Dana, vol. 11(2), pp. 65-130, 1996

Predator foraging in patchy environments: the interrupted Poisson process (IPP) model unit

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Abstract

This study addresses the heterogeneity of the prey environment perceived by a predator. The interrupted Poisson process (IPP) is presented as a starting point for modelling predator encounters with patchy prey. This theory is introduced thoroughly since it appears to offer a new entrance to modelling predator–prey interactions. The basis of the theory represents a coupling of the classical patch and prey encounter models of foraging theory. Specifically, the predator encounters prey in a Poisson process (1. parameter) but only while foraging in a food patch. The Poisson process is interrupted during exponentially distributed periods of interpatch travel (2. parameter). Patch residence times are also considered exponentially distributed (3. parameter). The interencounter times in this IPP become hyperexponentially distributed with a coefficient of variation, which is related to the index of dispersion for counts (*IDC*). Analytical expressions for such measures of the variability in encounters are derived and interpreted in relation to simple scenarios of patchiness. Using spherical patch geometry the IPP-parameters are derived for a cruising predator. The probability distribution of patch residence times is derived analytically as a function of intrapatch foraging speed and the patch radius. The effect of behavioural aspects is introduced and the optimum intrapatch foraging speed is derived in an example. The theory is exemplified with larval fish as predators.

Keywords: interrupted Poisson process (IPP), hyperexponential distribution, index of dispersion for counts (*IDC*), spherical patch geometry, foraging cycle, predator–prey encounters, optimal foraging.

Contents

Introduction

Very little is known about the specifics of predator–prey encounter events, since they usually cannot be observed *in situ* and therefore cannot be addressed without a unifying theory (see Rothschild 1986, 1988 for a discussion of this challenge). Thus, there is a need for simple models, which can be fully theoretically analysed and interpreted. 'Model unit' designates such a simple (stochastic) theory element and defines a starting point for the quantification of predator–prey encounters with an ultimate aim of understanding trophodynamic interactions in the sea. Apart from simplicity and inherent analytical tractability, a basic requirement for such a model unit is that its parameters can be interpreted biologically.

Animals (and particles) are not randomly distributed in space (for the small scale see e.g. Cassie 1959, and Owen 1989), which indicates that random encounters can not be described by homogeneous Poisson processes (PPs). On the other hand some predators most likely encounter prey at local scales approximately at random (e.g. Vlymen 1977). Hence a minor extension to a process that locally is Poissonian should be of benefit. This approach has been successfully applied in other areas where the subcomponents of the process can be observed. In telecommunications, for example, measurements of calls offered to an overflow trunk group exhibit more variability than the smooth traffic that would be generated by a simple Poisson process. However, this variability can be adequately described simply by introducing random periods of process interruptions (Kuczura 1979). In telecommunication theory such a pattern is termed an interrupted Poisson process (IPP). In recent years the IPP and similar processes have been used extensively to model sources, which generate traffic in an on-off pattern (e.g. Heffes & Lucantoni 1986). The present study introduces the IPP to biology as a possible means of creating a new theoretical basis for modelling prey–predator encounters in a wide ecological sense but with special reference to the marine environment. With this perspective the overall aim here is to present a thorough introduction to the stochastic IPP-theory.

The paper considers an individual predator's encounters with patchy prey (see Figure 1) without considering the possible causes of patchiness and without explicitly quantifying the relative velocity of predator–prey and the other components underlying the effective searching rate of any specific type of forager. However, a conceptual example with a cruising predator (see *Comment 8* (Comments constitute separate blocks for explanatory reasons or exemplifications)) introduces the link between this IPP-theory and simple encounter theory and spherical patch geometry. In

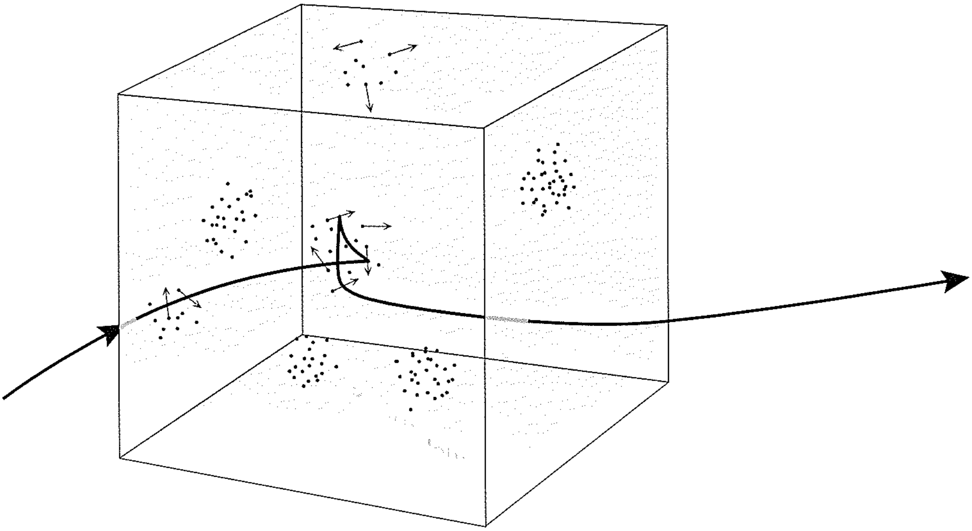
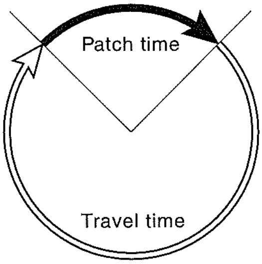


Figure 1. Illustrating a three-dimensional distribution of patchy prey and showing the track of a forager. It encounters six prey on the track in the cube. Redrawn after Beyer (1982) and Rothschild (1988).

such patch scenarios we also derive analytically the probability distributions of the time to first feeding (see *Comment 9*), which have bearings to the understanding of, for example, aspects of the early-life dynamics of marine fish. Furthermore, the probability distribution of patch residence times is derived analytically as a function of intrapatch foraging speed and the patch radius distribution (see *Comment 10*). These results for a cruising predator in spherical patch scenarios are finally used to introduce behavioural aspects and the optimum intrapatch foraging speed is derived when the reactive distance of the predator decreases with increasing speed (see *Comment 11*). These examples (*Comments 8-11*) serve merely as an introduction to the potential applications of the theory. The IPP model unit represents a building stone and more specific applications and elaborations will be considered in subsequent studies.

This study deals only with the basic theory. We specifically consider functional heterogeneity, i.e. heterogeneity as perceived by the predator rather than spatial heterogeneity measured at some arbitrary scale (see Kolasa & Rollo 1991 for discussion of this terminology). In doing this we adopt some of the concepts from foraging theory (see Figure 2) and assume that a predator encounters food patches in

Figure 2. The foraging cycle. Sequential encounter is assumed so the forager enters a patch residence period after an interpatch travel (search) time and, during the patch residence time, it encounters prey items sequentially one after the other (which could also be illustrated by this figure with patch time replaced by, e.g., handling time). After Mcnair (1983) (redrawn).



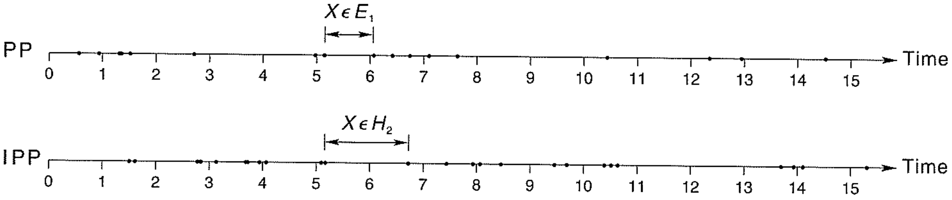


Figure 3. An individual realization of the predator–prey encounter process when it is governed by a Poisson process (PP) with intensity $\rho = 1$, i.e. with a mean interencounter (= interarrival) time of 1 and, alternatively, when it is governed by an interrupted Poisson process (IPP) (or a H_2-process) with $p = 8/11$ and intensities $\gamma_1 = 4$ and $\gamma_2 = 1/3$, i.e. also with mean interarrival time of 1 time unit. However, the coefficient of variation (c.v.) of the interarrival times for these patchy IPP-encounters is twice the c.v. for the non-patchy PP-encounters (which are characterized by mean = standard deviation, i.e. by c.v. = 1). Note, for example, the patchy encounters at the beginning of the shown IPP-realization: (1.515, 1.624), (2.775, 2.779, 2.822), 3.116 etc. The exponential and the hyperexponential p.d.f.'s of the interarrival times in the PP-case, respectively the IPP-case are shown in Figure 5.

a Poisson process and once inside a patch, that it also encounters individual prey items in a Poisson process (see Stephens & Krebs 1986 for a review of the patch and prey models in foraging theory). The present work deals only briefly with the two basic problems in foraging models: which prey items to consume and when to leave a patch (Stephens & Krebs op. cit.; *Comment 11*). We consider instead only encounters with one prey type and disregard for example possible density-dependent effects. In most of this study it is assumed that a predator leaves a patch at random at a rate, which is independent of, for example, the number of prey encountered, i.e. the patch residence times are exponentially distributed. Considering these elements together leads to the IPP because the process of encountering prey by an individual predator is interrupted by random periods of interpatch travel.

The outcome of such an encountering process is a signal comprising the points in time of the individual encounters. Figure 3 illustrates two such examples for cases of PP-encounters (i.e. non-patchy prey) and of IPP-encounters (i.e. patchy prey). With PP-encounters the interarrival times (= interencounter times), X, are exponentially distributed (E_1), i.e. with probability density function (p.d.f.) specified by one parameter, λ_0, the intensity or rate of encounters:

$$g(x) = \lambda_0 \cdot e^{-\lambda_0 x} . \tag{1}$$

The IPP-encounters lead to more dispersed interarrival times (i.e. with c.v. >1), which are hyperexponentially distributed as discussed below in the next section, i.e. with probability density function described by three parameters (see Figure 4),

$$f(x) = p\gamma_1 e^{-\gamma_1 x} + (1-p)\gamma_2 e^{-\gamma_2 x} \; ; \quad 0 < p < 1 . \tag{2}$$

This mixed exponential distribution has been used as the simplest patchy extension of the exponential or random model in Eq.1 (Rothschild 1991, but see also e.g. Cox 1962, Cox & Isham 1980, and, Nielsen 1988 and references herein, for an introduction). In the literature this hyperexponential distribution is often symbolized as H_2, a symbolism which we retain in this presentation.

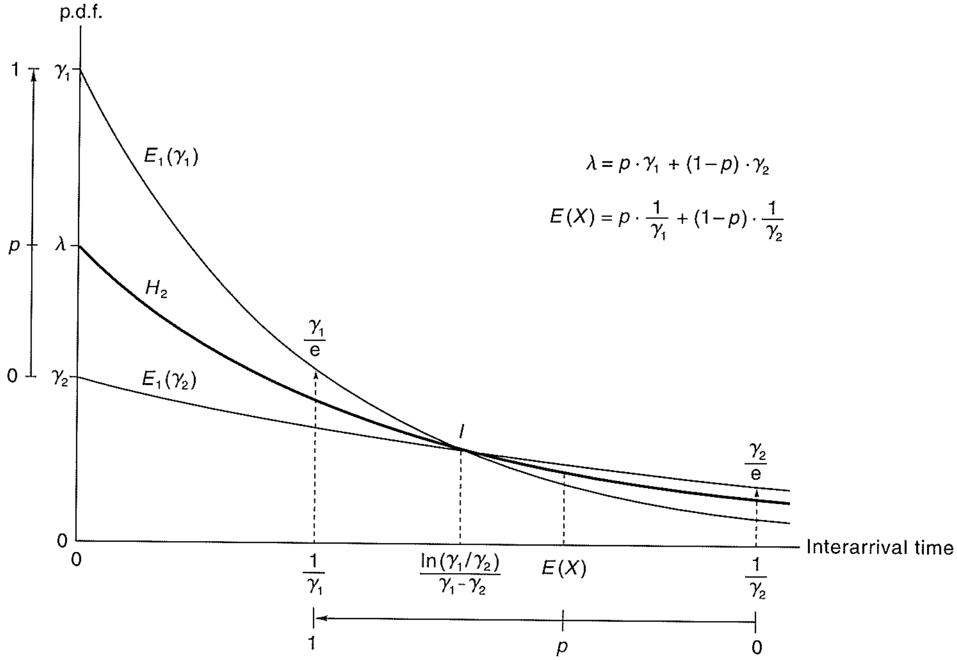


Figure 4. The probability density function (p.d.f.) of the hyperexponential distribution, H_2, and how it depends on the mixture (specified by p) of the two underlying exponential distributions, $E_1(\gamma_i)$ with mean = standard deviation = $1/\gamma_i$ ($i = 1, 2$). When p decreases from 1 towards 0 the H_2-curve moves from the γ_1-exponential curve, turning about the common E-point, I, (without maintaining the exponential shape) towards the γ_2-exponential curve. As p changes the displacement of the intercept, λ, the intensity of encountering prey items in a patch and, the displacement of $E(X)$, the mean interencounter time (between encountering consecutive prey items) are indicated by the p-arrows parallel to the ordinate and the abscissa, respectively. Such a change of H_2 towards the exponential density for the smallest γ-value actually takes place for the p.d.f. of the residual interarrival time when it is known that an encounter has not yet taken place after a specific period of time. This is a memory effect built into the H_2-distribution because it is only the exponential distribution, which is Markovian or memoryless (see Comment 1).

Comment 1: The H_2-process and pitfalls in its interpretation

The H_2-distribution in Eq. 2 thus provides an alternative specification of the IPP. In the terminology of stochastic processes each encounter forms a renewal point and the H_2-process is by definition a renewal process in which the intervals between renewals are H_2-distributed. The biological interpretation of this process is not that simple in contrast to the random PP or Eq. 1 in which the intensity λ_0 is proportional or in some other way directly linked to the local density of prey. For example, considering $\gamma_1 \gg \gamma_2$ implies that the interencounter times associated with γ_1 are less than those associated with γ_2 but this does not necessaryly imply a greater number of encounters associated with γ_1. The relative number of encounters of the two sources is determined by the parameter p, e.g. with p sufficiently small (almost) all the encounters will be associated with γ_2 whether or not $\gamma_1 \gg \gamma_2$. Secondly, considering again $\gamma_1 \gg \gamma_2$, it is misleading to interpret the H_2-process as describing a predator, which is foraging in an environment where γ_1 relates to the prey density in patches and γ_2 relates to an interpatch density. This point is best explained by first noting that any hyperexponential variable correctly can be considered as an exponentially distributed variable in which the intensity is chosen with a known probability, i.e. the hyperexponential distribution is a compound distribution (see e.g. Pielou 1969 for further explanations of this terminology). In this setting the conditional distributions are exponential distributions whereas the intensities are discretely distributed. Returning to the proposed (misleading) patch scenario, suppose a predator was dropped in such an environment at random with the result that it occupies a patch with probability p and an interpatch area with probability $1-p$. Then, assuming the predator can not leave the area without catching a prey item, the time interval until the first prey is encountered will be hyperexponentially distributed with the γ's relating to the prey densities in the two types of areas but, immediately after each encounter, a new random placement of the predator must take place, which in reality disqualifies this scenario. If such a replacement does not take place then an encounter does not become a renewal point, which invalidates the interpretation. In next section a useful interpretation of the H_2-process is suggested, which relates to the one-patch type of environment with *no* food outside patches (but which also is quite different from the interpretation of the IPP-process).

Finally the important equivalence between exponentially distributed time intervals and Poisson-distributed numbers of encounters in a given period of time is unique for the PP. Although an exponential distribution of time intervals is equivalent to Poisson-distributed numbers of encounter events, a compound exponential is *not* equivalent to a compound Poisson, i.e. it is incorrect to relate the mixed (or hyper) exponential time-interval distribution to a mixed Poisson distribution for numbers. The mixed Poisson distribution contains the Poisson distribution as a special case just as the H_2-distribution contains the exponential distribution as a special case ($\gamma_1 = \gamma_2$, $p \to 0$ or $p \to 1$) but this represents the only strict resemblance to the Poisson-exponential equivalence. The exact distribution of the numbers of encounters in the IPP or the H_2-process is not a mixed Poisson distribution and furthermore, it can apparently not be expressed in terms of nice looking analytical expressions for known distributions in any simple way (see *Comment* 7).

As an example, Figure 5 shows that, because of the parameter richness in Eq. 2, (infinitely) many p.d.f.'s exist with the same mean and the same variance (and, hence, constant c.v.). However, the parameters of the H_2-distribution in Eq. 2 are difficult to interpret biologically in any straightforward manner (cf. the attempts by Rothschild 1991, 1992) and a basic point of this study is therefore that the H_2-distribution of interarrival times does not (biologically) constitute our starting point but instead the distribution of interarrival times is derived as a consequence of the IPP-model, which is specified by the three biological parameters associated with the foraging cycle (see next section; Figure 6). Nevertheless, in the next section we also suggest a direct in-

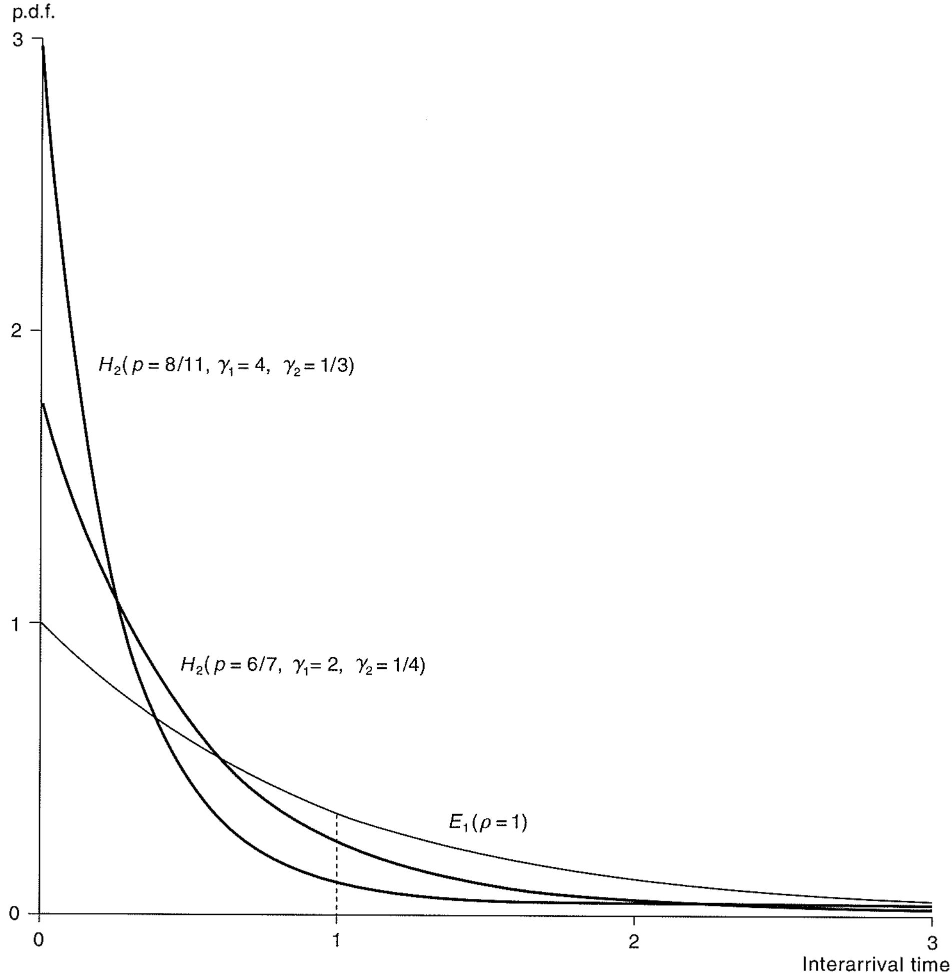


Figure 5. Examples of probability density functions (p.d.f.'s) of individual interarrival times when the mean interarrival time equals one. The exponential distribution, $E_1(\rho=1)$, implies that the predator encounters (non-patchy) prey items at random (in a homogeneous Poisson process) and the coefficient of variation, c.v., is also one (standard deviation = mean = $1/\rho = 1$). The hyperexponential distribution, $H_2(\gamma_1, \gamma_2, p)$, refers to encounters with patchy prey and, since it is described by three parameters, many different situations may give rise to the same mean and variance. The two p.d.f.'s shown have both c.v. = 2 (i.e. standard deviation = 2 · mean = 2). The top H_2 with most probability mass close to zero (i.e. intercept $\lambda = 3$ when $\gamma_1 = 4$, $\gamma_2 = 1/3$ and $p = 8/11$) is used as a recurrent example in this study. It differs from the other H_2 shown (i.e. the one with initial value or intercept $\lambda = 1.75$) by having a greater 3. moment (see Nielsen 1988, p. 131). It is of note that the E_1-distribution must tail off faster than any of the H_2-distributions (not shown).

terpretation of the H_2-parameters in terms of patchiness and a decision assumption (which refers to a choice the forager, on encountering a prey item, is assumed to make or that natural selection has made for it (e.g. Stephens & Krebs 1986)).

The analytical relationships between the parameter set of H_2 in Eq. 2 and that of the IPP (and vice versa) are presented (see *Comment 4*). The mean and variance of

H_2-distributed interarrival times are also given. In addition, we also consider the coefficient of variation (c.v.) of the H_2-distribution as a measure of functional heterogeneity. It is shown that functional heterogeneity (= c.v. of H_2-distribution) attains a maximum when the predator on average spends the same amount of time moving in patches as on travelling to locate patches.

Secondly, we consider the counting process of the number of prey encountered during a specific period of time. This number is of course known (by definition) to be Poisson-distributed in the PP case but in the case of the patchy IPP the distribution of numbers does not belong to any of the well-known discrete distributions, although some analytical resemblance to the mixed Poisson distribution is demonstrated. The mean and variance in this counting process are derived from renewal theory and presented on a closed analytical form as simple functions of the IPP-parameters. The index of dispersion for counts (*IDC*), which is defined as the variance to mean ratio in the counting process is used through out as a relative measure of the variability. Asymptotically *IDC* equals the c.v. squared for the interencounter distribution and thus constitutes an alternative measure of functional heterogeneity. As an example on the potential applications of the IPP-unit we consider the principal effects of patchy prey on the prey encounter rate for a cruising predator. We specifically put emphasis on the variability in counts (*IDC*). In a simple 3D-patch scenario the IPP-parameters, the time to first feeding, the distribution of patch residence times and the optimum intrapatch foraging speed are also considered as mentioned above (*Comments 8-11*).

This study is technically oriented because a proper introduction and presentation of the IPP predator–prey-encounter theory involves for example both IPP- and H_2-terminology. It also must indicate how and why, e.g. the distributions obtained differ from standard approaches such as the Poisson distribution or the negative binomial distribution. Such explanations and interpretations, which in principle can be considered independently of the main flow of the paper, are collected in *Comments 1-7*. It is, thus, possible and recommended to read the paper in different ways.

Comment 2: The non-Markovian property of the H_2-process

The 'lack of memory' or Markov property constitutes the fundamental property of the exponential distribution (or of the PP). In the context of the encounters between an individual predator and its prey items, the implication of exponentially distributed interarrival times is that whether a long time has passed or just a short period of time since the last encounter, the probability that an encounter will take place during the next small interval of time is constant and proportional to the rate of encounters (see also *Comment 3*). It is this independence of the past, which makes the exponential distribution attractive in its simplicity (and, which explains its many applications because in the limit the PP describes the superposition of many different and independent (but general) point processes (see e.g. Cox & Isham 1980)). The hyperexponential distribution does not possess this property (as will be shown mathematically below), which explains why it becomes more difficult to analyse a H_2-process (cf. *Comment 1*).

Mathematically the Markov property is expressed by the following requirement:

$$P\{X>t+u \mid X>u\} = P\{X>t\}$$

where X denotes the interarrival time and the distribution functions are (obtained by integrating the p.d.f.'s in Eqs 1 and 2),

$$P\{X>t\} = e^{-\lambda_0 t} \qquad ; X \epsilon E_1(\lambda_0)$$

$$P\{X>t\} = p \cdot e^{-\gamma_1 t} + (1-p) \cdot e^{-\gamma_2 t} \qquad ; X \epsilon H_2(p,\gamma_1,\gamma_2) \; .$$

In the exponential case the Markovian requirement is fulfilled because

$$P\{X>t+u \mid X>u\} = P\{X>t+u\} \,/\, P\{X>u\} = e^{-\lambda_0(t+u)} / e^{-\lambda_0 u} = e^{-\lambda_0 t} = P\{X>t\} \; .$$

That is, the remaining (or residual) interarrival time is still exponentially distributed with unchanged intensity, λ_0, in complete independence of the amount of time, u, which is known to have elapsed since the last encounter.

Inserting instead in $P\{X>t+u\} / P\{X>u\}$ the distribution function for H_2 and rearranging yields

$$P\{X>t+u \mid X>u\} = p_u \cdot e^{-\gamma_1 t} + (1-p_u) \cdot e^{-\gamma_2 t}, \qquad p_0 = p$$

where

$$p_u = p \,/\, [\, p + (1-p)\, e^{-(\gamma_2-\gamma_1)u}]$$

so when $\gamma_2 > \gamma_1$ then $p < \underset{\longrightarrow}{p_u} < 1$ as $0 < \underset{\longrightarrow}{u} < \infty$.

If $\gamma_1 > \gamma_2$ the inequality is replaced by $1-p < 1\underset{\longrightarrow}{-p_u} < 1$. As $p_u \neq p$ it follows that the Markov property is not fulfilled but instead

$$P\{X>t+u \mid X>u\} > P\{X>t\} \qquad ; X \epsilon H_2(p,\gamma_1,\gamma_2) \; .$$

A probabilistic interpretation of this result (which is valid also for hyperexponential distributions with more than two phases (Nielsen 1988)) is related to considering H_2 as a compound distribution, i.e. p represents the prior probability for selection of the (exponential phase with) intensity γ_1. After some time, u, without an encounter the probabilities of selecting the phases (or intensities), change from p and $1-p$ into the weighting factors p_u and $1-p_u$ but the (Markovian) exponential phases do not change (i.e. the intensities, γ_1 and γ_2, remain constant). Thus, the remaining (residual) interarrival time becomes $H_2(p,\gamma_1,\gamma_2)$-distributed and p_u represents the posterior probability for selection of the intensity γ_1. The result states that when some of the interarrival time is known already to have elapsed then this fact increases the probability that the actual exponential distribution (= phase) is governed by the smallest intensity, which again means that the mean residual time is greater than the mean (interencounter) time. The chance of obtaining a very long interarrival time hereby increases. In Figure 4 this H_2-memory effect implies that the p.d.f. of the residual interarrival time is obtained by turning the density about the cross-point (I) towards the γ_2-exponential density (which is memoryless).

