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FUNCTIONAL HETEROGENEITY:

USING THE INTERRUPTED POISSON PROCESS (IPP) MODEL UNIT
IN ADDRESSING HOW FOOD AGGREGATION MAY AFFECT FISH RATION

by

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ABSTRACT

Addressing how aggregating and dispersing food organisms affect fish ration, growth and survival is difficult without a theoretical approach. The IPP building stone provides a stochastic (individually-based), simple and well-defined starting point.

Functional heterogeneity or how a predator perceives and responds to patchy prey is quantified by considering the times of prey-predator encounters as an interrupted Poisson process (IPP) in the simplest case of one patch type and one prey type: the predator locates food patches at random (1. parameter), encounters prey in a Poisson process (2. parameter) when foraging inside a patch, and leaves a patch at random (3. parameter).

The interencounter times become hyperexponentially distributed (H_2) with parameters that are determined by the three (biologically interpretable) parameters of the IPP. As an example the model unit is applied to a cruising predator (e.g. larval herring) with food patches (e.g. copepod nauplii) from micro- to mesoscale and, maintaining a constant average prey density (on a macroscale averaging over patch- and interpatch volumes), the determination of the three IPP parameters is discussed.

INTRODUCTION

The purpose of this note is to introduce the IPP and to communicate the idea of using the IPP as a first step towards developing a new theory for predator-prey encounters in case of patchy prey (see OH1). This is done by using the overheads (referred to as OH1 to OH6) as the core of this note as well. Emphasis is on simplicity. However, even simple stochastic processes have a tendency to reveal complex behaviour and utmost care is needed to avoid misinterpretations and other pitfalls. As such the present note only serves as an appetizer and the interested reader is referred to Beyer and Nielsen (in press) for a more thorough examination of the IPP¹⁾.

The background for OH2 is the process of encountering prey by an individual predator. The outcome is a signal comprising the individual encounters, which may be specified by the inter-encounter times (T) or by the number of encounters (N_t =counts) during a specific period of time (t); see Fig 1.

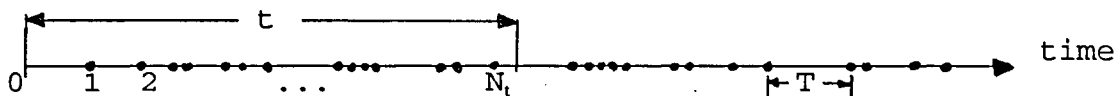


Fig 1.

Random encounters means that a predator encounters prey particles in a Poisson process (PP) at some rate λ_0 , i.e. the interencounter times are exponentially (EXP) distributed with mean = standard deviation = $1/\lambda_0$ and the number of counts is Poisson distributed with mean = variance = $\lambda_0 t$. Thus the coefficient of variation (= standard deviation/mean) of the interencounter times is one and so is IDC, the index of dispersion for counts (= variance to mean ratio for N_t), i.e. $c.v.(T) = IDC(t) = 1$ for all t . It is suggested to use IDC as a measure of the functional heterogeneity in encounters. We expect $IDC > 1$ in case of patchy prey.

Rothschild²⁾ (1991) considers a simple patchy extension of Poisson encounters by assuming the interencounter times to be described by a mixed exponential distribution (= hyper-exponential (H_2) = COMPOUND EXP in OH2). It is of note that the equivalence between the exponential and the Poisson distribution does not extend to the compound (or mixed) cases.

The three parameters of a H_2 -distribution (which will be introduced later) cannot be given a straightforward biological

- 1) Beyer & Nielsen, 1995: Predator foraging in patchy environments: the interrupted Poisson process (IPP) model unit. Dana. In Press.
- 2) Rothschild, B.J., 1991. Food-signal theory: population regulation and the functional response. J. Plank. Res. Vol. 13 no. 5: 1123-1135.

-interpretation in terms of patchiness..A basic point of this study is therefore that the H_2 -distribution of interencounter times does not (biologically) constitutes the starting point but instead is derived as a consequence of the IPP-model, which is specified by three biological parameters associated with the foraging cycle, i.e. the rates at which the predator encounters patches (ω_2), leaves patches (ω_1) and encounters prey particles (λ) while foraging inside patches. These three rates or parameters of the IPP are considered constant. The only real change, moving from Poisson to IPP encounters, is that the process of random encounters is interrupted by exponentially distributed periods of interpatch travel (during which the predator is assumed not to encounter prey particles).

EXAMPLE

A conceptual example is used to illustrate how the IPP-parameters can be obtained from simple encounter theory and the characteristics of patches. The simple scenario is shown in OH3 and comprises a cruising predator and a population of immobile prey particles (e.g. a fish larva and copepod nauplii, which are shown as dots).

Starting with randomly distributed prey in the water volume unit, the predator encounters these particles at a rate λ_0 , which equals the encounter rate kernel (= search volume rate) times the average prey density (ρ_0), i.e.

$$\lambda_0 = \pi d^2 v \rho_0 ; \quad \text{POISSON: prey encounter rate}$$

assuming constant swimming speed (v) and that the perceptive distance (d) is large compared to the radius of a prey particle (and that possible effects of crossing pathways can be neglected).

