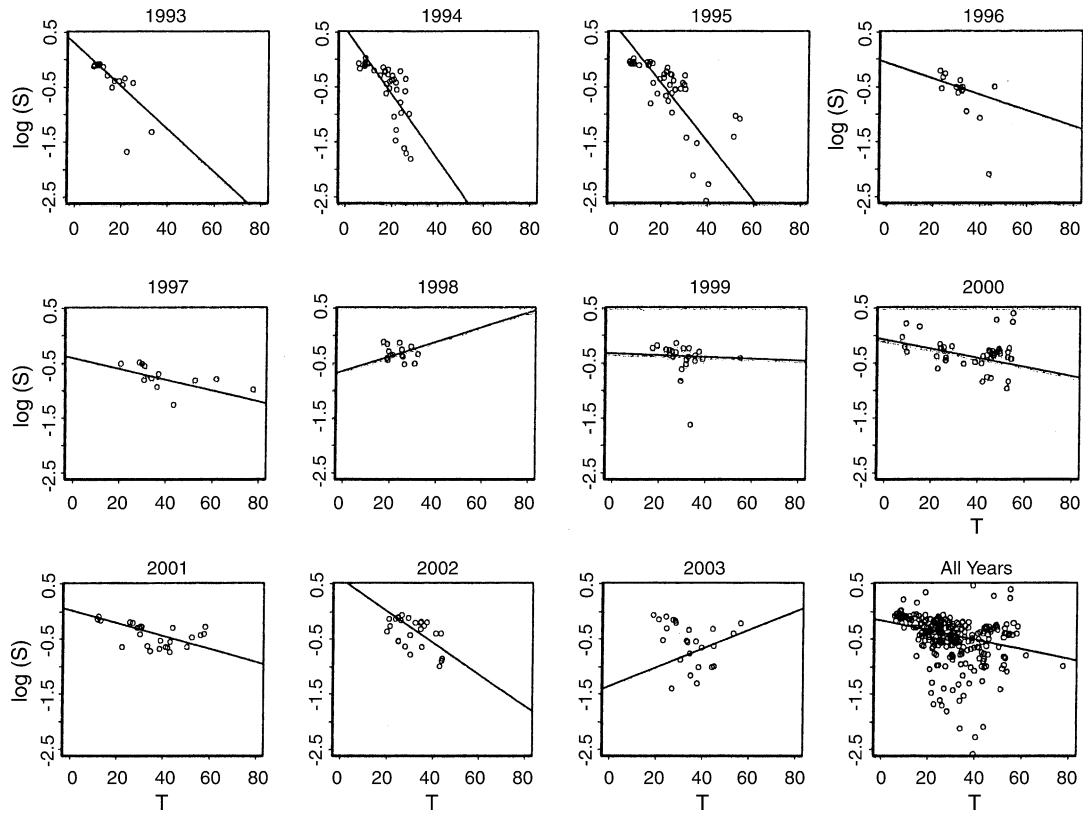


Fig. 6. Regression of log survival, $\log(S)$ vs. migration travel time, $T(d)$. Regressions are weighted by $1/(S.E.)^2$ of S .

Similar results were found in other studies. Muir et al. (2001), analyzing a subset (1992 through 1998) of the data used in our analysis, noted that the estimated survival from the hatcheries was inversely correlated with migration distance to Lower Granite Dam ($r^2=0.64$, $p<0.001$). In a linear regression, survival also had a weak inverse relationship with travel time to Lower Granite Dam ($r^2=0.17$, $p>0.07$). Studies have also noted that survivals of juvenile salmon migrating through the Columbia and Snake Rivers were significantly related to the distance traveled but not to travel time (Bickford and Skalski, 2000; Smith et al., 2002).

To apply the MFL model to the PIT tag data, we note that the juvenile salmon rapidly migrate through the tributaries while the predators are resident within the tributaries. Therefore, Eq. (14) is an appropriate form of the MFL model for fitting the juvenile salmon survival data. To estimate the model parameters, we

write Eq. (14) in a multiple-linear form

$$(\log S)^2 = ax^2 + br^2 \quad (22)$$

where the parameters are defined

$$\lambda = \frac{1}{\sqrt{a}} \quad \text{and} \quad \omega = \sqrt{\frac{b}{a}} \quad (23)$$

Because of the large difference in sample sizes, we weighted the individual survival estimates by one over the square of the standard error of the survival and fit Eq. (22) to each year and to the combined years (Table 1).