As an example, consider a specific encounter as the starting point and suppose the predator does not encounter a prey item during the first unit of time although the mean interarrival time also is 1 time unit. If encounters take place in a Poisson process (see PP-realization in Figure 3) then the interarrival time is governed by the (memoryless) exponential density in Figure 5 and the expected residual interarrival time is also 1 time unit so the expected duration of the entire interval becomes 2 time units. However, if encounters take place, say, in a $H_2(p = 8/11, \gamma_1 = 4, \gamma_2 = 1/3)$-process (see IPP-realization in Figure 3 with p.d.f. in Figure 5, top) the mean interarrival time is still 1 time unit but (with $u = 1$,) $p_1 = 0.064$ so the expected residual interarrival time becomes $0.064 \cdot 1/4 + 0.936 \cdot 3 = 2.82$ and, hence, the expected duration of the entire interval in this case becomes 3.82 (i.e. almost 4 times the average interarrival time, which is twice as long as in the PP-case). The prior probability $p = 0.727$ of encountering the next prey item with the high γ_1-rate has decreased by more than a factor of 10 and this change has occurred only because the interarrival time is known to exceed 1. The maximum effect of this length biased sampling in time (involving a mean residual time of $\gamma_2^{-1} = 3$) has almost been reached because $u = 1$ exceeds the relaxation time, which is $|\gamma_1 - \gamma_2|^{-1}$ or 0.3 (cf. the p_u-formula).

It is important to note that the Markov property of the exponential distribution implies that, in case of PP-encounters, the residual interarrival time (which in the terminology of renewal theory is known as the forward recurrence time) always is exponential distributed with unchanged parameter. Thus, considering PP-encounters with intensity $\lambda = 1$ and sampling a predator at a random point in time, the forward recurrence time (= residual interencounter time = the time until the next prey item would have been encountered had the predator not been sampled) and the backward recurrence time (= the time since the last encounter, which has implications for stomach content studies) are both exponentially distributed with mean 1 time unit. Thus, just as in the above case of knowing that the interencounter time exceeds u time units, the mean length of intervals sampled at random in the PP is also 2 time units, i.e. a bias of 100% compared to $\lambda^{-1} = 1$, the true mean length of the time intervals in the process. However, sampling the non-Markovian H_2-process at a random point in time, the forward and backward recurrence times become also H_2-distributed with intensities γ_1 and γ_2 but with another weighting factor (which is further explained in *Comment 7*),

$$p_{\text{rand}} = p \,/\, [p + (1 - p) \cdot \gamma_1/\gamma_2] = \frac{\dfrac{p}{\gamma_1}}{\dfrac{p}{\gamma_1} + \dfrac{1-p}{\gamma_2}} .$$

That is, p_{rand} is obtained by replacing the factor $\exp(-(\gamma_2 - \gamma_1)u)$ with γ_1/γ_2 in the denominator of the expression for p_u. The distributions become equal, $p_u = p_{\text{rand}}$, only in the special case of $u = (\gamma_1 - \gamma_2)^{-1} \cdot \ln(\gamma_1/\gamma_2)$. Considering again $H_2(p = 8/11, \gamma_1 = 4, \gamma_2 = 1/3)$ yields $p_{\text{rand}} = 8/(8 + 3 \cdot 12) = 2/11$ (i.e. the probability of selecting an interval governed by the largest phase has decreased by a factor of four), which produces a mean (forward or backward) recurrence time of 2.5 time units, i.e. the time intervals associated with random points in time will show a mean length of 5 time units although the true mean interval only is 1 time unit in the underlying H_2-process. This bias of 500% clearly does not disappear by increasing sampling. It simply occurs because a long interval (= interencounter time) is more likely to be sampled than a short interval. In general for a point process, the mean length of the intervals sampled equals the mean interval (= mean interarrival time) raised by a factor of one *plus* the c.v. squared of the interarrival times and, the residual interencounter time likewise is obtained by using half this factor, i.e. in mathematical notation $\mu_{\text{samp}} = \mu(1 + \text{c.v.}^2)$ and $\mu_{\text{res}} = \mu(1 + \text{c.v.}^2)/2$.

The interrupted Poisson process (IPP)

We consider one predator, which is foraging in an environment containing food patches. This implies that at any point in time the predator is characterized by being in one of two possible environmental states, which we label 0 and 1:

state 0: *non-patch (i.e. predator on interpatch travelling)*
state 1: *patch (i.e. predator doing patch residence)*

The process alternates between the two states and the patch model is completed (see Figure 6) by assuming that the predator encounters patches at random at rate ω_2 and that the duration of patch residences is exponentially distributed with mean $1/\omega_1$. The equilibrium probability distribution (see e.g. Cox & Miller 1965) becomes

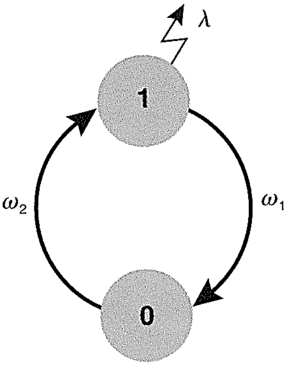


Figure 6. Transition diagram for the interrupted Poisson process (IPP) model unit. The forager encounters prey items in a Poisson process (PP) at rate λ but only while it occupies state 1 (patch). The event 'a prey encounter' represents a transition, which is not associated with a state change. The average patch residence time is $1/\omega_1$, i.e. a transition from state 1 to state 0 (interpatch travelling) occurs with intensity ω_1. In state 0 the forager does not encounter any prey and transition to state 1 occurs with intensity ω_2.

$$\pi_0 = \omega_1/(\omega_1 + \omega_2), \quad \pi_1 = \omega_2/(\omega_1 + \omega_2) \tag{3}$$

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 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.

Comment 3: The patch model foraging unit

The two-state Markov process, which controls the times spent by the individual forager in and outside patches, may be specified by alternating sequences of mutually independent (time interval) random variables, which are exponentially distributed with mean = standard deviation = $1/\omega_i$ ($i = 0{,}1$). An alternative specification of the process is in terms of the actual transitions between the two states. A predator, which at time t is in state 0 (non-patch), encounters a patch in $(t, t + \Delta t)$ with probability $\omega_2 \Delta t$ (hereby neglecting the factor $1 + O(\Delta t)$ because $O(\Delta t)$ vanishes for infinitesimal small Δt), independently of all occurrences before t. Similarly, if state 1 (patch) is occupied, transitions to state 0 occur at the constant rate ω_1. This simple representation of the foraging environment of the predator does not distinguish between specific patches of food particles. In principle food is considered to occur in such patches only. Residence in any of the patch areas simply implies occupancy of state 1 in the model. The parameter ω_2 denotes the rate at which a predator encounters patches. 'Encountering' refers to physical proximity but the operational definition, which is possible in a general study of the IPP model unit, is to consider a patch encounter as the forager is passing the only entrance into the food environment. Thus immediately after a patch encounter the forager is in a position to encounter prey items. A patch encounter in this model does not imply that the forager encounters an individual prey. The forager may actually pass through a patch without encountering any prey items. Thus patch encounter simply means that the patch comes within, for example, the visual range of the forager, which will depend on foraging behaviour, the conspicuousness of the patch, its geometrical properties etc. The rate of encountering patches (as well as the rate of encountering prey items inside patches) clearly depends on the searching behaviour of the predator, the motility of prey and on the passive relative motion of predator–prey caused by, for example, turbulence (Rothschild & Osborn 1988). Principles for simple applications of the IPP model unit are introduced in a later section (see also *Comments 8-11*) but further considerations must be tailored to specific predator–prey cases and considerations beyond 'encountering' (such as responding to encountered prey; attacking; prey escapement; pursuing prey; ingestions) are also outside the scope of this paper. Patch residence times or the point in time at which a predator leaves a patch may likewise be considered as an exponential variate of intensity ω_1.

Considering the dynamics of the process, let $\pi_i(t)$ ($i = 1{,}2$) denote the state probabilities at time t and assuming the initial conditions, $\pi_1(0)$ and $\pi_0(0) = 1 - \pi_1(0)$ to be specified, we obtain (e.g. Cox & Miller 1965),

$$\pi_1(t) = \pi_1 + [\pi_1(0) - \pi_1] \cdot e^{-(\omega_1+\omega_2)t}$$

$$\pi_0(t) = \pi_0 + [\pi_0(0) - \pi_0] \cdot e^{-(\omega_1+\omega_2)t}$$

Thus the relaxation time is $(\omega_1 + \omega_2)^{-1}$, which measures the speed at which the process reaches stationarity (i.e. the probability distribution is governed by π_0 and π_1 independently of the initial conditions).

The forager is considered not to encounter prey items on interpatch travelling. When state 1 (patch) is occupied, the forager encounters prey items in a Poisson process at a constant rate, λ. This completes the prey model and the IPP-model unit is thus specified by the three parameters λ, ω_1, ω_2 (Figure 6).

The IPP process is stochastically equivalent to a H_2 renewal process and the relationship between the parameters is given by (Kuczura 1973)

$$\begin{aligned} \lambda &= p \cdot \gamma_1 + (1 - p) \cdot \gamma_2 \\ \lambda + \omega_1 + \omega_2 &= \gamma_1 + \gamma_2 \\ \lambda \cdot \omega_2 &= \gamma_1 \cdot \gamma_2 \end{aligned} \tag{4}$$

Thus, starting with the IPP specification, the interarrival time becomes H_2-distributed with parameters (p, γ_1, γ_2) (Figure 7) and, hence, with p.d.f. given by Eq. 2. Figure 8 gives a graphical representation in one dimension of this parameter transformation, i.e. through Eq. 4 the figure shows the relationships that p, γ_1 and γ_2 bear to each of the three IPP-parameters (assuming the two other constant). For example, Figure 8 (mid panel) shows that, when the intensity of leaving a patch, ω_1, increases for constant intensities, ω_2 and λ, of encountering patches and prey items inside patches, the largest intensity of the two exponential H_2-phases, γ_1, increases almost linearly but the smaller intensity, γ_2, and p decrease towards zero. In the extreme, $\omega_1 \to \infty$, the forager leaves a patch immediately before having had a chance of encountering a prey item and then spends, on average, $1/\omega_2$ units of time on searching for the next patch. Translated into H_2-terminology, as $\omega_1 \to \infty$ the chance of selecting the first phase vanishes; so although the time required to encounter a prey item through this phase actually becomes very small, $1/\gamma_1 \to 0$, this event is not taking place because of $p \to 0$ and phase 2 is instead chosen with probability 1 but $1/\gamma_2 \to \infty$ so the interencounter time becomes infinitely large.

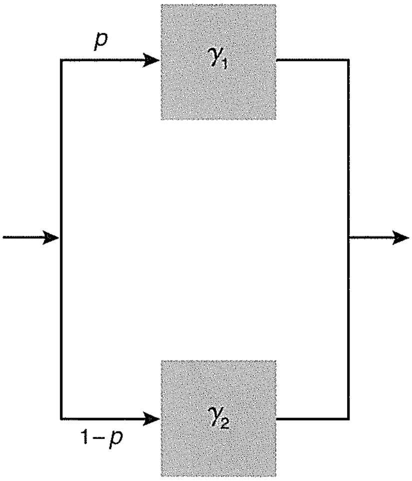
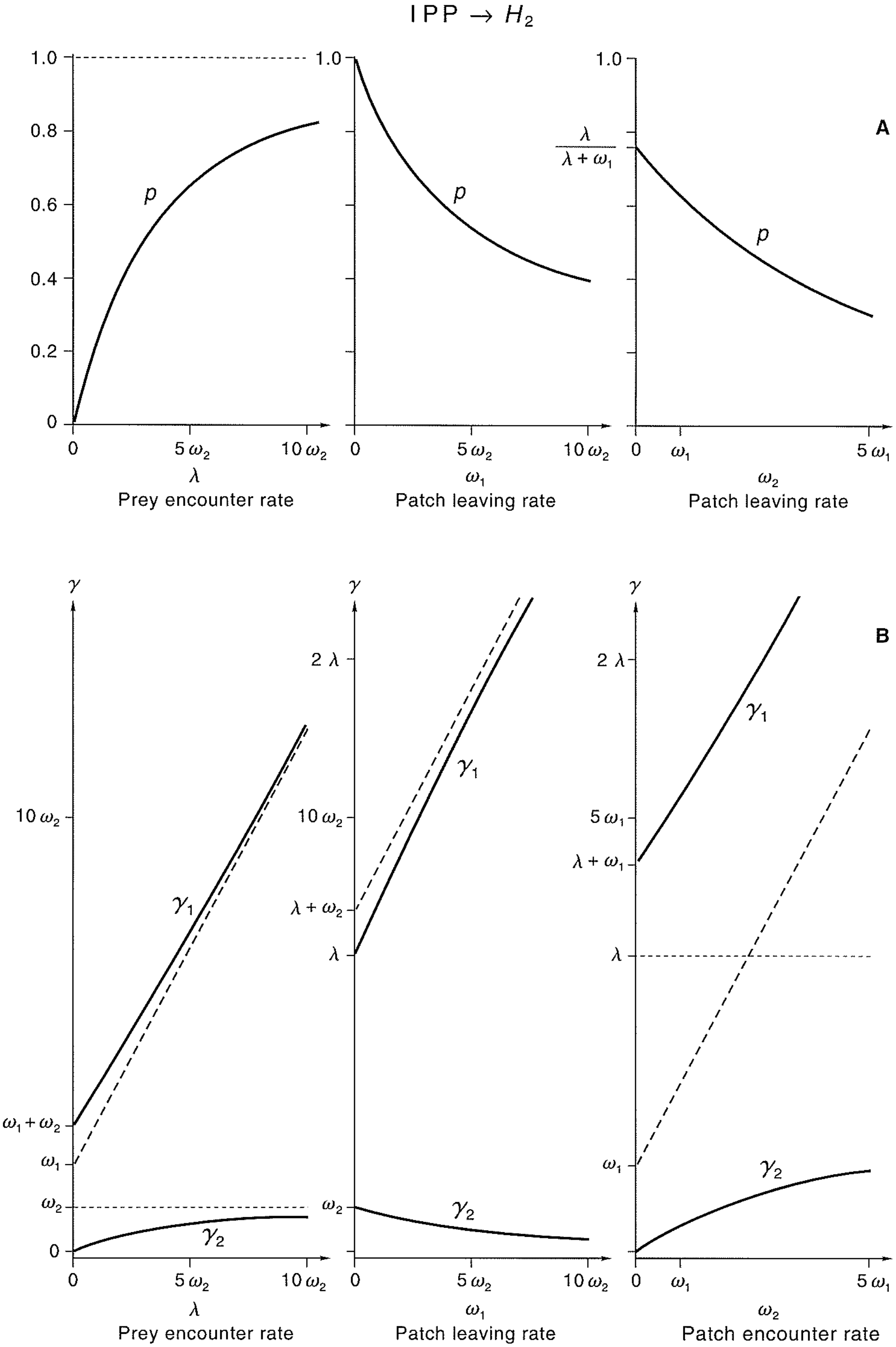


Figure 7. Phase diagram of hyperexponential distribution with two phases (H_2). The exponential phase governed by intensity γ_1 is selected with probability p and, similarly, γ_2 is selected with probability $1-p$. The distribution is therefore also known as the mixed exponential distribution. It governs the interencounter (= interarrival) times in the IPP model unit, i.e. IPP $\to H_2$. In the reverse argument, $H_2 \to$ IPP, a renewal process is defined by a H_2-model. A consistent biological interpretation of the H_2-parameters is as follows: on each prey encounter the forager stays in the patch with probability p (and thus encounter the next prey item at rate γ_1) or it leaves the patch with probability $1-p$ and encounters the next prey item (and, hence the next patch) at rate γ_2.


IPP → H_2
A
1.0
0.8
0.6
0.4
0.2
0
p
0
5 ω_2
10 ω_2
λ
Prey encounter rate
1.0
p
0
5 ω_2
10 ω_2
ω_1
Patch leaving rate
1.0
$\frac{\lambda}{\lambda+\omega_1}$
p
0
ω_1
5 ω_1
ω_2
Patch leaving rate
B
γ
10 ω_2
$\omega_1+\omega_2$
ω_1
ω_2
0
γ_1
γ_2
0
5 ω_2
10 ω_2
λ
Prey encounter rate
γ
2 λ
10 ω_2
$\lambda+\omega_2$
λ
ω_2
γ_1
γ_2
0
5 ω_2
10 ω_2
ω_1
Patch leaving rate
γ
2 λ
5 ω_1
$\lambda+\omega_1$
λ
ω_1
γ_1
γ_2
0
ω_1
5 ω_1
ω_2
Patch encounter rate

Alternatively, a renewal process is specified by $H_2(p, \gamma_1, \gamma_2)$ from which the parameters of the equivalent IPP-process likewise can be obtained through Eq. 4. Starting with the H_2-process specification, Figure 9 shows similarly the relationships that the IPP-parameters bear to each of the H_2-parameters. With reference to Figure 7 we interpret the H_2-renewal process in the following way assuming without loss of generality that $\gamma_1 > \gamma_2$. 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 phase, i.e. the interarrival time is 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) is governed by the second phase, i.e. the interarrival time is exponentially distributed with mean $1/\gamma_2 > 1/\gamma_1$. This interpretation of the H_2-parameters in relation to the interpretation of the IPP-parameters is useful for understanding the IPP-H_2 equivalence shown in Figures 8 and 9. For example, Figure 9A shows how the IPP-parameters depend on p assuming constant γ's. For $p \rightarrow 0$, in the H_2 patch interpretation, a forager leaves with certainty a patch after the first prey encounter and thus encounters prey items in a PP with intensity γ_2. The translation into IPP becomes $\lambda \rightarrow \gamma_2$ and $\omega_1 \rightarrow 0$ because the IPP interpretation now is that the forager stays in a (big) patch in order to be able to encounter prey in a PP at rate $\lambda = \gamma_2$. At the other extreme, $p \rightarrow 1$, the forager stays in a patch and encounters prey in a PP at rate γ_1, which in IPP-terminology again requires $\omega_1 \rightarrow 0$ (and, of course, $\lambda \rightarrow \gamma_1$). This is why the rate of leaving patches ω_1, attains a maximum (at that intermediate value of p for which $\lambda = \omega_2$).

←

Figure 8. IPP → H_2 parameter representation: The equivalent H_2-parameters depicted against each of the input IPP-parameters (assuming the two others constant). A: The dependency of the probability p (dimensionless) of selecting the first exponential phase (of intensity γ_1) on the IPP-parameters (with dimension of TIME^{-1}). It is of note that the patch concept in the interpretation of p as the probability of staying in the patch until the next prey encounter is different from the IPP-patch concept. B: The dependencies of the γ-intensities (with dimension of TIME^{-1}) on the IPP-parameters. The largest γ-intensity, which represents the rate of encountering prey within a patch in the H_2-interpretation, γ_1, bears an almost (= asymptotical as shown) linear increasing relationship to each of the IPP-parameters. The situations refer to the equivalent IPP-parameters for the H_2 case in Figures 3 and 5 (top), i.e. $\lambda = 3$, $\omega_1 = 8/9$ and $\omega_2 = 4/9$. The trends in the relationships can (with some care) be understood intuitively from the interpretations of the parameters. For example, when the rate of encountering patches increases, $\omega_2 \rightarrow \infty$, right panel, the forager locates a new patch immediately and therefore in reality encounters prey in a Poisson process (= PP) at the constant rate λ. This extreme situation is achieved in the H_2-model when the forager on each prey encounter decides with certainty (i.e. $1 - p \rightarrow 1$) to leave the patch and then encounters the next prey (and patch) with intensity $\gamma_2 = \lambda$. Another example (mid panel) is the γ_1-increase when the forager on average leaves a patch before encountering prey (i.e. $\omega_1 \rightarrow \infty$) in which case $\gamma_2 \rightarrow 0$ is selected in almost all cases (i.e. $1 - p \rightarrow 1$). However, in some rare cases the forager, by random chance, will succeed to encounter two prey items during one very short patch residence and such (rare) events are described by the high (but with $p \rightarrow 0$ very seldom) γ_1-rate.

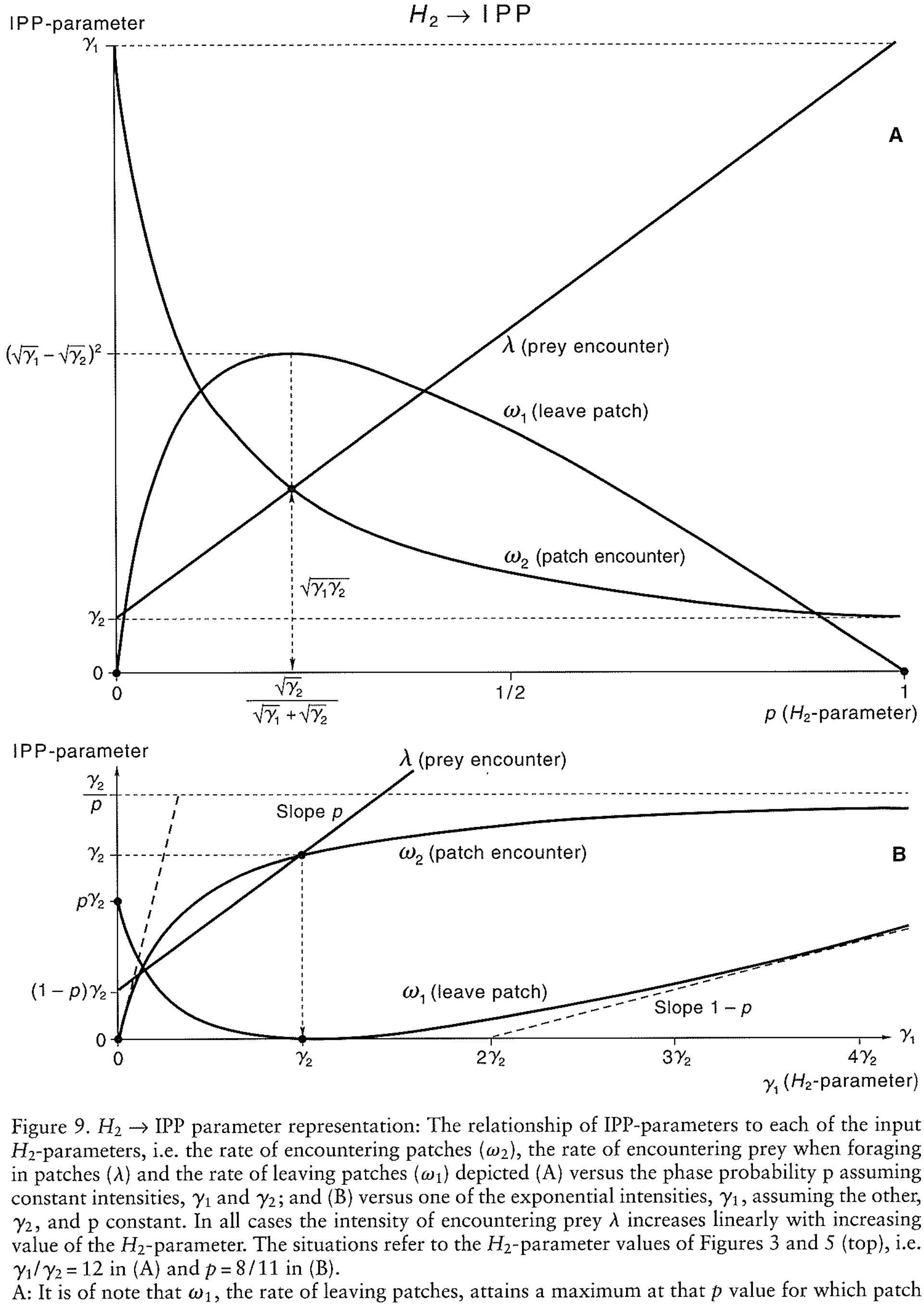


Figure 9. $H_2 \to$ IPP parameter representation: The relationship of IPP-parameters to each of the input H_2-parameters, i.e. the rate of encountering patches (ω_2), the rate of encountering prey when foraging in patches (λ) and the rate of leaving patches (ω_1) depicted (A) versus the phase probability p assuming constant intensities, γ_1 and γ_2; and (B) versus one of the exponential intensities, γ_1, assuming the other, γ_2, and p constant. In all cases the intensity of encountering prey λ increases linearly with increasing value of the H_2-parameter. The situations refer to the H_2-parameter values of Figures 3 and 5 (top), i.e. $\gamma_1/\gamma_2 = 12$ in (A) and $p = 8/11$ in (B).

A: It is of note that ω_1, the rate of leaving patches, attains a maximum at that p value for which patch encounters occur at the same rate as prey encounters (when foraging in a patch), i.e. $\lambda = \omega_2$. Note also that $\lambda \cdot \omega_2$ is constant ($= \gamma_1 \cdot \gamma_2$ independently of p). Identical average sojourn times in and outside patches, $1/\omega_1 = 1/\omega_2$, occurs when $p = p_\omega$ or $p = 1 - p_\omega$ (where $p_\omega = \frac{1}{2}\{1-[1-4\gamma_1/\gamma_2/(\gamma_1/\gamma_2-1)^2]^{\frac{1}{2}}\}$, which

continued next page

Comment 4: Stochastically equivalent prey encounters but biologically different patch encounters and interpretations in the IPP and the H_2-process

In a concrete case, specifying the IPP model unit, Eq. 4 offers an alternative specification in terms of the parameters of the H_2-distribution, which governs the interencounter times in the IPP. Such a *pure* transformation of parameters may be convenient for example in studying the moments and other statistics of the time intervals (= interencounter times). The non-trivial parameter relationships in Eq. 4 may be expressed in several ways and explicit equations for the IPP → H_2 and the H_2 → IPP transformations are given below. However, other expressions may be derived from Eq. 4, which are equally useful such as

$$\begin{aligned} p &= (\lambda - \gamma_2)/(\gamma_1 - \gamma_2) \\ \lambda \cdot \omega_1 &= p(1-p) \cdot (\gamma_1 - \gamma_2)^2 \\ \omega_1 + \omega_2 &= p \cdot \gamma_2 + (1-p) \cdot \gamma_1 \end{aligned}$$

IPP → H_2:

$$p = \frac{1}{2} \cdot \frac{(\lambda - \omega_1 - \omega_2) + \sqrt{(\lambda + \omega_1 + \omega_2)^2 - 4\lambda\omega_2}}{\sqrt{(\lambda + \omega_1 + \omega_2)^2 - 4\lambda\omega_2}}$$

$$\gamma_1 = \tfrac{1}{2}\left[(\lambda + \omega_1 + \omega_2) + \sqrt{(\lambda + \omega_1 + \omega_2)^2 - 4\lambda\omega_2}\right]$$

$$\gamma_2 = \tfrac{1}{2}\left[(\lambda + \omega_1 + \omega_2) - \sqrt{(\lambda + \omega_1 + \omega_2)^2 - 4\lambda\omega_2}\right]$$

H_2 → IPP:

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

$$\omega_1 = \frac{p(1-p)(\gamma_1 - \gamma_2)^2}{p\gamma_1 + (1-p)\gamma_2} = \frac{(\gamma_1 - \gamma_2)^2}{\dfrac{\gamma_1}{1-p} + \dfrac{\gamma_2}{p}}$$

$$\omega_2 = \frac{\gamma_1\gamma_2}{p\gamma_1 + (1-p)\gamma_2} = \frac{1}{\dfrac{p}{\gamma_2} + \dfrac{1-p}{\gamma_1}}\ .$$

---

implies that the forager spends more time in patches than outside patches, $1/\omega_1 > 1/\omega_2$, independently of the value of p if $0.17 = 3 - 2\sqrt{2} < \gamma_1/\gamma_2 < 3 + 2\sqrt{2} = 5.83$).