In creating patchiness with the same number of prey particles (mass balance), the patch volume fraction (η) determines the prey density inside patches ($\rho = \rho_0 / \eta$) and, assuming unchanged kernel, the prey parameter of the IPP is obtained as

$$\lambda = \lambda_0 / \eta ; \quad \text{IPP: prey encounter rate}$$

The concentration of patches (C) and the patch volume (V) are inversely related:

$$C \cdot V = \eta = \rho_0 / \rho$$

Consider a patch as a spherical particle with radius R and assume a patch encounter to take place when the predator actually encounters the patch surface then (assuming the chance of patch overlap is small)

$$\omega_2 = 3/4 v \eta / R ; \quad \text{IPP: patch encounter rate}$$

A patch encounter represents the only entrance to the food supply but (within the IPP concept) a predator may fail to

encounter prey particles during a (short) patch residence. Even if the predator was able to detect a patch surface at distance d the patch encounter rate above is not likely to change (because d is considered considerably smaller than R). The implication of ω_2 being inversely proportional to R appears to be that a prey population can reduce its chance of being predated by forming bigger but fewer patches. However, it also depends on the behaviour of the predator once a patch encounter has occurred.

Assuming that the patch volume fraction equals the fraction of time a predator spends in patches, $\omega_2/(\omega_1+\omega_2)$ (, see next section), the mean patch residence time, $1/\omega_1$, becomes equal to the time required for swimming the distance $4/3R$:

$$\omega_1 = \omega_2 \cdot (\eta^{-1} - 1) \approx 1 / 4/3R/v ; \quad \text{IPP: patch leaving rate}$$

where the approximation is valid for small η . Thus the average patch residence time will increase (as $1/\omega_2$, the mean interpatch travel time) in direct proportion to an increasing patch dimension, which will insure that the predator on average encounters prey particles at exactly the same rate independently of the degree patchiness (i.e. of η and R). This, of course, is convenient for comparisons of the variability in the IPP-counting process with that of random PP-encounters. But in reality it means that predator behaviour is neglected; a point I'll return to in the conclusion.

MODEL

In an environment containing food patches a predator is considered to alternate between two environmental states:

state 0: non-patch	(i.e. interpatch travelling)
state 1: patch	(i.e. foraging inside a patch)

The predator encounters patches at random (in a Poisson process) at rate ω_2 and once an encounter has taken place the predator also leaves the patch at random at rate ω_1 , i.e. the duration of patch residences is exponentially distributed with mean $1/\omega_1$. The equilibrium probability distribution is given by

$$\pi_0 = \omega_1 / (\omega_1 + \omega_2) , \quad \pi_1 = \omega_2 / (\omega_1 + \omega_2)$$

where π_1 may be interpreted as the proportion of time spent in food patches when the foraging behaviour of an individual predator is studied over a long period of time. An alternative empirical interpretation of the equilibrium distribution is that π_1 denotes the fraction of the total number of predators, which, at some fixed (but arbitrary) point in time, is foraging inside patches (assuming negligible effect of predatory interactions during the period of time considered).

The transition diagram of the complete IPP is shown on OH4. When state 1 (patch) is occupied, the forager encounters prey items in a Poisson process at a constant rate, λ . This completes the simple patch and prey IPP-model unit.

The IPP($\lambda, \omega_1, \omega_2$) process is stochastically equivalent to a $H_2(p, \gamma_1, \gamma_2)$ renewal process (i.e. with intercounter times being H_2 distributed - see Fig 2) and the (non-trivial) relationship between the parameters is given by

$$\lambda = p \cdot \gamma_1 + (1-p) \cdot \gamma_2$$

$$\lambda + \omega_1 + \omega_2 = \gamma_1 + \gamma_2$$

$$\lambda \cdot \omega_2 = \gamma_1 \cdot \gamma_2$$

The H_2 -renewal process may be interpreted in the following way assuming e.g. $\gamma_1 > \gamma_2$. On each prey encounter, the forager decides whether to stay in the patch or to leave: with probability p it stays and the probability of encountering the next prey item in that patch is then governed by the first exponential phase, i.e. the intercounter time becomes exponentially distributed with mean $1/\gamma_1$. With probability $1-p$ it leaves the patch and the time required to encounter the next prey item (and hence a patch) will be governed by the second exponential phase, i.e. the intercounter time becomes exponentially distributed with mean $1/\gamma_2 > 1/\gamma_1$. Note that the patch concept in this H_2 -interpretation is quite different from the more straightforward IPP-patch concept.

