



Markovian Building Blocks for Individual-Based Modelling

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Publication date:
2007

Document Version
Publisher's PDF, also known as Version of record

[Link back to DTU Orbit](#)

Citation (APA):
Nilsson, L. A. F., Nielsen, B. F., Thygesen, U. H., & Beyer, J. (2007). Markovian Building Blocks for Individual-Based Modelling. (IMM-PHD-2008-171).

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Markovian Building Blocks for Individual-Based Modelling

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Kongens Lyngby 2006
IMM-PHD-2006-XX

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IMM-PHD: ISSN 0909-3192

Summary

The present thesis consists of a summary report, four research articles, one technical report and one manuscript. The subject of the thesis is individual-based stochastic models.

The summary report is composed of three parts and a brief history of some basic models in population biology. This history is included in order to provide a reader that has no previous exposure to models in population biology with a sufficient background to understand some of the biological models that are mentioned in the thesis. The first part of the rest of the summary is a description of the dramatic changes in the degree of aggregation of sprat or herring in the Baltic during the day, with special focus on the dispersion of the fish from schools at dusk. The next part is a brief introduction to Markovian arrival processes, a type of stochastic processes with potential applications as sub-models in population dynamical models. The last part introduces Markov additive processes as a means of simplifying some individual-based models.

In the first part I present the background to article A and some extra material that were not included in the final article. The basic observation is that fish in schools migrate up toward the surface and disperse at dusk and aggregate in schools close to the bottom at dawn. This creates a periodically varying prey field to cod. Apart from humans, cod is the main predator of herring and sprat in the Baltic. In order to evaluate the consequences to cod of this variability it was necessary to describe this prey field. It was shown that the schools follow lines of constant light intensity and that they disperse below a critical light threshold. We propose that the dispersion is due to a random walk when light levels become sub-critical and provide time-scales for the dispersion of this type for different school geometries (random or on a regular square grid)—the time-scales are of the same order as those observed on the echosounder.

The second part is an introduction to Markovian arrival processes (MAPs), this is the background needed to understand papers C, B, E, and F, given some previous exposure to Markov chains in continuous time (see e.g. Grimmett and Stirzaker, 2001)). Markovian arrival processes are very general point processes that are relatively easy to analyse. They have, so far, been largely unknown to the ecological modelling community. The article C deals with a functional response in a heterogeneous environment. The functional response is a model of the mean ingestion rate of prey per predator as a function of prey and possibly predator density that appears in most models for populations. A previously proposed model for prey encounter in heterogeneous environments is reanalyzed, it is a stochastic process that easily can be implemented as a MAP. In article C we show that transferring a standard functional response to a heterogeneous environment does not preserve the functional form, contrary to previous assertions. In this simple case we provide a time-scale for when the heterogeneous environment can be assumed to be well-mixed, or close to a Poisson process, for the predator. It is also shown that in some cases the variability may be more important than the mean, thus the mean rate does not necessarily provide sufficient information for the population dynamics. Article B provides the mathematical apparatus for evaluating *any* moment of a MAP, and also the means for evaluating the *conditional moments* of a transient or terminating MAP. Transient MAPs are suitable as modelling tools when an important property of the system is that it can stop. This is the case for the young of many animals, where most of a large clutch die rather quickly, and yet it is the survivors that are interesting. The conditional moments can for instance be constructed such that one can evaluate the mean or the variance of the ingestion rate *given* that the animal did not die. Several different methods are used to obtain the formulas, which is an interesting aspect since some of these methods may be more suitable in situations where it is problematic to proceed using the standard formalism.

I provide material on how to model periodic MAPs in paper E. These are, or could be, important since most animals live in a periodic environment and a periodic system generally have dynamics that are different from the corresponding system with mean rates. The technical report F concerns how to model Markovian stomachs. Both aspects can be used in more advanced functional or numerical responses.

The third part concerns a larger class of Markov processes, to which the above mentioned MAPs belong. These are the Markov additive processes, which are bivariate Markov processes (X_t, N_t) where the transition probabilities depend on the X_t process only. The X_t process is marginally a Markov process, and the N_t process is a process with conditionally independent increments given the state of the X_t process. This class is rich enough to provide substantial realism into individual-based models yet it is so simple that it is not a great extra burden to solve the partial differential equations (PDEs) that arise for the evaluation of the moments. They are particularly useful in oceanographic contexts since

here the apparatus for solving the PDEs is usually present due to the need of solving fluid flow equations. The greatest benefit of the method is due to that it *circumvents* the need for statistical evaluation of the individual-based models.

In all three parts further work has been proposed.

Preface

This thesis was prepared at the department of Informatics and Mathematical Modelling at the Technical University of Denmark in partial fulfillment of the requirements for acquiring the Ph.D. degree in engineering.

The project has been carried out in collaboration with the Danish Institute for Fisheries Research. The research was supported by the SLIP research school under the Danish Network for Fisheries and Aquaculture Research (www.fishnet.dk) financed by the Danish Ministry of Food, Agriculture and Fisheries and the Danish Agricultural and Veterinary Research Council, and by the DTU.

The subject of the thesis is the application of Markovian stochastic models to the dynamics of biological systems. The thesis consists of a summary report, four research papers written during the Ph.D. study (one published elsewhere, two accepted, one submitted), and two technical reports.

Lyngby, August 2006

Fredrik Nilsson

Papers included in the thesis

- [A] L. A. Fredrik Nilsson, Uffe Høgsbro Thygesen, Bo Lundgren, Bo Friis Nielsen, J. Rasmus Nielsen, Jan E. Beyer. Vertical migration and dispersion of sprat (*Sprattus sprattus*) and herring (*Clupea harengus*) schools at dusk in the Baltic Sea. *Aquatic Living Resources* 2003. 16: 317–324.
- [B] Bo Friis Nielsen, Uffe Høgsbro Thygesen, L. A. Fredrik Nilsson, Jan E. Beyer. Higher order moments and conditional asymptotics of the Batch Markovian Arrival Process. Manuscript accepted for publication in *Stochastic Models*
- [C] L. A. Fredrik Nilsson, Bo Friis Nielsen, Jan E. Beyer, Uffe Høgsbro Thygesen. Heterogeneity may change the functional response—lessons from a simple stochastic encounter model. Manuscript to be submitted to *Oikos*.
- [D] Uffe Høgsbro Thygesen, L. A. Fredrik Nilsson, Ken H. Andersen. Eulerian techniques for individual-based models with additive components. Manuscript submitted to *Journal of Marine Systems*.
- [E] L. A. Fredrik Nilsson, Jan E. Beyer, Uffe Høgsbro Thygesen, Bo Friis Nielsen. A framework for functional and numerical responses in periodic environments. Manuscript.
- [F] L. A. Fredrik Nilsson. Stomachs as stochastic dams. Technical report.

Acknowledgements

I thank my supervisors for the large amount of support given despite being busy with their own research projects. Dr. Bo Friis Nielsen for remaining calm at times of stress and for sharing both his vast insight in queues and his good humour. For always finding time to discuss things, always being constructive, and postponing the summer vacation to the autumn! Dr. Jan Beyer for long talks about the project and for all interesting ideas. I learned a lot in these discussions. Dr. Uffe Høgsbro Thygesen for the always funny discussions and for his voodoo-like mathematical feeling, enthusiasm and talent.

This research was supported by the SLIP research school under the Danish Network for Fisheries and Aquaculture Research and I'm grateful to Prof. Henrik Gislason for inviting me to apply for a SLIP studentship in the first place and for running the network so smoothly.

I'm also grateful for an extra financial support from DTU of three months which enabled me to finish this dissertation.

I would like to thank the staff at IMM, Prof. Henrik Madsen for a creative atmosphere. Professor Poul Thyregood for always being willing to discuss statistical issues with a happy smile and for imparting some feeling for the subject. My sincerest thanks goes to Jonna Pedersen, Anne-Mette Lund, Ellen Brorup and Ulla Nørhave for help with practical issues. Henning Christiansen, Poul-Erik Thampdrup and Mogens Dybdal for help with the binary counting device. Our librarian, Finn Kuno Christensen, for help with articles and books. My fellow Ph.D. students for interesting discussions and help, in particular my room-mate, the late Thomas Kaare Christensen, but also Drs. Klaus Kaae Andersen, Søren Nymand Lophaven, Lasse Engbo Christiansen and Karl Skoglund. Dr. Niels Hermann Hansen for interesting conversations about the philosophical foundations of probability.

I'm very grateful for all the help from the PhD office, in particular from Inge Olesen and Aase Grundtvig.

I would like to thank Prof. Ulla Holst and Prof. Jan Holst. They made it possible for me to stay at the Lund University for more than a year. During this time I had Prof. Georg Lindgren the room opposite mine, which it has been very stimulating both due to his great energy and for helpful pointers when I was in doubt. I thank the staff for a pleasant visit and in particular the ones that presented theses, which were very inspiring. Thanks to Azra Kurbasic for giving me a hint about the ECMTB'05 conference and Dr. Magnus Wiktorsson for pointers to the literature on Markov additive processes.

The staff at DFU helped me with articles, data and with interesting discussions. In particular Drs. Stefan Neuenfeldt, Ken Haste Andersen and Christian Möllman.

Dr. Bo and Alice Lundgren deserves a special thanks. Bo for long phone talks in the middle of the night during the proof reading of the first article. Both Bo and Alice for nice company in Montpellier and for surviving a taxi trip.

My friends and my family for all the help and encouragement, in particular Marcus Romberg read and commented on most of the introductory chapters and my mother and father for uncessant support.

Finally, I thank my wife Stina for her enourmous support, help and endurance.

Note added in proof: The dissertation took place before the printing of this thesis. This enabled me to adress some questions raised by the examination committee: Professor Helle Holst, Professor Patsy Haccou and Professor Per Lundberg. I'm very grateful for the work of the examination committee, for making the dissertation such a rewarding experience. I am particularly indebted to Prof. Haccou who borrowed me her copy of the thesis. All errors and obscurities that remain are of course my own responsibility.

Contents

Summary	i
Preface	v
Papers included in the thesis	vii
Acknowledgements	ix
1 Introduction	1
1.1 Contents of the thesis	8
2 An brief history of birth, death and analysis	9
2.1 Further reading	23
3 The schooling behaviour of clupeids in the Baltic at dawn	25
3.1 Introduction	25
3.2 Materials and Methods	28
3.3 Results	31
3.4 Discussion	33
3.5 Contributions	34
3.6 Future work	35

4	Markovian Arrival Processes (MAPs) as tools in population dynamics	37
4.1	An introduction to MAPs via the Poisson process	38
4.2	Functional responses	49
4.3	Stomach models	59
4.4	Numerical responses	61
4.5	Discussion	61
4.6	Contributions	62
4.7	Future work	63
5	Markov additive processes can simplify individual-based models	65
5.1	Introduction	65
5.2	Markov additive processes	70
5.3	The backward equations	72
5.4	Discussion	74
5.5	Contributions	75
5.6	Future work	76
6	Postscript	79
7	Conclusion	83
A	Vertical migration and dispersion of sprat (<i>Sprattus sprattus</i>) and herring (<i>Clupea harengus</i>) schools at dusk in the Baltic Sea	85
A.1	Introduction	87
A.2	Materials and methods	87
A.3	Results	96
A.4	Discussion	98
A.5	Conclusion	100
B	Higher order moments and conditional asymptotics of the Batch	

Markovian Arrival Process	103
B.1 Introduction	105
B.2 The Batch Markovian Arrival Process	106
B.3 Formulas for moment matrices	107
B.4 Asymptotic behavior of low order moments of the BMAP and the tBMAP	120
B.5 Higher order moments of RAPs (BRAPs)	125
C Heterogeneity may change the functional response—lessons from a simple stochastic encounter model	131
C.1 Introduction	133
C.2 The models	134
C.3 Results	138
C.4 Discussion	149
D Eulerian Techniques for Individual-Based Models with Additive Components	155
D.1 Introduction	156
D.2 A Markov additive process modelling larval transport and growth	158
D.3 Discussion	168
D.4 Appendix A. Ensembles of Markov Additive Processes	171
E A framework for functional and numerical responses in periodic environments	175
E.1 Introduction	177
E.2 Key results on Markovian Arrival Processes	179
E.3 Transient Markovian Arrival Processes with periodic rates	181
E.4 Example 1: A planktonic organism and diel vertical migration . .	186
E.5 Discussion	192
E.6 Appendix A. Asymptotic analysis	195
E.7 Appendix B. Numerical implementation	198
E.8 Appendix C. Introducing a switch	199

E.9	Appendix D. Generation of T-translated solutions	199
E.10	Appendix E. Solutions to recursions by induction	200
F	Stomachs as stochastic dams	205
F.1	Introduction	206
F.2	Model formulation	208
F.3	Solution for the stationary distribution for a square-root model .	210
F.4	Numerical issues	216
F.5	Discussion	221

CHAPTER 1

Introduction

Biology needs a new approach which takes the living entity as a fundamental, starting unit. Only then will it be possible to have a theoretical biology which will have relevance to the needs of biologists.

Niels Bohr

Atomic Physics and Human Knowledge, 1963, p. 9.

This thesis concerns stochastic models and sub-models aimed at being tractable and applicable in fisheries models and population dynamical models and in particular individual-based population models. My aim in this theses is to use stochastic models as far as possible since I believe that these are both more fundamental and more appropriate in much of biological modelling than deterministic models. Stochastic models are more fundamental since, even if I agree with Bohr's assertion, there are always things that are left out when a model is made even if the model starts from the individual. These omissions may simply be ignored or included in the sense that there is uncertainty or stochasticity in the dynamics of the epiphenomenon, the population dynamics. These uncertainties may be due to differences in dynamics of subprocesses such as the individual hunting success, that individuals *are* different, that local conditions are different and that external factors, such as weather are unspecified. Some think that Lotka-Volterra models (a system of ODEs representing the time evolution of densities of species, ignoring differences in age and state) are fundamental in

biology, but I disagree. I think that multi-type birth-death processes are fundamental in population dynamical modelling on a similar level of abstraction as the Lotka-Volterra models. Since individuals produce offspring, the number of which is a positive integer, but the actual number is often random as is the time of reproductions as well as time of death. The continuous densities of animals used in Lotka-Volterra is a neat and often convenient abstraction, but sometimes it may be dangerous, e.g. the atto-fox phenomenon where concentrations of foxes with rabies that are effectively zero cause a “false” secondary wave of rabies invasion (see e.g. Mollison, 1991). Stochastic models are more appropriate to use in practical situations for the same reason; there are many things which the population dynamics depend upon which are either hard to specify, such as how an individual in the population allocates energy to reproduction or growth, or intrinsically stochastic such as food encounter. Their obvious drawback is that they are more difficult to analyse in general than deterministic models. Sometimes it is even necessary to analyse the model by simulations, which is both tedious and less robust than analytical results.

The most important aspect of models is that we always create a theory or model for our object of study. This will consciously and unconsciously shape our thinking and influence what to measure and observe—our observations are theory laden (Kuhn, 1970). Mathematical models are seemingly the best way to formalize our thinking and to draw the conclusions of our assumptions; as Haldane put it “...an ounce of analysis is worth a ton of verbal argument” (Maynard Smith, 1965). Their drawback, as with any model, is that the analysis in itself do not tell us when the assumptions are wrong and often one seek an extremely simplified model in order to make it analysable. Nevertheless, even these simple models may sometimes increase our understanding of a system and allow us to make predictions or even to control the system. But it is interesting to note that there is a feedback mechanism where the choice of framework influences the conclusions; the deterministic Lotka-Volterra system show neutrally stable oscillations whereas the stochastic counterpart will always go extinct. Extinction was a great problem in the reverse engineering attempts of Gause (1934) who tried to get stable oscillations in a predator-prey system in the lab (see Renshaw, 1991, for more details). Many deterministic models are formulated using probabilities (see e.g. de Roos, 1996) but often the final model does not contain stochasticity. When the models are analysed one ignores that the size of the system may not justify the assumption of a very large population or that the limited abilities of predators e.g. to move between different areas in the system makes it impossible to assume that all parts are equal. It is important to note that I do not think that there are a single best model, but that I think that a model that incorporates uncertainty is more robust, and that models that can be tested empirically are more interesting than those that can not. It is almost a truism, since the model approximates a system a model that includes an error term that represents that approximation will be more true.

Models of biological populations are important since they may help us to manage resources such as fish stocks in a sustainable way. In my opinion, sustainable means that the current exploitation of a resource does not significantly impair the possibilities for future usage. These models can help us preserve diversity, which is important since many of us think that this has a value in itself, and since diverse systems may be more productive (Tilman et al., 2001). The economical side of it is important since it is the short-term profits together with the large uncertainties in these systems that cause us to sacrifice the long-term gains. This greediness together with a small chance that things will mend themselves, e.g. that the recruitment can be enormously successful which would save a declining population make it difficult for an elected decision-maker to cut quotas (Walters and Martell, 2004). The long-term consequences of bad management often lead to expensive remedies which would have been unnecessary if we were to manage our fish stocks in a better way (Baum et al., 2005).

Biological populations are demanding to model since not only do they inhabit heterogeneous environments, but the individuals create heterogeneities on their own; by their movements, by reproducing, and that they differ from each other. The movements may be away from bad conditions towards good, so if the good conditions are patchy so will often the population tend to be (if e.g. dispersal between patches is a relatively slow process and patches exist for times longer than the generation time of the colonizer). It is not necessary that the initial conditions are patchy, they may be in a smooth gradient. This together with peculiarities of animal motion will sometimes create patchiness (Rohani et al., 1997). Organisms can move towards conspecifics in e.g. schools which also generates patchy distributions, or they can actively avoid the neighbourhood of their relatives which generates regular distributions. Reproduction creates a spatial dependency between offspring and parent since they are at the same place when the offspring is born. Such dependencies are well known problems in e.g. chemical reaction engineering (Epstein, 1995) and physics (Young et al., 2001). Individuals are different due to different environmental conditions during growth and different genetical compositions. The latter is very important since fisheries act as a selective predator, which tend to remove the largest fishes first (Ward and Myers, 2005). If there is differential mortality in a heritable trait, such as length of first reproduction, this will lead to evolutionary change. Such changes in natural populations of higher organisms has long been thought to be slow, but has been shown to occur quickly in both laboratory systems, such as Nicholson's blowflies (Stokes et al., 1988) and rotifers (Yoshida et al., 2003) as well as in the wild e.g. in Darwin's finches (Grant and Grant, 1993) and in fish (Reznick et al., 1997; Heath et al., 2003; Olsen et al., 2004; Shuter and Abrams, 2005). This is, in my opinion, the second most important task of population biology, maintaining sustainable populations, the first task, in such a way that we do not select for e.g. smaller and smaller cod, such that we in the end threaten the populations due to evolutionary change.

Many of the early models of modern population dynamics are based on an analogy with chemical reactions. The system is well-mixed and the reaction rates are low, when an “atom” of the prey type collides with an “atom” of the predator type the predator “atom” immediately annihilate the prey and produce a new predator “atom” or a fraction thereof. This fraction should be perhaps be interpreted as a probability of predator production since the “atoms” are identical. In chemical systems this would not necessarily be a problem since here 10^{23} is a relatively small number and the variations in the “atomic” interactions may average out, but not in population biology. Even in chemical engineering “well-mixing” is a Platonic ideal which is never met in reactors, and the deviations from it may be of utmost importance (as shown in e.g. Epstein, 1995).

My initial goal was to try create a population dynamical model where I would like to incorporate the fact that organisms are not identical “atoms” fizzling around and haphazardly bump into each other, but agents that sense and react to both their environmental conditions and their internal state. The internal state could be the energy reserves, hungry animals will try to find food more actively and starving animals will perhaps try even harder or for instance hibernate. The internal state could also be that the gonads are ripe, that the animal has a nest, or nestlings (see Mangel and Clark, 1988; Houston and McNamara, 1999; Clark and Mangel, 2000, for more examples). The effect of adaptive predator-prey behaviour has been studied in deterministic models (Abrams, 2005), but these have ignored differences in state. I believe that there could be interesting frequency dependent effects in an individual-based stochastic optimization model due to the fact that the resident strategy may be or become unstable or perhaps stabilising features due to the individual differences, there will often be some animals that are in a worse condition than other conspecifics. For instance suppose that prey can divert energy to defense at a cost in terms of reproduction, and that predators are able to divert energy against this defense with a reproductive cost. If the prey population is grazed down it will pay to defend oneself but it may be so that at some point the predator numbers are low enough to make the prey switch strategy. Then the remaining predators will change their strategy. Moreover, the incorporation of stochastic population dynamics would be different from the Lotka-Volterra type of equations that appear when the objective only is to maximize reproductive rate (Brown and Vincent, 1987; Abrams and Matsuda, 2004; Nowak and Sigmund, 2004) and between the mean-field equations of adaptive dynamics (Dieckmann and Law, 1996). The latter assume that the population dynamics are much faster than evolutionary dynamics.

Closest to my intended approach is probably Shertzer and Ellner (2002a) and Alonzo (2002). Shertzer and Ellner (2002a) studied the evolution of energy allocation strategies in the rotifer *Brachionus* using deterministic equations, and a genetic algorithm to find the optimum strategy. They found that no stan-

standard proxy for evolutionary goal function could describe the optimal strategy. Unfortunately, they did not study the evolutionary change in prey, which is more commonly observed (Johnson and Agrawal, 2003). Alonzo (2002) studied a Markov decision game between predators and prey. Here the predators and prey could choose between placing themselves in a rich or a poor patch, with perfect information. There were no changes in the population numbers, which is an interesting and relevant complication which I had hoped to be able to incorporate into my model. Moreover, the discrete dynamic games often have to include a certain amount of decision error in order to attain a stable strategy, which may not be necessary in the continuous time setting (cf. the logistic difference equation with the logistic differential equation). Alonzo (2002) noted that there has been a relatively clean cut between studies on the behavioural time-scale e.g. optimal foraging theory, where the importance of state has been recognized and that individual actions depend on other actors such as conspecifics and predators, and the population time-scale where such effects have largely been ignored, the main focus has been to describe the interaction between species.

I intended to base the model on data from the Baltic Sea, since the Baltic proper is a relatively simple system with few species. The purpose of this link to reality was to make it less probable to create a completely irrelevant model, e.g. simply by restricting the parameter space. In the Baltic proper sprat and herring are dominant planktivores and adult cod are top predators. The drawback with the Baltic Sea is that it is strongly forced by environmental conditions since the reproduction of the Baltic cod depends strongly on the inflow of fresh, aerated saltwater. Inflow occurs when there are strong winds over the sill, conditions which do not occur every year.

It would be natural to try to define a model where the food of the clupeids is spatial and continuous in time. This would give a staggering state space if one also would like to let the clupeids make their decision based on time of year and their internal state. It would be necessary to limit the states e.g. the environment could be defined on a coarse grid, with discrete states and transitions between seasons, the location of the clupeids and cod could be close to bottom or up, the internal states could perhaps be described by five internal states, yet this would give rise to an extremely difficult model. Some difficulties could possibly be solved using time-scale separation techniques, that it is possible to interpolate the decisions between days. The state of the system as a whole would depend on these individual daily decisions. This is problematic since the reproductive output and timing ought to be dependent on the environmental conditions, or as Charles Elton put it in 1930 (Hutchings, 2000): "Changes in the population of one animal are really changes in the habitat of other animals", and perhaps even more so since the change in the behaviour of one individual will change the environment of its conspecifics too. Thus the reproductive behaviour will depend on the behavioural interactions and the environment, which is periodic. When should the individuals of a certain species spawn in order to maximize their

reproductive value in some appropriately chosen future time? Cod has shifted its time of reproduction in the Baltic, which suggest that time of reproduction should be included as a decision variable (Hinrichsen et al., 2002).

As is common in many models of stochastic dynamic programming models there will be an enormous number of parameters concerning both the dynamics and the interactions at the behavioural and the reproductive time-scale—together these would form a very difficult system to analyse or to estimate the parameters. In optimal stochastic population dynamics this problem would be even worse due to the feedback between individual decisions and the state of the system, since this is a dynamic game. The great value of mechanistic models is, in my opinion, that it easier to give parameter values a meaning to see if they are reasonable or not. They provide functional relationships that provide basis functions for statistical analysis of data and are useful as submodels. It should be noted that this usefulness is not stronger than the assumptions, e.g. the Holling II functional response may be useless in a heterogeneous environment as shown in Article C. Nevertheless, mechanistically based models tend to be more robust than black-box models (Hilborn and Mangel, 1997).

The present work is far from the ambitious, and somewhat vague goal of optimal stochastic population dynamics, which would have needed a theoretical study on its own. (The goal is vague since it is uncertain what the goal function should be if Shertzer and Ellner (2002a) are right, or even how to analyze such a model with the ensuing large state-space if population numbers are allowed to change). But there are small bits and pieces that fit in. The aim of the work that preceded Article A was to describe the daily variations of the schooling behaviour of clupeids in the Baltic. If this work can be supplied with data of the pattern over the year and ancillary information on when, where and on what cod feeds it would give a picture of the profitabilities of different strategies during the day. This should be supplemented with data on with what success cod attacks clupeids in different states, and when and what clupeids eat. A difficulty here is to value the alternative; how should one define the possible gains and costs for a sprat which abandons its school and searches for food on its own if that never happen? The goal of describing the aggregation and dispersion of clupeids in the Baltic was far from reached. In Article A we described the dispersion pattern for 3 days, and found that the assumption of dispersion by means of Brownian motion could not be rejected. There was a link between schooling behaviour and light, such that the schools followed the declining light in a migration towards the surface or dispersed. The aggregation process remains unstudied but perhaps it could be due to some aggregation-fragmentation process (see e.g. Anderson, 1981; Niwa, 1998). It would be necessary for strong conclusions on these matters to have information of how the individuals of a dispersing school behave. Moreover, the relations between the internal state of individual fish to these phenomena are even less known, but see the laboratory studies of Krause et al. (1998) and Hensor et al. (2003).

The Markovian arrival process can be used as a neat device to derive functional and numerical responses. In particular this could come in handy when trying to capture the essence of the predatory interaction between cod and herring. Since schools form a rather extreme patchiness this could have large effects on the decisions of a cod to forage or not. On the other hand a cod could possibly follow a school during the day, attack when and if they are dispersed during foraging bouts of the sprat, and focus on feeding during dusk and dawn, if this is when clupeids are most active and easy to catch.

The daily shifts in light intensity provide a strong periodic variation that probably affects the profitability of feeding in cod. In order to explore these assumptions it was necessary to study periodic Markovian arrival processes (paper E) to find out what the consequences are to the cod. It could be objected that there is no decision in the Markovian arrival processes in general. But that is relatively easy to include, when and if one is able to specify the transitions between different states when different actions are chosen. A decision process based on the MAP has been developed by Hordijk and Koole (1992), called the Markovian decision arrival process (see also Altmann and Koole, 1993).

Mortality is an important factor in the life of many organisms, particularly the young. Since the risk of death is vital in the choice between different actions in the applications of Markov decision processes to ecological problems, we studied the conditional moments of Markovian arrival processes, which forms the basis of the article B. Here the derivations are done in full generality, but the aim is to be able to provide model input of e.g. the average ingestion rate of a survivor to another model on a longer time-scale.

It has been pointed out that the dynamics of the digestive apparatus constrain the energy assimilation of many organisms (Jeschke et al., 2002). Thus this may limit the value of different actions; it would be very costly to forage when the stomach is full. In Paper F I made an attempt to apply new results on fluid queues by Bekker et al. (2004) to the modelling of stochastic stomachs.

Finally, in Article D we take advantage of the Euler-Lagrange dichotomy in physics, where it is possible to either follow the particle (Lagrange) or to describe its probability distribution (Euler). Here we provide a framework for studying the evolution of “marks”, a property that the organism accumulates or loses during the path of the particle. This property could for instance be length, energy reserves or number of eggs. This has direct consequences for much of individual-based modelling, where the stochasticity inherent in a simulation is overridden. The advantage of this framework is that one avoids the relatively costly and imprecise simulation and instead works with probability distributions, or moments of these probability distributions (for the marks). The even simpler framework of Markovian IBMs could be useful in some epidemiological models (e.g. Hufnagel et al., 2004).

With further knowledge on branching processes and some measure of how strong mixing is necessary to make pair-correlations between offspring and parent sufficiently weak, which would enable reproduction to be included, this can have strong impact on the individual-based modelling community. Moreover, it would be interesting to study the relations between super-processes, or branching Brownian motions, and their Eulerian representation, to look for tools in modelling situations where the spatial dependencies are not weak.

These are small steps towards the goal of producing an individual-based population model with optimal behaviour. But that may come some sunny day.

1.1 Contents of the thesis

The thesis is organized as follows:

Chapter 2 contains a brief account on the models and methods of population biology based on the history of its development. The aim of this is to provide the background to the “basic” models of population biology to readers who have no previous experience of these. I have paid some extra attention to previous work on stochastic processes due to their presumed importance (to me), but also because it is interesting that e.g. Bartlett (1957) was so ahead of his time.

Chapter 3 provides an introduction to the temporally varying environment of a cod, in particular the distributional changes at dusk of schools of sprat and herring, the main food of large cod in the Baltic. These changes ought to be important in the foraging success of the cod.

In chapter 4 there is a brief introduction to Markovian arrival processes, then some example of their uses as tools to explore the ingestion and reproduction processes. In particular Markovian arrival processes can be used as devices to develop functional and numerical responses.

The Markov additive processes are a natural generalization of the Markovian arrival process. The simplifications of the Eulerian analysis of individual based models due to a Markov additive structure are presented in chapter 5 .

Chapter 7 contains a brief conclusion.

The last chapter of the summary is an afterword on what the implications are for the modelling of biological populations or perhaps the human interaction with biological populations.

Appendices A–F contain the papers that the thesis is based upon.

CHAPTER 2

An brief history of birth, death and analysis

Death is a lonely business.

Ray Bradbury 1985.

(Births are not, which is a biologically important point.)

The purpose of this chapter is to provide a brief historical background to the main notions and models in population biology.

Since taxation and prognoses thereof probably were one of the main tasks of early mathematicians there were almost certainly demographic studies and models from the early civilisations, but these are unknown to me. I include demography in population biology since even if there typically are differences in the amount of data that is available in human and non-human populations the task is essentially the same; to describe the time trajectory of a population whose components grow in age and size, move, produce offspring and die. Another reason for incompleteness is Stiegler's law of eponymy: "No law, theorem, or discovery is named after its originator" (Grimmett and Stirzaker, 2001, p. 19), which evidently is at work in this area too.

In 1202 Leonardo Pisano *alias* Fibonacci published a work on mathematics (reprinted in Pisano, 2003), which appears to be a resumé of what he has learnt from some Arabic masters which he had visited. Not only did he introduce

the Arabic numbers to the ignorant part of Europe but he also presented a population model on the growth of rabbits which shows geometric growth in an asymptotic manner. Geometric growth is so simple and has been known for so long that it has no name attached to it¹, it is simply that the present population size x_t is proportional to the population size at the previous time x_{t-1} . Thus $x_t = ax_{t-1}$, and if x_0 is known then $x_t = a^t x_0$, whence it is seen that if $a > 1$ then the population will explode and if $a < 1$ it will die out. The structure of Fibonacci's model is such that the population is composed of adult and juvenile pairs, there is no death and we start with one juvenile pair. Each adult pair get exactly one juvenile pair each month. The juvenile pairs will become fertile or adult the next month and contribute to the growth of the population. The total number of pairs at time $t + 1$ is $x_{t+1} = x_t + x_{t-1}$ with initial conditions $x_0 = 1$, $x_1 = 1$. This is a difference equation where the population asymptotically grows geometrically $x_{t+1} \sim \phi x_t$ when $t \rightarrow \infty$ with rate $\phi = \frac{\sqrt{5}+1}{2} \approx 1.618$ which is the famous golden ratio. That $\frac{x_{t+1}}{x_t} \rightarrow \phi$ as $t \rightarrow \infty$ was a discovery of Kepler. Interestingly, the Fibonacci sequence $\{x_t\}_{t=0}^{\infty} = 1, 1, 2, 3, 5, 8, \dots$ is encountered in many places in Nature, e.g. in the arrangement of seeds in sunflowers, the spirals of cones (which is called phyllotaxis, see Jean, 1994) and the shape of the nautilus.

In 1760, Leonhard Euler made one of the first contributions to the growth of age-structured populations and the stable age-distribution. If b_x is the number of offspring produced by an animal of age x and l_x is the survival probability to time x then the Euler-Lotka equation states that $1 = \sum_x e^{-rx} l_x b_x$ where r is the rate with which a population with stable age structure grows, under the assumption that l_x, b_x are constant. Euler states that this may not be true due to plague and war etc. thus recognizing some of the limits of deterministic and time-homogenous growth. He also dealt with economical problems such as the fair annual pay from a fund during the life-time of a person of age x who have deposited an amount of money in the fund, similar considerations were later used by Fisher to explain natural selection, and in particular reproductive value. The same year Daniel Bernoulli presented his analysis on small-pox and vaccination, but publication was delayed to 1766. Using the expected gain in life expectancy and the number of infants saved Bernoulli argued in favour of inoculation of small-pox. Bernoulli's analysis was based on life-table data by Edmund Halley, the astronomer.

Thomas Malthus proposed what has later been called the Malthusian law in 1798 where population growth is exponential. Surely exponential growth was known to Euler and before him, Newton and Leibniz, but perhaps Malthus got

¹But many riddles, such as the inventor of chess (or Krishna) and the king, where the King thinks it is a low price for losing a game of chess to put one rice corn on the first chess square and then two on the next and so on until the last square; the total weight is approximately $4.6 \cdot 10^{12}$ kg. Ambalappuzha Sri Krishna Temple in Kerala apparently serves a certain rice dish to celebrate this.

his name linked to the differential equation because of the conclusions drawn; that unbounded population growth would be controlled by war, sickness and famine. The ordinary differential equation for $N(t)$ is the population density at time t is

$$\frac{dN}{dt} = r \cdot N$$

and r is a constant. The solution is $N(t) = N_0 e^{r \cdot (t-t_0)}$, where N_0 is the initial population at time t_0 and it easily seen that if $r > 0$ then the population explodes and if $r < 0$ then it will decay to zero. A funny thing is that the Malthusian argument is that growth of populations is geometrical whereas growth of resources is at most linear which will cause famine; the reasoning was made in discrete time. The constant r is known as the rate of population growth or the Malthusian parameter.

Verhulst (1838) introduces the logistic growth where the exponential growth is dampened by the catastrophic factors in Malthus' model or competitive interactions. This is also within the differential equation framework:

$$\frac{dN}{dt} = r \cdot N \left(1 - \frac{N}{K} \right).$$

The equation was more or less forgotten and was rediscovered by Pearl and Reed (1920). It has an attractor for positive densities when $r > 0$ and $K > 0$; this means that all positive initial populations will eventually end up in $N = K$. There was a stupid paradox (see Gabriel et al., 2005), if r negative then positive population growth occurs for initial populations that are larger than K . The paradox comes from the fact that it is very useful mathematically to factor the terms in the analysis of population models. The model says that there is growth due to the numbers aN and less growth due to crowding $-bN^2$ using scaling, $b = \frac{a}{K}$. However the creators of the paradox seem to have forgotten "the interalienable right to think while using any technique" (Segel and Slemrod, 1989). The Verhulst-Pearl model can be interpreted such that both the birth rate and the death rate as a function of population size are quadratic functions $B(N) = bN + cN^2$, respectively $D(N) = dN + eN^2$. The population dynamics is, in the absence of immigration and emigration, controlled only by births and deaths. Thus $\dot{N} = (b-d)N - (e-c)N^2$ and in order to have interesting dynamics at low densities it is necessary that $b > d$ and in order to have stabilization at high densities that $(e - c) > 0$. Of course it is also biologically possible that $b \leq d$; the population dies out for all initial values. Were $e < c$ in this latter situation the model is ill-posed, there has to be higher order terms to correct for it.

Allee (1931) noted that in many cases there is a minimum population density needed for positive growth, and that the population will decrease when below this density. This effect may be due to social interactions between individuals or

e.g. that they are less able to defend themselves from predators at low densities. Thus while logistic population growth has a growth rate with a single maximum, the Allee effect creates growth rates that are negative in a range $(0, N_{min})$ and then positive for $N \in (N_{min}, N_{max})$ and then negative again for $N > N_{max}$. That population growth is dampened by the population size has been called “the logistic law”, but there are many functional relations that produce damping. For instance, already (Feller, 1939b) noted that many S-shaped functions fit the logistic data present at that time.

The origin of species was published in 1859. Although not very mathematical this work marks the beginning of modern biology, and as Dobzhansky put it in a famous essay in 1973: “Nothing in biology makes sense except in the light of evolution”, which of course is an exaggeration, but a rather mild one.

Darwin’s half-cousin Francis Galton asked about the extinction probability of family names in 1873 in the Educational Times. Watson provided an answer and together they wrote a paper on branching processes or Galton-Watson processes in 1874. Bienaymé had found these results earlier, and published them in a relatively obscure journal in 1845. Thus these are sometimes denoted Bienaymé-Galton-Watson processes. Oddly enough Bienaymé dealt with the same question as Galton-Watson; the extinctions of family names. The branching process starts with an initial population N_0 , the present number of males in a certain family in Galton’s example. Each male i in N_0 produce a random number of male offspring $X_0^{(i)}$, independently of the others. Then $N_1 = X_0^{(1)} + \dots + X_0^{(N_0)}$. The process continues as long as $N_i > 0$. Branching processes has found applications in nuclear reactor engineering and in biological populations, primarily in epidemiology. From an applied biological viewpoint it appears to me that too much emphasis has been put on asymptotic properties, such as with probability 1 this population will go extinct or explode, but, using numerical methods, Markovian multi-type branching processes in continuous time (see Dorman et al., 2004) seem to have much to offer to biology.

Alfred J. Lotka speculates on the possibility for oscillations in chemical reactions in 1910. In 1920 he presents a pair of coupled ordinary differential equations that are able to produce such oscillations. Interestingly, in 1921 Bley was able to produce similar oscillations in a simple chemical system, but these results were ignored since it was thought that these violated the second law of thermodynamics (see Murray, 1993, p. 141). Vito Volterra (1926) attempts to explain the fluctuations of fishes in the Adriatic. The system of ordinary differential equations were for the density of prey, N , and predators, P . They are identical to Lotka’s equations for chemical oscillations.

$$\begin{aligned}\frac{dN}{dt} &= aN - bPN \\ \frac{dP}{dt} &= cPN - dP,\end{aligned}$$

where a, b, c, d are positive constants. This set of equations exhibit neutrally stable oscillations, which can be seen from the phase-portrait, i.e. solving for N as a function of P , this provides a Lyapunov function (roughly a function that represents a positive quantity, such as energy in mechanical systems, if the time-change in this function is negative for all N , and P then energy is lost and there is a stable equilibrium and the system comes to rest at the point where the energy function is zero. In the Lotka-Volterra system the “energy” is preserved which corresponds to closed orbits). Note that these equations contain no spatial information, no age or stage-structure and that the interaction is based on the law of mass action or the law of Guldberg-Waage; the reaction rate is proportional to the product of the concentrations of P and N , this means that prey immediately turn into reproductive predators.

Lotka also made important contributions to age-structured populations. He derived the Lotka-Euler equation in 1907 which is the Euler-Lotka equation in the integral setting $1 = \int_0^\infty e^{-rx} l(x) m(x) dx$. He studied age-structured populations (Sharpe and Lotka, 1911) using integral equations. Let $B(t)$ be the number of births at time t , $b(a) da$ the (expected) reproductive output of an individual of age $[a, a + da]$, and $n(a, t)$ the number of individuals of age a at time t . Then

$$B(t) = \int_0^\infty n(a, t) b(a) da$$

Assume that the age-structure is stationary then $n(a, t)$ are the surviving individuals born at $t - a$, $B(t - a)$. Introduce the survival function, the probability to survive to age a , $l(a)$. Then, since $n(a, t)$ are the surviving newborns at time $t - a$,

$$B(t) = \int_0^\infty B(t - a) l(a) b(a) da. \quad (2.1)$$

Lotka assumed that $B(t) = K e^{rt}$ which gives the Lotka-Euler equation.

McKendrick (1926) and von Foerster (1959) provided an equivalent PDE formulation. Define a mortality rate $m(a)$ at age a . Then the number at age a satisfies

$$\frac{\partial n}{\partial t} + \frac{\partial n}{\partial a} = -\mu(a, t) n(a, t)$$

with boundary condition $n(0, t) = \int_0^\infty n(a, t) b(a) da$. There were intense work in the PDE formulation of general stage- and age-structured populations (see Metz and Diekmann, 1986), but it was found that PDEs are more difficult than the integral equations since the former have to deal with unbounded operators if there are jumps in rates since the derivative of that rate is infinite. Diekmann et al. (1998) formulated general linear physiologically structured population equations using the integral formalism, these lead to renewal equations, i.e. equations of the same type as equation (2.1). Naturally, there are non-linear interactions between the environment and the individual who is growing up, such

as density dependence (Gurtin and MacCamy, 1974), predation and cannibalism which lead to more difficult situations, which are dealt with in the single species formulation by Diekmann et al. (2001).

Volterra (1931) also considered competition processes; for instance when there are two species N_1 and N_2 which are governed by the following system:

$$\begin{aligned}\frac{dN_1}{dt} &= aN_1 - bN_1^2 - dN_1N_2 \\ \frac{dN_2}{dt} &= cN_2 - dN_2^2 - fN_1N_2,\end{aligned}$$

where a, b, c, d, e, f are positive constants. Will only one species survive or can they coexist? In a bold attempt of reverse engineering Gause (1934) tried to create a model system which could reproduce the Lotka-Volterra predator-prey equations. Gause had large difficulties in producing oscillations since the populations tended to go extinct rapidly. Even when there were refuges the predators became extinct and then the prey emerged from shelter. Only by adding one predator and one prey with regular intervals was he possible to obtain oscillations without extinction. In this work Gause also studied competition and logistic growth. The competition experiments lead to the conclusion that the stronger competitor always wins. This is not true if the interspecific competition is small enough and $\frac{b}{a}, \frac{d}{c}$ are about equal (see Murray, 1993, p. 78). Park (1954) studied a system of two different species of flour beetles (*Tribolium spp.*) which in certain circumstances had the interesting phenomenon that the outcome of equal initial conditions were that either species was out-competed. This lead to stochastic models by Leslie (1958) and Neyman and Scott (1959), where the state of the population may be seen as a ball on a saddle, and stochastic fluctuations will make it fall on one side or the other (see Renshaw, 1991, for more details). In a beautiful field-work combined with simple deterministic models Tilman (1994) showed that natural disturbances in the prairie lead to the persistence of several species of grass, whereas undisturbed competition experiments always led to monocultures of the stronger competitor. It was found that competitive abilities were negatively correlated with colonizing abilities; the least competitor was the best colonizer and the strongest was the worst. This work shows on the importance of disturbances and space and, in particular, biological trade-offs. Moreover it shows that it is not always relevant to look for the asymptotic outcomes of an unperturbed system if it always is perturbed (Hastings, 2004). Thus, fluctuations may provide the opportunity for another individual or species to survive.

Kermack and McKendrick (1927) created an important model class in epidemiology the SIR-model. The populations is divided into three groups S, susceptible, I, infected, and R, removed, i.e. dead or cured and not susceptible. Using a simple ODE-system, they found a good fit to the Bombay plague epidemic in

1905-1906. The system of equations is:

$$\begin{aligned}\dot{S} &= -rSI \\ \dot{I} &= rSI - aI \\ \dot{R} &= aI\end{aligned}$$

This class of models, SI, SIS, TSIR (T=time series), SIRS etc. are still fundamental in many epidemiological studies, where the stochastic (Bailey, 1964) and spatial analogues are used, e.g. Grenfell et al. (2001) a TSIR on measles, Hufnagel et al. (2004) on a global SARS epidemics and Stollenwerk et al. (2004) on bacterial meningitis. Dietz and Heesterbeek (2002) showed that Daniel Bernoulli's work could be cast into an SR-model and that some obscure statements by Bernoulli were absolutely right.

J. B. S. Haldane published an essay in 1928 "On Being the Right Size" (see Haldane, 1985) where he notes that the most important property of an organism is its size, a fact which he felt had been ignored. Here he argues that different forces e.g. gravity and surface tension are important to different animals, that oxygen supply by diffusion is sufficient for small organisms but not large, and using dimensional analysis that there is a scale invariance in the height that an animal can jump (ignoring air resistance, as Haldane did, Scholz et al. (2006) show that smaller creatures are better in transforming energy to motion, thus the conclusion does not hold strictly). To what extent other biologists have been inspired by this essay is unclear, since it has very few citations, but it contains many important points. How much bone that is needed for a leg not to snap leads to optimization of animal shape (see Alexander, 1982), and from there it is not far to go to the optimization of animal behaviour (Stephens and Krebs, 1986). Scale invariance is a very hot topic, but to me scale invariance is interesting only when the interval is specified, since almost always there are limits to it. Scaling "laws" have been reported; these are very interesting when it is possible to understand the mechanisms producing them, then they may be useful and robust. They seem to be less useful when e.g. there is disagreement on whether respiration rate should be proportional to body mass to the power of 2/3 or 3/4 even if this may be due to missuse of regression models (FARRELL-GRAY and GOTELLI, 2005).

The importance of size-structured models for population dynamics is connected with Haldane's essay, e.g. a cod can increase its length with a factor of about 1000 if it is lucky. This means that the environment and its possibilities to interact with its environment are very different during its life even if it were to stay at the same geographical position during this time.

Nicholson and Bailey (1935) made a discrete model for insect parasitoid-prey populations. They assumed random distribution of prey in an area A , and that each predator search an area a during its life-time. The probability that a given larva escapes a specific parasitoid is $(1 - \frac{a}{A})$. If P_t denotes the predator

population at time t and H_t the host population, then the fraction f of larvae that escapes parasitism is $f = (1 - \frac{a}{A})^{P_t}$, which can be rewritten as $f = e^{-\alpha P_t}$ where $\alpha = -\ln(1 - \frac{a}{A})$. They assumed that each host produce F eggs S of which survive then the host population next year will be:

$$H_{t+1} = (FSH_t)f = \kappa H_t e^{-\alpha P_t},$$

and they further assumed that each parasitized larva gives rise to a single adult parasitoid,

$$P_{t+1} = \kappa H_t (1 - f) = \kappa H_t (1 - e^{-\alpha P_t}).$$

This system of difference equations have a single unstable positive equilibrium; either both predator and prey goes extinct or the predator goes extinct and the prey population explodes. Nicholson and Bailey assumed that the parasites were host-limited; that the density of hosts were limiting the population growth. Getz (1998) notes that Thompson had earlier, in 1924, presented a model where the parasites were egg-limited, which gave $f = \exp(-\alpha \frac{P_t}{N_t})$, but Thompson's work was ignored until the end of the 1970ies, when one began to study such scenarios. Also the Nicholson-Bailey model gained renewed interest since it was shown that host-parasitoid populations on a lattice could survive indefinitely and that these interactions produced interesting spatial patterns (Hassell et al., 1991). It is of course most likely that parasites in general are both egg and host limited depending on densities (Gutierrez, 1996; Getz, 1998). These works are important for their use of random search, that encounters were Poisson distributed at a fixed time and Thompson's for using a ratio-dependent functional response.

The magnificent statistician Sir Ronald A. Fisher explains evolution by means of natural selection using genetical theory in 1930 (see Fisher, 1999). He states that the Lotka-Euler equation can be understood in a monetary sense. If one regards the birth of a child as a loan of life and the birth of this child's offspring as a repayment, then r is the appropriate rent. The unit investment (the child) has an expected return at $[x, x + dx]$ of $l_x b_x dx$. And the present value of this is $e^{-rx} l_x b_x dx$, summing these gives $1 = \int_0^\infty e^{-rx} l_x b_x dx$. This analogy can be taken further since one can ask for the future value of the reproductive output of a person who is of age x . This is $v_x = \frac{e^{rx}}{r} \int_x^\infty e^{-rt} l_t b_t dt$. Fisher ignored effects of inclusive fitness, that interrelated animals can benefit from helping their kin, since he thought these were small and stated that this is the value that the direct action of natural selection is proportional to. Together with J. B. S. Haldane and Sewall Wright, Fisher is considered to have founded population genetics. Fisher studied the spatial diffusion of a favourable gene 1937, this is called the Fisher equation $u_t = ku(1 - u) + Du_{xx}$. The even greater Andrej Kolmogorov, continued the study of similar equations the same year, $u_t = f(u)u + Du_{xx}$, in particular the wave-like properties of the solution (Kolmogorov et al., 1937). They found analytically that the asymptotic constant rate of spread is equal

to $2\sqrt{f(0)D}$. This is one of the starting points of reaction-diffusion equations which are widely used in chemistry, epidemiology, morphology, and genetics, although Murray (1993) states that Luther was first, in 1906, but forgotten. McKean (1975a,b) was able to provide an alternative proof of the asymptotic wave-speed for this equation using a branching Brownian motion. This work, and other e.g. by Watanabe, have lead to the study of superprocesses, or Brownian snakes (Dynkin, 2002). This analogy has been used in the analysis of integrodifference equations (see e.g. Kot et al., 2004). In the contact process by Mollison (1977) more general dispersal can be included, where the probability for a certain dispersal length comes from a distribution.

Feller (1939a) presented early analyses of simple stochastic population models, a pure death process, a pure birth process, a birth-death process, a diffusion approximation of a birth-death process which reflects accumulated energy, and a statement of Fokker-Planck equations for the the Lotka-Volterra two-species model. Feller is often said to have created the birth-death process, the birth process was introduced by Yule (1925) where he considered the evolution of new species. Feller also dealt with stochastic versions of logistic growth. Interestingly most logistic models have incorporated a decreasing reproduction rate in growth by letting the reproduction rate at population size n , λ_n be a quadratic function $\lambda_n = \alpha n - \beta n^2$, where α, β are non-negative. This makes the finiteness of the habitat explicit, since no growth can occur at $n > \frac{\alpha}{\beta}$. If one only had a death rate which increases quadratically with population size then there is no upper level defined. An interesting observation in Feller (1939a) is that the mean growth rate in a logistic stochastic population is less than its deterministic analogue.

Leslie (1945) introduces the Leslie-matrix, a neat scheme for age-structured populations with discrete state and in discrete time. In Leslie (1948) he shows that it is possible to incorporate density dependence. The basic structure of a general matrix model is that that the population of m stages at time t is characterized by a column vector $\vec{n}(t) = (n_1(t), \dots, n_m(t))^T$, and there is an $m \times m$ matrix A , which may depend on the present or past values of \vec{n} , time and have random components. The population at next time $\vec{n}(t+1)$ is

$$\vec{n}(t+1) = A \vec{n}(t). \quad (2.2)$$

Leslie was not first with this framework, Caswell (1989) writes that Bernadelli was first in 1941, with an article in the Journal of the Burma Research Society titled "Population waves". Bernadelli's model stemmed from his interest in fluctuations in the age-structure in the population in Burma. He came up with a model that could produce sustained oscillations where the matrix A is equal to

$$\begin{bmatrix} 0 & 0 & 6 \\ \frac{1}{2} & 0 & 0 \\ 0 & \frac{1}{3} & 0 \end{bmatrix}.$$

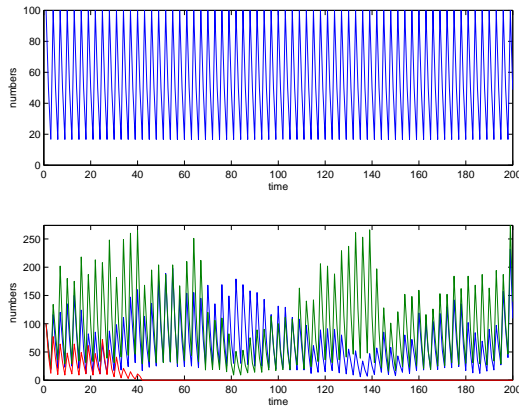


Figure 2.1: The expected version of Bernadelli's branching process (above) and 3 realisations of it. Note that one population (red) goes extinct.

This matrix should be interpreted such that the probability to survive the first year (or time period) is $\frac{1}{2}$, and the probability to survive the second is $\frac{1}{3}$. The three-year-old individuals produce (on average) 6 offspring then die, the offspring are then the newborns next year. From this it is hopefully clear that the Leslie-matrix is the expectation of a branching process, which in Bernadelli's case is critical. For an impression on the difference between stochastic outcomes and the expected version see Figure 2.1. Keyfitz and Keyfitz (1997) notes that Bernadelli was not first with this type of models either, in fact they originate from Cannan in 1895!

This framework is easily extended to stage-structured populations, which was realized in the 1960s. These are sometimes called the Lefkovich-matrix models, but it should not come as a surprise that Lefkovich was not first.

Another example, let b_i be the mean number of offspring produced by an animal of age i , let p_{i-1} be the survival probability from age $i-1$ to i . This means that the survival probability to age x is equal to $\prod_{i=0}^{x-1} p_i = l_x$. The Leslie matrix maps an initial population $n(t) = \{n_0(t), n_1(t), \dots\}$ to $n(t+1)$. Clearly the number of newborns next year will be $n_0(t+1) = \sum_{i \geq 0} n_i(t)b_i$ and for the other groups only grow older $n_{i+1}(t+1) = p_i n_i(t)$ for $i \geq 0$. In matrix form this can be put as:

$$\begin{bmatrix} b_0 & b_1 & b_2 & \cdots \\ p_0 & 0 & 0 & \cdots \\ 0 & p_1 & 0 & \cdots \\ \vdots & \vdots & \ddots & \vdots \end{bmatrix} \begin{bmatrix} n_0(t) \\ n_1(t) \\ n_2(t) \\ \vdots \end{bmatrix} = \begin{bmatrix} n_0(t+1) \\ n_1(t+1) \\ n_2(t+1) \\ \vdots \end{bmatrix}.$$

A population with stable age distribution has the property that $n(t+1) = an(t)$ and writing $a = e^r$ gives the Euler-Lotka equation. For finite state systems the Perron-Frobenius theorem states that there is a largest eigenvalue a which is real and positive. It is of course very important to know if a is greater than 1, which means that the population grows geometrically. For infinite state systems the Krein-Rutman theorem (see Zeidler, 1992, p. 290–291) generalise the Perron-Frobenius theorem and guarantees the existence of a unique largest eigenvalue if the operator is compact. An important matrix in age-structured branching processes is the ML-matrix (Dorman et al., 2004) which determines much of the behaviour of such a process, this is equivalent to a Leslie matrix.

The matrix formalism is essentially equivalent with the PDE or integral formulation of physiologically structured populations, and these can be seen as the expectation of a multi-type branching process (Diekmann et al., 1998), a property which I feel is sometimes taken too far e.g. when very small populations are studied using the deterministic models.

Another attempt to account for the fact that different stages have different impact on population growth was Hutchinson (1948) who represented the fact that only grown up individuals will contribute to interspecific competition. He proposed a delayed-logistic growth model.

$$\frac{dN}{dt} = (a - bN(t - \tau))N(t).$$

Expanding $N(t - \tau)$ in a Taylor series $N(t - \tau) = N(t) - \tau N'(t) + \frac{\tau^2}{2!} N''(t) + \dots$ it is clear that this equation corresponds to an infinite dimensional differential equation. Cunningham (1954) solved this equation for small enough τ , (see also Nisbet and Gurney, 1982). Time delays opens up for more complex dynamics than an ordinary first degree differential equation, in fact even chaotic dynamics (see Mackey and Glass, 1977). Delays have also been incorporated in Lotka-Volterra predation models (see Bartlett, 1957; Wangersky, 1978). An important example of its applications is that Gurney et al. (1980) were able to represent many characteristics of the time-series data set by Nicholson on blowflies, (see pp. 285–308 in Nisbet and Gurney (1982), and pp. 114–119 in Gutierrez (1996) for an alternative, meta-physiological, formulation). Introducing a weight function $w(\tau)$, where $\int_0^\infty w(\tau) d\tau = 1$ and a weighted memory of past populations is $N_w(t) = \int_0^\infty w(\tau) N(t - \tau) d\tau$, then the delay-differential equation may be viewed as a special case of integrodifferential equations.

Maurice E. Solomon introduced the terms functional response and numerical response in 1949 although these concepts had been used earlier (Holling, 1966). A functional response is the mean rate of removal of prey per predator given a certain prey and predator density. The numerical response is the average per capita production rate of predators given a certain prey and predator density. In discrete-time models the functional response is the mean number of consumed

prey per predator and time unit and the numerical response is the average number of offspring per predator and time. Holling (1959) is the pioneer of mechanically derived functional responses, he combined experiments with simple theory in what has become Holling's type II response. The Holling type II response is equivalent to Michaelis-Menten kinetics in enzyme reactions. Borghans et al. (1996) show that the functional response can arise from a singular perturbation of the fast process of handling prey and provide criteria for when the approximation is good. The fast process is assumed to be in quasi-stationary equilibrium and the rate of consumption of prey, or substrate in enzyme kinetics, is the functional response times the prey concentration. It has been shown that spatial heterogeneity and predator grouping may change the functional response (e.g. Cosner et al., 1999). Similarly, Poggiale (1998) derived different functional responses on the basis of fast movement of prey between shelter and a risky but rewarding habitat. Jeschke et al. (2002) review and classify most functional responses to that date. Numerical responses have, to my knowledge, a less solid theoretical foundation, and the standard procedure is to put the reproductive output as directly proportional to the functional response, which may be a good approximation in some animals. The aim of dynamic energy budget models aim to fix this broken link between ingestion and reproduction (see e.g. Shertzer and Ellner, 2002b), they generally use scaling arguments between size and energy needs and losses. For instance, the rate of ingestion may be proportional to surface area if it is a filtering moving organism whereas respiration is proportional to volume.

Alan Turing showed that pattern formation is possible by reaction-diffusion equations in 1952. Turing's interest seem to have been spurred by phyllotaxis, and in particular the appearance of Fibonacci sequences in Nature. This article has led to much interesting work, where one is able to reproduce the spots of a jaguar, and the stripes of a zebra (see Murray, 1993). Although there has been a large effort to find these diffusing morphogens to this date none has been found. The mechanism of animal patterns seems to be more intricate with gene regulation and cellular communication. Turing's work is important in population ecology too, since it shows that it is possible to have patterning in an initially homogenous environment (e.g. Kareiva and Odell, 1987) and as a means of including space in population dynamics (see Durrett and Levin, 1994, for illuminating comparisons between different approaches)

Moran (1953a,b) analyzed a data set on the Canadian lynx that had been published by Elton in 1942. Moran assumed that weather was an important factor in the oscillations and fitted a second order auto-regressive model to the lynx series. He showed that correlated noise synchronized any two processes with identical parameters, this is called the "Moran effect". This effect has been thoroughly studied in linear and non-linear models. Two other mechanisms cause population synchronization, dispersal from high to low densities and trophic interactions with other species that themselves are spatially syn-

chronous (Leibold et al., 2004). Renshaw (1991) notes that this data set has generated a fair amount of mathematical speculation and notes that Moran's explanation ignores the coupling to a fluctuating environment which could be provided by the snowshoe hare which is almost the only food of Canadian lynxes.