B: When $\gamma_1 = \gamma_2 = \gamma$ the H_2-process is reduced to an ordinary PP at rate $\gamma = \lambda = \omega_2$ and the rate of leaving patches, ω_1, becomes zero. The symmetry of p about ½ (because of interchanging γ-parameters) implies that the graphs for the IPP-parameters versus the second exponential intensity, γ_2, are similar with p replaced by $1-p$. It is of note that the intensity of encountering patches, ω_2, bears a Michaelis-Menten type of relationship to γ_1 (and, of course, also to γ_2). The asymptotic approach of ω_1 to a straight line is also indicated on the figure. The graph shows the existence of two γ_1-values between which $\omega_1 < \omega_2$. These values at which $\omega_1 = \omega_2$ are $\gamma_1 = \gamma_2 \cdot [1 + 1/2p(1-p) \cdot (1 \pm \sqrt{1 + 4p(1-p)})]$ or 0.145 and 6.90 (not shown) in the present case. Without loss of generality due to γ-symmetri, γ_1 has been selected to represent the largest of the γ-intensities in this study.

In addressing the question on the biological difference between stochastically equivalent IPPs and H_2-processes this comment is devoted to gaining more insight into the processes by analysing Figure 9B and using the H_2-example, which now can be translated into an IPP, i.e.

$$\begin{array}{llcll} & p = 8/11 & & & \lambda = 3 \\ H_2: & \gamma_1 = 4 & & \text{IPP:} & \omega_1 = 8/9 \\ & \gamma_2 = 1/3 & & & \omega_2 = 4/9 \end{array}$$

Starting with the H_2-process the comparison with the equivalent IPP (specified to the right) is instructive. First it is necessary to consider the basis and the suggested biological interpretation (see Figure 7) of the two types of intervals. Type 2 intervals, which are selected with probability $1 - p = 0.27$, are on average $\gamma_1/\gamma_2 = 12$ times longer than type 1 intervals. The occurrence of such a type 2 interval means that the forager has entered a patch by encountering a prey item in this patch. The concept of patch encounters is not considered explicitly in the H_2 interpretation. A type-2 interval in reality contains three subperiods; one for time spent on actually leaving the patch (since the last prey encounter), an intermediate one for interpatch travel and, one for entering the new patch (until first prey encounter). As an example, the actual series of interval types underlying the realization of the H_2-process or of the IPP in Figure 3 is,

$$\overbrace{2\ 1}\ \underbrace{2\ 1\ 1\ 1\ 1\ 1\ 1\ 1}\ \overbrace{2\ 1}\ \underbrace{2\ 1\ 1\ 1\ 1\ 1\ 1}\ \overbrace{2\ 1\ 1}\ \underbrace{2\ 1\ 1}$$

where ‘1’ refers to a time interval (and, hence, a prey encounter) generated by the phase γ_1 and, similarly, ‘2’ to phase γ_2. Square brackets indicate individual patch residences each starting somewhere in a 2-interval (i.e. the ‘2’ represents the first prey encountered during a patch residence) and ending somewhere in the beginning of the next 2-interval (i.e. the last ‘1’ before this next ‘2’ represents the last prey encounter). The simulation in Figure 3 was generated in this way, i.e. first drawing the type of the interval and secondly, the time for its exponential duration. The important point is that the H_2-process and the IPP are stochastically equivalent because the point processes of *prey* encountering (Figure 3) are identical (being governed by the same renewal process). But the processes are biologically different with respect to the interpretation of encountering *patchy* distributed prey. For example, foraging in a patch, the predator encounters on average $\gamma_1 = 4$ prey items per time unit in the H_2 interpretation but only $\lambda = 3$ items in the IPP interpretation. A realization of the interval types (such as the one shown above) can not be translated into a realization of state ‘0’ (non-patch) and state ‘1’ (patch) occupancies for the IPP. Figure 9B illustrates this point because when γ_1 increases, the above ‘1 and 2’ interval series continues to represent a realization of the H_2-phase process (being governed entirely by p, which remains constant) but the patch interpretation in the associated IPP changes drastically at the same time. For example, (reducing γ_1 by, e.g. a factor of 10), $\gamma_1 \approx \gamma_2$ implies $\omega_1 \approx 0$ and $\lambda \approx \omega_2 \approx \gamma_2$ so in the IPP, the forager stays in a patch and encounters prey at rate γ_2. With increasing γ_1, the length of time intervals of type 1 (and, hence, the patch residence time in the H_2 interpretation) are reduced proportionally. Figure 9B shows that the average patch residence time in the equivalent IPP, $1/\omega_1$, likewise decreases for increasing γ_1. When $\omega_1 = \omega_2$, which occurs for $\gamma_1 = \gamma_2 \cdot [1 + 1 / 2p(1-p)\ (1 + \sqrt{1 + 4p(1-p)})]$, the c.v. (or index of dispersion) of the prey interencounter time attains a maximum (see *Comment 5*). When γ_1 continues to increase (beyond the present case, which produces $\omega_1 = 2\omega_2$), then $\lambda \approx p\gamma_1$, $\omega_1 \approx (1-p)\gamma_1$ but, the intensity of encountering patches, ω_2, only increases slightly (which makes sense because γ_2 is constant) towards γ_2/p. That the average patch residence time, $1/\omega_1$, approaches $1/(1-p)\gamma_1$ can be explained by the series of type '1 and 2' intervals in the following way. The number of (consecutive) 1-intervals during a patch residence is geometrically distributed (i.e. probability of i 1-intervals $= p^i(1-p)$; $i = 0,1,\ldots$) with mean $p/(1-p)$. The mean number of prey items encountered during a patch residence is this number plus the first prey encountered, i.e. $1 + p/(1-p) = 1/(1-p)$. Multiplying with the average length of a 1-interval, $1/\gamma_1$, gives the asymptotic expression for the average patch residence time, $1/\omega_1$, which again indicates the equivalence between the two patch interpretations but only in the extreme cases.

The mean and the variance of the interencounter time are obtained in the standard procedure (e.g. Rothschild 1991) and using the p.d.f. of the H_2-distribution in Eq. 2 the results become

$$E(X) = \frac{p}{\gamma_1} + \frac{1-p}{\gamma_2} = \frac{1}{\lambda} \cdot \left(\frac{\omega_1 + \omega_2}{\omega_2}\right) \tag{5}$$

$$V(X) = 2 \cdot \left(\frac{p}{\gamma_1^2} + \frac{1-p}{\gamma_2^2}\right) - \left(\frac{p}{\gamma_1} + \frac{1-p}{\gamma_2}\right)^2 = \frac{1}{\lambda^2} \cdot \left(\frac{2\lambda\omega_1}{\omega_2^2} + \left(\frac{\omega_1 + \omega_2}{\omega_2}\right)^2\right). \tag{6}$$

Dividing the variance by the mean squared gives the coefficient of variation squared of the interencounter times, $[\text{c.v.}(X)]^2$, which constitutes an index of dispersion (*ID*) for the time intervals,

$$ID = 1 + 2p(1-p)\left(\frac{\gamma_1 - \gamma_2}{p\gamma_2 + (1-p)\gamma_1}\right)^2 = 1 + \frac{2\lambda\omega_1}{(\omega_1 + \omega_2)^2} \quad (= IDC_\infty)\ . \tag{7}$$

In a renewal process this $ID = [\text{c.v.}(X)]^2$ becomes equal to the asymptotic index of dispersion for counts (e.g. Cox & Isham 1980), IDC_∞, which is considered in the section on the counting process. For this reason it is convenient to introduce the *IDC* terminology and IDC_∞ is considered the appropriate measure of functional heterogeneity in this study.

In considering the dispersion index as a function of the IPP-parameters, using the last expression in Eq. 7, it is of note that IDC_∞ increases linearly with λ, the intensity of encountering prey within patches, assuming constant intensities of encountering and leaving patches. This trend is expected because whether an increase in λ is caused by an increase in prey density and/or, for example, by higher relative velocity of predator and prey (Rothschild & Osborn 1988), the result is a greater contrast in the prey environment perceived by the forager per unit of time and, hence, larger functional heterogeneity. If, however, the density of patches increases and/or the relative velocity between forager and patches increases, the intensity of encountering patches, ω_2, likewise increases (assuming constant intensities of encountering prey inside patches and of leaving them) but, then functional heterogeneity will decrease. This decrease in dispersion index happens because the forager spends less time on interpatch travelling and thus encounters a more and more homogeneous prey environment as ω_2 increases. Finally, assuming constant rates of encountering patches and of prey within patches, the forager stays in a patch if $\omega_1 = 0$ and, hence, encounters prey in a non-patchy PP resulting in the minimum value of one for the dispersion index. At the other extreme, $\omega_1 \to \infty$, the forager spends all the time outside patches and the dispersion index again becomes one (i.e. encountering prey in a PP at rate zero). Figure 10 shows that the dispersion index attains the maximum at the balance point in the rates of encountering and leaving patches, $\omega = \omega_1 = \omega_2$. This maximum increase in dispersion equals $\frac{1}{2}\lambda/\omega$ so, for example, everything equal, fewer but more dense patches gives rise to much higher functional heterogeneity if the forager on average spends equal amount of time in the patches as on interpatch travelling. The special log-like symmetry of the *IDC*-curve (see Figure 10) implies that exactly the same dispersion index results with an average patch residence time $(1/\omega_1)$ of, say, half or twice the interpatch travelling time $(1/\omega_2)$.

Alternatively, using the first expression in Eq. 7, Figure 11 shows the situations when the dispersion index is considered a function of the H_2-parameters. For constant phase intensities, the forager encounters prey in PP's when the same phase always is selected, and hence the dispersion index in Figure 11A attains its minimum value of 1 at the extremes, $p = 0$ and $p = 1$. Maximum dispersion occurs at $p = \gamma_1/\gamma_2/(1 + \gamma_1/\gamma_2)$ and Figure 11A shows the changes in this maximum for increasing values of the ratio γ_1/γ_2. If instead p and, for example, the smallest phase (γ_2) are constant then *IDC* increases as the largest phase, γ_1, increases. This situation is shown in Figure 11B and it has resemblance to the situation for increasing λ because γ_1, the largest phase denotes the rate of encountering prey items in the H_2-patch interpretation.

Comment 5: Index of dispersion and functional heterogeneity

In this study the term functional heterogeneity refers to the variability in encountering prey items as experienced by the individual forager. Absolute variability of interencounter times as measured by, e.g. $V(X)$ or $\text{Stdv}(X) = \sqrt{V(X)}$ must be considered relative to the mean interencounter time, $E(X)$, to obtain a relative (dimensionless) index, which is why the coefficient of variation, $\text{c.v.}(X) = \text{Stdv}(X)/E(X)$ is useful for the present purpose of quantifying various degrees of patchy encounters (i.e. $\text{c.v.}(X) > 1$) compared to random encoun-

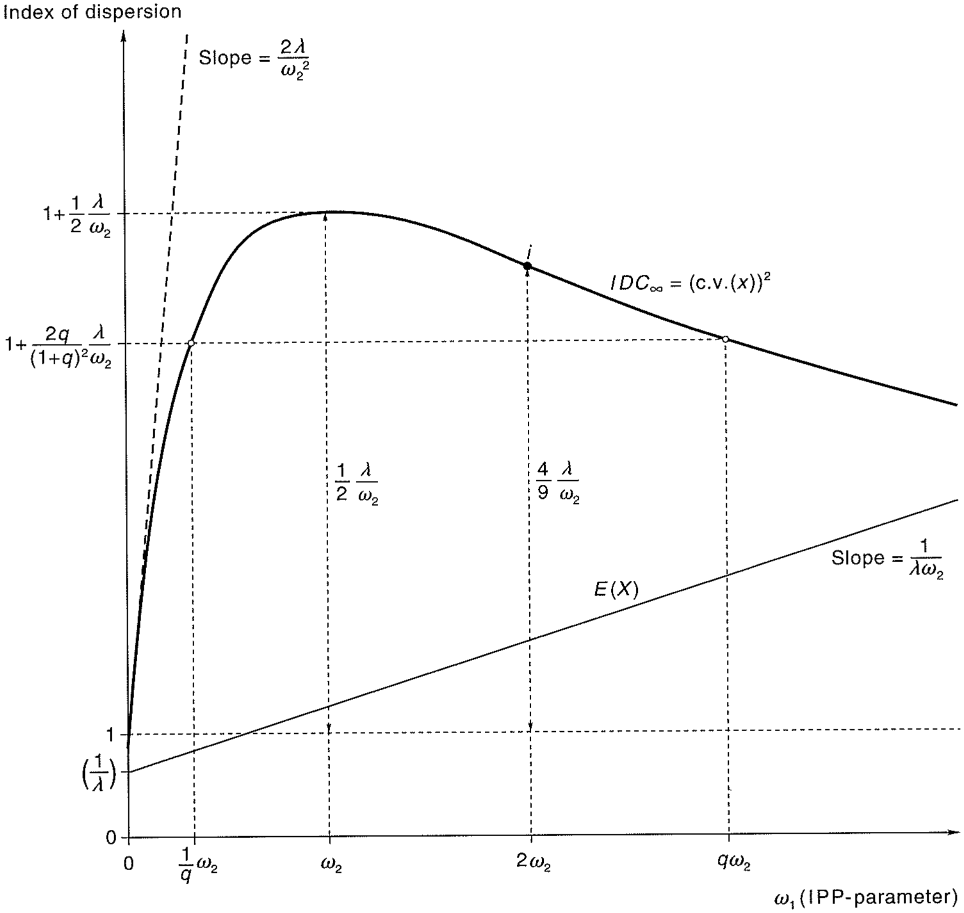
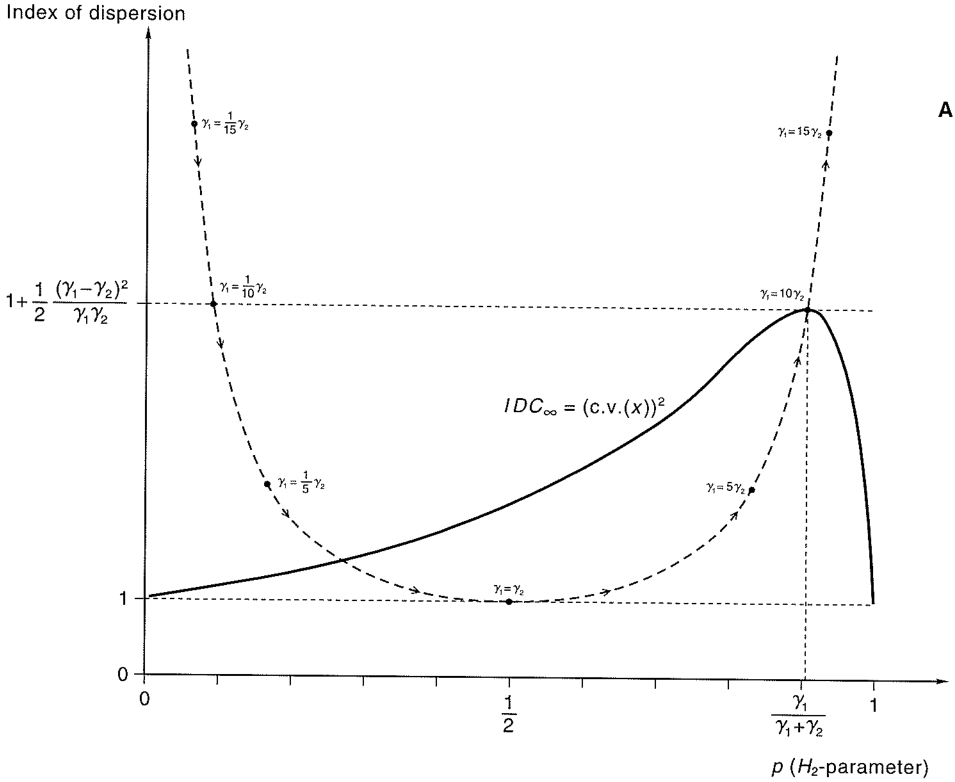
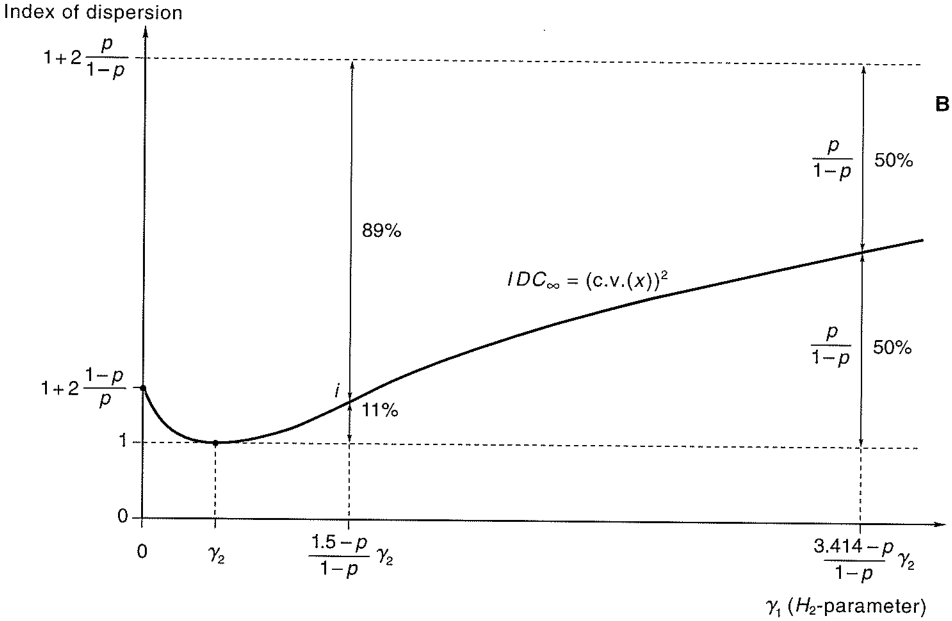


Figure 10. The coefficient of variation squared or the index of dispersion of the interencounter time in the IPP depicted against the intensity of leaving a patch, ω_1, for fixed intensities of encountering patches (ω_2) and of encountering prey items in a patch (λ). The index equals the asymptotic index of dispersion for counts, which is denoted by IDC_∞. This measure of functional heterogeneity attains a maximum with equal rates of encountering and leaving patches. The maximum value is determined by the rate ratio of encountering prey items in a patch to encountering patches. The index of dispersion approaches the minimum value of 1 for the Poisson process at the extremes. Log-like curve symmetry about $\omega_1 = \omega_2$ and, the point of inflexion for $\omega_1 = 2\omega_2$ are indicated. For relative comparison the linear course of the mean interencounter time, $E(X)$, is shown (although the position of its intercept, $1/\lambda$, is arbitrary because of different dimensions (i.e. TIME versus the dimensionless IDC)).

ters (i.e., c.v.$(X) = 1$). We choose to use the standard deviation to mean ratio squared because it equals IDC_∞, the index of dispersion for counts defined as the (asymptotic) variance to mean ratio for the counting process (as discussed in next section). In case of random encounters (i.e. PP) the number of encounters (counts) during a fixed period of time is Poisson-distributed, i.e. with a variance to mean ratio, $IDC(t) = 1$ independently of t. Other indices of vari-


Index of dispersion
A
$\gamma_1 = \frac{1}{15}\gamma_2$
$\gamma_1 = \frac{1}{10}\gamma_2$
$\gamma_1 = \frac{1}{5}\gamma_2$
$\gamma_1 = \gamma_2$
$\gamma_1 = 5\gamma_2$
$\gamma_1 = 10\gamma_2$
$\gamma_1 = 15\gamma_2$
$1 + \frac{1}{2}\frac{(\gamma_1 - \gamma_2)^2}{\gamma_1\gamma_2}$
$IDC_\infty = (\text{c.v.}(x))^2$
1
0
0
$\frac{1}{2}$
$\frac{\gamma_1}{\gamma_1+\gamma_2}$
1
p (H_2-parameter)


Index of dispersion
B
$1+2\frac{p}{1-p}$
$\frac{p}{1-p}$
50%
89%
$IDC_\infty = (\text{c.v.}(x))^2$
$\frac{p}{1-p}$
50%
$1+2\frac{1-p}{p}$
i
11%
1
0
0
γ_2
$\frac{1.5-p}{1-p}\gamma_2$
$\frac{3.414-p}{1-p}\gamma_2$
γ_1 (H_2-parameter)

ability will not be considered or discussed in this study (see Elliott 1977 for a basic introduction to contagious distributions and frequently used indices of variability).

The rest of this comment is devoted first to interpretations of the mean and the variance of the interencounter time in the IPP, $E(X)$ and $V(X)$, in comparison to in the PP. Secondly, Figures 10 and 11 on $IDC_\infty = V(X)/[E(X)]^2 = [\text{c.v.}(X)]^2$ versus one of the parameters (assuming the two others constant) are further exemplified and, supplemented with considerations of IDC_∞ versus one of the IPP-parameters assuming constant mean interencounter time, $E(X)$, (and that, only one of the remaining two IPP-parameters is constant).

The mean interencounter time in Eq. 5 can be obtained directly as $E(X) = 1/(\lambda\pi_1)$ because $\lambda\pi_1$ denotes the intensity in a randomly diluted PP (π_1 being the fraction of time the forager spends in patches during which it encounters prey items in a PP at rate λ).

The variance in Eq. 6 may be expressed as the mean squared plus a contribution, which accounts for how much the hyperexponential distribution deviates from the exponential distribution

$$V(X) = [E(X)]^2 + 2 \cdot \omega_1 / \lambda\omega_2^2 = [E(X)]^2 + 2p(1-p) \cdot (1/\gamma_1 - 1/\gamma_2)^2 .$$

If $\gamma_1 = \gamma_2$ (or $\omega_1 = 0$ see Figure 9B) the second term vanishes and $V(X) = [E(X)]^2$ or $\text{c.v.}^2 = 1$ because the H_2-distribution becomes an exponential distribution (or the IPP becomes a PP). For fixed γ's the maximum deviation from the exponential case (which occurs for $p=0$ and $p=1$) takes place for $p = \gamma_1/(\gamma_1 + \gamma_2)$. For this value of p both phases have the same contribution to the mean. The deviation is also proportional to the difference in phase means squared. In the example $p = 8/11$, $1/\gamma_1 = 1/4$ and $1/\gamma_2 = 3$ (or $\lambda = 3$ and $\omega_1 = 2\omega_2 = 8/9$), $E(X) = 1$ and the additional contribution to the variance becomes 3.

IDC tails off slowly for increasing ω_1, see Figure 10. The decrease is 25% at $\omega_1 = 3\omega_2$ and the 50% point is reached at $\omega_1 = (3 + 2\sqrt{2})\,\omega_2$ or when the aver-

←

Figure 11. The coefficient of variation squared or the index of dispersion of the interencounter time in the H_2-renewal process (stochastically = IPP) depicted against one of the H_2-parameters for the two other fixed. This index, which is a measure of functional heterogeneity, equals the asymptotic index of dispersion for counts denoted by IDC_∞.

A: the index attains a maximum as a function of p, the probability of selecting the exponential phase with intensity γ_1. The maximum is attained at a point where the two phases have the same contribution to the mean. The minimum value of 1, which governs the Poisson cases for the extreme values of p, is fixed and the γ-dynamics of the maximum is shown by the stipled curve. When $\gamma_1 = \gamma_2$, prey items are encountered in a Poisson process and the dispersion index becomes 1 for all values of p. The symmetry about $p = \frac{1}{2}$ (associated with interchanging γ-parameters) is indicated by the movements of the maximum.

B: for increasing γ_1 the dispersion index approaches an asymptotic value, which is the maximum for $p > \frac{1}{2}$ (e.g. the graph reflects the situation for $p = 8/11$). The asymptotic approach is slow; the inflexion point and the 50%-point are shown and specified. For decreasing values of p, the left part of the curve (i.e. for $\gamma_1 < \gamma_2$) would move up (higher index) and the right part (i.e. for $\gamma_1 > \gamma_2$) would move down, but, maintaining the minimum of 1 for $\gamma_1 = \gamma_2$. For $p = \frac{1}{2}$ the extremes coincides (i.e. the index becomes 3 both for $\gamma_1 = 0$ and for $\gamma_1 \to \infty$). This is just another way of showing the symmetry, i.e. the γ's can be interchanged by replacing p with $1-p$. In this study we assume for simplicity that $\gamma_1 > \gamma_2$.

age patch residence time, $1/\omega_1$, is reduced to $(3 - 2\sqrt{2}) \cdot 1/\omega_2$ or 17% of the mean interpatch travel time. In the example $\omega_1^{-1} = {}^1\!/_2\, \omega_2^{-1}$, which coincides with the inflexion point of the curve, and $IDC_\infty = 1 + 4/9 \cdot \lambda\, \omega_2^{-1}$ or 4 (with $\lambda = 3$ and $\omega_2 = 4/9$). The maximum IDC_∞ for $\omega_1^{-1} = \omega_2^{-1}$ becomes 4.375. The example case $\omega_1^{-1} = {}^1\!/_2\, \omega_2^{-1}$ and the case of $\omega_1^{-1} = 2\omega_2^{-1}$ both have $IDC_\infty = 4$ or c.v. = 2 but the mean interencounter time, $E(X)$, decreases from 1 to ${}^1\!/_2$. With increasing intensity of encountering prey, λ, IDC_∞ also increases but $E(X)$ decreases. If, for example, λ increases by a factor of 10 from $\lambda = 10\, \omega_2$ as on Figure 10 to $\lambda = 100\omega_2$ (e.g. denser patches) then the maximum dispersion also increases almost by a factor of 10. Figure 10 is also representative for this situation if the unit level for IDC and the slope of the $E(X)$-line both are reduced by a factor of 10.