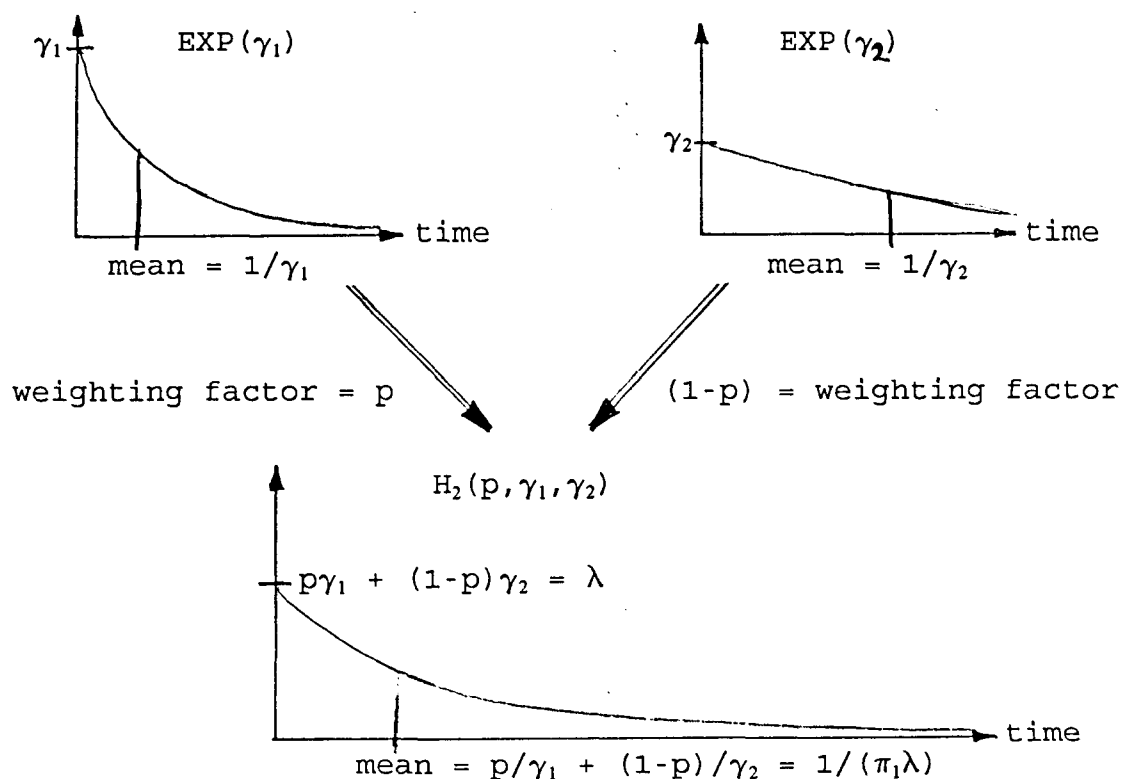


Fig 2. A graphical (pdf) representation of the phase diagram (see OH4) for a hyperexponential distribution with two phases (H_2) also known as a mixed exponential distribution or a compound exponential. Its pdf is given by the weighted sum of the two exponential pdf's, i.e. $p\gamma_1 \exp(-\gamma_1 t) + (1-p)\gamma_2 \exp(-\gamma_2 t)$.

RESULTS

Once the IPP is specified by the parameters $(\lambda, \omega_1, \omega_2)$ or by its H_2 -parameters (p, γ_1, γ_2) properties of the counting process (and thus the probability distributions governing the potential ration) can be studied. The results will differ for the time-stationary process and the event-stationary processes with respect to transient behaviour. The process is in equilibrium or time-stationary if it has been running a long time before observations starts ($t=0$) or simply, if is being observed from ($t=0$) a random point in time. The event stationary case implies that an encounter has just taken place at $t=0$. In this note, which serves as an IPP-introduction, focus is just on the mean counts and on the index of dispersion for counts (IDC) defined as the variance to mean ratio for counts. Only the asymptotic IDC is given below, i.e. the limit IDC, which is valid for counts in both the time- and event-stationary processes that pertain to periods of time large compared to $1/(\omega_1 + \omega_2)$.

The mean number of encounters in the time-stationary process is

$$\text{mean count} = \pi_1 \cdot \lambda t$$

This result was expected because λt is the mean count in a Poisson process but the predator is only occupying state 1 (patch) in the fraction π_1 of the time t . The result is exact for all t in the time-stationary case but only asymptotically correct in the event-stationary case. The asymptotic IDC becomes constant:

$$\text{IDC} = \text{variance}/\text{mean} = 1 + 2\lambda\omega_1/(\omega_1 + \omega_2)^2 = 1 + \frac{1}{2}\lambda/\omega_1 \cdot [2\pi_0]^2$$

Consider this IDC (, which also equals the c.v. squared of the interencounter time,) as a function of ω_1 , the rate of leaving patches for fixed rates of encountering patches (ω_2) and prey (λ) inside patches; see OH5. If $\omega_1=0$ the predatory will stay in the patch and thus continues to encounter prey particles in a Poisson process so IDC takes the minimum value of one. At the other extreme, considering very large ω_1 , the predatory will still encounter patches at a constant rate, ω_2 , but it will leave the patches so fast that the chance of encountering a prey is negligible, which represents a special (and unrealistic) case of Poisson so IDC=1 for this extreme as well. The maximum (in between these extremes) occurs when the predator leaves the patches at the same rate it is encountering patches, i.e. for $\omega_1=\omega_2$ when $\pi_0=\frac{1}{2}$,

$$\text{IDC}_{\max} = 1 + \frac{1}{2}\lambda/\omega ; \quad \omega_1=\omega_2=\omega$$

That is the maximum IDC for the IPP exceeds the variance to mean

ratio for the Poisson process with $\frac{1}{2}\lambda/\omega$, half the rate ratio of encountering prey in patches to encountering or leaving patches.