The lack of inclusion of such an obvious and seemingly necessary coupling to food is of course irritating to many people, including myself. Renshaw (1991) has a funny quote by Seton who remarks on the Canadian lynx and its prey the snowshoe hare: "It lives on Rabbits, thinks Rabbits, tastes like Rabbits, increases with them, and on their failure dies of starvation in the unrabbitted wood". A very neat study on the Canadian lynx and the snowshoe hare which incorporates detailed biological knowledge, e.g. that reproduction is lower in the hare when population is declining and that lynx forage more efficiently during the decline is found in Stenseth et al. (1998). They are able to use a simple self-exciting autoregressive model (SETAR), i.e. the dynamics are described by one autoregressive time-series model when the state is below a threshold and another when the state is over the threshold. This type of models belongs to a fairly recent trend in population biology that tries to infer ecological processes from time-series data, combined with what empirical knowledge there is (Royama, 1981; Turchin and Hanski, 2001; Kendall et al., 1999). Moran's study is also very important in the context of linking ecological processes to climate, in particular indices of weather such as the NAO (North Atlantic Oscillation—the yearly average pressure difference between the Azorean high-pressure and the low pressure over Iceland) and the (ENSO) El Niño Southern Oscillation (which is the Pacific equivalent to the NAO). The ENSO has been particularly studied, due to its drastic effects on fisheries in South America (Barber and Chavez, 1983; Chavez et al., 2003). The NAO has been successful as a component in explaining e.g. variation in recruits in Baltic herring (Axenrot and Hansson, 2003). Hallett et al. (2004) show that the reason that these large-scale fluctuations tend to predict population processes better than local weather is due to combinations of different time-lags. They argue that the specific mechanism of how weather influences populations is important since this may create an interaction between density-dependence and weather which would be missed by a large-scale index or inappropriate measures of local weather, such as mean monthly temperature.

Huffaker (1958) did not agree with Gause's conclusion that populations were self-annihilating without immigration. He realized that populations rarely mix homogeneously over the whole habitat, but develop within subsets of the habitat. Huffaker included the spatial component in a system where he had placed oranges regularly on a grid and he altered the available area of an orange and the degree of dispersion between the oranges. This system was equipped with two different species of mites as predators and prey. Huffaker was able to produce three cycles with 120 oranges and four with 252 oranges. In fact, Renshaw (1991) shows that it is theoretically possible to have sustained oscillations in a system with only ten sites. This work was important in the attempts to include

spatial variations in population models. A very similar system was used to study the mechanistic reasons to persistence by Ellner et al. (2001), and it was found that isolation by distance was the essential cause of persistence in their system.

Another very important work in the area of spatial models is the metapopulation model by Richard Levins (1969). He assumed that p is the probability that a patch is occupied, and that empty patches are colonized with rate C and occupied patches goes extinct with rate E . This leads to

$$\frac{dp}{dt} = (1 - p)C - pE.$$

Assume that the extinction rate is constant $E = e$ and that the colonization rate increases linearly with the number of occupied patches n , $C = cn$. Let N be the total number of patches and assume that this number is large enough to let the probability that a patch is occupied be $p = \frac{n}{N}$. Then

$$\frac{dn}{dt} = cn(N - n) - en.$$

The approximation that $p = \frac{n}{N}$ can only be valid when N is large, thus this model has also been studied in stochastic settings (see e.g. Etienne and Nagelkerke, 2002). The basic metapopulation model has been extended in many different ways e.g. to include Allee effect, rescue effect i.e. that extinction is less probable when more patches are occupied, detailed local dynamics, and heterogenous habitats etc. (see Hanski and Gilpin, 1997).

The focus on spatial models have remained in later years, where techniques from statistical mechanics (moment-closure, pair-correlations etc.) have been used to simplify spatial models (see Dieckmann et al., 2000). But also advanced statistical techniques have been increasingly popular in the analysis of data such as Markov Chain Monte Carlo methods (de Valpine and Hastings, 2002; de Valpine, 2003; Fujiwara et al., 2005) for non-linear models. The individual-based modelling approach, where the individuals that make up the population are modelled explicitly using computer simulations has been important (Grimm, 1999) for its conceptual appeal, and for the general message that individual differences in state are important. This has to some extent been found by other frameworks, e.g. the physiologically structured dynamics, which is related since the idea is to formulate interaction laws at the individual level and then integrate to the population level (Dieckmann et al., 1998) and study deterministic population phenomena. However the simulation-based individual-based models have suffered from the inability to analyse the model at the population level which requires a statistical analysis or the ability to transform the individual-level phenomena to the population-level (Gómez-Moureló, 2005). The mechanistically, or semi-mechanistically based models where the parameters can be interpreted have had large impact (Stenseth et al., 1997).

2.1 Further reading

Hilborn and Mangel (1997) present an inspiring account of biological modelling. Murray (1993) is a good source for mainly deterministic models in biology, with extra stress on reaction-diffusion models (see also Okubo and Levin, 2001; Shigesada and Kawasaki, 1997). Nisbet and Gurney (1982) and Gurney and Nisbet (1998) are very good general introductions to both stochastic (in the former) and deterministic models (the latter emphasizes spatial models at the expense of stochastic). The book by Renshaw (1991) is another treatise where the need for both stochastic and deterministic models is lucidly illustrated. Caswell (2001) provide a very broad introduction to much of structured population models but primarily matrix models, where many topics that were not present in second edition are included, such as the connection with branching processes. For more information on different ways to model structured populations, see Tuljapurkar and Caswell (1997).

Classical references for branching processes are Harris (1963) and Athreya and Ney (1972), for biological problems, see Haccou et al. (2005); Kimmel and Axelrod (2002).

For more examples on the practical side of modelling biological populations, this see Turchin (2003), Caswell (2001), Nisbet and Gurney (1982) and Gurney and Nisbet (1998).

Delay-differential equations and integro-differential equations in biology are covered by Cushing (1977). The modern (abstract) setting of delay-differential equations is functional differential equations (Diekmann et al., 1995).

Dynamic energy budgets are treated in Kooijman (2000), a meta-physiological alternative is found in Gutierrez (1996).

CHAPTER 3

The schooling behaviour of clupeids in the Baltic at dawn

Fish don't eat temperature.

Dr. Christian Möllmann on an explanation of why sprat are found in certain areas at certain times in the Baltic.

3.1 Introduction

The goal of this work is to describe a part of the time varying prey field of Baltic cod that are larger than 30 cm. Cod of this size feed primarily on sprat and on small herring (Essington and Hansson, 2004). Herring and sprat belongs to the family Clupeidae, hence they are sometimes called clupeids. They dominate the fish biomass of the Baltic Proper and they are found in schools during well-lit conditions. At the study site there were much more sprat than herring and since sprat is the primary target of cod, the schooling species seen on echograms will most of the time be called sprat or clupeids.

Almost 80 percent of the known species of fish aggregate in schools during some part of their life-history and approximately 25 percent of these school as adults (Shaw, 1978). Schools refer to a group of fish that are polarized and thus move in a coordinated manner. Other social aggregations of fishes that are not polarized

are called shoals (Pitcher and Parrish, 1993); these distinctions do not apply to earlier work nor are they adopted by all researchers. Since herring and sprat are known as obligate schooling fishes since they are always found in schools (during well-light conditions). The aggregations seen on echograms will be called schools even if it is possible that they are shoals.

One of the many interesting things with schools is that they change their shape and size during the day. Most species disperse to a disordered state or at least expand during dusk and then reform at dawn to compact schools. There are indications that feeding is most intense in both herring and cod during twilight conditions (Blaxter and Parrish, 1965; Adlerstein and Welleman, 2000). In the Baltic this feeding pattern was found by Cardinale et al. (2003) for herring, but not for sprat which fed during the day. Clupeids are known to be able to filter-feed also during night (Batty et al., 1990), although with a lower efficiency than during the day. In order to make a more precise description of prey encounter for cod we needed a model for the spatio-temporal behaviour of their main prey.

There are many different reasons to gather in a school, since a school may serve different purposes to its components, but the primary reason for most fishes is probably to avoid predation (Pitcher and Parrish, 1993) since “many eyes” will be better at detecting predators (Pitcher and Turner, 1986). However, it is possible that they save energy (Weihs, 1973; Herskin and Steffensen, 1998) and that fish in a school may find food faster (Peuhkuri et al., 1995; Grünbaum, 1998); some tunas form “soldier lines” to search an area efficiently (Cosner et al., 1999). Fish aggregated in schools have lower encounter rates with predators and are less likely to be consumed when attacked since the predator quickly becomes satiated and the remaining prey can escape (Pitcher and Parrish, 1993). Social interactions may also be an important cause, since it is easier to find a mate in school. An example of strong social interactions in schools is that some reef fishes form schools of entirely females and one male and when the male is removed the largest female will change sex (Warner and Swearer, 1991). There are of course costs to schooling such as increased intra-specific competition, faster transmission of disease and sometimes other species may benefit from the large local density of prey, such as whales, tunas (Brodie et al., 1978; Cosner et al., 1999) and humans (Parrish, 1999).

Vision seems to be the primary sense to maintain a school (Partridge and Pitcher, 1980) although the lateral line (Pitcher et al., 1976) is also important and possibly chemical and olfactory cues (Krause, 1993). When light levels decrease the schooling stops. The critical light levels are widely different between species (e.g. Shaw, 1961; Higgs and Fuiman, 1996) and between different sizes of the same species (Miyazaki et al., 2000). The dispersion and aggregation of sprat phenomenon in the Baltic is concurrent with a vertical migration which creates conspicuous shifts in echograms (see Figure 3.1). There may be a continuous formation of schools as light levels increase during the day since it

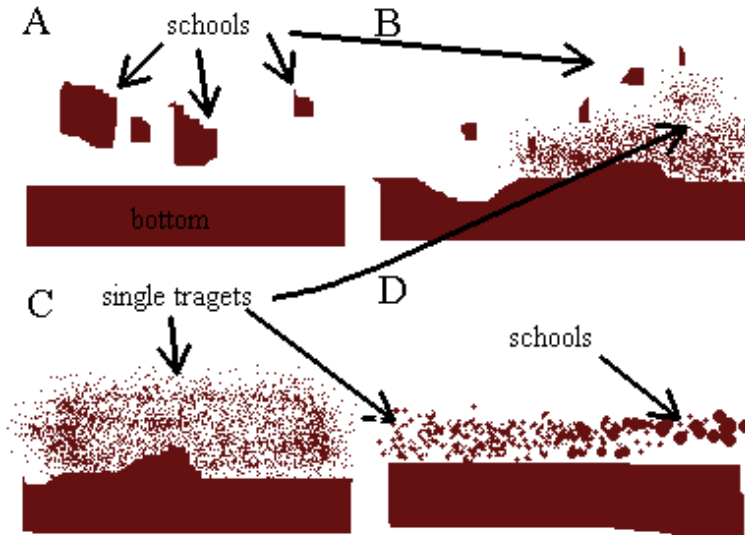


Figure 3.1: Schematic drawing of the daily shifts in echogram. A is during day time B during dusk C during night and D the transitions at dawn.

appears, from my limited experience, as if school sizes are larger at noon than in the late morning and in the afternoon. At dusk the schools have split into smaller schools, most of these disperse close to the bottom but some rise toward the surface before dispersion.

How do fish in a school disperse? We assume that the schools remain intact until light levels go below a threshold. Then the sprat disperse into an uncorrelated state by performing independent random walks. We built a model based on these assumptions and checked if the predictions match our observations. Our assumption are based on laboratory observations (Shaw, 1961; Batty et al., 1990; Higgs and Fuiman, 1996).

In this work we show that schools stay intact above ca 0.01 lux and that a diffusion model for the dispersion gives time-scales that are of the same order as the time scales observed. The most revealing observation was that the light levels 1, 0.1, 0.01 lux were chosen *a priori* based on literature data and that the pattern of dispersal in the field seemed to follow the 0.01 lux isolume very closely (see Figure A.3).

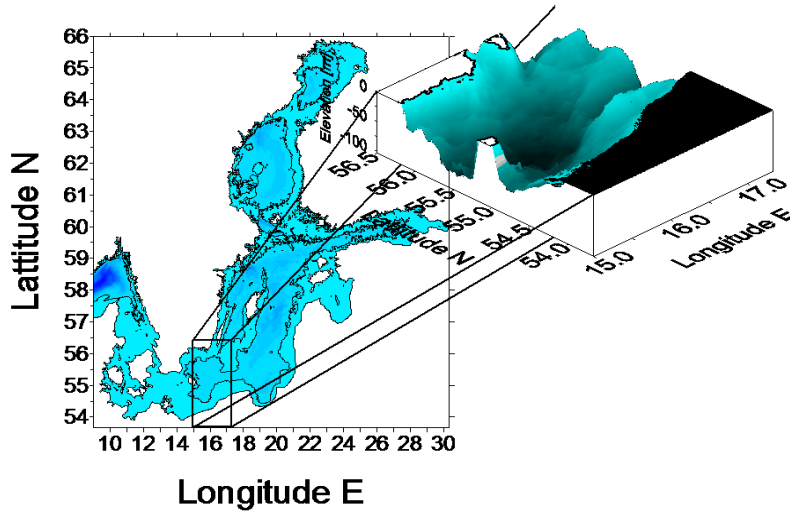


Figure 3.2: Map and topography of the Bornholm Basin

3.2 Materials and Methods

Echograms were collected during a cruise with R/V Dana (12-14 March 2002), on the north eastern slope of the Bornholm Basin (see figure 3.2). This position was chosen since cod were present; they are rarely found in the central parts during this time of the year. The echograms were stored electronically and analyzed using EchoView software (SonarData, 2002). At the same time of echogram registration we were trawling, mostly at the bottom but in the evening of March 14 we made some pelagic tows to ascertain that the fish seen closer to the surface on the echograms were indeed sprat and herring. We also registered currents, salinity, temperature and light attenuation at regular intervals. These light-depth profiles enabled us to calculate an approximate light level at the centre of a school and the measurements of the currents were used so that we could dispose of the catch downstream. The latter was unfortunately necessary to do since the storage facilities on board were limited. This caused unfortunate breaks in the otherwise continuous registration of events at the study site.

Schools were registered using the school-detection module of the EchoView programme. The identification parameters were set heuristically, to be able to discriminate between two schools but not identifying aggregations that may be two fishes standing close to each other. The light meter on the ship had limited sensitivity at the low light levels of dawn and dusk. It registered zero light levels even when the light levels at the surface were quite sufficient for reading, thus we had no accurate recording of the light levels at dusk. We used a programme

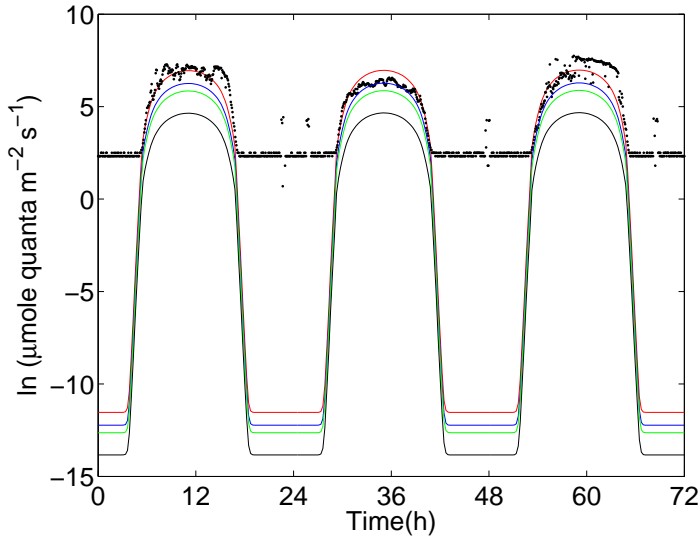


Figure 3.3: Model of light, different lines corresponds to different assumptions of cloud cover. Dots are the measurements from the light meter on Dana.

by Janiczek and De Young (1987) that allowed us to get an average value of the light intensity at the surface. The program is perhaps crude, but the link with actual light levels during periods of non-zero measurements on Dana was surprisingly good (see fig. 3.3). It is assumed that the atmosphere is isothermal and sea surface reflexions are not included which may have caused some of the positive deviations.

The light intensity at depth d , $I(d)$, was modelled using the Lambert–Beer’s law $\log I(d) = \log I_0 - K \cdot d$, where the attenuation coefficient K was estimated from regressions from the light profiles obtained by the light probe at the CTD. However, since the surface layer (0–20 m) contained phytoplankton which cause extra absorption of light we excluded this part of the light profile from the estimation of the rate of attenuation of light and the light meter had problems at log light levels lower than -2.7 ; the values below were excluded (see Figure 3.4). During the early morning of March 14th the weather changed to a gale with high waves and strong winds. This made the interpretation of the echograms harder, in particular the school identification algorithm performed badly. Both the echosounder and EchoView have bottom-detection algorithms but neither performed very well. The bottom is useful since it allowed us to remove much of the waviness of the echograms simply by applying a low-pass filter to the bottom lines and then aligning the echoes.

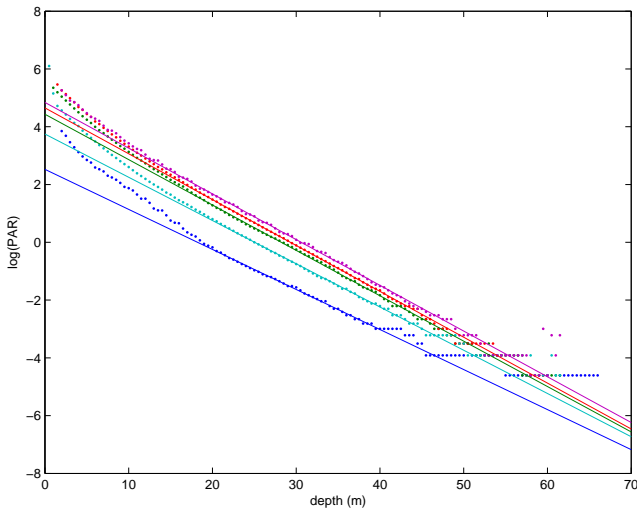


Figure 3.4: The logarithm of light profile (photosynthetically active radiation) at five stations versus depth and fitted regressions to the stable interval between 20 m and measurements above -2.7 .

In order to use the data we produced a program in Matlab to identify the bottom and a C++ program to change the echograms such that the bottom was better aligned. The former task was achieved using an identification of the bottom within a narrow band since the depth range was known and a low pass filter consisting of Gaussian weights. This improved the echograms enough to enable the school identification algorithm to be run. We did not correct for bubbles under the boat which cause the echosounder "miss" a ping or two, but this was a minor problem on the evening of March 14th since the wind had abated by then.

The relation between light and school depth was modelled using linear regressions. We modelled the light intensity at the centre of the i th school on day j , Y_{ij} as a linear regression of X_{ij} , the depth of the i th school on day j . It may seem as if it should be the other way around, that the depth should be a function of light, but our formulation allows us to have a zero slope if the schools follow the isolumes (lines of constant light intensity), which would not be the case in the alternative formulation.

In the modelling of the dispersion of fish in schools we assumed that the number of fish in a school is Poisson-distributed with mean \bar{N} , that the fish are all located in a single point and the dispersion is in the horizontal plane. At time 0 the light

levels go below a critical level and the fish in a school disperse by an unbiased random walk. This means that the density of fish $\rho(x, y, t)$ can be described by a diffusion equation:

$$\frac{\partial \rho(x, y, t)}{\partial t} = \frac{\sigma^2}{2} \nabla^2 \rho(x, y, t),$$

where $\frac{\sigma^2}{2}$ is the diffusivity. We evaluate the consequences of two different spatial arrangements of schools; either the schools are arranged on a regular square lattice with side length L or the schools themselves are Poisson distributed. In the former case the density can be expressed by its Fourier expansion:

$$\rho(x, y, t) = \frac{\bar{N}}{L^2} \sum_{j=-\infty}^{\infty} \sum_{k=-\infty}^{\infty} e^{-\frac{1}{2}\sigma^2\left(\frac{2\pi}{L}\right)^2(k^2+l^2)t} e^{i2\pi\left(\frac{kx+ly}{L}\right)}.$$

Here we compare two squares of size $\frac{L}{2} \times \frac{L}{2}$, one centred over a school and another centred over the point at the maximum distance from neighbouring schools (see Figure 3.5). Using the first Fourier modes, since these are dampened with the slowest rate, and a normal approximation we get an approximate time scale. For the randomly placed school centres we assume that the initial rate of increase of entropy is constant which gives a "mean" time until the schools have dispersed. For the analysis of the regular grid one has to specify a parameter α which is defined by the probability that there are more fish in the distant square than in the centred square is $\frac{1}{2} - \alpha$. Here we get a time-scale that also depends on the number of fish in the school: $T = -\frac{L^2}{2\pi^2\sigma^2} \ln\left(\frac{\pi}{4\sqrt{2N}}g\left(\frac{1}{2} + \alpha\right)\right)$ where $g\left(\frac{1}{2} + \alpha\right)$ is the $\left(\frac{1}{2} + \alpha\right)$ -quantile of the standard Normal distribution. The time scale does not depend on the school size when schools are Poisson distributed at $t = 0$, $T = \frac{L^2}{2\pi\epsilon\sigma^2}$ but the order of the time-scale of the dispersion is the same, i.e. proportional to $\frac{L^2}{\sigma^2}$ times a constant which typically is less than one.

3.3 Results

The model for the relation of light-levels and schools was significantly better at describing the data than $Y_{ij} = \alpha_i$ —that the logarithm of the light level at school centres were independent of depth. This means that the matching to the equal light intensities was not perfect. The data could be described by a model $Y_{ij} = \alpha_i + \beta X_{ij} + \varepsilon_{ij}$ where Y_{ij} is the log-light intensity at the centre of the j th school at the i th day, X_{ij} is the depth at which the j th school was found and ε_{ij} is an error term which has a normal distribution with zero mean. The estimate of the slope is $\beta = -0.0486$ (log-light per meter). The intercepts were $\alpha_1 = -2.51$, $\alpha_2 = -3.07$ and $\alpha_3 = -2.28$ but these are of minor importance since they indicate the deviation of the actual light levels from that of the model by Janiczek and De Young (1987). The model explained 38% of

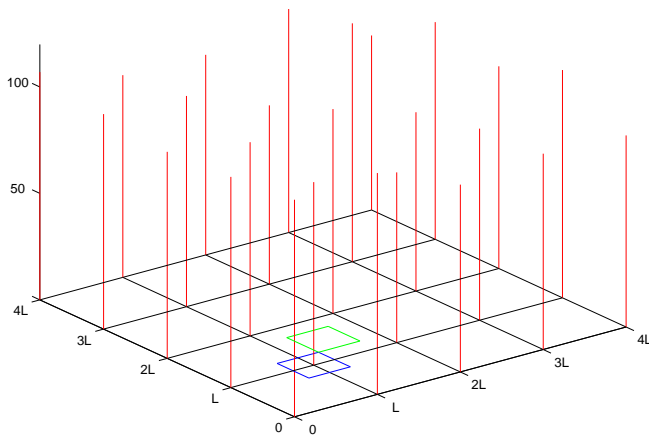


Figure 3.5: The model where schools (red) are located on a regular grid with inter-node distance L . The densities in the square centred at (L, L) (blue) is compared to the square centred at $(\frac{3}{2}L, \frac{3}{2}L)$ (green) in the derivation of the time to random dispersal.

the variation, which is low but not surprisingly low considering the frequently reported variability of schooling behaviour.

Based on data from EchoView we estimated the number of fish per school and the distance between schools. The estimate of numbers per school was obtained from the assumption that schools are shaped as vertical cylinders (MacLennan and Simmonds, 1992). We also assumed that the fish swim one body length per second which is a common cruising speed among fish (Niwa, 1994; Huse and Ona, 1996) and that their approximate mean length was 10 cm. This gave dispersion times that are in the range of 8 and 80 minutes, and the visual estimation of the transition time is ca 30 minutes which is within this range.

3.4 Discussion

There may be a slower transition taking place where the sprat move up toward the surface at a lower speed such that the transition between the phases take approximately 4 hours (see Orłowski, 2001, based on S_v patterns per 30 minutes not school detection). It is possible that this phenomenon occurs in our echograms too since there is a large initial concentration close to the bottom while somewhere round mid-night my impression is that the mode of the distribution has moved more toward the surface.

The fact that the slope, β , is negative seems a bit odd but perhaps it comes naturally from the dissolution process; if schools follow the isolumes but the ones that are on a higher light-level disperse faster this may have led to the negative slope. This may also be due to another bias—there are more schools at low depths and the fact that the density of fish is high at these points could make the school identification software to identify close aggregations of fish that are not schools. Nevertheless the slope is very small, in particular in the light of the large variations seen around the regression line. In this context it is appropriate to mention that the spawning season of sprat begins at this time in the Baltic. Sprat spawn at the bottom which may be the reason that there are so many schools that disperse close to the bottom, thus some aggregations that were registered as schools may have been spawning fish. In a related study on herring in the North Sea by Blaxter and Parrish (1965), there were no migration at dusk in August when herring spawn, but this could also be due to the low densities of herring observed at this point of the year in that study.

Weston and Andrews (1990) observed dispersion of schools on a horizontal sonar in UK, but some schools did not disperse. However it is unknown whether this was due to extreme light conditions, such as clear sky with moon-light or the physiological status of the fish. In laboratory studies it has been observed that swimming speed is reduced and nearest neighbour distance increase as light levels go down, the schools expand, the variation in nearest neighbour distances

increases and polarization is lost (Higgs and Fuiman, 1996). Since we do not observe the individual fish long enough we do not have information on whether they are polarised nor if the spatial arrangement is random. What is in favour of the latter hypothesis is that the point pattern on the echograms have a random appearance although there seems to be a gradual increase in the intensity toward the bottom. The pattern of points ought to be more regular in an expanded scenario. Due to the depth bias of the echosounder and uncertainties regarding the position of an object within a particular depth stratum we made no attempt to study the point pattern using e.g. Ripley's K-function (see Diggle, 1983) in order to see if there were any discrepancies from a Poisson point pattern.

In order to make any general statements concerning the dispersal behaviour of clupeids in the Baltic it is of course necessary to get much more data from the whole year and detailed data on the individual level.

3.5 Contributions

In article A we have described some aspects of the dispersion with a statistical model. The model for the light levels and school depth is to our knowledge the first although there is a similar graphical model for herring in Blaxter (1985), but here no dispersion occurs during the vertical migration phase. The figure in that article refers to an article by Blaxter and Parrish (1965) but neither data nor the figure is to be found. There is also a reference to Chortnoy who allegedly have said that herring follow isolumes all day and to Zusser who did not see this phenomenon. Appenzeller and Leggett (1995) studied the dynamics of the vertical distribution of rainbow smelt in a Canadian lake. They noted that the upper 5 percent of the distribution of biomass had a strong link to light levels of rainbow smelt, whereas the lower 95 percentile had a weak link and the distribution widened during the transition. However, they did not take into account if the vertical distribution was composed of schools or not. They also noted that several studies have shown a link between depth distribution and isolumes but that the evidence is circumstantial since these studies did not measure light levels *in situ*. Iida and Mukai (1995) studied the transition between schools and dispersed individuals of kokanee, *Onchorhynchus nerka* in a caldera lake in Japan using a bottom-mounted echo-sounder. This transition takes ca 50 minutes, but unfortunately there is no information on school sizes and school distances; data that would have enabled us to apply our dispersion model to their situation.

The dispersion model in article A is new and quite simple, it can be used to get rules of thumb measures of the time-scales. However it should be noted that we do not present strong evidence on the detailed process since we lack data on the individuals. It may well be that the fish disperse in a directed way from the

school during the initial phase and that they actively avoid the neighbourhood of other fishes during the whole process. It is also possible, although experimental data supports our assumption, that the schools remain polarized and what we observed was that the nearest neighbour distances increased dramatically. However that ought to have given more regular patterns on the echograms.

The smoothing of the echograms from the windy day is also new. This seems to be a useful thing that should be elaborated, using time-series techniques and perhaps using ancillary data on bottom topography to smooth the tracks further. It should also be possible to reconstruct the pings that are missed using filtering techniques, especially at low speeds when in general there is a high probability of having repeated echoes from single targets.

3.6 Future work

It would be interesting to have a stationary transducer mounted on the bottom in the Baltic to get a better description on what actually happens and not disturbing the fish by the boat and the trawl. This combined with a sonar or an array of transducers positioned at the bottom would be able to give us the large picture if one were able to record data from all seasons of the year.

In the near future there will be echosounders that transmit a signal with a wider frequency distribution; these will collect much more information of the targets seen. It may well be that species identification can be possible with these broadband echo-sounders (Au and Benoit-Bird, 2003), a feature that would greatly increase the utility of the echogram data. These new echo-sounders will give rise to interesting statistical problems on how to discriminate between species and how to cope with the large datasets that will be produced.

In order to answer the question why schools disperse I think that it will be necessary to account for the internal state of the sprat and the value of the alternative. This would require that one found schools that did not disperse and detailed information of the state of the sprat in different schools, within schools and how their environment changes such as the risk of being eaten by a cod. This seems to be a difficult and time-consuming problem that perhaps could be investigated using intensive stomach sampling of the sprat and the spatial location of these or perhaps in a laboratory. Some experimental work has been done in this area, e.g. Hensor et al. (2003) showed in laboratory studies that food-deprived killifish showed a higher propensity to leave a school than non-deprived.

How schools are formed is a very interesting question, perhaps this could be modelled as a coagulation process (see e.g. Jackson, 2001). It could also be important to study the daily cycle of the school sizes if it turns out e.g. that fish

in larger schools are safer or that fisheries target larger schools. Anderson (1981) has an approximate steady-state solution to a model of school size distributions, this model could possibly be used to fit the school sizes observed and to get a time-dependent solution when the forcing is periodic.

Higgs and Fuiman (1996) mention that the fish eye continues to grow and that it may develop more rods. Does this mean that larger cod are better at detecting prey than smaller cod? They show a nice graph that, when log-log-transformed (see Miyazaki et al., 2000), gives an indication of a scaling relation between eye size of different *species* and the light level at which they disperse. In relation to this is it very interesting to know the position of an attacking cod relative to a school; do they use the contrast against the surface and attack from below or do they attack from the side (Janssen, 1981)? The former could be a reason not to move up before the light levels go down in order to avoid predation.

Thus many issues remain, the most important for population oriented models would be to be able to statistically describe the spatial dynamics of the schooling fishes and their predators. A more complex but perhaps even more interesting project would be to understand why these patterns come about.

CHAPTER 4

Markovian Arrival Processes (MAPs) as tools in population dynamics

'It's perfectly intelligible,'
the Captain said, in an offended tone,
'to anyone that understand such things.'

Lewis Carroll 1885

Most encounters between an animal and its food has a random component. This may be due to difficulties in localizing the prey or that prey flee, that other foragers consumed the prey that the focal animal intended to eat etc. The number of offspring that an animal produce depends to some extent on foraging success, thus both consumption of food and production of new consumers will have random components. This means that even if the mean density of prey is lower than necessary some predators may have good luck and survive, and conversely, even if the average conditions are sufficient that there are some consumers with bad luck who die of starvation or fail to produce offspring. This kind of stochasticity is called demographic stochasticity, and it is generally assumed that it is negligible (e.g. Caswell, 2001). However, Chesson (1978) showed that this is generally not true in spatially subdivided habitats.

The Poisson process has been used as a model for random encounter since at least 1918 (Paloheimo, 1971) and it is still the most common model for such events since it is mathematically tractable. The Markovian arrival process (MAP) framework extends this tractability to more general point processes, where it is possible to have general inter-event times and dependence between events. This is useful in modelling more realistic situations such as prey encounter in heterogenous environments or when the searching activity of the predator depends on its internal state such as degree of satiation. The MAP can model any increasing sequence, which could represent prey eaten or the number of produced offspring. The structure of MAPs enables us to find the mean and the variance of such processes quite easily which makes MAPs interesting as a tool in ecology.

The stochastic property of many subprocesses makes it natural to use the MAP for the derivation of functional and numerical responses, and to use the relevant time-scales to see whether the mean rate is a good descriptor of the process or not. In this chapter I give a brief introduction to the general framework of MAPs, then I discuss functional and numerical responses and finally I present some possible parameterisations of well-known functional responses.

4.1 An introduction to MAPs via the Poisson process

The time-homogenous Poisson process is a basic stochastic process in continuous time. It is a counting process which has the important property that the expected number of events is directly proportional to the length of any interval. That is, take an interval or a set of intervals I then the expected number of events in this set is $\lambda|I|$ where $|I|$ is the length, or more precisely the Lebesgue measure, of the set. The constant of proportionality λ is called the intensity or the rate of the Poisson process. There is a dual representation of the Poisson process, let $N(t)$ be the number of events at time t where $N(0) = 0$ and let T_i be the times between the arrivals of the events. Then $\mathbb{P}\{N(t) \leq n\} = \mathbb{P}\{\sum_{i=1}^n T_i > t\}$. Thus the $N(t)$ process can be characterised by the T_i s—the inter-event times. The Poisson process have exponentially distributed inter-event times with a mean $\frac{1}{\lambda}$. The exponential distribution has a memoryless property which means that the residual waiting time for an event, an increase in $N(t)$, is exponential with the same parameter λ . The Poisson process is a Markov process, which means that the evolution of the process is completely characterised by the current state.

The Poisson process starting with 0 counts at time 0 can be described by a continuous time Markov Chain with states $\{0, 1, 2, \dots\}$ representing the number of events that has occurred and where the initial state is 0. The generator has

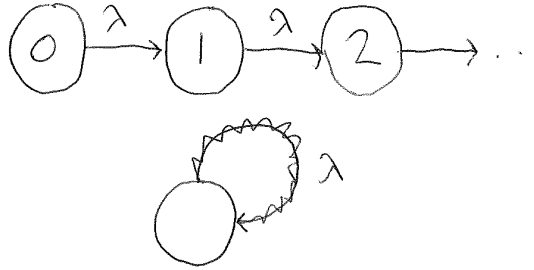


Figure 4.1: The Poisson process as a directed graph. In the upper directed graph the counting states are shown explicitly, in the lower they are implicit.

the following structure:

$$G = \begin{bmatrix} -\lambda & \lambda & 0 & 0 & \dots \\ 0 & -\lambda & \lambda & 0 & \dots \\ 0 & 0 & -\lambda & \lambda & \dots \\ \vdots & \vdots & \vdots & \vdots & \ddots \end{bmatrix}, \quad (4.1)$$

with $-\lambda$ on the diagonal and λ on the supradiagonal. The Poisson process is skip free; it can only increase its state by one. The generator can be interpreted as the rate of change of the process. If we are in state j then with probability $\lambda\Delta t + o(\Delta t)$ we make a jump to state $j+1$ in time Δt (small) and with probability $1 - \lambda\Delta t + o(\Delta t)$ we stay in j . The $o(\Delta t)$ denotes an arbitrary function $f(\Delta t)$ which has the property that $\frac{f(\Delta t)}{\Delta t} \rightarrow 0$ when $\Delta t \rightarrow 0$. For the Poisson process these transition probabilities are independent of both time and state. The Poisson process can be visualised as a directed graph (see Figure 4.1), these will become more important when more complicated models are introduced.

Given an initial probability distribution $\pi(0)$ the time evolution, $\pi(t)$, of a continuous-time Markov chain is governed by the Chapman–Kolmogorov forward equations $\dot{\pi}(t) = \pi(t)G$, the solution is $\pi(t) = \pi(0)e^{Gt}$ where e^{Gt} is the matrix exponential. The matrix exponential for this generator is quite simple, it is

$$e^{Gt} = \begin{bmatrix} e^{-\lambda t} & \lambda t e^{-\lambda t} & \frac{(\lambda t)^2}{2!} e^{-\lambda t} & \frac{(\lambda t)^3}{3!} e^{-\lambda t} & \dots \\ 0 & e^{-\lambda t} & \lambda t e^{-\lambda t} & \frac{(\lambda t)^2}{2!} e^{-\lambda t} & \dots \\ 0 & 0 & e^{-\lambda t} & \lambda t e^{-\lambda t} & \dots \\ \vdots & \vdots & \vdots & \vdots & \ddots \end{bmatrix}.$$

The matrix e^{Gt} is called the transition matrix, often denoted $\mathbf{P}(t)$, of the process. The j th element in the i th row $(\mathbf{P}(t))_{ij}$ is the probability of being in state j at time t if the process starts in i at time 0. Again, note the invariance of the

chain: starting at 0 and obtaining i has the same probability as starting at j and obtaining $i + j$ and that the time in each state $(\mathbf{P}(t))_{ii}$ is exponentially distributed $e^{-\lambda t}$.

4.1.1 PH-distributions

An extension of the exponential distribution to more general distributions are the Phase-type distributions or PH-distributions (see Latouche and Ramaswami, 1999). The PH-distributions are based on the method of stages, a technique introduced by A. K. Erlang in the early 20th century that was generalised by Marcel Neuts (Neuts, 1975).

A PH-distribution is the probability distribution of the time to be absorbed in a transient finite continuous or discrete time Markov Chain. The exponential distribution is of course a member of this class. Thus if we have a process with states $\{0, 1\}$ then the generator is

$$G = \begin{bmatrix} 0 & 0 \\ \lambda & -\lambda \end{bmatrix}.$$

If the process starts in state 1, i.e. with the initial vector $[0 \ 1]$, then the time until absorption is $\mathbb{P}\{X_t = 0 | X_0 = 1\} = 1 - e^{-\lambda t}$. More generally a continuous time PH-distribution has a generator of the form

$$G = \begin{bmatrix} 0 & \mathbf{0} \\ \mathbf{t} & \mathbf{T} \end{bmatrix},$$

where \mathbf{T} is an $m \times m$ matrix which is transient, i.e. the process is certain to leave the set of states in \mathbf{T} and eventually end up in state 0. Furthermore the PH-distribution has an initial probability distribution $\boldsymbol{\alpha}$, which is represented by an m dimensional row vector with the property that $\sum_{i=1}^m \alpha_i = \boldsymbol{\alpha} \mathbf{e} = 1$, where \mathbf{e} is a m -column vector with ones. Strictly speaking there could be an α_0 i.e. an initial probability of being absorbed, but in the following it will be assumed that $\alpha_0 = 0$. The probability that the chain has been absorbed before time x is $1 - \boldsymbol{\alpha} e^{\mathbf{T} \cdot x} \mathbf{e}$. The corresponding probability density is $\boldsymbol{\alpha} e^{\mathbf{T} \cdot x} \mathbf{t}$. The pair $(\boldsymbol{\alpha}, \mathbf{T})$ characterise a PH-distribution completely since \mathbf{t} can be obtained from the relation $\mathbf{t} = -\mathbf{T} \mathbf{e}$. The characterisation is unfortunately not unique, e.g. take $\boldsymbol{\alpha} = [p \ 1 - p]$, where $p \in (0, 1)$ and

$$G = \begin{bmatrix} 0 & 0 & 0 \\ \lambda & -\lambda & 0 \\ \lambda & 0 & -\lambda \end{bmatrix},$$

which is another representation of the exponential distribution.

An important question in conservation biology is the expected time to extinction. If one assumes that the process can be described by some, birth-death process, which could be quite elaborate e.g. with several types of individuals and catastrophic extinctions etc. Ecologists (should) know how to calculate the mean time until extinction in a population (e.g. Mangel and Tier, 1994). Diffusion approximations are often used but Nisbet and Gurney (1982) advice against using them. In fact, Doering et al. (2005) have shown that the diffusion approximation does not give the right time to extinction. An interesting feature in this context, is that PH-distributions are well-suited for the calculation of the extinction probabilities. Renshaw (1991) writes that there are few success stories in terms of exact results, and then continues with simulations to derive the numerical results for situations where there are no exact results. The PH-distributions offers a viable alternative to simulations, in particular with the use of uniformization (see Section 4.1.3.2).

4.1.2 PH-renewal processes

PH-distributions can also be used to construct a stochastic process where the inter-event times are identically and independently distributed; a PH-renewal process. This stochastic process starts in phase i with probability α_i and immediately after absorption from state j which happens with rate t_j the process restarts in state k with probability α_k etc. The interesting thing about PH-renewal processes is that many properties of the can be obtained using matrix algebra instead of integral equations which is the standard tool for renewal processes. This is similar to the relation of matrix population models and the integral formulation of stage-structured populations (cf. Caswell, 1989). The generator of a PH-renewal process has the following structure

$$\begin{bmatrix} \mathbf{T} & \mathbf{t} \cdot \boldsymbol{\alpha} & \mathbf{0} & \mathbf{0} & \cdots \\ \mathbf{0} & \mathbf{T} & \mathbf{t} \cdot \boldsymbol{\alpha} & \mathbf{0} & \cdots \\ \mathbf{0} & \mathbf{0} & \mathbf{T} & \mathbf{t} \cdot \boldsymbol{\alpha} & \cdots \\ \vdots & \vdots & \vdots & \vdots & \ddots \end{bmatrix}.$$

For the process to be well defined it is necessary that every state that is occupied immediately before absorption ($\forall j : t_j \neq 0$) can be reached from any initial state ($\forall i : \alpha_i \neq 0$), which is guaranteed if $\mathbf{T} + \mathbf{t} \cdot \boldsymbol{\alpha}$ is irreducible.

The basic idea of a PH-renewal is quite simple. Suppose that we have a realisation of a Poisson process with rate 2, if we remove every other arrival we get a process that will have mean rate 1, but it will not be a Poisson process, since the probability of having an arrival in Δt given that we had one at t is approximately $O(\Delta t^2) \neq O(\Delta t)$, this process will be more regular than a Poisson

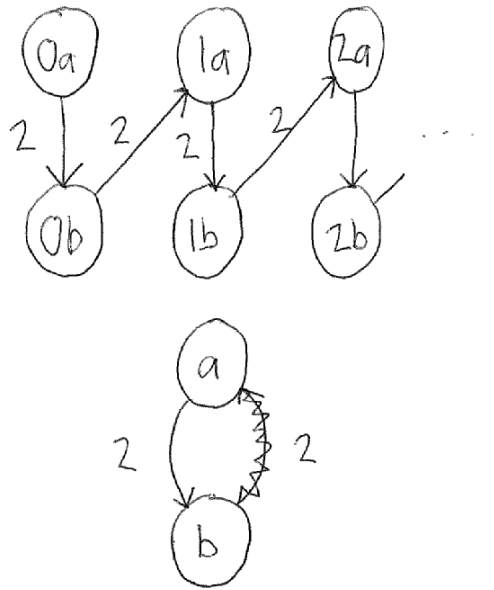


Figure 4.2: The Poisson process where only every second arrival is counted; upper graph shows explicit counting process and the lower graph the state representation.

process with rate 1. Here

$$\mathbf{T} = \begin{bmatrix} -2 & 2 \\ 0 & -2 \end{bmatrix} \text{ and } \mathbf{t} \cdot \boldsymbol{\alpha} = \begin{bmatrix} 0 & 0 \\ 2 & 0 \end{bmatrix}.$$

A more variable process can be obtained by having two Poisson processes one with rate $\frac{1}{2}$ and the other with rate 2, suppose that we choose the the inter-event time from the fast process with probability $\frac{1}{3}$ then we still have a mean inter-event time of 1 but the variability is higher than for an exponential. In this case

$$\mathbf{T} = \begin{bmatrix} -\frac{1}{2} & 0 \\ 0 & -2 \end{bmatrix} \text{ and } \mathbf{t} \cdot \boldsymbol{\alpha} = \begin{bmatrix} \frac{1}{3} & \frac{1}{3} \\ \frac{2}{3} & \frac{2}{3} \end{bmatrix}.$$

An alternative view of this process it that after an event an exponential time with rate 2 is chosen with probability $\frac{1}{3}$ and with probability $\frac{2}{3}$ an exponential time with rate $\frac{1}{2}$ is chosen. The process is illustrated in Figure 4.3.

To illustrate how different PH-renewals can be let us have 4 states, where it is only allowed to have transition rates of 1 per time unit to any other state. Then

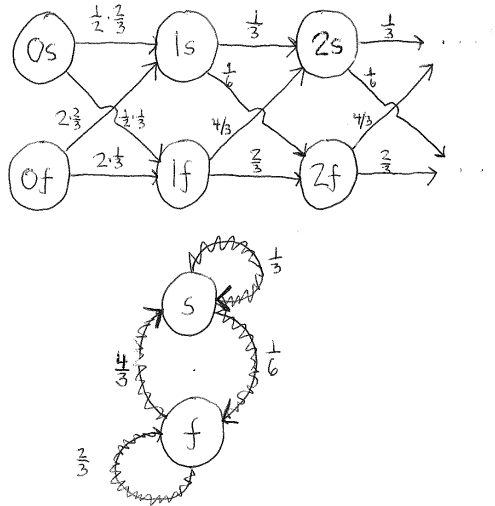


Figure 4.3: The random mixture of two Poisson processes, one with rate 2, the other with rate $\frac{1}{2}$ represented as directed graphs.

a PH-renewal process could have

$$\mathbf{D}_0 = \begin{bmatrix} -1 & 1 & 0 & 0 \\ 0 & -1 & 1 & 0 \\ 0 & 0 & -1 & 1 \\ 0 & 0 & 0 & -1 \end{bmatrix} \quad \text{and} \quad \mathbf{D}_1 = \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 \end{bmatrix}$$

This is an Erlang(4) process which is the most regular MAP possible with 4 states. The distribution of interarrival times can be seen in Figure 4.4. As a contrast take the 4 state MMPP with matrices:

$$\mathbf{D}_0 = \begin{bmatrix} -2 & 1 & 0 & 0 \\ 0 & -1 & 1 & 0 \\ 0 & 0 & -1 & 1 \\ 1 & 0 & 0 & -1 \end{bmatrix} \quad \text{and} \quad \mathbf{D}_1 = \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}$$

This will generate a process that is much more variable than a Poisson process; the interarrival distribution is shown in Figure 4.4, for reference an exponential distribution with the same mean as the two distributions above is included. Note that the \mathbf{D} matrix is the same for both the MMPP and the PH-renewal process but the behaviour is quite different.

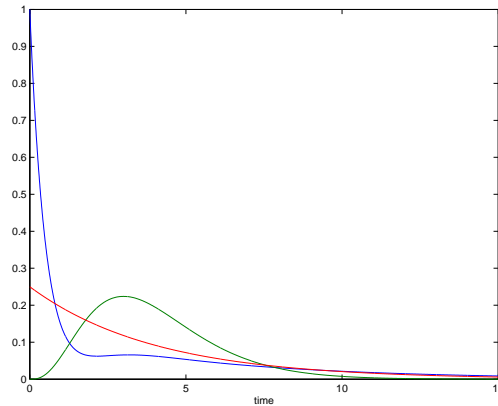


Figure 4.4: The Erlang(4)-process is green and the MMPP is blue; while an exponential variable with same mean is red. Note that the Erlang waiting time is much more regular and has less variance than the exponential and that the MMPP has a wider tail than the exponential distribution.

4.1.3 Markovian arrival processes

The Markovian arrival process (MAP) is another construction by Marcel Neuts (1979) although similar constructions had appeared earlier. The MAP generalise the PH-renewal process by removing the condition that the process should restart after an arrival, with probabilities specified by α and \mathbf{t} . One incentive for devising the MAP was that it could model phenomena that are bursty; such burstiness could have been modelled with time-dependent Poisson processes, but these are more difficult to work with (Neuts, pers. comm.). The MAP is described by the generator of a finite state continuous-time Markov Chain \mathbf{D} where some transitions are “marked”, these are collected in a matrix \mathbf{D}_1 , the transitions that do not generate marks are left in the matrix \mathbf{D}_0 , and $\mathbf{D} = \mathbf{D}_0 + \mathbf{D}_1$. The j th element in the i th row $(\mathbf{D}_1)_{ij}$ denotes the transition rate from state i to state j that produce a mark or event. Suppose that the number of states is m then \mathbf{D} , \mathbf{D}_0 and \mathbf{D}_1 are $m \times m$ matrices.

A MAP is a bivariate Markov process where there is a phase X_t and the number of events N_t . A state of a MAP ($X_t = i, N_t = n$) can be represented by the univariate Markov process ($Y_t = i + m \cdot n$), where m is the dimension of the

phase process. Thus, the generator of a MAP is the generator of Y_t

$$\begin{bmatrix} \mathbf{D}_0 & \mathbf{D}_1 & \mathbf{0} & \mathbf{0} & \cdots \\ \mathbf{0} & \mathbf{D}_0 & \mathbf{D}_1 & \mathbf{0} & \cdots \\ \mathbf{0} & \mathbf{0} & \mathbf{D}_0 & \mathbf{D}_1 & \cdots \\ \vdots & \vdots & \vdots & \vdots & \ddots \end{bmatrix}.$$

This generalisation allows for the construction of more general point processes than PH-renewals, e.g. there can be dependence between arrivals. Some special cases are the PH-renewal processes and the Markov modulated Poisson processes (MMPPs). The latter are characterised by the fact that \mathbf{D}_1 has non-zero entries on the diagonal only. The MMPPs are often used to produce sequences that are “bursty”. This is a property that has been used in telecommunications (Blondia, 1992; Heffes and Lucantoni, 1986), atomic physics (Burzykowski et al., 2003) and in the representation of heterogeneous encounter in marine larval ecology (Beyer and Nielsen, 1996).

The transitions between states or phases is described by a matrix $\mathbf{D} = \mathbf{D}_0 + \mathbf{D}_1$. Here the information contained in the counting process is ignored, and if \mathbf{D} is irreducible, which we assume, then there exists a unique stationary distribution. The chain will converge to this stationary distribution from all initial conditions and this stationary distribution can be found as the row vector θ that solves $\theta\mathbf{D} = 0$ and $\theta\mathbf{e} = 1$. Note that \mathbf{e} , the column vector with a one in every row, is a right-eigenvector to \mathbf{D} , i.e. $\mathbf{D}\mathbf{e} = 0$.

Given that the process starts in this time-stationary distribution then the mean number of events will be $\mathbb{E}\{N_t\} = \theta\mathbf{D}_1\mathbf{e}t = \lambda^*t$, thus the long term rate is λ^* . This is of primary interest when functional and numerical responses are produced and analysed. By dividing the entries of \mathbf{D}_0 and \mathbf{D}_1 with λ^* the time is scaled such that the rate of encounters is 1, which can be useful in some situations.

The long-time probability of being in a certain state immediately before an event, the event-stationary probability, is found from $\frac{\theta\mathbf{D}_1}{\theta\mathbf{D}_1\mathbf{e}}$. The event-stationary distribution can be used to derive the event-stationary mean rate of arrivals or Palm density, which is the renewal density if the MAP is a PH-renewal (see e.g. Asmussen, 2000). The event-stationary probability can be useful in complex ecological models of individual encounter to find out what state the predator will be most likely to be in when it is attacking.

4.1.3.1 Moments of MAPs

If we define a matrix function

$$M(t)_{ij} = \mathbb{E}\{N_t \mathbf{1}_{\{X_t=j\}} | X_0 = i, N_0 = 0\},$$

where $M(t)_{ij}$ describes the expected number of counts at time t if the process is in state j at this time and if it started in state i with no counts at time 0. $M(t)$ can be described by an ODE: $\dot{M} = M\mathbf{D} + P\mathbf{D}_1$ with initial condition $M(0) = \mathbf{0}$ and where $\dot{P} = P\mathbf{D}$, $P(0) = \mathbf{I}$ is the time evolution of the probability distribution of the states of the chain \mathbf{D} . This matrix function is useful for evaluating how different initial conditions will alter the accumulation of food. It is clear that starting the foraging season in a very rich patch will give more food initially than what the predator will get if it starts in a very bad patch.

The matrices of higher moments can be found as follows, define a matrix

$$M^n(t)_{ij} = \mathbb{E}\{N_t^n \mathbf{1}_{\{X_t=j\}} | X_0 = i, N_0 = 0\}.$$

Then solve the ODE

$$\dot{M}^n = M^n\mathbf{D} + \sum_{i=0}^{n-1} \binom{n}{i} M^i\mathbf{D}_1.$$

These matrices are useful for calculating the variance, and higher order central moments if these are of interest. The asymptotic variance is an affine function of t , (see Narayana and Neuts, 1992). Thus it is possible to speak about an asymptotic rate of the variance. For renewals this rate can be found from the quotient between the variance of the time between renewals and the mean of the time cubed $\frac{\sigma_t^2}{\mu^3}$ (Cox, 1962) which for PH-renewals is

$$\frac{2\boldsymbol{\alpha}(-\mathbf{T})^{-2}\mathbf{e} - (\boldsymbol{\alpha}(-\mathbf{T})^{-1}\mathbf{e})^2}{(\boldsymbol{\alpha}(-\mathbf{T})^{-1}\mathbf{e})^3}.$$

4.1.3.2 Uniformization

A tool that is very practical in the evaluation of transition and moment matrices is the uniformization technique (Jensen, 1953). The basic idea is that in order to calculate the transition probabilities $P = e^{\mathbf{D}t}$ one has to evaluate a matrix exponential $e^{\mathbf{D}t} = \sum_{i=0}^{\infty} \frac{(\mathbf{D}t)^i}{i!}$. There are many ways to calculate this and most of them are numerically unstable (Moler and Van Loan, 2003). However, if the original generator is replaced with a jump chain (in discrete time) based on the fastest phase, i.e. find $\tau \leq \min \mathbf{D}_{ii}$ and set $K = \frac{1}{\tau}\mathbf{D} + I$ then the continuous Markov chain is equivalent to a Poisson process with rate τ that drives the jump chain. This equivalence can be seen from the fact that the state in the jump chain will filter which jump that is counted as a transition in the continuous time Markov chain. The matrix exponential can be calculated as:

$$\exp(\mathbf{D}t) = \sum_{i=0}^{\infty} \frac{K^i}{i!} e^{-\tau t}.$$

This has the advantage of only adding positive numbers, which greatly reduces the accumulation of errors. It is also possible to use the Poisson distribution to control errors. The uniformization method has been extended to the first and second order factorial moments by Narayana and Neuts (1992) and to non-central moments of any order in Article B.

The calculation of the distribution of the counts (such as number of prey items eaten) at a certain time T given that the initial number is 0 and the initial distribution is γ can be done as follows: It is good to know approximately how many counts there will be $\lambda^*T + 2\sqrt{\lambda^*T}$ will often do as a first guess. Let n be the smallest integer larger than this number, then create an $(n \cdot m + 1) \times (n \cdot m + 1)$ matrix

$$Q = \begin{bmatrix} \mathbf{D}_0 & \mathbf{D}_1 & \mathbf{0} & \cdots & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{D}_0 & \mathbf{D}_1 & \cdots & \mathbf{0} & \mathbf{0} \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \cdots & \mathbf{D}_0 & \mathbf{D}_1 \cdot \mathbf{e} \\ 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix}.$$

Multiplying the $n \cdot m + 1$ -row vector $[\gamma \ \mathbf{0} \ \cdots \ \mathbf{0} \ 0]$ (where γ , the initial distribution, is an m row vector) from the left on e^{QT} will give the distribution. Note that this is a PH-distribution, which is simple to evaluate using uniformization. The additive property in the Markovian arrival process makes it easy to generalise this to cases when there is an initial distribution of preys eaten, since the prey distribution of a predator which has 1 prey initially, where the probability of being in the states is γ is the above distribution shifted one step to the right i.e. the initial vector is $[\mathbf{0} \ \gamma \ \cdots \ \mathbf{0} \ 0]$. The uniformization technique also has the advantage that it is possible to use recursion formulas such as $e^{QT} = e^{Q(T-b)}e^{Qb}$ where $0 \leq b \leq T$.

4.1.3.3 Different types of MAPs

There are a number of different types of MAPs, all of which exist both in continuous time versions and as discrete time versions. A transient MAP (Latouche et al., 2003) is a MAP where there is a possibility that the process terminates, which in biological models could represent that the animal dies or that it enters some specific state such as the first adult stage. This property may be important in some models, for instance the mortality rates among fish larvae may be very high, with survival rates of the order of one percent. An interesting measure in this context is the mean ingestion rate of the survivors. This can be found using results in Article B and it is only when the mortality rates are equal in all states that the conditional ingestion rate will be the same as the unconditional (see paper E). This has important consequences for larval ecology, inspecting the survivors may lead to a bias of the ingested number of food items and it

may just happen that the survivors were the ones that had the good fortune to be out of the dangerous zones for most of the time.

Another type is the Batch MAP (Lucantoni, 1991), where it is possible that several items arrives simultaneously. This is probably most easily understood from the generator of a continuous time BMAP,

$$\begin{bmatrix} \mathbf{D}_0 & \mathbf{D}_1 & \mathbf{D}_2 & \mathbf{D}_3 & \mathbf{D}_4 & \cdots \\ 0 & \mathbf{D}_0 & \mathbf{D}_1 & \mathbf{D}_2 & \mathbf{D}_3 & \cdots \\ 0 & 0 & \mathbf{D}_0 & \mathbf{D}_1 & \mathbf{D}_2 & \cdots \\ \vdots & \vdots & \vdots & \vdots & \vdots & \ddots \end{bmatrix},$$

where \mathbf{D}_i represents the rate arrival of a group of i items. The BMAP can be useful in settings where one has a prey distribution that one wishes to fit and to see the consequences of the the functional response. Since the BMAPs are weakly dense in the class of real-valued point processes (Asmussen and Koole, 1993) this is a very general framework.

A third type of MAPs is the periodic MAP. This has not been studied much, an exception is Breuer (2001) who provided ergodicity conditions and asymptotic distributions for the periodic BMAP(t)/PH/ c -queue, and Paper E. Time-dependent queues occur naturally both in telecommunications and in ecological applications but they are much more difficult to analyse, and in general one has to do numerical explorations. The periodic MAP have a property which makes it possible to gain some general insight if only the behaviour of the MAP is integrated over a period for any initial state. The same phenomenon applies to the higher order moments. This is due to the Floquet-Lyapunov theory (see e.g. Lukes, 1982) which states that the fundamental solution to $\dot{P} = PG(t)$ where $G(t)$ is periodic ($G(t + T) = G(t) \forall t$) can be written as an exponential matrix times a periodic matrix, i.e. $P(t) = e^{\mathbf{R}t} \cdot \Theta(t)$, where $\Theta(t)$ is periodic ($\Theta(t + T) = \Theta(t)$). However, the result of Floquet and Lyapunov is not constructive; there is no general way of finding \mathbf{R} and $\Theta(t)$ except from numerical approximation. If the fundamental solution is known at T , then the transition probabilities can be known at nT where $n \in \mathbb{N}$. If one knows transition probabilities of the MAP during the first period, then the phase of the periodic MAP is known at all times. The same results apply for the moments (see paper E). This suggests that when there is a periodicity on a fast time-scale then the dynamics on the slower time-scale may use the mean rates and variance of rates per period as input, which may be convenient.

A fourth type is the Marked MAP where there are several types of BMAPs that are governed by the same underlying chain (He and Neuts, 1998). These could be used to model different prey types with different energy contents or different types of offspring.

4.2 Functional responses

A typical predator–prey population model has the form

$$\begin{aligned}\mathcal{L} \cdot F(t) &= r(F(t))F(t) - f(F(t), C(t))C(t) \\ \mathcal{L} \cdot C(t) &= g(F(t), C(t))C(t) - d(C(t))C(t),\end{aligned}$$

where \mathcal{L} either is a differential operator $\frac{d}{dt}$ or a shift operator $\mathcal{L}F(t) = F(t+1)$. The prey species F increase at a rate $r(F)$ when predators C are absent. Predators consume prey at a rate $f(F, C)$ per predator, this is called the functional response. In the absence of prey the predators die at a rate $d(C)$ and when prey are present they produce new predators at a per capita rate $g(F, C)$. The latter is called the numerical response and in many situations it is assumed that there is a direct link between the prey consumption and predator production, such that the numerical response is $\epsilon f(F, C)$ where ϵ is a conversion efficiency, where $\epsilon \ll 1$ if the units for F and C are the same.