Eq. (23) requires that $a>0$ and $b\geq 0$, otherwise the model coefficients are imaginary. However, the regression puts no constraints on the values of a and b . This is somewhat problematic if the random speed ω , is near zero. In that case, b is also near zero and may take on a negative value as a result of estimation error. Therefore,

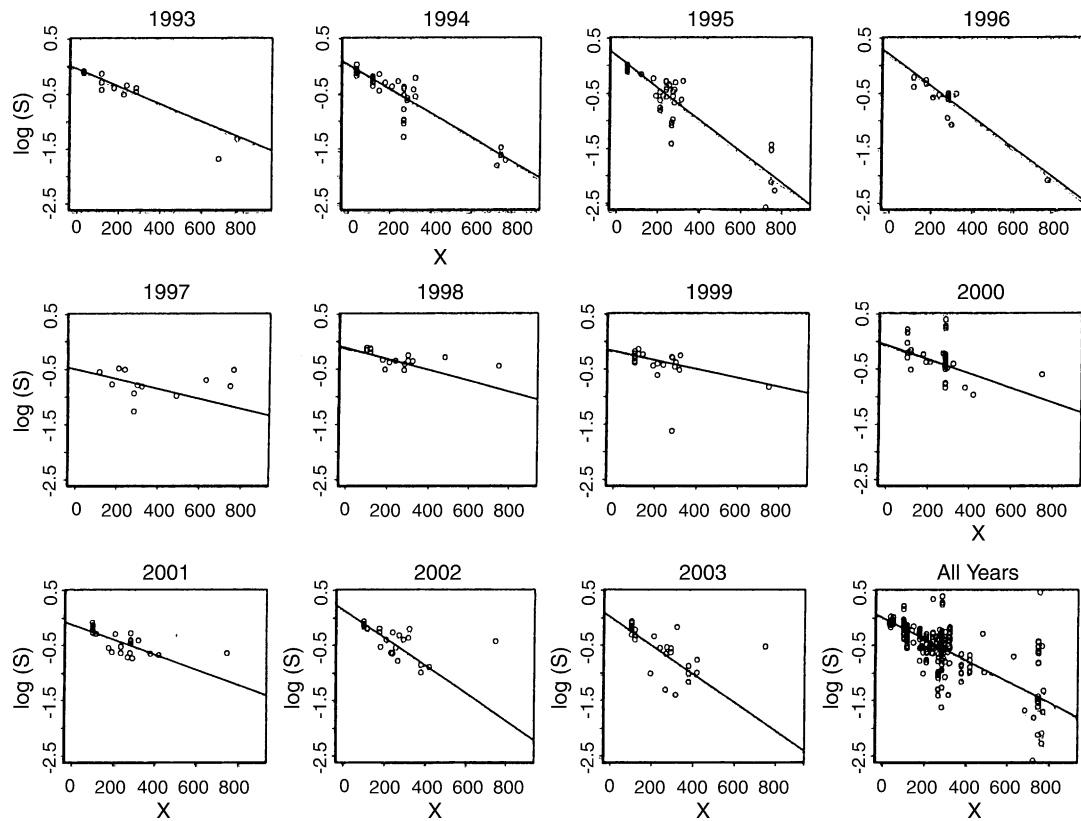


Fig. 7. Regression of log survival, $\log(S)$ vs. migration distance, X (km). Regressions are weighted by $1/(S.E.)^2$ of S .

we also calculate λ and ω using regression coefficients a and b plus and minus their standard errors (S.E.). We pair the estimates of a plus its standard error with estimates of b minus its standard error because a and b vary inversely in Eq. (22). That is, if due to estimation error the point estimate of a is low, then we expect that the point estimate of b will be high. In Table 2, NA indicates imaginary estimates of ω .