As an example consider a case,

$$\begin{aligned} H_2: \quad p &= 8/11 \\ \gamma_1 &= 4 \\ \gamma_2 &= 1/3 \end{aligned}$$

$$\begin{aligned} \text{IPP:} \quad \lambda &= 3 \\ \omega_1 &= 8/9 \\ \omega_2 &= 4/9 \end{aligned}$$

in which the mean counts is one per unit of time and $\text{IDC}=4$. The values of the IPP-parameters may also be obtained using $\lambda_0=1$ as the starting point (see OH3) and with a patch volume factor of $\eta=3$. The rate of leaving patches is double the rate of encountering patches, $\omega_1 = 2\omega_2$ (because $\eta^{-1}-1=2$), which coincides with the inflexion point on the IDC curve (OH5). The curve is rather flat (i.e. with a very long right tail) giving a maximum IDC of $4+3/8$ when ω_1 is reduced to $4/9$.

Based on this example OH6 shows a realization of the patchy IPP (right), which can be compared with a realization of the non-patchy Poisson process (left) specified by $\lambda_0=1$, i.e. the mean number of counts is one per unit of time in both cases. The top graphs show number of counts per 100 time units. The average count is thus 100 but the variability is much higher in the IPP case ($\text{IDC}=4$; standard deviation = 20) than in the Poisson case ($\text{IDC}=1$; standard deviation = 10). The graphs below are zooming in, magnifying 10% segments of the graphs above. IDC is still ca. 4 for the mid-cases because $t=10$ is considerably bigger than $1/(\omega_1+\omega_2) = 3/4$. OH6 (right) is based on a simulation of the H_2 process.

CONCLUSION

The three parameters of the IPP model unit are related directly to patch characteristics and foraging behaviour as illustrated by the basic example in OH3. The patch leaving rate was determined as $\omega_1 \approx \omega_2/\eta$ by assuming the patch volume fraction to equal the fraction of time spend by the predator in patches, i.e. $\eta = \pi_1$. This implies that the predator on average encounters prey particles at the same rate in different situations of patchiness (specified by η , the patch volume fraction and by R , the patch radius) including the random or non-patch (Poisson) situation for $\eta=1$. However, in reality η is usually small, say, in the order of $1/100$ for larval fish predators, which means first that the prey encounter rate may become very high and secondly that the patch leaving rate also becomes high (to ensure a constant mean encounter rate). In this case of a small η the mean count and the asymptotic index of dispersion for counts become

$$\text{mean counts per unit time} \approx \omega_2 \cdot \lambda / \omega_1 ; \quad \omega_1 \gg \omega_2$$

$$\text{IDC} \approx 1 + 2 \cdot \lambda / \omega_1 ; \quad \omega_1 \gg \omega_2$$

The important point is that the mean count and the IDC are approximately proportional to λ/ω_1 , the rate of encountering prey particles divided by the rate of leaving patches both of which are proportional to the average swimming speed of the predator when it is foraging inside a patch (denoted by, say, $v_{1\text{ pred}}$ where subscript 1 refers to the patch state). Thus, assuming $\omega_1 \propto v_{1\text{ pred}}/R$ as in OH3 but distinguishing between the swimming speeds of the predator when searching for patches (i.e. $\omega_2 \propto v_{0\text{ pred}}$) and the swimming speed ($v_{1\text{ pred}}$) when foraging inside patches, the mean count and the IDC will not change as long as $\omega_1 \gg \omega_2$. But, of course, for $v_{0\text{ pred}} > v_{1\text{ pred}}$ the average time spend in patches will exceed the average time spend on interpatch travel.

Mechanisms by which a predator is able to prolong its stay in patches will decrease ω_1 and hence cause an increase in both the prey encounter rate and in IDC (as long as $\omega_1 > \omega_2$). These considerations are but one example of incorporating behaviour into the IPP model. Other examples include the effects of mobile prey organisms and of turbulence on the contact rates. Some of the principal effects here can be examined by changing the speed of the predator. The effects of patchiness on encounters with predators operating with different feeding behaviours such as ambush feeders and pause-travel predators can be examined as well using the IPP model unit.

In this way I believe the IPP model unit may serve as a well-defined starting point for studying the variability in predator-prey encounter rates in ecology; a variability which is important for ensuring sufficient growth of the survivors and which at the other end may be responsible directly or indirectly for a major part of mortality during e.g. early life stages. In the marine environment the average survivor has most likely not survived based on the mean encounter rate with prey particles during early life. In the mortality context the IPP model unit can be used, for example, to derive analytical expressions for the probabilities of not encountering food during a critical time-frame for first feeding fish larvae depending on where the larvae are located when they are ready to commence feeding. Addressing many of these questions theoretically will lead to strong arguments for obtaining the empirical data, which are needed for further developing and testing the theory. However, it does required measurements on a scale similar to the one perceived by the predator in question, which is why further development of the concept of functional heterogeneity seems to be of importance.