Functional responses exist in many models of population dynamics, an important exception is the Leslie matrix model. Functional responses are based on a separation of time-scales, the consumption of prey is assumed to be a fast process whereas production of new predators is a slow process. Moreover there is a central limit type of assumption, that the number of prey items consumed are so large that the variance in mean is negligible. This is of course not necessarily the truth, since the consumption process may happen on a similar time-scale as the reproduction such as in parasite-host models and there may be strong non-linearities which make the approximation harder to justify. An important problem is that it is uncertain whether the functional form is right, since heterogeneities and behaviour may change the form. This is important since models with different functional responses can have dramatic differences, which can change conclusions about e.g. harvesting rates, (see Yodzis, 1994).

Here I will present some simple functional responses. Some other examples which are modelled with Markovian queues but are simpler to analyse using MAPs can be found in Sjöberg (1980) and Curry and DeMichele (1977).

4.2.1 The Holling functional responses

There are three “fundamental” functional responses due to Holling (1959), these are called the Holling type I–III functional responses. The Holling type I is a linear response, where ingestion rate is directly proportional to prey density. This is thought to be applicable mostly to filtering organisms and sometimes it is equipped with maximum ingestion rate for more realism. Sjöberg (1980) have made a model of such a saturating Holling I functional response based on a Markovian queue, where the organism has a stomach that saturates at higher

densities of prey. This saturating type I response can easily be recast into the MAP framework, but I will not show it here.

The basic idea of the Holling type II functional response is that the predators has to divide its time between searching for prey and handling a caught item. The handling time is the time spent per item before it can resume prey search again. It is often assumed that the encounter rate with prey λ is proportional to the prey density $\lambda = V_s F$ where V_s is the search volume. When a predator encounters a prey item it will be blocked from further encounters for a, possibly random time, T_h , the handling time. This gives a mean ingestion rate $f(F) = \frac{V_s F}{1 + V_s F t_h}$, where t_h is the mean handling time per prey item. The name handling time is a bit unfourtunate, since it can refer to the physical handling of a prey item, such as removing shell or other inedible parts, or digestion since the predator will not be able to eat more prey when the stomach is full. These two different processes may constrain the behaviour at different food densities, e.g. it is possible that the physical handling that is time-limiting at low densities because the predator is never satiated, but at high densities the predator will be satiated and it is the properties of the stomachs that are important. A way out of this problem is to model the stomach explicitly, see (Jeschke et al., 2002) and section 4.3 below.

A MAP formulation of the Holling II functional response, with exponential search and handling times, described by rates λ and $\alpha = \frac{1}{t_h}$ respectively, is as follows:

$$\mathbf{D}_0 = \begin{bmatrix} -\lambda & 0 \\ \alpha & -\alpha \end{bmatrix} \quad \text{and} \quad \mathbf{D}_1 = \begin{bmatrix} 0 & \lambda \\ 0 & 0 \end{bmatrix}.$$

The stationary ingestion rate is $\lambda^* = \theta \mathbf{D}_1 \mathbf{e} = \frac{\alpha \lambda}{\alpha + \lambda}$. Inserting $\lambda = V_s F$ one gets a Holling type II response: $I = \frac{V_s F t_h}{1 + V_s F t_h}$ which is a hyperbolic curve (see Figure 4.5). Here we have assumed that the handling time is exponential with rate $\alpha = \frac{1}{t_h}$ where t_h is the mean handling time. It is of course doubtful whether the actual handling time is exponential or not, but it turns out that the ingestion rate is not sensitive to this assumption. However the variance of this process *is* sensitive to the distribution of the handling time (see Figure 4.5). A more regular handling time can be created by adding a phase to the handling time.

$$\mathbf{D}_0 = \begin{bmatrix} -\lambda & 0 & 0 \\ 0 & -2\alpha & 2\alpha \\ 2\alpha & 0 & 2\alpha \end{bmatrix} \quad \text{and} \quad \mathbf{D}_1 = \begin{bmatrix} 0 & \lambda & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix}.$$

This is an Erlang(2) distributed handling time, the mean is the same $\frac{1}{\alpha}$, but the variance is $\frac{1}{2\alpha^2}$. Increasing the phases to n where each has mean residence time $\frac{1}{n\alpha}$ gives a variance of $\frac{1}{n\alpha^2}$. When n goes to infinity the variance will go to zero and in the limit the handling time is deterministic.

The Holling type III functional response is thought to be a consequence of active switching between prey types (Oaten and Murdoch, 1977). The predator does

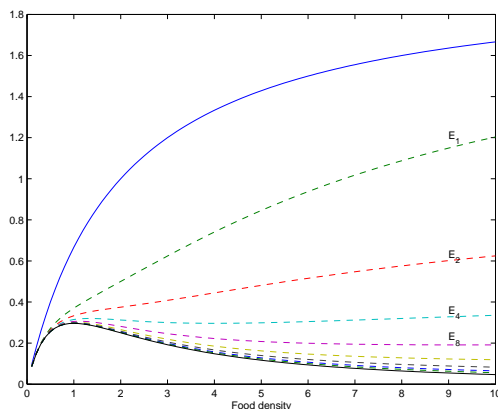


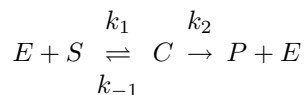
Figure 4.5: The mean (blue curve) and the variance for a sequence of Holling II models where the handling time is Erlang(n) distributed, here with $n = 1, 2, 4, \dots, 128$, and the variance from a model with deterministic handling time. If n , the number of phases in the Erlang distribution, $n \rightarrow \infty$ the variance will be the same as with deterministic handling time.

not hunt actively for a the focal prey type when it is scarce, but when densities increase the predator begins to search actively for it. This gives rise to a sigmoid shape of the functional response.

Another way that a general type III response may occur is by observing that the encounter rate λ may not be directly proportional to the prey density. If the encounter rate is proportional to the power of the prey density $\lambda = V_s N^\beta$ where $\beta > 1$ a type III functional response will follow (Getty and Pulliam, 1991)

4.2.2 The Michaelis-Menten derivation of functional responses

Michaelis and Menten (1913) studied the enzymatic degradation of sucrose. Here a small amount of the enzyme, β -fructofuranosidase (known as invertase at that time) transforms sucrose to glucose and fructose. In these reactions one has an enzyme with concentration E a substrate S , these form a complex C which dissociates either to E and S or into the product P and the free enzyme E .



Using the law of mass action these correspond to the following system of ODEs:

$$\begin{aligned}\dot{E} &= -k_1ES + (k_{-1} + k_2)C \\ \dot{S} &= -k_1ES + k_{-1}C \\ \dot{C} &= k_1ES - (k_{-1} + k_2)C \\ \dot{P} &= k_2C.\end{aligned}$$

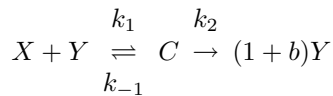
The initial conditions are that $E(0) = E_0$, $S(0) = S_0$, $C(0) = P(0) = 0$. The enzyme only facilitates the reaction, this means that $E(t) + C(t) = E_0$. The equations can consequently be rewritten as:

$$\begin{aligned}\dot{S} &= -k_1(E_0 - C)S + k_{-1}C \\ \dot{C} &= k_1(E_0 - C)S - (k_{-1} + k_2)C \\ \dot{P} &= k_2C\end{aligned}$$

Segel and Slemrod (1989) show that if the concentration of E_0 is small in comparison to S then these equations can be solved approximately using singular perturbations (see also Murray, 1993, for more details). The outer solution (which was found by Michaelis and Menten) assumes that the concentration of C is in a quasi-stationary equilibrium i.e. $\dot{C} \approx 0$. Solving for C gives $C^* = \frac{E_0S}{K_m + S}$, where $K_m = \frac{k_{-1} + k_2}{k_1}$ (K_m is called the Michaelis-Menten constant, but this form is actually due to Briggs and Haldane (1925)). Adding the equation for \dot{C} to S give that k_2C^* is the rate of consumption of S when the concentration of S is much larger than E_0 . This is essentially the same as the Holling derivation, where prey concentrations are assumed to be constant. Segel and Slemrod (1989) used scaling and comparisons between the outer and the inner approximation to derive conditions for when this approximation is valid. Their criterion is that $\frac{E_0}{S + K_m} \ll 1$.

This derivation differs from Holling's since it works with population entities, but the result is essentially the same. The analogy with predator-prey systems where the predators are assumed to reproduce at a much slower time-scale, thus acting as enzymes consuming substrate is evident.

Borghans et al. (1996) extended the results of Segel and Slemrod (1989) to situations where the initial concentration of E is not small in comparison to S . Here they introduce a new variable $\bar{S} = S(t) + C(t)$ and extend the quasi-stationary approximation to a wider range of situations. Borghans et al. (1996) use this technique to study a predator-prey system. Here they study the reaction

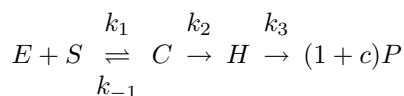


where X is the concentration of prey and Y the concentration of predators. They change variables by introducing $\bar{Y} \equiv C + Y$ and $\bar{X} \equiv X + C$ and find the

quasi-stationary equation for the complex C to be

$$0 = \frac{dC}{dt} = k_1 ((\bar{Y} - C)(\bar{X} - C) - K_m)$$

Then, they approximate this using a two point Padé approximation with $C^* = \frac{\bar{X}\bar{Y}}{\bar{X} + \bar{Y} + K_m}$, an approximation that is not overwhelmingly impressive (see Figure 4.9). This is a (special) Beddington-de Angelis functional response; through the introduction of an intermediate reaction step Huisman and de Boer (1997) were able to extend the result above to the general Beddington-de Angelis response. They used the reaction



An interesting feature here is that the predator dynamics are assumed to take place on a time-scale that is faster than the population dynamics of prey. There are of course numerous situations where this can be true, but often one would be more interested in situations where the prey dynamics are faster than the predator.

4.2.3 Functional responses in heterogeneous environments

An important question in ecology is how does the ubiquitous heterogeneity influence vital functions of an animal as, for instance, ingestion.

The Interrupted Poisson process (IPP) is the simplest model for heterogeneous encounter, i.e. an encounter process with prey that are more variable than the Poisson process. This has been proposed as a model unit in Beyer and Nielsen (1996), and has been used by Pitchford and Brindley (2001) and in Article C to study the consequences of this higher variability. The basic structure of the IPP is a MAP where the generator looks like:

$$\mathbf{D}_0 = \begin{bmatrix} -\omega_{01} & \omega_{01} \\ \omega_{10} & -(\omega_{10} + \lambda_{11}) \end{bmatrix} \quad \text{and} \quad \mathbf{D}_1 = \begin{bmatrix} 0 & 0 \\ 0 & \lambda_{11} \end{bmatrix}.$$

A biological interpretation is that patches are encountered as a Poisson process with rate ω_{01} and the residence time in the patch is exponential with mean ω_{10}^{-1} . While in the patch the animal encounters food in a Poisson process with rate λ_{11} . The IPP is stochastically equivalent to the hyperexponential renewal process (Kuczura, 1973), the latter has been used as a model for heterogeneous functional responses by Rothschild (1991) and Ruxton and Gurney (1994).

In Article C these models are analysed using three different scenarios, with exponential handling time for simplicity. It is also assumed that the mean

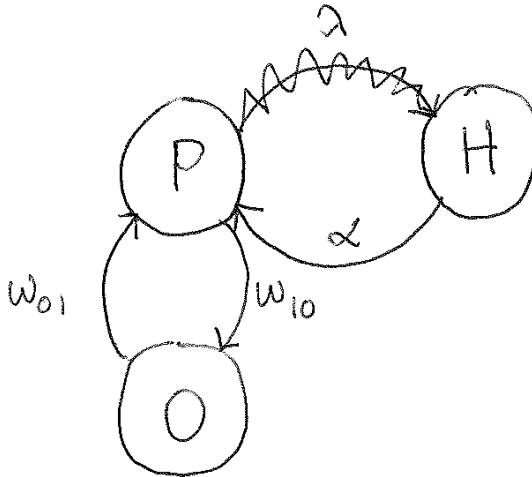


Figure 4.6: The situation when the predator is certain to start foraging in a patch after handling prey.

time between encounters in the heterogenous environment and the homogenous environment is the same if only the search phase is considered. In the first the predator is always able to start foraging in the patch after handling. This gives a model with generator

$$\mathbf{D}_0 = \begin{bmatrix} -\omega_{01} & \omega_{01} & 0 \\ \omega_{10} & -(\omega_{10} + \lambda) & \lambda \\ 0 & 0 & -\alpha \end{bmatrix} \quad \text{and} \quad \mathbf{D}_1 = \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & \alpha & 0 \end{bmatrix}.$$

This gives the same functional response as in the homogeneous environment i.e. a Holling II functional response if $\lambda = V_s F$, since the mean encounter rates are equal and the predator is certain to resume the search phase in the patch.

Rothschild (1991) supposed that the predator continuously encounters prey, i.e. the predator encounters prey also when it temporarily handles a prey item but it cannot catch these extra encounters. The encounter rate with prey is the same when it handles a prey and when it is searching. The structure of the

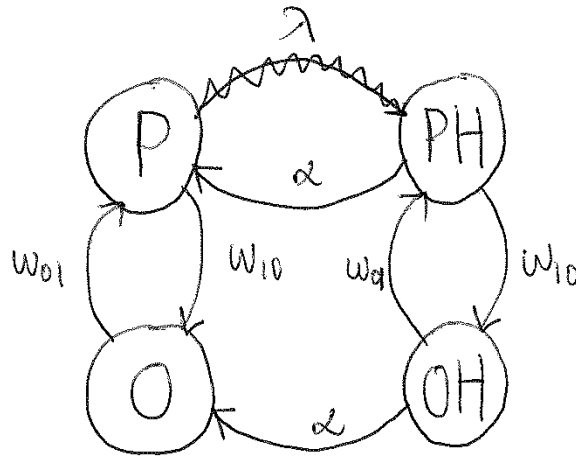


Figure 4.7: The IPP when the forager continues to encounter and leave patches when handling prey. O refers to out-of-patch, P that the predator is in a patch, PH that the predator is in a patch handling prey, and OH that the predator is out of the patch handling prey.

MAP of this model is:

$$\mathbf{D}_0 = \begin{bmatrix} -\omega_{01} & \omega_{01} & 0 & 0 \\ \omega_{10} & -(\omega_{10} + \lambda) & 0 & \lambda \\ 0 & 0 & -(\omega_{01} + \alpha) & \omega_{01} \\ 0 & 0 & \omega_{10} & -(\omega_{10} + \alpha) \end{bmatrix}$$

$$\mathbf{D}_1 = \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ \alpha & 0 & 0 & 0 \\ 0 & \alpha & 0 & 0 \end{bmatrix}.$$

The predator in this scenario suffers from the heterogeneity since there is a chance that it moves out of the patch while handling. This cost cannot not occur in the homogeneous environment. The directed graph representation of this scenario is shown in Figure 4.7.

The most important point in the latter model is that the ingestion rate depends on two parameters e.g. ω_{01} and ω_{10} when the third parameter of the encounter process, λ , is specified by the mean inter-encounter time. The challenge of this model is to prescribe how ω_{01} and ω_{10} change as the prey density changes. There is no given answer, since it not even certain that these should be functions of F only. If and only if these are constant is it certain that the functional response is a strict Holling II functional response, but then the maximum ingestion rate

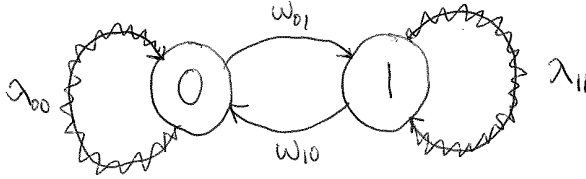


Figure 4.8: The directed graph of the switched Poisson process (SPP).

is lower than in the homogenous environment.

If ω_{01} and ω_{10} vary with prey density such that the coefficient of variation of the inter-encounter times in the IPP is fixed then the functional response is similar to the Holling II, but where the handling time distribution influences the similarity and the initial slope is less steep. Many other parameterisations are possible, most of these do not conserve the Holling II shape, not even approximately, as claimed in Ruxton and Gurney (1994), see Article C.

The IPP is a crude generalisation, but it the simplest stochastic model for heterogeneous encounter. More advanced models for the encounter process could, for instance, specify the encounter rates with prey in habitat i , λ_i and the transition rates between these habitats. A simple extension of the IPP is the switched Poisson process (SPP), which has the property that there are prey encounters also in the out-of-patch habitat. The generator of the phase and the counting process are

$$\mathbf{D}_0 = \begin{bmatrix} -(\omega_{01} + \lambda_{00}) & \omega_{01} \\ \omega_{10} & -(\omega_{10} + \lambda_{11}) \end{bmatrix} \quad \text{and} \quad \mathbf{D}_1 = \begin{bmatrix} \lambda_{00} & 0 \\ 0 & \lambda_{11} \end{bmatrix}.$$

The graphical representation of the SPP is shown in Figure 4.8. The SPP is not a renewal process as it has some dependence between the inter-encounter times. Both the IPP and the SPP are MMPPs (Markov modulated Poisson processes), which has the property that the stationary distribution does not change if the encounter rates are changed. The MMPPs subclass of MAPs has been more studied than the subclass of MAPs that neither are PH-renewals nor MMPPs. There are results on parameter estimations particular to this subclass (see e.g. Rydén, 1996). Unfortunately models based on MMPPs will not be MMPPs when the model is equipped with one or several states where the encountered item is handled since the inclusion of handling means that a successful encounter gives a jump from the encounter state to the handling state, i.e. a non-diagonal entry in the \mathbf{D}_1 matrix.

4.2.4 Predator dependent functional responses

In the simple functional responses above it is assumed that the predators behave independently of each other and that the concentrations of prey and predators are approximately constant. This is similar to the dilute gas approximation of the Lotka-Volterra equations where the predators are so scarce that the likelihood of any interaction between them is negligible. In many circumstances the predator density is not sufficiently low to warrant this approximation and even if densities were low enough there can be social interactions which invalidate this approximation. When there are interactions between predators then the functional response will be predator dependent. Such functional responses have empirically been found to be better than pure prey dependent functional responses (see e.g. Jost and Ellner, 2000; Skalski and Gilliam, 2001). Borghans et al. (1996) found that a predator dependent functional response emerges naturally from a general quasi-steady-state assumption in a simple predator prey model where predators interact directly only with prey. The apparent interaction between predators is due to that the number of predators handling prey depends on both the prey and the predator density.

The Beddington-de Angelis functional response was derived explicitly by Beddington (1975) and proposed heuristically by DeAngelis et al. (1975). In Beddington's version predators encounter prey with rate λN and other predators with rate κP . A prey encounter leads to an handling time $t_h = \frac{1}{\alpha}$ and a predator encounter blocking $t_b = \frac{1}{\beta}$.

A possible MAP formulation the Beddington-de Angelis functional response is: A predator encounters prey with rate proportional to density N and after encounter it gets it and is able to resume foraging after an exponential handling time with rate α . There are also direct interactions between predators where the rate of encounter with other predators is proportional to their density. When a predator encounters another predator then they form a complex which last for an exponentially distributed time with mean $\frac{1}{\beta}$. This MAP has

$$\mathbf{D}_0 = \begin{bmatrix} -(\lambda N + \kappa(P-1)) & \lambda N & \kappa(P-1) \\ 0 & -\alpha & 0 \\ \beta & 0 & -\beta \end{bmatrix} \text{ and } \mathbf{D}_1 = \begin{bmatrix} 0 & 0 & 0 \\ \alpha & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix}.$$

The mean ingestion rate is $\lambda^* = \frac{\alpha\beta\lambda N}{\alpha\beta + \beta\lambda N + \alpha\kappa(P-1)} = \frac{\lambda N}{1 + t_h\lambda N + t_b\kappa(P-1)}$. This is the stochastic analogue of the derivation in Beddington (1975) where the number prey is decreased by one since the predator cannot interfere with itself. The assumptions are that there is no interaction between predators that handle prey and predators that search for prey, and that only pair interactions are formed. There is an implicit assumption that predators are scarce or that the interaction is weak, due to the asymmetry in the derivation. The rate of encounter with other predators ought to be proportional to the number of predators that

are searching, which is approximately $\kappa P \pi_0!$ This gives a functional response $f(N, P) = \lambda N \left(\frac{\sqrt{\beta^2(\alpha + \lambda N)^2 + 4\kappa P \alpha^2 \beta} - \beta(\alpha + \lambda N)}{4\kappa P \alpha} \right)$.

A formulation close to Borghans et al. (1996) is to work with the matrix

$$\begin{bmatrix} -\lambda NP & \lambda NP & 0 & \dots & 0 \\ \alpha & -(\lambda(N-1)(P-1) + \alpha) & \lambda(N-1)(P-1) & \dots & 0 \\ 0 & 2\alpha & -(\lambda(N-2)(P-2) + 2\alpha) & \dots & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & 0 & \dots & \lambda(N-m+1)(P-m+1) \\ 0 & 0 & 0 & \dots & -m\alpha \end{bmatrix},$$

where $m = \min(\{P, N\})$. Here one assumes that the N prey and P predators are (quasi)-constant, and when a predator encounters a prey item it is blocked for an exponentially distributed time with mean $\frac{1}{\alpha}$. Then a continuous approximation of P and N is used to find the C such that $\lambda(N - C)(P - C) - \alpha C = 0$ which amounts to finding the level where the upward movement is equal to the downward. This is simpler than finding the mean of the stationary distribution, but it seems to be a good approximation, see Figure 4.9. Borghans et al. (1996) then use a two-point Padé approximation at P and N equal to 0 respectively ∞ . This gives $C \approx \frac{NP}{N+P+\frac{\alpha}{\lambda}}$ which gives the Beddington response when C is multiplied with α , since this is the rate with which C are left per time unit. Thus $f(N, P) = \frac{\lambda N}{\lambda(N+P)t_h + 1}$. The Padé approximation used is quite rough as can be seen in Figure 4.9. Huisman and de Boer (1997) adopts exactly the same strategy as Borghans et al. (1996) but they include an extra state which enables them to produce a Padé approximated functional response of the general Beddington type, $f(N, P) = \frac{\lambda N}{\lambda N t_h + \lambda \epsilon P t_h + 1}$, where $0 < \epsilon < 1$.

Another predator dependent functional response is the ratio-dependent functional response. This has caused a lot of debate due to its “unnatural” behaviour at the origin (see Abrams and Ginzburg, 2000), it predicts positive predator growth at very low prey densities if only predator densities are lower, this gives extra stability of course. Suppose that the focal animal interacts with $P - 1$ conspecifics in a contest of prey; it gets it with probability $1/P$.

$$\mathbf{D}_0 = \begin{bmatrix} -\lambda N & \lambda N \\ \alpha(P-1) & -\alpha P \end{bmatrix} \quad \mathbf{D}_1 = \begin{bmatrix} 0 & 0 \\ \alpha & 0 \end{bmatrix}.$$

Here the stationary distribution in the states is $\pi = [\lambda P \ \alpha N](\lambda P + \alpha N)^{-1}$ and consequently the mean ingestion rate is $\lambda^* = \frac{\lambda \alpha N}{\alpha P + \lambda N} = \frac{\lambda N}{P + t_h \lambda N}$. This derivation is strange in a similar way to Beddington’s derivation since there is no symmetry in the interaction i.e. the focal animal interacts with conspecifics when it has caught a prey item, but it does not interact with other when they have caught a prey. A model with symmetry gives a Holling II response. A possible model

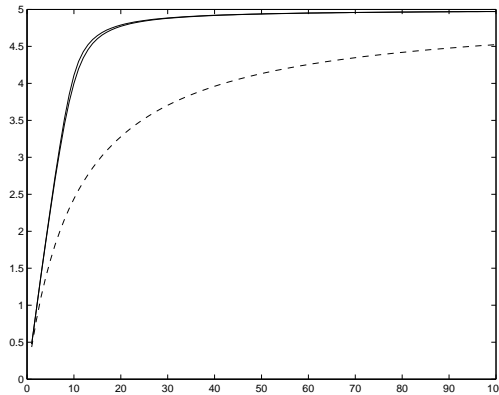


Figure 4.9: lower line (green) traditional Beddington-de Angelis functional response, upper (blue) the true Borghans and (red) my approximation. $P = 10$ and $\tau_h = 2$. Larger P make the traditional Beddington-de Angelis approximation even worse.

for this would be that the population hunts as one group, and the caught prey item is shared in a scramble competition, this is similar assumptions to one derivation of a ratio-dependent functional response in Cosner et al. (1999).

4.3 Stomach models

The MAP is suitable not only for modelling the external state of an animal but also the internal or both. Here \mathbf{D} would model the transitions between internal states, where the internal states could be size or stomach contents. Jeschke et al. (2002) argue that it is necessary to separate the handling time and the digestion time, since most predators are digestion limited. Even an amoeba search for food during only 17% of the time (Jeschke et al., 2002). The level of satiation could be modelled with a Markovian arrival process, where prey of different sizes increase the state with a suitable amount and in absence of food the satiation decrease. Another possibility is to link the energy reserves to growth, where food increases energy reserves, and when energy reserves reach a critical level then the organism grows to next state. Interesting output could be the amount of food needed reach the adult state given certain environmental conditions or the time that it takes, which is a PH-distribution.

An advanced way to include satiation effects into functional responses is to use an elaboration of stochastic dams. Stochastic dams are stochastic models

where precipitation arrives instantaneously as a stochastic point process. Each “rain” has a certain distribution (the amount of rain), which increases the dam content. The dam empties with a deterministic rate. The elaboration is to let the deterministic rate depend on the level in the dam (Bekker et al., 2004; Thygesen et al., 2005) and to allow more general arrival processes than Poisson (Bekker et al., 2004). Recent advances in Bekker et al. (2004) were used in a search for analytic formulas for stationary stomach distributions in Paper F. The stomach emptied with a rate that was proportional to the square-root of the stomach contents, which is similar to how a barrel with a small hole in the bottom filled empties (assuming Bernoulli flow). This rate has empirically been found to be the best fit to stomachs of whiting (Andersen, 1998). The solution to Poisson distributed prey was relatively simple and for Erlang-2 distributed food an analytical solution was found which was relatively intractable.

In many applications it may be useful to discretize the stomach content and use a MAP. A particular example where it is useful is a stomach where the emptying rate is $\kappa \cdot x^2$, where x is the stomach content. The problem with this rate is that the algebraic apparatus is much more difficult due to the fact that the dam never empties, which results in a singular Volterra equation that is difficult to solve (Bekker et al., 2004). However for a discretisation it is quite simple to get the stationary distribution.

The work of Metz and van Batenburg (1985a,b) describes the detailed process of hunting, which is subdivided into the tasks, encounter, stalking, strike, and eating. The basis for this work is the detailed observations by Holling (1966) on a mantid, *Hierodula crassa*, where it was shown that some of these activities depend on the level of satiation. In particular the encounter rate could be described as a function of satiation, $g(S)$ times the prey density, x , i.e. $\lambda = xg(S)$, the eating time and strike success were constant. Metz and van Batenburg (1985a) derive an integro-differential equation for a system of this kind based on Markovian dynamics, then they derive various simplifications to it. This important work has not been the source of much experimental work, which I believe is due to the difficult formalism, and to some extent the lack of detail in their exposition. This could easily be modelled as a MAP, where the stomach is divided into n equal subunits, i.e. we have $\{S_0, S_{\Delta s}, \dots, S_{n\Delta s} = S_{max}\}$. There is no difficulty, using a MAP, in having prey size distributions, which seems to be somewhat problematic in the model of Metz and van Batenburg (1985a).

Interestingly, Taylor (1976) studies the value of clumping to prey and the evolutionary response to ambush predators using a finite queue where the predator encounters aggregated prey. He finds that during most conditions clumping is valuable to prey, when the predator is an ambush predator that only can kill one item per group. This could be similar to the conditions that a cod encounters during the day, during dusk and dawn the prey would be dispersing and at night fully dispersed. Cod stomachs often contain a group of equally sized sprats in

similar states of digestion, which suggests that a cod can make multiple kills per group encounter, during some conditions. Together with data on cod stomachs and on the dispersal strategies of sprat and herring a stomach-based encounter model could be one important component in devising optimal life strategies of these species in the Baltic.

4.4 Numerical responses

The numerical response is the per capita production rate of offspring. This is a first order approximation as is the functional response. It is often used even if there is no separation of time-scales that justifies the approximation. In Paper E it is shown that in some cases it may be a good approximation, when there is plenty of food even if the functional response is varying wildly due to heterogeneities. However this particular model of a numerical response will vary much when food becomes scarce. Thus it will be a bad approximation during those conditions. The numerical response is often assumed to be the functional response times a small factor ε , the conversion efficiency. It intrigues me that this assumption is so common, since there are a number of other things that a predator can do that would decouple the processes, some of these are evident in humans.

Another thing which can make the numerical response less appropriate is strong non-linearities. For instance, in Article C we construct a hypothetical scenario where the the number of recruits to next generation is a step function. This makes a numerical response unsuitable in a model of this population since the variability or more precisely the tail of the distribution will influence the outcome.

The use of functional and numerical responses in situations where there reproduction and consumption of prey are on similar time-scales such as in lion-zebras, epidemiological and parasitological models may be a rough approximation since variations in encounter or contact rates will be important. Here I think it is important to include stochasticity in the population models.

4.5 Discussion

The MAP is a very general framework for formulating and analysing functional and numerical responses. A complication it is that there may be many rates to specify. These may possibly be fitted if experiments are made using the methods in Breuer (2002a) or Nielsen and Beyer (2006). An important aspect is that it may be possible to equip animals with tags that record feeding events (e.g. Block et al., 2002). This information together with spatial information of

local prey densities may substantially increase our knowledge on how functional responses look outside the laboratory.

The MAP may also indicate when a time-scale approximation is suitable with and when it is not. The functional response approximation is a “law of large numbers” approximation, perhaps would it be suitable to explore the consequences of “functional central limit” approximations where the variance is included. In a continuous approximation this gives stochastic differential equations, instead of the ordinary differential equation of e.g. Lotka and Volterra type. There is a large literature on averaging methods in stochastically perturbed dynamical systems e.g. Freidlin and Wentzell (1998), and Berglund and Gentz (2005), these contain some guidelines on how and when functions that depend on a stochastic process may be approximated by the same function of the mean of that process.

To my knowledge, apart from the previously cited work, there is only one article that use MAPs in biology, although the model is not denoted as a MAP in the article. It is the work by Recer and Caraco (1989) which contains a possible explanation for the empirical deviations from the predictions of optimal foraging theory. Standard optimal foraging theory produce result that state that the predator should always or never eat a certain prey type. However, this is not how the actual diets of real animals look like. The model of Recer and Caraco (1989) is a environment with two types of patches and two types of prey. The predator maximises the energy uptake, but there is a discrimination cost. For many parameter values they find that the predator should eat a certain percentage of the less profitable prey. Thus, MAPs have a potential for providing new views on ecological processes.

4.6 Contributions

This chapter introduces the Markovian arrival process, a class of point processes that has a large potential for ecological applications. In the Article C which concerns functional responses in a heterogeneous environment it is shown that previous analysis by Ruxton and Gurney (1994) was wrong; the functional response is not of the Holling II type when the environment is heterogeneous. The purpose of this article is also to introduce doubts about the validity of functional and numerical responses in general and we show that variability may be very important in these matters.

In Paper E it is shown that periodicities are an important complication, although it lacks the experimental basis for fitting different functional forms for the rates. The framework with periodicities can be embedded in a discrete time setting where everything is analysable (using discrete-time BMAPs) which can be useful on time-scales much longer than that of the period.

The article on moments, Article B, contain important tools for calculating any conditional moment, and a mathematical treatment of the inner workings of the moments. We provide numerical methods for calculating the moments, an extension of results in Narayana and Neuts (1992).

4.7 Future work

I would like to experimentally study the simplest possible predator-prey system and explore the variances in e.g. offspring production. Is it so that at high densities there is a large variation and at low there is less? It would also be important for population biology to look at the death process of the predator population when there is no food, since the commonly assumed exponential decline obviously does not apply to many systems. It may be that the number of deaths are well approximated by a Poisson process at high densities, if the total death process is a superposition of independent processes. This approximation will be less well suited at low densities, which are important in conservation biology and perhaps in the population dynamics of subdivided habitats where local extinctions may be common.

It would also be interesting to obtain data (e.g. by data storage tags or stomachs) and try to fit more general MAPs as an extension of the estimation procedure in Nielsen and Beyer (2005) or in Breuer (2002a). Could one determine how many states there should be in the MAP, as a generalization of Rydén (1997)?

Another interesting question in relation to stomachs and stomach fullness is what are the optimal prey choice consequences when these are considered? Is it due to the $\kappa\sqrt{x}$ emptying rate that one sees so many empty stomachs? This rate favours full stomachs since the emptying rate is faster the more there are in the stomach. Does this mean that large prey are more profitable, and if the stomach is almost full why not eat something small? What constraints are active when a predator is satiated; can they swim as usual or not? To find the meal size distribution when the stomach size distribution is known using the methods in paper F could be relevant, in particular in relation to the actual densities of prey, and contribute to the parameterisation of multi-species models.

Finally, theoretical results on when a given Markovian arrival process is close to another, or to a Markov additive process, would be needed to parallel the simplifications in Metz and van Batenburg (1985a). This would probably make the important models in Metz and van Batenburg (1985a) more accessible to experimental work.

CHAPTER 5

Markov additive processes can simplify individual-based models

An ounce of analysis is worth a ton of simulation

Lande et al. (2003) paraphrasing Haldane.
Monte Carlo is an extremely *bad* method; it should only be used when all alternative methods are worse.

Alan D. Sokal (1996a) before “embarking on 9 hours of lectures on Monte Carlo methods”.¹

5.1 Introduction

In this chapter I will present a structure that is useful for the analysis and simplification of some individual-based models (IBMs). The framework is directly

¹The same Sokal who wrote *Transgressing the Boundaries: Towards a Transformative Hermeneutics of Quantum Gravity* Sokal (1996c) a non-sensical text that was written to “...combat a currently fashionable postmodernist/poststructuralist/social-constructivist discourse – and more generally a penchant for subjectivism – which is, I believe, inimical to the values and future of the Left.” (Sokal, 1996b).

applicable to situations where the individuals change their state according to a Markov process and there is some property of interest, such as energy reserves, that decrease or increase depending only on what state the individual is in. This is the essence of Markov additive processes which we will make precise below. Moreover, many IBMs may be approximated by Markovian rules which makes this type of models generally interesting to IBM-modellers. The advantage of this framework is perhaps most evident in marine spatial IBMs where there is a flow field that advects and disperses the organisms and this flow field is calculated by a circulation model. Modern circulation models solve the partial differential equations for the flow numerically and in many of these there is a possibility to include additional partial differential equations to model e.g. the distribution of a chemical. These equations are of the same type and dimension as the ones governing the distribution of individuals, or the moments of the property of interest. Thus, it is relatively easy and cheap to include the latter type of models in a circulation-based IBM.

During the last decade there have been several such models where the effects of circulation on larval growth, survival and subsequent recruitment have been studied (see Heath and Gallego, 1997; Werner et al., 2001, for reviews). The main motivation for these studies is to improve the understanding of variability in recruitment and ultimately to make better models and predictions of the recruitment of fishes. This is a weak spot in many fisheries models since the number of successful recruits will determine much of the future development of the stock and the possibility to forecast would make control easier. Traditionally the number of recruits have been studied with time-series methods or a stock-recruitment relationship, usually with low success.

Individual-based models have increased our understanding of the effects of variability, but they are difficult to evaluate for large numbers of individuals and for long times, which may be of interest to the modeller. These issues are easier to study with Eulerian models which follow the evolution of the population densities relative to a fixed grid. The most obvious drawback with Eulerian models is that these generally are partial differential equations (PDEs) or even partial integro-differential equations (PIDEs). These are very computationally demanding to solve if the state space is high-dimensional. We show in Article D that if the models have a Markov additive structure then it is possible to obtain the moments of the Eulerian density by solving PDEs on a smaller state space. Possible extensions such as IBMs covering full population dynamics will be discussed at the end of the chapter.

There are many different definitions of individual-based models e.g. DeAngelis and Mooij (2005) include the physiologically structured models of Metz and Diekmann (1986) in this class. Here I will refer to individual-based models only in the sense that they model individuals, or possibly super-individuals, directly i.e. these are followed explicitly in a simulation model. In this sense, Lagrangian

or individual-based models are attractive since they take the individual in biology or, the atom or particle in physics as the starting point of the modelling process. They define how different types of individuals change their state by specifying how an individual of each type interacts with its environment. A large number of particles are followed individually and higher order properties of the system such as population density, carrying capacity or pressure and temperature in physics emerge from these models; they are not defined from the beginning. Since these properties in general are determined by the stochastic evolution of the system it is only in the simplest systems that it is possible to derive these higher order properties directly. In most other cases it is necessary to analyse these higher order properties by simulation which will be called the Lagrangian, or Monte Carlo method. Here it is important to note that each simulation is only one possible realisation of the system and that these simulations may yield quite different outcomes.

The conceptual advantages of IBMs are clear since the modelling begins with something that the biologist can relate to or have data on. Individual-based models can also be seen as tool to incorporate more variability than traditional models (Grimm, 1999). The disadvantages are that most individual-based models produce a realisation of a stochastic simulation, that they often are very complex with many parameters, and they are not well suited for long time-scales or for the study of extreme events. In order to analyse an IBM it is necessary to perform statistical experiments using several simulations, although this is not as frequently done as it should be. Hinckley et al. (2001) is an exception, where the different factors that could affect the successful recruitment to the nursery grounds of walleye pollock in Alaska were studied using contingency tables. The analysis of Lagrangian simulations may be very time consuming since there is scant prior knowledge on what mechanisms are important at the population level and which are not. It is also possible that the phenomena of interest are extreme events such as the survival of cod larvae. Such rare events may be very difficult to capture in a simulation, which it probably why mortality is excluded in most marine IBMs (sic!). An alternative is to use super-individuals (Scheffer et al., 1995), here the simulated particle represent a certain fixed number of individuals initially, say 10^6 individuals, this number decreases when the individuals that make up the super-individual die. When all are dead the super-individual have deceased. This allows mortality to be included but it creates a strict dependence between the individuals that constitute the superindividual. The interactions between individuals, perhaps of different types such as in predator-prey interactions, or of similar type in aggressive or cannibalistic interactions are typically difficult to model in IBMs since this concerns the relative distances of individuals. There are computing techniques such that it is not necessary to keep track of all the $n - 1$ possible interacting particles in an n particle simulation. Interestingly, these techniques have an Eulerian character since they keep track of the inter-particle distances

within a fixed grid. The difficulties with interacting particles is particularly large in marine systems due to the range of scales that are important from the individual interactions at the metre scale to the transport phenomena above the kilometre scale.

The Eulerian view is dual to the Lagrangian, here the particles are not followed but instead the densities of particles within a fixed coordinate system are calculated based on the Lagrangian properties. The disadvantages of the Eulerian view are that the individual trajectory is lost, which may provide information to the modeller, in general it is difficult to translate directly between the Eulerian and the Lagrangian reference frame (e.g. Grünbaum (1994) use a linearisation to convert a Lagrangian model to an Eulerian), and the Eulerian model typically involves the solution of partial differential equations (PDEs), which may be of high dimension: a four-dimensional PDE is demanding to solve numerically and only very special cases can be solved analytically. Each extra dimension in a PDE increases the number of computations with a multiplicative factor, which is proportional to the number of discretization points in the new dimension. Thus if the PDE is a function of t, x, y then a discretization with 1000 grid-cells in each dimension requires a number of calculations in the order 10^9 operations, adding an extra dimension z with 1000 cells will require 10^{12} operations and take at least 1000 times longer to solve.

The advantages of an Eulerian model is that it not necessary to perform statistical experiments since the Eulerian view deals with the outcomes of the statistical experiments that should be performed in the Lagrangian simulations i.e. the distributions themselves. When the interaction between individuals may be translated to an interaction between the densities or mean fields this it is much simpler to do in an Eulerian model. In some cases the PDE formulation allows for the use of a sophisticated mathematical machinery, e.g. to study asymptotic or global properties of the solution (see e.g. Stevens, 2000, and references therein). The properties of the solution at longer time-scales are easier to evaluate in Eulerian models than in Lagrangian models. Extreme or rare events are easier to handle too, such as the successful recruitment of a herring from a batch of eggs, since such events require very large amounts of particles initially to describe the rare event with some precision.

Thus, one of the major difficulties of Eulerian models is that they result in PDEs of high dimension. However, when the temporal evolution of the phenomenon that we are interested in, e.g. length of fish larvae, can be described by the moments of the additive component of a Markov additive process substantially less computing power is needed, since PDEs of low dimension are solved. Another important fact is that the translation between the Lagrangian to the Eulerian framework is straightforward when the individuals behave independently of each other.

It is important to note that the Lagrangean, simulation based, or Monte Carlo

method is one way to solve difficult problems, but they are stochastic, which makes them expensive to use. As a simple example, suppose that we would like to calculate the probability density of an exponentially distributed random variable with rate 2 at a particular time, say 0.7. (We assume that we cannot evaluate $2 \exp(-2 \cdot 0.7)$ directly). We could simulate 10000 times, count the ones that are in the interval $[0.65, 0.75]$ and then estimate $2 \exp(-2 \cdot 0.7) \approx \frac{\sum_i 1_{X_i \in [0.65, 0.75]}}{10000 \cdot 0.1}$. From the central limit theorem we will estimate this better and better as the number of points increases. The Eulerian view, in this context is to note that the pdf satisfies the ODE $y' = -2y$ with initial condition $y(0) = 2$. Solving this using 10000 steps to arrive at $x = 0.7$ we find that the approximation is The thing to note is that the Eulerian analysis give us an numerical approximation if we can't find the analytical solution, but the error is much less than that of the Lagrangean. However the Eulerian analysis cannot give us an impression of how it would look in the field (were we to observe 10000 exponentially distributed times with rate 2). If we only are interested in the probability distribution and possibly expectation of functions of the pdf then the Eulerian alternative is to be preferred (except in high-dimensional problems where such integrals become more cumbersome than simulating particles).

Perhaps a better alternative is the evaluation of the distribution of counts in a system such as a MAP at a given time. Either one could simulate the system, or one could use the pdf, which will have to be evaluated using e.g. the uniformization method. Here it is possible to control the error, which is much more difficult in the simulation (one knows that the error is approximately proportional to $n^{1/2}$). (Skall vara med?)

The problems in Article D are of this type where a number of parameters define the characteristics of the time-evolution of particles and their rewards. The main purpose in this article is to show that the framework is able to represent the same system that is realized from a Lagrangean simulation with an Eulerian analysis. It is less interesting in this respect to evaluate the sensitivity to parameters values, since for the purposes of comparing the same system these are exact. However, it is of course conceivable, and indeed usually the case in practical situations, that these parameters are only known with a certain amount of imprecision. This will increase the uncertainty in the model. In both frameworks one would have to integrate out the uncertainty in the parameters, which leads to a much more difficult problem, involving the determination of the joint probability distribution of the parameters, and then obtaining the true probability of being in a set of states as $\mathbb{P}\{X_t \in A\} = \int \mathbb{P}\{X_t \in A|\theta\} f(\theta) d\theta$, where $f(\theta)$ is the pdf of the parameters.

5.2 Markov additive processes

A Markov additive process (see e.g. Breuer, 2002b; Asmussen, 2003) (MAdP) is a bivariate Markov process $Y = \{X_t, S_t\}_{t \geq 0}$ where the first component X_t is a Markov process. The second component S_t is a process with conditionally independent increments given the state of the first process in the sense that:

$$\mathbb{E}\{f(S_{t+s} - S_t)g(X_{t+s})|\mathcal{F}_t\} = \mathbb{E}\{f(S_s)g(X_s)|X_t, S_t = 0\}.$$

where \mathcal{F}_t is the σ -algebra of the process Y up to time t (this represents the past history of the process), f and g are arbitrary measurable functions. Thus there is a translation invariance in the S_t process. The X_t process will be called the state process.

Some examples of Markov additive processes are:

- The Markovian arrival process, i.e. a Markov chain in discrete or continuous time with integer valued rewards. The conditional formulas for transient process derived in Article B are of extra importance in ecological settings where mortality is important.
- Markov reward processes. Here the transitions between states is specified by a Markov chain and a reward, positive or negative, which is accumulated continuously, where the rate of accumulation depend on the state in the Markov chain. These have been extended to have white noise in the reward process by Horváth et al. (2004).
- A variation of the Markov reward model where there are rewards also in transitions in state.
- Another variation of Markov reward models are Markov fluids. Rogers (1994) showed that it is possible to analyse the behaviour of these using Wiener-Hopf techniques on the corresponding (normal) Markov reward process. A Markov fluid can be imagined as a bath tub of finite size which has a number of pipes which can be open or closed, when open they fill the tub with rate θ and there is a number of taps which also may be open or closed. When a tap is open the flow out of it is ρ . Let Z_t be the number of open taps and Y_t the number of open pipes then the content of the tub, ξ_t obeys the differential equation

$$\frac{d\xi_t}{dt} = \theta Y_t - \rho Z_t,$$

when $0 \leq \xi_t \leq a$. When the tank is empty it remains empty until there is some inflow, and when the tub is full it remains full until the outflow is larger than the inflow. The dynamics of Y_t and Z_t are governed by a Markov Chain. These could be interesting to use in models for e.g. stomachs.

- Diffusions with continuous rewards, for an example see Article D. In this article the reward denotes length and the individual particle moves in two-dimensional turbulent flow.
- Diffusions with diffusive rewards or even more generally with rewards that are jump-diffusions which are diffusions that have sudden jump-discontinuities whose size have a certain distribution.

By direct products of state spaces it is possible to combine diffusions with Markov chains, which makes it possible to have state-dependent models of very high complexity.

In Article D we show how the Markov additive framework is applied to larvae that grow and die in a two-dimensional flow. Furthermore, we derive the moment formulas for this case and how the covariances can be calculated when there are two continuous rewards.

5.2.1 Marked Poisson and Markov Additive Processes

The beauty of the Markovian framework is most easily explained when both the state space, \mathcal{X} , of the Markov process and the reward space, Σ , are discrete.

Suppose that the initial distribution of individuals is such that their number of individuals in each state i and each initial reward j is Poisson distributed with parameter λ_{ij} for $i \in \mathcal{X}$ and $j \in \Sigma$. Then the total number of particles is also Poisson distributed with parameter $\Lambda = \sum_{i,j} \lambda_{ij}$. This is an example of a marked Poisson process on a discrete state space, and the initial distribution represents a measure, which can be formed into a probability measure for the individual particle, i.e. the probability that a randomly picked particle belongs to state i and has reward j is $\frac{\lambda_{ij}}{\Lambda}$. If the particles act independently of each other and change their state from state i and reward j at time 0 to state k and reward l at time t with probability $p(k, l, t|i, j, 0)$, the transition probabilities of the Markov (additive) process, then the number of individuals in state m and reward n at time t are Poisson distributed with $\lambda_{mn}(t) = \sum_{i,j} \lambda_{ij} p(m, n, t|i, j, 0)$. This follows from the fact that superposition of independent Poisson processes are still a Poisson process and that independent random thinning of Poisson processes are still Poisson (e.g. Grimmett and Stirzaker, 2001, p. 255).

Thus, the Markov (additive) process maps marked Poisson processes to marked Poisson processes. From the formula above, and the fact that the process is additive, it follows that e.g. the mean reward in state m at time t is equal to the weighted sum of the mean initial reward in each state i at time 0 plus a contribution from the change of state during this time. This latter contribution is simply the mean number of particles times the mean change in state of a particle that starts in state i at time 0 and ends up in m at time t times the

probability that a particle is i initially, summed over all states i . The weights in the initial mean reward is the transition probability of an i state particle at time 0 ends up in m at time t . Or equivalently,

$$\begin{aligned} \mathbb{E}\{S_t 1_{\{X_t=j\}} | X_0 = i\} &= \mathbb{E}\{S_0 | X_0 = i\} p(i, 0 | j, t) \\ &\quad + \mathbb{E}\{S_t 1_{\{X_0=j\}} | X_0 = i, S_0 = 0\} \end{aligned}$$

where $p(i, 0 | m, t)$ is the transition probability from state i at time 0 to state m at time t and $p(i, 0)$ is the probability of being in state i at time 0. Thus, for the calculation of the mean it is not necessary to know the distribution of the marks on the reward space, we only need to know the initial mean, the marginal density $p(i, 0)$ which specifies the probability of being in state i at time 0 and the mean change in reward from all initial states! This type of formula for moments are generic in Markov additive processes, thus the moment formulas are very similar for different additive processes, and their dimension are equal to the dimension of the state space \mathcal{X} .

These properties are also true on more general state and reward spaces, the difference is that one has to introduce a slightly more complicated measure for the marked Poisson process.

An example of the benefits of the Eulerian framework can be seen in a preliminary model to Article D which models the growth of larvae that diffuse in one dimension. Here 1000 particles were released at the origin, a convergent-divergent flow accumulate these in areas around $\pm \frac{\pi}{2}(2n + 1)$, $n \in \mathbb{Z}$, and they grow and die with different rates depending on spatial position. In Figure 5.1 the individual lengths are shown as red dots, the mean of the particle length in each computational cell is shown as a blue line and the Eulerian mean is shown as a solid black line.

From the figure it is obvious that the Lagrangian mean is only well-defined in cells with many particles. The flow profile is such that the determination of the mean in the areas where there are few particles would require very large amounts of initial particles. In addition, the Eulerian framework provides information on the distribution, see Figure 5.2.

A possible application would be to determine the different nursery grounds, and status (length) of settled larvae during different flow regimes when the spawning ground is known. This is a typical problem for marine IBMs (see e.g. Ådlandsvik et al., 2004; Skogen et al., 2003).

5.3 The backward equations

We present the forward equations in Article D, these describe how the probability distribution of the state space or the moment of the additive property

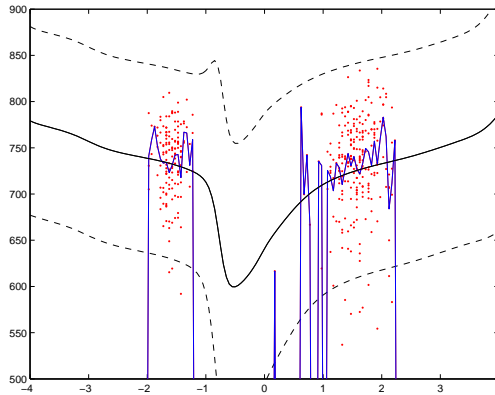


Figure 5.1: The solid black line shows the mean calculated using the Eulerian approach in a one-dimensional divergent flow. The blue lines show the cell means in of the length of the simulated particles, which are indicated by red dots. Approximate 95-percent confidence limits are indicated with black dashed lines. Based on an 1000 particles initially, 377 were alive at this time.

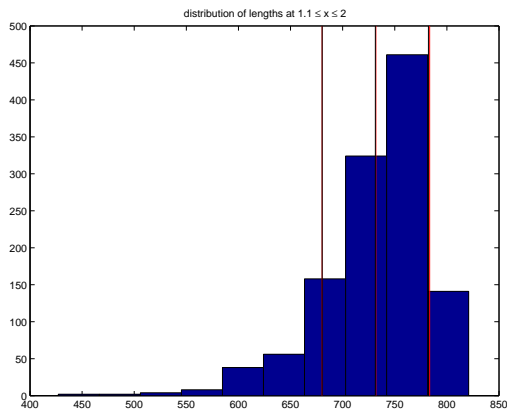


Figure 5.2: A histogram of the length of all particles in the area $1.1 \leq x \leq 2$ at time 10. The sample mean is 731.3 and the mean from the Eulerian scheme is 731.9 (middle red vertical line), the standard deviation is 51.02 resp 51.63. Based on a simulation with 10122 particles initially, where 1194 are in the region at the terminal time.

evolves forward in time, i.e. given the state at time s , what is the probability that the individual is in the set of states A at some future time $t > s$ or what is the expected reward at time t in states A given the initial state and mean reward at time s ?

The converse questions are possible where the probability asked for is: “What is the likelihood that the individual in state x at time t were in some set of phases A at time $s < t$?” These evolution of these probabilities are governed by the backward Kolmogorov equations and the Eulerian framework applies with some minor changes in the governing equations to these situations too. The backward equations are interesting to use when one observes an individual and would like to say something on its past state. Some difficulties will arise since the hydrodynamical equations are solved in forward time; concurrent solutions are not possible. However the method in Hermann et al. (2001) where low-pass filtered time-series of the flow are stored could be used in this context.

In marine larval ecology these could help to infer the possible spawning grounds of larvae that arrive to nursery areas, which seems to be a common problem (see e.g. Allain et al., 2003; Marinone et al., 2004). Possibly the information in otoliths could be used to increase accuracy in the backwards equations. The otoliths or ear-stones are bones in the ear of fish which aid them to keep their balance. These stones grow continuously with daily increments, similar to the rings of trees. The isotopic composition of different metals in the ambient water is thought to be mirrored in the deposits in the ear.

It would be very interesting to apply this framework to real situations. There are interesting statistical difficulties with this, but possibly the ancillary information of length and age plus the isotopic profiles in the otoliths could make inference possible. An interesting case would be to compare this method with the method of Schmidt (1922) where contour charts with the minimum length of eel larvae (leptocephali) was used to place the spawning location of European eel in the Sargasso Sea. The size of this area in the Sargasso Sea is so large that the actual spawning location of eel is still quite uncertain; the size is approximately 10^6 km^2 , twice the size of Spain.

Another application of the backwards equations would be to try to find the location which is most suitable for the reintroduction of an organism with planktonic dispersal in an archipelago.

5.4 Discussion

The Eulerian perspective in Markov additive processes can contribute to many individual-based models. The framework can be used to obtain answers to questions that are difficult in the Lagrangian view, such as the extreme events.

Since it is possible to let the state to depend on a Markov chain it is very flexible and will often be computationally efficient for phenomena of interest in marine situations. It is possible to include interactions with nutrient, and prey fields such as the nutrient, phytoplankton, and zooplankton-fields in Hermann et al. (2001).

The real difficulty with IBMs is to capture the biology to a sufficient degree (but not to much), since most information on the behaviour will come from laboratory experiments which are non-trivial to extrapolate to the field and in most cases the assumed field behaviour is an educated guess. Many organisms, even as small as bacteria, react on their environment and change their movement patterns such that the probability of being in a favourable place increases. When the cue is external such as food density this is easy to add to the movement pattern of a particle. It can be difficult when the cue is produced by the organisms themselves, which would pose a problem e.g. to modelling schools of fish with such techniques.

Reproduction is not included in most marine IBMs, possibly due to the enormous uncertainties that develop. A crude way of incorporating reproduction would be change the sign of the mortality in some states and associate this type of transitions with a birth of an individual in the Lagrangian simulation, and possibly link this with a jump to another developmental state if such are included. A disadvantage of this is that whereas death occurs to single individuals, reproduction creates a spatial dependence between offspring and parent, thus there is a pair-correlation that is important and the Poisson framework is no longer exact (Young et al., 2001). However, if the time-scales are different between reproduction and movement a Poisson approximation ought to be good.

If reproduction is included in this way, spawning can be turned on and off at suitable times. This option should be used with caution since e.g. Baltic cod seem to have shifted their spawning season due to the decline of the food of cod larvae (*Pseudocalanus*) in the Bornholm Basin (Hinrichsen et al., 2002). More realistic models would have to include an energetic reserve that can be emptied at suitable spawning times. Here the important question arises: "How do cod come to spawn at a certain time?". As we show in Article D it is possible to have the rate of accumulation of rewards to depend linearly on the reward itself. This increases the possibility for complex biological applications dramatically, since it is possible to introduce a linear feed-back in the reward.

5.5 Contributions

The current framework offers a possibility to get both the Lagrangian and the Eulerian information in models that can be quite elaborate. The Eulerian framework based on Markov additive processes is directly applicable to many of the

models that are used in marine larval IMBs.

There are many possible extensions, but the most important work is to show that the framework can provide much of the information that is sought and that the Lagrangian simulations are random which means that replication is needed to analyse their behaviour, whereas the Eulerian framework removes this need.

5.6 Future work

The most important thing is to apply the models to real data, then their value will be evident but also what elaborations are needed. The analysis of spawning grounds using otoliths would be both a statistically challenging and biologically relevant question.

The inclusion of reproduction could be modelled using branching Brownian motions; there is an equivalence between the expectation of these and some PDEs (Dynkin, 2002). Nowadays even interacting branching Brownian motions have been studied. It would be fantastic if it were possible to represent the internal dynamics of an individual using a Markov Chain, and to be able to have the particles annihilate other particles, reproduce, and to be able to describe the probability densities of their spatial distributions.

A difficulty is the interaction with other particles, here possibly the recent framework in economics with heterogeneous Markovian interacting agents (e.g. Aoki, 2002) could be of interest, or the Fokker-Plank formulation of living fluids by Willander et al. (2004), which is formulated in very general terms. Agent based models have been used to reproduce macroeconomic characteristics in e.g. stock price fluctuations from micro-behaviour. Willander et al. (2004) states that fluids where some components are alive cannot be modelled using standard statistical mechanics, hence they have developed a new framework to include such fluids. But they do not provide any examples on how this can be done.

A simpler possibility that deserves mentioning is to combine Markov chains with diffusions which has not been explored in any IBM to my knowledge and to derive the Eulerian equations of for the probability of being in a certain state and position. This is simpler than the additive framework but also powerful. For instance, Hufnagel et al. (2004) analysed the global spread of SARS (severe acute respiratory syndrome) using diffusion approximations of SIR-dynamics within countries and a continuous Markov chain that modelled the rate of movement of people by airlines between countries. The spatial spread of the epidemic starting with an infected individual in Hong Kong was analysed using 1000 realisations of the stochastic model², then they computed the mean number of infected individuals at each node. This could easily have been done using the Eulerian

²The second IBM to my knowledge that use replicates

framework for Markov processes.

Postscript

And perhaps worst of all, there is now quite a large community of scientists who are willing to sell modeling to managers as an alternative to hard, expensive experimentation, and this is too often an easy sell.

Walters and Martell (2004).

In this thesis we present a number of different tools that are or could be useful to the applied population biologist. The Markovian arrival process can be used as a simple tool to include the effects of stochasticity in encounter and foraging success of the individual dynamics which enables the modeller to investigate how this will affect the food source and the reproduction process of the individual. These models can be used to link the effects of internal states, such as energy reserves or stomach fullness, to the propensity to feed or ability to reproduce.

More work needs to be done for the Markov chain with discrete or continuous reward structure to be practically useful. First, it is necessary to be able to estimate the rates in the transitions, here some work has been done (Nielsen and Beyer, 2005; Breuer, 2002a) but more has to be done both regarding the procedures but also on making it known in biology. Second, there is a need to know how to reduce the state space, to make model reduction, similar to the reductions used by Metz and van Batenburg (1985a) in a continuous-state Markov process. Third, a practical case study is needed to show how this could be done to make it applicable.