The maximum of IDC_∞ on Figure 10 for $\omega_1 = \omega_2$, assuming λ and ω_2 constant, is different from the maximum of IDC_∞ on Figure 11A, assuming constant γ's. In the example the maximum on Figure 11A becomes 6.04 and occurs at $p = 12/13$. Considering instead p and γ_2 constant, the asymptotic maximum of IDC_∞ on Figure 11B for increasing γ_1 becomes 6.33. It is of note that the H_2-distribution of the prey interencounter times for $\gamma_1 \rightarrow \infty$ has $IDC_\infty = (1 + p)/(1 - p)$ and degenerates towards an atom in zero with probability mass p and, for interencounter times >0, the unchanged exponential density (for the second phase) with mean $1/\gamma_2$.

It is instructive to consider the dispersion index for constant mean interencounter time, i.e. for μ constant in

$$\mu = E(X) = 1/\lambda\ (1 + \omega_1/\omega_2) \qquad \text{or} \qquad \lambda = 1/\mu\ (1 + \omega_1/\omega_2)\ .$$

With the aim of considering the equivalence to Figure 10 of the dependency of IDC_∞ on the rate of leaving patches, ω_1, but with constant λ replaced by constant μ, Eq. 7 is rewritten,

$$IDC_\infty = 1 + 2\omega_1 / \mu^2 \lambda \omega_2^2 = 1 + 2/\mu\omega_2 \cdot \omega_1/\omega_2 \cdot (1 + \omega_1/\omega_2)^{-1}\ .$$

When the rate of leaving patches, ω_1, increases, assuming constant μ and a constant rate of encountering patches (ω_2), the rate of encountering prey in patches, λ, must increase linearly with ω_1 (to keep μ constant) and the dispersion index increases towards an asymptotic value of $1 + 2/\mu\omega_2$, which becomes 5.5 in the example. Alternatively, and perhaps more realistically, suppose μ and λ are constant when ω_1 increases, then the rate of encountering patches must increase in proportion to ω_1 (to keep μ constant), $\omega_2 = \omega_1 /(\mu\lambda - 1)$, and, the dispersion index will decrease,

$$IDC_\infty = 1 + 2\,(1 - 1/\mu\lambda)^2\, \lambda/\omega_1\ .$$

The asymptotic decline towards the minimum value of 1 represents a PP of rate $1/\mu$ because the forager is shifting incredibly fast between state 1 (patch) and state 0 (non-patch) virtually without realizing the patchy environment (i.e. $\omega_1 \rightarrow \infty$ and $\omega_2 \rightarrow \infty$ but with ω_1/ω_2 constant). Translated into H_2-notation, this asymptotic situation is described by $1 - p = 1$, $\gamma_2 = 1/\mu$ (and $p = 0$, $\gamma_1 \rightarrow \infty$).

The counting process

The important variable for potential growth and survival is N_t, the number of prey items a forager encounters during a specific period of time, t, when the process of encountering prey items is governed by an IPP$(\lambda, \omega_1, \omega_2)$ or by the equivalent $H_2(p, \gamma_1, \gamma_2)$ distribution of the interencounter times.

The mean and the variance for the number of counts in the time-stationary process can be obtained from renewal theory (Cox 1962) yielding (e.g. Heffes & Lucantoni 1986),

$$E(N_t) = \frac{\lambda\omega_2}{\omega_1 + \omega_2} \cdot t \tag{8}$$

$$V(N_t) = \frac{\lambda\omega_2 t}{\omega_1 + \omega_2} + \frac{2\lambda^2\omega_1\omega_2 t}{(\omega_1 + \omega_2)^3}\left[1 - \frac{1}{(\omega_1 + \omega_2)t}\left(1 - e^{-(\omega_1+\omega_2)t}\right)\right] \tag{9}$$

and, hence, the variance to mean ratio or the index of dispersion for counts, $IDC(t)$, which is shown graphically in Figure 12 as a function of time,

$$IDC(t) = V(N_t)/E(N_t) = 1 + \frac{2\lambda\omega_1}{(\omega_1 + \omega_2)^2}\left[1 - \frac{1}{(\omega_1 + \omega_2)t}\left(1 - e^{-(\omega_1+\omega_2)t}\right)\right] \tag{10}$$

For t large compared to $(\omega_1 + \omega_2)^{-1}$ the exponential term vanishes and the approach towards the asymptotic index of dispersion for counts, IDC_∞ in Eq. 7, then becomes

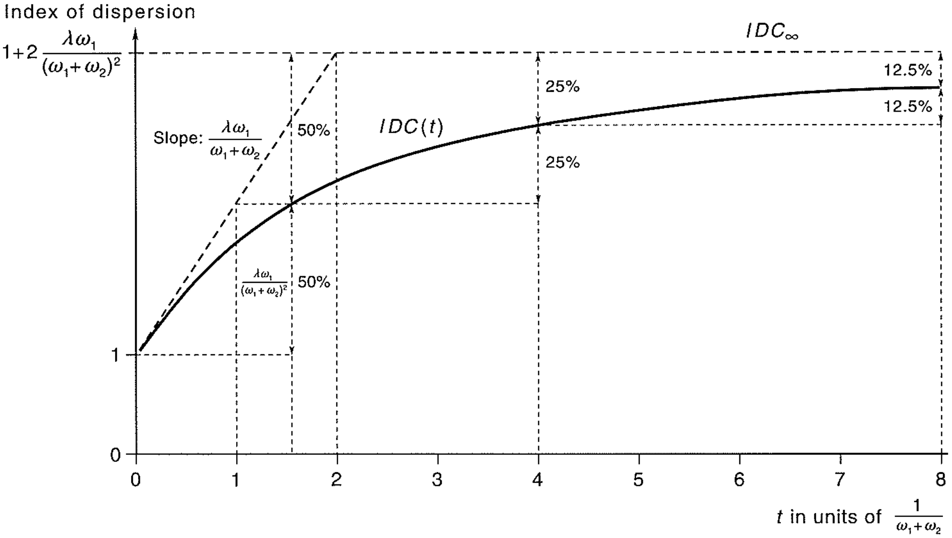


Figure 12. The variance to mean ratio of counts in a period of time, t, or $IDC(t)$, the index of dispersion for counts depicted as a function of time in the time-stationary IPP. The dispersion index increases towards an asymptotic value, IDC_∞. The difference between this maximum and the actual IDC diminishes inversely proportional to time, i.e. to ca. 3 decimal places, $IDC(t) = IDC_\infty - 2\lambda\omega_1/[(\omega_1 + \omega_2)^3 t]$ when $t \geq 5/(\omega_1 + \omega_2)$. The relationships between IDC_∞ and each of the IPP or H_2-parameters are shown in Figures 10 and 11. The graph refers to the example, i.e. IPP$(\lambda = 3$, $\omega_1 = 8/9$ and $\omega_2 = 4/9)$.

inversely proportional to t, i.e.

$$IDC(t) \cong IDC_\infty - \frac{2\lambda\omega_1}{(\omega_1+\omega_2)^3} \cdot \frac{1}{t} \;; \qquad t \gg \frac{1}{\omega_1+\omega_2} \tag{11}$$

where the IDC_∞-relationships, which the maximum bears to each of the IPP or the H_2-parameters, are shown in Figures 10 and 11. The results in Eqs 8-11 refer to the time-stationary situation, i.e. the period of time considered, $(0, t)$, starts at a random point in time. Hence, at time 0 the predator is foraging in a patch with probability $\pi_1 = \omega_2/(\omega_1 + \omega_2)$ or it is travelling interpatch with probability $\pi_0 = \omega_1/(\omega_1 + \omega_2)$. In either case the predator is locally encountering prey in a Poisson process (at rate λ, respectively, 0), which is why the IDC curve in Figure 12 starts at 1 for $t = 0$. The speed of the asymptotic approach is determined by the total intensity of encountering and leaving patches, $\omega_1 + \omega_2$.

If the period of time instead starts exactly at a point in time at which the forager has encountered (a random) prey item then N_t^e refers to the number of counts during a period of time, t, in the so-called event-stationary process. In this case the predator is known to be foraging in a patch at time 0 and $IDC(0) = 1$. The asymptotic approaches for $E_{\text{event}}(N_t^e)$, $V_{\text{event}}(N_t^e)$ and $IDC_{\text{event}}(t)$ will be different compared to Eqs 8-11 but IDC_∞ as given by Eq. 7 is also the asymptotic maximum in the event-stationary process. In the following the more precise notation N_t^e for event-stationary case is assumed understood and N_t is simply used.

Comment 6: Variability in the counting process.

A process is in equilibrium or time-stationary if it has been running a long time before observation starts $(t = 0)$ or if it is being observed from $(t = 0)$ at a random point in time. It follows from equilibrium renewal theory (Cox 1962) that the asymptotic mean number of encounters equals $t/E(X)$ and the asymptotic variance (i.e. Eq. 9 for large t) equals $t \cdot V(X)/[E(X)]^3$ plus a constant where $E(X)$ and $V(X)$ are the mean and the variance of the interencounter times as given by Eqs 5 and 6. This explains that the asymptotic variance to mean ratio of the number of counts (= renewals) becomes equal to the coefficient of variation squared for the interencounter time, i.e. $V(N_t)/E(N_t) \approx V(X)/[E(X)]^2$.

The event-stationary case implies that an encounter has just taken place at time 0. Following the general procedure of Laplace transforming moments in the counting process, which is shown by Cox (1962), decomposing and rearranging, the mean and the variance of the number of counts in this case become

$$E_{\text{event}}(N_t) = \frac{\lambda\omega_2 t}{(\omega_1+\omega_2)} + \frac{\lambda\omega_1}{(\omega_1+\omega_2)^2}\left(1 - e^{-(\omega_1+\omega_2)t}\right)$$

$$\begin{aligned} V_{\text{event}}(N_t) = {} & \frac{\lambda\omega_2 t}{(\omega_1+\omega_2)} + \left(\frac{\lambda\omega_1}{(\omega_1+\omega_2)^2} - \frac{4\lambda^2\omega_1\omega_2}{(\omega_1+\omega_2)^4}\right)\left(1 - e^{-(\omega_1+\omega_2)t}\right) \\ & + \frac{2t\lambda^2\omega_1\omega_2}{(\omega_1+\omega_2)^3}\left(1 - e^{-(\omega_1+\omega_2)t}\right) \\ & + \frac{\omega_1^2\lambda^2}{(\omega_1+\omega_2)^4}\left(1 - 2t(\omega_1+\omega_2)e^{-(\omega_1+\omega_2)t} - e^{-2(\omega_1+\omega_2)t}\right). \end{aligned}$$

In comparing, for example, the means in the two cases it is instructive to consider the expected number of counts in a small interval of time (Δt). In the event-stationary case the important point is that the forager is known to occupy state 1 (patch) at time 0. It does not really matter whether or not an encounter has taken place at time 0 because of the lack of memory property of the exponential interarrival distribution in state 1. Considering a first order approximation the probability of encountering 1 prey item during Δt is $\lambda \Delta t$ or (neglecting the probability of encountering two or more prey items in this small interval of time), $E_{\text{event}}(N_{\Delta t}) = 1 \cdot \lambda \Delta t$, which is the result above (using $1 - \exp(-x) = x$ for x small). In the time-stationary case, Eq. 8, π_1 is the probability of being in state 1 at time 0, and the result becomes similarly $E(N_{\Delta t}) = \pi_1 \lambda \Delta t$.

In the example, $\lambda = 3$ and $\omega_1 = 2\omega_2 = 8/9$ (or $p = 8/11$, $\gamma_1 = 4$ and $\gamma_2 = 1/3$), the mean and variance of the counts in the two cases become

$$\begin{aligned} E(N_t) &= t \\ V(N_t) &= 4t - 9/4\,(1 - e^{-4/3\,t}) \end{aligned}$$

$$\begin{aligned} E_{\text{event}}(N_t) &= t + 3/2\,(1 - e^{-4/3\,t}) \\ V_{\text{event}}(N_t) &= 4t - 3/4 + 3\,e^{-4/3\,t} - 9/4\,e^{-8/3\,t} - 3\,t\,e^{-4/3\,t} \end{aligned}$$

After 5 units of time the exp-terms have virtually vanished so $E_{\text{event}}(N_t) = E(N_t) + 3/2$ and $V_{\text{event}}(N_t) = V(N_t) + 3/2$ for $t > 5$. The probability distributions for the number of counts are shown in Figure 13 in both cases.

The mathematical expression for the exact probability distribution of the number of encounters, N_t, is complicated and cannot be formulated in a simple analytical way as a function of well-known distributions. Figure 13 gives an example of how the distribution develops as time progresses in the time- and the event-stationary cases. The distributions can be regarded as asymptotically normal with mean and variance proportional to time, t, (cf. Eqs 8 and 9 for the time-stationary case) and, the index of dispersion for counts rapidly approaches IDC_∞ as given by Eq. 7 (cf. Figure 12). However, the example in Figure 13 demonstrates that the distributions are considerably skewed and hence do not show resemblance to normal distributions (during the first ca. 20 units of time) although the mean and variance (already after ca. 5 units of time) are almost represented by the asymptotic expressions. In many applications the tail probabilities are of importance and the dynamics of the transient behaviour is then likely to be of more significance than the (asymptotical) normal behaviour. It is difficult to obtain exact expressions for the right tail. However, the left tail, in particular the probability of zero counts, is more easy to handle.

No encounters or the event $\{N_t = 0\}$ occurs if the interencounter time exceeds t, i.e. the event $\{X > t\}$. Using renewal theory (see *Comment 7*) and denoting by $p_i(0,t)$, $(i = 0,1)$, the probability that a forager, which occupies state i at time 0, does not encounter any prey items during the interval of time $(0,t)$, yields,

$$\begin{aligned} p_1(0,t) &= P\{N_t = 0 \mid \text{foraging in patch (state 1) at } t = 0\} \\ &= p \cdot e^{-\gamma_1 t} + (1 - p) \cdot e^{-\gamma_2 t} \end{aligned} \tag{12}$$

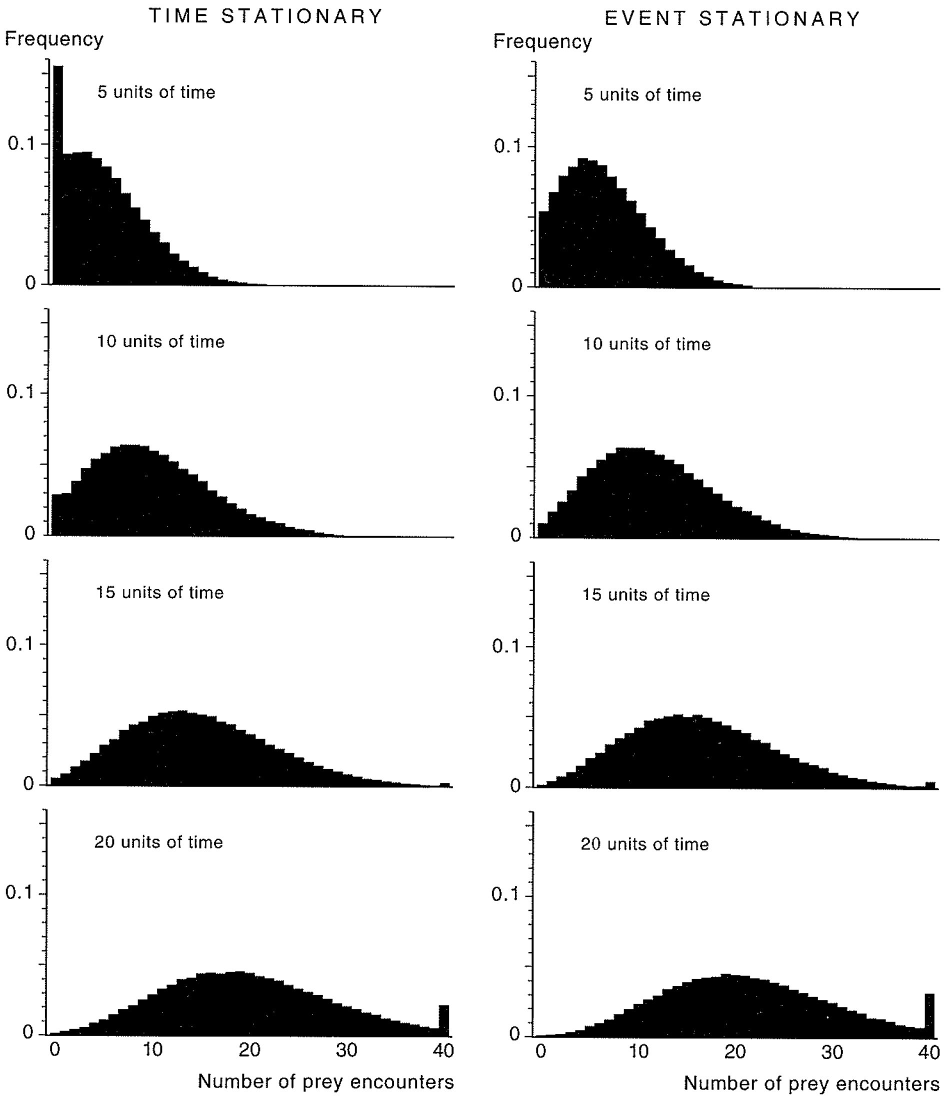


Figure 13. The probability distributions of the total number of prey encounters during 5, 10, 15 and 20 units of time in the stationary IPP($\lambda = 3, \omega_1 = 8/9, \omega_2 = 4/9$) or $H_2(p = 8/11, \gamma_1 = 4, \gamma_2 = 1/3)$ renewal process. The left column refers to the *time*-stationary situation, i.e. the period of time starts at a random point in time. The right column refers to the *event*-stationary situation, i.e. the period of time starts immediately after an encounter has occurred. Thus at time 0 the predator is foraging in a patch in case of the event-stationary distributions. Compared to the case of time-stationary distributions this event of being in a patch implies a smaller probability of not encountering any prey items the effect of which shows up in the first bar for zero counts (and also in the last bar for cumulative counts at 40+). The probability distributions can not be expressed in a simple way analytically and were instead obtained based on simulating 100 000 realizations of the $H_2(p = 8/11, \gamma_1 = 4, \gamma_2 = 1/3)$ process over the period of time in question. As t tends to infinity the distributions are asymptotically normal (Cox 1962).

$$p_0(0,t) = P\{N_t = 0 \mid \text{interpatch travelling (state 0) at } t = 0\}$$

$$= \frac{\gamma_2}{\gamma_2 - \gamma_1} \cdot e^{-\gamma_1 t} + \frac{\gamma_1}{\gamma_1 - \gamma_2} \cdot e^{-\gamma_2 t} \ . \tag{13}$$

The first situation represents the event-stationary case and $p_1(0,t)$ is simply obtained as $P\{X > t\}$ directly from the $H_2(p,\gamma_1,\gamma_2)$ distribution because the lack of memory property of the PP (governing prey encounters in a patch) makes the interencounter time (assuming an encounter at $t = 0$) stochastically equivalent to the residual interencounter time (= forward recurrence time) (assuming being in a patch at $t = 0$ but without an encounter at $t = 0$; see *Comment* 2). If, alternatively, the forager at $t = 0$ is in the interpatch area then, according to Eq. 13, the residual interencounter time is not H_2 distributed because the weighting factor associated with the largest γ-intensity is negative (and, consequently, the other factor exceeds 1 by the same amount). In fact Eq. 13 is the tail probability of a generalized Erlang distribution with intensities γ_1 and γ_2. This distribution occurs when considering sums of independent exponentially distributed random variables (e.g. Cox 1962, Nielsen 1988). Thus it is interesting to note that the probability distributions of the time until the next encounter are governed by the same two exponential variables; in the case of the predator being in the interpatch area at time $t = 0$, it is the sum of these variables (Eq. 13), whereas in the case of the predator being in the patch area at time $t = 0$, it is just one of these variables (Eq. 12) chosen with probability p and $1-p$, respectively. The generalized Erlang distribution is an underdispersed distribution (c.v. < 1) while the H_2 distribution always is overdispersed (c.v. > 1). We have no intuitive biological interpretation of this shift in distributional properties as the conditioning scenario changes, though some analytical insight in the phenomenon can be gained by considering the time until the first encounter as a two-dimensional phase-type distribution (Nielsen 1988, pp. 38-43).

In the time-stationary case the period starts at a random point in time so state i is occupied at $t = 0$ with probability π_i (see Eq. 3) and, hence, $p(0,t) = \pi_1 \cdot p_1(0,t) + \pi_0 \cdot p_0(0,t)$, yielding

$$p(0,t) = P\{N_t = 0 \mid t = 0 \text{ is a random point in time}\}$$

$$= \frac{\dfrac{p}{\gamma_1}}{\dfrac{p}{\gamma_1} + \dfrac{1-p}{\gamma_2}} \cdot e^{-\gamma_1 t} + \frac{\dfrac{1-p}{\gamma_2}}{\dfrac{p}{\gamma_1} + \dfrac{1-p}{\gamma_2}} \cdot e^{-\gamma_2 t} \ . \tag{14}$$

This tail probability, $p(0,t)$, belongs to a H_2-distribution, but the weighting factor associated with the smallest γ-intensity has increased compared to the event-stationary case described by Eq. 12. This implies $p(0,t) > p_1(0,t)$ as reflected by the difference in the first bars (for $N_t = 0$) in Figure 13 (because of the non-Markovian property of the H_2 distribution – see *Comment* 2).

It appears from Eqs 12 and 14 that the probability of zero counts in the IPP in the event and time-stationary cases can be expressed as a probability for zero counts in a mixed Poisson distribution (with parameters $\gamma_1 t$ and $\gamma_2 t$). Unfortunately, this is not true for the probabilities of non-zero counts. Since the time- dependent terms in the expression for $P\{N_t = n\}$ (see *Comment 7*) are the time- dependent terms of the mixed Poisson distribution with parameters $\gamma_1 t$ and $\gamma_2 t$ it is tempting to search for some analogy. Nevertheless, in spite of the inherent analytical equivalence several discrepancies must be noted. First a normal distribution constitutes the limiting distribution of the number of counts in any renewal process with finite mean and variance in the interarrival time distribution. However, the limiting distribution of the mixed Poisson distribution is a mixture of two normal distributions (which will be bimodal when $\gamma_1 t$ and $\gamma_2 t$ are not too close). Secondly, the mixed Poisson distribution and other well-known discrete distributions such as the negative binomial are well suited as models for describing individual random variables. Thus the weighting factor in the mixed Poisson distribution (denoted by u in *Comment 7*) represents the probability of a once for all choice, e.g. considering the prey-encounters of predators, which spend whole life in area with prey density proportional to γ_i (see also *Comment 1* in relation to special (and misleading) γ_i-associated prey density interpretations of the H_2-renewal process). This is in contrast to the IPP or H_2-renewal process where the predator dynamically moves between areas with different prey densities. The mixed Poisson distribution is thus valid as a descriptor of prey encounters in a very limited setting.

Comment 7: The probability distribution of the number of prey encounters in the IPP. In this comment, following some considerations on the conditional distributions of the number of prey encountered, the Laplace transforms of the probability distributions of the (unconditional) counts, N_t, are presented and by decomposing etc., the probabilities of none and of one count are obtained for analytical comparison with the mixed Poisson distribution.

If the predator during the entire period of time $(0,t)$ is known to have been foraging in a patch then it has encountered prey in a Poisson process at rate λ and the total number of counts has been Poisson-distributed with mean λt, i.e.

$$P\{N_t = n \mid \text{non-interrupted patch residence during } (0,t)\}$$
$$= \frac{(\lambda t)^n}{n!} \cdot e^{-\lambda t} \quad ; \qquad n = 0,1,2, \ldots$$

However, being in state 1 (patch), the next event occurs with intensity $\omega_1 + \lambda$ (cf. Figure 6) and the probability that this event is a transition to state 0 (*OFF* = interpatch) is $\omega_1/(\omega_1+\lambda)$ or, alternatively, a prey encounter occurs with probability $\lambda/(\omega_1+\lambda)$. Thus in an interarrival time, the number of times the forager moves from one patch to another patch (i.e. visits state 0) is geometrically distributed with mean ω_1/λ, i.e.

$$P\{i \text{ periods of interpatch travel between two consecutive prey encounters}\}$$
$$= \left(\frac{\omega_1}{\lambda + \omega_1}\right)^i \frac{\lambda}{\lambda + \omega_1} \quad ; \qquad i = 0,1,2, \ldots$$

The average interpatch residence time is $1/\omega_2$ so between two consecutive encounters the forager on average spends $\omega_1/\lambda \cdot 1/\omega_2$ units of time searching for patches. By a similar argument, it follows that the number of prey encountered during one patch residence time is geometrical distributed with mean λ/ω_1 and variance $\lambda(\lambda + \omega_1)/\omega_1{}^2$, i.e.

$$P\{i \text{ prey items encountered during one patch residence}\}$$
$$= \left(\frac{\lambda}{\lambda + \omega_1}\right)^i \frac{\omega_1}{\lambda + \omega_1} \quad ; \qquad i = 0,1,2, \ldots$$

Thus, in a Poisson process the number of counts in a fixed period of time is Poisson-distributed but the number of counts in an exponentially distributed period of time is geometrically distributed (= special case of negative binomial).

Returning to the probability distribution of the unconditional number of counts, N_t, define $\mathrm{P}(n,t)$ as the 2×2 matrix of elements,

$$\mathrm{P}_{ij}(n,t) = \mathrm{P}\{N_t = n \text{ and the forager occupies state } j \text{ at time } t \mid \text{the forager started (at time 0) in state } i\} \quad ; \qquad (i = 0,1;\ j = 0,1)$$

The matrices $\mathrm{P}(n,t)$ satisfy the Chapman-Kolmogorov equations (see e.g. Cox & Miller 1965 for an introduction to the standard procedure) and taking the Laplace transformed yields

$$\mathrm{P}^*(0,s) = \frac{1}{s^2 + s(\lambda + \omega_1 + \omega_2) + \lambda\omega_2} \cdot \begin{bmatrix} s + \omega_2 & \omega_1 \\ \omega_2 & s + \lambda + \omega_1 \end{bmatrix}$$

$$\mathrm{P}^*(n,s) = \frac{\lambda^n (s + \omega_2)^{n-1}}{(s^2 + s(\lambda + \omega_1 + \omega_2) + \lambda\omega_2)^{n+1}} \cdot \begin{bmatrix} (s + \omega_2)^2 & (s + \omega_2)\omega_1 \\ (s + \omega_2)\omega_2 & \omega_1\omega_2 \end{bmatrix} \quad ; \quad n \geq 1$$

where the H_2-parameters (γ_1, γ_2) are the roots in the 2nd degree polynomium in the denominator and P^* denotes the Laplace-transformed, i.e.

$$\mathrm{P}^*(n,s) = \int_0^\infty e^{-st}\,\mathrm{P}(n,t)\,dt$$

For zero counts, $n = 0$, we obtain after decomposing and back-transforming into the time domain,

$$\mathrm{P}(0,t) = \frac{1}{\gamma_2 - \gamma_1} \begin{bmatrix} \omega_2 - \gamma_1 & \omega_1 \\ \omega_2 & \lambda + \omega_1 - \gamma_1 \end{bmatrix} e^{-\gamma_1 t} + \frac{1}{\gamma_1 - \gamma_2} \begin{bmatrix} \omega_2 - \gamma_2 & \omega_1 \\ \omega_2 & \lambda + \omega_1 - \gamma_2 \end{bmatrix} e^{-\gamma_2 t}$$

from which the probabilities of no counts, $p_0(0,t)$ and $p_1(0,t)$, in Eqs 12 and 13 are obtained by adding the columns, i.e.