FUNCTIONAL HETEROGENEITY:
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AGGREGATION MAY AFFECT FISH
RATION

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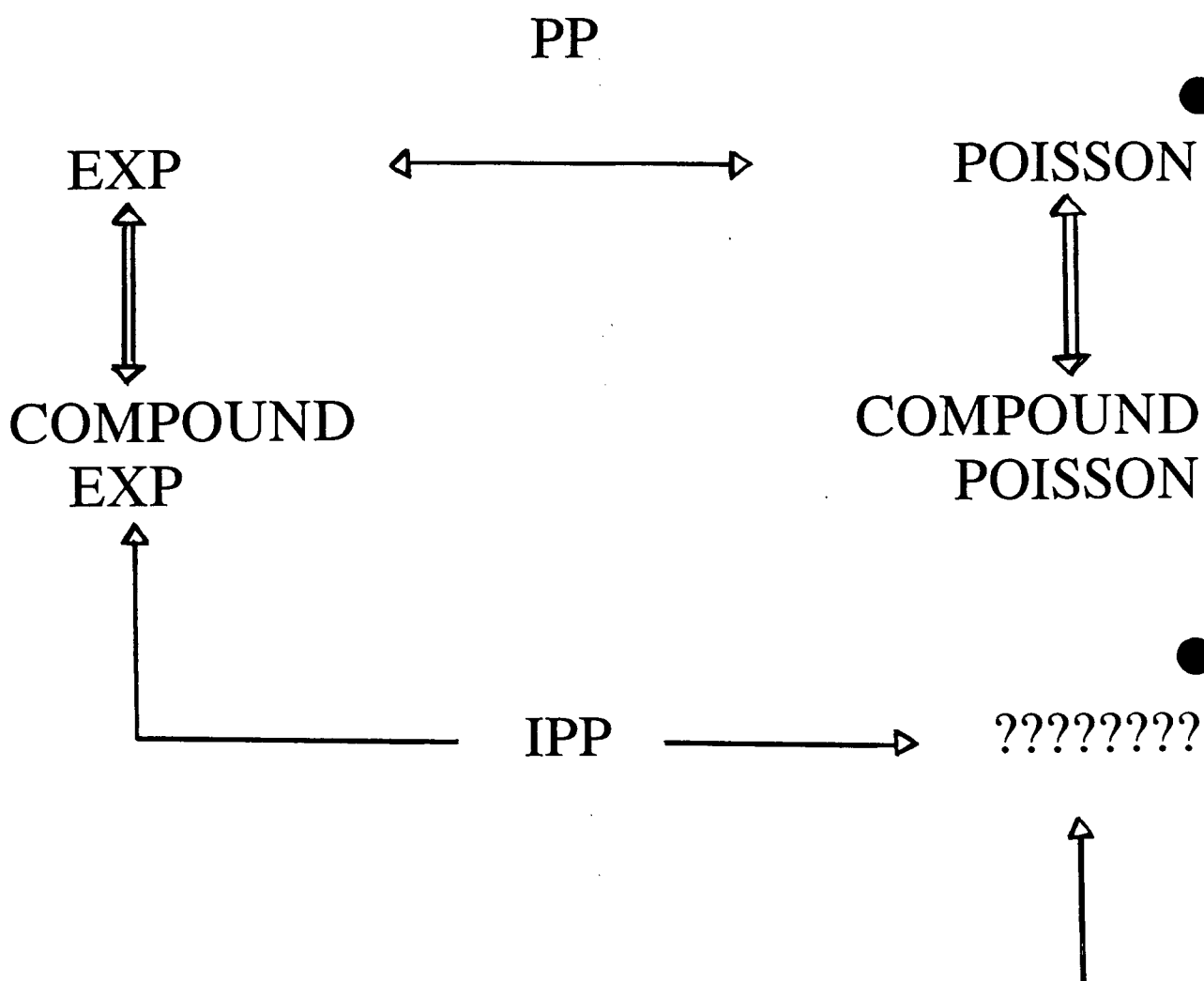
- Need for simple but mechanistic models because predator-prey encounters usually cannot be observed and therefore cannot be addressed without a unifying theory
- Functional heterogeneity = how a predator perceives and responds to patchy prey
- The IPP building stone provides a stochastic (individually-based), simple and well-defined starting point.