In general I think there is a need for more work on how to incorporate sub-model stochasticity into population models. When are the law of large numbers arguments (which underlies the use of functional and numerical responses) appropriate, and when should these be replaced by functional central limit arguments, which would give a first order noise structure, be used and when is it necessary to have higher order moments?

Regarding the Markov additive processes of ensembles I believe they are already useful in answering the type of questions that currently are investigated in marine larval ecology. They provide modellers with the opportunity to get the whole picture in cases where the simulation based view only provides bits and pieces. Accompanied with particle trajectories from Lagrangian simulations they will further our understanding of variability in larval fish recruitment. Markov additive processes would also benefit from being applied to new situations where some property needs to be investigated. An obvious, and both biologically and statistically interesting question is given that we catch a larva at position x what is the most likely spawning ground? Using the ancillary information in otoliths such as age, concentrations of different isotopes and perhaps growth patterns this could perhaps be found with some precision.

It would be worth investigating how to include reproduction and how to cope with the spatial dependencies that this and other behaviours, such as schooling, generates. How close would these be to the marked Poisson process framework? Can one use Poisson approximations, there are results on this stemming from the work by Barbour, Chen and Stein (see Grimmett and Stirzaker, 2001), but will they provide error bounds? Reinert (2001) is able to provide error bounds for an epidemic process using Stein's method. Poisson approximation used in many other situations using moment-closures (e.g. Keeling et al., 2000) and the Durrett-Levin transform of Cantrell and Cosner (2004) without any error bounds. Could other frameworks that could provide alternative ways of deriving an Eulerian formulation the situations when Poisson approximations are not good, Brownian branching processes, the agent-based framework in economics, or the living-fluid formulation of statistical mechanics?

Regarding the issue of sustainability I think it necessary that we do not fool ourselves. There will almost certainly be sufficient amounts of uncertainties present in any relevant future model of fish populations that enable, or force, the decision-makers not to manage the "unmanaged commons" (cf. Hardin, 1968), i.e. to preserve and rebuild fish stocks. Empirical support for this claim can e.g. be found in the management of the Baltic cod. Here the total allowable catch (TAC) for cod was set to 39 000 tonnes in 2005. The International Council for the Exploration of the Seas recommended that the quotas should be reduced to 14 000 tonnes in 2006 to keep this threatened stock within safe limits. Yet the negotiations within the European Union lead to an increase in TAC for 2006 to 45 000 tonnes, and only one country objected to this!

Optimal dynamics of stochastic populations can come later.

Conclusion

It has been shown that the dispersion process of schools of sprat and herring in the Baltic can be described by a process where the schools follow lines of equal light intensity, and that they disperse below this light intensity. We were able to approximate the dispersion process with a model with uncorrelated random walkers and the time-scales for dispersion found in these models were of the same order as those seen on echograms.

The Markovian arrival process is used for biological applications, notably to model functional and numerical responses. We clarify some obscurities concerning a simple functional response in a heterogeneous environment, and provide moment formulas for survivors, along with numerical approximation schemes. The MAP in periodic environment is shown to be embeddable in discrete time with possible applications where time-scales are well separated. This is important since most systems are periodic, and their properties cannot be derived from the mean rates.

A fluid dam model is used for the modelling of stochastic stomachs, here an analytical formula is found for exponentially distributed meal sizes, and also a recursion formula for Erlang-2 distributed meal sizes, the latter is quite difficult to normalize (analytically).

Markov additive processes can be used as a tool to avoid the tedious statistical evaluations of individual-based models. We show that the moments can be obtained with a relatively small effort. These tools will probably be of great value, in particular to larval biology in marine environments.

APPENDIX A

**Vertical migration and
dispersion of sprat (*Sprattus
sprattus*) and herring (*Clupea
harengus*) schools at dusk in
the Baltic Sea**

Published in Aquatic Living Resources 2003. 16:317-324.

Vertical migration and dispersion of sprat (*Sprattus sprattus*) and herring (*Clupea harengus*) schools at dusk in the Baltic Sea.

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Abstract

In populations of herring (*Clupea harengus*) or sprat (*Sprattus sprattus*), one typically observes a pattern of schools forming at dawn and dispersing at dusk, usually combined with vertical migration. This behaviour influences interactions with other species; hence a better understanding of the processes could contribute to deeper insight into ecosystem dynamics. This paper reports field measurements of the dispersal at dusk and examines two hypotheses through statistical modelling: that the vertical migration and the dissolution of schools is determined by decrease in light intensity, and that the dissolution of schools can be modelled by diffusion, i.e. active repulsion is not required. The field measurements were obtained during 3 days in March at one location in the Baltic Sea and included continuous hydroacoustical monitoring, trawl samples, and hydrographical CTD data. Echogram patterns were analysed using the school detection module in Echoview® and local light intensities were calculated using a model for surface illuminance. The data and the analysis support that schools migrate upwards during dusk, possibly trying to remain aggregated by keeping the local light intensities above a critical threshold, that schools initiate their dissolution when ambient light intensity drops below this critical threshold, and that fish subsequently swim in an uncorrelated random walk pattern.

Keywords: Random walk; Dispersion of schools; Light; Clupeids; Baltic

A.1 Introduction

When collecting hydroacoustic data in the Baltic, one commonly sees a fast change in the echogram structure at dawn and dusk. The day situation is often characterized by aggregations of clupeids close to the bottom, whereas there are disperse targets in the whole water column during the night. The pattern is similar to that of herring in the North Sea (Blaxter and Parrish, 1965; Blaxter, 1985), however, in the Baltic, a large proportion of the schools do not migrate vertically—they disperse in the initial phase of the transition close to the bottom. It is possible that most of the predator-prey interactions take place during the twilight period (Major, 1977; Clark and Levy, 1988); the swift changes seen on the echograms may be an indication of this. There are indications that both herring and sprat, and their main predator, cod, are feeding during dusk and dawn (Blaxter and Parrish, 1965; Adlerstein and Welleman, 2000) and consequently these periods could be very important for the population dynamics. This motivates an investigation of the spatial structure and how it changes during dusk and dawn.

The dominant species of fish in the Baltic Proper are sprat (*Sprattus sprattus*), herring (*Clupea harengus*), cod (*Gadus morhua*), and flounder (*Platichthys flesus*). Due to the relative scarcity of species, especially among schooling fishes, the Baltic is a well-suited study area for the transition between schooling and dispersed state in clupeids, since it is relatively easy to know what species one is studying and since the possible number of interactions between different species is few.

While there is some consistency as to where and when schools can be found, it remains much less clear why and how the transitions occur. One specific question is if schooling fish actively spread out at dusk, or if schools simply diffuse as their members cease to maintain the structure. This article approaches this question by estimating the time constant of dissolution, assuming passive diffusion, and comparing with observed transition times. Another open question is how directly the dispersal is related to the decrease in light. We examine this issue by estimating the local light intensity at the position of observed schools.

A.2 Materials and methods

A.2.1 Data sampling and analysis

Data were collected during a survey with R/V Dana 12-14 March 2002. Two Simrad EY500 split-beam echosounders were continuously recording at 38 and 120 kHz, respectively. The hydroacoustical data were stored electronically. The transducers were hull mounted, and the echosounders were calibrated using stan-

dard procedures (Foote et al., 1986). Fish were collected using a TV3-trawl; it was used as a bottom trawl except for night hauls on March 14, when it was used for pelagic hauls. Hydrographical data were collected several times a day with a Seabird SBE911PLUS CTD equipped with a light sensor (Biospherical/Licor) that measures the photosynthetically active radiation (PAR). The collection of fish was performed during both day and night on approximately the same site.

The location at approximately $16^{\circ} 20' E$, $55^{\circ} 45' N$ was chosen to be representative of the Bornholm basin with respect to species composition and depth range; the depth at this location was 55-65 m. The fish caught were minced and afterwards discarded into the sea at a dumping site 5 nmi away downstream in order to avoid disturbances to the study site. Steaming speed to and from the dumping site was 12 knots, otherwise the ship was operated at approximately 3 knots in order to make the acoustical data independent of whether the ship was trawling or not. The current direction was registered using an acoustic Doppler current profiler. The hydroacoustical data were analysed using the Echoview software, version 2.20. The lower threshold for acceptance of volume backscattering values, S_v was set to -60 dB for echo-integration and school-detection procedures. The school detection parameters were set heuristically and the distances were based on GPS positions. The settings for the 38 kHz sounder were (120 kHz settings within parentheses): minimum school length 2 (1.20) m, minimum school height 2 (1.20) m, minimum connected height 1.5 (0.6) m, maximal vertical linking distance 3 (2) m, maximal horizontal linking distance 3 (7) m.

Both the EY500 and the Echoview software have algorithms for detecting the bottom. However, due to bad weather with high swell on March 14, the bottom identification did not perform well. Improved bottom values for pings were identified using a Matlab program searching for the maximum increase of echo level between samples near the expected depth obtained from nearby pings. Furthermore, to compensate for ship movements due to the swell, a C++ program was used to produce new raw data files in which data in relevant telegrams were shifted up or down in order to get bottom points aligned with a smoothed bottom line obtained by a moving average with Gaussian weights. The end result was a smoother bottom (see Fig. A.1) and echogram patterns more comparable with the days with calm weather. We did not correct for bubbles under the ship. Regions that evidently were affected by this phenomenon were excluded from the analysis. Data from 0.5 m above bottom to 15 m below surface were included in the echo-integration and school-detection procedures. The upper limit was chosen since observed fish densities were very low above this depth and in order to exclude bubble noise on March 14.

The ship is equipped with a Licor PAR light sensor placed on the top of the ship, but its sensitivity was insufficient for measuring light intensities at dawn and dusk. Instead the light variations for twilight were estimated using a model by Janiczek and De Young (1987), which gives surface illuminance given time, date,

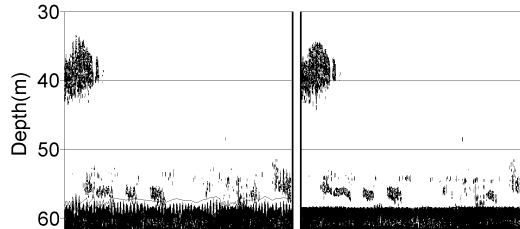


Figure A.1: Detail of echogram from March 14. Bottom is unsmoothed in the left panel, smoothed in the right.

geographical position and cloudiness. The cloudiness is given as four factors, corresponding to:

- a Average clear sky, less than 70% of the sky covered by (scattered) clouds; the direct rays of the Sun or Moon are unobstructed relative to the location of interest.
- b The Sun or Moon is easily visible but direct rays are obstructed by thin clouds.
- c The direct rays of the Sun or Moon are obstructed by average clouds.
- d Dark stratus clouds cover the entire sky (rare).

In the computer program, these conditions a-d correspond to dividing the calculated illuminance with a factor 1, 2, 3, 10, respectively. The model is quite crude (see Fig. A.2). Since the sky was clear for most of the time, we have chosen to use the factor 1 or condition a.

The attenuation of light by water was estimated from the Seabird PAR data using a linear regression of the logarithm of light intensity on depth:

$$\ln I(z) = \ln I(0) - K \cdot z \quad (\text{A.1})$$

where $I(z)$, $I(0)$ are the light intensities at z and 0 m depth, respectively, and K is the attenuation coefficient. K was found to vary between 0.131 and

0.167 m^{-1} . We chose to proceed with a value of 0.16 m^{-1} , which is higher than the average value for the layer of interest, arguing that the rays of light during dusk come from a more or less horizontal light source. The attenuation

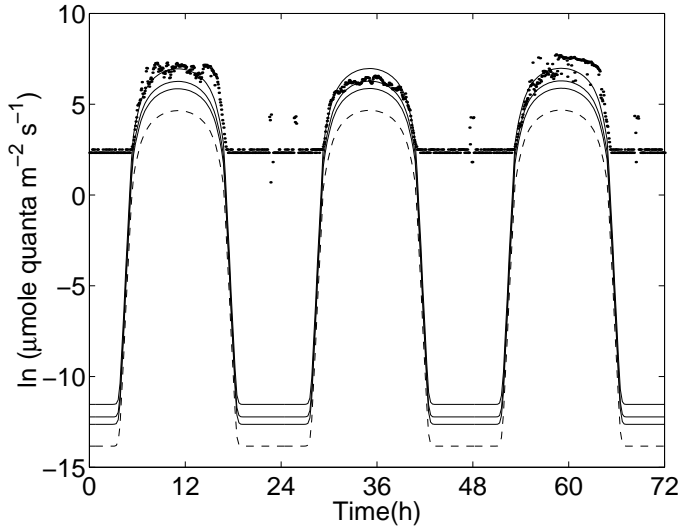


Figure A.2: Plot of logarithmic light intensities $\ln(\mu\text{mole quanta} \cdot \text{s}^{-1} \cdot \text{m}^{-2})$. The dots are the measurements from the quantum light meter on R/V Dana. The black lines correspond to the four different cloud situations in the model for illumination (uppermost—clear, lowest—sky covered with stratus clouds). Horizontal scale is hours.

is somewhat higher in the layer 0–10 m but we do not take this into account, since the relative effect of this is the same for all days and since only data below 15 m were analysed. The surface illuminance from the model is given in lux, but the attenuation constant is based on PAR. We choose to use the factor $0.01953 \mu\text{mole quanta} \cdot \text{s}^{-1} \cdot \text{m}^{-2} \cdot \text{lux}^{-1}$ (Brock, 1981) to convert illuminance to surface PAR irradiance, assuming a standard daylight spectral distribution.

A.2.2 Migration process in relation to light levels

For every ping, the depth at which the local light intensities would correspond to 0.01, 0.1, 1 lux, respectively, were calculated using the daylight model and the attenuation coefficient. These light levels were chosen a priori since it has been reported that schooling ceased in this interval (Blaxter and Parrish, 1965; Iida and Mukai, 1996). The data were then displayed in the echograms as lines of equal irradiance. The schools followed the lines (see Fig. A.3). With the Echoview school-detection module, we obtained the mean depth of a school and

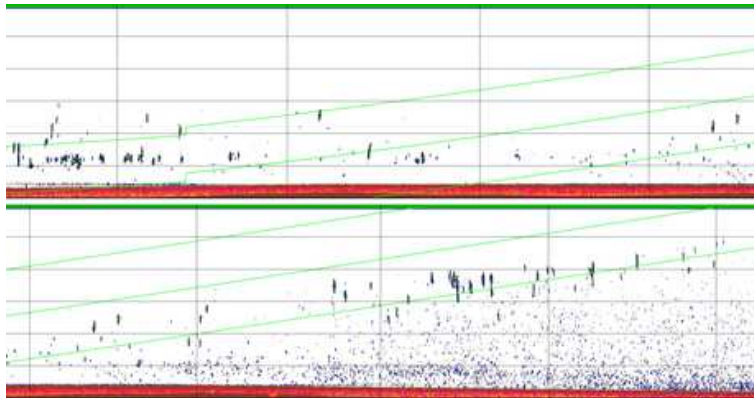


Figure A.3: The vertical migration of schools and dissolution at dusk on March 13. The three green parallel lines that rise from left to right are lines of equal light intensity. The step in the lines (left, top) is due to sunset. Distance between horizontal lines are 10 m and 0.5 nmi between vertical lines.

the time at which the school was recorded. In the same way as above, time was used to calculate the light intensity at the mean depth of the school. For data well within the transition period (17.25–18 UMT), we tested the model:

$$Y_{ij} = \alpha_i + \beta_i X_{ij} + \epsilon_{ij} \quad (\text{A.2})$$

where Y_{ij} is the natural logarithm of the light intensity at the depth of the centre of the j^{th} school at the i^{th} day, α_i , β_i are constants for day i , and X_{ij} is the depth of the j^{th} school on day i , and ϵ_{ij} are independent and identically distributed normal variables with zero mean and variance σ^2 . The logtransformation was necessary to meet the standard assumptions for linear regression.

A.2.3 Modelling the dissolution of schools by diffusion

This section constructs a model of the diffusion of schools and proposes three different time constants describing the duration of the process. With all three approaches, the number of fish in a typical school is Poisson distributed with mean \bar{N} and the sizes of different schools are stochastically independent. At the starting point (dusk), all fish in the school are positioned at a single point in the plane. Then, instantly, all social forces are removed and each fish performs an independent random walk. The difference between the models is in how schools are placed at the starting point, and which criterion is used for the schools to have dissolved.

A.2.4 Dispersion from regularly spaced schools

At time $t = 0$ (dusk), a school is located at each node in a regular two-dimensional grid with grid length L . At times $t > 0$, each individual fish performs a random walk in two dimensions with intensity σ^2 . The expected time until an individual fish has displaced itself a distance Δx from its starting point is (e.g. Berg, 1992).

$$\frac{\Delta x^2}{2\sigma^2}. \quad (\text{A.3})$$

If we insert $L/2$ for Δx , then we obtain roughly the time until the individual is halfway between two school centres; hence we cannot determine from which school the individual originated. Based on this argument, we would find that the time to dissolution of the schools is

$$\frac{1}{8} \frac{L^2}{\sigma^2}. \quad (\text{A.4})$$

Although this argument is somewhat sketchy, we shall see below that more elaborate modelling leads to similar answers.

A.2.4.1 Statistical detection of school structure

Using the same model as above, the individual fish constitute a Poisson point process (Stoyan et al., 1995) which is fully specified by its density $\rho(x, y, t)$. This density satisfies the partial differential equation (e.g. Berg, 1992):

$$\frac{\partial \rho(x, y, t)}{\partial t} = \frac{1}{2} \sigma^2 \nabla^2 \rho(x, y, t) \quad (\text{A.5})$$

and can be expressed in terms of its Fourier series (Farlow, 1983):

$$\rho(x, y, t) = \sum_{k=-\infty}^{\infty} \sum_{l=-\infty}^{\infty} A_{kl}(t) \exp\left(i2\pi \frac{kx + ly}{L}\right). \quad (\text{A.6})$$

Here, the coefficients $A_{kl}(t)$ are determined by the initial conditions, and are equal to:

$$A_{kl}(t) = \frac{\bar{N}}{L^2} \exp\left(-\frac{1}{2} \sigma^2 \left(\frac{2\pi}{L}\right)^2 (k^2 + l^2) t\right). \quad (\text{A.7})$$

The shape of the solution is quickly dominated by the smallest non-zero eigenvalue, $-1/2\sigma^2(2\pi/L)^2$, obtained with wave numbers $k^2 + l^2 = 1$.

At time T , we hypothetically sample two square regions, each of area $L^2/4$. One area, A , is centred around $(x, y) = (0, 0)$ so that the initial position of the school

is in the dead centre. The other, B , is centred at $(x, y) = (L/2, L/2)$ i.e. the point in space furthest away from the schools.

The number of fish found in region A , N_A , is then Poisson distributed with mean EN_A :

$$EN_A = \int_A \rho(T) dx dy = \sum_{k,l} A_{kl}(T) H_A(k, l) \quad (\text{A.8})$$

where

$$H_A(k, l) = \int_A \exp\left(2\pi i \frac{kx + ly}{L}\right) dx dy = f(k)f(l) \quad (\text{A.9})$$

and

$$f(k) = \int_{-L/4}^{L/4} \exp\left(2\pi i \frac{kx}{L}\right) dx. \quad (\text{A.10})$$

We have that $f(k)$ is equal to $L/2$ when k is zero, otherwise it is $\frac{L}{2\pi ik} (\exp(\frac{\pi}{2} ik) - \exp(-\frac{\pi}{2} ik))$. The latter expression is equal to 0 when k is even and non-zero. When k is odd, we have $f(k) = L/(\pi k)$, if $k = \dots, -11, -7, -3, 1, 5, 9, \dots$, and $f(k) = -L/(\pi k)$, if $k = \dots, -9, -5, -1, 3, 7, 11, \dots$. Now, focusing on the long-term behaviour, we consider only the lowest eigenvalue obtained with $k^2 + l^2 = 1$. Then

$$\begin{aligned} EN_A \approx & \frac{L^2}{4} A_{0,0}(T) + \frac{L^2}{2\pi} (A_{0,1}(T) + A_{1,0}(T) + A_{0,-1}(T) \\ & + A_{-1,0}(T)) = \frac{\bar{N}}{4} + \frac{2\bar{N}}{\pi} \exp\left(-\frac{\sigma^2}{2} \left(\frac{2\pi}{L}\right)^2 T\right). \end{aligned} \quad (\text{A.11})$$

Correspondingly,

$$\begin{aligned} EN_B \approx & \frac{L^2}{4} A_{0,0}(T) - \frac{L^2}{2\pi} (A_{0,1}(T) + A_{1,0}(T) + A_{0,-1}(T) \\ & + A_{-1,0}(T)) = \frac{\bar{N}}{4} - \frac{2\bar{N}}{\pi} \exp\left(-\frac{\sigma^2}{2} \left(\frac{2\pi}{L}\right)^2 T\right). \end{aligned} \quad (\text{A.12})$$

The criterion for the schools to have dissolved is that the $N_B > N_A$ with a certain probability $P = 1/2 - \alpha$. Approximating the Poisson distributions with Gaussians, we find

$$N_B - N_A \sim N\left(\frac{4\bar{N}}{\pi} e^{-\frac{\sigma^2}{2} \left(\frac{2\pi}{L}\right)^2 T}, \frac{\bar{N}}{2}\right). \quad (\text{A.13})$$

And P is the probability of $N_B - N_A > 0$ which can then be approximated as

$$P = \frac{1}{2} - \alpha = \Phi\left(-\frac{4\sqrt{2\bar{N}}}{\pi} e^{-\frac{\sigma^2}{2} \left(\frac{2\pi}{L}\right)^2 T}\right) \quad (\text{A.14})$$

where Φ is the standard Gaussian distribution function. Equivalently,

$$T = -\frac{L^2}{2\pi^2\sigma^2} \ln \left(\frac{\pi}{4\sqrt{2\bar{N}}} q \left(\frac{1}{2} + \alpha \right) \right) \quad (\text{A.15})$$

where $q(1/2 + \alpha)$ is the $(1/2 + \alpha)$ -quantile of the standard Gaussian distribution.

According to this expression for T , the natural time scale of the dissolution process is L^2/σ^2 . In this time unit, we may plot T as a function of α for different values of N . This is done in Fig. A.4. The most striking feature of the plot is the plateau, implying a fairly rapid transition from high levels of aggregation ($\alpha \approx 0.4$) to low levels of aggregation ($\alpha \approx 0.1$). This is comforting since it implies that the estimated transition time is not very sensitive to the exact choice of α , i.e. the critical level of aggregation. With this approach, the dependence on $\ln N$ is also quite natural; more fish in the school makes it easier to detect differences when they exist.

A.2.4.2 Dispersion from randomly placed schools

This model is a Poisson cluster model, using the terminology of stochastic geometry (Stoyan et al., 1995): schools are placed randomly in the plane according to a Poisson point process in 2D with intensity λ_s . To obtain the same density as in the previous model, we must have $\lambda_s L^2 = 1$. As before, school sizes are independent and identically Poisson distributed with mean \bar{N} , all fish within a school are co-located at the school centre at time $t = 0$, and for time $t > 0$, each individual performs an independent Brownian motion with intensity σ^2 .

At some later time t , the stochastic geometry becomes a Cox process, i.e. a conditional Poisson point process. To be specific, given the school centres, the density of the fish originating from the particular school is a Gauss bell, and the total density is the superposition of all these Gauss bells. For a Poisson process, we can define the entropy as

$$I = -E \ln \rho(x, y) \quad (\text{A.16})$$

i.e. minus the logarithmic density at a “typical point”.

If only one school is present at position $(x, y) = (0, 0)$, then at time t , individual fish will be distributed according to a Poisson process with density

$$\rho(x, y, t) = \frac{\bar{N}}{2\pi\sigma^2 t} e^{-\frac{1}{2} \frac{x^2 + y^2}{\sigma^2 t}} \quad (\text{A.17})$$

leading to an entropy

$$I = 1 + \ln 2\pi + \ln \sigma^2 t - \ln \bar{N} \quad (\text{A.18})$$

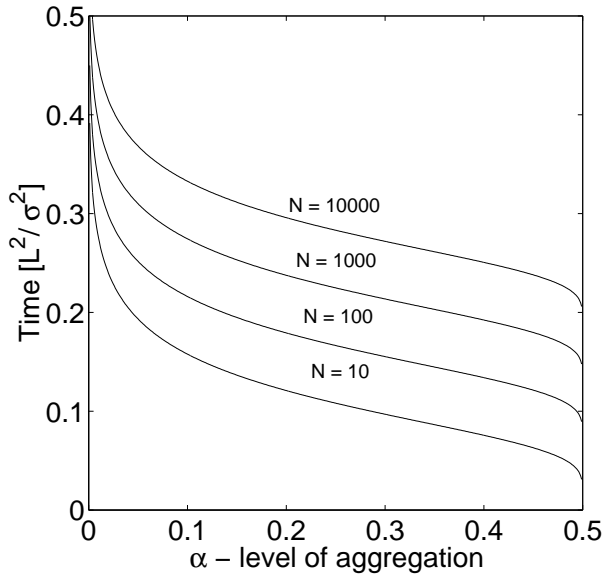


Figure A.4: Time against level of aggregation.

where $\sigma^2 t$ is the variance in the 2D Gauss bell at time t . For low values of t , the schools do not interact and the same expression holds for the Poisson cluster model. As t grows, the entropy will gradually approach its limit in which the density is constant

$$\rho_\infty = \bar{N}\lambda_s \quad (\text{A.19})$$

which leads to an entropy of $-\ln \bar{N}\lambda_s$. One way of assessing the time duration of the transition is to assume that the initial growth of entropy continues and then report the time where this entropy reaches the steady-state value. We find:

$$1 + \ln 2\pi + \ln \sigma^2 t - \ln \bar{N} = -\ln \lambda_s - \ln \bar{N} \quad (\text{A.20})$$

Table A.1: The weight and percentage of the species caught in the bottom hauls

Species	Common name	Fraction in bottom hauls	Fraction in pelagic hauls
Sprattus sprattus	Sprat	0.636	0.798
Clupea harengus	Herring	0.094	0.177
Platichthys flesus	Flounder	0.011	0
Gadus morhua	Cod	0.257	0.025
	Other species	0.002	≤ 0.001
Total weight (kg)		4387	914

or

$$t = \frac{1}{2\pi e\lambda_s\sigma^2}. \quad (\text{A.21})$$

A.2.5 Estimation of parameters

The inter-school distance was obtained with Echoview's school-detection module. Mean target strength was calculated from the TS relation (Foote, 1987) for clupeids and the length-distribution of caught herring and sprat. This was used to calculate the number of fish per school, assuming that schools could be described as vertical cylinders. The mean school area is (MacLennan and Simmonds, 1992) $\bar{A} = \frac{3\pi}{8} \bar{L}_0^2$, where \bar{L}_0^2 is the mean of squared length of schools.

A.3 Results

For the bottom and pelagic hauls, the catch consisted of more than 70% and 97% of clupeids, respectively (see Table A.1). The size distributions were the same for bottom and pelagic hauls for sprat and herring (Fig. A.5); the schools on the echograms are most likely sprat and herring.

The model for the relation between depth of school centres and local light conditions was significantly better at describing data than $Y_{ij} = \alpha_i$, i.e. that the logarithm of the light was independent of depth ($P < 0.002$). The model could be reduced to a model with a common slope; all β_i are equal (see Fig. A.6). The model could not be reduced more, e.g. to zero slope or a common intercept. The residual plots did not indicate that the model was inappropriate. Since the error variance was high, the part of the variation that could be explained by the model was rather low, 0.22.

The distance between schools was found to be 70–200 m, the number of clupeids per school was 400–900, and the mean area was in the range 120–220 m^2 .

Comparing the three suggested time constants of the transition, only the second time constant is based on statistical identification of school structures and hence grows with the number of fish in a typical school. Except for this difference, the time constants scale identically. Furthermore, for a school size between 10 and 10 000 fish, the estimated time constants are all of the same order of magnitude, i.e. between 0.05 and 0.3, measured in the time unit L^2/σ^2 . In summary, a useful time constant of the dissolution process is about 0.1 L^2/σ^2 and after 0.3 L^2/σ^2 , it is fair to say that the process has ceased.

To estimate L^2 , we note that the average distance between schools during the daytime is 70–200 m. Since the width of the transect at the bottom is 7–8 m (7° beam width), this implies a school density of maximum one school per 490

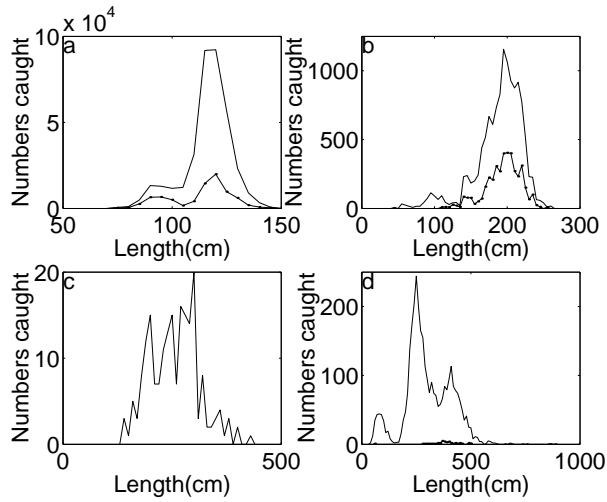


Figure A.5: The total numbers caught '—' in 20 hauls within a certain length-class of the dominant species sprat, herring, flounder and cod (top left, top right, bottom left, bottom right). The line joining dots '·—' shows fish caught with pelagic hauls (three hauls).

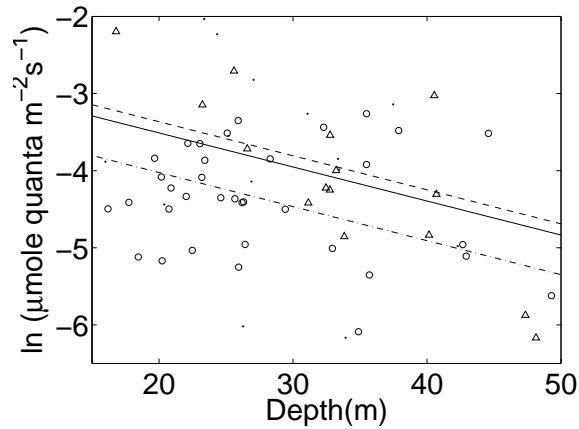


Figure A.6: Relationship between logarithm of light intensity at school centre and depth of school centre for 12–14 March 2002. Data from 12 March '●', 13 March '○' and 14 March '△'. Fitted model for 12 March '—', 13 March '---', and 14 March '—·—'.

m^2 and minimum one school per 1600 m^2 .

To obtain a rough estimate of the diffusivity, we assume a swimming speed of one body length per second and a body length of 0.1 m, and a relaxation time (time between turns) of the swimming direction of 10 s. This yields $\sigma^2 = 0.1m^2s^{-1}$ (Berg, 1992). The fraction $\frac{L^2}{\sigma^2}$ is then in the interval between 4900 and 16,000 s. Multiplying the former with 0.1 and the latter with 0.3, we obtain that the time for schools to dissolve is in the range between 8 and 80 min.

These models all assume that the fish in a school at time $t = 0$ are located at the same point. In reality, the size of a school is measurable compared to the typical distance between schools and thus the time constants should be seen as upper bounds.

A.4 Discussion

Some authors (Weston and Andrews, 1990; Fréon et al., 1996) have proposed that the dissolution, or expansion of schools may be due to a diffusion process, but not specified the underlying mechanism. In this paper, a simple model for the dissolution of schools is proposed, where the fish in a school disperse as uncorrelated random walkers. The models presented are based on few parameters and should be easy to use to compare with data in different regions. The estimated transition times are comparable to those observed, indicating that active dispersal is not required to explain the observed change in the pattern. Iida and Mukai (1995) obtained similar values for the dispersion of Kokkanee schools, 50 min; whereas Fréon et al. (1996) showed that, in Senegalese waters, the transition took several hours, but the expected values depend on the local conditions.

The results given by Orlowski (2001) suggest that there is a slower transition in the Baltic at dusk for herring and sprat that takes approximately 4 h; however that result is based on S_v per 30 min, not school identification. The slower transition could be explained with planktonic prey emerging from the bottom at dusk and that the fish dispersing close to the bottom are hungry enough to risk feeding and dispersing where the predation risk probably is very high since cod are close to the bottom. If the planktonic prey are rising slowly, then may be the dispersed fish close to the bottom follow their prey toward the surface, which would give rise to a slower transition phenomenon. This leads to an anisotropy that may give different time scales depending on whether the solution is determined in the horizontal or in the vertical plane. In a similar approach to Orlowski (2001), Giannoulaki et al. (1999) obtained a transition for sardines in the northern Aegean Sea that took several hours; it may be that the averaging done using S_v and the modelling of the vertical migration with relatively low order trigonometric polynomials give longer dispersion times.

Schools follow roughly the lines of equal light intensity, but with high variation. The fact that the schools rise faster than the lines of equal irradiance (i.e. $\beta < 0$) is difficult to explain. However, it should be noted that the differences between the light intensities at the end points of the fitted lines are very small and perhaps the estimated slope β is an artefact of the methodology. In any case, the slope β being significantly different from 0 in the statistical sense should not overshadow the observation that schools appear to remain at similar light levels. It is encouraging that the models catch this feature despite the simplicity in their assumptions and the uncertainty on the parameters. The log-transformation of the light data makes biological sense, since the response of eyes is approximately logarithmic.

The fact that the model could not be reduced to a common intercept may be due to real differences between days or that the cloudiness factor in the model for the light illuminance is the same for the different days, while the light levels seem to differ between days (see Fig. A.2).

The high variation in the results is partly due to few measurements. However, diurnal vertical migration is highly variable (e.g. Blaxter and Parrish, 1965; Appenzeller and Leggett, 1995); it can vary over season, and is probably dependent on tides, the physiological status of the fish as well as predators (Blaxter and Parrish, 1965).

Appenzeller and Leggett (1995) showed that the modus and the upper 95 percentile of the biomass distribution of rainbow smelt (*Osmerus mordax*) closely follow the lines of constant local light intensities, whereas the lower 95 percentile did so to a lesser extent. The range of the vertical distribution was narrower during day than night. They also noted that the smelt formed dense schools during day, which dispersed during night. Based on our results, it is possible that the widening of the distribution is due to schools dissolving, and that the upper parts that followed light levels more closely were schools rising.

Future work should be aimed at describing the internal and external state of the schooling fish in the Baltic. Is the crepuscular period the time at which the clupeids are eating, being eaten, neither or both? Stomach data of both clupeids and cod with high temporal resolution could help to answer that question. If the dispersion pattern of a school were studied with sonar, this could possibly give the local swimming speeds of the fish, and a better overview of the process. In addition, it would be interesting to follow the individual fish during the dispersal of schools in laboratory tanks, such as was done by Blaxter and Parrish (1965). With modern tracking techniques, it should be able to obtain more information about the behaviour and motion of the individual fishes, and it might be important and informative to incorporate the predatory behaviour of cod in relation to clupeids, since predation is not a static risk but a dynamic process dependent on prey behaviour (Lima, 2002).

A.5 Conclusion

Schools of herring and sprat tend to follow lines of equal light intensity when they migrate towards the surface at dusk in the Baltic, whereas this is not the case for the dispersing fish. In contrast to other studies showing the phenomenon that migrating fish follow lines of equal light intensity, we have found that a large part of the schooling fish dispersed close to the bottom. This causes a widening of the depth distribution, which may be attributed to differences in hunger or some other internal factor. Three different measures for the time until schools are dispersed are presented, these agree quite well with the time-scales viewed on the echograms. The times depend on few parameters and should be useful in comparisons.

Acknowledgements

We wish to thank the crew of the R/V Dana for excellent work and the DIFRES personnel for processing the fish. The research was supported by the SLIP research school under the Danish Network for Fisheries and Aquaculture Research (www.fishnet.dk) financed by the Danish Ministry for Food, Agriculture and Fisheries and the Danish Agricultural and Veterinary Research Council. The work is part of a larger project 'Development of improved models of fisheries impact on marine fish stocks and ecosystems' also funded by the Danish Ministry for Food, Agriculture and Fisheries.

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APPENDIX B

Higher order moments and conditional asymptotics of the Batch Markovian Arrival Process

Manuscript accepted for publication in *Stochastic Models*.

Higher order moments and conditional asymptotics of the Batch Markovian Arrival Process

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Abstract

We consider the number of arrivals in a Batch Markovian Arrival Process (BMAP) and derive matrix analytic expressions for its moments of arbitrary order. These expressions consist of decomposition formulas connected to the semigroup structure of the moments, forward and backward differential equations, and recursive as well as direct integral formulas. This extends earlier work by Narayana and Neuts on the first two factorial moment matrices. We next turn to the *terminating* BMAP, i.e. a BMAP with an absorbing state in which no arrivals occur. We consider the asymptotic behavior of the moments conditional on the process not yet having terminated. We show that the conditional mean and variance possess affine asymptotics and derive the coefficients explicitly. Finally we discuss how parts of our work also applies to the more general class of Rational Arrival Processes (RAPs).

B.1 Introduction

The Markovian Arrival Process (MAP), a point process associated with transitions in a finite Markov chain (Lucantoni, 1993; Neuts, 1979), is a highly versatile construction. The MAP extends the analytic and numeric virtues of the Poisson process to non-exponential waiting time distributions and non-trivial dependence structures.

There exists an extensive literature on the MAP, in particular in a queuing context. Neuts 1979 presented a thorough discussion of the MAP which was used by Ramaswami 1980 in his detailed analysis of a single server queue with MAP input. The modern parameterization of the MAP was introduced by Lucantoni et al. in 1990; see also Lucantoni (1991, 1993). In an essential reference for our work, Narayana and Neuts 1992 derived properties of the first and second order moment matrices. Pacheco and Prabhu 1995 studied the properties of Markov additive processes of arrivals, which are more general processes with BMAPs as a subset. Breuer 2002b generalized this work further to Markov-additive jump processes on general phase spaces and with arrivals in a general (real) vector space. Asmussen and Koole 1993 showed that any marked point process can be approximated in the weak convergence sense by the slightly more general class of Markovian Arrival Streams. It follows that the BMAPs with an appropriate scaling are dense in the class of stationary point processes with positive real marks. The versatility of the MAP has been used for sensitivity analysis and for characterization of point processes (Andersen and Nielsen, 2000; Andersen et al., 2004).

The MAP literature has primarily focused on continuous time although discrete time MAPs have been applied to packet based transmission systems such as the Asynchronous Transmission Mode protocol (ATM) (Blondia and Casals, 1992) and Integrated Services Digital Networks (ISDN) (Blondia, 1992).

In this work we generalize well known first and second order moment formulas for the *Batch* MAP (BMAP) to moments of arbitrary order. It also allows for a unified treatment of non-central and factorial moments, and of the continuous-time and the discrete-time case. These results are given in section B.3. Based on these results we present a numerical algorithm for the calculation of moments of arbitrary order generalizing results by Narayana and Neuts (1992) and Neuts and Li (1995).

While earlier approaches in this direction employ generating functions, we present alternative derivations based on elementary probabilistics, the semigroup structure of the transition probabilities, and the stochastic geometry of the point process. In section B.3 we compare the approaches. Most importantly, the semigroup-based approach has the advantage of indicating generalizations to wider classes of processes, but at the expense of considerable abstraction rela-

tive to the elementary probabilistic reasoning. In addition, we find it elucidating to have the different approaches in parallel, in particular so because they connect to different bodies of literature within the theory of stochastic processes.

The original motivation behind this paper was an application to ecology where points in the MAP correspond to a particular foraging individual ingesting a prey item. This application calls for *terminating* MAPs, i.e. processes that eventually enter an absorbing state where no arrivals occur, corresponding to death. Such terminating MAPs have recently been considered in Latouche et al. (2003). Moreover, in this ecological application the fate of the survivors were of main interest. This lead us to investigate the *conditional* moments of the number of arrivals occurring in a long time interval. Here the conditioning is on the process not having terminated, which in the ecological application corresponds to averaging over survivors only. This situation is analyzed in section B.4. The asymptotic behavior of the conditional mean and variance turns out to be affine in time and we find explicit formulas for the linear asymptotes.

Finally we show, in section B.5, that our results carry over verbatim to the more general class of rational arrival processes (RAPs), introduced in Asmussen and Bladt (1999). This is hardly surprising because the RAPs still employ a matrix machinery, although without an underlying Markov Chain.

B.2 The Batch Markovian Arrival Process

A Batch Markovian Arrival Process (BMAP) in continuous time is a Markov process (N, J) with two components: a *phase* process $J = \{J(t) \in \{1, \dots, m\} : t \geq 0\}$, and a non-decreasing and additive *counting* process $N = \{N(t) \in \mathbb{N}_0 : t \geq 0\}$. We may represent the BMAP as the univariate Markov process $X = \{X(t) = m \cdot N(t) + J(t) : t \geq 0\}$; the generator of X is an infinite matrix

$$\mathbf{G} = \begin{pmatrix} \mathbf{D}_0 & \mathbf{D}_1 & \mathbf{D}_2 & \mathbf{D}_3 & \cdots \\ \mathbf{0} & \mathbf{D}_0 & \mathbf{D}_1 & \mathbf{D}_2 & \cdots \\ \mathbf{0} & \mathbf{0} & \mathbf{D}_0 & \mathbf{D}_1 & \cdots \\ \vdots & \vdots & \vdots & \vdots & \ddots \end{pmatrix}. \quad (\text{B.1})$$

Here the m -by- m matrices \mathbf{D}_n , $n \in \mathbb{N}_0$, parameterize the BMAP. It is required that $\mathbf{D} = \sum_{n=0}^{\infty} \mathbf{D}_n$ is finite and a generator; in fact \mathbf{D} is the generator of the phase process J which is in itself Markov. The matrix \mathbf{D}_n specifies the rates of transitions in J occurring simultaneously with a batch of n events occurring in the point process.

By restricting the parameters of \mathbf{D}_n one obtains sub-classes of special interest: The Markov Modulated Poisson Processes (e.g. Fischer and Meier-Hellstern,

1992) has \mathbf{D}_1 diagonal and $D_k = 0$ for $k \geq 2$; the two-state case is termed a *Switched Poisson Process* (van Hoorn and Seelen, 1983), and when only one of the two diagonal elements in \mathbf{D}_1 is positive one obtains the *Interrupted Poisson Process* (Kuczura, 1973) which is perhaps the simplest MAP, save the Poisson process itself.

As a note on nomenclature, the literature is slightly inconsistent regarding the terms MAP and BMAP. Here, we shall reserve the term MAP for a BMAP with individual arrivals only, i.e., $\mathbf{D}_k = \mathbf{0}$ for $k > 1$. We will derive results in the general BMAP setting, but whenever there is a significant and useful simplification in the MAP case we will state this result explicitly.

In our analysis of non-central moments of $N(t)$ it becomes convenient to introduce

$$\mathbf{D}_n^* = \sum_{i=0}^{\infty} i^n \mathbf{D}_i \quad \text{and} \quad \mathbf{D}_n^f = \sum_{i=0}^{\infty} i^{[n]} \mathbf{D}_i .$$

Here, $i^{[n]}$ is the factorial power $i \cdot (i - 1) \cdots (i - n + 1)$, and we take $0^0 = 0^{[0]} = 1$ so that

$$\mathbf{D}_0^* = \mathbf{D}_0^f = \sum_{i=0}^{\infty} \mathbf{D}_i = \mathbf{D} .$$

Note that $\mathbf{D}_1^f = \mathbf{D}_1^*$, and that these expressions for the MAP simplify to

$$\mathbf{D}_0^* = \mathbf{D}_0^f = \mathbf{D}_0 + \mathbf{D}_1 , \quad \mathbf{D}_n^* = \mathbf{D}_1 , \quad \text{for } n \geq 1, \quad \mathbf{D}_n^f = \mathbf{0} \text{ for } n \geq 2 .$$

Throughout, when we make use of \mathbf{D}_n^* or \mathbf{D}_n^f we assume they are finite.

B.3 Formulas for moment matrices

This section considers the *non-central moment matrices* $\Psi_n(t)$, which are given by their (i, j) -elements, for $t \geq 0$, $p \in \mathbb{N}_0$

$$[\Psi_p(t)]_{ij} = \mathbb{E}^i \{ N^p(t) \mathbf{1}(J(t) = j) \} , \tag{B.2}$$

as well as *factorial moment matrices*, $\mathbf{M}_p(t)$, for which the corresponding (i, j) -element is

$$[\mathbf{M}_p(t)]_{ij} = \mathbb{E}^i \left\{ N^{[p]}(t) \cdot \mathbf{1}(J(t) = j) \right\} .$$

Here, $\mathbf{1}(A)$ denotes the indicator variable of the event A while \mathbb{E}^i denotes expectation w.r.t. \mathbb{P}^i , the law of the BMAP with initial condition $J(0) = i$, $N(0) = 0$.

We shall use the notation $\mathbb{P}^{i,k}$ and $\mathbb{E}^{i,k}$ when the counting process N starts in state $N(0) = k$.

The factorial moment matrices were studied thoroughly by Narayana and Neuts (1992), who obtained explicit matrix expressions for first and second order using generating function techniques. In this section we generalize their results to arbitrary order.

B.3.1 A decomposition formula

Theorem B.1 *The non-central moment matrices $\Psi_p(t)$ satisfy*

$$\Psi_p(t_1 + t_2) = \sum_{i=0}^p \binom{p}{i} \Psi_i(t_1) \Psi_{p-i}(t_2) ; p \in \mathbb{N} . \quad (\text{B.3})$$

The same holds for the factorial moment matrices $\mathbf{M}_p(t)$

$$\mathbf{M}_p(t_1 + t_2) = \sum_{i=0}^p \binom{p}{i} \mathbf{M}_i(t_1) \mathbf{M}_{p-i}(t_2) ; p \in \mathbb{N} .$$

Proof: The result follows from the observation that the restrictions of the arrival process to the intervals $(0, t_1]$ and $(t_1, t_1 + t_2]$ are independent, when conditioning on the phase $J(t_1)$ at time t_1 . For notational brevity we introduce $N(t_1, t_2) = N(t_1 + t_2) - N(t_1)$.

Then

$$\begin{aligned} [\Psi_p(t_1 + t_2)]_{ij} &= \mathbb{E}^i \{ N^p(t_1 + t_2) \mathbf{1}(J(t_1 + t_2) = j) \} \\ &= \mathbb{E}^i \{ (N(t_1) + N(t_1, t_2))^p \mathbf{1}(J(t_1 + t_2) = j) \} \\ &= \sum_{l=0}^p \binom{p}{l} \mathbb{E}^i \{ N(t_1)^l N(t_1, t_2)^{p-l} \mathbf{1}(J(t_1 + t_2) = j) \} . \end{aligned}$$

We continue the manipulation of each term in this sum to obtain

$$\begin{aligned} &\mathbb{E}^i \{ N(t_1)^l N(t_1, t_2)^{p-l} \mathbf{1}(J(t_1 + t_2) = j) \} \\ &= \mathbb{E}^i \{ \mathbb{E}^i \{ \{ N(t_1)^l N(t_1, t_2)^{p-l} \mathbf{1}(J(t_1 + t_2) = j) \mid J(t_1), N(t_1) \} \} \} \\ &= \mathbb{E}^i \{ N(t_1)^l \} \mathbb{E}^i \{ N(t_1, t_2)^{p-l} \mathbf{1}(J(t_1 + t_2) = j) \mid J(t_1), N(t_1) \} \\ &= \mathbb{E}^i \left\{ N(t_1)^l \sum_{k=1}^m \mathbf{1}(J(t_1) = k) \right\} [\Psi_{p-l}(t_2)]_{kj} \\ &= \sum_{k=1}^m [\Psi_l(t_1)]_{ik} [\Psi_{p-l}(t_2)]_{kj} . \end{aligned}$$

Combining these we obtain

$$[\Psi_p(t_1 + t_2)]_{ij} = \sum_{l=0}^p \binom{p}{l} \sum_{k=1}^m [\Psi_l(t_1)]_{ik} [\Psi_{p-l}(t_2)]_{kj} ,$$

which is the element-wise version of the stated matrix equation.

To see that the results also hold for the factorial moment matrices, note that all computations in the proof of the theorem remain valid when replacing the powers n^p with factorial powers $n^{[p]}$. In particular we use the result

$$(a + b)^{[p]} = \sum_{i=0}^p \binom{p}{i} a^{[i]} b^{[p-i]} ,$$

which is known as the Chu-Vandermonde identity (Weisstein, 2003).

□

Corollary 1 The matrices $\Psi_p(t)$ satisfy the forward and backward differential equations

$$\Psi'_p(t) = \sum_{i=0}^p \binom{p}{i} \Psi_i(t) \mathbf{D}_{p-i}^* , \quad \Psi'_p(t) = \sum_{i=0}^p \binom{p}{i} \mathbf{D}_i^* \Psi_{p-i}(t) .$$

Similarly, $\mathbf{M}_p(t)$ satisfy

$$\mathbf{M}'_p(t) = \sum_{i=0}^p \binom{p}{i} \mathbf{M}_i(t) \mathbf{D}_{p-i}^f , \quad \mathbf{M}'_p(t) = \sum_{i=0}^p \binom{p}{i} \mathbf{D}_i^f \mathbf{M}_{p-i}(t) . \quad (\text{B.4})$$

□

Proof: The forward equation for $\Psi_p(t)$ is proved by choosing $(t_1, t_2) = (t, dt)$ in Theorem B.1 and letting $dt \searrow 0$.

We find

$$\begin{aligned} \Psi_p(t + dt) - \Psi_p(t) = \\ \sum_{i=0}^{p-1} \binom{p}{i} \Psi_i(t) (\mathbf{D}_{p-i}^* dt + o(dt)) + \Psi_p(t) (\mathbf{I} + \mathbf{D}_0^* dt + o(dt)) - \Psi_p(t) \end{aligned}$$

reducing to the forward equation as $dt \searrow 0$. Here and in the following $o(\cdot)$ is Landau's o , in this case associated with the limit $t \searrow 0$. The estimates

$$\Psi_0(t) = I + D_0^* dt + o(dt) \quad \text{and} \quad \Psi_p(t) = D_p^* dt + o(dt) \quad (p \in \mathbb{N})$$

as $dt \searrow 0$ are standard and come directly from the generator (B.1).

The backward equation can be proved correspondingly by choosing $(t_1, t_2) = (dt, t)$, and the equations for the factorial moment matrices follow analogously.

□

Corollary 2 The non-central moment matrices satisfy the recursive integral equation

$$\Psi_p(t) = \int_0^t \sum_{i=0}^{p-1} \binom{p}{i} \Psi_i(u) D_{p-i}^* e^{D(t-u)} du$$

for $t \geq 0, p \in \mathbb{N}$. For the factorial moment matrices $\mathbf{M}_p(t)$ the corresponding equations are

$$\mathbf{M}_p(t) = \int_0^t \sum_{i=0}^{p-1} \binom{p}{i} \mathbf{M}_i(u) D_{p-i}^f e^{D(t-u)} du .$$

□

Proof: This result was derived by Narayana and Neuts for the first two factorial moments, and their method applies verbatim in our case:

The solution to the forward equation in $\Psi_p(t)$ is found by convolving the driving function $\sum_{i=0}^{p-1} \binom{p}{i} \Psi_i(u) D_{p-i}^*$ with the impulse response, $\exp(Du)$ (Råde and Westergren, 2004).

Similar recursive integral expression may be derived from the backwards equations. Note that in the case of the MAP, the recursive formula for the factorial moment simplifies to

$$M_p(t) = p \cdot \int_0^t M_{p-1}(u) D_1 e^{D(t-u)} du .$$

B.3.2 An alternative derivation based on the semigroup structure

We now reconsider Theorem B.1 taking the semigroup structure of the transition probabilities into account. At the end of this section we discuss the benefits of this approach. Let x denote a state (n, j) in the univariate representation X of (N, J) and let $f : x \mapsto f(x)$ denote a function on state space. Now, recall from standard Markov theory that the transition probabilities $\{\mathbf{P}(t) : t \geq 0\}$ form a

continuous semigroup of linear operators, which each map an initial distribution π of $X(0)$ to the terminal distribution $\pi\mathbf{P}(t)$ of $X(t)$. Dually, $\mathbf{P}(t)$ maps the function f to its expectation

$$[\mathbf{P}(t)f](x) = \mathbb{E}^x \{f(X(t))\} \quad ,$$

which is a function of the initial condition $X(0) = x$, whenever the expectation exists. We note that f can be represented as an infinite vector of function values and that one can represent the operation of $\mathbf{P}(t)$ on f directly as a matrix vector product. We will generally interpret $\mathbf{P}(t)f$ in the general, more abstract, sense. In the following we will use $f(n, j)$ for $f(x)$ to avoid the somewhat cumbersome expressions that extract j and n from x .

Let \mathcal{V} be a linear space of such functions f with the property that \mathcal{V} is invariant under the semigroup, i.e. $\forall t \geq 0 : \mathbf{P}(t)\mathcal{V} \subset \mathcal{V}$. Then, trivially, the restrictions $\mathbf{P}_{\mathcal{V}}(t)$ of the operators $\mathbf{P}(t)$ to \mathcal{V} also form a semigroup, i.e. we may write

$$\mathbf{P}_{\mathcal{V}}(t + s) = \mathbf{P}_{\mathcal{V}}(t) \star \mathbf{P}_{\mathcal{V}}(s) \quad .$$

Here \star indicates operator concatenation, $(P \star Q)(f) = P(Q(f))$. If \mathcal{V} is finite dimensional, then $\mathbf{P}_{\mathcal{V}}(t)$ admits a finite matrix representation and thus the composition rule \star involves only matrix algebra.

We now show that Theorem B.1 is exactly the algebraic representation of the composition rule \star for a suitable function space \mathcal{V} . In fact, let \mathcal{V} be the linear space of functions f of the form

$$f(n, j) = \sum_{i=0}^p \alpha_{ij} n^i \quad ,$$

for some coefficients $\alpha_{ij} \in \mathbb{R}$, $i = 0, \dots, p$, $j \in 1, \dots, m$. Thus, for fixed phase j , the function $f(\cdot, j)$ is a polynomial of order no greater than p . This space \mathcal{V} has dimension $m(p + 1)$.

Proposition B.2 *The space \mathcal{V} thus defined is invariant under $\mathbf{P}(t)$, for any $t \geq 0$.*

Proof: The claim follows from the additive structure of the BMAP:

$$\mathbb{E}^{j,n} \{f(N(t), J(t))\} = \mathbb{E}^{j,0} \{f(n + N(t), J(t))\} \quad ,$$

which holds for any f whenever the expectation exists. Now, let $f \in \mathcal{V}$ and let

α_{ij} be the corresponding coefficients. We then obtain:

$$\begin{aligned}
(\mathbf{P}(t)f)(j, n) &= \mathbb{E}^{j,n} \{f(N(t), J(t))\} \\
&= \mathbb{E}^{j,0} \left\{ \sum_{i=0}^p \alpha_{iJ(t)} (N(t) + n)^i \right\} \\
&= \sum_{i=0}^p \mathbb{E}^{j,0} \left\{ \alpha_{iJ(t)} \sum_{l=0}^i \binom{i}{l} N^{i-l}(t) n^l \right\} \\
&= \sum_{l=0}^p \left[\sum_{i=l}^p \binom{i}{l} \mathbb{E}^{j,0} \{ \alpha_{iJ(t)} N^{i-l}(t) \} \right] n^l = \sum_{l=0}^p \beta_{lj} n^l \quad (\text{B.5})
\end{aligned}$$

with the obvious definition of β_{lj} . We now have a polynomial in n of order no greater than p , for fixed phase j , and thus an element in \mathcal{V} .

□

We collect the coefficients α_{ij} , that uniquely identifies $f \in \mathcal{V}$, in $(p+1)$ column vectors $\boldsymbol{\alpha}_i, i = 0, \dots, p$ each of dimension m . The $p+1$ tuple of the $\boldsymbol{\alpha}_i$'s is denoted by $\boldsymbol{\alpha}^p$. We are now ready to give the algebraic representation of $P_{\mathcal{V}}(t)$.

Proposition B.3 *Let $f \in \mathcal{V}$ be represented by $\boldsymbol{\alpha}^p = (\boldsymbol{\alpha}_0, \dots, \boldsymbol{\alpha}_p)$ and let $t \geq 0$. Define $g = P(t)f$ and let g be represented by the $p+1$ tuple of column vectors $\boldsymbol{\beta}^p = (\boldsymbol{\beta}_0, \dots, \boldsymbol{\beta}_p)$, i.e.*

$$g(j, n) = \sum_{i=0}^p \beta_{ij} n^i .$$

Then

$$\boldsymbol{\beta}_l = \sum_{i=l}^p \binom{i}{l} \Psi_{i-l}(t) \boldsymbol{\alpha}_i \quad (\text{B.6})$$

holds for $l = 0, \dots, p$.

Proof: The result follows immediately from Equation (B.5) in Proposition B.2. Since

$$\mathbb{E}^{j,0} \{ \alpha_{iJ(t)} N^{i-l}(t) \} = \sum_{k=1}^m \alpha_{ik} \mathbb{E}^{j,0} \{ \mathbf{1}(J(t) = k) N^{i-l}(t) \} = \sum_{k=1}^m [\Psi_{i-l}(t)]_{jk} \alpha_{ik}$$

we obtain the element-wise version of (B.6).

□

The restriction $\mathbf{P}_\nu(t)$ may thus be represented by the $p + 1$ -tuple $\Psi^p(t) = (\Psi_0(t), \dots, \Psi_p(t))$, and we may write

$$\beta^p = \Psi^p(t) \circ \alpha^p$$

where the rule \circ is defined by (B.6) for $l = 0, \dots, p$.

Finally, we must give the algebraic representation of operator concatenation \star . By the semigroup property we immediately have

$$\Psi^p(t + s) \circ \alpha^p = (\Psi^p(t) \star \Psi^p(s)) \circ \alpha^p = \Psi^p(t) \circ (\Psi^p(s) \circ \alpha^p) .$$

Writing out the first and last term using (B.6) and comparing terms we obtain

$$\mathbf{Z}^p = \mathbf{X}^p \star \mathbf{Y}^p \Leftrightarrow Z_n = \sum_{i=0}^n \binom{n}{i} X_i Y_{n-i} ,$$

where $\mathbf{Z}^p = (Z_0, \dots, Z_p)$ is a $p + 1$ -tuple of m -by- m matrices and similarly for \mathbf{X}^p and \mathbf{Y}^p . With this definition of \star , Theorem B.1 is simply the semigroup property

$$\Psi^p(t + s) = \Psi^p(t) \star \Psi^p(s) .$$

Alternatively, the composition rule can be represented as matrix multiplication, but less compact. Introduce the block matrix Ψ^p with $(p + 1) \times (p + 1)$ blocks each of size $m \times m$, where the (i, j) th block entry is $[\Psi^p]_{ij} = \binom{j-1}{i-1} \Psi_{j-i}$ for $j \geq i$ and $\mathbf{0}$ for $i > j$. If we re-interpret the $p + 1$ tuples β^p and α^p as column vectors, then $\beta^p = \Psi^p \alpha^p$ and $\Psi^p(t + s) = \Psi^p(t) \Psi^p(s)$.