4. Results

The r^2 of the XT model fit to data over the years 1993–2003 range from 0.54 to 0.97; the fit to all years is 0.65, and the p -values are significant at the 0.005 level or greater for all years (Table 1). Estimates of λ range between 354 and 917 km and estimates of ω range between 0.5 and 12 cm/s. Including all years together, the encounter velocity is less than 0.6 cm/s and

Table 2
Model parameters, λ in km, ω in cm/s

Year	λ_{\max}	λ_{ave}	λ_{\min}	ω_{\max}	ω_{ave}	ω_{\min}
1993	601	567	539	5.0	NA	NA
1994	469	458	449	5.3	3.1	NA
1995	400	371	348	7.3	5.0	NA
1996	365	354	345	NA	NA	NA
1997	3131	800	575	12.0	9.9	7.4
1998	975	871	794	8.6	7.3	5.7
1999	1127	917	793	6.9	5.5	3.5
2000	1026	864	761	7.1	6.1	4.9
2001	815	719	651	5.7	4.9	3.9
2002	481	439	406	1.9	NA	NA
2003	412	381	356	2.4	0.5	NA
All years	466	454	443	0.6	NA	NA

Subscripts min and max are defined by standard errors on the parameters. NA indicates estimate not computable because of a negative b estimate.

the mean free-path length is 454 km. In some years, because b is negative, the random encounter velocity ω cannot be calculated, but in all years except 1996 the upper estimate of ω can be calculated. An estimate of ω is not possible in 1996 because b is negative and the standard error is less than the absolute value of b . However, λ is not affected by this negative b estimate in 1996. Regressing $\log S$ against x gives $\lambda = 354$, which is identical to λ obtained by Eq. (22) that includes the negative b . We conclude that in 1996 $\omega = 0$, which implies survival is best characterized by a gauntlet process of Eq. (17).

5. Comparison with independent predictions

To evaluate the model, we compare parameters estimated from the XT model to estimates derived from other methods using independent observations.

5.1. Encounter distance

From Eq. (4), the predation encounter distance, r , characterizing the average distance at which a predation event occurs can be written

$$\frac{1}{\sqrt{\pi\rho\lambda}} \quad (24)$$

To estimate r , the predator density over the migration path is required. To derive a very approximate estimate of ρ , we use population estimates of northern pikeminnow and smallmouth bass, which are the major predators of juvenile salmon in the river (Poe et al., 1991; Knutsen and Ward, 1999). Estimated populations for Lower Granite Reservoir are 26,000 northern pikeminnow larger than 250 mm (NMFS, 2000) and 20,911 smallmouth bass larger than 174 mm (Bennett et al., 1997). Dividing the combined populations by the volume of Lower Granite Reservoir, $597 \times 10^6 \text{ m}^3$, the predator density approximation is $\rho = 7.9 \times 10^{-5} \text{ predators m}^{-3}$. Using the range of the mean estimates of λ , from Table 2, the predator–prey encounter distance varies between 6.6 and 10.7 cm with the estimate for the combined years of $r = 9.4 \text{ cm}$. Because λ is derived from survival estimates of fish migrating for several weeks, the encounter distance represents an average of day and night conditions over the migratory period.

For an independent estimate of the encounter distance, consider observations of predator reaction distance, which should be somewhat greater than the encounter distance because reaction distance identifies the distance at which a predator first reacts to a prey while the encounter distance, by definition, is the distance within which on average a predation event occurs. Reaction distance depends on water clarity and light level (Vogel and Beauchamp, 1999). In 1997, the water clarity based on horizontal secchi disk readings in the Grande Ronde, a tributary of the Snake River, ranged between 20 and 100 cm, with a mean of about 50 cm (Steel, 1999). This equates to a turbidity reading of about 40 NTU (Steel and Neuhauser, 2002). Additionally, secchi disk readings in Lower Granite Reservoir typically vary between 10 and 50 cm (CRDART, 1998). Using the Vogel and Beauchamp (1999) reaction distance formula for the response of lake trout to rainbow and cutthroat trout prey, the reaction distance is 37 cm under midday conditions (100 lx) and a turbidity of 40 NTU, while in a midcrepuscular period (0.17 lx) the reaction distance is 5 cm. Additionally, note that laboratory studies on brook trout (Sweka and Hartman, 2001) and rainbow trout (Barrett et al., 1992) found reaction distances less than 20 cm for turbidity levels greater than 30 NTUs. Furthermore, because the reaction distance is zero at night, the reaction distance averaged over the day should be about half the midday values and thus between 10 and 20 cm.