INTRODUCTION

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Interencounter time

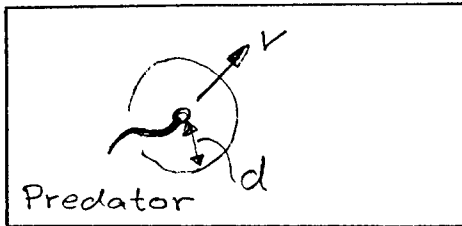
Counting process



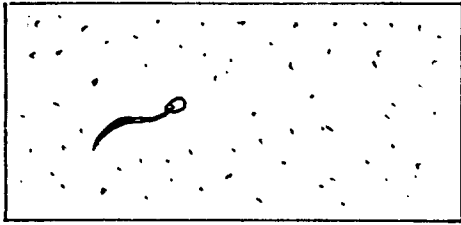
INDEX OF DISPERSION FOR COUNTS
= IDC = VARIANCE TO MEAN RATIO

BASIC EXAMPLE

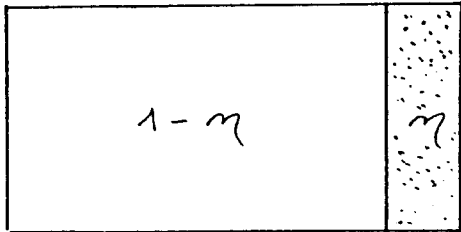
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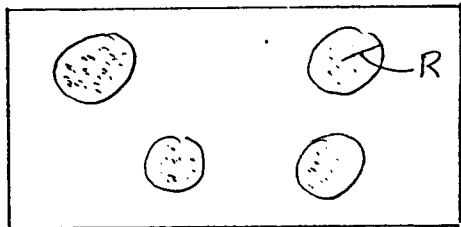
swimming speed v
 visual range d
 search volume rate $\beta_{\text{prey}} = \pi d^2 v$
 (encounter rate kernel)



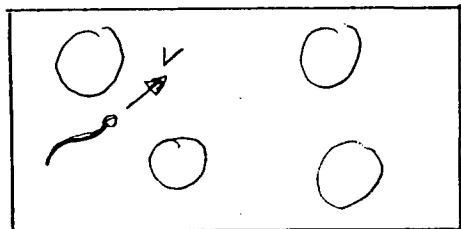
average prey density ρ_0
 encounter rate $\lambda_0 = \beta_{\text{prey}} \cdot \rho_0$



patch volume fraction $\eta = \rho_0 / \rho$
 intrapatch prey density $\rho = \rho_0 / \eta$
 prey encounter rate $\lambda = \lambda_0 / \eta$



patch radius R
 patch volume $V = 4/3 \pi R^3$
 patch concentration $C = \eta / V$



patch encounter kernel $\beta_{\text{patch}} = \pi R^2 v$
 patch encounter rate $\omega_2 = \beta_{\text{patch}} \cdot C$

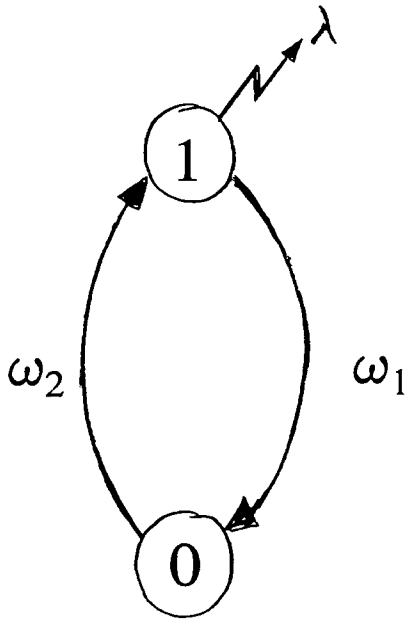
$$\text{PATCH ENCOUNTER RATE} = \omega_2 = 3/4 \cdot v \cdot \eta / R$$

$$\text{PATCH LEAVING RATE} = \omega_1 \approx \omega_2 / \eta = 1 / 4/3 \cdot R / V$$

MODEL

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IPP transition diagram

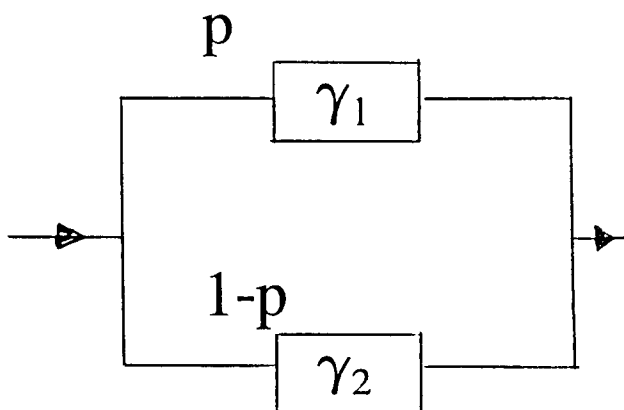


patch = state 1

probability = $\omega_2 / (\omega_1 + \omega_2)$ ●

IPP is stochastically equivalent to a H_2 renewal process

H_2 phase diagram



H_2 process interpretation:

different patch concept !