We have now established theorem B.1, and may turn to some consequences of the result which follow easily from this approach. First, the infinitesimal generator of the semigroup $\Psi^p(\cdot)$ is

$$\lim_{t \searrow 0} \frac{1}{t} (\Psi^p(t) - \Psi^p(0)) = (D_0^*, \dots, D_p^*)$$

and since a continuous semigroup of operators is characterized by its generator, we immediately obtain the following:

Theorem B.4 *The matrix family $\Psi_i(t)$ for $i = 0, \dots, p$ and $t \geq 0$ is uniquely specified by the decomposition rule (B.3) and the behavior near $t = 0$*

$$\Psi_0(t) = \mathbf{I} + \mathbf{D}_0^* t + o(t) \quad \text{and} \quad \Psi_p(t) = \mathbf{D}_p^* t + o(t) ; \quad p \in \mathbb{N} .$$

Similarly, we immediately recognize the equations of corollary 1 as the standard differential equations of semigroups

$$\frac{d}{dt} \Psi_0^p(t) = (D_0^*, \dots, D_p^*) \star \Psi_0^p(t) = \Psi_0^p(t) \star (D_0^*, \dots, D_p^*) .$$

Also the similar statements for the factorial moments are, from this perspective, immediate. This is because the sub-space of polynomials of order no greater than p is also the sub-space of *factorial* moments of order no greater than p ; the difference merely amounts to choosing a different basis when performing the calculations. In this case the behavior near $t = 0$ is such that

$$M_0(t) = I + D_0^f t + o(t) \quad \text{and} \quad M_p(t) = D_p^f t + o(t) ; \quad p \in \mathbb{N} ,$$

and thus the generator of the semigroup $M_0^p(\cdot) = (M_0(\cdot), \dots, M_p(\cdot))$ is (D_0^f, \dots, D_p^f) .

Finally, we remark that we could have taken the *dual* point of view, i.e. instead of considering functions f on state space we could have argued in terms of probability distributions π on state space. In appendix B.5 we pursue this thread.

It is now fair to compare the approach of this section with the original proof of Theorem B.1. The original proof has the advantage of relying solely on elementary probability theory while the alternative argumentation in this section is more abstract. However, it is appealing that this abstraction allows us to conceptualize Theorem 1, after which it becomes simply a matter of filling in the specific details to obtain the exact form of the decomposition rule. This also lets us anticipate similar results in a more general setting, allowing us e.g. to replace the Markov Chain $J(t)$ with a diffusion process. The computational tool will then be partial differential equations rather than matrix algebra. Finally, the semigroup perspective seems to provide the easiest proof of the uniqueness result of theorem B.4, without which one could imagine some confusion from the fact that $\Psi_p(t)$ and $\mathbf{M}_p(t)$ satisfy the *same* decomposition rule.

B.3.3 Product densities and integral formulas for moments

We now turn to the stochastic geometry of point processes as presented in Stoyan et al. (1995b). Recall from this framework that a key descriptor of a point process is the product density, from which the factorial moments are obtained by integration. Here, we first establish such product densities for the MAP, and state the corresponding integral formulas for the factorial moments.

The motivation for the material in this section is twofold. First, the numerical evaluation presented in section B.3.4 are the discretized or uniformized version of the product densities. Second, the material is natural to include when discussing moment properties of point processes.

To this end, we first need a product density which takes into account the phase process. This is the p th order product density matrix

$$R_{1,\dots,1}(t_1, \dots, t_p; t) ,$$

an m -by- m matrix, the (i, j) element of which is given by

$$[R_{1,\dots,1}(t_1, \dots, t_p; t)]_{ij} \cdot dt_1 \cdots dt_p = \mathbb{E}^i \left\{ \prod_{k=1}^p N(t_k, t_k + dt_k) \cdot \mathbf{1}(J(t) = j) \right\} + o(dt_1 \cdots dt_p) .$$

The subscripts in $R_{1,\dots,1}$, the number one repeated p times, are motivated by the generalization to the BMAP below. The (i, j) element of this product density matrix specifies the probability, when starting in phase $J(0) = i$, of having an arrival near each point of time t_1, \dots, t_p , and ending in phase $J(t) = j$.

It is then a result from the theory of point processes (Stoyan et al., 1995b) that the p th order factorial moment of $N(t)$, partitioned according to the phase $J(t)$, is obtained as

$$\mathbb{E}^i \left\{ N^{[p]}(t) \mathbf{1}(J(t) = j) \right\} = \int_0^t \cdots \int_0^t [R_{1,\dots,1}(t_1, \dots, t_p; t)]_{ij} dt_p \cdots dt_1 .$$

Lemma B.5 Consider the MAP. Let $p \in \mathbb{N}$ and $0 < t_1 < \cdots < t_p < t$, then

$$R_{1,\dots,1}(t_1, \dots, t_p; t) = \left(\prod_{i=1}^p e^{D(t_i - t_{i-1})} D_1 \right) e^{D(t - t_p)} ,$$

where we take $t_0 = 0$.

The lemma is easy to prove by first verifying the case $p = 1$, and then using the Markovian structure of the process $(J(t), N(t))$ to perform induction on p , by conditioning on the phase at some time s so that $t_{p-1} < s < t_p$.

Since the product density matrix is invariant under permutations of the times t_1, \dots, t_p , the lemma specifies the product density matrix for $(t_1, \dots, t_p) \in [0, t]^p$, except on a set of measure zero where two or more arguments t_i and t_j coincide. Since there are $p!$ such permutations, we obtain:

Corollary B.6 For the MAP

$$\mathbf{M}_p(t) = p! \int_{0 < t_1 < \cdots < t_p < t} \left(\prod_{i=1}^p e^{D(t_i - t_{i-1})} D_1 \right) e^{D(t - t_p)} dt_1 \cdots dt_p .$$

We now generalize these results to the BMAP. Let us first note that $N^{[p]}(t)$ equals the number of p -tuples which can be constructed from the set of arrivals $\{1, \dots, N(t)\}$ such that each element occurs at most once. Let us agree to call such a p -tuple *valid*, and compute its expected number by partitioning according to which batches the arrivals are part of. Throughout, we let the BMAP start in phase $J(0) = i$ and count only realizations for which $J(t) = j$. First, the

expected number of valid p -tuples for which all arrivals stem from the same batch, is the (i, j) -element of

$$\int_0^t e^{Dt_1} D_p^f e^{D(t-t_1)} dt_1 \ .$$

Next, the expected number of valid p -tuples which first contain $p_1 \in \{1, \dots, p-1\}$ arrivals from one batch and next $p_2 = p - p_1$ arrivals from a later batch, is the (i, j) -element of

$$\int_0^t \int_{t_1}^t e^{Dt_1} D_{p_1}^f e^{D(t_2-t_1)} D_{p_2}^f e^{D(t-t_2)} dt_2 dt_1 \ .$$

Each such tuple can, in turn, be shuffled to form a total of $p!/(p_1!p_2!)$ valid p -tuples.

In general, for any n natural numbers (p_1, p_2, \dots, p_n) which sum to p , the expected number of valid p -tuples where the first p_1 arrivals stem from one batch, the next p_2 from a later batch, etc, is the (i, j) -element of

$$\int_0^t \int_{t_1}^t \dots \int_{t_n}^t \left(\prod_{i=1}^n e^{D(t_i-t_{i-1})} D_{p_i}^f \right) e^{D(t-t_n)} dt_n \dots dt_2 dt_1 \ .$$

Since each such tuple can be rearranged in $p!/(p_1! \dots p_n!)$ different ways, we obtain:

Theorem B.7 *Let $p \in \mathbb{N}$, then*

$$\mathbf{M}_p(t) = \sum_{n=1}^p \sum_{\substack{\sum_{r=1}^n p_r = p \\ p_r \geq 1}} \frac{p!}{p_1! \dots p_n!} \int_{0 < t_1 < \dots < t_n < t} R_{p_1, \dots, p_n}^f(t_1, \dots, t_n; t) dt_n \dots dt_1 \ , \quad (\text{B.7})$$

where, for $0 = t_0 < t_1 < \dots < t_n < t$,

$$R_{p_1, p_2, \dots, p_n}^f(t_1, \dots, t_n; t) = \left(\prod_{i=1}^n e^{D(t_i-t_{i-1})} D_{p_i}^f \right) e^{D(t-t_n)} \ .$$

We note that Theorem B.7 could be proved alternatively by verifying that the expression in (B.7) satisfies the forward equation (B.4) of Corollary 1.

This result has an immediate analogy for non-central moments. Since the derivation is completely parallel to the one just given, we simply state the result

without proof:

$$\Psi_p(t) = \sum_{n=1}^p \sum_{\substack{\sum_{r=1}^n p_r = p \\ p_r \geq 1}} \frac{p!}{p_1! \cdots p_n!} \int_{0 < t_1 < \cdots < t_n < t} R_{p_1, \dots, p_n}^*(t_1, \dots, t_n; t) dt_n \cdots dt_1 ,$$

for $p \in \mathbb{N}$, where

$$R_{p_1, \dots, p_n}^*(t_1, \dots, t_n; t) = \left(\prod_{i=1}^n e^{D(t_i - t_{i-1})} D_{p_i}^* \right) \cdot e^{D(t - t_n)} .$$

B.3.4 Numerical evaluation

We now turn to the numerical evaluation of the non-central moments matrices $\Psi_i(t)$ for $i \in \mathbb{N}$ and $t > 0$. First, it should be noted that since the tuple $(\Psi_0(t), \dots, \Psi_p(t))$ satisfies a homogeneous linear time-invariant system, it can be computed numerically by evaluating the matrix exponential to a square matrix of side length $(p + 1) \cdot m$. Although this straightforward approach is sufficient when the side length is moderate, more efficient algorithms are soon required.

Narayana and Neuts demonstrated how to calculate the first and second order moment matrices efficiently using information for small values of t and then applying equation (B.3) recursively. We now generalize their results for non-central moment matrices of arbitrary order.

The calculation of the matrix exponential by uniformization is now standard (Neuts and Li, 1995)

$$e^{\mathbf{D}t} = e^{-\lambda t} \sum_{k=0}^{\infty} \frac{(\lambda t)^k}{k!} \mathbf{K}^k ,$$

where

$$\mathbf{K} = \mathbf{I} + \frac{1}{\lambda} \mathbf{D} \quad \text{and} \quad \lambda \geq \max_i (-D_{ii}) .$$

The extension of this method to the first order moment matrix was given in Narayana and Neuts (1992):

$$\Psi_1(t) = e^{-\lambda t} \sum_{k=0}^{\infty} \frac{(\lambda t)^{k+1}}{(k+1)!} \mathbf{E}_1(k) ,$$

where

$$\mathbf{K}_j^* = \frac{1}{\lambda} \mathbf{D}_j^* \quad \text{and} \quad \mathbf{E}_i(k+1) = \mathbf{E}_i(k) \mathbf{K} + \mathbf{K}^{k+1} \mathbf{K}_i^* .$$

The generalization to arbitrary moment order matrices is:

Corollary 3 The matrices Ψ_p ($p \geq 1$) are given by

$$\Psi_p(t) = e^{-\lambda t} \sum_{n=1}^p \sum_{\substack{\sum_{r=1}^n p_r = p \\ p_r \geq 1}} \sum_{k=0}^{\infty} \frac{p!}{p_1! \cdots p_n!} \frac{(\lambda t)^{k+n}}{(k+n)!} \mathbf{E}_{p_1, \dots, p_n}(k) \quad , \quad (\text{B.8})$$

with

$$\mathbf{E}_0(k) = \mathbf{K}^k \quad \mathbf{E}_{p_1, \dots, p_n}(0) = \prod_{r=1}^n \mathbf{K}_{p_r}^*$$

$$\mathbf{E}_{p_1, \dots, p_n}(k+1) = \mathbf{E}_{p_1, \dots, p_n}(k) \mathbf{K} + \mathbf{E}_{p_1, \dots, p_{n-1}}(k+1) \mathbf{K}_{p_n}^* \quad .$$

□

Proof: We prove the result by induction. The formula is obviously true for $p = 1$. We assume it holds for all $i \leq p$, and apply corollary 2 for Ψ_{p+1} to find

$$\begin{aligned} \Psi_{p+1} &= \int_0^t e^{-\lambda u} \sum_{k_1=0}^{\infty} \frac{(\lambda u)^{k_1}}{k_1!} \mathbf{K}^{k_1} \lambda \mathbf{K}_{p+1}^* \sum_{k_2=0}^{\infty} e^{-\lambda(t-u)} \frac{(\lambda(t-u))^{k_2}}{k_2!} \mathbf{K}^{k_2} du + \\ &\int_0^t \sum_{i=1}^p \binom{p+1}{i} e^{-\lambda u} \sum_{n=1}^i \sum_{\substack{\sum_{r=1}^n p_r = i \\ p_r \geq 1}} \quad . \\ &\sum_{k_1=0}^{\infty} \frac{i!}{p_1! \cdots p_n!} \frac{(\lambda t)^{k_1+n}}{(k_1+n)!} \mathbf{E}_{p_1, \dots, p_n}(k_1) \lambda \mathbf{K}_{p+1-i}^* \cdot \\ &\sum_{k_2=0}^{\infty} e^{-\lambda(t-u)} \frac{(\lambda(t-u))^{k_2}}{k_2!} \mathbf{K}^{k_2} du \quad . \end{aligned}$$

Using the Beta integral formula

$$\int_0^t \frac{(\lambda u)^{k_1}}{k_1!} \lambda \frac{(\lambda(t-u))^{k_2}}{k_2!} du = \frac{(\lambda t)^{k_1+k_2+1}}{(k_1+k_2+1)!} \quad ,$$

we get

$$\begin{aligned}
& e^{-\lambda t} \sum_{k_1=0}^{\infty} \sum_{k_2=0}^{\infty} \frac{(\lambda t)^{k_1+k_2+1}}{(k_1+k_2+1)!} \mathbf{K}^{k_1} \mathbf{K}_{p+1}^* \mathbf{K}^{k_2+} \\
& \quad e^{-\lambda t} \sum_{i=1}^p \binom{p+1}{i} \sum_{n=1}^i \sum_{\substack{\sum_{r=1}^n p_r = i \\ p_r \geq 1}} \frac{i!}{p_1! \cdots p_n!} \cdot \\
& \quad \sum_{k_1=0}^{\infty} \sum_{k_2=0}^{\infty} \frac{(\lambda t)^{k_1+k_2+l+1}}{(k_1+k_2+n+1)!} \mathbf{E}_{p_1, \dots, p_n}(k_1) \mathbf{K}_{p+1-i}^* \mathbf{K}^{k_2} \quad .
\end{aligned}$$

Now the first term equals

$$e^{-\lambda t} \sum_{k=0}^{\infty} \frac{(\lambda t)^{k+1}}{(k+1)!} \sum_{r=0}^k \mathbf{K}^r \mathbf{K}_{p+1}^* \mathbf{K}^{k-r} = e^{-\lambda t} \sum_{k=0}^{\infty} \frac{(\lambda t)^{k+1}}{(k+1)!} E_{p+1}(k) \quad ,$$

corresponding to the first term in the sum of (B.8) ($n = 1$). For the second term we get

$$\begin{aligned}
& e^{-\lambda t} \sum_{n=1}^p \sum_{i=n}^p \sum_{\substack{\sum_{r=1}^n p_r = i \\ p_r \geq 1}} \frac{(p+1)!}{(p+1-i)! i!} \frac{i!}{\prod_{r=1}^n p_r!} \cdot \\
& \sum_{k=0}^{\infty} \frac{(\lambda t)^{k+n+1}}{(k+n+1)!} \sum_{s=0}^k \mathbf{E}_{p_1, \dots, p_n}(s) \mathbf{K}_{p+1-i}^* \mathbf{K}^{k-s} \\
& = e^{-\lambda t} \sum_{n=2}^{p+1} \sum_{i=n-1}^p \sum_{\substack{\sum_{r=1}^{n-1} p_r = i \\ p_r \geq 1}} \frac{(p+1)!}{\prod_{r=1}^{n-1} p_r! \cdot (p+1-i)!} \sum_{k=0}^{\infty} \frac{(\lambda t)^{k+n}}{(k+n)!} \mathbf{E}_{p_1, \dots, p_{n-1}, p+1-i}(k) \\
& = \sum_{n=2}^{p+1} \sum_{\substack{\sum_{r=1}^n p_r = p+1 \\ p_r \geq 1}} \frac{(p+1)!}{\prod_{r=1}^n p_r!} \sum_{k=0}^{\infty} \frac{(\lambda t)^{k+n}}{(k+n)!} \mathbf{E}_{p_1, \dots, p_n}(k),
\end{aligned}$$

where the last equality can be verified by straightforward calculations.

B.3.5 Results for discrete time processes

For the discrete BMAP the matrix $\mathbf{D} = \sum_{n=0}^{\infty} \mathbf{D}_n$ is stochastic. The decomposition rule of Theorem B.1 applies for t_1 and t_2 integer. Special cases are

$$\Psi_i(1) = \mathbf{D}_i^* \quad , \quad \Psi_n(2) = \sum_{i=0}^n \binom{n}{i} \mathbf{D}_i^* \mathbf{D}_{n-i}^* \quad ,$$

and the forward and backward difference equations

$$\Psi_n(t+1) = \sum_{i=0}^n \binom{n}{i} \Psi_i(t) \mathbf{D}_{n-i}^* = \sum_{i=0}^n \binom{n}{i} \mathbf{D}_i^* \Psi_{n-i}(t) \quad .$$

Also for the discrete time case, we may solve these difference equations using the unit pulse response and the transfer function technique (Råde and Westergren, 2004), thus establishing recursive equations analogous to those of Corollary 2

$$\Psi_n(t) = \sum_{j=1}^t \sum_{i=0}^{n-1} \binom{n}{i} \Psi_i(j-1) \mathbf{D}_{n-i}^* \mathbf{D}^{t-j}, \quad n \geq 1, t \geq 1 \quad . \quad (\text{B.9})$$

B.4 Asymptotic behavior of low order moments of the BMAP and the tBMAP

We now consider a BMAP of dimension $m+1$, $m \in \mathbb{N}$, for which the $m+1$ 'st state is an absorbing state in which no arrivals occur. We will denote this process a *terminating* BMAP (tBMAP) Latouche et al. (2003). We aim to analyze the behavior of the process, under the condition that the process has not terminated, in the limit $t \rightarrow \infty$.

B.4.1 Asymptotics in the continuous time case

For such a continuous tBMAP, the parameter matrices \mathbf{D}_n can be partitioned as

$$\mathbf{D}_n = \begin{bmatrix} \mathbf{C}_n & \mathbf{c}_n^0 \\ \mathbf{0} & 0 \end{bmatrix} \quad ,$$

where \mathbf{C}_n is $m \times m$. This block structure of the process applies also to the moment matrices: Let $\Psi_p(t)$ be the $m \times m$ -matrix with (i, j) 'th-element

$$\mathbb{E}^i \{N(t)^p \mathbf{1}(J(t) = j)\} \quad .$$

Then the matrix functions $\Psi_p(t)$ depend on the blocks \mathbf{C}_i for $i = 0, \dots, p$, and are independent of the blocks \mathbf{c}_n^0 . The usefulness of this observation is that it allows a unified treatment of the terminating case where $C = \sum_{i=0}^{\infty} \mathbf{C}_i$ is a sub-generator, and the persistent case where C is a generator. In the persistent case the partitioning of \mathbf{D}_n is irrelevant. Thus, in the persistent case it is most natural to think of \mathbf{C}_n as \mathbf{D}_n .

In both cases, the analysis assumes that \mathbf{C} is irreducible, implying that there is a unique eigenvalue λ_1 of maximum real part (Seneta, 1981). Then \mathbf{C} admits the block diagonalization

$$\mathbf{C} = \begin{bmatrix} \mathbf{v}_1 & V_2 \end{bmatrix} \begin{bmatrix} \lambda_1 & \cdot \\ \cdot & \Lambda_2 \end{bmatrix} \begin{bmatrix} \mathbf{u}_1 \\ U_2 \end{bmatrix} .$$

Here the dominant eigenvalue λ_1 is 0 in the persistent case and negative in the transient case. We require that

$$\begin{bmatrix} \mathbf{u}_1 \\ U_2 \end{bmatrix} \begin{bmatrix} \mathbf{v}_1 & V_2 \end{bmatrix} = I .$$

Let λ_2 be a bound on the spectrum of Λ_2 , i.e. a negative number with $\lambda_2 < \lambda_1$ such that $\Lambda_2 - \lambda_2 I$ is asymptotically stable.

Theorem B.8 *If C is irreducible, then*

$$\Psi_1(t) = te^{\lambda_1 t} \mathbf{v}_1 \rho \mathbf{u}_1 + e^{\lambda_1 t} (\Pi \mathbf{C}_1^* \mathbf{v}_1 \mathbf{u}_1 + \mathbf{v}_1 \mathbf{u}_1 \mathbf{C}_1^* \Pi) + o(e^{\lambda_2 t}) \quad (\text{B.10})$$

and

$$\Psi_2(t) = \frac{1}{2} t^2 e^{\lambda_1 t} \cdot \Xi_2^2 + te^{\lambda_1 t} \cdot \Xi_2^1 + e^{\lambda_1 t} \cdot \Xi_2^0 + o(e^{\lambda_2 t}) \quad , \quad (\text{B.11})$$

where $\frac{o(e^{\lambda_2 t})}{e^{\lambda_2 t}} \rightarrow 0$ as $t \rightarrow \infty$. Here

$$\rho = \mathbf{u}_1 \mathbf{C}_1^* \mathbf{v}_1$$

is the fundamental rate of the dominant mode,

$$\Pi = V_2 (\lambda_1 \mathbf{I} - \Lambda_2)^{-1} U_2 = (\mathbf{v}_1 \mathbf{u}_1 + \lambda_1 \mathbf{I} - \mathbf{C})^{-1} - \mathbf{v}_1 \mathbf{u}_1$$

is a pseudo-inverse of $\lambda_1 \mathbf{I} - \mathbf{C}$, and

$$\begin{aligned} \Xi_2^2 &= 2 \mathbf{v}_1 \rho^2 \mathbf{u}_1 \\ \Xi_2^1 &= \mathbf{v}_1 \mathbf{u}_1 \mathbf{C}_2^* \mathbf{v}_1 \mathbf{u}_1 \\ &\quad + 2 (\mathbf{v}_1 \mathbf{u}_1 \mathbf{C}_1^* \mathbf{v}_1 \mathbf{u}_1 \mathbf{C}_1^* \Pi + \mathbf{v}_1 \mathbf{u}_1 \mathbf{C}_1^* \Pi \mathbf{C}_1^* \mathbf{v}_1 \mathbf{u}_1 + \Pi \mathbf{C}_1^* \mathbf{v}_1 \mathbf{u}_1 \mathbf{C}_1^* \mathbf{v}_1 \mathbf{u}_1) \\ \Xi_2^0 &= (\Pi \mathbf{C}_2^* \mathbf{v}_1 \mathbf{u}_1 + \mathbf{v}_1 \mathbf{u}_1 \mathbf{C}_2^* \Pi) + \\ &\quad 2 (\Pi \mathbf{C}_1^* \Pi \mathbf{C}_1^* \mathbf{v}_1 \mathbf{u}_1 + \Pi \mathbf{C}_1^* \mathbf{v}_1 \mathbf{u}_1 \mathbf{C}_1^* \Pi + \mathbf{v}_1 \mathbf{u}_1 \mathbf{C}_1^* \Pi \mathbf{C}_1^* \Pi) \\ &\quad - 2 (\Pi \Pi \mathbf{C}_1^* \mathbf{v}_1 \mathbf{u}_1 \mathbf{C}_1^* \mathbf{v}_1 \mathbf{u}_1 + \mathbf{v}_1 \mathbf{u}_1 \mathbf{C}_1^* \Pi \Pi \mathbf{C}_1^* \mathbf{v}_1 \mathbf{u}_1 + \mathbf{v}_1 \mathbf{u}_1 \mathbf{C}_1^* \mathbf{v}_1 \mathbf{u}_1 \mathbf{C}_1^* \Pi \Pi) . \end{aligned}$$

Proof: The matrix functions $\Psi_p(t)$ solve backward equations similar to those in corollary 1, but with \mathbf{D}_i^* replaced by \mathbf{C}_i^* . In Laplace domain, the system may be written

$$s \tilde{\Psi}_p(s) - I \cdot \mathbf{1}(p=0) = \sum_{i=0}^p \binom{p}{i} \mathbf{C}_i^* \tilde{\Psi}_{p-i}(s) \quad . \quad (\text{B.12})$$

Here $\tilde{\Psi}_p(s)$ denotes the usual Laplace transform of $\Psi_p(t)$. For a given p the solution is readily found using the tridiagonal structure of the system. The first three elements are

$$\begin{aligned}\tilde{\Psi}_0(s) &= (sI - \mathbf{C})^{-1} , \\ \tilde{\Psi}_1(s) &= (sI - \mathbf{C})^{-1} \mathbf{C}_1^* (sI - \mathbf{C})^{-1} , \text{ and} \\ \tilde{\Psi}_2(s) &= (sI - \mathbf{C})^{-1} \mathbf{C}_2^* (sI - \mathbf{C})^{-1} + 2(sI - \mathbf{C})^{-1} \mathbf{C}_1^* (sI - \mathbf{C})^{-1} \mathbf{C}_1^* (sI - \mathbf{C})^{-1} .\end{aligned}\tag{B.13}$$

We now obtain from the block diagonalization that

$$\tilde{\Psi}_0(s) = \frac{1}{s - \lambda_1} \mathbf{v}_1 \mathbf{u}_1 + V_2 (sI - \Lambda_2)^{-1} U_2 ,$$

which in time domain implies the well known result

$$\Psi_0(t) = \mathbf{v}_1 \mathbf{u}_1 e^{\lambda_1 t} + o(e^{\lambda_2 t}) \quad \text{as } t \rightarrow \infty .$$

Substituting this into the expression for $\tilde{\Psi}_1$, multiplying out and using

$$\frac{1}{s - \lambda_1} (sI - \Lambda_2)^{-1} = \frac{1}{s - \lambda_1} (\lambda_1 \mathbf{I} - \Lambda_2)^{-1} - (\lambda_1 \mathbf{I} - \Lambda_2)^{-1} (sI - \Lambda_2)^{-1}$$

to reduce, we obtain

$$\begin{aligned}\tilde{\Psi}_1(s) &= \frac{1}{(s - \lambda_1)^2} \mathbf{v}_1 \mathbf{u}_1 \mathbf{C}_1^* \mathbf{v}_1 \mathbf{u}_1 \\ &\quad + \frac{1}{s - \lambda_1} (\Pi \mathbf{C}_1^* \mathbf{v}_1 \mathbf{u}_1 + \mathbf{v}_1 \mathbf{u}_1 \mathbf{C}_1^* \Pi) \\ &\quad - V_2 (sI - \Lambda_2)^{-1} U_2 \Pi \mathbf{C}_1^* \mathbf{v}_1 \mathbf{u}_1 \\ &\quad - \mathbf{v}_1 \mathbf{u}_1 \mathbf{C}_1^* \Pi V_2 (sI - \Lambda_2)^{-1} U_2 \\ &\quad + V_2 (sI - \Lambda_2)^{-1} U_2 \mathbf{C}_1^* V_2 (sI - \Lambda_2)^{-1} U_2 .\end{aligned}$$

Note that the last three terms in $\tilde{\Psi}_1(s)$ are analytic for $\Re s > \lambda_2$. In time domain this implies (B.10).

For $p = 2$ we repeat the exercise. Using $\Omega(\cdot)$ to denote a function which is analytic in the open right half plane, we obtain

$$\tilde{\Psi}_2(s) = \frac{1}{(s - \lambda_1)^3} \Xi_2^2 + \frac{1}{(s - \lambda_1)^2} \Xi_2^1 + \frac{1}{(s - \lambda_1)^1} \Xi_2^0 + \Omega(s - \lambda_2) ,$$

where Ξ_2^0 , Ξ_2^1 , and Ξ_2^2 are as in the theorem. In time domain, this implies (B.11).

□

Using $\Pi = (\mathbf{v}_1 \mathbf{u}_1 + \lambda_1 \mathbf{I} - \mathbf{C})^{-1} - \mathbf{v}_1 \mathbf{u}_1$ for the first moment of the BMAP we get the expression stated in Narayana and Neuts (1992). Using the expansion method of that paper for the integral formulas we obtained (B.11). We find the proposed method somewhat more transparent and slightly less cumbersome. In addition this method elegantly unifies the derivations for the continuous, discrete, and transient cases.

We now turn to the conditional moments for the tBMAP

$$\mathbb{E}^{\boldsymbol{\pi}} \{N^p(t) \mid J(t) \in B\} \quad ,$$

for $p = 1, 2$. Here $B \subset \{1, \dots, m\}$ is a non-empty set of transient states such that $\mathbf{u}_1 e_B \neq 0$, where e_B is the indicator vector corresponding to B . The expectation is w.r.t. the law of the tBMAP starting with $N(0) = 0$ and with $J(0)$ distributed on $\{1, \dots, m\}$ according to m -vector $\boldsymbol{\pi}$. These conditional moments are obtained as

$$\mathbb{E}^{\boldsymbol{\pi}} \{N^p(t) \mid J(t) \in B\} = \frac{\boldsymbol{\pi} \Psi_p(t) e_B}{\boldsymbol{\pi} \Psi_0(t) e_B} \quad .$$

Corollary 4 As $t \rightarrow \infty$, the conditional expectation admits an affine asymptote given by

$$\mathbb{E}^{\boldsymbol{\pi}} \{N(t) \mid J(t) \in B\} = \rho \cdot t + \frac{\boldsymbol{\pi} \Pi \mathbf{C}_1^* \mathbf{v}_1}{\boldsymbol{\pi} \mathbf{v}_1} + \frac{\mathbf{u}_1 \mathbf{C}_1^* \Pi e_B}{\mathbf{u}_1 e_B} + o(e^{(\lambda_1 - \lambda_2)t}) \quad .$$

Furthermore, the conditional mean-square has the parabolic asymptote

$$\mathbb{E}^{\boldsymbol{\pi}} \{N^2(t) \mid J(t) \in B\} = t^2 \rho^2 + t \frac{\boldsymbol{\pi} \Xi_2^1 e_B}{\boldsymbol{\pi} \mathbf{v}_1 \mathbf{u}_1 e_B} + \frac{\boldsymbol{\pi} \Xi_2^0 e_B}{\boldsymbol{\pi} \mathbf{v}_1 \mathbf{u}_1 e_B} + o(e^{(\lambda_1 - \lambda_2)t}) \quad .$$

Thus the variance has the affine asymptote

$$\mathbb{V}^{\boldsymbol{\pi}} \{N(t) \mid J(t) \in B\} = t \cdot (\mathbf{u}_1 \mathbf{C}_2^* \mathbf{v}_1 + 2\mathbf{u}_1 \mathbf{C}_1^* \Pi \mathbf{C}_1^* \mathbf{v}_1) + \Phi + o(e^{(\lambda_1 - \lambda_2)t}) \quad ,$$

where we have used the shorthand

$$\begin{aligned} \Phi &= \frac{\boldsymbol{\pi} \Pi \mathbf{C}_2^* \mathbf{v}_1}{\boldsymbol{\pi} \mathbf{v}_1} + \frac{\mathbf{u}_1 \mathbf{C}_2^* \Pi e_B}{\mathbf{u}_1 e_B} \\ &+ 2 \frac{\boldsymbol{\pi} \Pi \mathbf{C}_1^* \Pi \mathbf{C}_1^* \mathbf{v}_1}{\boldsymbol{\pi} \mathbf{v}_1} + 2 \frac{\mathbf{u}_1 \mathbf{C}_1^* \Pi \mathbf{C}_1^* \Pi e_B}{\mathbf{u}_1 e_B} \\ &- 2 \frac{\boldsymbol{\pi} \Pi \Pi \mathbf{C}_1^* \mathbf{v}_1 \mathbf{u}_1 \mathbf{C}_1^* \mathbf{v}_1}{\boldsymbol{\pi} \mathbf{v}_1} - 2 \mathbf{u}_1 \mathbf{C}_1^* \Pi \Pi \mathbf{C}_1^* \mathbf{v}_1 - 2 \frac{\mathbf{u}_1 \mathbf{C}_1^* \mathbf{v}_1 \mathbf{u}_1 \mathbf{C}_1^* \Pi \Pi e_B}{\mathbf{u}_1 e_B} \\ &- \left(\frac{\boldsymbol{\pi} \Pi \mathbf{C}_1^* \mathbf{v}_1}{\boldsymbol{\pi} \mathbf{v}_1} \right)^2 - \left(\frac{\mathbf{u}_1 \mathbf{C}_1^* \Pi e_B}{\mathbf{u}_1 e_B} \right)^2 \quad . \end{aligned} \tag{B.14}$$

□

Note that the intercept for the conditional expectation contains two terms; one depending on the target set B , and one depending on the initial distribution and vanishing when $\boldsymbol{\pi} = \mathbf{u}_1$, i.e., when the process is quasi-stationary.

B.4.2 Asymptotics in the discrete time case

The derivations of this section carry over virtually unchanged to the discrete time case and we get the slightly surprising result that the asymptotic expansions are almost identical in continuous and discrete time.

For the discrete time case, we assume that C is a stochastic or sub-stochastic matrix. The dominant eigenvalue λ_1 is in the interval $[0, 1]$, taking the value 1 in the persistent case and a value less than 1 in the transient case. That λ_1 (and λ_2) dominate Λ_2 now means that all eigenvalues of Λ_2 are within the open disk with radius λ_1 (λ_2).

To proceed, introduce the z-transform

$$\tilde{\Psi}_n^D(z) = \sum_{\nu=0}^{\infty} z^{-\nu} \Psi_n^D(\nu)$$

The superscript D indicates discrete time. We have

$$\tilde{\Psi}_0^D(z) = z(zI - \mathbf{C})^{-1} .$$

while for $n \in \mathbb{N}$ equation (B.9) implies

$$\tilde{\Psi}_n^D(z) = \sum_{i=0}^{n-1} \binom{n}{i} \tilde{\Psi}_i^D(z) \mathbf{C}_{n-i}^* (zI - \mathbf{C})^{-1} .$$

Thus in general

$$\tilde{\Psi}_n^D(z) = z \tilde{\Psi}_n(z) ,$$

where $\tilde{\Psi}_n(\cdot)$ are the matrix algebraic expressions for the Laplace transforms of equations (B.12) and (B.13). The spectral decomposition is therefore identical in discrete and continuous time. We obtain

$$\tilde{\Psi}_1^D(z) = \frac{z}{(z - \lambda_1)^2} \mathbf{v}_1 \rho \mathbf{u}_1 + \frac{z}{z - \lambda_1} (\Pi C_1^* \mathbf{v}_1 \mathbf{u}_1 + \mathbf{v}_1 \mathbf{u}_1 C_1^* \Pi) + \Omega\left(\frac{z}{\lambda_2}\right)$$

and

$$\tilde{\Psi}_2^D(z) = \frac{z}{(z - \lambda_1)^3} \Xi_2^2 + \frac{z}{(z - \lambda_1)^2} \Xi_2^1 + \frac{z}{z - \lambda_1} \Xi_2^0 + \Omega\left(\frac{z}{\lambda_2}\right) .$$

Here, $\Omega(\cdot)$ indicates a function which is analytic outside the unit disk.

In the time domain, this implies

$$\Psi_1^D(\nu) = \nu \lambda_1^{\nu-1} \mathbf{v}_1 \rho \mathbf{u}_1 + \lambda_1^\nu (\Pi C_1^* \mathbf{v}_1 \mathbf{u}_1 + \mathbf{v}_1 \mathbf{u}_1 C_1^* \Pi) + o(\lambda_2^\nu)$$

and

$$\Psi_2^D(\nu) = \Xi_2^0 \lambda_1^\nu + \Xi_2^1 \nu \lambda_1^{\nu-1} + \Xi_2^2 \left(\frac{1}{2} \nu^2 \lambda_1^{\nu-2} - \frac{1}{2} \nu \lambda_1^{\nu-2} + o(\lambda_2^\nu) \right) ,$$

where $\lambda_1 = 1$ in the persistent case.

The affine asymptotes therefore become

$$\mathbb{E} \{ N_\nu | J_\nu \in B \} = \nu \cdot \frac{\rho}{\lambda_1} + \frac{\pi \Pi C_1^* \mathbf{v}_1}{\pi \mathbf{v}_1} + \frac{\mathbf{u}_1 C_1^* \Pi e_B}{\mathbf{u}_1 e_B} + o((\lambda_2/\lambda_1)^\nu)$$

and

$$\mathbb{V} \{ N_\nu | J_\nu \in B \} = \nu \cdot \left[\frac{\mathbf{u}_1 C_2^* \mathbf{v}_1}{\lambda_1} - \left(\frac{\rho}{\lambda_1} \right)^2 + 2 \frac{\mathbf{u}_1 C_1^* \Pi C_1^* \mathbf{v}_1}{\lambda_1} \right] + \Phi + o((\lambda_2/\lambda_1)^\nu) ,$$

where Φ is as in (B.14).

B.5 Higher order moments of RAPs (BRAPs)

Rational Arrival Processes (RAPs) are a class of point processes introduced by Asmussen and Bladt in 1999; see also Bladt and Neuts (2003) for interpretations and applications. Letting $\phi = \{t_i : i \in \mathbb{N}\}$ denote the random set of arrival times, the defining property of a RAP is the existence of a finite-dimensional space \mathcal{V} , the linear span of laws of point processes, such that the conditional law of the future arrival times $\{t_i - t : t_i \in \phi, t_i > t\}$, given the past process $\phi \cap [0, t]$, takes value in \mathcal{V} for all t and all realizations. Thus, the information obtained by observing the point process on $[0, t]$ can be summarized by a finite-dimensional statistic, which is sufficient for prediction. See Asmussen and Bladt (1999) for an in-depth treatment.

This property clearly holds for the MAP, where the past is summarized in the conditional probabilities $\mathbb{P} \{ J(t) = j | \mathcal{F}_t \}$ for $j = 1, \dots, m$. Here, \mathcal{F}_t is the information $\sigma(\phi \cap [0, t])$, and we take as basis for \mathcal{V} the m laws of the MAP when starting in phase $J(0) = j$, for $j = 1, \dots, m$. Thus, RAPs generalize MAPs. The relationship between the two classes is similar to the relationship between Matrix Exponential (ME) distributions and Phase Type distributions. Thus, in general analytical expressions are identical for RAPs and MAPs. One example, apart from those in Asmussen and Bladt (1999), is the quasi-birth-and-death-process with RAP components Bean and Nielsen (2005). A simple example of a RAP is the renewal process where inter-arrival times have density $2e^{-t}(1 - \cos(t))$. This cannot be a MAP because the density vanishes for some $t > 0$. See Mitchell (2001) for such cascaded Matrix Exponential distributions.

With this background, we proceed to show that also our Theorem B.1 holds in the RAP setting. To this end, let m be the dimension of the space \mathcal{V} in the

definition of the RAP, choose a basis for this space consisting of m laws, and let $A(t) = (A_1(t), \dots, A_m(t))$ be the coordinates of the conditional law of the future arrival times w.r.t. this basis.

Define m -by- m matrices

$$[\Psi_p(t)]_{ij} = \mathbb{E}^i \{ N^p(t) A_j(t) \} \quad ,$$

where \mathbb{E}^i is expectation w.r.t. the law of the RAP starting with $A(0) = e_i$, an m -vector with a 1 at position i and zeros elsewhere. Note that for the MAP, this definition of Ψ_p is consistent with (B.2) since in this case the initial condition $A(0) = e_i$ implies $J(0) = i$ w.p. 1, and

$$\begin{aligned} \mathbb{E}^i \{ N^p(t) A_j(t) \} &= \mathbb{E}^i \{ N^p(t) \mathbb{E}^i \{ \mathbf{1}(J(t) = j) | \mathcal{F}_t \} \} \\ &= \mathbb{E}^i \{ \mathbb{E}^i \{ N^p(t) \mathbf{1}(J(t) = j) | \mathcal{F}_t \} \} \\ &= \mathbb{E}^i \{ N^p(t) \mathbf{1}(J(t) = j) \} \quad . \end{aligned}$$

We then obtain

$$\begin{aligned} [\Psi_p(t+s)]_{ij} &= \mathbb{E}^i \{ \mathbb{E}^i \{ [N(t) + N(t, t+s)]^p \cdot A_j(t+s) | \mathcal{F}_t \} \} \\ &= \sum_{k=0}^p \binom{p}{k} \mathbb{E}^i \{ \mathbb{E}^i \{ N^k(t) N^{p-k}(t, t+s) A_j(t+s) | \mathcal{F}_t \} \} \\ &= \sum_{k=0}^p \binom{p}{k} \mathbb{E}^i \left\{ N^k(t) \sum_{l=1}^m A_l(t) [\Psi_{p-k}(s)]_{lj} \right\} \\ &= \sum_{k=0}^p \binom{p}{k} \sum_{l=1}^m [\Psi_k(t)]_{il} [\Psi_{p-k}(s)]_{lj} \quad . \end{aligned}$$

This is the element-wise version of the matrix equation

$$\Psi_p(t+s) = \sum_{k=0}^p \binom{p}{k} \Psi_k(t) \Psi_{p-k}(s)$$

i.e. also for the RAP the semigroup structure of theorem B.1 holds. It is immediately clear that also forward and backward equations of corollary 1 apply to the RAP as well, as do the corresponding results for the factorial moments, i.e. the matrix functions $M_p(t)$.

Acknowledgements

This research was supported by the SLIP research school under the Danish Network for Fisheries and Aquaculture Research (www.fishnet.dk). Bo Friis

Nielsen also wants to acknowledge the support by the Technical University of Denmark for providing the opportunity of a sabbatical leave, the Technical Research Council of Denmark for the support under grant no. 26-02-0155, and the Department of Statistics University of California at Berkeley for the hospitality of hosting him under his sabbatical leave. The authors thank Kasper Kristensen for helpful discussions.

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Appendix A. Duality in the semigroup approach

In section B.3.2 we derived theorem B.1 from the semigroup perspective, considering the transition probabilities $\mathbf{P}(t)$ operating on functions on the state

space. We noted in passing that it was possible to adopt the dual point of view where $\mathbf{P}(t)$ operate on probability distributions. For the sake of completeness, this appendix outlines this dual point of view.

The duality between functions on the state space and distributions on the state space is a standard construction where one takes distributions to represent linear operators: applying a distribution to a function amounts to taking expectation of the function w.r.t. this distribution.

In section B.3.2 we established invariance under $\mathbf{P}(t)$ of the space \mathcal{V} of p th order polynomials in n , and we now pursue the dual of this result. The dual space \mathcal{V}^* contains finite-valued linear operators on \mathcal{V} . Clearly, a probability distribution π is a finite-valued linear operator on \mathcal{V} if and only if it has finite p th order moments, i.e.

$$\mathbb{E}^\pi \{N^p \mathbf{1}(J = j)\} < \infty \quad ,$$

for all $j = 1, \dots, m$. Here \mathbb{E}^π denotes expectation w.r.t. the distribution π . Moreover, any linear operator on \mathcal{V} can be obtained as a linear combination of such probability distributions. Thus, \mathcal{V}^* is spanned by probability distributions on the state space with finite p th order moments.

However, two probability distributions π and ψ define the *same* linear operator on \mathcal{V} if all their moments up to order p coincide, i.e. $\mathbb{E}^\pi \{N^i \mathbf{1}(J = j)\} = \mathbb{E}^\psi \{N^i \mathbf{1}(J = j)\}$ holds for any $j \in \{1, \dots, m\}$ and any $i \in \{0, \dots, p\}$. In this case we say that that π and ψ are equivalent, $\pi \sim \psi$.

Let π be a fixed but arbitrary element in \mathcal{V}^* . To characterize π as an operator on \mathcal{V} , it suffices to know the image under π of the basis functions in \mathcal{V} , which are the functions $g_{ij}(n, k) = n^i \mathbf{1}(k = j)$ for $i = 0, \dots, p$ and $j = 1, \dots, m$. We therefore define

$$\beta_{ij} = \langle \pi, g_{ij} \rangle$$

and note that when π is a probability distribution, this amounts to specifying the moments up to order p and restricted to each phase j . For a fixed but arbitrary element g in \mathcal{V} ,

$$g = \sum_{i=0}^p \sum_{j=1}^m \alpha_{ij} g_{ij} \quad ,$$

we then obtain

$$\langle \pi, g \rangle = \sum_{i=0}^p \sum_{j=1}^m \alpha_{ij} \beta_{ij} \quad .$$

As $\mathbf{P}(t)$ operates on \mathcal{V} , we introduce the dual operators $\mathbf{P}^*(t)$ which operate on \mathcal{V}^* ; defined as usual by $\langle \pi, \mathbf{P}(t)g \rangle = \langle \mathbf{P}^*(t)\pi, g \rangle$ whenever $t > 0$, $\pi \in \mathcal{V}^*$, $g \in \mathcal{V}$. A convenient notation is obtained by taking distributions in \mathcal{V}^* to be infinite row vectors. With this appeal to matrix notation, we shall write $(\mathbf{P}^*(t))(\pi)$ as simply $\pi \mathbf{P}(t)$.

We can now state the dual of proposition B.2:

Proposition B.9 *Give $t \geq 0$. The equivalence relation \sim is invariant under $\mathbf{P}^*(t)$, i.e. if $\pi \sim \psi$ then $\pi\mathbf{P}(t) \sim \psi\mathbf{P}(t)$. Furthermore, \mathcal{V}^* is invariant under $\mathbf{P}^*(t)$.*

The invariance of the equivalence relation simply says that the statistics $\mathbb{E}\{N^i(0)\mathbf{1}(J(0) = j)\}$ for all $(i, j) \in \{0, \dots, p\} \times \{1, \dots, m\}$ are sufficient to determine the p th moment of $N(t)$ - given these, other statistics of the initial distribution are irrelevant. Next, that \mathcal{V}^* is invariant under $\mathbf{P}^*(t)$ says that if the initial distribution has finite p th order moments, then so has the distribution at time t .

The proof of the proposition can now follow that of proposition B.2; however we shall take the latter for granted and employ duality. As before, let g be a fixed but arbitrary element in \mathcal{V} . First, since \mathcal{V} is invariant under $\mathbf{P}(t)$ we have $\mathbf{P}(t)g \in \mathcal{V}$; thus $\langle \pi, \mathbf{P}(t)g \rangle$ is well defined. This implies that $\langle \pi\mathbf{P}(t), g \rangle$ is well defined. Since $g \in \mathcal{V}$ is arbitrary this implies that $\pi\mathbf{P}(t) \in \mathcal{V}^*$ and thus \mathcal{V}^* is invariant under $\mathbf{P}^*(t)$. Next, assume $\pi \sim \psi$, then $\langle \pi - \psi, \mathbf{P}(t)g \rangle = 0$ which implies $\langle \pi\mathbf{P}(t) - \psi\mathbf{P}(t), g \rangle = 0$. Again, since g is arbitrary this implies that $\pi\mathbf{P} \sim \psi\mathbf{P}$.

To finally obtain the algebraic representations, organize the moments β_{ij} in $p+1$ row-vectors $(\beta_0, \dots, \beta_p)$, each corresponding to the same order moments and with m elements, one for each phase. We then have, using (B.6):

$$\langle \pi, \mathbf{P}(t)g \rangle = \sum_{l=0}^p \beta_l \sum_{i=l}^p \binom{i}{l} \Psi_{i-l}(t) \alpha_i = \sum_{i=0}^p \left[\sum_{l=0}^i \binom{i}{l} \beta_l \Psi_{i-l}(t) \right] \alpha_i .$$

The term in the brackets is the algebraic representation of $\mathbf{P}^*(t)$: Given the moments of the initial distribution, this specifies the moments at time t .

We can now obtain theorem B.1 by operator concatenation as in B.3.2; the derivation would be entirely analogous.

APPENDIX C

**Heterogeneity may change
the functional
response—lessons from a
simple stochastic encounter
model**

Manuscript to be submitted to *Oikos*.

Heterogeneity may change the functional response—lessons from a simple stochastic encounter model

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Abstract

We use a stochastic model with an appealing geometric interpretation to demonstrate how heterogeneity may change the functional response. In our model food is encountered as a Poisson process in non-depletable patches. We express the three free parameters of the model as functions of the mean density of prey. This formulation enables us to show that the functional response is, in general, not of Holling type II form. We present some special cases with Holling type II responses and other examples that do not belong to the type II class of functional responses.

Even if the mean ingestion rate of prey, i.e. the functional response, is equal in heterogeneous and homogeneous environments the variance in the heterogeneous environment will be larger. This higher variance is primarily determined by the rates of encountering and leaving patches. We present a critical time-scale for this phenomenon and demonstrate that in some cases the functional response can be an inadequate and insufficient descriptor of the encounter process.

Our work is motivated by earlier work by Rothschild [J. Plankton Res., 1991. 13: 1123–1135] and Ruxton and Gurney [Am. Nat., 1994. 144: 537–541]. Our approach is linked to a geometric formulation that allow biologically relevant interpretation and an extension of the Poisson process to heterogeneous environments.

keywords

Functional response, patchiness, stochastic encounter, interrupted Poisson process, renewal process, Markovian arrival process.

C.1 Introduction

All predator-prey systems exhibit spatial and temporal heterogeneity. This has profound effects on the behaviour of these systems (e.g. Tilman, 1994). However, heterogeneous systems are more difficult to analyse than homogeneous, therefore one often assumes homogeneity at one or several levels in a model. This assumption may be that the spatial distribution is homogeneous at certain spatial scales or that all individuals of a certain type, such as juveniles, are equal. Such simplifying assumptions are vital to arrive at models that are analytically tractable, and to remove sub-processes that are of little importance to the overall dynamical behaviour.

A common micro-level descriptor that is used in many models of population dynamics is the functional response or the mean rate of ingestion of prey per predator in continuous time models. Here one assumes that the process of catching and consuming prey is fast compared to reproduction. This fast process is assumed to be in a quasi-stationary equilibrium (Segel and Slemrod, 1989; Poggiale, 1998) and so intense that it can be approximated with a deterministic flow. Then the mean rate of the fast process is sufficient to describe what happens at the slower time-scale. The functional response contains a wealth of biological information and its shape is important for properties of models of population dynamics, such as stability (Oaten and Murdoch, 1975) and sensitivity to harvesting (Yodzis, 1994). Since encounters between predator and prey are inherently random it is reasonable that the analysis of these types of interactions should be based on stochastic models. This has long been recognized, e.g. Paloheimo (1971) mentions several works of the first half of the 20th century where prey were encountered according to random sampling of a randomly distributed population. This leads to prey encounters described by a Poisson process. Thus, the essentially deterministic derivation of Holling (1959) of the type II response has been redone using queues (Curry and DeMichele, 1977; Sjöberg, 1980) and renewal theory (Hassell, 1978; Mangel and Clark, 1988).

Our analysis is based on a description of a functional response in a heterogeneous environment by Rothschild (1991), also analysed by Ruxton and Gurney (1994). Here the Poisson process that governs encounter in a homogeneous environment was replaced with a more variable encounter process, the hyperexponential renewal process, to account for spatial variability. The assumptions were that there are no depletion effects of the prey, and that a predator that did not interfere with prey would encounter the prey with the same mean rate as in a homogeneous environment. Furthermore it is assumed that the predators do not interfere directly with each other and that the predator density is low enough to avoid predator dependence in the functional response. Predator dependence will arise from non-interacting predators when predator densities are high because a searching predator will not encounter the true quasi-stationary

density of prey since a fraction of the prey-population will be handled by other predators (Borghans et al., 1996). We replace the hyperexponential renewal process with an equivalent formulation which relates the encounter to a model of geometrical patchiness. Using the assumption that the heterogeneity of the prey can be described by the mean density of prey we show that the ability to resume foraging in a patch will be critical for the shape of the functional response. Similarly to the derivations in Rothschild (1991) and Ruxton and Gurney (1994) we assume that there are no interactions between predators, and that patches are not

A fundamental problem in deriving functional responses from a model for stochastic encounter in a heterogeneous environment is the difficulty in parametrising how the spatial distribution of prey items changes with the total density of prey. Not only is it necessary to specify how the mean time between encounters changes as the prey density changes but also how the patchiness changes as the prey density changes. Furthermore, the behaviour of the predator while it is handling prey also has to be specified. Is it able to stay in the patch during the handling time, does it continue to encounter patches while handling prey or is it certain that it starts the search phase of a new foraging session outside the patch? The inability to always resume foraging in a patch may be due to limited sensory apparatus of a predator, that prey flee from the patch after an attack, or that the predator is disturbed by other factors while handling prey in the patch which cause it to leave the patch. Another possibility is that the predator consumes its prey outside of the patch and have difficulties in relocating a patch when it has finished handling the current prey item.

In Section C.2 we present the encounter process and three scenarios that represent different behaviour of the predator. We then show how the ability to start in a patch at the beginning of a search cycle will influence the functional response, and that changes in patchiness as the mean density changes can alter the shape of the functional response in Section C.3. Finally, we discuss the findings and their implications in Section C.4.

C.2 The models

In the classical Holling type II response the predator is thought to alternate between a phase where it searches for food and a phase where it handles food. These two phases form a search cycle. In a stochastic version of the Holling type II response the total length of a search cycle is a random time which is independently and identically distributed for all cycles. However, within a cycle it is possible that the length of one phase depends on the other. Under these assumptions the ingestion process is a renewal process (Cox, 1962).

The functional response is the mean ingestion rate which can be defined as

$I = \lim_{t \rightarrow \infty} \mathbb{E}\{N_t/t\}$, where N_t is the number of prey a predator has caught during time t . For renewal processes this mean ingestion rate can be found from the renewal reward theorem (cf. Wolff, 1989), where the reward is one prey per cycle, as

$$I = \frac{1}{\mathbb{E}\{T_c\}},$$

where $\mathbb{E}\{T_c\}$ is the mean of T_c , the time to complete a search cycle. This result applies both for populations and individuals provided that the process can be observed for a long time period and that the densities of prey and predators are constant during this time. In classical functional responses the random time T_c is decomposed into two mutually exclusive phases. A search phase, T_s , and a handling phase, T_h of random lengths. We have that $\mathbb{E}\{T_c\} = \mathbb{E}\{T_s + T_h\} = \tau_s + \tau_h$ where $\mathbb{E}\{T_s\} = \tau_s$ and $\mathbb{E}\{T_h\} = \tau_h$.

If the environment is homogeneously random from the viewpoint of the predator when searching, then the encounter process is a homogeneous Poisson process (also known as random search, see Rogers, 1972). For a homogeneous encounter process, let V_s be the volume searched per time unit and F the prey density, then the encounter rate is $V_s F$. Now the ingestion rate will be $\frac{1}{\frac{1}{V_s F} + \tau_h}$ which can be rewritten as:

$$I = \frac{V_s F}{1 + V_s F \tau_h} \quad \text{or} \quad I = \frac{I_{max} F}{F_0 + F}.$$

This is the Holling respectively the Michaelis-Menten form, where $F_0 = \frac{1}{V_s \tau_s}$ and $I_{max} = \frac{1}{\tau_h}$. It should be noted that if the encounter rate is proportional to $V_s F^\alpha$, where $\alpha > 1$; then a sigmoid, or type III, functional response will follow. For instance, (Getty and Pulliam, 1991) stated that a predator that move to a point in the plane, search for the nearest prey item, then move to a new random position in the plane will have an encounter rate that is proportional to $F^{3/2}$ if the encounter rate with prey while searching is proportional to the angle subtended on the retina. This angle is approximately proportional to the inverse distance cubed and the average nearest neighbour distance to the nearest prey is proportional to $F^{-1/2}$ for Poisson distributed prey.

In our model we assume that the environment consists of patches containing prey and empty space between patches. Here, a forager encounters patches as a Poisson process with rate ω_{01} . The residence time in a patch is exponentially distributed with mean residence time $\frac{1}{\omega_{10}}$. This time is independent of the number of prey items caught i.e. there are no satiation effects. While in the patch the forager encounters prey according to a Poisson process with rate λ . This encounter process is called an Interrupted Poisson Process (IPP) (Kuczura, 1973). Beyer and Nielsen (1996) introduced the IPP as the simplest way to extend the random encounter of a homogeneous environment to a more variable, heterogeneous environment. An important difference between the IPP and a

Poisson process is that the time between encounters in the IPP has a coefficient of variation, $CV = \frac{\sqrt{\mathbb{V}\{T_s\}}}{\mathbb{E}\{T_s\}}$, that is larger than one, whereas it is equal to one in the Poisson process. The IPP has a clear, biologically meaningful interpretation since it refers to being in a patch or not, moreover it is stochastically equivalent to the hyperexponential renewal process (Kuczura, 1973).

The hyperexponential renewal process is generated by independent hyperexponentially distributed inter-encounter times. Such inter-encounter times are produced by choosing an exponentially distributed time with mean $\frac{1}{\gamma_1}$ with probability p , and with $1 - p$ an exponentially distributed time with mean $\frac{1}{\gamma_2}$. Thus the expected time to the next encounter is

$$\tau_s = \frac{p}{\gamma_1} + \frac{1-p}{\gamma_2}.$$

A weakness of the hyperexponential renewal process is that it is difficult to relate the parameters (p, γ_1, γ_2) to actual patchiness (see Beyer and Nielsen, 1996). But it is always possible to convert these to the three parameters of the IPP ($\omega_{01}, \omega_{10}, \lambda$) and vice versa (see e.g. Kuczura, 1973; Beyer and Nielsen, 1996). Rothschild (1991) used hyperexponentially distributed search times to model that the time between encounters in a heterogeneous environment is more variable than in a homogeneous environment. This model concerned a swimming organism that encounters prey continuously but is unable to catch new prey while it is busy handling. In this scenario, called “continuous encounter” below, the predator suffers from the heterogeneous environment since it may catch the first item in a cluster, then it is blocked for some time and it is quite probable that it resumes foraging in the space between clusters. Clearly, a cruising predator in a homogeneous environment would not encounter this kind of problem.

Ruxton and Gurney (1994) analysed this model for deterministic handling times, and found that the functional response is Holling type II. Their result requires a particular scaling of (p, γ_1, γ_2). In the analysis below, we repeat the analysis without these particular assumptions and find that the response is in general not Holling type II.

We will base our analysis on the IPP noting that there is always an equivalent hyperexponential formulation. In the following we will assume that the predator does not have the capability to aggregate in patches of prey. This makes the comparison with the homogeneous situation easier since an inclusion of this, quite natural, possibility would introduce at least one more parameter. Our analysis will be based on three scenarios that illustrate different assumptions concerning the ability to restart the search phase in a patch.

In the first scenario the predator is always able to start foraging in a patch when the handling phase is completed. This behaviour may apply to a fast predator

pursuing slow prey. One example would be a whelk feeding on barnacles that are located in large patches. To simplify the reading we will call this scenario for “total control”.

In the second scenario the forager is continuously encountering prey from a patchy process but the predator is unable to catch all prey since it is blocked by handling. This could apply to a cruising predator with limited ability to control its movement, e.g. in a turbulent environment as originally proposed by Rothschild (1991). Another appropriate biological scenario would be patchily distributed prey that sweep by a sessile predator such as a sea anemone. This scenario will be called “continuous encounter”.

A forager in the third scenario will always start its search for prey outside a patch. This could apply to situations where the prey move with similar speed as the predator. Another example would be an ambush predator that attacks schools or herds. After an attack the ambush predator will handle the prey and then resume search outside of the patch. In the forthcoming this scenario will be called “ambush”.