$p_0(0,t) = \mathrm{P}_{00}(0,t) + \mathrm{P}_{01}(0,t)$, and
$p_1(0,t) = \mathrm{P}_{10}(0,t) + \mathrm{P}_{11}(0,t)$

In the time-stationary process the probability of no counts, $p(0,t) = \pi_0 p_0(0,t) + \pi_1 p_1(0,t)$, in Eq. 14 follows directly from the requirement to a time- stationary (= equilibrium) renewal process, i.e. the p.d.f. of the first forward recurrence time is $[1-F(t)]/\mu$ (e.g. Cox 1962, Cox & Miller 1965) where $1-F(t)$ is the probability that an interencounter time exceeds t, which equals the probability, $p_1(0,t)$, of no counts in the event-stationary process; and $\mu = p/\gamma_1 + (1-p)/\gamma_2$ is the mean interencounter time. This produces a posterior p in the H_2-expression for no counts in the time-stationary process, which becomes $p_{\text{rand}} = p/[p+(1-p)\gamma_1/\gamma_2]$ (see also *Comment* 2).

The situation $\gamma_1 = \gamma_2 = \gamma$ leads to PP-encounters at rate λ implying $p_1(0,t) = p(0,t) = \exp(-\gamma t)$ due to the Markov property of the exponential distribution. However, the situation is different when the forager starts in state 0,

$$p_0(0,t) = (1+\gamma t)\,\mathrm{e}^{-\gamma t} \quad ; \qquad \gamma_1 = \gamma_2 = \gamma,$$

which is the tail probability of a homogeneous Erlang-2 distribution (E_2) obtained from the generalized Erlang-2 as γ_1 and γ_2 tend to be equal.

In principle, following the same procedure as for $n = 0$, decomposing $\mathrm{P}^*(n,s)$ and back transforming into the time domain, yields the probabilities for $N_t = 1, 2, 3 \ldots$, which, however, rapidly become mathematically complicated. The result for $N_t = 1$ count becomes, in the case of an event-stationary IPP,

$$\begin{aligned} p_1(1,t) &= P\{N_t = 1 \,|\, \text{the predator is foraging in a patch at } t = 0\} \\ &= A[\mathrm{e}^{-\gamma_1 t} - \mathrm{e}^{-\gamma_2 t}] + Ct\,\mathrm{e}^{-\gamma_1 t} + Dt\,\mathrm{e}^{-\gamma_2 t} \end{aligned}$$

where

$$A = \frac{\lambda}{(\gamma_1-\gamma_2)^3} \cdot [(\gamma_1-\omega_2)^2 + (\gamma_2-\omega_2)^2 - (\gamma_1-\gamma_2)^2 + \omega_1((\omega_2-\gamma_1)+(\omega_2-\gamma_2))]$$

$$C = \frac{\lambda}{(\gamma_1-\gamma_2)^2} \cdot [(\gamma_1 \sim \omega_2)^2 + \omega_1(\omega_2-\gamma_1)]$$

$$D = \frac{\lambda}{(\gamma_1-\gamma_2)^2} \cdot [(\gamma_2-\omega_2)^2 + \omega_1(\omega_2-\gamma_2)]$$

It is the first term associated with A, which makes the probability of $N_t = 1$ different from the equivalent probability in a mixed Poisson distribution, which consists of the two terms of type $t \cdot \mathrm{e}^{-\gamma t}$:

$$\begin{aligned} &P\{N_t = n \,|\, N_t \text{ is mixed Poisson-distributed } (u, \gamma_1 t, \gamma_2 t)\} \\ &= u \cdot \frac{(\gamma_1 t)^n}{n!}\mathrm{e}^{-\gamma_1 t} + (1-u) \cdot \frac{(\gamma_2 t)^n}{n!}\mathrm{e}^{-\gamma_2 t}\ . \end{aligned}$$

In this mixed Poisson distribution the variance to mean ratio, $IDC_{\text{mix Poisson}}(t)$, bears a linear relationship to time,

$$IDC_{\text{mix Poisson}}(t) = 1 + \frac{u(1-u)(\gamma_1 \sim \gamma_2)^2}{u\gamma_1 + (1 \sim u)\gamma_2} \cdot t\ .$$

Requiring that the mean count, $[u\gamma_1 + (1-u)\gamma_2] \cdot t$, coincides with the mean count in the IPP, which as noted in *Comment* 6 equals $t/E(X)$ where $E(X) = p/\gamma_1 + (1-p)/\gamma_2$, yields $u = p/\gamma_1/E(X)$ and *IDC* takes the form,

$$IDC_{\text{mix Poisson}}(t) = 1 + \frac{\omega_1}{\omega_1 + \omega_2} \cdot \lambda t \quad ; \qquad u = \frac{\dfrac{p}{\gamma_1}}{\dfrac{p}{\gamma_1} + \dfrac{1-p}{\gamma_2}} \; (= p_{\text{rand}})$$

Thus, using the mixed Poisson distribution for counts, which produces the same mean count as in the IPP, implies that the weighting factor becomes equal to the p-weight ratio of the exponential phase means in the IPP (e.g. $u = 2/11$ in the example) and; the *IDC* equals the contribution of 1 from a Poisson distribution plus a term, which equals the mean count had the forager stayed in a patch during all t time units weighted by π_0, the fraction of the time spent on average in the non-patch state. The mixed Poisson distribution in other words generates much more variability in the number of prey encounters than the IPP. In the IPP-example (see Figure 13), IDC_∞ is 4 but $IDC_{\text{mix Poisson}}(t) = 1 + 2t$ and thus has already increased to 11 after 5 units of time. The distributions clearly show considerable differences. At $t = 5$ the unimodal count distribution in IPP (Figure 13, top right) peaks at 4 counts or close to the mean count of 5. In the bimodal mixed Poisson distribution the major peak occurs already at 1 count (26% chance; caused by $\gamma_2 t = 5/3$) but a second, local peak at 20 counts (chance 1.6%; caused by $\gamma_1 t = 20$) creates a long tail. Thus the chance of obtaining extreme counts (i.e. very low or very high compared to the IPP-mean) is much greater in the mixed P-case than in the IPP. The coefficient of variation,

$$\text{c.v.}\,(N_t) = \sqrt{IDC(t)/\text{mean}},$$

which in the IPP diminishes towards zero with increasing time (e.g. c.v. decreases from ca. 0.7 to 0.4 when t increases from 5 to 20; Figure 13), becomes (asymptotically) constant, $\text{c.v.}_\infty = \sqrt{\omega_1/\omega_2} = \sqrt{2}$, in case of the mixed Poisson distribution (e.g. in the example, c.v. decreases from 1.5 to 1.4 when t increases from 5 to 20). The *IDC*'s (and, hence, the c.v.'s) are equal when $t = 2/(\omega_1 + \omega_2)$ (e.g. 1.5 in the present example).

Conceptual example

Principal effects of encountering patchy prey are here considered in a conceptual example with emphasis on simplicity and generality. Focus is placed on functional heterogeneity as measured by *IDC* when the average rate of encountering food organisms is kept constant. The aim is to show that the actual rates of encounters experienced by the individual predators may deviate considerably from the average due exclusively to the aggregation of food particles into patches. As a special aspect of variability, the effect of the position of the predator (i.e. the state occupied = start condition) on the time to encounter the first food organism is also considered. The purpose of the entire section is at the same time to exemplify the concepts of the IPP model unit and thereby to elucidate the biological interpretation of the three IPP-parameters.

The scenario comprises a cruising predator foraging in a large volume of water containing (a specified number of) one type of food organisms. The idea is to compare the variability in encounter rates for the artificial situation in which the food organisms are randomly distributed in the water with situations in which these food organisms instead are more or less aggregated and occur in few big patches or in many small patches. The conceptual link to patch geometry and densities is created by introducing two dimensionless parameters without considering absolute measures of, e.g. patch dimensions (but see *Comments 8 and 9*).

Starting with a non-patch situation (i.e. with the food organisms randomly distributed in space) the predator is supposed to encounter food particles in a Poisson process at a constant rate, λ_0, which is directly proportional to the concentration (density) of food particles. Thus λ_0 is considered a measure of the food density and it constitutes the first of the environmentally related IPP-parameters we are about to introduce. Such a non-patch scenario is depicted in Figure 14A(left). The number of counts during a specific period of time, t, becomes Poisson-distributed with mean = variance = $\lambda_0 t$, and, hence, $IDC = 1$ for all t. As a simplifying assumption we assume that the mean time between consecutive encounters, μ, is directly proportional to the prey density also in the case where the food particles are clustered in patches. This yields the relationship $\mu = 1/\lambda_0$. The assumption also provides us with a framework for a comparison of the randomly distributed case with the case of patchy distributed prey. The first step in creating a patch situation from the non-patch situation consists of concentrating the food particles in a smaller volume of water as illustrated in Figure 14A from left to right. Let η denote this patch volume fraction, i.e. on average one volume-unit of water consists of $1 - \eta$ units of water without food and η units of water, which contains food organism at a η^{-1} times higher density than in the non-patch situation. Thus $\eta = 1$ denotes the non-patch situation and the smaller η the denser the intrapatch concentration of food organisms ($\eta < 1$). Similarly, everything equal, the predator foraging inside a patch will encounter food particles at a rate, which is η^{-1} higher than in the non-patch situation:

$$\lambda = \eta^{-1} \cdot \lambda_0 \quad \text{or} \quad \eta = \lambda_0 / \lambda . \tag{15}$$

The criterion of maintaining the average interencounter time, $\mu = 1/(\lambda \pi_1)$ (or maintaining the average number of encounters, $E(N_t) = \lambda \pi_1 \cdot t$, during a specific period of time, t) is equivalent to assume that the fraction of the sea, η, which is occupied by patches, equals the proportion of time spent by the predator in patches, π_1, i.e.

$$\omega_1 / \omega_2 = \eta^{-1} - 1 \quad \text{if} \quad \eta = \pi_1 . \tag{16}$$

Furthermore assuming non-overlapping patches, the density of patches (= the mean number of patch centres in a volume of water) must be inversely proportional to the average patch volume because their product equals η, which is considered constant. Figure 14B illustrates this variation in patch geometry pertaining to a specific patch volume fraction (η) and, hence, to a specific intrapatch prey density ($\propto \lambda_0$).

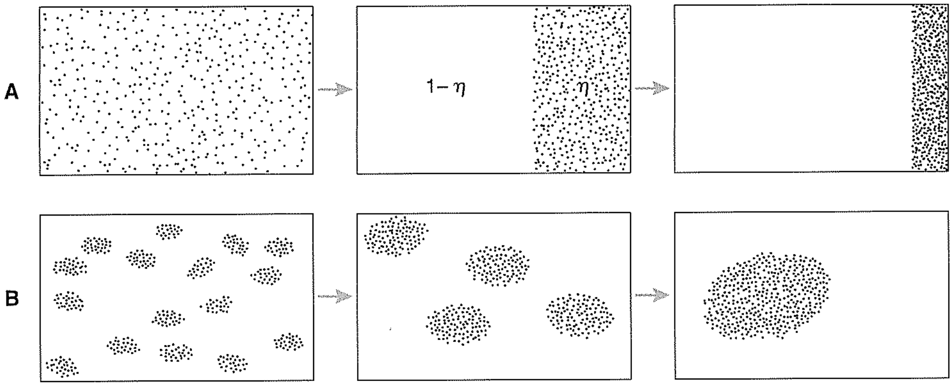


Figure 14. A conceptualization of patchiness simplified to two dimensions. A square represents a volume unit of water in which a prey particle is shown by a dot. The redistribution of prey particles (initially randomly distributed, A, left) in forming aggregations with almost identical patches is considered to take place in two steps. Through conservation of prey mass, the first step (A) links total patch volume to intrapatch prey concentration. The second step likewise links patch concentration to the individual patch volume. Thus, in the top squares (A), the number of prey particles is constant (i.e. constant λ_0; see text) and, moving to the right, these particles are concentrated in a smaller and smaller patch volume fraction of the sea, η. The bottom squares represents a situation for a fixed η (and λ_0) and, moving to the right, this total patch volume comprises fewer but bigger patches (i.e. decreasing ξ; see text).

Everything equal, the rate at which the predator encounters patches, ω_2, is likely to decrease as the situation changes from one of many smaller patches (Figure 14B, left) to one of fewer but bigger patches (Figure 14B: right). Let ξ denote the patch encounter rate relative to λ_0:

$$\omega_2 = \xi \cdot \lambda_0 \quad ; \qquad \xi = \omega_2/\lambda_0 \tag{17}$$

Thus ξ measures the intensity of encountering patches per unit of one average prey interencounter time in the non-patchy case. Alternatively, ξ^{-1} denotes the average number of food organisms the predator encounters in the non-patchy case during an average patch search time.

Comment 8: Specification of the IPP *model unit based on simple encounter theory and patch geometry*

This comment is devoted to an example of deriving the IPP-parameters in relation to the patch scenarios with a cruising predator in Figure 14. Simple encounter theory with spherical patch geometry is used to express the relationships that encounter rates bear to search volume rates and to prey and patch concentrations. For this purpose it is necessary to introduce several new symbols, e.g. for predator speed, prey concentrations and patch dimensions. Emphasis is also put on dimensions using, e.g. cm^3 for volume and s for time. Larval herring is used as an example. Secondly, returning to the environmental parameter representation of the IPP, (λ_0, $\eta = \pi_1$, ξ), the relationships for obtaining the equivalent H_2-parameter set (p, γ_1, γ_2) of the IPP are given together with approximations for extreme cases.

The prey encounter rate in the non-patch case, λ_0 [encounters $\cdot$ s^{-1}], is obtained as the search volume rate, β_{prey} [cm$^3 \cdot$ s^{-1}], multiplied by the prey density, $\rho_{0\,\text{prey}}$ [ind. $\cdot$ cm^{-3}]:

$$\lambda_0 = \beta_{\text{prey}} \cdot \rho_{0\text{prey}} .$$

Denoting by D_{pred} [cm] the perceptive distance of the forager while searching for immobile prey particles with speed $v_{1\,\text{pred}}$ [cm $\cdot\, s^{-1}$] the search volume rate becomes approximately (assuming negligible effects of crossing pathways),

$$\beta_{\text{prey}} = \pi(D_{\text{pred}} + \text{r}_{\text{prey}})^2\, v_{1\,\text{pred}} \approx \pi D_{\text{pred}}{}^2\, v_{1\,\text{pred}}$$

where r_{prey} [cm] is the equivalent spherical radius of the prey particles (= prey size), which usually is small compared to the visual range of the predator, D_{pred}. In a patch scenario the predator, when it is foraging inside a patch, will likewise encounter (per unit time) the prey organisms contained in this β-volume (assuming that its swimming speed and perceptive distance remain almost constant; continuous search, e.g. that refractory periods can be neglected etc.). Thus the rate at which the predator encounters prey particles in a patch becomes approximately

$$\lambda = \beta_{\text{prey}} \cdot \rho_{\text{prey}} \quad ; \qquad \rho_{\text{prey}} = \eta^{-1} \cdot \rho_{0\text{prey}} .$$

The fraction of the sea, η [dimensionless], which is occupied by patches, must equal the concentration of patches, C_{patch} [number of patch centres $\cdot$ cm^{-3}], multiplied by the average patch volume, V_{patch} [cm^3]:

$$\eta = C_{\text{patch}} \cdot V_{\text{patch}} .$$

Considering a patch as a collection of (randomly distributed) prey particles enclosed by a sphere with radius R_{patch} [cm] gives:

$$V_{\text{patch}} = 4/3 \cdot \pi R_{\text{patch}}{}^3$$

and, then

$$C_{\text{patch}} = 3/4 \cdot \pi^{-1} \cdot \eta \cdot R_{\text{patch}}{}^{-3} .$$

Per unit time the predator will encounter the patches in the volume, β_{patch} [cm$^3 \cdot$ s^{-1}], given by:

$$\beta_{\text{patch}} = \pi v_{0\,\text{pred}} \cdot R_{\text{patch}}{}^2$$

where $v_{0\,\text{pred}}$ denotes the swimming speed of the predator when searching for food patches. In this equation it is assumed that a patch encounter requires physical contact between predator and patch sphere perimeter. If the predator is able to perceive the sphere perimeter at distance D, the patch radius, R_{patch}, must be replaced with $D + R_{\text{patch}}$ in the β-kernel above. However, in most cases such a 'patch perceptive distance' is probably small compared to the patch dimensions and the β-kernel will not change. The rate at which the predator encounters patches, ω_2, equals this β-kernel multiplied by the density of patches:

$$\omega_2 = \beta_{\text{patch}} \cdot C_{\text{patch}} = 3/4 \cdot v_{0\text{pred}} \cdot \eta / R_{\text{patch}} .$$

It is of note that ω_2 is proportional to η / R_{patch} where $\eta = \rho_{0\,\text{prey}} / \rho_{\text{prey}}$ may be estimated as the ratio of the average prey density in the sea (sampling over patch and interpatch areas) to the average intrapatch density of prey particles. Basically η measures the fraction of the sea occupied by patches and the relationship states (with constant η) that, prey organisms, for example, can halve their risk of group encounter with predators by aggregating eight times as many in (eight times) fewer and bigger patches (i.e. by doubling R_{patch}).

Assuming that patch centres are randomly distributed in space, patch overlap is not likely to occur when the patch volume fraction (η) is very small because for any patch, the probability of an interpatch centre distance less than $2R_{\text{patch}}$ is $1 - \exp(-8C_{\text{patch}} V_{\text{patch}}) \approx 8\eta$. This expression is based on the cumulative distribution function (c.d.f.) of the nearest neighbour distance, d_{NND}, which is $1 - \exp(-4/3 \cdot \pi d_{\text{NND}}^3 \cdot \rho)$ for randomly distributed particles at density ρ (e.g. Pielou 1969).

The dimensionless measure ξ of the rate of encountering patches per average prey interencounter time $1/\lambda_0$ (in the non-patchy case of Figure 14A (left)) becomes

$$\xi = \omega_2 / \lambda_0 = \frac{3}{4} v_{0\,\text{pred}} \cdot \frac{\eta}{\lambda_0} \cdot \frac{1}{R_{\text{patch}}}$$

where η / λ_0 may be replaced by $1/\lambda$. If η is halved then ω_2, the rate of patch encounters is also halved (because of half as many patches) but λ, the rate of prey encounter doubles (because the intrapatch prey density, ρ_{prey} doubles) so ξ is also halved. Suppose R_{patch} at the same time is halved then ω_2 and ξ remain constant. However, the idea in Figure 14B is to consider patch situations for fixed η, and ξ then decreases (like ω_2) in inverse proportion to increasing patch dimension, R_{patch} (with decreasing number of patches).

In the present case of maintaining a constant average rate of encountering prey, the rate of leaving patches, ω_1, decreases in proportion to the rate of encountering patches (see Eq. 16), which implies that the speed of the predator is the same (whether it is searching for food patches or on intrapatch search for individual prey organisms):

$$\omega_1 = (1 - \eta) \cdot \omega_2 / \eta = 3/4 (1 - \eta)\, v_{\text{pred}} / R_{\text{patch}}$$

where $v_{\text{pred}} = v_{1\,\text{pred}} = v_{0\,\text{pred}}$. For a small patch volume fraction, η, the factor $(1 - \eta)$ vanishes and $1/\omega_1 \approx 4/3 \cdot R_{\text{patch}} / v_{\text{pred}}$, i.e. the average patch residence time equals the time required to move the distance $4/3 \cdot R_{\text{patch}}$. This result and the distribution of patch residence times are derived and discussed further in *Comment 10* (assuming the predators are moving through patches in straight paths). The assumption of no behavioural changes during patch residences (e.g. constant speed $= v_{1\,\text{pred}} = v_{0\,\text{pred}}$) (which is the essence of the requirement $\eta = \pi_1$) is discussed in *Comment 11* and the effect of reducing the speed during patch residences is considered.

As an example consider 1.2 cm herring larvae (ca. 2 weeks old) swimming at $v_{\text{pred}} = 1\ \text{cm} \cdot \text{s}^{-1}$ with a perceptive distance of $D_{\text{pred}} = 1.5$ cm searching for copepod nauplii with $r_{\text{prey}} \approx 0.01$ cm (e.g. Rosenthal & Hempel 1970, Munk &

Kiørboe 1985). The encounter rate kernel becomes $\beta_{\text{prey}} \approx 7\ \text{cm}^3 \cdot \text{s}^{-1}$. According to Munk & Kiørboe (1985) this kernel (of ca. $25\ \text{l} \cdot \text{h}^{-1}$) appears to be 2-3 times too high (e.g. because, according to Rosenthal & Hempel (1970), the perceptive field should only comprise the half-circular field of vision above the head). However, it is only the right order of magnitude, which matters in the present context. Considering the average prey density in the sea to be $\rho_{0\ \text{prey}} = 10^{-4}$ ind. $\cdot\ \text{cm}^{-3}$ (= 0.1 ind. $\cdot\ \text{l}^{-1}$) gives a Poisson prey encounter rate of $\lambda_0 = 7 \times 10^{-4}$ ind. $\cdot\ \text{s}^{-1}$, i.e. with an average interencounter time $(1/\lambda_0)$ of 24 min. The average nearest neighbour distance of these randomly distributed (non-patchy) nauplii is $0.55 \cdot (\rho_{0\ \text{prey}})^{-1/3}$ or ca. 12 cm. Assuming these nauplii aggregates in patches at an intrapatch density of $\rho_{\text{prey}} = 10^{-2}$ ind. $\cdot\ \text{cm}^{-3}$ (= 10 ind. $\cdot\ \text{l}^{-1}$) implies a patch volume fraction of $\eta = 1/100$ and the IPP prey encounter rate increases likewise by a factor of 100, i.e. $\lambda = 7 \cdot 10^{-2}$ ind. $\cdot\ \text{s}^{-1}$ and the average interencounter time $(1/\lambda)$ becomes 14 s as long as the predator remains inside a patch. Hence the average *NND* of the nauplii inside a patch decreases by a factor of $100^{-1/3} \approx 1/5$ and becomes 2.5 cm. A patch radius of $R_{\text{patch}} = 10$ cm or a spherical patch volume of $V_{\text{patch}} = 4200\ \text{cm}^3$ (= 4.2 l) gives a concentration of patches of $C_{\text{patch}} = 2.4 \cdot 10^{-6}$ patches $\cdot\ \text{cm}^{-3}$ (= 2.4 patches $\cdot\ \text{m}^{-3}$) with an average patch *NND* of 41 cm. The rate of encountering patches becomes $\omega_2 = 3/4 \cdot 1 \cdot 0.01 \cdot 1/10 = 0.75 \cdot 10^{-3} \cdot \text{s}^{-1}$ or $2.7 \cdot \text{h}^{-1}$. However, the rate of leaving patches, which is necessary to produce the (non-patch) average interencounter time of 24 min, is $\omega_1 \approx 100\ \omega_2 = 0.075 \cdot \text{s}^{-1}$ giving an average patch residence time of only 13 s. A herring larva encounters on average $\xi = 1$ patches during a 24-min period. The index of dispersion for counts (*IDC*) for this IPP is ca. 3 (see e.g. Eq. 21). Maintaining a patch volume fraction of $\eta = 0.01$ but increasing the patch radius by a factor of 10 (to 1 m) causes the patch volume to increase 1000-fold and, hence, the patch concentration to decrease by a factor of 1000 and consequently, the average patch *NND* to increase by a factor of 10 (to 4 m). The rates of encountering and leaving patches as well as ξ decrease by a factor of 10 and *IDC* becomes 21, which implies a 7-fold increase in the variance of counts (because the mean is constant corresponding to the average interencounter time of 24 min).

If the parameters λ_0, $\eta = \pi_1$ and ξ are known then the IPP- or the H_2-parameters can be obtained as follows:

IPP:

$$\lambda = \lambda_0 / \eta$$

$$\omega_1 = (1 - \eta) \cdot \frac{\xi}{\eta} \lambda_0$$

$$\omega_2 = \xi \cdot \lambda_0$$

H_2:

$$p = \frac{1}{2} \cdot \frac{1 - \xi + \sqrt{(1 + \xi)^2 - 4\xi\eta}}{\sqrt{(1 + \xi)^2 - 4\xi\eta}}$$

$$\gamma_1 = \frac{1}{2} \cdot \frac{\lambda_0}{\eta} \left[(1+\xi) + \sqrt{(1+\xi)^2 - 4\xi\eta}\,\right]$$

$$\gamma_2 = \frac{1}{2} \cdot \frac{\lambda_0}{\eta} \left[(1+\xi) - \sqrt{(1+\xi)^2 - 4\xi\eta}\,\right]$$

which for small η may be linearized as follows:

$$p \approx \frac{1}{1+\xi} \cdot \left(1 + \frac{\eta\xi(1-\xi)}{(1+\xi)^2}\right) \simeq \frac{1}{1+\xi} \quad ; \qquad \eta = \pi_1 \ll 1$$

$$\gamma_1 = \frac{\lambda_0}{\eta}(1+\xi) - \frac{\lambda_0\xi}{1+\xi} \simeq \frac{\lambda_0}{\eta}(1+\xi) \quad ; \qquad \eta = \pi_1 \ll 1$$

$$\gamma_2 = \lambda_0 \cdot \frac{\xi}{1+\xi} \cdot \left(1 + \frac{1}{4} \cdot \frac{\xi\eta}{(1+\xi)^2}\right) \simeq \lambda_0 \cdot \frac{\xi}{1+\xi}\,.$$

Thus as the patch volume fraction decreases (and hence the intrapatch prey concentration increases) p and γ_2 remain more or less constant but γ_1 increases in inverse proportion to η. The last example with $R_{\text{patch}} = 100$ cm is characterized by $\eta = 0.01$ and $\xi = 0.1$ and the approximation above give directly that $p = 0.9$, $\gamma_1 = 110 \cdot \lambda_0$ and $\gamma_2 = \lambda_0/11$.