Thus, the 9 cm encounter distance derived from the XT model is reasonable because it is close to the reaction distances estimated above. Consequentially as has been found in other systems (Gregory and Levings, 1998), we may expect that, in the Snake River tributaries, water visibility may be an important determinant of predator–prey encounter distance and therefore of juvenile salmon survival.

5.2. Random encounter velocity

The predator–prey random encounter velocity depends on the random prey velocity u^* , and the random predator velocity v^* , according to Eq. (11). An upper estimate of u^* can be derived from Zabel (2002) in which the distribution of smolt migration travel times was modeled with an advection–diffusion equation controlled by two parameters: migration velocity u , and a spread term σ^2 . The travel time distribution is inversely

related to the migration velocity distribution and, based on Tweedie (1957), the variance in the migration velocity is

$$\text{Var}\left(\frac{x}{t}\right) = \frac{u}{x}\sigma^2 + \frac{2}{x^2}\sigma^4 \quad (25)$$

where x is the migration distance. The square root of Eq. (25) provides an upper estimate of u^* . From 4 years of data, wild Snake River spring chinook migrating 233 km from the Salmon River to Lower Granite Dam $\sqrt{\text{Var}(x/t)}$ ranged between 9.0 and 16.1 cm/s.

For a second measure of the encounter velocity, consider predator velocities determined from radio-tagged Northern pikeminnow in John Day Reservoir. Using fish positions determined several times per day in May 1993 and 1994, an average velocity over the ground was 7 cm/s in the tailrace and 1 cm/s in mid-reservoir (Martinelli and Shively, 1997; Martinelli et al., 1993). Additionally, the coefficients of variation were about one in both areas so the random velocity about equals the average velocity, and to a first order the predator random velocity is expected to be a few cm/s.

In comparison, the XT model estimated encounter velocity for the Snake River tributaries ranges between 0 and 12 cm/s. Although these estimates are relatively close, a direct comparison between them is problematic. First, uncertainty in all estimates is large and it is not possible to put meaningful confidence intervals on any of them. Second, the estimates derived from prey and predator movements only represent components of the combined estimate of the XT model. Third, the prey random velocity estimated from Eq. (25) contains additional elements other than the actual random swimming velocity. Eq. (25) is derived from a difference in arrival times of fish after traveling the distance x . Because early in migration juvenile salmon mostly migrate at night and are presumed to hold station near the bottom during the day (Zabel, 2002), the spread in a release group's arrival time at a downstream location is the result of both their actual random swimming velocity and their diel station holding behavior. Thus, the velocity derived from Eq. (25) should represent an upper limit of u^* . Considering these caveats, XT model's estimate of ω on the order of a few cm/s is reasonable.

6. Discussion

The MFL model was motivated by the finding that the survival of migrating juvenile salmon was independent of their migration time (Muir et al., 2001; Smith et al., 2002). While many predator–prey models do not easily explain this puzzling result, the mean free-path perspective provides an intuitive explanation that is valuable for exploring how behavior affects the spatial-temporal characteristics of predator–prey encounters. Furthermore, while the MFL model does not provide spatial details of predator–prey encounters, it implicitly contains spatial scales and directionality and so provides a way to characterize the dynamics within homogeneous cells frequently used in individual based models (IBMs). Below we elaborate on these ideas.

The contrast in the way the MFL model treats spatial scales compared to IBMs is illustrated by comparing our model to an IBM of salmon predator–prey interactions (DeAngelis and Peterson, 2001). One problem with IBMs is that model response is often sensitive to the cell size. DeAngelis and Peterson (2001) explored this problem in their model of salmon smolts migrating through a river described by a series of cells and suggested a sharp increase in smolt mortality as cell size increased from 4 to 50 km was an artifact of improperly characterizing the ecological neighborhood of the predator–prey interaction. The MFL model is continuous and overcomes this problem by avoiding the need of setting the correct cell size; in effect, the data determine the scale of the model.