Given a certain food density, F , the encounter rate in the homogeneous scenario depends on only one parameter, V_s . We assume that the mean time between encounters of a predator that did not interfere with prey would be equal to that of a predator in a homogeneous environment, i.e. $\tau_S(F) = \frac{1}{V_s F}$.

There are many ways to choose the two free parameters of the IPP. Here we choose to define the encounter rate with prey in the patch, $\lambda = \lambda(F)$, and the squared coefficient of variation minus one, $CV^2 - 1 = \rho(F)$, of the search times as some functions of the mean density, F , that will be specified later. The encounter rate with patches ω_{01} and the rate with which patches are left ω_{10} are functions of τ_S , $\lambda(F)$ and $\rho(F)$,

$$\omega_{01}(F) = \frac{2V_s F(\lambda(F) - V_s F)}{\rho(F)\lambda(F)} \quad \text{and} \quad \omega_{10}(F) = \frac{2(\lambda(F) - V_s F)^2}{\rho(F)\lambda(F)}, \quad (\text{C.1})$$

which are found using formulas in Beyer and Nielsen (1996). We have $\lambda(F) > V_s F$ and $\rho(F) > 0$, since ω_{01} and ω_{10} are greater than zero.

A major difference between deterministic and stochastic models for functional responses is that in the latter there are fluctuations in the number of ingested items. For large t the mean number of ingested prey of a predator will be approximately It , where I is the mean ingestion rate. The variance in this number will approach an affine asymptote; let σ_a^2 denote its slope. Thus the variance in the observed ingestion rate will be approximately $\frac{\sigma_a^2}{t}$. For the population the mean per capita ingestion rate will asymptotically be I and its variance is asymptotically $\frac{\sigma_a^2}{P^2 t}$, where P is the number of predators in the population which encounters the same environment. This means that the time t has to be large in relation to the encounter and handling process, such that the mean rate is

well-defined, but short in relation to the time-scales of appreciable change in prey and predator population densities and that the population should be large. If σ_a^2 is large then the ingestion rate will be less well approximated by the mean (for a fixed t) or longer times are needed to obtain the same precision in the mean rate approximation. For renewal processes the asymptotic slope of the variance σ_a^2 , which we call the variance rate, is equal to the ratio of the variance in time between captures σ_T^2 with the mean time between encounters cubed μ_T^3 (Cox, 1962).

The Holling type II functional response is one of several responses in the class of type II functional responses, sometimes referred to as hyperbolic (Jeschke et al., 2002). These have ingestion rates that are increasing for increasing prey densities $I'(F) > 0$, an asymptotic maximum ingestion rate $I(F) \rightarrow I_{max}$ when $F \rightarrow \infty$, and the increase in ingestion rate will be lower for higher prey densities, i.e. $I''(F) < 0$ for all prey densities.

C.3 Results

In this section we derive functional responses based on the IPP encounter model and present the differences between the three scenarios that models the effect of the position of the predator when it restarts the search phase. We first examine the effect of the three scenarios on the functional response. Then we discuss an interpretation of the hyperexponential renewal process proposed in Ruxton and Gurney (1994). Finally, we show that even if the mean rates are equal in the homogeneous case and in the total control, the variance may be much larger in the latter. The potential effect of this is shown in a simple example.

C.3.1 Results for the three scenarios

We now turn to the three scenarios: First, the "total control" scenario, where the predator resumes searching within a patch, having completed handling of a prey item. Next, the "continuous encounter", where the predator leaves and enters patches during handling, according to the same rules as when searching. Finally, the "ambush" scenario, where the predator resumes searching outside patches.

C.3.1.1 Total control

When the predator is certain to begin its search for food in the patch the mean time to catch a new prey is τ_s —the mean time between encounters in the IPP. Thus the ingestion rate I will be $\frac{1}{\tau_s + \tau_h}$ which is the same rate as in

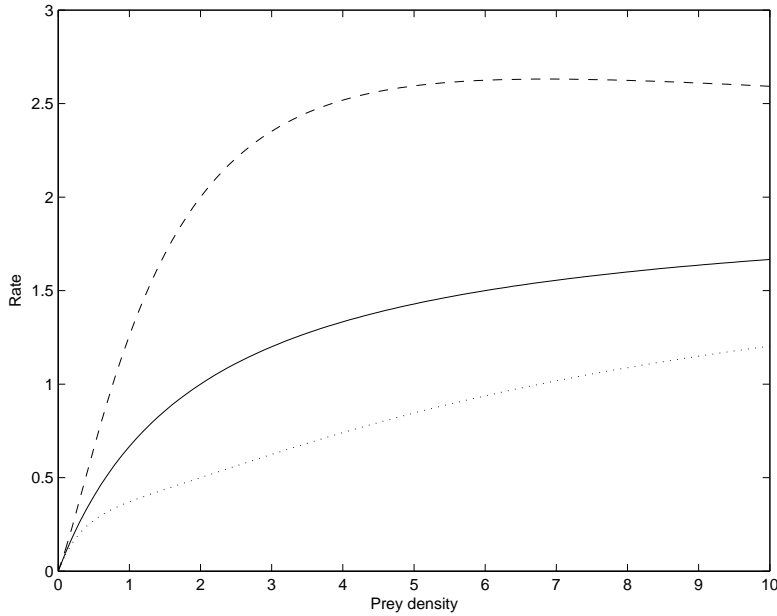


Figure C.1: The functional response from a homogeneous environment and the total control scenario in a heterogeneous environment (solid line) are equal. The asymptotic slope of the variance of the number of prey items for the homogeneous (dotted) respectively the heterogeneous situation (dashed) is shown for $V_s = 1$, $\omega_{01} = \frac{4}{9}$, $\omega_{10} = \frac{8}{9}$ and exponentially distributed handling time with mean $\frac{1}{2}$.

the homogeneous situation. The variance of the number of encountered items may be much larger in this scenario than in the homogeneous situation; see Figure C.1. The variance rate in the homogeneous situation with exponentially distributed handling times is $(\tau_s^2 + \tau_h^2)/(\tau_s + \tau_h)^3$ whereas the corresponding variance rate in the heterogeneous situation will be $(\tau_s^2(1 + \rho(F)) + \tau_h^2)/(\tau_s + \tau_h)^3$. Thus if $\rho(F) < F^2$ the asymptote of the variance rate will be equal for the heterogeneous and the homogeneous situation, but even if this is true (as in Figure C.1) it is possible to have large differences at intermediate prey densities. The importance of this phenomenon will be shown in Section C.3.3 using a discrete time model, where the effects are most obvious.

C.3.1.2 The continuous encounter

For the predator that continues to encounter prey during the handling phase the probability of being out of the patch if the handling time was t_h is $p_{10}(t_h) = \frac{\omega_{10}}{\omega_{01} + \omega_{10}}(1 - e^{-(\omega_{10} + \omega_{01})t_h})$ (see e.g. Cox and Miller, 1965, p. 172). Thus conditional expectation of X , the time between encounters, given a certain handling time, t_h , is

$$\mathbb{E}\{X|T_h = t_h\} = t_h + \tau_s(1 - p_{10}(t_h)) + \left(\tau_s + \frac{1}{\omega_{01}}\right)p_{10}(t_h),$$

where the second term is the expected time to next encounter if the predator resumes searching in the patch and the third is if it begins out of the patch. Taking expectation with respect to T_h gives

$$\mathbb{E}\{X\} = \tau_h + \tau_s + \frac{1}{\omega_{01}} \frac{\omega_{10}}{\omega_{01} + \omega_{10}} (1 - F_h^*(\omega_{10} + \omega_{01})), \quad (\text{C.2})$$

where $F_h^*(s) = \mathbb{E}\{e^{-sT_h}\}$ is the Laplace transform of the probability distribution of the handling time. For small enough $\omega_{01} + \omega_{10}$

$$\mathbb{E}\{X\} = \tau_h + \tau_s + \frac{\omega_{10}}{\omega_{01}} \left(\tau_h - (\sigma_h^2 + \tau_h^2)(\omega_{01} + \omega_{10}) \frac{1}{2} + O((\omega_{01} + \omega_{10})^2) \right),$$

where σ_h^2 is the variance of the handling time. Thus when $\omega_{01} + \omega_{10}$ is small it is always beneficial with a more variable handling time distribution given that the mean can be kept constant.

With $CV^2 = \frac{2\lambda\omega_{10}}{(\omega_{10} + \omega_{01})^2} + 1$ and $\tau_s = \frac{\omega_{01} + \omega_{10}}{\lambda\omega_{01}}$ one can rewrite the mean ingestion rate as

$$I = \frac{1}{\tau_h + \tau_s \left(1 + \frac{1}{2}(CV^2 - 1)(1 - F_h^*(\omega_{01} + \omega_{10}))\right)}.$$

This result was obtained, for deterministic handling times, by Ruxton and Gurney (1994) for the hyperexponential encounter process using a different approach. They rewrote the mean ingestion as

$$I = \frac{I_{max} \cdot F}{\tilde{F}_0 + F} = \frac{\frac{1}{\tau_h} \cdot F}{\frac{1}{\tau_h V_s} \left(1 + \frac{1}{2}(CV^2 - 1)(1 - F_h^*(\omega_{01} + \omega_{10}))\right) + F}, \quad (\text{C.3})$$

and interpreted this as a Holling type II functional response similar to the homogeneous situation. The only difference would be that the half-saturation constant is larger, i.e. the initial slope is less steep.

For Equation (C.3) to be a Holling II functional response, I_{max} and \tilde{F}_0 must be constant when F is changed, and this restricts the way the size, number and richness of patches change as the mean density changes. First $CV^2 - 1$, or

equivalently $\rho(F)$, must be constant. Second $\omega_{01} + \omega_{10}$ must be constant. Using the $\rho(F), \lambda(F)$ formulation

$$\omega_{01} + \omega_{10} = \frac{2(\lambda(F) - V_s F)}{\rho(F)}.$$

This means that it is necessary for the rate of encounter with prey in the patch, $\lambda(F)$, to have the form $V_s F + c_1$, where c_1 is a positive constant. Note that this result is not structurally stable since a small perturbation of $\lambda(F)$ such that $\lambda(F) = (1 + \xi)V_s F + c_1$ where $\xi > 0$ will not give a strict Holling type II response; there will be a factor that decreases to zero as the food density increases, but the rate with which it does so will depend on the handling time distribution. When $\xi > 0$ the functional response will still be type II, but if $\xi < 0$ the functional response is not necessarily type II and will only be defined for prey densities $F < \frac{c_1}{-\xi V_s}$.

To further investigate how patchiness changes with mean density we explore the effects of keeping two of the three parameters ω_{01} , ω_{10} and λ constant. This leads to different explicit assumptions about the habitat. To assume that both ω_{01} and ω_{10} are constant corresponds to an environment where the size and number of the patches are fixed and increasing the food level increases the density within these fixed patches. From Equation (C.2) it is clear that there will be a constant which adds to the handling time. Then both I_{max} and F_0 will be lower than in the homogeneous environment. In Michaelis-Menten form:

$$I = \frac{\frac{1}{\tau_h + \frac{\omega_{10}}{\omega_{01}(\omega_{01} + \omega_{10})}}(1 - F_h^*(\omega_{01} + \omega_{10}))}{\frac{1}{V_s(\tau_h + \frac{\omega_{10}}{\omega_{01}(\omega_{01} + \omega_{10})}}(1 - F_h^*(\omega_{01} + \omega_{10}))} + F} \cdot F.$$

If either λ and ω_{01} , or λ and ω_{10} are assumed to be constant one does not get a Holling type II functional response see Figure C.2. The models are only valid for mean prey densities below $\frac{\lambda}{V_s}$. Both are very close to having linear increase (type I) for high densities respectively for low densities (see Appendix C.4 for formulas when the handling time is exponentially distributed). In general the functional response is not Holling type II when the predator is not certain to resume search in a patch, not even type II. An immense variety of functional responses are possible. For instance, let $\lambda(F)$ be equal to $V_s F + \rho(F)$ and $\rho(F) = e^{\kappa F} - 1$ with $\kappa > 0$. This is a pathological scenario for $F \rightarrow \infty$, but suppose that this parametrisation is applicable for the densities encountered in nature. This gives a functional response of the form:

$$I = \frac{V_s F}{1 + (e^{\kappa F} - 1)(1 - F_h^*(2)) + V_s F \tau_h},$$

which is decreasing at high prey densities as can be seen in Figure C.2. This type of functional response is not entirely unrealistic, since there are situations

where prey become increasingly difficult to catch when prey densities increase due to e.g. schooling behaviour (Sandin and Pacala, 2005) (see also Jeschke et al., 2002, Note 16 in Table 1).

The Laplace transform of the handling-time probability distribution appears in the functional response of continuous encounter. Numerical investigations on the maximum difference between the ingestion rate of a predator with exponentially distributed handling time and one with a deterministic handling time, show that a deterministic handling time gives a constant reduction of 12.2 percent in the domain $\tau_h \times \tau_s \in [0.001, 1000] \times [0.001, 1000]$. Thus the distribution of the handling time can make a sizable difference. Although it seems unlikely that a forager can choose between handling time distributions while keeping the mean handling time constant this is an important complication of the description of the process.

C.3.1.3 Ambush

The ingestion rate for the ambush scenario is always less than for the continuous encounter since the predator is certain to resume its search outside a patch. This means that the considerations of patch formulation will apply to this scenario but only through the dependence of ω_{01} on prey densities F . Here the ingestion rate will depend only on the mean of the handling time not on its distribution

$$I = \frac{1}{\tau_s + \tau_h + \frac{1}{\omega_{01}}}.$$

This scenario forms the lower limit of the severity of the effect of patchiness.

C.3.2 On the interpretation of the hyperexponential renewal process

Some confusion has been generated by different interpretations of the hyperexponential renewal process, see Beyer and Nielsen (1996) for a discussion. Ruxton and Gurney (1994) suggest a model with a fraction p_1 of patches with food density γ_1 and a fraction $p_2 = 1 - p_1$ of patches with food density γ_2 . The predator forages in patch of either type for a fixed time T . Upon completion it resumes foraging in a patch of type i , $i = 1, 2$ with probability p_i . One can derive the marginal distribution of time between encounters by allowing the foraging times to be exponentially distributed rather than constant, see Appendix C.4 for the derivations. We call this approximation the approximate Ruxton-Gurney scheme (ARGS) and the original scheme for RGS. The marginal density of this process, which is a switched Poisson process (SPP) is then

$$F_{SPP}(t) = 1 - \tilde{p}e^{-\tilde{\gamma}_1 t} - (1 - \tilde{p})e^{-\tilde{\gamma}_2 t},$$

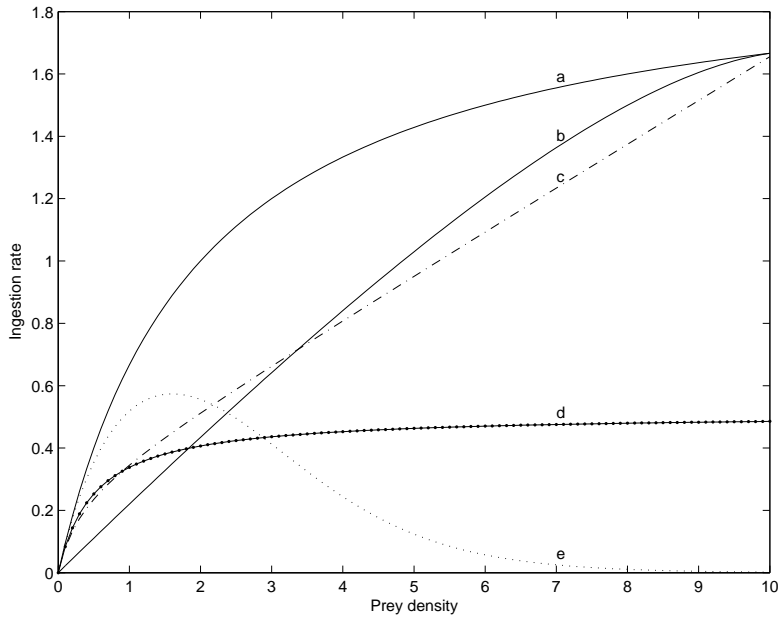


Figure C.2: The functional response for the different assumptions on parameters in continuous encounter. For reference the corresponding ingestion rate for total control is included (line a). The other line (marked with b) is when $\omega_{01} = \frac{4}{9}$ and $\lambda = 11$, The dash-dotted line is when $\omega_{10} = \frac{8}{9}$ and $\lambda = 11$ (c), and the line with points (d) is the ingestion rate when both ω_{01} and ω_{10} are constants ($\frac{4}{9}$ resp. $\frac{8}{9}$). The dotted line (e) is when $\rho(F) = e^F - 1$ and $\lambda(F) = \rho(F) + V_s F$. An exponentially distributed handling time was used with mean $\tau_h = \frac{1}{2}$, and $V_s = 1$ in all scenarios.

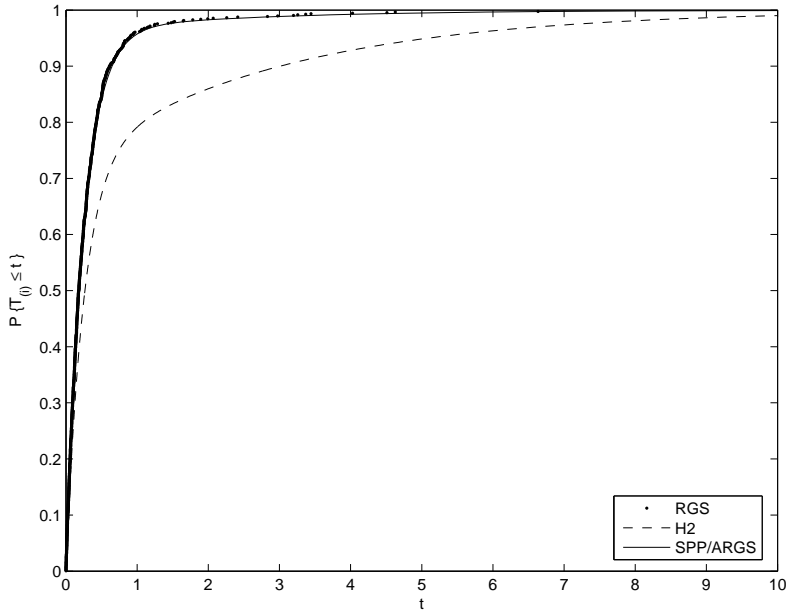


Figure C.3: The cumulative density function (cdf) of a hyperexponential distribution with parameters $p = \frac{8}{11}$, $\gamma_1 = 4$, $\gamma_2 = \frac{1}{3}$ (dashed). The empirical cdf of 1000 inter-encounter times generated by the Ruxton-Gurney scheme (RGS) with time T in a particular habitat equal to 10 (dots) and the corresponding marginal cdf of the SPP/ARGS (line). The main difference between RGS and the original hyperexponential distribution is that the latter have longer inter-arrival times.

thus hyperexponential as stated by Ruxton and Gurney (1994) but not with parameters $(p_1, \gamma_1, \gamma_2)$ as one might assume at a first glance. Figure C.3 illustrates the difference. Clearly, the times between encounters are not independent which means that this is not a renewal process. Functional responses where the inter-encounter times are dependent can often be modelled using Markovian arrival processes (see Nilsson, 2006), a class of stochastic processes that contains both the SPP and the IPP.

C.3.3 The importance of the variability and its critical time-scale

There are many situations where the value of functional or numerical responses would be doubtful. This is particularly clear in discrete time models. To illustrate this, we follow the female population of an annual species. Females are born in the beginning of the year, are juveniles for 2 months and then become adult. We assume that the fecundity of a female is so large that if one female survives the year there will be enough eggs to maintain the population. Furthermore, density dependence affects the juveniles such that if there are eggs then a Poisson distributed number of females with mean 500 will have the potential to reproduce if they find sufficient amount of food. If an adult female eats at least 70 prey items in 10 months she will be able to reproduce. Suppose that the expected number of prey encountered during this time is 50.

Here we compare three possibilities, the deterministic situation, the stochastic situation either in a homogeneous environment or in a heterogeneous environment, and in all scenarios the initial population is a Poisson distributed number of females with mean 500. In the deterministic situation all adult females will get 50 prey items and the population goes extinct in 1 year.

The stochastic scenarios are constructed such that if the initial population N_1 produce at least one adult female then there will be N_2 females in the next generation. These will also be Poisson distributed with mean 500. The expected number of encountered prey is the same as in the deterministic situation, and in the heterogeneous environment the predator has total control. We assume that the handling time distribution is exponentially distributed with mean 0.01 month.

The probability of obtaining less than 70 food items is found numerically (see Nilsson, 2006). Denote the probability that an individual female obtained less than 70 prey items during the foraging season with p_d , then the probability of extinction in the n th time step given N_1, \dots, N_n is $(1 - p_d^{N_1}) \cdots (1 - p_d^{N_{n-1}}) p_d^{N_n}$. Taking the expectation with respect to the Poisson distributions and using the independence between years one finds that the probability of extinction in the n th year is $(1 - e^{-500(1-p_d)})^{n-1} e^{-500(1-p_d)}$. Thus the time to extinction is a geometric random variable with mean $e^{500(1-p_d)}$.

In the homogeneous environment the $p_d \approx 0.9972$ and we find that the expected time to extinction is approximately 5.1 years. Assume that the heterogeneous habitat is such that half is patch with twice the density of the homogeneous environment and half of the habitat is empty. The rate of encounter is equal to the rate with which patches are left, here it is set to 1month^{-1} . The females are randomly distributed at the start of each season, i.e. the probability of being in patch in the beginning of the season is $\frac{1}{2}$. One finds that $p_d \approx 0.8789$ and that

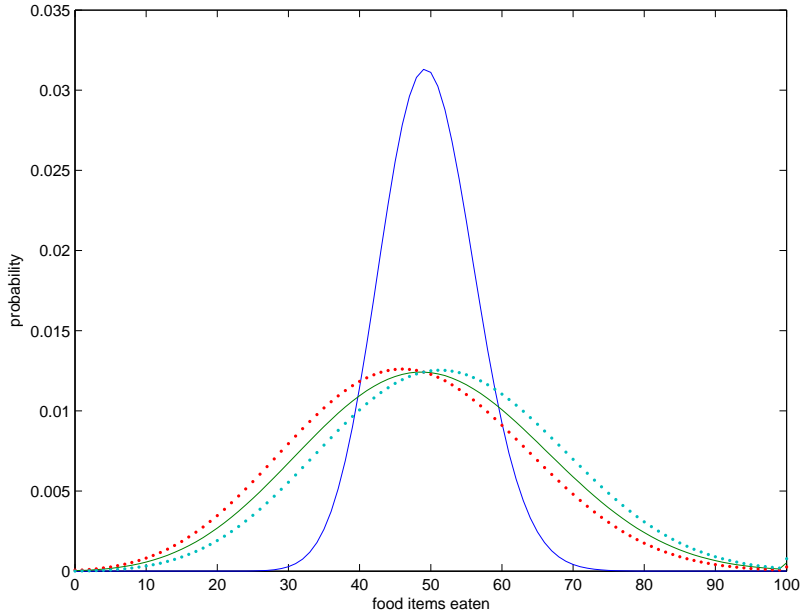


Figure C.4: A comparison between the distribution of prey in a homogeneous environment (dashed line) and in a heterogeneous (solid line), when the handling time is exponentially distributed with mean 0.01. The rings and the dots refer to the probability of getting a certain number when starting in respectively out of a patch, where the latter has the mode to the left of the mean.

the expected time to extinction is $1.9 \cdot 10^{26}$ years!

Here stochastic encounter combined with a non-differentiable nonlinearity means that the average clearly is not a sufficient descriptor of the system and the variance in the heterogeneous population is much larger than in the homogeneous, which greatly enhances the probability of survival of the population. The distributions are seen in Figure C.4. In the heterogeneous model the rate of leaving and entering patches was not very large and this is a key to the result. Suppose that the residence time in a patch is very short and that the time to find a new patch also is very short. Then the switching between patches is so fast that the predator will experience essentially the same environment as in the homogeneous Poisson scenario and thus heterogeneity does not have significant effects. Conversely, suppose that the residence times in or out of patches are comparable to the life time of an individual, then this effectively creates a metapopulation model and the variance in encountered prey items is very large.

This suggests that a critical time scale exists, such that environmental heterogeneity at faster scales can safely be ignored. To identify this time scale, we keep the fraction of patches, π_1 in the habitat constant, the prey encounter rate, λ , and the exponentially distributed prey handling rate α constant. Then the rate of patch encounter can be expressed as a function of the rate of leaving, $\omega_{01} = \frac{\pi_1}{1-\pi_1}\omega_{10}$ for total control.

The variance of the number of prey items eaten at time t , N_t will be asymptotically be linear in t . The slope can be found as the ratio of the variance in time between capture σ_T^2 with the mean time between encounters cubed μ_T^3 (Cox, 1962).

This gives

$$\lim_{t \rightarrow \infty} (\mathbb{V}\{N_t\}/t) = \left(\frac{\sigma_T^2}{\mu_T^3} \right) = \frac{1}{\mu_T^3} \frac{2\lambda\alpha^2(1-\pi_1)^2 \frac{1}{\omega_{10}} + ((\alpha + \lambda\pi_1)^2 + \lambda^2\pi_1^2)}{\pi_1^2\lambda^2\alpha^2}.$$

The numerator $(2\lambda\alpha^2(1-\pi_1)^2 \frac{1}{\omega_{10}} + ((\alpha + \lambda\pi_1)^2 + \lambda^2\pi_1^2))$ is approximately constant when ω_{10} is large and proportional to $\frac{1}{\omega_{10}}$ when ω_{10} is small. The pivot point marking the transition between these two scalings, is:

$$\omega_{10}^* = \frac{2\lambda\alpha^2(1-\pi_1)^2}{(\alpha + \lambda\pi_1)^2 + \lambda^2\pi_1^2},$$

as is illustrated in Figure C.5. The critical rate of leaving the patch is found to be approximately 4.7 for the example above. Thus for rates that is much higher than this the variance is close to that of the homogeneous ingestion process and for much lower rates the variance will be substantially higher. Although this is an asymptotic result it is still valid for the example (since the foraging season T is much longer than the mean residence time in the patch $\frac{1}{\omega_{10}^*}$) where time was finite as can be seen in Figure C.5. Another break-point at $\frac{1}{T}$ occurs for the variance in finite time (see Figure C.5) which shows the metapopulation effect.

For general handling times with mean μ_H and variance σ_H^2 the frequency below which the variance becomes important is

$$\omega_{10}^* = \frac{2\lambda(1-\pi_1)^2}{(1 + \lambda\pi_1\mu_H)^2 + \lambda^2\pi_1^2\sigma_H^2}$$

or equivalently when the residence time in the patch is longer than $\frac{1}{\omega_{10}^*}$. Here $\mu_T = \frac{\omega_{10} + \omega_{01}}{\lambda\omega_{01}} + \mu_H$ and $\sigma_T^2 = 2\frac{\omega_{10}}{\lambda\omega_{01}^2} + \mu_T^2 + \sigma_H^2$.

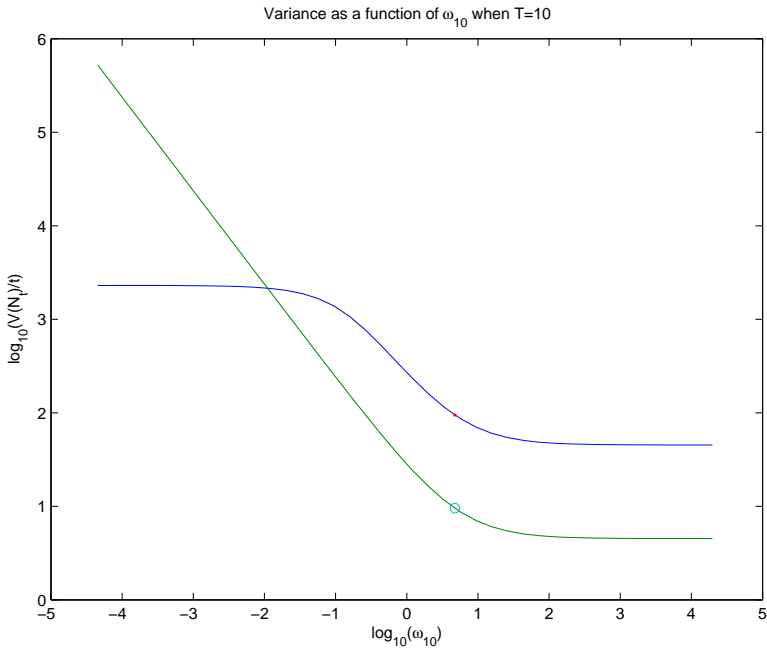


Figure C.5: The pivot-point at 4.7 both for the asymptotic result (solid line) and for the $\log(\mathbb{V}\{N_t\}/t)$ of the example (dashed) with $t = 10$. Note the other break-point for finite time at $\omega_{10} = \frac{1}{T} = 0.1$. $\pi_1 = \frac{1}{2}$, $\alpha = 0.01$ and $\lambda = 100$.

C.4 Discussion

We show in the present work how important the location may be for the shape of the functional response when a predator with a limited behavioural repertoire starts its search phase in a heterogeneous environment. It is not new that behaviour may change the functional response, Abrams (1982) showed that optimal behaviour may change the shape of the functional response. Using another approach Cosner et al. (1999) showed that the spatial grouping of predators and prey changes the functional response (see also Poggiale, 1998). In this article we have assumed that there is a functional relationship between average food density and patchiness and shown that this dependency is vital to the functional forms that emerge. This assumption is a reasonable starting point, however in real systems there may be a certain amount of memory in the system such that the patchiness may be different at the same mean prey density depending on e.g. whether the prey population is receding or recovering.

Another assumption is that the handling time is independent of prey density and search time. It may well be that more refined functional responses should be used where there is a separation of prey handling and prey digestion as Jeschke et al. (2002) suggest. This is not possible using the renewal formalism, but easily done using e.g. Markovian arrival processes (Neuts, 1979; Nilsson, 2006) which are well suited for the derivation of more advanced stochastic functional responses (Nilsson, 2006). It is also possible to let the patch residence time depend on the number of prey items encountered using Markovian arrival processes.

An important point is that given a certain average density it is impossible to increase the mean ingestion rate in the heterogeneous situation. If patchiness increases the mean ingestion rate above the rate of the homogeneous situation this must be due to patch accumulation abilities of individuals, such that these will encounter a higher than average ration, provided that the mortality rates are equal in patch and out-of-patch. Mortality is not included in our models, but may produce a bias in the survivors if the difference between patch and non-patch is large (Nilsson, 2006).

The IPP is arguably simplistic, but it is much more versatile than the Poisson process. Interestingly, Currie et al. (1998) showed that a towed plankton recorder observed patches but within patches the prey distribution was not significantly different from the Poisson distribution. The IPP has the nice property that when the time between encounters of patches and time in patches is small relative to the time between encounters in the patch then the IPP is very close to be a Poisson process. It is important to recognize that if the level of “mixing” is reduced in the system the Poisson process may rapidly lose its applicability. This may be particularly important for threatened populations living in an increasingly fragmented habitat. The use of a functional response in some

parasitoid models, where only one or a few host encounters are needed for the reproduction, seems questionable since here one would expect stochastic effects to be important at the population level. Also when there are non-differentiable non-linearities, as in the population example, the mean field approximation will encounter severe difficulties. To some extent such non-linearities are to be expected in models of population dynamics since there is a minimum investment in offspring to make it viable. Since renewal reward processes will be well approximated by a normal distribution when time is large, some of these difficulties could possibly be avoided using second order approximations, i.e. stochastic differential equations, instead of ordinary differential equations.

This article has demonstrated that a heterogeneous encounter process can destroy the type II form of the functional response if the predator is unable to restart its search for food in a patch. We have advocated the use of the IPP as a model for heterogeneity; this process is flexible, tractable and has parameters which can be estimated from data (see e.g. Nielsen and Beyer, 2006). Such data could come from archival devices that are fitted to individual predators and would be very informative on the type of heterogeneity that a predator experiences in the field. For instance, the more than 400-fold reduction in maximal ingestion rate found in the comparison of laboratory experiments with field estimates by Aljetlawi et al. (2004) could be due to habitat heterogeneity with e.g. fixed ω_{01} , ω_{10} and the ambush scenario. Although other factors such as predation risk of the predator could be equally important for this result, we have shown that in many circumstances it is necessary to consider the heterogeneous and stochastic nature of encounter.

Acknowledgements

The research was supported by the SLIP research school under the Danish Network for Fisheries and Aquaculture Research (www.fishnet.dk) as well as by the REX project, financed by the Danish Ministry for Food, Agriculture and Fisheries and the Danish Agricultural and Veterinary Research Council.

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Appendix A. Functional responses for continuous encounter

If λ and ω_{01} are assumed to be constant which can be interpreted as the number of patches and the prey density within the patches are fixed, only the size of the patches vary. The model is valid only for prey densities below $\frac{\lambda}{V_s}$. The rate of leaving the patch is $\omega_{10} = \frac{\omega_{01}(\lambda - V_s F)}{V_s F}$. For exponentially distributed

handling times one finds that:

$$I = \frac{V_s F (V_s F + \omega_{01} \tau_h \lambda)}{(1 + V_s F \tau_h)(\omega_{01} \lambda \tau_h + V_s F) + (\lambda - V_s F) V_s F \tau_h},$$

which is not Holling type II.

Suppose instead that λ and ω_{10} are constant. Here the environment has a fixed density within patches and a fixed size; increasing the mean density of prey increases the number of patches. We have that $\omega_{01} = \frac{V_s F \omega_{10}}{\lambda - V_s F}$. As in the previous example this only applies for $\lambda > V_s F$. Here the functional response will be:

$$I = \frac{V_s F (\lambda - V_s F) (\lambda (1 + \tau_h) - V_s F)}{(\lambda (1 + \tau_h) - V_s F) - V_s F (\lambda - V_s F) + \tau_h V_s F (\lambda - V_s F) (\lambda (1 + \tau_h) - V_s F)}$$

for exponentially distributed handling times.

Appendix B. The calculations for ARGs

Our approximation of the Ruxton and Gurney (1994) procedure is that the predator can be in 2 patches, in patch 1 prey are found with rate γ_1 and in patch 2 they are found with rate γ_2 . The rate of switching between patch 1 to patch 2 is $\frac{q}{T}$ and the rate of switching from patch 2 to patch 1 is $\frac{p}{T}$. The above procedure is based on the similarity between a geometrically distributed and an exponentially distributed random variable. The ‘‘continuous approximation’’ will be good when $T > \max\{\frac{1}{\gamma_1}, \frac{1}{\gamma_2}\}$ and when the simulation time $T_{sim} \gg T$.

The state of a process of this type at time t will be described by (X_t, N_t) where X_t is the type of patch the forager is in and N_t is the number of prey eaten. Then system can be described by a Markovian arrival process (Neuts, 1979; Nilsson, 2006), i.e. a continuous time Markov Chain where transitions between states that do not increase N_t is described by \mathbf{D}_0 and transitions between states that do generate an increase in N_t described by \mathbf{D}_1 . We have:

$$\mathbf{D}_0 = \begin{bmatrix} -(\frac{q}{T} + \gamma_1) & \frac{q}{T} \\ \frac{p}{T} & -(\frac{p}{T} + \gamma_2) \end{bmatrix} \quad \text{and} \quad \mathbf{D}_1 = \begin{bmatrix} \gamma_1 & 0 \\ 0 & \gamma_2 \end{bmatrix}.$$

The stationary probabilities of being in a state can be found from the row vector θ that solves $\theta \cdot (\mathbf{D}_0 + \mathbf{D}_1) = 0$, and the stationary probability of being in a state before an arrival is $\theta_{arr} = \theta \mathbf{D}_1$ normalized to sum to one.

$$\theta = [p, q], \quad \theta_{arr} = [p\gamma_1, q\gamma_2](p\gamma_1 + q\gamma_2)^{-1}$$

and the SPP_1 cdf is

$$F_{s_1}(t) = 1 - \theta_{arr} e^{\mathbf{D}_0 t} \mathbf{e}.$$

The eigenvalues of \mathbf{D}_0 are

$$\lambda_{1,2} = \frac{-(\gamma_1 + 1/T + \gamma_2)}{2} \pm \sqrt{\left(\frac{\gamma_1 + (q-p)/T - \gamma_2}{2}\right)^2 - \frac{pq}{T^2}}.$$

This gives that

$$\begin{aligned} F_{s_1}(t) &= 1 - \frac{e^{\lambda_1 t}}{2\sqrt{\zeta}(p\gamma_1 + q\gamma_2)} \left(p\gamma_1 \left(\sqrt{\zeta} + \frac{1/T + \gamma_2 - \gamma_1}{2} \right) + q\gamma_2 \left(\sqrt{\zeta} - \frac{1/T + \gamma_1 - \gamma_2}{2} \right) \right) \\ &\quad + \frac{e^{\lambda_2 t}}{2\sqrt{\zeta}(p\gamma_1 + q\gamma_2)} \left(p\gamma_1 \left(\sqrt{\zeta} - \frac{1/T + \gamma_2 - \gamma_1}{2} \right) + q\gamma_2 \left(\sqrt{\zeta} + \frac{1/T + \gamma_1 - \gamma_2}{2} \right) \right) \\ &= 1 - \tilde{p}e^{-\lambda_1 t} - (1 - \tilde{p})e^{-\lambda_2 t} \end{aligned}$$

where $\tilde{p} = \frac{1}{2} + \frac{p\gamma_1(1/T + \gamma_2 - \gamma_1) - q\gamma_2(1/T + \gamma_1 - \gamma_2)}{4\sqrt{\zeta}(p\gamma_1 + q\gamma_2)}$ and $\sqrt{\zeta} = \frac{\lambda_1 - \lambda_2}{2}$. That is the distribution of times is marginally hyperexponential.

The event-stationary number of counts is:

$$\theta_{arr} M_1(t)e = (p\gamma_1 + q\gamma_2)t + \frac{Tpq(\gamma_1^2 + \gamma_2^2)}{p\gamma_1 + q\gamma_2}(1 - e^{t/T})$$

whereas in the hyperexponential model one has (the renewal function):

$$H(t) = \frac{\gamma_1\gamma_2}{q\gamma_1 + p\gamma_2}t + \frac{(\gamma_1 - \gamma_2)^2 pq}{(q\gamma_1 + p\gamma_2)^2}(1 - e^{(q\gamma_1 + p\gamma_2)t}).$$

The rates of these can only be (asymptotically or time-stationary) equal if and only if it is a Poisson process we study.

APPENDIX D

Eulerian Techniques for Individual-Based Models with Additive Components

Manuscript submitted to *Journal of Marine Systems*

Eulerian Techniques for Individual-Based Models with Additive Components

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Abstract

Individual-based models appeal to marine ecologists because of the emphasis on the individual as the fundamental ecological unit, but their analysis often includes computationally demanding statistical analysis of stochastic Lagrangian simulations. This paper shows that certain individual based models, those based on Markov additive processes, lend themselves to a simplified Eulerian analysis where low order statistics can be computed exactly with relatively modest effort. We illustrate the framework with a hypothetical example from larval transport and growth, where the approach leads to partial differential equations for the mean and variance of larval length, as a function of position and time. We discuss the general applicability of the framework, and the merits of an Eulerian analysis versus individual-based simulation.

Keywords: Marine ecology, Individual-based models, Dispersion, Growth, Survival, Eulerian analysis

PACS: 92.20.Sg, 92.10.Lq, 92.20.jm, 92.10.Lq, 92.20.jp

1991 MSC: 82C70, 82C31, 65C20

D.1 Introduction

Individual-based models (IBM's) are popular within the fields of biological oceanography and fisheries science, as well as in many other fields. Typical

applications of IBM's in a marine context is the analysis of transport, growth and survival of fish larvae (see e.g. Ådlandsvik et al., 2004; Bartsch et al., 2004; Hinrichsen et al., 2002; Werner et al., 2001).

The appeal of an individual-based model is that the mathematical description targets the individual, rather than the population or other more abstract objects to which it is more difficult to relate. Furthermore, IBM's capture variability among individuals, which is an essential feature in much of marine ecology. Despite this, it is not always favourable to *analyse* individual-based models by means of extensive numerical simulations, where each individual is represented explicitly in the simulation program as an object. This is because a successful interpretation of the output requires large amounts of data as well as sufficient statistical techniques in both planning and analysis of the experiments. When simple population properties are the aim of the study, simulation of IBM's may not be the most effective approach.

An alternative to individual-based simulation is an Eulerian analysis of the model. That is, rather than explicitly following individuals over time as they move in space, we follow the density of animals or other continuous fields as they evolve over time. In principle, the Eulerian approach holds the advantage that the statistical part of the study is eliminated, because the object of analysis is in itself the statistics we are after, but the downside is that the Eulerian analysis typically involves solving partial differential equations. In oceanographic applications this may not in itself be a great extra burden, because the biology is already embedded in a physical environment which is governed by partial differential equations. However, when many biological state variables are included, the Eulerian analysis targets the joint probability density function of a high-dimensional variable, leading to partial differential equations with many independent variables.

The objective of this paper is to direct attention to a particular mathematical structure, that of individuals governed by independent and identically distributed Markov *additive* processes. The word “additive” indicates that some quantity, e.g. length, is cumulated along the trajectory but does not affect the trajectory. The class of Markov additive processes is well known within the theory of stochastic processes; here we take the small extra step of considering ensembles, or populations, where each individual is governed by such a process. It is interesting to note that the simplest example of an additive component is *age*, in that the age of every individual increases with constant rate 1. Thus the framework generalises the notion of *water age*, which has been the subject of study in recent years within physical and biological oceanography (Deleersnijder et al., 2001; Bendtsen et al., 2006).

The advantage of processes with additive components is that we can explicitly pose partial differential equations for the statistics of the processes, as functions of space and time. The aim of this paper is to present these equations as well

Parameter	Description	Example
H	Water depth	20 m
z_0	Bottom roughness	10^{-4} m
\mathbf{u}	Flow profile	$u_x = \frac{U_f}{\kappa} \log(z/z_0 + 1)$, $u_z = 0$
κ	von Kármán constant	0.41
U_f	Friction velocity	0.0168 m/s
D	Eddy diffusivity	$D_{xx} = D_{xz} = 0$, $D_{zz} = U_f \kappa z (1 - z/H)$
μ	Mortality	$\frac{2}{3}(z/H + 1/2)$ hour $^{-1}$
r	Local hatching rate	0
kL_∞	Growth rate	17 cm/year $\cdot (1 + 2z/H)$

Table D.1: The parameters in the general model, and their specific form in the example.

as a minimal example, which illustrates the potential of the framework in the context of biological oceanography. To this end, section D.2 presents the example of larval dispersal and growth, starting with the Eulerian and Lagrangian formulations of transport, and next including individual length as an additive component. The objective of the analysis is to pose Eulerian partial differential equations for the mean and variance of the length of a larvae caught at a given point in time and space. Section D.3 offers a discussion of generalisations and applicability of the framework.

D.2 A Markov additive process modelling larval transport and growth

In this section we develop the application of Markov additive processes to larval transport and growth. We do this in generality, but at the same time we will illustrate with a particular, simple example.

Consider fish larvae which move in space while growing. The larvae are mainly planktonic, i.e. passive drifters, but also subject to some diffusion, which accounts for turbulent mixing and the motility of the larvae. Finally, the larvae are subject to a mortality which varies in space and time.

In our specific example, we consider a two-dimensional space with one horizontal coordinate x and one vertical, z . We let the velocity, diffusivity and mortality depend on depth only and thus be independent of horizontal position and time, as in figure D.1.

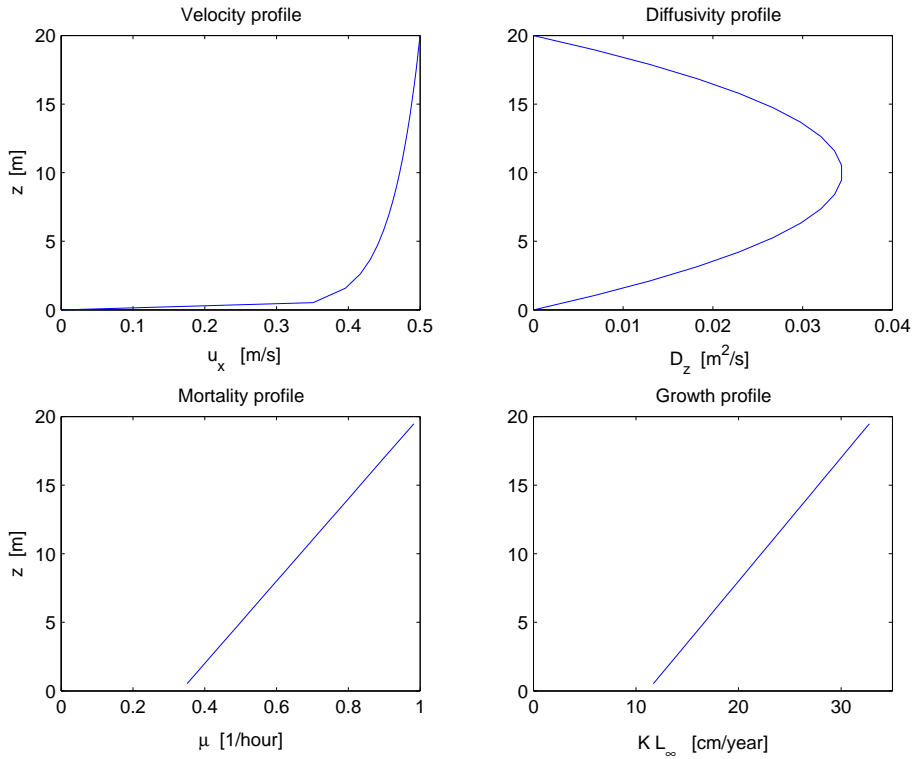


Figure D.1: The velocity field, diffusion rate, mortality rate, and growth rate. The flow regime is that of open channel flow, see table D.1. The growth and mortality profiles are chosen as simple as possible while having the feature that high growth rates coincide in space with high mortalities.

D.2.1 Eulerian and Lagrangian analysis of motion

Combining the model in the previous, and adopting the Eulerian view, the population of larvae is described by its density $C(\mathbf{x}, t)$ as a function of position \mathbf{x} and time t , and this density satisfies the partial differential equation (PDE)

$$\dot{C} = -\nabla \cdot (\mathbf{u}C - D\nabla C) - \mu C + r \quad . \quad (\text{D.1})$$

Here \mathbf{x} is the vector position (x, z) , $\mathbf{u}(\mathbf{x}, t)$ is the mean flow while $D(\mathbf{x}, t)$ is the diffusivity or dispersion, which can be a scalar (when the diffusion is isotropic) or a tensor. In our example we ignore the horizontal diffusivity D_{xx} , since horizontal dispersal is presumably dominated by longitudinal diffusion (Taylor, 1954), i.e. the combined effect of a velocity gradient and vertical mixing. The mortality rate is $\mu(\mathbf{x}, t)$ while $r(\mathbf{x}, t)$ is the local production rate of larvae, e.g. due to hatching of eggs. The PDE is completed with spatial boundary conditions. In our example we take the *no-flux* condition that $\mathbf{u}C - D\nabla C$ vanishes at the boundary of the domain. Finally, we prescribe an initial condition $C(\cdot, 0)$. In our example we start with a batch of larvae located at a single point in space. Contour lines of the solution are seen in figure D.2.

The corresponding Lagrangian approach is to simulate the random movements of an ensemble of larvae. Initially, individuals are placed randomly in space so that their density is $C(\cdot, 0)$, for example according to a spatial Poisson process (Stoyan et al., 1995a). During the simulation, the position of each larva is updated according to some stochastic recursion, a prototype of which is (Visser, 1997)

$$\mathbf{X}_{t+h}^{(j)} = \mathbf{X}_t^{(j)} + \tilde{\mathbf{u}}(\mathbf{X}_t^{(j)}, t)h + \sqrt{2D(\mathbf{X}_t^{(j)})}(\mathbf{B}_{t+h}^{(j)} - \mathbf{B}_t^{(j)}) \quad . \quad (\text{D.2})$$

Here $\mathbf{X}_t^{(j)}$ is the (vector) position in space of larva j at time t . $\mathbf{B}_{t+h}^{(j)} - \mathbf{B}_t^{(j)}$ is a multivariate random variable, with the same number of elements as $\mathbf{X}^{(j)}$, each element following a Gaussian distribution with mean 0 and variance h . When the diffusivity is anisotropic, the square root is to be understood in the matrix sense. The drift field $\tilde{\mathbf{u}}$ is the advection field corrected for heterogeneity in the diffusivity (see Visser, 1997):

$$\tilde{\mathbf{u}}(\mathbf{x}, t) = \mathbf{u}(\mathbf{x}, t) + \nabla D(\mathbf{x}, t) \quad .$$

In addition each larva is removed from the ensemble with probability $\mu(\mathbf{X}_t^{(j)}, t)h$ in each time interval. The movement scheme must be completed with a boundary behaviour which matches the boundary condition (Gard, 1988). In our example the no-flux boundary condition at the surface and bottom corresponds to reflection of particles at the boundary (Wilson and Flesch, 1993); we circumvent the associated difficulties by using the technique in Thygesen and Ådlandsvik (2006).

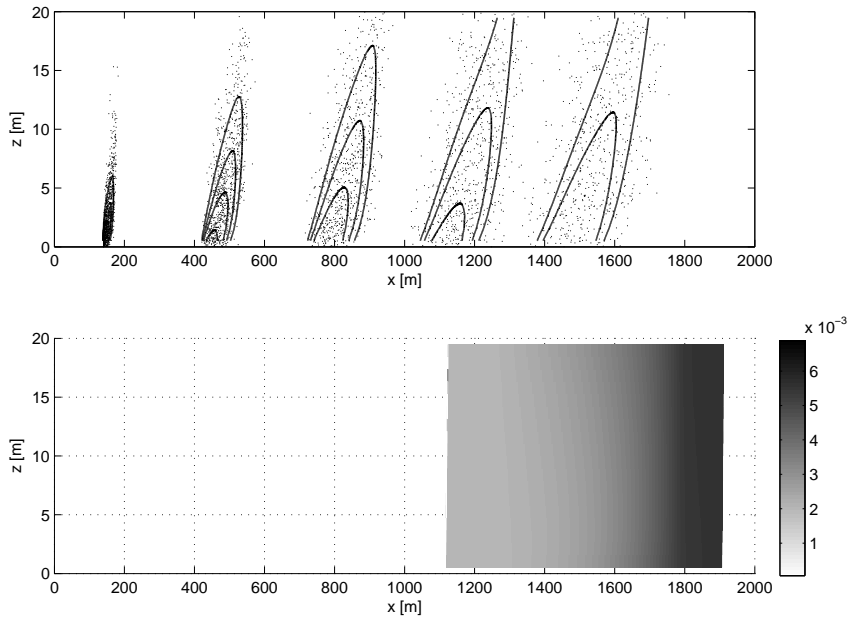


Figure D.2: Upper panel: Ensemble of surviving larvae in the IBM simulation, at times 400, 1200, 2000, 2800 and 3600 seconds. Overlaid are contour levels for the density, as computed by solving (D.1). The contour lines are chosen so the expected number of individuals between lines are 200. Lower panel: Mean length-at-position of larvae, at 3600 seconds.

Finally, as the simulation progresses new larvae are introduced to the ensemble and placed randomly in space: In each (short) time interval $[t, t + h]$ new larvae are placed randomly so that they have density $r(\cdot, t) \cdot h$, for example according to a spatial Poisson process.

The movement scheme ensures that the position of a larva is a Markov process (Gardiner, 1985). The defining property of Markov processes can be loosely be stated as “Given the present state, the future state is independent of past states”; so the position of a larva being Markov means that the instantaneous velocity is not needed to compute the future position. More specifically, the scheme (D.2) is the Euler scheme Kloeden and Platen (1995) for discretising the continuous-time *diffusion* process $\mathbf{X}_t^{(j)}$, which is the solution to the (Itô) stochastic differential equation (Øksendal, 1995; Gardiner, 1985)

$$d\mathbf{X}_t^{(j)} = \tilde{\mathbf{u}}(\mathbf{X}_t^{(j)}, t) dt + \sqrt{2D(\mathbf{X}_t^{(j)}, t)} d\mathbf{B}_t^{(j)} \quad ,$$

with killing rate μ . This connection provides us with an arsenal of more sophisticated numerical algorithms, in situations where the simple recursion (D.2) leads to problems (Kloeden and Platen, 1995). In turn, the transport terms in the Eulerian model (D.1) agree with the Fokker-Planck equation (also known as the forward Kolmogorov equation), governing the transition probabilities of the process $\mathbf{X}_t^{(j)}$.

With this Lagrangian model, the ensemble of larvae will at each time t constitute a spatial point process with intensity $C(\cdot, t)$, disregarding the effect of finite time steps. This is seen in figure D.2 (top panel), which combines a scatter plot from the IBM simulation with the densities computed with the Eulerian model. If the initial point pattern of larvae is Poissonian, and new larvae are also added to the ensemble according to a Poisson process at each time step, then the ensemble remains Poissonian.

D.2.2 Including growth

Now, we turn to the internal state of each larvae, viz. its length $L_t^{(j)}$. To keep things simple, we assume that all larvae have length L_0 at the time of hatching, and that the length thereafter follows the growth model

$$\frac{dL_t^{(j)}}{dt} = L_\infty \cdot k(\mathbf{X}_t^{(j)}, t) \quad .$$

Thus the growth rate depends on local conditions e.g. temperature, food availability, but given these, the growth rate is independent on the present length. This corresponds to the initial phase of von Bertalanffy growth. In an individual-based or Lagrangian simulation model, it is a matter of adding a few lines of

code to keep track of the length $L_t^{(j)}$ of each larvae. A snap-shot of such a simulation run would display a collection of points in space, indicating the position of the larvae, where each point is equipped with a *mark*, viz. the length of the particular larvae. In the terminology of stochastic geometry (Stoyan et al., 1995a), such a snap-shot is a realization of a marked point process.

Alternatively, to adopt an Eulerian setting, we would need the joint density $\phi(\mathbf{x}, l, t)$ of position $\mathbf{X}_t^{(j)}$ and internal state $L_t^{(j)}$: What is the expected number of larvae in a given region in space, at a given time, which has a length in a specified range? This density satisfies the “forward”, “Boltzmann”, or “Master”, equation (Fennel and Neuman, 2004)

$$\dot{\phi} = -\frac{\partial}{\partial \mathbf{x}}(\phi \tilde{\mathbf{u}} - D \frac{\partial}{\partial \mathbf{x}} \phi) - \frac{\partial}{\partial l}(\phi L_\infty k) - \mu \phi + r \delta(l - L_0) \quad . \quad (\text{D.3})$$

Note the term $-\frac{\partial}{\partial l}(\phi L_\infty k)$: Growth of individuals correspond to a flow along the “length” axis, and the local accumulation is minus the divergence of the advective flux. The last term, $r \delta(l - L_0)$ where δ is the Dirac delta, corresponds to the local production of larvae, which all have length L_0 . From a computational point of view, the extra dimension introduced by the internal state of the larva increases the burden enormously. In a 3-D environment, or with more than one attribute to the state, numerical resolution of a full Eulerian description is prohibitively expensive.

The key to making progress is to note that $(\mathbf{X}_t^{(j)}, L_t^{(j)})$ is an example of a Markov additive process (Asmussen, 2003, chapter 11), where $L_t^{(j)}$ is the additive component. We can recognise this by noticing that none of the coefficients in (D.3) depend on l . Loosely, this means that the position $\mathbf{X}_t^{(j)}$ evolves according to its own dynamics, while $L_t^{(j)}$ is simply cumulated along the trajectory. More precisely, $(\mathbf{X}_t^{(j)}, L_t^{(j)})$ is Markov, and the transition probability from (\mathbf{x}, l) to (\mathbf{x}', l') is the same as the transition probability from $(\mathbf{x}, 0)$ to $(\mathbf{x}', l' - l)$. See also Breuer (2002b) for a comparison of these characteristics with the more abstract definitions used in the specialised literature.

It follows that we are able to write up explicitly partial differential equations which govern the moments (i.e., mean, variance, etc.) of the length of a fish larva at a given position. This technique is standard within the field of Markov additive process; in appendix D.4 we present the result with the minor extension of considering not just one larva, but an ensemble of larvae, and allowing for multiple states with linear dynamics. The end result is that to determine the mean and variance of the length of a randomly selected larvae at a given position and time, we must first solve the system of equations

$$\dot{\rho}_i = -\nabla \cdot (\mathbf{u} \rho_i - D \nabla \rho_i) - \mu \rho_i + i L_\infty k \rho_{i-1} + L_0^i r \quad (\text{D.4})$$

where the subscript $i = 0, 1, 2, \dots$ corresponds to the order of the moment we are considering. Thus $\rho_0(\mathbf{x}, t)$ corresponds to the density of larvae at position

\mathbf{x} and time t , and the governing equation agrees with equation (D.1). Next, ρ_1 corresponds to density of larval *length*. To be precise, if we let $S_B^{(1)}(t)$ be the total length, summed over all larvae present in a region B at time t , then the expected value of $S_B^{(1)}(t)$ is

$$\mathbb{E}S_B^{(1)}(t) = \int_B \rho_1(\mathbf{x}, t) d\mathbf{x} \quad . \quad (\text{D.5})$$

From ρ_0 and ρ_1 we can form the mean length of a larva as a function of position and time (see appendix D.4):

$$\frac{\rho_1(\mathbf{x}, t)}{\rho_0(\mathbf{x}, t)} \quad .$$

To analyse the model, we therefore solve equations (D.4) numerically. Figure D.2 (lower panel) shows the conditional mean length as a function of position, colour coded. Note that the mean length varies quite strongly along the x -axis, but little along the z -axis. This is because individuals which have moved far must have been exposed to fast flow, which in turn coincides with high growth rates (compare figure D.1), so these individuals must have grown much. Note also that the Eulerian model determines accurately also the mean length of larvae in regions of space where very few larvae are present. This feature is particularly important in recruitment studies, where the length of the survivors, which constitute a small fraction of the initial ensemble, is of interest.

Similarly, ρ_2 corresponds to density of larval length squared, and from ρ_2 we may form the variance of the length of a larva sampled at position \mathbf{x} and time t :

$$\frac{\rho_2(\mathbf{x}, t)}{\rho_0(\mathbf{x}, t)} - \left(\frac{\rho_1(\mathbf{x}, t)}{\rho_0(\mathbf{x}, t)} \right)^2 \quad .$$

Thus, solving also for ρ_2 provides us with approximate confidence limits to the mean length. In figure D.3 we show the mean length as a function of horizontal position, with confidence limits, as well as the distribution of the horizontal position.