The parameter set $(\lambda_0, \eta = \pi_1, \xi)$ determines an IPP and represents one way of linking predator behaviour to prey density, patch density and average patch volume. In this IPP assuming time-stationarity the mean counts during t is $\lambda_0 t$ independent of the values of the patch volume fraction, η, and of the patch volume measure, ξ, but the variability in counts will depend on these values. As an example suppose the predator on average encounters $\lambda_0 = 1$ prey per unit of time in case of randomly distributed prey. If these prey organisms are aggregated in patches, which takes up, say, one third of the water volume, $\eta = 1/3$, the (intrapatch) rate of prey encounters becomes $\lambda = 3$ (Eq. 15). Assuming the predator spends one third of the time in patches ($\eta = \pi_1$) implies that it leaves patches at twice the rate it encounters patches, $\omega_1 = 2\,\omega_2$. This yields the example used throughout the text when $\omega_2 = 4/9$, i.e. $(\lambda, \omega_1, \omega_2) = (3, 8/9, 4/9)$ or in the H_2-representation, $(p, \gamma_1, \gamma_2) = (8/11, 4, 1/3)$ (see *Comment* 4), which now is represented by $\lambda_0 = 1$, $\eta = \pi_1 = 1/3$ and $\xi = 4/9$. Figure 5 shows the distribution of interencounter times in this setting. The mean interencounter time is 1 ($= 1/\lambda_0 = 1/(\lambda\pi_1)$). The probability distribution of the numbers of encounters during 5, 10, 15 and 20 units of time are furthermore shown in Figure 13 both for the time-stationary and the event-stationary cases. For small t the distributions differ greatly with respect to the probability of no counts. The mean and the variance in both cases are given in *Comment* 6. As an illustration Figure 3 shows a realization of individual encounters during a small time segment, and, Figure 15 (top) shows the variation in the (cumulated) number of counts during 100 time units in the Poisson process (left) and the IPP (right). Zooming in, Figure 15 also illustrates the variation in counts during 10 time units (mid graphs) and during 1 time unit (bottom graphs). The variation in number of encounters up to time t, which

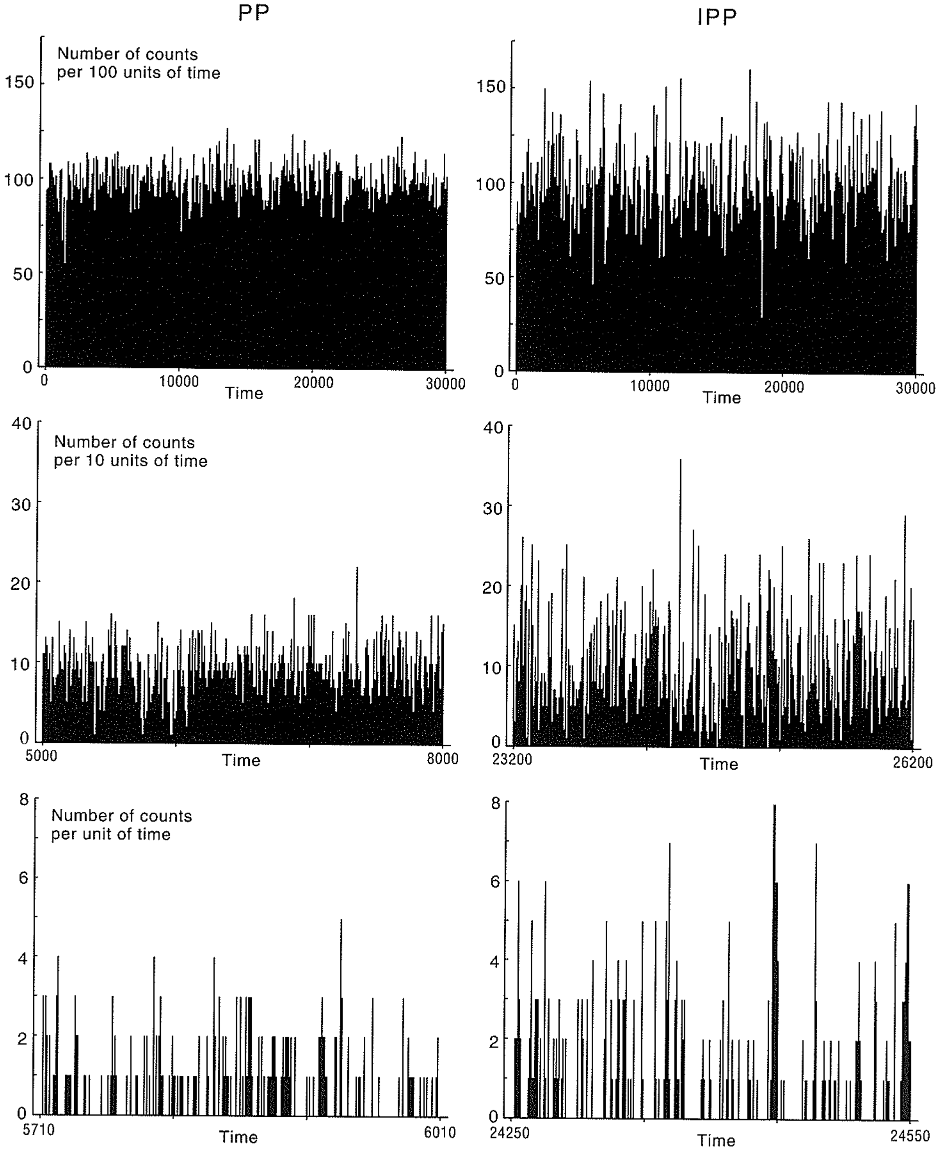


Figure 15. Comparing the variability in number of encounters in realizations of the non-patchy Poisson process (left) with realizations of the patchy IPP or H_2 process (right). The realizations are obtained by simulation. In both cases the mean number of counts is one per unit of time, e.g. in each of the top graphs, 100 encounters is the mean count of each bar in the realizations shown. In the Poisson ($\lambda_0 = 1$) case the number of encounters is Poisson distributed with variance = mean, i.e. with index of dispersion for counts, $IDC = 1$. In the IPP($\lambda = 3$, $\omega_1 = 8/9$, $\omega_2 = 4/9$) or H_2(p = 8/11, $\gamma_1 = 4$, $\gamma_2 = 1/3$) case the variance to mean ratio is ca. $IDC_\infty = 4$ (see Figure 12), which gives rise to higher variability. The graphs below are zooming in, magnifying 10% segments of the graphs above, and showing the variation in the number of counts per 10 time units (mid) and per 1 time unit (bottom). The IPP realization is based on simulation of the H_2-process.

always is higher in the IPP than in the PP, increases with increasing $IDC(t)$, the index of dispersion for counts at time t. $IDC(t)$ is defined as the variance to mean ratio for the counting process, $V(N_t)/E(N_t)$, ($E(N_t) = t$ in this example for the time-stationary case) (see Eqs 8-10), and for large t this ratio approaches a limit, IDC_∞, (as shown in Figure 12 for the present case), which is the same for the time- and event-stationary processes and equals the coefficient of variation squared of the inter-encounter times (see Eqs 5-7), i.e. after a translation into (λ_0, η, ξ)-notation,

$$IDC_\infty = 1 + 2 \cdot \frac{1-\eta}{\xi} \quad ; \qquad \eta = \pi_1 \quad ; \qquad t \gg \frac{\eta}{\xi\lambda_0} \; . \tag{18}$$

The speed at which this approach takes place is determined by a critical time unit, which expresses a balance between η and ξ:

$$t_{\text{crit}} = \frac{1}{\omega_1 + \omega_2} = \frac{\eta}{\xi} \cdot \frac{1}{\lambda_0} \tag{19}$$

or, in the example, $t_{\text{crit}} = (1/3)/(4/9) = 3/4$. Hence $IDC_\infty = 4$ represents the index of dispersion for IPP-counts in Figure 15 (top) and also in Figure 15 (mid) because $t = 10$ is still considerably bigger than t_{crit}. In Figure 15 (top) the expected number of counts during 100 time units is 100 in both cases but in the IPP case IDC is four times greater than in the equivalent Poisson process, i.e. in the IPP the standard deviation of counts, $\text{Stdv}(N_{100}) = [IDC]^{1/2} \cdot [\text{MEAN}]^{1/2} = 20$, is twice the standard deviation for the Poisson case (= $[\text{MEAN}]^{1/2} = 10$). The coefficient of variation for counts likewise is halved from c.v. $(N_{100}) = [IDC/\text{MEAN}]^{1/2} = 0.2$ in the IPP (see end of *Comment* 7) to 0.1 in the Poisson case. Thus, when $IDC \approx IDC_\infty = 2^2$, c.v. for counts in the IPP is twice the c.v. for the Poisson but the absolute value of the c.v. for counts decreases towards zero for increasing t.

For smaller t, IDC must be calculated from the exact expression in Eq. 10, i.e. translated into (λ_0, η, ξ)-notation,

$$\begin{aligned} IDC(t) &= 1 + 2\,\frac{1-\eta}{\xi}\left[1 - \frac{\eta}{\xi\lambda_0 t} \cdot \left(1 - e^{-\frac{\xi}{\eta}\lambda_0 t}\right)\right] \quad ; \qquad \eta = \pi_1 \\ &\approx IDC_\infty - 2\,\frac{(1-\eta)\eta}{\xi^2\lambda_0 t} \quad ; \qquad \eta = \pi_1,\; t \gtrsim \frac{\eta}{\xi} \cdot \frac{5}{\lambda_0} \; . \end{aligned} \tag{20}$$

As the patch volume fraction of the sea decreases (i.e. η is small and λ becomes big), IDC_∞ approaches a maximum, which according to Eq. 18 becomes,

$$IDC_{\max\,\infty} = 1 + 2/\xi \quad ; \qquad \eta = \pi_1 \ll 1 \; . \tag{21}$$

Consider for example the same case as before but with $\eta = 1/10$, i.e. the IPP with parameters $\lambda = 10$, $\omega_2 = \xi = 4/9$ and $\omega_1 = 9\omega_2 = 4$ or the equivalent $H_2(p = 0.7011, \gamma_1 = 14.13, \gamma_2 = 0.3145)$ process. Thus, decreasing the patch volume fraction ca. three times so $\eta = 1/10$, IDC_∞ increases from 4 to $1 + 4.5 \cdot 0.9 = 5.05$, which is close to the maximum dispersion index of 5.5 (with $\xi = 4/9$). Increasing patchiness further by considering fewer but bigger patches, suppose ξ also takes a value of 1/10, IDC_∞ becomes 19, i.e. a variance of counts, which is ca. 5 times higher than for the IPP case shown in Figure 15. The IPP-parameters for this case ($\eta = \xi = 1/10$) are IPP($\lambda = 10, \omega_2 = 0.1, \omega_1 = 0.9$) or $H_2(p = 0.9161, \gamma_1 = 10.91, \gamma_2 = 0.0917)$. Compared to the IPP-situation in Figure 15 (top), the standard deviation of counts more than doubles and becomes 44 (because $IDC_\infty^{1/2} = 19^{1/2} = 4.4$). The approximately 95% confidence interval for the number of prey particles a predator will encounter during 100 units of time thus expands from (80,120) in the Poisson case ($\lambda_0 = 1$) to (60,140) in the IPP case shown in Figure 15 ($\eta = 1/3$, $\xi = 4/9$) with a further expansion to (12,188) in the present IPP case of $\eta = \xi = 1/10$. Thus, in all these cases a predator, on average, encounters one prey per unit of time but due to patchiness, individual predators are likely to experience encounters with prey which deviate considerably from this average.

The variability in counts has important implications for very short periods of time and the rest of this example is devoted to considering the consequences of the start conditions (i.e. which state the predator occupies at time 0) on the time, T, required to encounter the very first food organism. We specifically consider the probability that the first encounter time exceeds a certain critical period of time denoted by τ, i.e. $P\{T > \tau\} = P\{N_\tau = 0\}$. These probabilities of zero counts at time τ are given by Eqs 12 and 13, i.e.,

$$p_1(\tau) = p \cdot e^{-\gamma_1\tau} + (1-p) \cdot e^{-\gamma_2\tau} \tag{22}$$

$$p_0(\tau) = \frac{\gamma_2}{\gamma_2 - \gamma_1} \cdot e^{-\gamma_1\tau} + \frac{\gamma_1}{\gamma_1 - \gamma_2} \cdot e^{-\gamma_2\tau} \tag{23}$$

where p_1 denotes the probability that the first encounter time exceeds $t = \tau$ if the predator at $t = 0$ is foraging in a patch, and the larger probability, p_0, likewise refers to the situation when the predator at $t = 0$ is located in the interpatch area. If the predator instead was foraging in a patch at $t = 0$ with probability $\eta = \pi_1$ (and travelling interpatch at $t = 0$ with probability $1 - \eta = \pi_0$) then its chance of not encountering a food organism during the first τ units of time becomes $\pi_1 p_1 + \pi_0 p_0$ and, hence, intermediate to p_1 and p_0 as expressed by Eq. 14 for the time-stationary case.

As an example consider again the situation in which the predator on average encounters $\lambda_0 = 1$ food organism in case of randomly distributed food organisms. The chance of not encountering a food organism during, say, $\tau = 1$ unit of time is $p_{\text{Poisson}}(1) = \exp(-1) = 0.37$ irrespectively of the predator's position at $t = 0$. Redistributing this $\lambda_0 = 1$ random food situation into the standard IPP-patch example used above, i.e. $(p, \gamma_1, \gamma_2) = (8/11, 4, 1/3)$ or $(\lambda, \omega_1, \omega_2) = (3, 8/9, 4/9)$ or $(\lambda_0, \eta = \pi_1, \xi) = (3, 1/3, 4/9)$, causes the probability of not encountering a food organism during 1 time unit to decrease when the predator starts inside a patch; $p_1(1) = 0.21$. However, starting outside the patches this probability increases by a factor of ca. 4 and becomes $p_0(1) = 0.78$ reflecting that the chance of encountering at least one patch (which on average requires $1/\omega_2 = 2.25$ time units) and then encountering a food organism within 1 time unit only is 12%. If the predator starts in a patch and remains there for at least 1 unit of time (which occurs with probability $\exp(-\omega_1) =$

0.41) then its chance of not encountering a food organism is only $\exp(-\lambda) = 0.050$ (cf. *Comment 7*). The higher value, $p_1(1) = 0.21$, is obtained because the predator may pass through the patch without encountering any food organism (see also *Comment 7*), which also is reflected by the fact that $p_1(1)$ is determined almost entirely by γ_2, i.e. $p_1(1) \approx (1-p)\exp(-\gamma_2) = 0.20$. This also explains why p_1 decreases slower than p_{Poisson} for increasing τ. Suppose, for example, that $\tau = 5$ then $p_{\text{Poisson}}(5) = \exp(-5) = 0.0067$ but $p_1(5) = 0.052$ and $p_0(5) = 0.21$. The balance of $p_1 = p_{\text{Poisson}}$ occurs with the present parameter values for $\tau = 2.0$. During longer period than 2 time units a higher proportion of zero counts is likely to occur in the IPP compared to the Poisson process (with the same mean) which causes $p_1 > p_{\text{Poisson}}$ (but also a higher proportion of many encounters).

Dividing Eq. 23 with Eq. 22, rearranging and using Eq. 4 yields an expression for how many times p_0 exceeds p_1, i.e.

$$p_0(\tau) = p_1(\tau)\left[1 + \frac{\lambda}{\gamma_1-\gamma_2}\cdot\frac{1}{1-p}\cdot\frac{1-e^{-(\gamma_1-\gamma_2)\tau}}{1+\dfrac{p}{1-p}\cdot e^{-(\gamma_1-\gamma_2)\tau}}\right]. \tag{24}$$

The last factor in the bracket with the exponential terms vanishes when $\tau(\gamma_1-\gamma_2)$ is considerably greater than one, which gives

$$p_0(\tau) \approx p_1(\tau)\left[1 + \frac{\lambda}{\gamma_1-\gamma_2}\cdot\frac{1}{1-p}\right] \quad ; \quad \tau \gg \frac{1}{\gamma_1-\gamma_2}. \tag{25}$$

In the standard example above this factor (= bracket) becomes 4. It is of note that the factor in Eq. 25 alternatively may be written $\gamma_1/(\gamma_1-\gamma_2)\cdot 1/(1-p)$ because the approximation is equivalent to neglect the γ_1-terms and, hence calculate p_0 and p_1 in Eqs 22-23 based entirely on the γ_2-terms. Transforming into $(\lambda_0, \eta = \pi\pi_1, \xi)$-notation (see *Comment 8*) and linearizing for small patch volume fractions, η, yields Eq. 25 on the form

$$p_0(\tau) \approx p_1(\tau)\left[1+\frac{1}{\xi}\left(1+\frac{\eta}{1+\xi}\right)\right] \approx p_1(\tau)\left[1+\frac{1}{\xi}\right];\ \eta = \pi\pi_1 \ll 1,\ \tau \gg \frac{\eta}{\lambda_0}\cdot\frac{1}{1+\xi}. \tag{26}$$

The last expression, $p_0/p_1 = 1 + 1/\xi$, shows resemblance to the maximum index of dispersion for counts in Eq. 21, $IDC_{\max\infty} = 1 + 2/\xi$. As an example consider again the patchy case of $\eta = \xi = 1/10$ (maintaining $\lambda_0 = 1$) with the alternative parameter specification IPP$(\lambda = 10, \omega_2 = 0.1, \omega_1 = 0.9)$ or $H_2(p = 0.9161, \gamma_1 = 10.91, \gamma_2 = 0.0917)$. It follows from Eq. 26 that p_0 is ca. 12 times greater than p_1. The probabilities become $p_0(\tau) \approx \gamma_1/(\gamma_1-\gamma_2)\cdot\exp(-\gamma_2\tau)$ and $p_1(\tau) \approx (1-p)\cdot\exp(-\gamma_2\tau)$ or $p_0 = 0.92$ and $p_1 = 0.077$ when $\tau = 1$. As above these probabilities are to be compared with $p_{\text{Poisson}} = 0.37$. The time period required for $p_{\text{Poisson}} = p_1$ has now increased to $\tau \approx -(\ln(1-p))/(1-\gamma_2) = 2.7$. Increasing τ to 5 time units these probabilities of not encountering food decrease to $p_{\text{Poisson}} = 0.0067$, $p_1 = 0.053$ and $p_0 = 0.64$. Thus, in all these examples, the predator, on average, encounters one food organism per unit of time but due to patchiness, the probability that the predator does not encounter food during τ units of time depends not only on τ and on the average food density but very much on the position of the predator at time 0.

Comment 9: The probability characteristics of the time to first feeding

The time required to encounter and ingest the very first food organism, T, is of particular importance for survival in early life. Blaxter & Hempel (1963) worked with first-feeding herring larvae and introduced a concept of 'point-of-no-return' (*PNR*), referring to the point in time starving larvae are too weak to feed. Suppose time 0 defines the point in time at which a herring larva is ready to start exogenous feeding. At this point in time the larva still have some yolk-sac left (e.g. Blaxter & Hempel op. cit., Kiørboe *et. al.* 1985). If τ denotes *PNR* then $p_1(\tau)$ and $p_0(\tau)$ give the probabilities of reaching *PNR* and, hence, of death due to starvation depending on the position of the larva at time 0. Thus, the IPP theory offers the possibility of analysing the effects of patchiness on first feeding.

This comment starts with considering the probability distributions of the time to first feeding from which the standard statistics (i.e. mean, variance and c.v.) are obtained. The standard example is considered again and then first-feeding scenarios of larval herring are introduced in continuation of the example given in *Comment 8*.

The notation for the time to first feeding is T_{Poisson} in case of randomly distributed food organisms and, in case of patchiness, T_1, T_0 or T_{rand} when the predator at time 0 is located inside a patch, outside the patches or, respectively, inside a patch with probability π_1. This time to first feeding is equal to or greater than the time to the first prey encounter because not all encounters lead to successful attacks. However, suppose the attack success, ϵ, gives the probability that an encounter results in prey ingestion then the point process of ingestions is simply obtained by multiplying the intensity of encounters, λ, with ϵ. For example, considering a cruising predator (*Comment 8*),

$$\lambda_0 = \epsilon \cdot \beta_{\text{prey}} \cdot \rho_{0\,\text{prey}} \qquad \text{(non-patchy or Poisson)}$$
$$\lambda = \epsilon \cdot \beta_{\text{prey}} \cdot \rho_{\text{prey}} \qquad \text{(patchiness)}$$

where β_{prey} is the encounter rate kernel and ρ is the density of food organisms. In the rest of this comment such a ϵ-dilution of the encountering process is assumed to have taken place so an encounter actually implies prey ingestion.

In case of non-patchy food, i.e. the predator is considered to encounter food organisms in a Poisson process, the time to first feeding is exponentially distributed with intensity λ_0, i.e. with p.d.f. given by Eq. 1 so $E(T_{\text{Poisson}}) = 1/\lambda_0$, $V(T_{\text{Poisson}}) = [1/\lambda_0]^2$ and c.v.$(T_{\text{Poisson}}) = 1$. In case of patchiness and if the predator already is inside a food patch at time 0 then the time to first feeding, T_1, follows the same hyperexponentially distribution, $H_2(p, \gamma_1, \gamma_2)$, as the interencounter time with mean and variance given by Eqs 5 and 6, and with a $[\text{c.v.}(T_1)]^2 = IDC_\infty$, which is *greater* than 1; see Eq. 7. However, if the predator is on interpatch travel at time 0 then the c.d.f. of the time to first feeding, T_0, equals $1 - p_0(t)$ and, is the (generalized Erlang) distribution of the sum of two stochastic independent variables, which are exponentially distributed with intensities γ_1 and γ_2, respectively (see Eq. 13 and the discussion hereafter). Adding the means and adding the variances of these exponential variables yield,

$$E(T_0) = \frac{1}{\gamma_1} + \frac{1}{\gamma_2} = \frac{1}{\omega_2} + \frac{1}{\lambda} \cdot \frac{\omega_1 + \omega_2}{\omega_2}$$

$$V(T_0) = \left(\frac{1}{\gamma_1}\right)^2 + \left(\frac{1}{\gamma_2}\right)^2 = \left(\frac{\lambda + \omega_1 + \omega_2}{\lambda \omega_2}\right)^2 - \frac{2}{\lambda \omega_2}$$

with a variance to mean ratio of

$$(\text{c.v.}(T_0))^2 = 1 - \frac{2}{\gamma_1 \gamma_2 \left(\frac{1}{\gamma_1} + \frac{1}{\gamma_2}\right)^2} = 1 - \frac{2\lambda\omega_2}{(\lambda + \omega_1 + \omega_2)^2} \; .$$

This coefficient of variation squared is *smaller* than one and attains a minimum of 1/2 for $\gamma_1 = \gamma_2$ (see also *Comment 7*). Thus, not surprisingly, the average T_0 exceeds the average T_1 by the average time required to locate a patch, $1/\omega_2$, but the relative variability of T_0 is always smaller (and can be much smaller) than the relative variability of T_1. It is of note that the distribution of T_0 is independent of p with a density function, $f_0(t)$, which is unimodal, starting in zero with the maximum at $t_{\text{mode}} = [\ln(\gamma_1/\gamma_2)]/(\gamma_1 - \gamma_2)$ and tailing off being skewed to the right.

Consider the standard example $H_2(p = 8/11,\ \gamma_1 = 4,\ \gamma_2 = 1/3)$ or IPP$(\lambda = 3,\ \omega_1 = 8/9,\ \omega_2 = 4/9)$ in which case the average time to first feeding becomes $E(T_1) = 1$ and c.v.$(T_1) = 2$ with an intrapatch starting point. However, the average time to first feeding becomes $E(T_0) = 3.25$ and c.v.$(T_0) = 0.93$ with an interpatch starting point. If p varies then the IPP-parameters and therefore the T_1-characteristics change but the T_0-characteristics remain constant. For example, $E(T_1)$ decreases linearly with increasing p from $E(T_1) = 1/\gamma_2 = 3$ for $p = 0$ to $E(T_1) = 1/\gamma_1 = 0.25$ for $p = 1$ but $E(T_0) = 3.25$ for all values of p. Similarly, according to Figure 11A, c.v.$(T_1) = 1$ at the extreme (i.e. $p = 0$ or $p = 1$) and attains a maximum of

$$\text{c.v.}_{\max}(T_1) = \sqrt{1 + \frac{1}{2} \cdot \frac{(\gamma_1 - \gamma_2)^2}{\gamma_1 \gamma_2}} \quad \text{for} \quad p = \frac{\gamma_1}{\gamma_1 + \gamma_2}$$

i.e. in the present case, c.v.$_{\max}(T_1) = 2.5$ and $E(T_1) = 0.46$ for $p = 0.92$. Thus, changing the IPP-patch characteristics through p, c.v.(T_1) takes values between 1 and 2.5 but c.v.(T_0) = 0.93 for all values of p.