Further comparisons between the MFL model and the Peterson and DeAngelis model emphasize the consequences of how predator–prey interactions are specified. The MFL model encounter rate depends on the predator and prey random speeds and the prey migration rate, and so if fast migrating prey pass a gauntlet of slow predators, survival depends on the gauntlet length but not the rate of passage since a predator only gets one chance at a prey. In the Peterson and DeAngelis model, encounter rate is characterized by the GS equation, which depends on predator and prey random speeds, but not on the mean prey velocity (Peterson and DeAngelis, 2000). Consequentially, a prey can encounter a predator multiple times and so mortality depends on the migration rate since it determines cell residence time. These alternative encounter representations produce diametrically opposed survival relationships. At

low smolt density, cell-based survival increases in an exponential-like manner with increasing flow, while MFL-based survival asymptotically approaches a constant as flow increases (Fig. 3). These differences illustrate the importance of properly characterizing how animals move between cells and what they do within a cell. We emphasize this issue because cells and grids are powerful constructs for modeling animal dynamics in complex landscapes (Tischendorf, 1997; Nestler et al., 1997; Bian, 2003; Booker et al., 2004). Furthermore, the MFL model can readily be incorporated into a Peterson/DeAngelis-type cell-based model.

How animals move and interact with their environment is fundamental in determining predator–prey encounter rates and therefore population dynamics. For example, in an individual-based model, Mitchell and Lima (2002) found that random search predators are more efficient at finding stationary prey than randomly moving prey while the opposite is true if the predators have a spatial memory of the prey distribution. From studies on sit-and-wait invertebrate predators in streams, Woodward and Hildrew (2002) suggested that prey availability, effectively the product of density and encounter rate, may be more important in determining predator impact than prey density itself. They also noted that the impact of sit-and-wait predators might be different from the impact of search predators. Luttbeg and Schmitz (2000) found that differing assumptions about prey behavior and risk perception could produce similar or different community dynamics, community persistence and resource use. They emphasized the importance of better understanding and representing the behavioral and cognitive capabilities of the prey. Blaine and DeAngelis (1997), analyzing an herbivore-periphyton model, found that the conditions in which the herbivore moved between patches affected how spatial heterogeneity and biomass responded to nutrient inputs. These studies and others illustrate the importance of animal behavior, memory, and adaptive responses to population dynamics. However, the specific behaviors are not readily represented by the traditional sit-and-wait and searching categories of predator–prey interactions (Hart, 1997). In contrast the MFL approach, offers a simple and unique quantification of fundamental behaviors in terms of the random and directed motions of both predators and prey. Furthermore, because encounters are described by speeds, the energetic costs of the predator–prey strategies can be quantified and ranked.

Undoubtedly, behavior and environmental covariates can add formable layers of complexity to a model. However, by linking covariates to the effective predator density and predator encounter distance, which together determine the mean free-path length, we can potentially reduce the complexity. For example, Anderson and Van Holmes (manuscript in review) relate encounter distance to transparency based on a study of Gregory and Levings (1998) and effective predator density to temperature based on how predator digestion changes with temperature (Vigg and Burley, 1991). In principle, the effect of the prey consumption rate on predator satiation could also be formulated in terms of the effective predator density, although a simple analytical solution is unlikely. However, instead of incorporating more complex predator dynamics into a prey survival model, it is feasible to use the MFL theory to define prey encounters in a detailed predator foraging model, for example as in Jeschke et al. (2002). In the present model, the effects of predator satiation are reflected in the effective predator density, which in turn affects the mean free-path length. Therefore, we expect a longer mean-free path length as predators become satiated.

While the statistically derived mean-free path characterization of animal movement is relatively unique in ecology, which typically considers individual-based animal movements, the two approaches have similarities. Matthiopoulos (2003) studied an animal's use of space limited by preference and accessibility in terms of the total path length (l) and the maximum distance (ρ) achieved over the path. The MFL model contains similar concepts: l is equivalent to λ , and ρ is equivalent to Ut . Cuddington and Yodzis (2002), considering individual random walks through a spatially complex fractal environment, characterized how environmental constraints, such as a river valley, limit animal mobility. The number of new sites a walker visits depends on the fractal, or spectral dimension, of the environment. On a one-dimensional landscape, the number of new sites visited is proportional to the square-root of time while the number of sites visited on a two-dimensional surface is proportional to time. Thus, reduced fractal dimensionality of the environment reduces encounters with new sites. The MFL model has an analogous interpretation. In the form, $S = \exp\left(-\frac{\omega}{\lambda}t\sqrt{1+(W/\omega)^2}\right)$, the term W/ω is a fractal-like dimension. When $W/\omega > 1$

predators and prey tend to move at some fixed angle to each other and prey survival over a fixed migration distance is greatest and independent of time. As the ratio decreases, movements of predator and prey take on higher dimensions, while mortality increases and becomes dependent on time. Thus, we see that fractal characteristics of movement can affect predator–prey dynamics in both restricted and unrestricted environments. Furthermore, the equation's rate coefficient, ω/λ , characterizes the strength of mortality per unit time. We suggest that the mean free-path length concept, quantified by these two ratios, provide a very basic way to compare and contrast diverse predator–prey systems.