D.2.3 Interpretation of the governing equations

The equation (D.4) for the density ρ_1 of length may be interpreted as follows: length is a quantity which is being transported and lost with its carrier, i.e. the fish larvae, hence the terms $-\nabla \cdot (u\rho_1 - D\nabla\rho_1) - \mu\rho_1$ in its governing equation. In addition, length is being produced by two processes: The growth, which gives a local production of length which is the local density of fish larvae, ρ_0 , times the growth rate of each larvae $L_\infty k$. Secondly, length is being produced by new larvae hatching with rate r , each contributing with the initial length L_0 to the

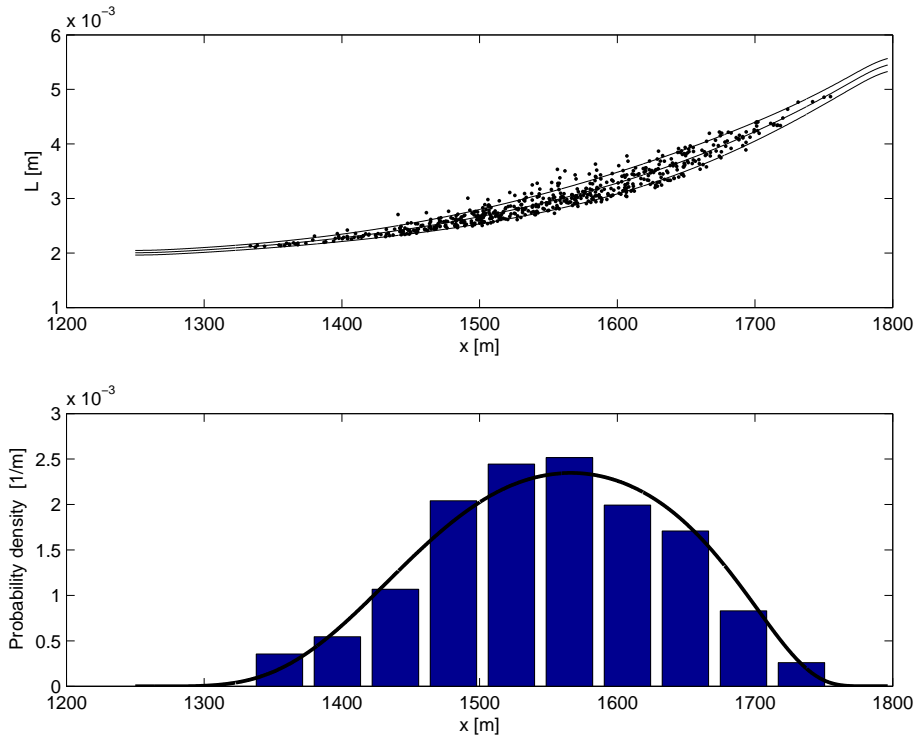


Figure D.3: *Top panel:* Scatter plot of length $L_t^{(j)}$ versus horizontal displacement $X_t^{(j)}$. Included are the mean length, and upper and lower limits in 95 % confidence intervals from the Eulerian model. *Lower panel:* Histogram of $X_t^{(j)}$ (bars). Included is the probability density function of $X_t^{(j)}$, as computed with the Eulerian model.

local length density. The combined effect of transport, mortality loss, growth, and production, is the governing equation (D.4) with $i = 1$.

The dynamic equation for ρ_2 is analogous: length squared is a quantity which is transported and lost with its carrier, the fish larvae. Furthermore length squared is introduced by new hatchlings with rate $L_0^2 r$ and finally the local production of length squared is $2L_\infty k \rho_1$. Re-writing this production rate as

$$2L_\infty k \frac{\rho_1}{\rho_0} \quad ,$$

we see that it is the local density of larval length times the average rate of increase of length squared at that position, using the chain rule

$$\frac{d(L_t^{(j)})^2}{dt} = 2L_t^{(j)} L_\infty k \quad .$$

These interpretations should illuminate the structure of the evolution equations (D.4). The reasoning can be extended to cover higher order moments as well, but this is probably of less practical interest.

D.2.4 Multiple additive components

There will be situations where we are interested in more than one internal state of the individuals. As a simple example, we may be interested in somatic growth and otolith growth, and in particular the correlation between the two. This section states the Eulerian equations for the mean, variance, and covariance of several additive components.

Rather than introducing new features into the model, however, we may simply re-inspect the governing equations (D.3) for our simple example and see that the coefficients neither depend on x nor on l , because the fields \mathbf{u} , D , K , μ only varies with the vertical position. Therefore the vertical position $Z_t^{(j)}$ is in itself Markov, and both $X_t^{(j)}$ and $L_t^{(j)}$ are additive components. It follows that we can write up a partial differential equation for the vertical distribution of larvae $\phi_{00}(z, t)$, and next for the joint statistics of horizontal displacement and length, as a function of vertical position. We end up with the system of equations

$$\partial_t \phi_{\alpha\beta} = \partial_z (D \partial_z \phi_{\alpha\beta}) - \mu \phi_{\alpha\beta} + \alpha u \phi_{(\alpha-1)\beta} + \beta g \phi_{\alpha(\beta-1)} \quad .$$

Here the subscripts α, β correspond to the order of the moments of horizontal position and length. The mean horizontal position is determined from ϕ_{10} , the mean length is determined from ϕ_{01} , and variance-covariance statistics are determined from ϕ_{02} , ϕ_{11} , and ϕ_{20} . We give the exact formulae in table D.2. The table also contains formulae for the unconditional moments, i.e. disregarding or averaging over the vertical position.

Statistic	Symbol	Formula
Vertical distribution		$\phi_{00}(z, t)$
Mean x at z	$\bar{m}_{X Z}(z, t)$	$\frac{\phi_{10}(z, t)}{\phi_{00}(z, t)}$
Mean l at z	$\bar{m}_{L Z}(z, t)$	$\frac{\phi_{01}(z, t)}{\phi_{00}(z, t)}$
Variance of x at z	$V_{X Z}(z, t)$	$\frac{\phi_{20}(z, t)}{\phi_{00}(z, t)} - (\bar{m}_{X Z}(z, t))^2$
Variance of l at z	$V_{L Z}(z, t)$	$\frac{\phi_{02}(z, t)}{\phi_{00}(z, t)} - (\bar{m}_{L Z}(z, t))^2$
Covariance between x and l at z	$\text{COV}_{XL Z}(z, t)$	$\frac{\phi_{11}(z, t)}{\phi_{00}(z, t)} - \bar{m}_{X Z}(z, t)\bar{m}_{L Z}(z, t)$
Mean x	$\bar{m}_X(t)$	$\frac{\int \phi_{10}(z, t) dz}{\int \phi_{00}(z, t) dz}$
Mean l	$\bar{m}_L(t)$	$\frac{\int \phi_{01}(z, t) dz}{\int \phi_{00}(z, t) dz}$
Variance of x	$V_X(t)$	$\frac{\int \phi_{20}(z, t) dz}{\int \phi_{00}(z, t) dz} - (\bar{m}_X(t))^2$
Variance of l	$V_L(t)$	$\frac{\int \phi_{02}(z, t) dz}{\int \phi_{00}(z, t) dz} - (\bar{m}_L(t))^2$
Covariance of x and l	$\text{COV}_{XL}(t)$	$\frac{\int \phi_{11}(z, t) dz}{\int \phi_{00}(z, t) dz} - \bar{m}_X(t)\bar{m}_L(t)$

Table D.2: Formulae for the statistics, computed with the fields $\phi_{\alpha\beta}$. For brevity, we write x , z and l for “horizontal position”, “vertical position”, and “length”.

These low-order statistics may be computed with very little effort. For our simple example, where the Markov component Z_t is one-dimensional and the governing equations are time-invariant, we may discretise the vertical dimension into n layers. The coupled system for $\phi_{\alpha\beta}$ with $0 \leq \alpha + \beta \leq 2$ is thus approximated by $6n$ coupled linear time-invariant differential equations, so that the solution for any particular time may be obtained by evaluating the exponential to a matrix of dimension $6n \times 6n$.

Clearly, just having information of up to second order does not describe all features of the distributions. If we take the usual approach and consider Gaussians with the same statistics, then we would approximate the density and histogram in figure D.3 (lower panel) with a Gauss bell, which is reasonable, but we would also approximate the conditional mean length as a function of x in the upper panel with a straight line, which is less reasonable. To discover that conditional mean length is an accelerating function of x , we would need third order information. Whether this feature is critical and justifies the extra computation, or the covariance information is sufficient, depends on the application at hand. Note that as time progresses, these approximations become more and more accurate; a Central Limit Theorem applies to these processes.

D.3 Discussion

In this paper, we have stated Eulerian equations for the mean and variance structure in a population of individuals which each is characterised by its position as well as some internal state, which is cumulated along the trajectory. We have illustrated with a minimalistic example for maximum clarity, but we stress that the framework is applicable in much greater generality; a point we shall elaborate on below.

Our aim has been to show that an Eulerian analysis of individual-based models is possible, also from a practical point of view. We believe that many practical problems with individual-based models can be avoided by adopting the Eulerian view. One particular such problem is statistical and regards the number of particles required for a reliable analysis, especially with large mortality; numerical issues regarding implementations of random-walk schemes is another example. A benefit of Eulerian models in this respect is that a large toolbox is available and already well-known within the oceanographic scientific community. This holds for “ecosystem” modules for the reaction kinetics of multiple biological fields which are subject to (active or passive) transport. But also analytical techniques are available, which may assist in making coarse first estimates without solving the actual equations. One set of techniques which should be very useful is model reduction based on time scale separation in the model, either using adiabatic elimination of fast variables or averaging of periodicities (Gardiner, 1985; Murdock, 1999). In our example, with sufficiently large time scales of interest, the vertical mixing could be considered a fast process so that vertical position is eliminated adiabatically, resulting in a simple advection-diffusion model for growth and horizontal transport.

When simulating individual-based models it is easy to add arbitrarily complex internal state dynamics, whereas an Eulerian analysis requires a simpler model structure. This can be a limitation, but can also serve as a reminder to maintain focus during modelling. In larval drift studies, for example, a prominent source of uncertainty is our inability to parameterise the mortality and the way it varies with internal states and external environmental factors. In this situation, adding complexity to other parts of the model is not likely to increase the overall fidelity of the model predictions.

We do not claim that Eulerian analysis is always superior to individual-based simulation, but merely that it is an advantage to be able to choose the better approach for the problem at hand. Individual-based simulation are likely to be computationally superior when few particles would suffice, but the Eulerian model would have to resolve a large space. Also, individual-based models yield actual trajectories of individuals, which can be a great help in understanding the life history of animals. Another limitation is that the methods we have presented for additive processes yield only moments, whereas other information about the

distribution, e.g. tail characteristics, would require a full Eulerian analysis, or an individual-based simulation. Finally, non-linear dynamics cannot be solved exactly with this approach. Reparameterisations in terms of cumulated exposure, or moment closure techniques, are possible, but have to be specific for the problem at hand.

In our analysis we have concentrated on the forward equations, which govern how probability densities evolve from a given initial condition. In the theory of stochastic processes there is a well established duality, so that we could equally well have concentrated on equations evolving backwards in time. This could e.g. govern the expected length of a larva when it reaches a nursery ground, as a function of spawning time and position, and averaged only over those larvae which actually reach the nursery ground.

Regarding the generality of the framework, we should emphasise that our results do not hinge on the particularities of the example. For instance, the dynamics of the vertical position $Z_t^{(j)}$ may include vertical preferences or migrations, and the entire system may be time-varying. Neither is it critical that the additive component, here $L_t^{(j)}$, grows continuously and deterministically given the position. It may contain a diffusive component, and it may display random jumps, as will be the case if the additive component measures encounters with prey or cumulated feeding intake.

The dynamics of the additive component may also contain a *linear* term in the additive component itself. This can extend our simple example to cover the full von Bertalanffy growth model, and can lead to general matrix dynamics for the internal state vector when multiple internal states are considered.

One particular problem with individual-based models is the representation of interactions among the individuals in the model. In simulation models, realistic interactions require realistic densities of individual, which leads to overwhelming computational burdens when studying larvae. In an Eulerian analysis of larval growth, a reasonable heuristic is to let the local growth and mortality depend on the local density, thus adding non-linear terms to the equations (D.4). However, it is not trivial to determine which non-linear terms in the Eulerian model corresponds to which individual interactions in a simulation.

The common feature of Eulerian analysis of individual-based models is that we need “ecosystem” modules on top of circulation models, which can resolve the transport, both passive and active, and production of multiple scalar fields. Driven by applications to food-web models, such modules are becoming standard extensions to common circulation models and their performance and flexibility are rapidly increasing. These modules may be used to use to gain a deeper knowledge about the fate of marine organisms, than what is obtained by merely keeping track of numbers or biomass, by including also non-mass state variables. In this respect, additive processes provide a framework which is both general

and tractable, and is particular well suited for non-mass state variables such as length, age, and cumulated exposure to environmental cues. Most importantly, the framework is an evidence to the fact that individual variability can be captured also in Eulerian models.

Acknowledgements

The research was supported by the SLIP research school under the Danish Network for Fisheries and Aquaculture Research (www.fishnet.dk) as well as by the REX project, financed by the Danish Ministry for Food, Agriculture and Fisheries and the Danish Agricultural and Veterinary Research Council.

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D.4 Appendix A. Ensembles of Markov Additive Processes

A Markov Additive Process is a stochastic processes with two components, say $X_t \in \mathbf{X}$ and $L_t \in \mathbf{L}$, so that the combined process (X_t, L_t) is Markov, and so that the transition probabilities are invariant under shifts in L_t . Formally, let $p(s, t, (x_s, l_s), A \times B)$ be the probability that the process satisfies $X_t \in A$ and $L_t \in B$, given that it starts in (x_s, l_s) at time s , then

$$p(s, t, (x_s, l_s), A \times B) = p(s, t, (x_s, 0), A \times (B - l_s))$$

must hold for every initial state (x_s, l_s) , every target sets A and B , and every initial and terminal times s and t .

Consider the particular Markov additive process of a fish moving in space while growing, as in section D.2.2. Let $\phi(\mathbf{x}, l, t)$ be the joint density of $(\mathbf{X}_t^{(j)}, L_t^{(j)})$, which then satisfies the forward Kolmogorov equation (compare e.g. Øksendal,

1995; Gardiner, 1985; Kloeden and Platen, 1995; Fennel and Neuman, 2004)

$$\frac{\partial \phi}{\partial t} = [-\partial_{\mathbf{x}}(u\phi - D\partial_{\mathbf{x}}\phi)] + \{-\partial_l(L_{\infty}k\phi)\} \triangleq A\phi \quad . \quad (\text{D.6})$$

Here we have decomposed the equation in two terms: The first, in square brackets, corresponds to redistribution of $\mathbf{X}_t^{(j)}$, which does not involve l , while the second term in curly brackets corresponds to redistribution of $L_t^{(j)}$, and is shift invariant in l .

We proceed to consider an ensemble of individuals, which each evolve according to independent realisations of this Markov additive process. If the ensemble at time 0 constitutes a Poisson process in state space, and if no individuals are added to or removed from the ensemble, then the ensemble will remain a Poisson process with a density in state space which is governed by the same equation (D.6). If individuals are added to the ensemble according to a Poisson process in state space and time with density $r(\mathbf{x}, l, t)$, and if each individual is removed from the ensemble with probability $\mu(\mathbf{x}, t)$, then the equation governing the density of the ensemble in state space becomes

$$\partial_t \phi = A\phi - \mu\phi + r \quad . \quad (\text{D.7})$$

A Poisson process in state space $\mathbf{X} \times \mathbf{L}$ can be thought of as a *marked* Poisson process in \mathbf{X} , where \mathbf{L} is the mark space (Stoyan et al., 1995a). The density of this process in \mathbf{X} at time t is $\rho_0(\cdot, t)$ where

$$\rho_0(\mathbf{x}, t) = \int_{\mathbf{L}} \phi(\mathbf{x}, l, t) \, dl \quad ,$$

while the mark distribution, giving the probability density of the mark (i.e., the length) of a “typical” fish larvae sampled at location \mathbf{x} , is

$$\frac{\phi(\mathbf{x}, l, t)}{\rho_0(\mathbf{x}, t)} \quad .$$

It follows that the i th moment of the length of a typical fish sampled at position \mathbf{x} is

$$\int_0^{\infty} l^i \frac{\phi(\mathbf{x}, l, t)}{\rho_0(\mathbf{x}, t)} \, dl = \frac{\rho_i(\mathbf{x}, t)}{\rho_0(\mathbf{x}, t)} \quad ,$$

where $\rho_i(\mathbf{x}, t) = \int_{\mathbf{L}} l^i \phi(\mathbf{x}, l, t) \, dl$. To derive dynamic equations for ρ_i , differentiate this expression with respect to time and insert (D.6) to find, for $i \geq 1$:

$$\dot{\rho}_i = -\frac{\partial}{\partial \mathbf{x}}(\rho_i \tilde{u}) + \frac{\partial^2}{\partial \mathbf{x}^2}(D\rho_i) + L_{\infty}k i \rho_{i-1} - \mu \rho_i + \int_{\mathbf{L}} l^i r(\mathbf{x}, t, l) \, dl \quad . \quad (\text{D.8})$$

The last term corresponds gives the production rate of the i th moment due to introduction of new individuals to the ensemble. For comparison with (D.4), take $r(\mathbf{x}, l, t) := r(\mathbf{x}, t)\delta(l - L_0)$.

To obtain the result (D.8) from (D.7), use partial integration to evaluate the term

$$\int_0^\infty l^i \frac{\partial}{\partial l} (\phi L_\infty k) dl = [l^i \phi L_\infty k]_0^\infty - \int_0^\infty i l^{i-1} \phi L_\infty k dl$$

and the observation that $l^i \phi L_\infty k$ must vanish both at $l = 0$ (since $i \geq 1$) and in the limit $l \rightarrow \infty$ (for ρ_i to be finite). Note that if the Markov process $(\mathbf{X}_t^{(j)}, L_t^{(j)})$ did not have the additive structure, these equations would involve higher order moments, i.e. the dynamic equations for the low-order moments would not be closed.

The result is easily extended to the case of several additive components: For example, if we have two additive components, $L_t^{(j)} \in \mathbf{L}$ and $M_t^{(j)} \in \mathbf{M}$, then we establish the Master equation for the joint density in $\mathbf{X} \times \mathbf{L} \times \mathbf{M}$, multiply with $l^\alpha m^\beta$ and integrate over $\mathbf{L} \times \mathbf{M}$, to obtain dynamic equations for the joint moments.

Note that it is not essential that the Markov state $\mathbf{X}_t^{(j)}$ is a advection-diffusion process; it could be any Markov state, for example including discrete behavioural or physiological states. Also, the additive component $L_t^{(j)}$ may evolve according to more general dynamics than growing with a rate $L_\infty k(\mathbf{x}, t)$, of which we now list a few:

Diffusive components: If the increment in $L_t^{(j)}$ over a small time interval has a small random component, this will appear in the Master equation as a term $E \partial_u \phi$. This will not affect the mean growth, i.e. ρ_1 , but it will increase the variance through an additional production term $2E \rho_0$ appearing in the dynamic equation for ρ_2 .

Discrete jumps: These may appear if $L_t^{(j)}$ models weight, stomach contents, or encounters, rather than length. Jumps will give rise to a convolution term in the Master equation. In the equation for ρ_1 a term $\lambda \overline{\Delta L}$ will appear; here λ is the jump rate while $\overline{\Delta L}$ is the mean jump height.

Linear relaxation: For example, we may replace the growth rate $k L_\infty$ with the full von Bertalanffy model $k(L_\infty - L_t^{(j)})$. This will give rise to an additional term $\partial_l(\phi k l)$ in the Master equation, and thus the additional term $-k \rho_1$ in the equation for ρ_1 , and the additional term $-2k \rho_2$ in the equation for ρ_2 . When multiple internal states are included, this can give rise to quite sophisticated models.

APPENDIX E

A framework for functional and numerical responses in periodic environments

Manuscript

A framework for functional and numerical responses in periodic environments

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Abstract

Markovian Arrival Processes are very general point processes where the generation of points is controlled by an underlying finite state Markov chain. This dependence makes it possible to approximate inter-arrival times from all positive distributions and to include correlations between events. One of the biggest advantages of MAPs is that it is often possible to obtain analytical or algorithmically tractable results i.e. key properties of the stochastic process can be acquired without simulating it.

In this article we will present transient Markovian Arrival Processes with periodic rates that we believe can be used as a tool to understand the effects of stochasticity at the individual level e.g. on the number of food items acquired during a time period, or the offspring produced. We use transient models since the risk of death is a very important factor in at least parts of the life of most organisms. Moreover, in order to study and describe situations with periodicities our models are equipped with periodic rates since temporal variations in prey, light, temperature etc. are vital to how biological systems work.

We present the asymptotics of conditional moments in order to characterise the long-term survivors and propose that these moments can be used in time-scale separation techniques. We will also present a sequence of examples where the transient MAPs can be seen as logical and plausible extensions of a Poisson process, in order to account for heterogeneities or regularities in nature. It will also be shown that even if food intake is highly variable, another process such as offspring production which depends on feeding success can be underdispersed relative to a Poisson process.

E.1 Introduction

Most ecosystems have periodic or almost periodic external forcing; evident examples are daily and annual variations in light and temperature. Most organisms respond to these external periodicities and behave periodically due to adaptations to different profitabilities or availabilities of prey, or probabilities of encountering predators or a partner during a period. This is an effect that often is ignored. If the aim is to build mechanistically derived models then it is important to include these variations since they may have large effects. For instance, periodical variations in time make it, at least theoretically, feasible for some organisms to exist in a system where it would have been impossible to survive without periodicities (see e.g. Ebenhöh, 1988).

Periodicity is a fundamental property of the environment of many organisms, but even if the cause of the periodicity is deterministic its effects on the individual may not be so. A periodic variation may give an organism the opportunity to exploit an otherwise inaccessible resource; Clark and Levy (1988) showed that the daily variations in light enables small fish to search for food at dusk and dawn with relatively low risk since the light levels are low enough to hamper the foraging success of their predators but high enough to not impede their own foraging. The actual outcome of such phenomena, such as foraging, is typically stochastic and in many cases depend on the state of the organism, since for instance, it is not possible to ingest food if the stomach is full. Periodicity is a regular temporal variation, but spatial variability is often important too, e.g. spatial variability in resources can lead to persistence of populations over several generations even if the average, or homogeneous, situation leads to extinction in much less time. A splendid illustration of this is Brodie et al. (1978) who noted that the average densities of euphasiids estimated via nets and acoustics were insufficient to feed fin whales in an area off the coast of Nova Scotia; the whales would need to swim at speeds of $900 \text{ km} \cdot \text{h}^{-1}$ to fill their stomachs in 8 hours.

Since variation in resources and in encounters with prey are important to the fitness of an organism we believe that it is important to construct and analyze stochastic models even if they in general are more cumbersome to deal with than their deterministic counterpart.

The Markovian Arrival Process (MAP) offers a possible starting point for studying the effect of stochasticity at the individual level; it is a very general stochastic point process and yet, due to the Markov property, it is possible to analyze models without having to use simulation. For a MAP the rate of generation of points depends on a finite state Markov chain. MAPs has found many applications in queueing theory (see e.g. Heffes and Lucantoni, 1986), but it has not been widely used in biology. The two-state Markov chain with arrivals of points in one state only, the interrupted Poisson process is a MAP. It has been used as a simple model-unit to describe that in many instances patchiness makes the number of

prey encountered more variable than the Poisson distribution, see Beyer and Nielsen (1996) for a thorough introduction and Pitchford and Brindley (2001) for applications to fish larvae.

We assume that the behaviour of an organism can be described as being in a finite number of states, called phases, and that the transitions between phases can be described by a finite Markov chain. Certain transitions in the Markov chain generate counts, these represent some discrete quantity of interest such as captured prey, offspring produced. Since the risk of mortality probably is the most important aspect of life for many organisms, in particular for the juvenile stages, we explore the dynamics of transient processes where death is the absorbing state. An absorbing state has the property that once entered it cannot be left. Other states with a non-zero probability of an eventual transition to the absorbing state are called transient—it is certain that they are left. Our models are constructed with only one absorbing state where no counts are generated after death. Moreover it is assumed that the models are constructed such that the transient states are communicating; the probability of transition from any state to any other state is non-zero given that the process did not terminate. In order to characterise the number of points of the survivors or the dead in the long run we are interested in finding the asymptotic moments for the number of counts *given* that the organism is in a certain state or set of states—these are the conditional moments for the MAP.

In this article we will first present MAPs briefly in Section E.2, then we will present the conditional mean and variance of counts for transient MAPs with periodic rates in Section E.3. Finally, in Section E.4 we will produce some scenarios on a vertically migrating planktonic organism that will illustrate the flexibility of the MAP and show that it is possible to have different counting processes, the effect of including death on the survivors, and possibilities for time-scale separation. It will be shown that the framework of Markovian Arrival Processes will enable us to analyse situations where under- and over-dispersing mechanisms compete.

Notation

In the following vectors are denoted with a bold lower case letter, such as \mathbf{a} , these are always assumed to be column vectors; row vectors will appear as transposed column vectors (\mathbf{a}^T is a row vector). There are some special vectors $\mathbf{e} = [1, \dots, 1]^T$, \mathbf{e}_x is a vector with a 1 in position x and zeros in all other positions, and if C is a set of states that the organism can be in, then \mathbf{e}_C is a vector with 1 in positions corresponding to phases in C , the rest of the positions are equal to zero. Matrices will appear as uppercase bold letters such as \mathbf{M} and the scalar positioned in the j th column of the i th row of the matrix will be denoted $(\mathbf{M})_{ij}$. Special matrices are \mathbf{I} , the identity matrix, and $\mathbf{0}$, the

zero matrix, where the dimension depends on the context. We will denote the indicator function with $\mathbf{1}\{x \in A\}$ which is equal to 1 if x belongs to A and 0 if not. Let $\mathbb{E}^{x,n,t}[\cdot]$ and $\mathbb{V}^{x,n,t}[\cdot]$ denote the expectation respectively the variance with respect to the law of the Markovian Arrival Process X_t, N_t starting at (x, n) at time t .

E.2 Key results on Markovian Arrival Processes

Marcel Neuts introduced the versatile Markovian process in 1979. The versatile Markovian process was later redescribed as the Markovian arrival process (MAP) by Lucantoni et al. (1990) which is the commonly used term. Here we will present the basic structure of MAPs such that a reader with some knowledge of continuous-time Markov chains will be able to follow the subsequent theory. For a more complete presentation of MAPs we refer to the afore-mentioned works and to Neuts (1989). A sufficient background for continuous-time Markov chains can be found in Grimmett and Stirzaker (2001).

A Markovian arrival process is a stochastic point process where the generation of counts depend on a finite state Markov chain. The MAP owes much of its flexibility to this dependence since this makes it possible to approximate interarrival times from almost any positive distribution (Asmussen and Koole, 1993).

The MAP is the counting process $\{N_t\}$ generated by a two-dimensional Markov process $\{X_t, N_t\}$ for $t > 0$ where X_t denotes the phase, *i.e.* the state in the finite Markov chain, at time t and N_t the counts accumulated to that time. Let the number of phases be m , then the behaviour of the MAP for $t > 0$ is fully described by $(\phi, \mathbf{D}_0, \mathbf{D}_1, n_0)$, where ϕ is the probability of being in phase i at $t = 0$, \mathbf{D}_1 and \mathbf{D}_0 are two $m \times m$ matrices, and n_0 is the initial number of counts. Without loss of generality we will assume that n_0 is equal to zero, hence the state space is $\{(i, n) : i \in \{1, 2, \dots, m\}, n \in \mathbb{N}\}$.

When the rates of the MAP are independent of time then the matrices \mathbf{D}_0 and \mathbf{D}_1 are constant; \mathbf{D}_0 has non-negative off-diagonal elements and the matrix \mathbf{D}_1 has non-negative elements. The j th off-diagonal element in the i th row of \mathbf{D}_0 , $(\mathbf{D}_0)_{ij}$ determines the instantaneous rate out of state (i, n) into (j, n) without generating a point. The j th element in the i th row of the matrix \mathbf{D}_1 , $(\mathbf{D}_1)_{ij}$, determine the rate out of state (i, n) into state $(j, n+1)$ – transitions from phase i to j that generate a point. Note that transitions from (i, n) to $(i, n+1)$ are allowed, then $(\mathbf{D}_1)_{ii}$ is positive.

In order to preserve probability, the rate by which state (i, n) is left has to be balanced by the rate by which other states are entered from this state, this

means that

$$(\mathbf{D}_0)_{ii} = - \left(\sum_{\substack{1 \leq k \leq m \\ k \neq i}} (\mathbf{D}_0)_{ik} + \sum_{k=1}^m (\mathbf{D}_1)_{ik} \right).$$

The general structure of a MAP can be seen from the infinite-dimensional transition matrix \mathbf{Q} , where the m first rows correspond to being in some of the m phases and having 0 counts, the next m rows to having 1 count *etc.*, where

$$\mathbf{Q} = \begin{bmatrix} \mathbf{D}_0 & \mathbf{D}_1 & \mathbf{0} & \mathbf{0} & \cdots \\ \mathbf{0} & \mathbf{D}_0 & \mathbf{D}_1 & \mathbf{0} & \cdots \\ \mathbf{0} & \mathbf{0} & \mathbf{D}_0 & \mathbf{D}_0 & \ddots \\ \vdots & \vdots & \ddots & \ddots & \ddots \end{bmatrix}.$$

Ignoring the counts the rate of one-step transitions between phases is described by the matrix $\mathbf{D} \equiv \mathbf{D}_0 + \mathbf{D}_1$. If \mathbf{D} is irreducible, and time-independent, then the stationary probability distribution can be found as the column vector $\boldsymbol{\theta}$ that solves:

$$\boldsymbol{\theta}^T \mathbf{D} = \mathbf{0}^T \quad \text{and} \quad \boldsymbol{\theta}^T \mathbf{e} = 1,$$

where \mathbf{e} is a column vector with all ones and $\mathbf{0}$ is a vector of zeros.

The first two moment-matrices of the counting process of a MAP are described in Narayana and Neuts (1992) together with a discussion on algebraic and algorithmic properties of these. The moment-matrix describes the first two fractional moments of counts at time t given that the present state is j and that the initial state was i , where the n th fractional moment of a random variable X is $\mathbb{E}\{X(X-1)(X-2)\cdots(X-n+1)\}$.

Latouche et al. (2003) describe fundamental results for transient MAPs with time-invariant rates. Transient MAPs occur when there are catastrophic events which cause the process to stop. In biological models transient chains could e.g. be used to represent the death of an animal. In Nielsen et al. (2007) the results of Narayana and Neuts (1992) were generalized to any moment for transient MAPs with rates that are independent of time; these can be used to derive formulas for the conditional mean, variance and higher order central conditional moments.

E.2.1 Some basic building blocks of MAPs

The *PH-renewal process* and the *Markov-modulated Poisson Process (MMPP)* are often used in MAP constructions. Let (α, \mathbf{T}) be the irreducible representation of a phase-type distribution—a phase-type distribution is defined as the

time to absorption in a finite Markov chain with one absorbing state (see Neuts, 1989). Then a PH-renewal process has the matrices:

$$\mathbf{D}_0 = \mathbf{T} \quad \mathbf{D}_1 = \mathbf{t}^o \alpha,$$

where $\mathbf{t}^o = -\mathbf{T}\mathbf{e}$. An *MMPP* has the rate matrices:

$$\mathbf{D}_0 = \mathbf{D} - \Lambda \quad \mathbf{D}_1 = \Lambda,$$

where Λ is a diagonal matrix. The MMPPs have the nice property that it is possible to multiply the generation of counts without altering the probability distribution of the phases. For instance, if the rate matrix is multiplied with a scalar α the the expected counts will be increased with this factor.

To illustrate this let us have 4 states, where it is only allowed to have transition rates of 1 per time unit to other states. An example of a PH-renewal process is a MAP with

$$\mathbf{D}_0 = \begin{bmatrix} -1 & 1 & 0 & 0 \\ 0 & -1 & 1 & 0 \\ 0 & 0 & -1 & 1 \\ 0 & 0 & 0 & -1 \end{bmatrix} \quad \text{and} \quad \mathbf{D}_1 = \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 \end{bmatrix}.$$

This is an Erlang(4) process which is the most regular MAP possible with 4 states. The distribution of interarrival times can be seen in Figure E.1. As a contrast take the 4 state MMPP (it is also a PH-renewal) with matrices:

$$\mathbf{D}_0 = \begin{bmatrix} -2 & 1 & 0 & 0 \\ 0 & -1 & 1 & 0 \\ 0 & 0 & -1 & 1 \\ 1 & 0 & 0 & -1 \end{bmatrix} \quad \mathbf{D}_1 = \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}$$

This will generate a process that is much more variable than a Poisson process; the interarrival distribution is shown in Figure E.1, for reference an exponential distribution with the same mean as the two distributions above is included. Note that the \mathbf{D} matrix is the same for both the MMPP and the PH-renewal process but the behaviour is quite different.

E.3 Transient Markovian Arrival Processes with periodic rates

Here we present terminating MAPs where the rates are varying periodically with minimal period T , and results for the asymptotics of their conditional mean and variance. For convenience phase 0 is the absorbing state where no counts are

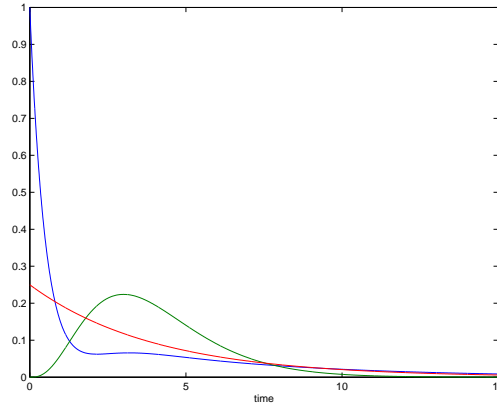


Figure E.1: The Erlang(4)-process is green and the MMPP is blue; while an exponential variable with same mean is red. Note that the Erlang waiting time is much more regular and has less variance than the exponential and that the MMPP has a wider tail than the exponential distribution.

generated. All the other m phases are transient and communicating in the absence of death. The $(m + 1) \times (m + 1)$ rate matrixes for one-step transitions with and without producing a count are

$$\mathbf{D}_1(t) = \begin{bmatrix} 0 & \cdots & 0 \\ h_{1,0}(t) & \cdots & h_{1,m}(t) \\ \vdots & \ddots & \vdots \\ h_{m,0}(t) & \cdots & h_{m,m}(t) \end{bmatrix}, \quad \mathbf{D}_0(t) = \begin{bmatrix} 0 & \cdots & 0 \\ g_{1,0}(t) & \cdots & g_{1,m}(t) \\ \vdots & \ddots & \vdots \\ g_{m,0}(t) & \cdots & g_{m,m}(t) \end{bmatrix}$$

respectively. We assume that the functions $h_{i,j}(t)$ are non-negative as well as the off-diagonal functions in \mathbf{D}_0 . The diagonal functions in \mathbf{D}_0 are defined as

$$g_{i,i}(t) = - \left(\sum_{\substack{0 \leq j \leq m \\ j \neq i}} g_{i,j}(t) + \sum_{j=0}^m h_{i,j}(t) \right)$$

for $i = 1, \dots, m$. We assume that the functions $g_{i,j}(t)$ and $h_{i,j}(t)$ are sufficiently well-behaved to assure existence and uniqueness for the solutions; piece-wise continuous functions are examples of such (see p. 107 in Lukes, 1982, for exact criteria). The periodicity in the rates implies that $\mathbf{D}_1(t + T) = \mathbf{D}_1(t)$ and $\mathbf{D}_0(t + T) = \mathbf{D}_0(t)$ for all t . Consequently the time-dependent rate of one-step transitions between phases is $\mathbf{D}(t)$ is also periodic.

In order to be able to answer questions such as: “What is the expected number of prey eaten given that the predator is alive now (time $t+t_s$) and that it started in phase i with nothing at some previous time t_s ?”, we will need to compute the following matrices $\mathbf{P}(t_s, t+t_s)$, $\mathbf{M}_1(t_s, t+t_s)$, and $\mathbf{M}_2(t_s, t+t_s)$. Their interpretation is that the j th element in row i of $\mathbf{P}(t_s, t+t_s)$, $(\mathbf{P}(t_s, t+t_s))_{i,j}$, is the probability of being in phase j at time $t+t_s$ given that the process was in phase i t time units before. The corresponding entry on the i th row in the j th column of $\mathbf{M}_1(t_s, t+t_s)$ (or $\mathbf{M}_2(t_s, t+t_s)$) are the expectation of the number of counts (or squared counts) *and* that the present phase is j given that the initial state was $(i, 0)$ t time units before at time t_s .

These can be found (see Article B from the solutions to the following system of ordinary differential equations:

$$-\frac{d}{d\tau} \begin{bmatrix} \mathbf{P} \\ \mathbf{M}_1 \\ \mathbf{M}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{D}(\tau) & 0 & 0 \\ \mathbf{D}_1(\tau) & \mathbf{D}(\tau) & 0 \\ \mathbf{D}_1(\tau) & 2\mathbf{D}_1(\tau) & \mathbf{D}(\tau) \end{bmatrix} \begin{bmatrix} \mathbf{P} \\ \mathbf{M}_1 \\ \mathbf{M}_2 \end{bmatrix} \quad (\text{E.1})$$

with initial conditions $\mathbf{P}(0) = \mathbf{I}$, $\mathbf{M}_1(0) = \mathbf{M}_2(0) = \mathbf{0}$ for $\tau < 0$. These are the backward Kolmogorov equations which fix the end time and state, the time is usually set to 0, which means that the initial time will be negative. The interpretation for the moments is actually: “Given that we start in state i at time 0 what is the expected number of *lost* prey when running things backwards?” This slightly awkward point of view can be taken care of by changing the time to $t \rightarrow -\tau$. In what follows the boundary value will be taken at time 0, since it is always possible to translate the time $t' \rightarrow t - t_s$. For simplicity the matrix $\mathbf{P}(\tau, 0)$ (in the original time scale) will be denoted $\mathbf{P}(t)$ except where distinctions are necessary.

In the forward Kolmogorov equations the starting time is fixed (usually to $t = 0$) and the question to be answered is: “Given that the initial phase is i (and no rewards) what is the probability (or expected number of counts) given that the phase at time t positive is j ?” The difference is slight and the solutions are equal at each period. However the backward Kolmogorov has some properties that makes it more suitable in our calculations since the system to be integrated can be reduced by multiplying from the right with \mathbf{e}_B , whereas in the forward setting reductions can be made with the given initial distribution.

The conditional mean can be found as

$$\mathbb{E}^{x,0,\tau}[N_0|X_0 \in C] = \frac{\mathbf{e}_x^T \mathbf{M}_1(\tau) \mathbf{e}_C}{\mathbf{e}_x^T \mathbf{P}(\tau) \mathbf{e}_C},$$

and the conditional variance as

$$\mathbb{V}^{x,0,\tau}[N_0|X_0 \in C] = \frac{\mathbf{e}_x^T \mathbf{M}_2(\tau) \mathbf{e}_C}{\mathbf{e}_x^T \mathbf{P}(\tau) \mathbf{e}_C} - \left(\frac{\mathbf{e}_x^T \mathbf{M}_1(\tau) \mathbf{e}_C}{\mathbf{e}_x^T \mathbf{P}(\tau) \mathbf{e}_C} \right)^2$$

for $\tau < 0$ as was shown in Article B.

Due to the fact that the matrices $\mathbf{D}_0(t)$, $\mathbf{D}_1(t)$, and $\mathbf{D}(t)$ are time-dependent an analytical solution cannot be found, but the periodicity provides structure; the system can be integrated numerically over a period T and then recursive equations can be used. These recursions can be used to calculate the state of the system for $t + T$. This is due to the fact that if $\mathbf{f}(t)$ is a solution such that $\mathbf{f}(t_0) = \mathbf{x}_0$ for the n -dimensional ODE system $\frac{d}{dt}\mathbf{x}(t) = \mathbf{A}(t)\mathbf{x}(t)$ where $\mathbf{A}(t)$ is a T -periodic matrix then the solution starting from \mathbf{x}_0 at time $t_0 + T$ is $\mathbf{f}(t - T)$. This means that if the solutions to n linearly independent starting conditions are known over a period, then any initial condition can be written as a combination of these and this solution will form a vector at the end of the period, which can be written as a linear combination of the n vectors and so to proceed as the initial condition in the next period. The periodic system can be embedded into a discrete time-invariant system.

This is illustrated in Figure E.2 where there is only one periodic state (it is actually the solution $\mathbf{P}_{1,1}(t)$ from Example 1). Using periodicity the following equations are derived (see appendix E.9):

$$\mathbf{P}(t + T) = \mathbf{P}(t)\mathbf{P}(T) \quad (\text{E.2})$$

$$\mathbf{M}_1(t + T) = \mathbf{M}_1(t)\mathbf{P}(T) + \mathbf{P}(t)\mathbf{M}_1(T) \quad (\text{E.3})$$

$$\mathbf{M}_2(t + T) = \mathbf{M}_2(t)\mathbf{P}(T) + 2\mathbf{M}_1(t)\mathbf{M}_1(T) + \mathbf{P}(t)\mathbf{M}_2(T) \quad (\text{E.4})$$

If we denote \mathbf{P} as \mathbf{M}_0 then these equations can be generalised for the n th moment:

$$\mathbf{M}_n(t + T) = \sum_{i=0}^n \binom{n}{i} \mathbf{M}_{n-i}(t)\mathbf{M}_i(T)$$

(see Article B for the time-invariant case). These recursions make it possible to calculate the development of the system if only the solutions are known during the first period for $\mathbf{P}(t)$, $\mathbf{M}_1(t)$, and $\mathbf{M}_2(t)$. Note that in general $\mathbf{P}(0, s + t) = \mathbf{P}(0, s)\mathbf{P}(s, s + t) \neq \mathbf{P}(0, s)\mathbf{P}(0, t)$. The above recursions use the T -translational invariance, $\mathbf{P}(T, t + T) = \mathbf{P}(0, t)$. The essence of the recursions is natural; let the expected number of counts at time nT be n_{nT} and the expected number of squared counts be m_{nT} . Then it is easy to see that:

$$m_{nT+T} = m_{nT} + 2n_{nT}(n_{nT+T} - n_{nT}) + (n_{nT+T} - n_{nT})^2$$

which essentially is the relation in Equation (E.4) where care has been taken to sum over all possible intermediate states at time nT and the probability of arrival is included.

The asymptotic analysis is based on sampling the system every period and solving the recurrence equations for $\mathbf{P}(T)$, $\mathbf{M}_1(T)$, and $\mathbf{M}_2(T)$ that are obtained by putting $t = nT$ in Equations (E.2, E.3, E.4). The matrices $\mathbf{P}(T)$, $\mathbf{M}_1(T)$, and

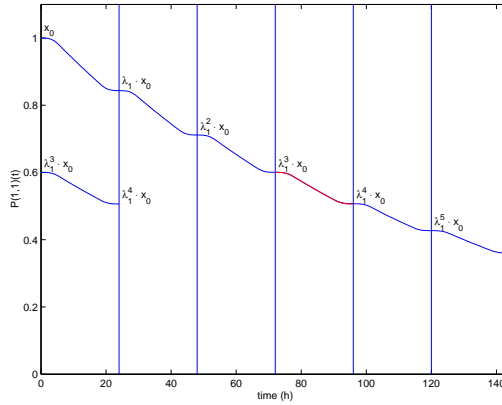


Figure E.2: An illustration that the solution to a periodic ODE can be written as a $x(t) = e^{\mu t} p(t)$, where $p(t+T) = p(t)$. This introduces a mapping of the solution at periodic times; no need for the actual shape of the periodic function $p(t)$ is needed if system is inspected at periodic times. Starting at $\lambda_1^3 x_0$ at any period, the solution will be $\lambda_1^4 x_0$ one period after.

$\mathbf{M}_2(T)$ are found through numerical integration of the system (E.1) with initial conditions $\mathbf{P}(0) = \mathbf{I}$, $\mathbf{M}_1(0) = \mathbf{0}$, and $\mathbf{M}_2(0) = \mathbf{0}$. The asymptotic behaviour of the system is determined by the stationary phase if the target set C contains phase 0. The stationary phase has a left eigenvector \mathbf{e}_0^T and a right eigenvector \mathbf{e} . If the target set does not contain phase 0, then the asymptotic behaviour is determined by the quasi-stationary distribution \mathbf{u}_1^T and its right eigenvector \mathbf{v}_1 and the eigenvalue λ_1 . We write the $\mathbf{P}(T)$ matrix according to its Jordan decomposition (see Gantmacher, 1959) as:

$$\mathbf{P}(T) = \mathbf{e}\mathbf{e}_0^T + \mathbf{v}_1\lambda_1\mathbf{u}_1^T + \mathbf{V}_2\Lambda_2\mathbf{U}_2,$$

where it turns out that \mathbf{V}_2 , \mathbf{U}_2 , and Λ_2 are not necessary to compute (see Appendix E.7 for details).

If the set of phases C contains the absorbing state it is shown in appendix E.6 that the conditional expectation and conditional variance have constants as asymptotes. These are:

$$\mathbb{E}^{x,0,0}[N_{nT}|X_{nT} \in C] = \mathbf{e}_x^T(\mathbf{I} - \mathbf{P}(T) + \mathbf{e}\mathbf{e}_0^T)^{-1}\mathbf{M}_1(T)\mathbf{e} + O(n\lambda_1^{n-1}) \quad (\text{E.5})$$

and:

$$\begin{aligned} \mathbb{V}^{x,0,0}[N_{nT}|X_{nT} \in C] &= \mathbf{e}_x^T(\mathbf{I} - \mathbf{P}(T) + \mathbf{e}\mathbf{e}_0^T)^{-1}\mathbf{M}_2(T)\mathbf{e} \\ &+ \mathbf{e}_x^T(\mathbf{I} - \mathbf{P}(T) + \mathbf{e}\mathbf{e}_0^T)^{-1}\mathbf{M}_1(T)(\mathbf{I} - \mathbf{P}(T) + \mathbf{e}\mathbf{e}_0^T)^{-1}\mathbf{M}_1(T)\mathbf{e} \\ &- (\mathbf{e}_x^T(\mathbf{I} - \mathbf{P}(T) + \mathbf{e}\mathbf{e}_0^T)^{-1}\mathbf{M}_1(T)\mathbf{e})^2 + O(n\lambda_1^{n-1}) \end{aligned} \quad (\text{E.6})$$

respectively, where $O(n\lambda^{n-1})$ denotes some function $f(n)$ which is such that $\frac{f(n)}{n\lambda^{n-1}}$ bounded by some constant when n goes to infinity.

When the set C does not contain the absorbing state, the asymptotes of the conditional mean and variance are linearly increasing each period:

$$\mathbb{E}^{x,0,0}[N_{nT}|X_{nT} \in C] = \mathbf{u}_1^T\mathbf{M}_1(T)\mathbf{v}_1 n\lambda_1^{-1} + O(1) \quad (\text{E.7})$$

and

$$\begin{aligned} \mathbb{V}^{x,0,0}[N_{nT}|X_{nT} \in C] &= \mathbf{u}_1^T\mathbf{M}_2(T)\mathbf{v}_1 \frac{n}{\lambda_1} \\ &+ 2\mathbf{v}_1\mathbf{M}_1(T)\mathbf{V}_2(\lambda_1\mathbf{I} - \Lambda_2)^{-1}\mathbf{U}_2\mathbf{M}_1(T)\mathbf{v}_1 \frac{n}{\lambda_1} \\ &- (\mathbf{u}_1\mathbf{M}_1(T)\mathbf{v}_1)^2 \frac{n}{\lambda_1^2} + O(1) \end{aligned} \quad (\text{E.8})$$

respectively.

E.4 Example 1: A planktonic organism and diel vertical migration

In many aquatic environments there is a diel vertical movement of planktonic and nektonic organisms. In the “normal” migrational pattern the organisms are deeper during the day and closer to the surface during the night. There is also a “reverse” pattern where an organism is down in the deep during the night and more close to the surface during the day. The commonly held view is that diel vertical migration (DVM) is a response of daily fluctuations in risk of predation and possibility of feeding (see Clark and Levy, 1988; Pearre, 2003). It is clear that daily fluctuations in light intensity are an integral part of the process, which can be seen from phenomena at solar eclipses (*e.g.* Backus et al., 1965).

Pearre (2003) reviews the many factors that influence the strength and type of DVM, but he claims that a central problem in the understanding of vertical migration by plankton is that few data exist on individuals, evidence is indirect where *e.g.* the timing of presence of food in guts of animals in layers where this type of food is absent indicates DVM. We believe that the same is true for fish and that electronic archival devices could be used to solve this problem. The data from these devices could be fitted to MAP models (Nielsen and Beyer, 2006).

In the following we will present a series of examples on a planktonic organism such as a copepod or a cladoceran that will illustrate some of the flexibility in

transient MAPs. The examples should only be seen as an illustration of how the periodicities that naturally occur in the environment of an organism could be incorporated in different models with increasing levels of complexity.

E.4.1 A herbivore that follows isolumes

Our simplest example is of a herbivorous zooplankter that follows an isolume, in many taxa it appears as if the vertical migration is closely tied to isolumes Pearre (2003). Here, we assume that the water column is vertically stratified, with homogenous food in the upper part of the water column and no food below this upper stratum. The food of the plankter is assumed to be equally sized, and equally profitable prey which is encountered as a Poisson process when in the upper layer. When the organism follows an isolume the rate of predation is assumed to be constant, which may a reasonable approximation if most predators are visual and the hydrodynamical signal when migrating is sufficiently weak. Hence, if the light levels were higher, *i.e.* a higher isolume were chosen then the mortality rates would be higher. It may well be that other migrating organisms arrive later in the night which could create a change in the predation rate during this period, however we have chosen to ignore this possibility.

The animal can be in two states; alive (1), or dead (0). When the migrating organism enters the food rich stratum it will start to feed, eventually it will leave the isolume, stay on approximately the same depth until it encounters higher light levels which will make it follow the corresponding isolume downwards. We assume that the depth at which it abandons the isolume is constant. The generator will be

$$\mathbf{D}_0(\tau) = \begin{bmatrix} 0 & 0 \\ \delta(\tau) & -(\delta(\tau) + \phi(\tau)) \end{bmatrix} \quad \mathbf{D}_1(\tau) = \begin{bmatrix} 0 & 0 \\ 0 & \phi(\tau) \end{bmatrix}$$

where $\phi(\tau)$ is the feeding rate, and $\delta(\tau)$ is the mortality rate. A graphical representation is seen in Figure E.3. Possible functional forms for these are given in Figure E.4.

It is interesting to note that due to its simplicity, this system is explicitly solvable, and the conditional feeding rate is equal to that of a model where no death is included. In more elaborate models the system will in most circumstances lack the structure currently known that makes it explicitly solvable (see Lukes, 1982). Given that $\Delta(\tau) = \int_0^\tau \delta(\xi) d\xi$, and $\Phi(\tau) = \int_0^\tau \phi(\xi) d\xi$, the backwards solution for $\tau < 0$ for $\mathbf{P}(\tau)$ and $\mathbf{M}_1(\tau)$ will be

$$\mathbf{P}(\tau) = \begin{bmatrix} 1 & 0 \\ 1 - e^{\Delta(\tau)} & e^{\Delta(\tau)} \end{bmatrix}$$

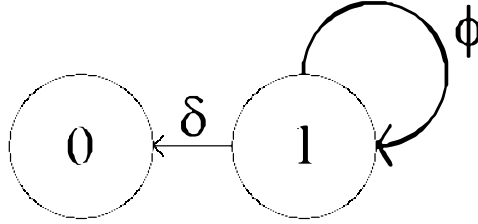


Figure E.3: The transient periodic Poisson process. Phase 0 represents that the organism is dead, phase 1 that it is alive. While alive it feeds with rate $\phi(t)$, which is indicated with a bold arrows since this generates a mark and it dies with rate $\delta(t)$.

$$\mathbf{M}_1(\tau) = \begin{bmatrix} 0 & 0 \\ e^{\Delta(\tau)}(\Phi(\tau) - \int_0^\tau \phi(\xi)e^{-\Delta(\xi)}d\xi) & -e^{\Delta(\tau)}\Phi(\tau) \end{bmatrix}$$

The model is a periodic transient Poisson process, since it is a Poisson process with parameter $|\Phi(\tau)|$ conditional on not being absorbed.

In our particular example $\Phi(T)$ is simple; let ξ be the time where $\phi(\tau)$ is non-zero during the period then $\Phi(T) = 10\xi$. In this case it is 110, the ODE-solver give a slightly higher value 110.26 (or 110.22 from the variance).

Ignoring the periodicity, this is about as simple as one can do a stochastic encounter model and it is often the level at which most encounter models are made if they are stochastic (see Hassell, 1978; Mangel and Clark, 1988). However, it is clear that many organisms are not randomly distributed in their habitat, nor do they move in such manners as to encounter prey with exponential waiting times. In some cases heterogeneity may give more variable encounters (e.g. Beyer and Nielsen, 1996), but in other cases it makes it possible to exploit a resource that would not be possible to use were it random—such as fishing for schooling fish or perhaps the situation for the fin whales off Nova Scotia.

The MAP framework allows us to produce models that can be analysed and to include e.g. spatial heterogeneity. The next example will show on a case where patchiness increases the variability in prey encounter, whereas the third example will show how the internal structure may decrease the effects of this variability on another process, egg production.

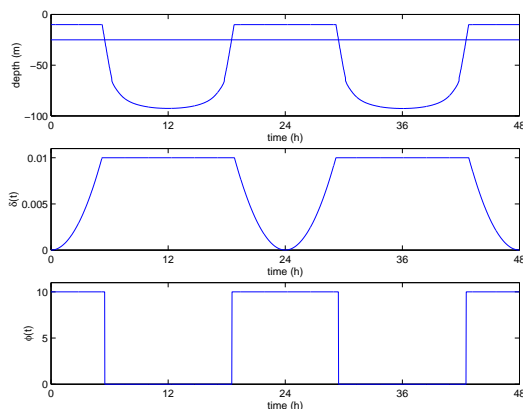


Figure E.4: Upper panel shows the depth that a planktonic organism is assumed to follow. Middle panel shows the mortality rate $\delta(t)$, and the lowest graph shows feeding rate $\phi(t)$.

E.4.2 Example 2: Inclusion of spatial variability

Suppose that the plankter is following an isolume as before but that the food is heterogenous in distribution in the upper stratum. Now we assume that the animal can be in 3 states; (1) alive not in food patch, (2) alive in food patch, and (0) dead. The patches are entered with rate $\alpha(t)$ and left with rate $\beta(t)$. This process could be called the periodic transient interrupted Poisson process. Even if this is a rather simple system it is analytically intractable in general.

Being in a food-patch is often more dangerous (see *e.g.* Lima, 1998); patches may be more easy to locate for a predator and the higher feeding rate in the patch may give stronger hydrodynamic signals and less time to avoid predators in. In order to study the effect of different predation rates in different states on the asymptotic feeding rate we assume that the predation in state (1) is $\xi \cdot \delta(t)$ and $(1 - \xi) \cdot \delta(t)$ in state (2) where $\xi \in [0, 1]$. Here and in the following we will assume that the mortality rate, $\delta(t)$, is twice the mortality rate in Example 1 such that the mortality rate will be $\delta(t)$ in each state when $\xi = \frac{1}{2}$. We let the feeding rate $\phi(t)$ is the same as in Example 1.

When the light is increasing the organism is forced to leave the feeding zone; it cannot be in a patch. The easiest solution to this is only to change the mortality rate when the isolume exits the feeding zone, but then some animals will stay in a patch during the night and so commence to feed immediately next day without having to locate a patch. We have chosen a seemingly more consistent model, where the meaning of the states is fixed, where a deterministic switch is

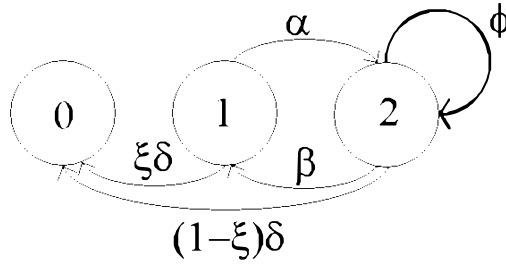


Figure E.5: A plot over the state-flow when the food is patchily distributed, state 0 corresponds to being dead, state 1 to alive but not in patch, and state 2 to alive and feeding in patch. Food items are found with rate $\phi(t)$, patches of food are entered with rate $\alpha(t)$ and left with rate $\beta(t)$. The mortality rate is $(1 - \xi)\delta(t)$ and $\xi\delta(t)$ in respectively out of the patches.

used at the time of exit from the photic zone, where all individuals will be in the out-of-patch phase immediately after exit (see appendix E.8 for details).

However introducing a switch changes the autocorrelation structure such that the number of eaten food-items during a day will be an i.i.d. stochastic variable and it introduce “well-mixing” such that the process can be viewed as a discrete renewal reward process.

For more motile organisms such as fish or whales it may be that the patches are followed even if the prey organisms are out of the patch during some period of the day; the patches may be the food of the prey and more easily detected. Here the $\alpha(t)$ and $\beta(t)$ will probably be on a much lower level. Changing ξ changes the asymptotic ingestion rate although the effect is rather slight when the mortality rates are moderate. When ξ is low i.e. it is more dangerous in the patch, then the asymptotic ingestion rate will be lower than when ξ is high. This effect is caused by being a patch during a long time will increase the risk of being dead. Consequently the survivors will have spent lesser time there than the dead and there will be a reduction in the conditional rate of feeding.

A process with non-zero elements on the diagonal of \mathbf{D}_1 only is called a Markov Modulated Poisson Process (see *e.g.* Latouche et al., 2003). These have among other things the nice property that the eigenstructure of $\mathbf{P}(T)$ is invariant to scaling of the rates in \mathbf{D}_1 . This means that multiplying \mathbf{D}_1 with a factor α will increase the rate linearly with α (and the variance as a second degree polynomial). Thus with a knowledge of the conditional mean for the living states with the same $\phi(t)$ as in Example 1 (75.9) it is easy to find out that a feeding rate of $1.5\phi(t)$ is needed to yield the same rate of ingestion as in Example 1.

E.4.3 Example 3: Including egg production

Suppose that we study the planktonic organism from Example 2 where the food is found only in patches, but now we are interested in the egg production. We assume that the egg production is dependent on some internal reserves which are reversibly allocated to egg production. When the reserves are high enough an egg or a batch of eggs is produced and the internal energy reserves decrease to a low level. The reserves are used to cover energetic needs irrespective of whether food was caught. If the energy level reach a critical lower level then the animal dies from starvation. Here we assume that the other energetic needs consume one energy unit with a constant rate m independent on which phase the organism is in. We assume that there are 10 energy levels; we order the states from 0 to 20 where state 0 means that the organism is dead, state $2k - 1$ is when the organism has energy reserves k but are not in a food-patch, and it has the same reserves and is in a patch when it is in state $2k$. After egg production the organism returns to energy level 1 (state 2). The rate of energy requirements, m , is set to 0.1, and ξ , the parameter controlling the difference in mortality between patch and non-patch, is set to 0.1.