Considering the example with herring larvae in *Comment 8* but increasing the prey densities by a factor of 10 (i.e. $\rho_{0\text{prey}} = 1\,\text{nauplii} \cdot \text{l}^{-1}$ and $\rho_{\text{prey}} = 100$ nauplii $\cdot\, \text{l}^{-1}$) and adopting an attack success at the onset of feeding of about 10% (i.e. $\epsilon \approx 0.1$; see e.g. Rosenthal & Hempel 1970, Blaxter & Staines 1971, and Kiørboe *et.al.* 1985). Assuming unchanged encounter rate kernels, this leads to the same prey encounter rates as in *Comment 8*, i.e. $\lambda = 100 \cdot \lambda_0 = 7 \times 10^{-2} \cdot \text{s}^{-1}$. Thus, $E(T_{\text{Poisson}}) = 1/\lambda_0 \approx 24$ min but inside a patch a larva encounters food organisms, which are $\eta^{-1} = 100$ times more dense so $1/\lambda \approx 14$ s. In *Comment 8* the rates of leaving and encountering patches were obtained by considering $\pi_1 = \eta = 0.01$ and furthermore spherical patches with radius of 10 cm giving

$\omega_1 \approx 100 \cdot \omega_2 = 7.5 \times 10^{-2} \cdot s^{-1}$. Thus, the patch volume measure, ξ, which equals the average number of patches encountered during $1/\lambda_0 \approx 24$ min, is one. The H_2-parameters are easily obtained from the approximations given at the end of *Comment 8*, i.e. $p = 1/(1+\xi) = \frac{1}{2}$, $\gamma_1 = \lambda_0(1+\xi)/\eta = 200 \cdot \lambda_0$ and $\gamma_2 = \lambda_0\xi/(1+\xi) = \frac{1}{2} \cdot \lambda_0$. Thus, $\gamma_1 = 400\gamma_2$ and the average time to first feeding becomes $E(T_0) \approx 1/\gamma_2 \approx 2/\lambda_0$ (= 48 min) when the larvae is at an interpatch location at time 0. If the prey encounter rate kernel is reduced by, say, a factor of 10 (to account for less speed and smaller visual field at first feeding) then λ_0 and λ, and to the extend the reduction refers to speed also ω_1 and ω_2 are reduced by this factor. Hence, the patch volume measure, ξ, may increase slightly and $E(T_0)$ will almost increase by a factor of 10 and becomes 8 hours. If instead the patch radius is increased by a factor of 10 (to 1 m but maintaining a patch volume fraction of $\eta = \pi_1 = 0.01$; see also the end of *Comment 8*), then ξ decreases by a factor of 10 yielding $p = 0.9$, $\gamma_1 = 110 \cdot \lambda_0$ and $\gamma_2 = \lambda_0/11$ so $E(T_0) \approx 11/\lambda_0$. Thus, in the present case, increasing the volume of a patch 1000 fold and thereby decreasing the number of patches per unit volume by a factor of 1000 causes the average time for first feeding to increase from 48 min to 4.4 hours when the larva is on interpatch travel at the onset of feeding.

In the example above the average interencounter time is kept constant by assuming $\eta = \pi_1$. This means that the average time required for first feeding is $E(T_1) = 1/\lambda_0$ (or 24 min in the example) when the larva is inside a patch at time 0. The rate of leaving a patch, ω_1, is high because there is no behavioural changes incorporated in the model (on patch encounter) so even though the average time to first feeding only is 14 s if the larva remains in the patch, the high chance of leaving the patch causes the increase in $E(T_1)$. At the other extreme, suppose that the predator actually is able to remain in a food patch once encountered. This situation is achieved with $p = 1$ or $\omega_1 = 0$, which implies $\lambda = \gamma_1$ and $\omega_2 = \gamma_2$. If $\gamma_1 \gg \gamma_2$ as in the examples above, then $E(T_0) \gg E(T_1)$ and the probability of dying of starvation before first feeding, $p_0(\tau) \approx \exp(-\gamma_2\tau)$, cannot be neglected although the larva will get high rations once the first food organism successfully is ingested (i.e. before time τ).

Discussion

Understanding the mechanisms, which govern the contact rates between predators and their prey organisms, represents the essential entrance to quantifying trophodynamics. The task constitutes a tremendous challenge and requires exceptional theoretical development (see discussion by Rothschild 1986 (pp. 247), 1988). We do not attempt to address this challenge directly in the present paper. Our standpoint is that a well-defined and simple starting point is required to form a sort of analytical building stone for beginning conceptually to address the effects of a heterogeneous environment on the encounter rates. The basic question dealt with in this theoretical study is how to describe from first principles the variability in the number of encounters between a predator and its patchy prey and, using such a consistent theory, to investigate under which conditions this variability considerably exceeds the variability that would be created in a random setting of the prey organisms. The building stone must therefore be a stochastic one and we are advocating that the interrupted Poisson process (IPP), which as a double stochastic process represents the simplest version of a Markov-modulated Poisson process (MMPP; see e.g. Cox & Isham 1980, Fischer & Meier-Hellstern 1992), represents such a starting point. Although the IPP has been used intensively, e.g. in telecommunications, we believe that this is the first time it has been applied to biology and the phenomenon of patchiness.

The term 'patchiness' is used to designate a prey environment in which the spatial distribution of the individual prey particles is more aggregated than a completely random distribution. The important point, however, concerns the scale of patchiness under investigation. We use patchiness as a concept to designate characteristics of the heterogeneous prey environment perceived by the predator. Thus the scales of patchiness, which are of relevance in this study, depend on the perceptive distance and other properties of the predator considered rather than on the type of sampling devices applied in acquiring general knowledge of patchiness in the sea. In this terminology a vertical plankton haul or a bottom trawl should for example be considered a predator sweeping a volume of water basically in one and two dimensions, respectively. The idea is that the model unit developed in this study in principle should be applicable to any type of predator, and cruising predators such as larval fish are used only to exemplify part of the theory. The consequences of the patchiness, as encountered by the individual predator, is sometimes referred to as 'functional heterogeneity' (Kolosa & Rollo 1991), which represents the patchy elaboration of the predator's encounter and response to a specific density of randomly or homogeneously distributed prey, i.e. to the patchy extension of the functional response (Holling 1965). It may be noted that the term 'randomness' or 'randomly distributed' is taken to imply completely spatial randomness in the sense that the particles are considered homogeneously Poisson-distributed in space, i.e. a distribution where the number of points (e.g. prey organisms or patch centres) in a given set such as a volume of water is Poisson distributed with a mean proportional to the measure of the set (see Cressie 1991). Apparently this is the only distribution leading to analytical tractability which is why we, in the extension from a random to a patchy setting, tend to maintain the assumption of randomness as far as possible (e.g. randomly distributed patch centres in the geometrical interpretation and applications of the IPP model unit). We use the Index of Dispersion of Counts (*IDC*) as a measure of functional heterogeneity in this study, i.e. the variance to mean ratio of the distribution of the number of encounters a predator experiences during a specific period of time. This variance to mean ratio (*IDC*) is 1 for the Poisson distribution which suggests that a patchy distribution has a variance to mean ratio which is bigger than 1. However, there is no generally accepted definition of how to measure departure from the Poisson process or completely spatial randomness (see Ripley 1981 (chapter 6) and Cressie 1991 (chapter 8) for a discussion). Thus for this study it is sufficient to specify patchiness relative to randomness using the *IDC* for the IPP, which is fortunate because otherwise it is difficult to define and quantify what is meant by patchiness in any general sense. This is also illustrated by the fact that a satisfactory and general index of patchiness has not yet been established (Elliot 1977, Downing 1991).

Our strategy for developing a model unit concerning the effects of patchiness is therefore not the usual one of starting by specifying the statistical nature of contagious prey distributions whether this is done by the negative binomial distribution for the global distribution, by the distributions of clusters or in any concrete case by spectral analysis or some other type of data analysis (e.g. Fasham 1978). Instead we consider the effects of patchiness directly by a mechanistic parameterization of the individual predator's encounter with (patchy) prey. In doing this we do of course assume a patchy nature of the prey environment (which we, as stated above, do not specify initially) and we then attempt to parameterize the heterogeneous nature of the encounter rate, which is caused by patchiness and the foraging behaviour of the predator. The simplest model unit for the encounter rate we can imagine resembles a binary variable, which can only distinguish between two states referred to as a 1 and 0 state. Such an ON and OFF signal captures the principal effect of prey patchiness. Any predator will experience periods of foraging during which no encounters take place simply because no appropriate food organisms are passing by (temporal resource heterogeneity) or present in the parcel of water searched for food (spatial heterogeneity). This OFF-event is associated with time spent in the interpatch domain in the IPP model unit. The ON-event represents all other situations (i.e. various types of food are present to a smaller or larger degree whether or not the predator succeeds to encounter any of these food items), which are simply associated with patch residence times in the IPP model unit. Thus the ON-OFF abstraction is first used to distinguish between patch encounters and 'interpatch encounters' and then, the ON part is used again for individual prey encounters during patch residence times. The OFF-part would here represent the dead period after a prey encounter during which the predator is engaged in pursuing, attacking and otherwise handling that prey. This is but one example of an elaboration of the IPP model unit, which is important in many applications and will be treated in a separate paper (but see Rothschild 1991 for an introduction).

Thus our conceptual starting point for modelling the encounter effect of patchiness does not directly involve any considerations of the sizes and shapes of the individual patches. The ON-OFF patch signal divides the habitat (as perceived by the predator) into two compartments as shown in Figure 16. The intensities ω_1 and ω_2 of leaving and encountering patches can thus be considered as a simple, stochastic model of a predator migrating forth and back between a food and a non-food environment. It is in the food environment, which in this scenario is represented by all the food patches in the habitat considered, the forager is considered to encounter food organisms in a traditional Poisson process with intensity λ.

The three IPP-parameters represent a simple and direct characterization of an individual predator foraging in a patchy environment. The parameters may be said to specify completely the predator's chance of encountering prey and thus represent a quantification of the encounter effect of patchiness on the spatial and temporal scales which are defined by the searching behaviour of the predator. In addition to Poisson encounters with prey inside a patch the basic assumption in this simple representation of patchy encounters is exponentially distributed sojourn times of inter- and intrapatch travelling. This leads to a simple three parameter representation.

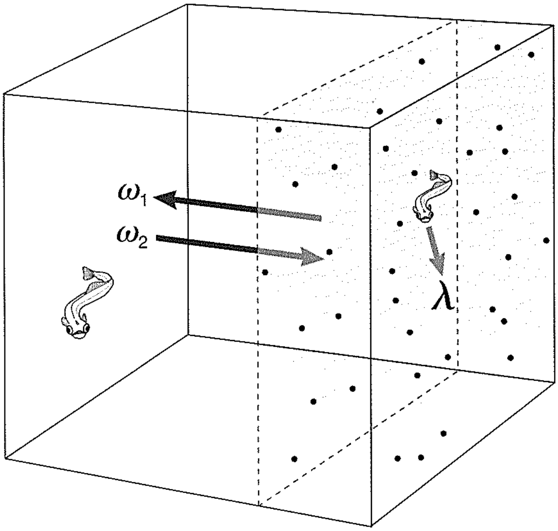


Figure 16. The conceptual starting point for using the IPP as a model unit for the phenomenon of patchiness. The domain of foraging, which is symbolized as a cube, is considered to comprise two types of water masses; one without food and one which contains food organisms. A predator changes between these two types of environment with constant intensities, ω_1 and ω_2, and, while occupying the food environment, it encounters food organisms at a constant intensity, λ. In a specific application the next step involves a redistribution of the food compartment into discrete (non-overlapping) patches in the cube (not shown but see Figures 1, 14 & 17A). Such a 3d-conceptualization of resource patchiness provides the basis for expressing the IPP-parameters as functions of the heterogeneous food environment and the foraging behaviour of the predator.

Thus, in the IPP, specifying values of ω_2, λ and ω_1, we are not only saying that if the predator at time *t* is located in the non-food environment then $1/\omega_2$ denotes its expected time to encounter the food environment, or, alternatively, if the predator at time *t* is located in the food environment, its expected time to encounter a food organism is $1/\lambda$ provided it stays in the food-environment and $1/\omega_1$ is the expected time to leave this environment, but we are also saying that these encounter times are exponentially distributed, which for example implies that the above mean (forward) times remain constant (i.e. no memory effects cf. *Comment* 2) and that the variability of the sojourn or encounter times is completely specified (with standard deviations equal to the means). In general it seems safe to assume that the actual encounters (as a result of the searching behaviour of a predator during a relatively small interval of time) in a first approximation can be described by an IPP with constant parameters. It is in this respect that the IPP may serve as a fundamental unit for modelling patchy encounters. The key question concerning the validity of such a constant three-parameter system is the spatial and temporal dynamics which govern changes in these three parameters. This question must be considered in relation to the specific applications but possible causes for the necessity for such parameter changes include environmental changes in the physical structure of patch and prey distributions, changes in the relative velocity between predator and food particles and, behavioural changes in foraging.

The IPP model unit may alternatively be specified by the three (statistical) parameters of the H_2-distribution of the interencounter times, and Figures 8 & 9 show the one-to-one relationship between the two sets of parameters. In stochastic terminology this means that an IPP process of encounters is stochastically equivalent to a H_2 renewal process of interencounter times and we may choose either parameter representation according to convenience in the various applications of the IPP model unit. However, if the H_2 renewal process was taken as the starting point for modelling patchy encounters (Rothschild 1991) then the underlying (biological) interpretation of resource patchiness and foraging behaviour would be quite different. A new and consistent interpretation of the H_2-process has been given in this study in which the parameter p designates a decision variable of the predator, i.e. on each prey encounter the predator stays with probability p and encounters the next prey in that patch according to the first exponential phase of the H_2-distribution (see Figure 7 and *Comment 4*). Operating with a decision assumption of the forager, this interpretation of the IPP model unit, which is based on the equivalent H_2-parameters, is associated with foraging theory (e.g. Stephens & Krebs 1986) and may be useful as a new starting point for modelling certain insect predators such as bumble bees searching for patchy flowers. However, in the present study focus is placed on the more direct patch concept, which is associated with the interpretation of the IPP parameters. It may be noted that the two intensities of the H_2-distribution, γ_1 and γ_2, cannot be interpreted and related directly to local prey densities such as the IPP parameter, λ, of encountering prey in a patch (see *Comment 1*). The description of a predator foraging in two different prey environments requires four parameters, i.e. an elaboration of the transition diagram of the IPP in Figure 6 with a second λ-arrow such that the predator encounters prey with intensity $\lambda = \lambda_{\text{intra}}$ in state 1 (intrapatch) and intensity λ_{inter} in state 0 (interpatch). Such MMPP models of patchiness will be considered in a separate paper. These models are mathematically complicated and difficult to treat on an analytically closed form because they do not represent renewal processes. It is only in the simple IPP which deals with just one type of prey patches (because $\lambda_{\text{inter}} = 0$) that all encounters occur in the same prey environment and a (H_2-) renewal process of the interencounter times is formed.

In a specific application the biological interpretation and quantification of the IPP model unit becomes more transparent when its three parameters are modelled such that they can be derived from specifications of the environmental conditions and the predator's foraging behaviour. The environmental specification includes for example patch (centre) density, patch geometry and (intrapatch) prey density. Graphically this step implies that Figure 16 can be replaced by a picture of the modelled patch structure, which is illustrated by the procedure in Figure 14. The specification of predator behaviour includes for example, as a minimum, swimming speed and reactive distance. The model of the IPP parameters for a cruising predator based on simple encounter theory and spherical patch geometry (*Comment 8*) constitutes one such example. The assumption that patch encounters as well as intrapatch prey encounters occur at random is often used in established foraging and encounter theories (see e.g. Stephens & Krebs 1986). The third assumption about exponentially distributed patch residence times (i.e. as a consequence of a constant

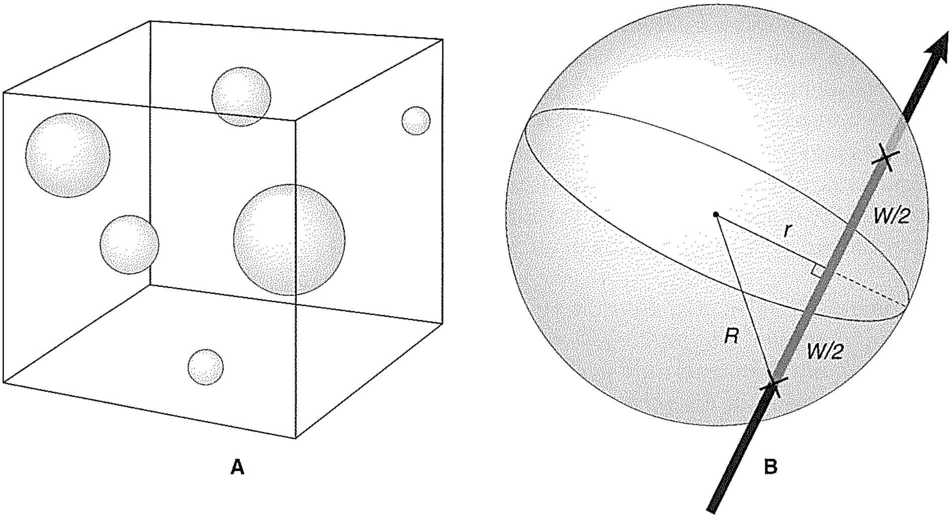


Figure 17. A: simple spherical patch scenario with randomly distributed patch centres assuming non-overlapping patches. This is an example of a 3d-conceptualization of patchiness in the redistribution of the food compartment shown in Figure 16; B: illustrating that a predator is considered to move through a spherical patch of radius R in a straight path of random direction. The distance travelled through the patch is denoted by w. Used in comment 10 for a simple derivation of the distribution of patch residence time.

intensity of leaving patches) is perhaps more questionable. The probability distribution of patch residence times is difficult to derive even in the most simple cases. As an example Figure 17A illustrates a scenario comprising spherical patches of various sizes. If a predator moves through such a spherical patch approximately in a straight path of a specific but random direction with constant speed (see Figure 17B) then the average (intrapatch) distance travelled exceeds the patch radius by 33% (see *Comments 8* & *10*). The distribution of patch residence times can now be derived if the probability distribution of the sizes of the patches encountered is known (*Comment 10*). Alternatively, considering the inverse problem, the probability distribution of encountered patch sizes, which produces an exponential patch residence time as assumed in the IPP, can be derived. This distribution of the radius in the patches encountered is, as a new result, shown in *Comment 10* to become a 50% mixture of an exponential distribution and an E_2-distribution (= distribution of the sum of two identical, exponentially distributed, variables which becomes more narrow with less variance than the exponential). The variability of the exponential residence time is in this scenario caused by the variability in the sizes of the patches encountered described by the mixed distribution mentioned above combined with the variability in the individual patch transfer times due to the random direction of travel through patches. However, the probability distribution of the actual sizes of patches in the sea may differ considerably from the probability distribution of the sizes of the patches encountered. This principal problem known as length-biased sampling has been illustrated in *Comment 2* where a simple example showed a bias of 500%

in estimating the average time between consecutive encounters simply because a long interencounter interval is more likely to be sampled than a short interval. Similarly a cruising predator will encounter patches of a certain radius four times more frequently than patches of half this radius assuming both sizes of patches were equally abundant (because the patch searching rate of the predator is approximately proportional to the patch radius squared – cf. *Comment 8*). Thus even the apparent simple task of deriving the distribution of patch residence times becomes complicated. These questions concerning the validity of the assumptions of the various exponential sojourn times will be dealt with in a separate paper.

Comment 10: The distribution of patch residence times derived from simple encounter theory and patch geometry

This comment deals only with what happens after the predator has encountered a patch and not with the chance of actually encountering patches. Consider the scenario where the predator is moving in one direction when it is occupying the intrapatch state. In continuation of *Comment 8*, the aim is to derive the probability distribution of the intrapatch distance travelled, W, when the predator is moving with constant speed $v_1 = v_{1\text{pred}}$ in such straight paths through spherical patches of radius $R = R_{\text{patch}}$. We will show that the mean distance travelled, $E(W)$, becomes $4/3 \cdot R$, which yields a mean patch sojourn time of $4/3 \cdot R/v_1$ in accordance with $\omega_1 = 3/4 \cdot v_1 \cdot 1/R$ as obtained in *Comment 8* for small patch volume fractions, $\eta = \pi_1$, i.e. when interpatch travelling occurs with the same speed as intrapatch foraging. This assumption of $v_0 = v_1$ is not considered here. Thus the speed within patches could be different from the speed of the predator when doing interpatch travelling hereby incorporating some behavioural aspects (an example of which is considered in *Comment 11*). We specifically consider the effect of random patch sizes and show that the patch sojourn time becomes exponentially distributed (as assumed in the IPP model unit) when the variability in the patch radius is described by a specific distribution.

Whenever a predator enters a patch there exists a circle with radius R (on the sphere) orthogonal on the moving direction of the predator; see Figure 17B. The distance from the point of entering the patch (sphere) to the plane of this circle is $W/2$ or half the distance of total intrapatch travel. This distance can be expressed by the x, y coordinates of the point of predator intersection with the circular section mentioned above. In fact only the distance $r = (x^2 + y^2)^{1/2}$ from the centre of this circular section to the point of intersection is of interest. Assuming that all points in the circular section are equally probable it is easy to derive the probability distribution of r and thus of W. The probability of having a point of intersection in the annulus $\{r \mid r_0 \le r \le r_0 + \Delta(r)\}$ is

$$\frac{\pi((r_0 + \Delta(r))^2 - r_0^2)}{\pi R^2} = \frac{2r_0 \Delta r + (\Delta(r))^2}{R^2}$$

Thus the density of r becomes

$$f(r_0) = \frac{2r_0}{R^2} \quad ; \qquad 0 \le \gamma_0 \le R$$

and the c.d.f. of r

$$F(r_0) = \left(\frac{r_0}{R}\right)^2 \quad ; \qquad 0 \le \gamma_0 \le R$$

Noting that $r^2 + (W/2)^2 = R^2$, the distribution of W is obtained in a straightforward manner:

$$P\{W \le w\} = P\{2\sqrt{R^2 - r^2} \le w\} = P\left\{R^2 - r^2 \le \left(\frac{w}{2}\right)^2\right\} = P\left\{\sqrt{R^2 - \left(\frac{w}{2}\right)^2} \le r\right\}$$

$$= 1 - P\left\{r \le \sqrt{R^2 - \left(\frac{w}{2}\right)^2}\right\} = \left(\frac{w}{2R}\right)^2 .$$

The density becomes

$$f(w) = \frac{w}{2R^2}$$

from which the mean $E(W) = 4/3 \cdot R$ easily is obtained. The question is how the distribution of W changes when also the patch radius, R, is a random variable. The notation $R = \mathrm{r}$ below is just to indicate a patch of radius r not to be confused with the distance $r = (x^2 + y^2)^{1/2}$ above.

For a sphere of radius $R = \mathrm{r}$ the average distance through the sphere will thus be $4/3 \cdot \mathrm{r}$. Moreover the distance will be a random variable, W, with the distribution function $F(w \mid R = \mathrm{r}) = (w/2\mathrm{r})^2$ and density $f(w \mid R = \mathrm{r}) = w/(2\mathrm{r}^2)$. The time spent in the patch by a predator moving with constant speed will be proportional to W and thus have the same distribution apart from a scaling factor. Considering patches of random sizes, R becomes a random variable with density, say, $g(\mathrm{r})$, and then the distribution of W is given by

$$f(w) = \int_{w/2}^{\infty} f(w \mid \mathrm{r})\, g(\mathrm{r})\, d\mathrm{r}$$

$$f(w) = \int_{w/2}^{\infty} \frac{w}{2\mathrm{r}^2}\, g(\mathrm{r})\, d\mathrm{r}$$

If reasons exist to assume a specific distribution for w then the particular distribution of R, which yields this distribution, can be derived. This means, solving for $g(\mathrm{r})$ in the above equation, which for $w > 0$ reads after a multiplication with $2/w$,

$$2\,\frac{1}{w}\, f(w) = \int_{w/2}^{\infty} \frac{1}{\mathrm{r}^2}\, g(\mathrm{r})\, d\mathrm{r}$$

or, with the substitution $z = w/2$,

$$\frac{1}{z}\, f(2z) = \int_{z}^{\infty} \frac{1}{\mathrm{r}^2}\, g(\mathrm{r})\, d\mathrm{r} .$$

Differentiating with respect to z yields

$$-\frac{1}{z^2} f(2z) + 2\frac{1}{z} f'(2z) = -\frac{1}{z^2} g(z)$$

and finally

$$g(\mathrm{r}) = f(2\mathrm{r}) - 2\mathrm{r}f'(2\mathrm{r}) \ .$$

In the IPP model unit the distribution $f(w)$ is exponential. More specifically

$$f(w) = \frac{\omega_1}{v_1} \mathrm{e}^{-\frac{\omega_1}{v_1}} \cdot w \ .$$

This is because the predator will stay in the patch for an exponentially distributed time interval with mean $\omega_1{}^{-1}$ and, hence, assuming a constant speed v_1, the distance travelled within the patch is also exponentially distributed with mean $v_1 \cdot \omega_1{}^{-1}$. Denoting $\phi = \omega_1/v_1$,

$$f(w) = \phi \mathrm{e}^{-\phi w}$$

which, using the f-to-g transformation above, is produced by encountered patches with randomly distributed radii of density:

$$g(\mathrm{r}) = \phi \mathrm{e}^{-2\phi \mathrm{r}} + 2\mathrm{r}\ 2\phi^2\ \mathrm{e}^{-2\phi \mathrm{r}}$$

$$g(\mathrm{r}) = \frac{1}{2} 2\phi\ \mathrm{e}^{-2\phi \mathrm{r}} + \frac{1}{2} 2\phi (2\phi \mathrm{r}) \mathrm{e}^{-2\phi \mathrm{r}} \ .$$

This last expression is a mixture of an exponential distribution and an Erlang-2 distribution. It is to some degree intuitively clear that an exponential distribution of the patch sojourn only can be obtained with a distribution of the patch radius, which show less variability than an exponential distribution. The intuitive reasoning is that on top of the uncertainty of the patch radius comes the uncertainty of the entering point and since the combined effect has to become exponential each individual effect has to be of less variability than the exponential.

Thus considering spherical patch distributions of this kind the predator stays in a patch for an exponentially distributed period of time, which is consistent with the IPP-model.

Nevertheless, a model where the predator moves according to a more complicated scheme is clearly more realistically. Upon an encounter it is natural to assume that the predator will slow down or stop completely with the purpose of entering some kind of attack sequence. This, however, introduces the notion of behavioural aspects, we have not generally addressed in the present study. For the IPP-model to remain valid it must be assumed that the combined effects of the distribution of patch size, distribution of patches, and the behaviour of the predator still results in patch sojourn times and interpatch times, which can be adequately described by exponential distributions.

The examples with a cruising predator in a food environment of identical, spherical patches comprising immobile prey at a constant density (e.g. *Comment 8*) showed that the expected time to encounter a patch, $1/\omega_2$, is proportional to patch radius and inversely proportional to speed and the patch volume fraction, η. Once encountered the expected time to leave a patch, $1/\omega_1$, is clearly also proportional to patch radius. The expected prey interencounter time during patch residence, $1/\lambda$, is inversely proportional to (intrapatch) prey density, speed and perceptive distance squared. This is but one example of a simple model of the IPP parameters. If the foraging environment (patch volume fraction, patch radius, prey density) and predator behaviour (speed, perceptive distance) and hence the IPP parameters for this simple scenario of a larval predator remain reasonably constant then a situation of statistical equilibrium will be reached. We distinguish between the time-stationary IPP, which is being observed from a random point in time and the event-stationary IPP, which is being observed from a point in time at which an encounter has just taken place (see *Comment 6*). The exact properties of the counting process are different in the two cases as illustrated by the example in Figure 13. This difference is vital for solving problems concerning rare events or generally the tails of the distributions of encounters during a relative short period of time, i.e. an initial period of time, which is not very much larger than $t_{\text{crit}} = (\omega_1 + \omega_2)^{-1}$.