Returning to the issue that motivated our work, we find that the model fit to smolt survival data produced random encounter velocities of a few cm/s with within-year variations of about 50% and an across-year variations of about 100% (Table 2). These rather large variations may be associated with environmental properties such as water transparency or river hydraulics that affect the parameters in ways not explicit in the model. The large random encounter velocity in 1997, which was a year of high flow and low transparency, supports this possibility. On the other hand, our data represent fish survival from 17 hatcheries located on different tributaries between 31 and 772 km above Lower Granite Dam, and so we may expect variations in fitting such a diverse set of data with a two-parameter model. In any case, with random encounter and migration velocities about 5 and 15 cm/s respectively, then U/ω is about 3, and from Fig. 3 we see that survival is largely independent of migration velocity. In other words, fish pass a gauntlet of predators so that migration distance, not migration velocity, is a major factor determining the survival of juvenile spring chinook migrating through the tributaries of the Snake River.

Finally, as a check on the model, we estimated the parameters using independent methods and data. The predator encounter length scale, derived from predator density and the prey's mean free-path length, was close to the predator's visual field during the migration. Estimates of the random encounter velocity from direct observations of predator and prey swimming speeds agreed with the model estimated random encounter velocity. The fact that our model-derived parameters are consistent with these independent estimates demonstrates the feasibility of the model.

Acknowledgement

We are thankful to the Bonneville Power Administration for funding this project.

References

- Addicott, J.F., Aho, J.M., Antolin, M.F., Padilla, D.L., Richardson, J.S., Soluk, D.A., 1987. Ecological neighborhoods: scaling environmental patterns. *Oikos* 49, 340–346.
- Arditi, R., Ginzburg, L.R., 1989. Coupling in predator–prey dynamics: ratio-dependence. *J. Theor. Biol.* 139, 311–326.
- Barrett, J.C., Grossman, G.D., Rosenfeld, J., 1992. Turbidity-induced changes in reactive distance of rainbow trout. *Trans. Am. Fish. Soc.* 121, 437–443.
- Bennett, D.H., Madsen, M.A., Angela, S.M., Cichosz, T., Dresser, T.J., Davis, M., Chipps, S.R., 1997. DRAFT: fish interactions in lower granite reservoir, idaho-washington. Completion report submitted to the Army Corporations of Engineers, Walla Walla, Washington, USA.
- Berryman, A.A., 1992. The origins and evolution of predator–prey theory. *Ecology* 73, 1530–1535.
- Bian, L., 2003. The representation of the environment in the context of individual-based modeling. *Ecol. Model.* 159, 279–296.
- Bickford, S.A., Skalski, J.R., 2000. Reanalysis and interpretation of 25 years of Snake-Columbia River juvenile salmon survival studies. *N. Am. J. Fish. Manag.* 20, 53–68.
- Blaine, T.W., DeAngelis, G.L., 1997. The interaction of spatial scale and predator–prey functional response. *Ecol. Model.* 95, 319–328.
- Booker, D.J., Dunbar, M.J., Ibbotson, A., 2004. Predicting juvenile salmonid drift-feeding habitat quality using a three-dimensional hydraulic-bioenergetic model. *Ecol. Model.* 177, 157–177.
- Columbia River Data Access in Real Time (CRDART), 1998. Online interactive database of the University of Washington Columbia Basin Research. University of Washington. Available at www.cbr.washington.edu/dart/dart.html.
- Cuddington, K., Yodzis, P., 2002. Predator–prey dynamics and movement in fractal environments. *Am. Nat.* 160, 119–134.
- DeAngelis, D.L., Peterson, J.H., 2001. Importance of the predator's ecological neighborhood in modeling predation on migrating prey. *Oikos* 94, 315–325.
- Evans, G.T., 1989. The encounter speed of moving predator and prey. *J. Plank. Res.* 11, 415–417.
- Feynman, R.P., Leighton, R.B., Sands, M., 1963. The Feynman Lectures on Physics, vol. 1. Addison-Wesley Publishing Company Inc. Reading, Massachusetts.
- Gerritsen, J., 1984. Size efficiency reconsidered: a general foraging model for free-swimming aquatic animals. *Am. Nat.* 123, 450–467.
- Gerritsen, J., Strickler, J.R., 1977. Encounter probabilities and community structure in zooplankton: a mathematical model. *J. Fish. Res. Bd. Can.* 34, 73–82.
- Gregory, R.S., Levings, C.D., 1998. Turbidity reduces predation on migrating juvenile Pacific salmon. *Trans. Am. Fish. Soc.* 127, 275–285.