RESULTS

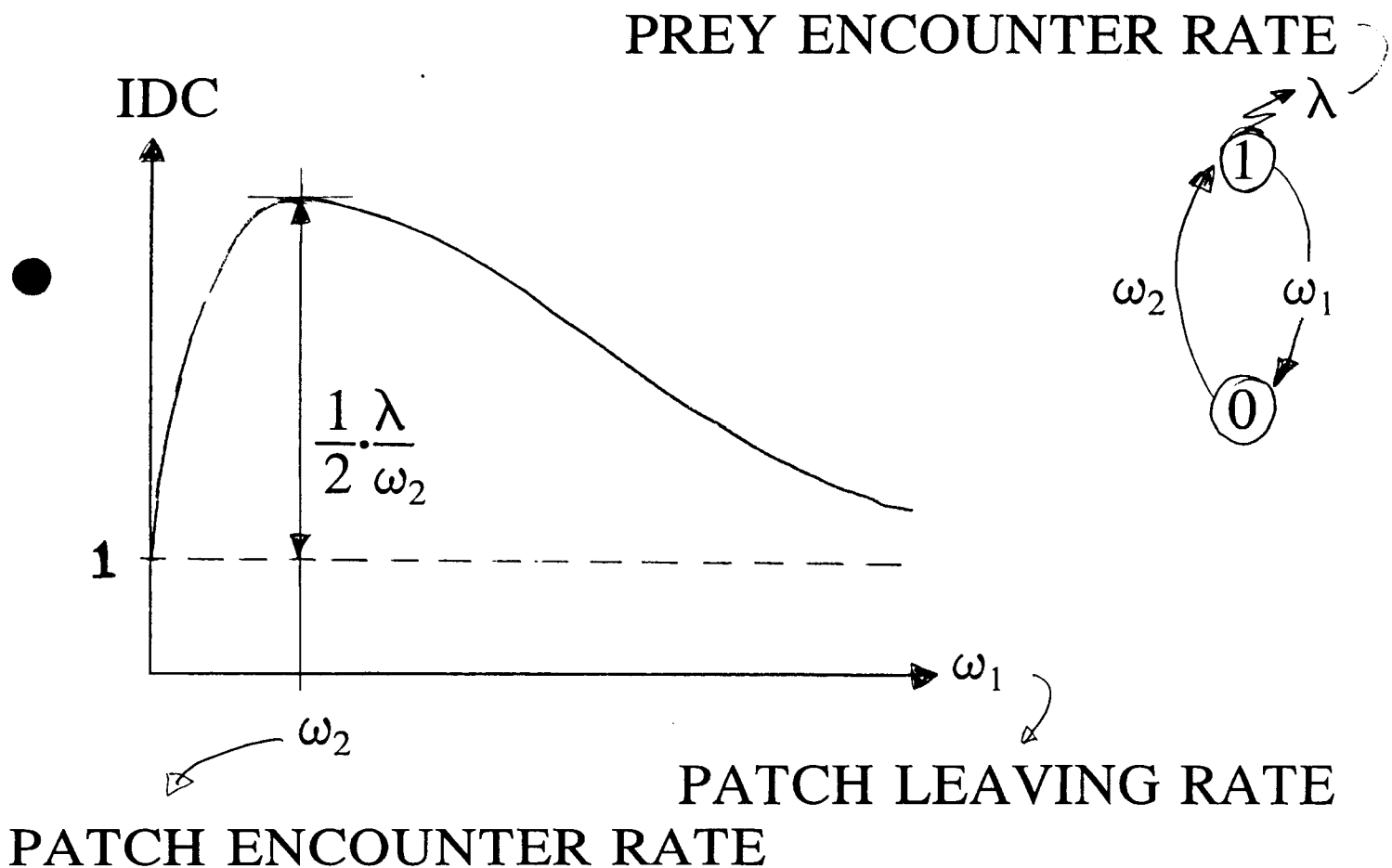
EXAMPLE:

Mean interencounter time = 1

IDC = variance to mean ratio = 4

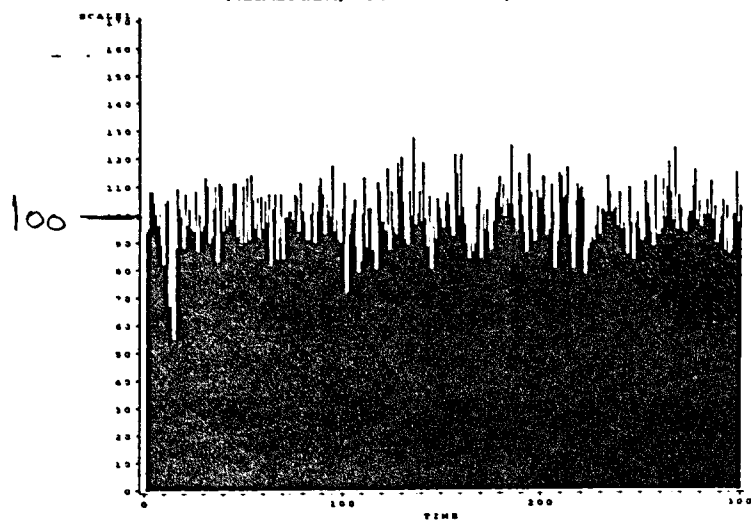


INDEX OF DISPERSION FOR COUNTS

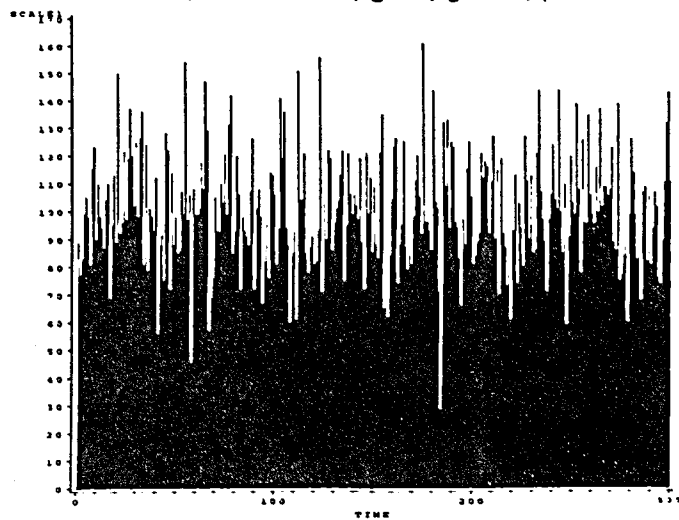


IPP

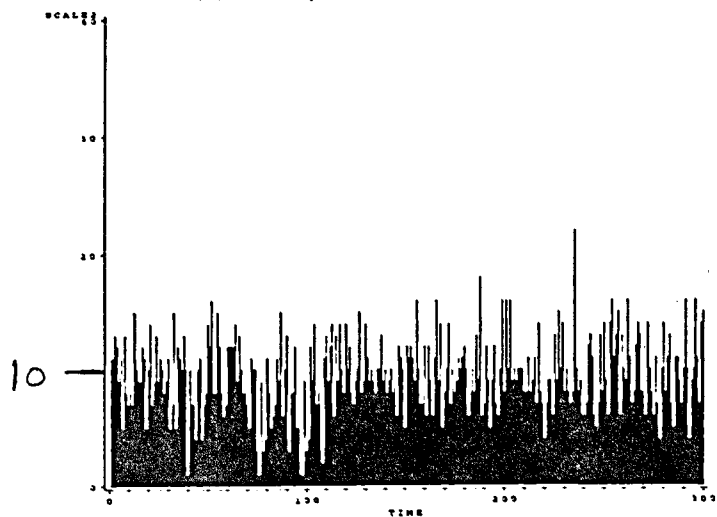
Realization, 100 time units, Poisson



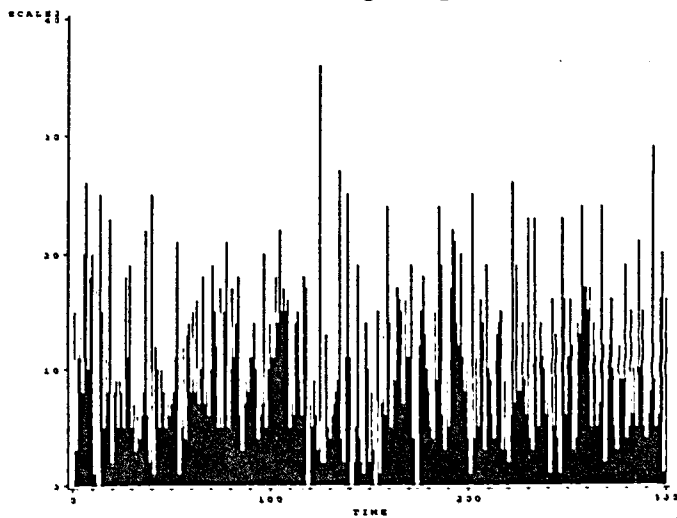
Realization, 100 time units, $g_1=4$, $g_2=1/3$, $p=8/11$



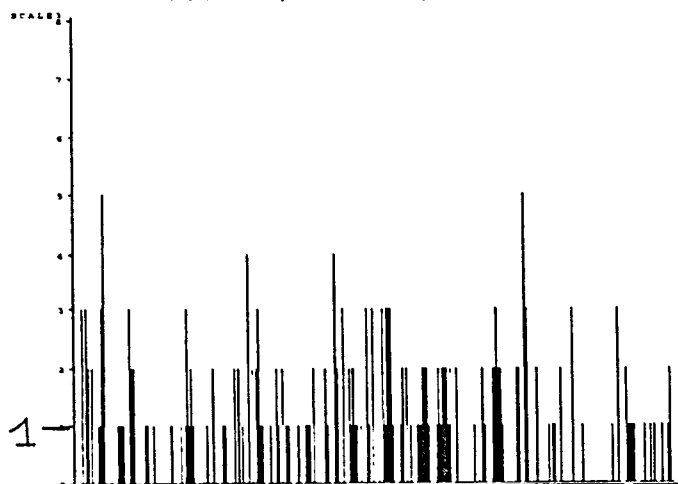
Realization, 10 time units, Poisson



Realization, 10 time units, $g_1=4$, $g_2=1/3$, $p=8/11$



Realization, 1 time units, Poisson



Realization, 1 time units, $g_1=4$, $g_2=1/3$, $p=8/11$