One such example is the probability distribution of the time required for first feeding (see *Comment 9*). In case of non-patchy food the distribution becomes exponential. In case of patchy food this distribution turns into the overdispersed H_2-distribution when the fish larva happens to be located in a patch at the onset of first feeding. This case is equivalent to the event-stationary situation. In the time-stationary case first feeding is also described by a H_2-distribution but with quite different properties (Eq. 14 and *Comments 2 & 7*). Finally, if the larva is located in the interpatch domain the distribution of the time to first feeding changes into a generalized Erlang distribution with the same intensities as in the H_2-distributions (Eqs 13 & 23; *Comments 7 & 9*). The implications of these new results for the dynamics of first feeding larvae will be treated further in a separate paper. However, it may be noted that the independence of the H_2-parameter p in the underdispersed Erlang distribution implies that the chance of encountering food before the point of no return for most first feeding larvae will be the same under quite different situations of patchiness in the sea, i.e. the situations described by all the combinations of IPP-parameters shown in Figure 9A as p varies, (which, as shown by Figure 11A, in case of a considerable difference in the γ-intensities is associated with a considerable range of variation in *IDC*).

Figure 13 and *Comment 7* also show another important point. The probability distributions of encounters in the IPP are not compound Poisson (= mixed Poisson) or equal to any of the other well-known distributions although they, as for any renewal process, become asymptotically normal. Thus the parallel between exponentially distributed interencounter times and Poisson distributed encounters in the non-patchy case is not maintained in the patchy IPP-case although the interencounter times here are compound exponential (= mixed exponential or H_2).

The patchy IPP can produce much higher variability in number of encounters than the non-patchy Poisson. Figure 15 introduces this point by comparing the variability when the mean rate of encounters is the same in the non-patchy and patchy case. Since the variance to mean ratio always is 1 for the non-patchy case such a comparison implies that the value of *IDC* obtained in the patchy case directly gives the number of times the variance increases from the non-patchy to the patchy scenario. Thus the square root of *IDC* denotes the multiplicative increase in the standard deviation or coefficient of variation of the distributions of encounters. We use the asymptotic *IDC* which overestimates the correct (time-dependent) index by less than 10% if the time period in question exceeds ca. $10t_{\text{crit}} = 10/(\omega_1 + \omega_2)$ – see Figure 12. In Figure 15 $IDC = 4$ so the c.v. of encounters has doubled. The construction of such comparable scenarios has been done starting by specifying the non-patchy case and then following the procedure shown in Figure 14. The example in *Comment 8* for small herring larvae, as modified in *Comment 9* by assuming that only 10% of the encounters result in ingestion, considers an average prey density of 1 nauplii per litre in the sea. A herring larva in this non-patchy scenario will on average ingest a prey every $1/\lambda_0 = 24$ min, i.e. the expected ration during a 12-hour feeding day becomes 12×60/24 or 30 nauplii. The standard deviation for this non-patchy Poisson ration distribution becomes 5.5 and the c.v. equals 18%. Considering instead these prey concentrated at a density of 100 nauplii per litre (i.e. $\eta = 1/100$) in spherical patches of radius 1 m the larva will on average encounter a patch every $1/\omega_2 = 3.7$ hours assuming unchanged speed (i.e. the larva encounters $\xi = 0.11$ patches during a non-patchy mean interencounter time). Once in a patch the larva will now encounter nauplii 100 times more frequently than in the non-patchy case. With such a high rate of prey encounters the larva can only stay on average $1/\omega_1 = \eta/\omega_2$ or 2.2 min in a patch in order to achieve the same mean ration of 30 nauplii per day as in the non-patchy scenario. The *IDC* for this patchy scenario is $1 + 2/\xi$ (Eq. 21) or 20, i.e. the variance of the ration distribution has increased 20-fold and the c.v. becomes 82%. This will give rise to a considerable variation in the rate of growth. The instantaneous growth rate of larval fish is approximately proportional to the daily ration (e.g. Beyer 1989, Example 10) and using a normal approximation for the ration distribution it follows that ca. 10% of the larvae will succeed to grow at least at double the average rate during the day considered, i.e. these larvae obtain a ration of 60 or more nauplii per day. The probability of such growth rates in the non-patchy case is only 2×10^{-8}. At the other extreme the probability that a larva fails to ingest just one nauplius during a feeding day is virtual zero (i.e. $\exp(-\lambda_0\tau) = \exp(-30)$; $\tau = 12$ h) in the non-patchy case. However, 6.5% of the larvae ($\exp(-\gamma_2\tau) = \exp(-30/11)$; see *Comment 9*), which at the start of the feeding day are travelling interpatch, will not succeed to ingest any food during that day. Considering that successful daily growth almost immediately improves the swimming speed and generally the larva's ability to grow and survive the next day, these results indicate the potential importance of patchiness for fish population dynamics. The implications of spatial patchiness on larval fish population dynamics and recruitment will be investigated further in a separate paper by using the IPP to govern daily rations in an individually based, time-discrete model such as the Beyer & Laurence (1979) model.

The comparative scenarios are based on a constant, average rate of prey encounters, which is achieved by assuming that the foraging behaviour of the predator does not change when food is aggregated into micropatches. Thus the speed of the predator is constant in all the comparative scenarios we have presented and the patch volume fraction (η) becomes equal to the proportion of time spent in patches (π_1). However, the high speed in intrapatch foraging often results in relative short patch residence times and unrealistic high rates of prey encounter. For example, in the scenario mentioned above, the fish larva ingests on average a prey every 14 s during intrapatch foraging and each ingestion represents, on average, the outcome of 10 encounters (i.e. $\epsilon = 0.1$). It is therefore of note that such comparative scenarios with a constant mean encounter rate alternatively can be produced with a simple behavioural adaptation to patch foraging. The principle in this new amendment to the mechanistic model of the IPP-parameters is as follows. Suppose the speed of the predator generally decreases with increasing food density. The speed in the non-patchy scenario with the low food density, say, $v_{\text{non-patch}}$, must then be slightly smaller than the speed during interpatch travel (v_0) in the absence of food and the speed in intrapatch foraging (v_1) must be considerably lower. If, for example, $v_{\text{non-patch}} = 0.9v_0$ then it can be shown that the requirement to a constant mean encounter rate implies that $v_1 = 0.1v_0$. Thus compared to the scenarios described above, the fish larva will now on average spend 9-fold more time foraging in patches than the patch volume fraction suggests (i.e. $\pi_1 = 9\eta$). This higher mean patch residence time and the ca. 10% larger rate of patch encountering are on average counteracted by the 10-fold reduction in intrapatch searching rate. The *IDC* is reduced by ca. 20% compared to the equivalent patch scenario above with constant speed. Figure 10 shows that *IDC* actually increases as ω_1 decreases (towards ω_2) but since λ also decreases (by ca 90% and ω_2 increases by 10%) the maximum *IDC* will decrease even more and the combined effect is the 20% reduction in the *IDC* for this patch scenario with prey-density-dependent behaviour.

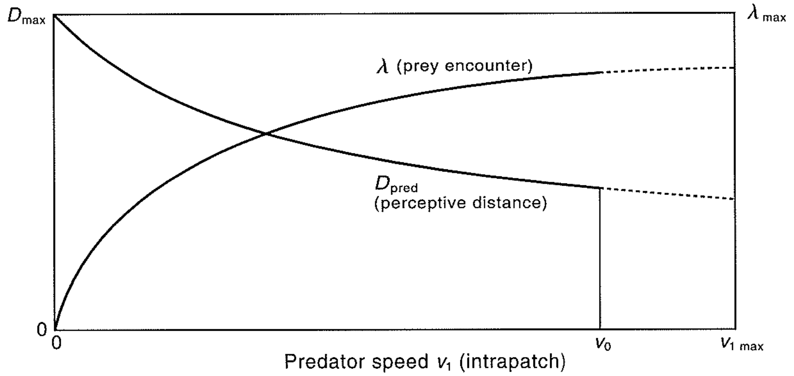


Figure 18. Illustrating the effect on the rate at which the predator encounters prey in a patch when its perceptive distance decreases with increasing speed. Used in *Comment 11* to derive the (optimum) intrapatch speed which maximises the average rate of prey encounters assuming the predator moves interpatch with speed v_0. Arbitrary scales.

The perceptive distance is the other characteristic of predator behaviour in the simple model of the IPP parameters considered in this paper. Figure 18 shows that the linear relationship which the intrapatch prey encounter rate bears with speed in the simple model is changed into a Michaelis-Menton type of relationship when the perceptive distance is considered to decrease with increasing speed. This model is examined in *Comment 11* and the optimum encounter rate with food organisms is derived. The result is similar to the considerations above.

The basis model of the IPP parameters can similarly be elaborated with respect to the characteristics of the foraging environment. One such example, which also pertains to larval fish as predators, is to incorporate the effect of mobile prey (Gerritsen & Strickler 1977) and further the effects of turbulence on the encounter rates (Rothschild & Osborn 1988, Ewans 1989, Davis *et al.* 1991, Kiørboe & Saiz 1995). This would constitute another important example of the interactive effect between predator behaviour and the environmental impact on the encounter rate.

Comment 11: Optimum encounter rate with food organisms – an example of including the effect of predatory behaviour

In *Comments 8 and 9*, the analysis of the variability in counts created by patchiness (as described by the IPP with simple encounter theory and spherical patches) was based on a comparative approach maintaining a constant average interencounter time, $\mu = 1/(\lambda \pi_1)$. This implies that the average rate of encounters with food organisms, e, was equal to $\lambda \cdot \eta$, i.e.

$$e = E(N_t)/t = \lambda \pi_1 = \lambda \cdot \frac{w_2}{w_1 + w_2}$$

where π_1, the proportion of time spent by the predator in patches was equal to η, the fraction of the sea, which is occupied by patches. The essence of this requirement is that there is no behavioural changes during patch residences, which in the present context implies that the predator continues to forage inside patches with unreduced speed (i.e. $v_1 = v_0$) and with unchanged perceptive distance, D_{pred} (which here is considered equal to the reactive distance).

In this comment the reactive distance for a cruising predator is considered to decrease with increasing speed and the intrapatch foraging speed, $v_{1\,\text{opt}}$, which maximizes the average encounter rate with food organisms, $e(v_{1\,\text{opt}}) = e_{\max}$, is derived. An example pertaining to larval herring is included.

The food patchiness is specified by the prey densities $\rho_{0\,\text{prey}}$ and ρ_{prey} (or $\eta = \rho_{0\,\text{prey}}/\rho_{\text{prey}}$) and by the average patch radius, R_{patch}. Predator behaviour is specified by a (constant) sustained cruising speed on interpatch travel, v_0, and by a constant (but unknown) intrapatch foraging speed, v_1, and also by the reactive distance, $D_{\text{pred}}(v_1)$, which is considered a function of v_1. This leads to a specification of the encounter rate kernels (β_{patch} and β_{prey}, see *Comment 8*) and then to the patch and prey encounter rates of the IPP. The rate of leaving patches, ω_1, can not be obtained from the (λ_0, η, ξ)-specification as in *Comments 8 and 9* because η is *not* equal to π_1 in the present scenario. In total, results from *Comments 8* to *10* are used to specify the IPP-parameters as follows:

$$\omega_2 = \beta_{\text{patch}} \cdot C_{\text{patch}} = 3/4 \cdot v_0 \cdot \eta / R_{\text{patch}} \quad ; \quad v_0 = v_{0\,\text{pred}}$$

$$\lambda = \epsilon \cdot \beta_{\text{prey}} \cdot \rho_{\text{prey}} \approx \epsilon \cdot \pi (D_{\text{pred}}(v_1))^2\, v_1 \cdot \rho_{\text{prey}} \quad ; \quad v_1 = v_{1\,\text{pred}}$$

$$\omega_1 = 3/4 \cdot v_1 \cdot 1/R_{\text{patch}} \quad ; \quad v_1 = v_{1\,\text{pred}}$$

First, the equation for the patch encounter rate, ω_2, is from *Comment 8*. The second equation is from *Comment 9* and specifies the prey encounter rate, λ, by also taken the attack success, ϵ, into consideration. The third equation specifies the average patch residence time, $1/\omega_1$, as it was derived in *Comment 10*.

In a specific patch scenario it is only the perceptive distance, D_{pred}, and the speed, v_1, which are not determined and the equations show that the rate of encountering patches, ω_2, is constant whereas the (intrapatch) rate of prey encounter and the rate of leaving patches both are proportional to speed, i.e. $\lambda \propto D_{\text{pred}}{}^2 \cdot v_1$ and $\omega_1 \propto v_1$. If the reactive distance was constant independently of the speed then the average prey-encounter rate, $e \propto v_1/(\text{constant} + v_1)$, bears an increasing relationship to speed and the predator would benefit from using its maximum speed (when the energetic cost of locomotion are neglected). If the reactive distance bears some decreasing relationship to speed then it seems sensible to assume that this decrease still allows the prey-encounter rate kernel (= search volume rate), $\beta_{\text{prey}} \approx \pi (D_{\text{pred}}(v_1))^2 \cdot v_1$, to increase with increasing speed. Suppose $D_{\text{pred}}(v_1)^2$ is inversely proportional to a constant plus v_1, i.e. introducing a convenient notation for the constants,

$$D_{\text{pred}}(v_1) = \sqrt{\frac{\beta_{\text{prey max}}/\pi}{v_{1\,\text{max}} - v_0 + v_1}}$$

then the encounter rate kernel becomes

$$\beta_{\text{prey}}(\text{v}_1) = \beta_{\text{prey max}} \cdot \frac{v_1}{v_{1\,\text{max}} - v_0 + v_1}$$

where $v_{1\,\text{max}}$ is the speed that would result in the maximum kernel, $\beta_{\text{prey max}}$, if the reactive distance was constant and equal to the reactive distance during interpatch travel at the sustained speed, $v_0 < v_{1\,\text{max}}$ (see Figure 18). The speed $v_{1\,\text{max}}$ is considered the maximum possible speed of the predator. Such a burst speed can only be maintained during short periods of time which is why the predator is considered to travel interpatch at the lower speed v_0. That is

$$v_{1\,\text{max}} = v_0 \cdot \beta_{\text{prey max}} / \beta_{0\,\text{prey}}$$

with $\beta_{0\,\text{prey}}$ denoting the encounter kernel at speed v_0. The prey encounter rate becomes

$$\lambda = \lambda_{\text{max}} \cdot \frac{v_1}{v_{1\,\text{max}} - v_0 + v_1}$$

where $\lambda_{\text{max}} = \epsilon \cdot \beta_{\text{prey max}} \cdot \rho_{\text{prey}}$. The probability of being in a patch is

$$\pi_1 = \frac{\eta v_0}{\eta v_0 + v_1}$$

and the average prey-encounter rate becomes

$$e = \lambda_{\max} \cdot \eta v_0 \cdot \frac{v_1}{v_{1\max} - v_0 + v_1} \cdot \frac{1}{\eta v_0 + v_1} \ .$$

This rate shows a maximum at an intermediate speed, $v_{1\,\mathrm{opt}}$, because e becomes very small at small speeds (due to small kernel) as well as at large speeds (due to small residence time). The maximum becomes

$$e_{\max} = \lambda_{\max} \cdot \left(\frac{\sqrt{\eta v_0}}{\sqrt{\eta v_0} + \sqrt{v_{1\max} - v_0}} \right)^2 = \lambda_{\max} \cdot \left(\frac{v_0}{v_0 + v_{1\,\mathrm{opt}}/\eta} \right)^2$$

and it is attained at the speed

$$v_{1\,\mathrm{opt}} = v_0 \sqrt{\eta \left(\frac{v_{1\max}}{v_0} - 1 \right)} = v_0 \sqrt{\eta \left(\frac{\beta_{\mathrm{prey\ max}}}{\beta_{0\ \mathrm{prey}}} - 1 \right)} \ .$$

This optimal swimming speed is smaller than the sustained cruising speed, v_0, unless v_0 is very small. It can be shown that

$$\frac{\eta}{1+\eta} \cdot v_{1\max} < v_{1\,\mathrm{opt}} < v_0 \quad \text{if} \quad \frac{\eta}{1+\eta} \cdot v_{1\max} < v_0 < v_{1\max} \cdot \frac{1}{1+\eta} \ .$$

In continuation of the larval herring example from *Comments 8 and 9* suppose the equivalent random (non-patchy) prey density is $\rho_{0\ \mathrm{prey}} = 1$ nauplii $\cdot\, \mathrm{l}^{-1}$ with a $\eta^{-1} = 100$ times more dense intrapatch prey density, $\rho_{\mathrm{prey}} = 100$ nauplii $\cdot\, \mathrm{l}^{-1}$. The attack success is put to 10% ($\epsilon = 0.1$). With a speed of $v_0 = 1\ \mathrm{cm} \cdot \mathrm{s}^{-1}$ and a perceptive distance of $D_{0\,\mathrm{pred}} = D_{\mathrm{pred}}(v_0) = 1.5$ cm the prey-encounter rate kernel becomes $\beta_{0\,\mathrm{prey}} = 7\ \mathrm{cm}^3 \cdot \mathrm{s}^{-1}$. Suppose the maximum kernel represents an increase of 50%, i.e. $\beta_{\mathrm{prey\ max}} = 10.5\ \mathrm{cm}^3 \cdot \mathrm{s}^{-1}$. Then $v_{1\max} = 1.5\ \mathrm{cm} \cdot \mathrm{s}^{-1}$ and the optimum speed becomes $v_{1\,\mathrm{opt}} = 0.07\ \mathrm{cm} \cdot \mathrm{s}^{-1}$. The perceptive distance at this speed is $D_{\mathrm{pred}}(v_{1\,\mathrm{opt}}) = 2.4$ cm and the equivalent maximum average rate of prey-encounters becomes $e = 5.8\ \mathrm{h}^{-1}$ with a maximum rate of $\lambda_{\max} = 0.105\ \mathrm{s}^{-1}$ (= $378\ \mathrm{h}^{-1}$). The interpretation of this result is as follows. On encountering a patch the predator continues to swim in a straight path but with reduced swimming speed thereby increasing its reactive distance and its probability of staying longer time in the patch. In the present case the reduction in speed is more than 10-fold, which increases the average sojourn time ($1/\omega_1$) in a patch of radius 10 cm from 13 s (with $v_1 = v_0$) to more than 3 min. The reactive distance is considered to increase ca. 60% at this reduced speed and the combined result is that the larva, on average, encounters food organisms at a rate of 5.8 per hour, which is more than double the rate, $e(v_0) = \epsilon \cdot \beta_{0\,\mathrm{prey}} \cdot \rho_{\mathrm{prey}} \cdot \eta = 2.5\ \mathrm{h}^{-1}$, had the larva continued through patches with unreduced speed. The fraction of time the larvae are foraging inside patches become $\pi_1 = 0.125$, i.e 12.5% compared to 1% in case of $\pi_1 = \eta$ when $v_1 = v_0$. The index of dispersion for counts, IDC_∞, increases likewise from 3 to 4.8 in case of $R_{\mathrm{patch}} = 10$ cm.

The main purpose of this herring case is to exemplify the effect of introducing behaviour into the IPP patch–prey model. Some of the input-parameter values are questionable or difficult to assess. For example, the attack success for 1.2 cm herring larvae feeding on copepod nauplii is more likely in the order of 50% (Munk & Kiørboe 1985). We maintained the 10% value used for first-feeding larvae in *Comment 9* for comparative reasons because the average prey density of 1 per litre (with 100 per litre in patches) then produces the same encounter rates as the case considered in *Comment 8* with an average of 0.1 (with 10 in patches) nauplii per litre without considering the effect of a limited attack success (i.e. $\epsilon = 1$). In general estimates of parameter values are difficult to obtain. An example is estimates of searching rates for similar-sized herring larvae, which vary by more than one order of magnitude (see Munk & Kiørboe op. cit. and references herein).

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Notation

c.d.f.	Cumulative (probability) density function
C_{patch}	Concentration of patches, i.e. number of patch centres per unit of volume
c.v.	Coefficient of variation, i.e. standard deviation to mean ratio
d_{NND}	Nearest neighbour (particle) distance
D_{pred}	Perceptive distance of a predator
e	Average rate of encounters
E_1	Exponential distribution (= Erlang with one phase)
E_2	Erlang distribution with two phases
$E(.)$	Expectation or mean of the stochastic variable in the bracket; referring to the time-stationary IPP
E_{event}	Expectation operator in the event-stationary process (i.e. an encounter took place at time 0)
f	Probability density function
F	Cumulative probability function
g	Probability density function
H_2	The hyperexponential distribution (with two exponential phases) or the mixed exponential distribution; specified by the three parameters (p, γ_1, γ_2)
i, j	Indices mainly used to designate states or phases
IBM	Individually Based Modelling or Models
ID	Index of dispersion
$IDC(t)$	Index of dispersion for counts, i.e. the variance to mean ratio for counts during time/period t
IDC_∞	Asymptotical limit for the index of dispersion for counts, used as a measure of functional heterogeneity
$IDC_{\max\infty}$	Maximum dispersion for counts when patches only constitute a small fraction of the sea, which equals the proportion of time spent by the predator in patches (i.e. $\eta = \pi_1 \ll 1$)
$IDC_{\text{mix Poisson}}$	Index of dispersion for counts for the mixed Poisson distribution

IPP	Interrupted Poisson process; specified by the three parameters $(\lambda, \omega_1, \omega_2)$
MMPP	Markov-modulated Poisson process
n	Integer indicating a specific value of the number of encounters
N_t	Random variable denoting the number of encounters in the interval $(0, t)$
$O(\Delta t)$	Continuous function tending to 0 as Δt tends to 0
p	First parameter of the H_2 distribution, which gives the probability of an exponentially distributed interencounter time with mean $1/\gamma_1$. In the H_2 patch scenario p is the probability that the predator stays in the patch
p_0	The value of p_u, as explained below, at time 0
p_u	Given the time interval u has elapsed since the last encounter, p_u is the probability that the time until the next encounter is exponentially distributed with intensity γ_1
p_{rand}	Probability that a randomly sampled predator will encounter the next prey according to an exponential distribution with intensity γ_1. In the H_2 interpretation this is equivalent to the probability that a randomly sampled predator is doing interpatch foraging
$p_i(0, t)$, $i = 0, 1$	The probability of no encounters up to time t given that the predator was in state i at time 0. State 0 = interpatch area; state 1 = patch area
$p(0, t)$	The probability of no encounters up to time t, given that the predator is occupying state i with probability π_i at time 0, i.e. the probability of no encounters in an interval of length t for a stationary process
$P\{A \mid B\}$	Conditional probability. The probability of event A given event B has occurred
$p_{ij}(0, t)$	The probability of no encounters up to time t under the condition that the predator is in state i at time 0 and in state j at time t
$\mathbf{P}(0, t)$	Matrix with the probabilities $p_{ij}(0, t)$
$p_{ij}(n, t)$	The probability of n encounters up to time t under the condition that the predator is in state i at time 0 and in state j at time t
$\mathbf{P}(n, t)$	Matrix with the probabilities $p_{ij}(n, t)$
$\mathbf{P}^*(0, s)$	The Laplace transform of the probability $P(0, t)$
$\mathbf{P}^*(n, s)$	The Laplace transform of the probability $P(n, t)$

p.d.f.	Probability density function
PNR	Point of no return, referring to the point in time where a starving animal is too weak to feed
r_{prey}	Equivalent spherical radius of prey particles
r	Random variable denoting the closest distance from the centre of a spherical patch that the predator will come when passing through the patch
R, R_{patch}	Radius of spherical patches
s	Parameter of the Laplace transform
$Stdv(X)$	Standard deviation of the interencounter time
t	Specific time value. Used with X and N_t
t_{crit}	Critical time unit or relaxation time determining the speed at which e.g. the index of dispersion approaches IDC_∞
T	Random variable denoting the time to the first feeding
u	Mixing probability of the mixed Poisson distribution, i.e. with probability u the number of encounters will be distributed according to a Poisson distribution with parameter $\gamma_1 u$
$v_{1\ pred}, v_1$	Swimming speed of predator inside patches
$v_{0\ pred}, v_0$	Swimming speed of predator in the interpatch area
v_{pred}	Swimming speed of predator when assuming constant speed
V_{patch}	Average patch volume
$V(N_t)$	Variance of the number of encounters in the interval $(0, t)$
$V(X)$	Variance of the interencounter time
W	Random variable denoting the distance travelled through a spherical patch by a predator travelling at a constant speed
w	Specific value of the variable W described above
X	Random variable denoting the interval between successive encounters referred to as the interencounter time or interarrival time
x	Specific value of the interencounter time, $X = x$, indicating the value of the interval between successive encounters
β_{prey}	Prey search volume rate of predator
β_{patch}	Patch search volume rate of predator

γ_1	Second parameter of the H_2 distribution. In the H_2 patch scenario γ_1^{-1} is the mean time between two successive encounters within a patch
γ_2	Third parameter of the H_2 distribution. In the H_2 patch scenario γ_2^{-1} is the mean time between two successive encounters when the predator leaves the patch
ϵ	Probability of successful pursuit, i.e. an encounter leads to ingestion
λ_0	Rate of prey encounters assuming a non-patchy environment, i.e. the food particles are assumed to be completely randomly distributed in space. Parameter of the environmental representation of the IPP
λ	Rate of prey encounters when the predator is moving inside a patch. λ^{-1} is the mean interencounter time as long as the predator is foraging inside a patch
η	Fraction of the sea occupied by patches. Parameter of the environmental representation of the IPP
ρ	Density of food particles (prey) randomly distributed in space
$\rho_{0\text{prey}}$, ρ_{prey}	Density of food particles in the case of a non-patchy environment and the higher intrapatch density, $\rho_{\text{prey}} = \eta^{-1} \cdot \rho_{0\text{prey}}$, when these food particles form a patchy environment
μ	Mean value of the time between encounters
μ_{samp}, μ_{res}	Mean value of the time to next encounter and time between the preceding and the next encounter for a randomly sampled predator
$\pi_1, \pi_0, \pi_1(t), \pi_0(t)$	Stationary and time varying probabilities of being in state 1 (patch area) or in state 0 (interpatch area)
ω_1	Rate by which the predator leaves a patch. ω_1^{-1} is the mean patch residence time
ω_2	Patch encounter rate. ω_2^{-1} is the average time spent on encountering a patch
τ	Specific value, $T = \tau$, of the time to first feeding
ξ	The ratio between the patch encounter rate and the prey encounter rate of the equivalent non-patchy scenario. ξ^{-1} denotes the average number of food organisms the predator encounters in the non-patchy case during an average patch search time. Parameter of the environmental representation of the IPP.