- Hart, P.J.B., 1997. Foraging tactics. In: Godin, J.J. (Ed.), *Behavioral Ecology of Teleost Fishes*, pp. 104–133.
- Hollings, C.S., 1959. The characteristics of simple types of predation and parasitism. *Can. Entomol.* 91, 385–398.
- Hosseini, P.R., 2003. How localized consumption stabilizes predator–prey systems with finite frequency of mixing. *Am. Nat.* 161, 567–585.
- Jeschke, J.M., Kopp, J.M.M., Tollrian, R., 2002. Predator functional responses: discriminating between handling and digesting prey. *Ecol. Monogr.* 72, 95–112.
- Knutsen, C.J., Ward, D.L., 1999. Biological characteristics of northern pikeminnow in the Lower Columbia and Snake Rivers before and after sustained exploitation. *Trans. Am. Fish. Soc.* 128, 1008–1009.
- Lima, S.L., 2002. Putting predators back into behavioral predator–prey interactions. *Trends Ecol. Evol.* 17, 70–75.
- Lotka, A.J., 1925. *Elements of Physical Biology*. Williams and Wilkins, Baltimore, pp. 460.
- Luttbeg, B., Schmitz, O.J., 2000. Predator and prey models with flexible individual behavior and imperfect information. *Am. Nat.* 155, 669–683.
- Martinelli, T.L., Shively, R.S., 1997. Seasonal distribution, movement, and habitat associations of Northern squawfish in two lower Columbia River reservoirs. *Reg. Riv.: Res. Manag.* 13, 543–556.
- Martinelli, T.L., Shively, R.S., King, T.P., 1993. Distribution, movement and behavior of radio-tagged northern squawfish (pikeminnow) near The Dalles and John Day Dams as determined by radio-tracking. *Annual Report of Research to Bonneville Power Administration, Project No. 82-003, Contract DE-A179-88BP 91964*, Portland, Oregon, USA.
- Matthiopoulos, I., 2003. The use of space by animals as a function of accessibility and preference. *Ecol. Model.* 159, 239–268.
- May, R.M., 1974. Stability and complexity in model ecosystems. In: *Monographs in Population Biology #6*. Princeton University Press, Princeton, NJ, pp. 235.
- Mitchell, W.A., Lima, S.L., 2002. Predator–prey shell games: large-scale movement and its implications for decision-making by prey. *Oikos* 99, 249–259.
- Muir, W.D., Smith, S.G., Williams, J.G., Hockersmith, E.E., Skalski, J.R., 2001. Survival estimates for migrating yearling chinook salmon and steelhead tagged with passive integrated transponders in the Lower Snake and Lower Columbia Rivers, 1993–1998. *North Am. J. Fish. Manag.* 21, 269–282.
- Murdoch, W.W., McCauley, R., Nisbet, R.M., Gurney, W.S.C., de Roos, A.M., 1992. Individual-based models: combining testability and generality. In: DeAngelis, D.L., Gross, L.J. (Eds.), *Individual-based models and approaches in ecology: populations, communities and ecosystems*. Chapman and Hall, New York, pp. 18–35.
- Nestler, J.M.R.A., Goodwin, T.M., Cole, D., Degan, D., Dennerline, 1997. Simulating movement patterns of blueback herring in a stratified southern impoundment. *Trans. Am. Fish. Soc.* 131, 55–69.
- National Marine Fisheries Service (NMFS), 2000. *Predation on Salmonids Relative to the Federal Columbia River Power System*. Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 2725 Montlake Blvd. E. Seattle, Washington 98112. Available at www.nwfsc.noaa.gov/publications/whitepapers/Predation.PDF.
- National Research Council (NRC), 1996. *Upstream: Salmon and Society in the Pacific Northwest*. National Academy Press, Washington, DC, USA.
- Okubo, A., Levin, S.A., 2001. *Diffusion and ecological problems: modern perspectives*, second ed. Springer-Verlag, New York.
- Pascual, M., Levin, S.A., 1999. From individuals to population densities: searching for the intermediate scale of nontrivial determinism. *Ecology* 80, 2225–2236.
- Peterson, J.H., DeAngelis, D.L., 2000. Dynamics of prey moving through a predator field: a model of migrating juvenile salmon. *Math. Biosci.* 165, 97–114.
- Poe, T.P., Hansel, H.C., Vigg, S., Palmer, D.E., Penderdast, L.A., 1991. Feeding on predaceous fishes on out-migrating juvenile salmonids in John Day Reservoir, Columbia River. *Trans. Am. Fish. Soc.* 120, 405–420.
- Prentice, E.F., Flagg, T.A., McCutcheon, C.S., 1990. Feasibility of using implantable passive integrated transponder (PIT) tags in salmonids. *Am. Fish. Soc. Symp.* 7, 317–322.
- Rieman, B.E., Bearnederfer, R.C., Vigg, S., Poe, T.P., 1991. Estimated loss of juvenile salmonids to predation by northern squawfish, walleyes and small mouth bass in John Day Reservoir, Columbia River. *Trans. Am. Fish. Soc.* 120, 448–458.
- Roby, D.D., Craig, D.P., Collis, K., Adamany, S.L., 1998. Avian predation on juvenile salmonids in the lower Columbia River, 1997 Annual Report. Bonneville Power Administration and U.S. Army Corps of Engineers, Portland, Oregon.
- Smith, S.G., Muir, W.D., Williams, J.G., Skalski, J.R., 2002. Factors associated with travel time and survival of migrant yearling chinook salmon and steelhead in the lower Snake River. *North Am. J. Fish. Manag.* 22, 385–405.
- Steel, E.A., 1999. In-stream factors affecting juvenile chinook salmon migration, Ph.D. dissertation. University of Washington, Seattle, USA.
- Steel, E.A., Neuhauser, S., 2002. A comparison of methods for measuring water clarity. *J. North Am. Bentho. Soc.* 21, 326–335.
- Sverdrup, H.U., Johnson, M.W., Fleming, R.H., 1942. *The Oceans: Their Physics, Chemistry and General Biology*. Prentice-Hall, Englewood Cliffs, New Jersey, pp. 1087.
- Sweka, J.A., Hartman, K.J., 2001. Influence of turbidity on brook trout reactive distance and foraging success. *Trans. Am. Fish. Soc.* 130, 138–146.
- Tischendorf, L., 1997. Modeling individual movement in heterogeneous landscapes: potentials of a new approach. *Ecol. Model.* 103, 33–42.
- Tweedie, M.C.K., 1957. Statistical properties of inverse Gaussian distribution I. *Annal. MathStat.* 28, 362–377.
- Vigg, S., Burley, C.C., 1991. Temperature dependent maximum daily consumption of juvenile salmonids by northern squawfish (*Ptychocheilus oregonensis*) from the Columbia River. *Can. J. Fish. Aquat. Sci.* 48, 2491–2498.
- Vogel, J.L., Beauchamp, D.A., 1999. Effects of light, prey size and turbidity on reaction distances of lake trout (*Salvelinus namaycush*) to salmonid prey. *Can. J. Fish. Aquat. Sci.* 56, 1293–1297.
- Volterra, V., 1926. Fluctuation in the abundance of a species considered mathematically. *Nature* 118, 558–560.

- Waage, P., Guldberg, C.M., 1864. Forhandler: Videnskabs-Selskabet i Christiana, vol. 35.
- Ward, D.L., Peterson, J.H., Loch, J.L., 1995. Index of predation of juvenile salmonids by northern squawfish in the Lower Columbia and Snake Rivers. *Trans. Am. Fish. Soc.* 124, 321–334.
- Woodward, G., Hildrew, A.G., 2002. the impact of sit-and-wait predators: separating consumption and prey emigration. *Oikos* 99, 409–418.
- Zabel, R.W., 2002. Using “travel time” data to characterize the behavior of migrating animals. *Am. Nat.* 159, 372–387.