The generators will have the following structure

$$\mathbf{D}_0 = \begin{bmatrix} 0 & \mathbf{0} & \mathbf{0} & \mathbf{0} & \cdots & \cdots & \mathbf{0} \\ \mathbf{k} + \mathbf{Me} & \mathbf{S} & \mathbf{F} & \mathbf{0} & \cdots & \cdots & \vdots \\ \mathbf{k} & \mathbf{M} & \mathbf{S} & \mathbf{F} & \ddots & \vdots & \vdots \\ \mathbf{k} & \mathbf{0} & \mathbf{M} & \mathbf{S} & \ddots & \ddots & \vdots \\ \vdots & \ddots & \ddots & \ddots & \ddots & \ddots & \vdots \\ \mathbf{k} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \cdots & \mathbf{M} & \mathbf{S} \end{bmatrix}, \quad \mathbf{D}_1 = \begin{bmatrix} 0 & \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & \mathbf{F} & \mathbf{0} & \cdots & \mathbf{0} \end{bmatrix}$$

where

$$\mathbf{k} = \begin{bmatrix} \xi\delta(t) \\ (1 - \xi)\delta(t) \end{bmatrix}, \quad \mathbf{M} = \begin{bmatrix} m & 0 \\ 0 & m \end{bmatrix}, \quad \mathbf{F} = \begin{bmatrix} 0 & 0 \\ 0 & \phi(t) \end{bmatrix},$$

and

$$\mathbf{S} = \begin{bmatrix} -(\xi\delta(t) + m + \alpha(t)) & \alpha(t) \\ \beta(t) & -((1 - \xi)\delta(t) + m + \beta(t) + \phi(t)) \end{bmatrix}.$$

Here the \mathbf{k} is the rate by which the animal dies from some external factor which does not depend on the energetic state only on whether the organism is in a foraging patch or not. The \mathbf{Me} vector is death from starvation, this occurs only in states 1 and 2. The \mathbf{M} matrix is determined by the rate by which the energetic state is reduced by one, and the \mathbf{F} matrix the corresponding increase in energetic state, except for when the proces is in the highest phase, then it

denotes a reproductive event. The matrix \mathbf{S} controls the rates by which the animal enters and exits patches of food. The feeding rate $\phi(t)$, the mortality rate $\delta(t)$, and the rates of entering and leaving patches $\alpha(t)$ respectively $\beta(t)$ are the same as in example 2.

The asymptotic rate of egg production given that the organism is alive is 6.94 and the asymptotic variance is 4.15. Had 100 internal energy levels been used the rate would have been 0.692 and the asymptotic variance 0.0416. This example shows how important the phases are; even if the subsystem of finding food is highly variable compared to a Poisson process, the system as a whole generates eggs with a rate that is much less variable than a Poisson process.

E.5 Discussion

The previous examples have shown that given a detailed knowledge of an organism in a periodic environment it is possible to construct transient Markovian arrival processes that are able to model some of the vital elements of this behaviour.

The periodic MAP can not be replaced by its average. Other than that, there is nothing really that comes as a fundamental property of being periodic. The tMAPs are state-dependent models, which can be used to model a wide range of animal behaviour. These models do not include optimality, it is assumed that they describe what animals do.

The tMAP as presented here has only one arrival at a time. There are various extensions to this; the batch Markovian arrival process (BMAP) can include arrivals of several items at a time. This could be used to model for instance birth of batches where the batches have certain probabilities, or when there are more or less distinct types of prey that have different value to the animal.

It is also possible to use Marked Markovian Arrival Processes (MMAP) (He and Neuts, 1998), these are a generalization of the MAP and the BMAP, where it is possible to include several different types of arrivals. Thus, in a MMAP it is possible to both keep track on food and egg production. In chains where there are different types of mortalities, such as Example 3 where the organism can die both of predation and by energy deficit it is possible to put a new type of marks on *e.g.* death by predation, which enables the modeller to distinguish between the two probabilities. It is also possible that some events that lead to absorption are in fact not death of the organism but that it enters a new state with different properties. Putting yet a new type of marks on these transitions will make it possible to find out the probabilities of the occurrence of such an event.

The transient IPP can be seen as a model-unit describing the fact that many

organisms have the possibility of staying (relatively safe) or feeding at the expense of increased risk. Due to the dependence on the underlying state space it is possible to model encounter rates from many different distributions which would make it possible to go one step further than the standard assumption of Poisson encounters. The influence on the variability in survival using a stomach model and non-Poissonian food arrivals is an interesting issue; especially in fisheries where the recruitment of fish is a difficult and important issue.

The ongoing development and use of archival devices that register activities of tagged animals is a promising development. There are already ambitious tagging programmes (see e.g. Block et al., 2002) where marine mammals, large fish and marine reptiles are studied. The tMAPs can be used on such data to give a detailed description of an organism which is manageable. This description can then be used on other time-scales to produce *e.g.* functional and numerical responses, perhaps diffusion approximations will also be useful. It is also possible to fit and discriminate between different models of behaviour when data from archival tags are available. These models could then be used as inputs to population-level models.

In order to derive population level properties from a system that is composed of individuals that are described by tMAPs then it is necessary to connect the individual tMAPs but it is not easy to see how this could be done since the MAPs are linear. The introduction of feedbacks, e.g. that the encounter rate with prey is decreased as the predator population grows in numbers would introduce non-linearities that makes the analysis much more difficult. Were one to consider the direct product of individual state-spaces for the population model it would in most cases be a staggering construction. A possibility could be if the individual tMAPs were dependent on the distribution of other tMAPs.

Acknowledgements

The research was supported by the SLIP research school under the Danish Network for Fisheries and Aquaculture Research (www.fishnet.dk) financed by the Danish Ministry for Food, Agriculture and Fisheries and the Danish Agricultural and Veterinary Research Council. The work is part of a larger project, 'Development of improved models of fisheries impact on marine fish stocks and ecosystems' also funded by the Danish Ministry for Food, Agriculture and Fisheries.

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E.6 Appendix A. Asymptotic analysis

The conditional mean and variance are found by first solving the system:

$$-\frac{d}{d\xi} \begin{bmatrix} \mathbf{P} \\ \mathbf{M}_1 \\ \mathbf{M}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{D}(\xi) & 0 & 0 \\ \mathbf{D}_1(\xi) & \mathbf{D}(\xi) & 0 \\ \mathbf{D}_1(\xi) & 2\mathbf{D}_1(\xi) & \mathbf{D}(\xi) \end{bmatrix} \begin{bmatrix} \mathbf{P} \\ \mathbf{M}_1 \\ \mathbf{M}_2 \end{bmatrix}$$

with $\mathbf{P}(0) = \mathbf{I}$ and $\mathbf{M}_1(0) = \mathbf{M}_2(0) = \mathbf{0}$, for $-T < \xi < 0$ (see Article B). A change of variables $t = -\xi$ enables us to get rid of the negative sign on the left side and to solve the equations for positive time.

$$\frac{d}{dt} \begin{bmatrix} \mathbf{P} \\ \mathbf{M}_1 \\ \mathbf{M}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{D}(-t) & 0 & 0 \\ \mathbf{D}_1(-t) & \mathbf{D}(-t) & 0 \\ \mathbf{D}_1(-t) & 2\mathbf{D}_1(-t) & \mathbf{D}(-t) \end{bmatrix} \begin{bmatrix} \mathbf{P} \\ \mathbf{M}_1 \\ \mathbf{M}_2 \end{bmatrix}$$

Integrating this numerically over $[0, T]$ gives $\mathbf{P}(T)$, $\mathbf{M}_1(T)$, and $\mathbf{M}_2(T)$ after which the recursion equations can be solved. If necessary the rows in $\mathbf{P}(T)$ are adjusted such that they sum to 1. The corresponding entries in $\mathbf{M}_1(T)$ and $\mathbf{M}_2(T)$ should probably be weighted according to the adjustments in $\mathbf{P}(T)$. Another option is to do a direct Eulerian ODE solution since this would retain the Markovian nature of the problem.

The solutions to the recursions are:

$$\begin{aligned}
 \mathbf{P}(nT) &= \mathbf{P}(T)^n, \\
 \mathbf{M}_1(nT) &= \sum_{i=1}^n \mathbf{P}(T)^{i-1} \mathbf{M}_1(T) \mathbf{P}(T)^{n-i} \text{ and} \\
 \mathbf{M}_2(nT) &= \sum_{i=1}^n \mathbf{P}(T)^{i-1} \mathbf{M}_2(T) \mathbf{P}(T)^{n-i} \\
 &\quad + 2 \sum_{i=1}^{n-1} \mathbf{P}(T)^{i-1} \mathbf{M}_1(T) \sum_{j=1}^{n-i} \mathbf{P}(T)^{j-1} \mathbf{M}_1(T) \mathbf{P}(T)^{n-i-j}.
 \end{aligned}$$

In the analysis of the asymptotic behaviour the following assumptions are made:

1. $\mathbf{P}(T)$ can be written as

$$[\mathbf{e} \ \mathbf{v}_1 \ \mathbf{V}_2] \begin{bmatrix} 1 & 0 & 0 \\ 0 & \lambda_1 & 0 \\ 0 & 0 & \Lambda_2 \end{bmatrix} \begin{bmatrix} \mathbf{e}_0^T \\ \mathbf{u}_1^T \\ \mathbf{U}_2 \end{bmatrix},$$

where \mathbf{e} is a column-vector with ones, \mathbf{e}_0^T a row-vector with a one in the absorbing state, \mathbf{v}_1 the right eigenvector corresponding to the quasi-stationary state and \mathbf{V}_2 a matrix of all the other right eigenvectors $\mathbf{V}_2 = [\mathbf{v}_2 | \dots | \mathbf{v}_n]$. Correspondingly, \mathbf{u}_1^T is the left quasi-stationary eigenvector and \mathbf{U}_2 a matrix with the rest of the left eigenvectors. The vectors are ortho-normalized such that:

$$\begin{bmatrix} \mathbf{e}_0^T \\ \mathbf{u}_1^T \\ \mathbf{U}_2 \end{bmatrix} [\mathbf{e} \ \mathbf{v}_1 \ \mathbf{V}_2] = \mathbf{I}$$

2. The subdominant, or quasi-stationary, eigenvalue λ_1 is unique, real and less than 1. This will be guaranteed if the transient states are communicating. Since there is only one quasi-stationary state the modulus of any eigenvalue in Λ_2 is less than λ_1 .
3. In steady state no marks are generated; $\mathbf{e}_0^T \mathbf{M}_1(T) = \mathbf{0}$, consequently are there no squared marks; $\mathbf{e}_0^T \mathbf{M}_2(T) = \mathbf{0}$.
4. The target set C is observed in the dominant or subdominant mode; $\mathbf{e}_0^T \mathbf{e}_C \neq 0$ or $\mathbf{u}_1^T \mathbf{e}_C \neq 0$.
5. The initial state x excites the subdominant mode $\mathbf{e}_x^T \mathbf{v}_1 \neq 0$.

In the asymptotic analysis we use, for notational convenience, the following symbols; $O(n^i \lambda^n)$ which denotes a class of functions such that a function $f(n)$ is a member of this class if $f(n) = n^i \lambda^n H(n)$ where $H(n)$ is bounded when $n \rightarrow \infty$. Similarly let $o(n^i \lambda^n)$ denote a class of functions where a member of the class, $g(n)$, is such that

$$\lim_{n \rightarrow \infty} \frac{g(n)}{n^i \lambda^n} \rightarrow 0.$$

It should be noted that if $|\lambda_1| > |\lambda_2|$, then any function which is $O(n^i \lambda_2^n)$ is also $o(n^i \lambda_1^n)$, for any i . Moreover, we use the following facts:

1. If $\mathbf{e}_0^T \mathbf{A} = \mathbf{0}$ for some matrix \mathbf{A} then:

$$\left(\mathbf{v}_1 \frac{1}{1 - \lambda_1} \mathbf{u}_1^T + \mathbf{V}_2 (\mathbf{I} - \Lambda_2)^{-1} \mathbf{U}_2 \right) \mathbf{A} = (\mathbf{I} - \mathbf{P}(T) + \alpha \mathbf{e} \mathbf{e}_0^T)^{-1} \mathbf{A}$$

for any non-zero $\alpha \in \mathbb{R}$ (see Article B. Where $\mathbf{P}(T) = \mathbf{e} \mathbf{e}_0 + \mathbf{v}_1 \lambda_1 \mathbf{u}_1 + \mathbf{V}_2 \Lambda_2 \mathbf{U}_2$ as above.

2. For any square matrix \mathbf{B} where 1 is not an eigenvalue:

$$\sum_{i=0}^n \mathbf{B}^i = (\mathbf{I} - \mathbf{B}^{n+1})(\mathbf{I} - \mathbf{B})^{-1} = (\mathbf{I} - \mathbf{B})^{-1}(\mathbf{I} - \mathbf{B}^{n+1}).$$

3. For any square matrix \mathbf{B} where 1 is not an eigenvalue:

$$\sum_{i=1}^n i \mathbf{B}^i = (\mathbf{I} - \mathbf{B}^{n+1})(\mathbf{I} - \mathbf{B})^{-2} - n \mathbf{B}^n (\mathbf{I} - \mathbf{B})^{-1}.$$

From the Jordan decomposition it follows that

$$\mathbf{P}(nT) = \mathbf{e} \mathbf{e}_0^T + \mathbf{v}_1 \lambda_1^n \mathbf{u}_1^T + \mathbf{V}_2 \Lambda_2^n \mathbf{U}_2.$$

Case i) $\mathbf{e}_0^T \mathbf{e}_C \neq 0$:

When $\mathbf{e}_0^T \mathbf{e}_C \neq 0$ we expand all terms in \mathbf{e} and \mathbf{e}_0^T . Then

$$\mathbf{M}_1(nT) = (\mathbf{I} - \mathbf{P}(T) + \mathbf{e} \mathbf{e}_0^T)^{-1} \mathbf{M}_1(T) \mathbf{e} \mathbf{e}_0^T + O(n \lambda_1^{n-1}),$$

where the $O(n \lambda_1^{n-1})$ term comes from the term that only contains \mathbf{v}_1 and \mathbf{u}_1 which is natural since the quasi-stationary mode is the one that vanishes with the slowest rate. Similarly,

$$\begin{aligned} \mathbf{M}_2(nT) &= (\mathbf{I} - \mathbf{P}(T) + \mathbf{e} \mathbf{e}_0^T)^{-1} \mathbf{M}_2(T) \mathbf{e} \mathbf{e}_0^T \\ &\quad + 2(\mathbf{I} - \mathbf{P}(T) + \mathbf{e} \mathbf{e}_0^T)^{-1} \mathbf{M}_1(T) (\mathbf{I} - \mathbf{P}(T) + \mathbf{e} \mathbf{e}_0^T)^{-1} \mathbf{M}_1(T) \mathbf{e} \mathbf{e}_0^T \\ &\quad + O(n^2 \lambda^{n-2}). \end{aligned}$$

Given that the initial state is $(x, 0)$ at time $t = 0$ the conditional mean is

$$\mathbb{E}^{x,0,nT}[N_0|X_0 \in C] = \mathbf{e}_x^T (\mathbf{I} - \mathbf{P}(T) + \mathbf{e}\mathbf{e}_0^T)^{-1} \mathbf{M}_1(T) \mathbf{e} + O(n\lambda_1^{n-1}).$$

The conditional variance is found to be

$$\begin{aligned} \mathbb{V}^{x,0,nT}[N_0|X_0 \in C] &= \mathbf{e}_x^T ((\mathbf{I} - \mathbf{P}(T) + \mathbf{e}\mathbf{e}_0^T)^{-1} \mathbf{M}_2(T)) \mathbf{e} \\ &+ 2\mathbf{e}_x^T (\mathbf{I} - \mathbf{P}(T) + \mathbf{e}\mathbf{e}_0^T)^{-1} \mathbf{M}_1(T) (\mathbf{I} - \mathbf{P}(T) + \mathbf{e}\mathbf{e}_0^T)^{-1} \mathbf{M}_1(T) \mathbf{e} \\ &- (\mathbf{e}_x^T (\mathbf{I} - \mathbf{P}(T) + \mathbf{e}\mathbf{e}_0^T)^{-1} \mathbf{M}_1(T) \mathbf{e})^2 + O(n\lambda_1^{n-1}). \end{aligned}$$

Case ii) $U_0 \vec{e}_B = 0$: Expanding terms with \mathbf{v}_1 and \mathbf{u}_1 gives

$$\begin{aligned} \mathbf{M}_1(nT) &= \mathbf{v}_1 \mathbf{u}_1^T \mathbf{M}_1(T) \mathbf{v}_1 \mathbf{u}_1^T n\lambda_1^{n-1} + \mathbf{v}_1 \mathbf{u}_1^T \mathbf{M}_1(T) \mathbf{V}_2 (\lambda_1 \mathbf{I} - \Lambda_2)^{-1} \mathbf{U}_2 \lambda_1^n \\ &+ \mathbf{V}_2 (\lambda_1 \mathbf{I} - \Lambda_2)^{-1} \mathbf{U}_2 \mathbf{M}_1(T) \mathbf{v}_1 \mathbf{u}_1^T \lambda_1^n + o(\lambda_1) \end{aligned}$$

We find that as $t \rightarrow \infty$:

$$\mathbb{E}^{x,0,t}[N_0|X_0 \in C] = (\mathbf{u}_1^T \mathbf{M}_1(T) \mathbf{v}_1) n\lambda_1^{-1} + O(1).$$

And the conditional variance is:

$$\begin{aligned} \mathbb{V}^{x,0,t}[N_0|X_0 \in C] &= (\mathbf{u}_1^T \mathbf{M}_2(T) \mathbf{v}_1) \frac{n}{\lambda_1} \\ &+ 2\mathbf{u}_1^T \mathbf{M}_1(T) \mathbf{V}_2 (\lambda_1 \mathbf{I} - \Lambda_2)^{-1} \mathbf{U}_2 \mathbf{M}_1(T) \mathbf{v}_1 \frac{n}{\lambda_1} \\ &- (\mathbf{u}_1^T \mathbf{M}_1(T) \mathbf{v}_1)^2 \frac{n}{\lambda_1^2} + O(1). \end{aligned}$$

E.7 Appendix B. Numerical implementation

When λ_1, \mathbf{v}_1 and \mathbf{u}_1 are identified it may be useful to note that:

$$\mathbf{V}_2 (\lambda_1 \mathbf{I} - \Lambda_2)^{-1} \mathbf{U}_2 = (\lambda_1 \mathbf{I} - \mathbf{P}(T) + \alpha \mathbf{v}_1 \mathbf{u}_1^T)^{-1} (\mathbf{I} - \mathbf{v}_1 \mathbf{u}_1^T) - \mathbf{e} \frac{1}{\lambda_1 - 1} \mathbf{e}_0^T$$

for any non-zero α , which does not require a knowledge of the rest of the eigenstructure.

For very large systems for instance ARPACK (Lehoucq et al., 1998) could be used to identify some of the largest eigenvalues. To avoid numerical noise it may be useful to identify the eigenvalues of $\mathbf{P}(T) - \mathbf{e}\mathbf{e}_0^T$ since the numerical identification of λ_0 will introduce some numerical noise which may give rise to a very small complex part on the eigenstructure of λ_1 which is unnecessary since we know the stationary state.

It is also advised to adjust the rows in $\mathbf{P}(T)$ so that they sum to 1.

E.8 Appendix C. Introducing a switch

Suppose that we have a fixed time $\tau_0 < 0$ at which there is a deterministic (or probabilistic) instantaneous reshuffling of the process. For instance, we could perhaps like to set the probability of being in a certain set of states to 0 after some time τ_0 .

It is clear that:

$$\begin{aligned}\mathbf{P}(0, t + \xi) &= \mathbf{P}(t, t + \xi)\mathbf{P}(0, t) \\ \mathbf{M}_1(0, t + \xi) &= \mathbf{P}(t, t + \xi)\mathbf{M}_1(0, t) + \mathbf{M}_1(t, t + \xi)\mathbf{P}(0, t) \\ \mathbf{M}_2(0, t + \xi) &= \mathbf{P}(t, t + \xi)\mathbf{M}_2(0, t) + 2\mathbf{M}_1(t, t + \xi)\mathbf{M}_1(0, t) + \mathbf{M}_2(t, t + \xi)\mathbf{P}(0, t)\end{aligned}$$

Let \mathbf{A} be the transition matrix for $\mathbf{P}(\tau^+, \tau^-)$. Then, since this is such a short time step, where no counts are generated, we find that:

$$\begin{aligned}\mathbf{P}(0, \tau^-) &= \mathbf{A}\mathbf{P}(0, \tau^+) \\ \mathbf{M}_1(0, \tau^-) &= \mathbf{A}\mathbf{M}_1(0, \tau^+) \\ \mathbf{M}_2(0, \tau^-) &= \mathbf{A}\mathbf{M}_2(0, \tau^+)\end{aligned}$$

If the reshuffling is deterministic then the matrix \mathbf{A} have only one entry per row which is 1, this corresponds to $\mathbb{P}(X_{\tau^+} = i | X_{\tau^-} = j) = \delta_{x,j}(i)$; there is a deterministic change from state j to state x . It is of course possible to assign probabilities for the transition to different states.

E.9 Appendix D. Generation of T-translated solutions

We have that $\mathbf{P}(t + T) = \mathbf{P}(t)\mathbf{P}(T)$.

Let $\mathbf{P}(t)$ be the solution to $\dot{\mathbf{P}}(t) = \mathbf{D}(t)\mathbf{P}(t)$ where $\mathbf{D}(t + T) = \mathbf{D}(t)$ for all t , with initial condition $\mathbf{P}(0) = \mathbf{I}$.

Then $\mathbf{P}(t) = e^{\int_0^t \mathbf{D}(\tau) d\tau}$. Using the fact that $\mathbf{D}(t + T) = \mathbf{D}(t)$ we see that:

$$\begin{aligned}\mathbf{P}(T + t) &= e^{\int_0^T \mathbf{D}(\tau) d\tau + \int_T^{T+t} \mathbf{D}(\tau) d\tau} = e^{\int_0^T \mathbf{D}(\tau) d\tau + \int_0^t \mathbf{D}(\xi + T) d\xi} \\ &= e^{\int_0^t \mathbf{D}(\xi) d\xi} e^{\int_0^T \mathbf{D}(\tau) d\tau} = \mathbf{P}(t)\mathbf{P}(T)\end{aligned}$$

Note. One could be lead to the erroneous conclusion that $\mathbf{P}(t + T) = \mathbf{P}(T)\mathbf{P}(t)$ that is not true since $\int_0^t \mathbf{D}(\xi) d\xi$ and $\int_0^T \mathbf{D}(\tau) d\tau$ do not commute (if $\mathbf{A}\mathbf{B} \neq \mathbf{B}\mathbf{A}$ for two quadratic matrices \mathbf{A} and \mathbf{B} then $e^{\mathbf{A}+\mathbf{B}} = e^{\mathbf{A}}e^{\mathbf{B}} \neq e^{\mathbf{B}}e^{\mathbf{A}} = e^{\mathbf{A}+\mathbf{B}}$). This could perhaps be more easily seen by solving $\dot{\mathbf{P}}(t) = \mathbf{D}(t)\mathbf{P}(t)$ subject to the initial condition $\mathbf{P}(T)$. Then $\mathbf{P}(t + T) = e^{\int_T^{T+t} \mathbf{D}(\tau) d\tau} \mathbf{P}(T) = \mathbf{P}(t)\mathbf{P}(T)$.

We have that $\mathbf{M}_1(t+T) = \mathbf{M}_1(t)\mathbf{P}(T) + \mathbf{P}(t)\mathbf{M}_1(T)$.

Let $\mathbf{M}_1(t)$ be the solution to $\dot{\mathbf{M}}_1(t) = \mathbf{D}(t)\mathbf{M}_1(t) + \mathbf{D}_1(t)\mathbf{P}(t)$ where $\mathbf{D}(t+T) = \mathbf{D}(t)$ and $\mathbf{D}_1(t+T) = \mathbf{D}_1(t)$ for all t , with initial condition $\mathbf{M}_1(0) = \mathbf{0}$.

Then $\mathbf{M}_1(t) = e^{\int_0^t D(\tau)d\tau} \int_0^t e^{-\int_0^\xi D(\tau)d\tau} \mathbf{D}_1(\xi) e^{\int_0^\xi D(\tau)d\tau} d\xi$. Solving the differential equation from T gives:

$$\begin{aligned} \mathbf{M}_1(T+t) &= e^{\int_T^{T+t} D(\tau)d\tau} \mathbf{M}_1(T) \\ &\quad + e^{\int_T^{T+t} D(\tau)d\tau} \int_T^{T+t} e^{-\int_T^\xi D(\tau)d\tau} \mathbf{D}_1(\xi) e^{\int_T^\xi D(\tau)d\tau} \mathbf{P}(T) d\xi \\ &= \mathbf{P}(t)\mathbf{M}_1(T) \\ &\quad + e^{\int_0^t D(\tau)d\tau} \int_0^t e^{-\int_T^{\zeta+T} D(\tau)d\tau} \mathbf{D}_1(\zeta+T) e^{\int_T^{\zeta+T} D(\tau)d\tau} d\zeta \mathbf{P}(T) \\ &= \mathbf{P}(t)\mathbf{M}_1(T) + \mathbf{M}_1(t)\mathbf{P}(T). \end{aligned}$$

We have that $\mathbf{M}_2(t+T) = \mathbf{M}_2(t)\mathbf{P}(T) + 2\mathbf{M}_1(t)\mathbf{M}_1(T) + \mathbf{P}(t)\mathbf{M}_2(T)$.

Let $\mathbf{M}_2(t)$ be the solution to $\dot{\mathbf{M}}_2(t) = \mathbf{D}(t)\mathbf{M}_2(t) + 2\mathbf{D}_1(t)\mathbf{M}_1(t) + \mathbf{D}_1(t)\mathbf{P}(t)$, where $\mathbf{D}(t+T) = \mathbf{D}(t)$ and $\mathbf{D}_1(t+T) = \mathbf{D}_1(t)$ for all t , with initial condition $\mathbf{M}_2(0) = \mathbf{0}$.

Then $\mathbf{M}_2(t) = e^{\int_0^t D(\tau)d\tau} \int_0^t e^{-\int_0^\xi D(\tau)d\tau} (2\mathbf{D}_1(\xi)\mathbf{M}_1(\xi) + \mathbf{D}_1(\xi)\mathbf{P}(\xi)) d\xi$. Solving the differential equation from T gives:

$$\begin{aligned} \mathbf{M}_2(T+t) &= \mathbf{P}(t)\mathbf{M}_2(T) \\ &\quad + e^{\int_T^{T+t} D(\tau)d\tau} \int_T^{T+t} e^{-\int_T^\xi D(\tau)d\tau} (2\mathbf{D}_1(\tau)\mathbf{M}_1(\xi) + \mathbf{D}_1(\xi)\mathbf{P}(\xi)) d\xi \\ &= \mathbf{P}(t)\mathbf{M}_2(T) \\ &\quad + e^{\int_0^t D(\tau)d\tau} \int_0^t e^{-\int_T^{\zeta+T} D(\tau)d\tau} (2\mathbf{D}_1(\zeta+T)\mathbf{M}_1(\zeta+T) \\ &\quad\quad + \mathbf{D}_1(\zeta+T)\mathbf{P}(\zeta+T)) d\zeta \\ &= \mathbf{P}(t)\mathbf{M}_2(T) + 2\mathbf{M}_1(t)\mathbf{M}_1(T) + \mathbf{M}_2(t)\mathbf{P}(T). \end{aligned}$$

E.10 Appendix E. Solutions to recursions by induction

We have $\mathbf{P}(nT+T) = \mathbf{P}(nT)\mathbf{P}(T)$ for $n \geq 1$, where $\mathbf{P}(T)$ is given. Then $\mathbf{P}(2T) = \mathbf{P}(T)\mathbf{P}(T) = \mathbf{P}(T)^2$.

Assume that $\mathbf{P}(nT) = \mathbf{P}(T)^n$.

Then $\mathbf{P}(nT + T) = \mathbf{P}(nT)\mathbf{P}(T) = \mathbf{P}(T)^n\mathbf{P}(T) = \mathbf{P}(T)^{n+1}$. Hence

$$\mathbf{P}(nT) = \mathbf{P}(T)^n \quad \forall n \geq 1$$

We have that $\mathbf{M}_1(nT + T) = \mathbf{M}_1(nT)\mathbf{P}(T) + \mathbf{P}(nT)\mathbf{M}_1(T)$ for $n \geq 1$ and $\mathbf{M}_1(T)$ given. Then

$$\mathbf{M}_1(2T) = \mathbf{M}_1(T)\mathbf{P}(T) + \mathbf{P}(T)\mathbf{M}_1(T) = \sum_{i=1}^2 \mathbf{P}(T)^{i-1}\mathbf{M}_1(T)\mathbf{P}(T)^{2-i}$$

Assume that $\mathbf{M}_1(nT) = \sum_{i=1}^n \mathbf{P}(T)^{i-1}\mathbf{M}_1(T)\mathbf{P}(T)^{n-i}$.

Then

$$\begin{aligned} \mathbf{M}_1(nT + T) &= \mathbf{M}_1(nT)\mathbf{P}(T) + \mathbf{P}(nT)\mathbf{M}_1(T) \\ &= \sum_{i=1}^n \mathbf{P}(T)^{i-1}\mathbf{M}_1(T)\mathbf{P}(T)^{n+1-i} + \mathbf{P}(T)^n\mathbf{M}_1(T) \\ &= \sum_{i=1}^{n+1} \mathbf{P}(T)^{i-1}\mathbf{M}_1(T)\mathbf{P}(T)^{n+1-i} \end{aligned}$$

Thus,

$$\mathbf{M}_1(nT) = \sum_{i=1}^n \mathbf{P}(T)^{i-1}\mathbf{M}_1(T)\mathbf{P}(T)^{n-i} \quad \forall n \geq 1$$

Lemma. For matrices \mathbf{A} and \mathbf{B} and integers n greater than one we have:

$$\begin{aligned} \sum_{i=1}^n \mathbf{A}^{i-1}\mathbf{B} \sum_{j=1}^{n+1-i} \mathbf{A}^{j-1}\mathbf{B}\mathbf{A}^{n+1-i-j} = \\ \sum_{i=1}^{n-1} \mathbf{A}^{i-1}\mathbf{B} \sum_{j=1}^{n-i} \mathbf{A}^{j-1}\mathbf{B}\mathbf{A}^{n+1-i-j} + \sum_{i=1}^n \mathbf{A}^{i-1}\mathbf{B}\mathbf{A}^{n-i} \end{aligned}$$

Proof.

$$\begin{aligned} \sum_{i=1}^n \mathbf{A}^{i-1}\mathbf{B} \sum_{j=1}^{n+1-i} \mathbf{A}^{j-1}\mathbf{B}\mathbf{A}^{n+1-i-j} = \\ \sum_{i=1}^{n-1} \mathbf{A}^{i-1}\mathbf{B} \sum_{j=1}^{n+1-i} \mathbf{A}^{j-1}\mathbf{B}\mathbf{A}^{n+1-i-j} (\mathbf{1}_{\{j=n+1-i\}} + \mathbf{1}_{\{j < n+1-i\}}) + \mathbf{A}^{n-1}\mathbf{B}\mathbf{B} \\ = \sum_{i=1}^{n-1} \mathbf{A}^{i-1}\mathbf{B} \sum_{j=1}^{n-i} \mathbf{A}^{j-1}\mathbf{B}\mathbf{A}^{n+1-i-j} + \sum_{i=1}^n \mathbf{A}^{i-1}\mathbf{B}\mathbf{A}^{n-i} \end{aligned}$$

QED.

We have that $\mathbf{M}_2(nT + T) = \mathbf{M}_2(nT)\mathbf{P}(T) + \mathbf{P}(nT)\mathbf{M}_2(T) + 2\mathbf{M}_1(nT)\mathbf{M}_1(T)$ for $n \geq 1$ and $\mathbf{M}_2(T)$ given. Then

$$\begin{aligned} \mathbf{M}_2(2T) &= \mathbf{M}_2(T)\mathbf{P}(T) + \mathbf{P}(T)\mathbf{M}_2(T) + 2\mathbf{M}_1(T)\mathbf{M}_1(T) \\ &= \sum_{i=1}^2 \mathbf{P}(T)^{i-1}\mathbf{M}_2(T)\mathbf{P}(T)^{2-i} \\ &\quad + 2 \sum_{i=1}^1 \mathbf{P}(T)^{i-1}\mathbf{M}_1(T) \sum_{j=1}^{2-i} \mathbf{P}(T)^{j-1}\mathbf{M}_1(T)\mathbf{P}(T)^{2-i-j} \end{aligned}$$

Assume that

$$\begin{aligned} \mathbf{M}_2(nT) &= \sum_{i=1}^n \mathbf{P}(T)^{i-1}\mathbf{M}_2(T)\mathbf{P}(T)^{n-i} \\ &\quad + 2 \sum_{i=1}^{n-1} \mathbf{P}(T)^{i-1}\mathbf{M}_1(T) \sum_{j=1}^{n-i} \mathbf{P}(T)^{j-1}\mathbf{M}_1(T)\mathbf{P}(T)^{n-i-j} \end{aligned}$$

Then

$$\begin{aligned} \mathbf{M}_2(nT + T) &= \mathbf{M}_2(nT)\mathbf{P}(T) + \mathbf{P}(nT)\mathbf{M}_2(T) + 2\mathbf{M}_1(nT)\mathbf{M}_1(T) \\ &= \sum_{i=1}^{n+1} \mathbf{P}(T)^{i-1}\mathbf{M}_2(T)\mathbf{P}(T)^{n+1-i} \\ &\quad + 2 \sum_{i=1}^{n+1} \mathbf{P}(T)^{i-1}\mathbf{M}_1(T)\mathbf{P}(T)^{n+1-i}\mathbf{M}_1(T) \\ &\quad + 2 \sum_{i=1}^n \mathbf{P}(T)^{i-1}\mathbf{M}_1(T) \sum_{j=1}^{n-i} \mathbf{P}(T)^{j-1}\mathbf{M}_1(T)\mathbf{P}(T)^{n+1-i-j} \\ &= \sum_{i=1}^{n+1} \mathbf{P}(T)^{i-1}\mathbf{M}_2(T)\mathbf{P}(T)^{n+1-i} \\ &\quad + 2 \sum_{i=1}^n \mathbf{P}(T)^{i-1}\mathbf{M}_1(T) \sum_{j=1}^{n+1-i} \mathbf{P}(T)^{j-1}\mathbf{M}_1(T)\mathbf{P}(T)^{n+1-i-j}. \end{aligned}$$

where the lemma is used to get the last equality. Consequently the expression for $\mathbf{M}_2(nT)$ is true for all n greater than zero.

Note. The interpretation of the expressions for $\mathbf{M}_1(nT)$ and $\mathbf{M}_2(T)$ are quite simple. $\mathbf{M}_1(nT)$ is the sum of the n different sequences of length n that have one occurrence of $\mathbf{M}_1(T)$ and the rest are $\mathbf{P}(T)$ s. $\mathbf{M}_2(nT)$ have one part which

is exactly corresponding to the $\mathbf{M}_1(nT)$; which are the n different sequences with exactly one $\mathbf{M}_2(T)$ and the rest are $\mathbf{P}(T)$ s. The other part are the $\binom{n}{2}$ sequences which exactly two $\mathbf{M}_1(T)$ occurrences and all the $n - 2$ positions are filled with $\mathbf{P}(T)$ s.

This makes the proof for the formula for $\mathbf{M}_2(nT + T)$ easy to understand. The sum containing the $\mathbf{M}_1(T)$ terms are just the sequences of length n with exactly two occurrences of $\mathbf{M}_1(T)$ with a $\mathbf{P}(T)$ padded on the right PLUS the sequences of length n with exactly one occurrence of $\mathbf{M}_1(T)$ with a $\mathbf{M}_1(T)$ padded on the right; this generates all the different sequences with exactly two occurrences of $\mathbf{M}_1(T)$ of length $n + 1$.

APPENDIX F

Stomachs as stochastic dams

Technical report.

Stomachs as stochastic dams L. A. Fredrik Nilsson^{a,*},

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Abstract

In many, and in particular marine, ecosystems it is difficult to observe the interaction of organisms with their prey. Stomach analysis is often the only information available on what prey they eat, their consumption rate and to some extent the periodicities of feeding and the feeding preferences. These types of information are vital for the performance of multi-species population assessments, and to human exploitation of fish. Thus, good models for stomachs are needed in order to maximize the information obtained by extensive stomach sampling.

This technical report concerns the modelling of stomachs as a stochastic dam. The work is based on a recent article by Bekker et al. (2004) where new results on the stationary behaviour of stochastic dams are presented and another where the stomach contents of whiting is described by an infinite stochastic dam Thygesen et al. (2005).

The report contains a brief review of different types of stomach models, then a presentation of developments of Bekker et al. (2004) and Thygesen et al. (2005). The analytical solution to a stationary infinite dam i.e. a dam with no upper limit on food contents with exponentially distributed meal sizes and a release rate that depends on the square-root of the total contents is presented. Then a relatively intractable solution to the same dam with Erlang-2 distributed meal sizes is shown and attempts to solve for stomachs with fixed meal sizes analytically. The reason for these endeavours is that there were some hope that if either of these results were available one could obtain results for the class of Erlang- n , $n \in \mathbb{N}$, distributed meal sizes. In the end there are some comments on numerical issues and a brief discussion on the inverse problem: given a stomach size distribution what is the meal size distribution?

F.1 Introduction

Animal guts are interesting since they provide information on what and how much the specific animal is eating. A good model and the state of the ingested meal makes it possible to obtain information on when the food was caught.

Using sampling programmes it is possible to describe how the diet varies over some time period in relation to the “available” food. Basic facts, such as the evacuation rate of the gut and the speed of deterioration of an individual prey item must be obtained by controlled experiments. With ancillary data one could use stomachs as archival devices that tell us when, what, how often and how much a certain animal eat. Beyer (1998) presents the historical background on stomach sampling programmes in fisheries science and states that with the introduction of multispecies models the need for this type of data have increased.

There are many ways to model stomachs. In a review Yearsley et al. (2001) states that in animal science the idea of ‘eating to requirements’ have been very successful for intensive farming of domestic animals. The assumption underlying this model that the food intake is determined by an animal’s protein deposition requirements when food is unlimiting. It is very uncertain if it this model is applicable in the wild. For ecological systems, Yearsley et al. (2001) state that digestion part have been modelled using compartment models or gut-reactor models. While equivalent in principle the compartment models are more empirical whereas gut-reactor models are based on biologically detailed description.

It is common with large variations in gut contents, probably due to the stochastic nature of encounter and other factors. This variation makes it necessary to model the contents as a stochastic process. There are many different approaches to this; e.g. Magnússon and Aspelund (1997) modelled the intake rate and meal size of capellin using a compound Poisson process, Beyer (1998) modelled the stomach content of whiting using a renewal reward process. Hall et al. (1995) modelled a finite stomach without satiation effects in a stochastic dam approach with linear evacuation rate.

The focus in present work is on the modelling of stomachs in a way that is equivalent to the stochastic modelling of dams. Let the gut contents at time t be denoted by V_t then, given that there is something in the stomach, the contents is evacuated deterministically with a rate $r(V_t)$ in the absence of new food arriving. New food arrives with a rate $\lambda(t, V_t)$ i.e. the arrival rate can depend both on time and gut contents. The latter enables us to model satiation effects. This type of model have been used in the modelling of dams (see references in Bekker et al., 2004). To my knowledge Hall et al. (1995) initiated the work on stochastic dam–stomachs using a linear evacuation rate and a finite stomach; they estimated the parameters of the model for a data set by visual fitting.

In a recent article Thygesen et al. (2005) provide a time-dependent solution to a stomach–dam with periodically varying arrival rates and a rate of evacuation that depends on the square-root of the stomach contents. They estimate the parameters of the periodic arrival rate, a satiation parameter, and the meal-size distribution, which is assumed to be log-normal, based on a real data set. Their dam is not finite, but they include satiation effects in the arrival rate and all results are obtained numerically.

Bekker et al. (2004) study the stationary behaviour of queues, or dams, with workload dependent arrival and service rates. They provide criteria for when there is an atom in 0, and prove congruence properties of two independent queues where the quotients between release rates and arrival rates of the respective queue are equal; this make it possible to prove results for classes of queues. They also provide results for general and independent arrival processes. Using Palm theory they are able to link the results from the time-stationary queue to the event-stationary queue and to reprove some results obtained from the queues with state-dependent Poisson arrivals.

This report has the purpose of presenting the results for the square-root stomach with a Poisson arrival process, and to present some ideas on numerical issues. The inverse problem will also be treated briefly and some further developments discussed.

F.2 Model formulation

Here I present some background to the modelling of stomachs in fish, where particularly good information exists on whiting, a close relative to cod. Then these considerations are put into a stochastic dam model of stomachs of fishes not to dissimilar to whiting.

F.2.1 Evacuation rates

There is no consensus on how to choose the deterministic evacuation rates for fish. The main choices are linear, square-root, exponential, or surface dependent. There are evidence in favour for each of them, but the detailed study of Andersen (1998) indicated that the square-root should be chosen for whiting. Thus, in the absence of new food arriving the dynamics of the total stomach contents can be written as:

$$\dot{V}_t = -RL^p \sqrt{V_t},$$

where L is the length of the whiting, while R and p are parameters. Thygesen et al. (2005) use a normalized stomach content such that $\tilde{V}_t = \frac{V_t}{L^{2p}}$ which removes the need for length.

Generally, the evacuation rate $r(x)$ has to be a strictly positive function (right continuous with left limits) for $x > 0$, have a strictly positive limit, and $r(0) = 0$ (Bekker et al., 2004).

The models that are studied here will have an evacuation rate, with $r(x) = \kappa\sqrt{x}$, where κ is constant.

F.2.2 The arrival rate

Thygesen et al. (2005) model the arrival rate $\lambda(x, t)$ as the product of a periodic function and an exponential damping due to satiation.

Bekker et al. (2004) allow the arrival rate to depend on stomach contents, but their analysis is stationary, independent on t .

In this report the arrival rate is assumed to be constant, since analytical formulas for the stationary problem is the main focus and the major difficulty introduced is to have other meal size distributions than exponentially distributed meals.

F.2.3 The meal size distribution

Let $B(x, t)$ be the probability of obtaining a meal of less than or equal to x at time t , let the corresponding density be $b(x, t)$ and its mean β . Typical choices are meal sizes from a log-normal distribution or a gamma distribution. Sometimes these are truncated at some maximum stomach size, which is a crude way to incorporate satiation effects.

F.2.4 The dynamical model

Bekker et al. (2004) derive the steady-state equation for the stomach using level-crossing arguments under the assumption that the queue is ergodic and a stationary distribution exists. To prevent drift to infinity they provide a criterion which has to be fulfilled; the mean meal size β , the encounter rate $\lambda(x)$ and the evacuation rate $r(x)$ have to satisfy that the $\limsup_{x \rightarrow \infty} \frac{\beta\lambda(x)}{r(x)} < 1$.

Let $F(x, t|v) = \mathbb{P}\{V_t \leq x | V_0 = v\}$ then the PASTA (Poisson Arrivals See Time Averages (see e.g. Wolff, 1989)) property of Markovian queues is used to arrive at the following partial-integro-differential equation which is a minor generalization of (Gaver and Miller, 1962):

$$\frac{\partial}{\partial t} F(x, t) = r(x, t) \frac{\partial}{\partial x} F(x, t) - \int_0^x \lambda(y, t) (1 - B(x - y, t)) d_y F(y, t), \quad (\text{F.1})$$

where $d_y F(y, t)$ denotes a Lebesgue-Stieltjes integration; if there is a jump in the cdf this will correspond to a point measure. The stationary workload satisfies:

$$r(x) \frac{\partial}{\partial x} F(x) = \int_0^x \lambda(y, t) (1 - B(x - y, t)) d_y F(y). \quad (\text{F.2})$$

Thygesen et al. (2005) arrive at the essentially the same equation, the difference is that they work with pdfs instead of cdfs, where they use that the square-root

model has an atom in 0. The corresponding equation for the densities $f(x, t)$ is then

$$\begin{aligned}\frac{\partial f}{\partial t}(0, t) &= \lim_{x \rightarrow 0^+} (\kappa\sqrt{x}f(x, t)) - \lambda(0, t) \cdot f(0, t) \\ \frac{\partial f}{\partial t}(x, t) &= \frac{\partial}{\partial x} (\kappa\sqrt{x}f(x, t)) - \lambda(x, t) \cdot f(x, t) \\ &\quad + \int_{0^+}^x \lambda(v, t)b(x-v)f(v, t)dv \\ &\quad + \lambda(0, t)b(x)f(0, t) \quad \text{for } x > 0.\end{aligned}$$

F.3 Solution for the stationary distribution for a square-root model

It is convenient to have analytical solutions to check if the numerical schemes work well. Here I present one analytical solution to the square-root stomach with exponential meal sizes, and attempts to solve for Erlang-2 or deterministic meal sizes, since then it could have been possible to use results from Asmussen et al. (2002) to get the stationary distribution for all Erlang distributions.

Bekker et al. (2004) provide a result for when there is an atom in 0. They define

$$R(x, z) := \int_z^x \frac{1}{r(y)} dy, \quad 0 \leq z < x < \infty,$$

to represent the time to move from state x to z in the absence of arrivals. Particularly interesting is $R(x, 0) := R(x)$ the time to drain the workload x if no arrivals. A related quantity is

$$\tilde{R}(x, z) := \int_z^x \frac{\lambda(y)}{r(y)} dy, \quad 0 \leq z < x < \infty.$$

In particular $\tilde{R}(x) := \tilde{R}(x, 0)$ determines whether or not the workload has an atom at 0. If $\tilde{R}(x) < \infty$ for all $0 < x < \infty$ then there is an atom in 0, otherwise 0 cannot be reached by the workload process. If there is an atom in zero the cumulative density function can be written

$$F(x) = \begin{cases} F_0 & \text{if } x = 0 \\ F_0 + \int_{0^+}^x f(\xi) d\xi & \text{for } x > 0 \end{cases}$$

The stomach is positive recurrent if and only if

$$a := \int_0^\infty f(x) dx < \infty.$$

If $F(0) = 0$ then the pdf $f(x)$ is normalized by multiplication with α^{-1} , otherwise if $F(0) > 0$ then

$$\lim_{x \rightarrow 0+} r(x)f(x) = \lambda F(0).$$

For the square-root stomach with constant arrival rate and a finite meal size we have that $\limsup_{x \rightarrow \infty} \frac{\lambda}{\beta \kappa \sqrt{x}} = 0$, and that $\tilde{R}(x) < \infty$ for all $x : 0 < x < \infty$; we have an atom at 0.

F.3.1 Exponentially distributed meal sizes

We assume an exponential distribution of the workload with mean $\frac{1}{\mu}$. Here we have from Equation F.2 that

$$r(x)f(x) = \lambda F(0)e^{-\mu x} + \int_{0+}^x \lambda f(y)e^{-\mu(x-y)} dy.$$

Writing $g(x) := r(x)f(x)e^{\mu x}$ we get:

$$g(x) = \lambda F(0) + \int_{0+}^x \frac{\lambda}{r(y)} g(y) dy.$$

This is a Volterra equation of the second kind and can be solved using a Neumann kernel. But it is so simple that it can be solved by differentiation. Solving the ensuing ODE gives; $g(x) = Ce^{\frac{2\lambda}{\kappa}\sqrt{x}}$. Thus $f(x) = \frac{C}{\kappa\sqrt{x}}e^{-\mu x + \frac{2\lambda}{\kappa}\sqrt{x}}$. From the conditions above it is clear that there is an atom in 0 and the dam is positive recurrent; one finds that:

$$f(x) = \frac{\lambda F(0)}{\kappa\sqrt{x}} e^{-\mu x + \frac{2\lambda}{\kappa}\sqrt{x}}.$$

Then

$$F(0) = \frac{1}{1 + \int_0^\infty \frac{f(x)}{F(0)} dx} = \frac{1}{1 + \sqrt{\frac{\pi}{\mu}} \frac{2\lambda}{\kappa} e^{\frac{\lambda^2}{\mu\kappa^2}} \Phi\left(\frac{\lambda}{\kappa} \sqrt{\frac{2}{\mu}}\right)},$$

where $\Phi(x)$ is the cdf for a standard normal variable and the solution is complete. For an illustration of the probability density function see Figure F.1.

F.3.2 A solution for the Erlang-2 distribution

Here we have $B(x) = 1 - e^{-\mu x} - \mu x e^{-\mu x}$. Iterating to find a solution, which is what the Neumann kernel does infinitely many times starting with $g_0(x) = 0$,

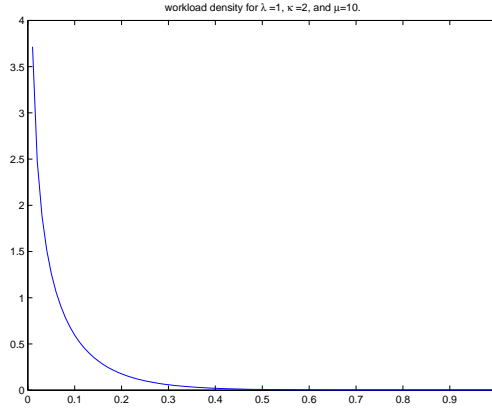


Figure F.1: The stationary distribution of stomach contents for a square-root stomach model with $\kappa = 2$, $\lambda = 1$ and exponentially distributed meal-size with mean $\mu^{-1} = 10^{-1}$.

using the recursion $g_i(x) = \lambda F(0)B^c(x) + \int_{0+}^x \frac{\lambda}{r(y)}B^c(x-y)g_{i-1}(y) dy$ to find $g_\infty(x) = \lambda F(0)(1 + \mu x)e^{-\mu x} + \int_{0+}^x \frac{\lambda}{r(y)}(1 + \mu(x-y))e^{-\mu(x-y)}g_\infty(y) dy$ gives:

$$\begin{aligned}
 g_0(x) &= 0; \\
 g_1(x) &= \lambda V_0(1 + \mu x)e^{-\mu x} \\
 g_2(x) &= \lambda V_0 e^{-\mu x} \left(1 + \frac{2\lambda}{\kappa} x^{1/2} + \mu x + \frac{2\lambda}{\kappa} \mu x^{3/2} + \frac{2\lambda}{\kappa} \frac{2}{15} \mu^2 x^{5/2} \right) \\
 g_3(x) &= \lambda V_0 e^{-\mu x} \left(1 + \frac{2\lambda}{\kappa} x^{1/2} + \left(\mu + \frac{2\lambda^2}{\kappa^2} \right) x + \frac{2\lambda}{\kappa} \mu x^{3/2} + \frac{2\lambda^2}{\kappa^2} \mu x^2 \right. \\
 &\quad \left. + \frac{4\lambda}{15\kappa} \mu^2 x^{5/2} + \frac{19\lambda^2}{45\kappa^2} \mu^2 x^3 + \frac{\lambda^2}{45\kappa^2} \mu^3 x^4 \right) \\
 g_4(x) &= \lambda V_0 e^{-\mu x} \left(1 + \frac{2\lambda}{\kappa} x^{1/2} + \left(\mu + \frac{2\lambda^2}{\kappa^2} \right) x + \left(\frac{2\mu\lambda}{\kappa} + \frac{4\lambda^3}{3\kappa^3} \right) x^{3/2} \right. \\
 &\quad \left. + \frac{2\mu\lambda^2}{\kappa^2} x^2 + \left(\frac{4\mu^2\lambda}{15\kappa} + \frac{4\mu\lambda^3}{3\kappa^3} \right) x^{5/2} + \frac{22\lambda^3\mu^2}{63\kappa^3} x^{7/2} \right. \\
 &\quad \left. + \frac{19\lambda^2\mu^2}{45\kappa^2} x^4 + \frac{2\lambda^3\mu^2}{63\kappa^3} x^{9/2} + \frac{4\lambda^3\mu^4}{4455\kappa^3} x^{11/2} \right)
 \end{aligned}$$

There is no obvious structure in this, but some will emerge in what follows.

Differentiating the integral equation twice gives a second order ODE:

$$\frac{d^2 g}{dx^2} - \frac{\lambda}{\kappa\sqrt{x}} \frac{dg}{dx} + \frac{\frac{1}{2x} - \mu}{\kappa\sqrt{x}} \lambda g(x) = 0,$$

where $g(x) = r(x)f(x)e^{\mu x}$ as above and the initial conditions $g(0) = \lambda F_0$ and $\lim_{x \rightarrow 0^+} \text{sqr}t x \frac{d}{dx}(g'(x)\sqrt{x}) = \frac{\lambda^2 F_0}{\kappa} + \lambda F_0 \mu$. This solution was found using Maple, when the initial conditions were included the solution covers several pages. Maple was not able to solve the ODE for $f(x)$.

$$g(x) = e^{\frac{\lambda\sqrt{x}}{\kappa}} \cdot (C_1((\lambda^2 + 8\mu\kappa\lambda\sqrt{x} + 16\mu^2\kappa^2x) {}_0F_1(\cdot, \frac{5}{3}, \xi) + 8\kappa^2\mu {}_0F_1(\cdot, \frac{2}{3}, \xi)) + C_2((\frac{\lambda^3}{64} + \frac{3\mu\sqrt{x}\kappa\lambda^2}{16} + \frac{3\mu^2\kappa^2\lambda x}{4} + \mu^3\kappa^3x^{3/2})\lambda {}_0F_1(\cdot, \frac{7}{3}, \xi) + \frac{\kappa^2\mu}{3}(\frac{\lambda^2}{4} + \mu\kappa\lambda\sqrt{x} + 4\kappa^2\mu) {}_0F_1(\cdot, \frac{4}{3}, \xi))),$$

where $\xi = \frac{\lambda(\lambda+4\mu\kappa\sqrt{x})^3}{144\mu^2\kappa^4}$. The ${}_0F_1(\cdot, a, x)$ is called the confluent hypergeometric limit function, it can be expressed as:

$${}_0F_1(\cdot, a, x) = \sum_{n=0}^{\infty} \frac{1}{(a)_n n!} x^n,$$

where $(a)_n = a \cdot (a + 1) \dots (a + n - 1)$. It can be expressed as a Bessel function (see e.g. Petkovsek et al., 1996, p. 38):

$$J_n(x) = \frac{(\frac{1}{2}x)^n}{n!} {}_0F_1(\cdot, n + 1, -\frac{1}{4}x^2)$$

but this does not simplify the expression for $g(x)$. One would rather like to see the function that is related to ${}_0F_1(\cdot, n + 1, -\frac{1}{4}x^3)$ and there does not seem to be such a (known) function.

The constants C_1 and C_2 are determined from the initial conditions

$$g(0) = \lambda F(0) \quad \text{and} \quad \lim_{x \rightarrow 0^+} \sqrt{x} \frac{d}{dx}(2g'(x)\sqrt{x}) = \frac{\lambda^3 F(0)}{\kappa^2} + \lambda \mu F(0).$$

However, in order to evaluate $F(0)$ one has to integrate this ugly expression from 0^+ to infinity!

F.3.2.1 Another attempt

We have the equation

$$g(x) = \lambda V_0(1 + \mu x) + \int_{0^+}^x \frac{\lambda}{\kappa\sqrt{y}} (1 + \mu(x - y)) g(y) dy$$

where $g(x) := \kappa\sqrt{x}f(x)e^{\mu x}$. Using the ansatz $g(x) = \sum_{i=0}^{\infty} b_i x^{i/2}$ and that $\frac{\lambda}{\kappa} \int_0^x y^{\frac{n-1}{2}} dy = \frac{\lambda}{\kappa} \frac{2}{n+1} x^{\frac{n+1}{2}}$ and $\frac{\lambda\mu}{\kappa} \int_0^x (x-y)y^{\frac{n-1}{2}} dy = \frac{4\lambda\mu}{\kappa} \frac{1}{(n+1)(n+3)} x^{\frac{n+3}{2}}$ gives:

$$\begin{aligned} b_0 + b_1 x^{\frac{1}{2}} + b_2 x^2 + \dots + b_n x^{\frac{n}{2}} + \dots = \\ \lambda F_0 (1 + \mu x) + \frac{2\lambda}{\kappa} \left(b_0 x^{\frac{1}{2}} + \frac{1}{2} b_1 x + \frac{1}{3} b_2 x^{\frac{3}{2}} + \dots + \frac{1}{n} b_{n-1} x^{\frac{n}{2}} + \dots \right) \\ + \frac{4\lambda\mu}{\kappa} \left(\frac{1}{3} b_0 x^{\frac{3}{2}} + \frac{1}{4 \cdot 2} b_1 x^2 + \dots + \frac{1}{n \cdot (n-2)} b_{n-3} x^{\frac{n}{2}} + \dots \right) \end{aligned}$$

Identifying coefficients of equal powers gives:

$$\begin{aligned} b_0 &= \lambda F_0 \\ b_1 &= \frac{2\lambda}{\kappa} b_0 \\ b_2 &= \frac{2\lambda}{2\kappa} b_1 + \lambda F_0 \mu \\ b_3 &= \frac{2\lambda}{3\kappa} b_2 + \frac{4\lambda\mu}{\kappa} \frac{1}{3} b_0 \\ &\vdots \\ b_n &= \frac{2\lambda}{n\kappa} b_{n-1} + \frac{4\lambda\mu}{\kappa} \frac{1}{n \cdot (n-2)} b_{n-3} \end{aligned}$$

This is a neat recursion formula but it is not easily solved analytically. If μ were 0 there is obviously an $\exp \frac{2\lambda}{\kappa} \sqrt{x}$ term. The solution from Maple with hyperexponential formulas gives an $\exp \frac{\lambda}{\kappa} \sqrt{x}$ term times a sum of four hyperexponential functions. The ansatz $g(x) := e^{\frac{\lambda}{\kappa} \sqrt{x}} \sum b_i x^{\frac{i}{2}}$ gives awkward recursions.

Trying generating functions, $B(z) := \sum_{i=0}^{\infty} b_i z^i$ gives a differential equation:

$$\frac{1}{z} B''(z) - \left(\frac{\kappa + 2\lambda z}{\kappa z^2} \right) B'(z) + (1 - 2\mu z^2) \frac{2\lambda}{\kappa z^2} B(z) = 0$$

with initial conditions from above. (Interestingly $b_1 = \frac{2\lambda}{\kappa} b_0$ is redundant). The general solution is (surprise):

$$\begin{aligned} B(z) &= -C1 \left(\left(\frac{1}{4} \lambda + \mu z \kappa \right)^2 {}_0F_1 \left(\frac{5}{3}, \frac{\lambda (\lambda + 4\mu z \kappa)^3}{\mu^2 \kappa^4 144} \right) \right. \\ &\quad \left. + \frac{1}{2} {}_0F_1 \left(\frac{2}{3}, \frac{\lambda (\lambda + 4\mu z \kappa)^3}{\mu^2 \kappa^4 144} \right) \mu \kappa^2 \right) e^{\frac{\lambda z}{\kappa}} \\ &\quad + -C2 e^{\frac{\lambda z}{\kappa}} \left(\left(\frac{1}{4} \lambda + \mu z \kappa \right)^3 \lambda {}_0F_1 \left(\frac{7}{3}, \frac{\lambda (\lambda + 4\mu z \kappa)^3}{144 \mu^2 \kappa^4} \right) \right. \\ &\quad \left. + {}_0F_1 \left(\frac{4}{3}, \frac{\lambda (\lambda + 4\mu z \kappa)^3}{144 \mu^2 \kappa^4} \right) \kappa^2 \left(\frac{1}{4} \lambda^2 + \lambda \mu z \kappa + \mu \kappa^2 \right) \mu \right) \end{aligned}$$

This is the same solution obtained before, where $g(z) = B(\sqrt{z})$. Which is rather obvious with hindsight, since this is just to make the variable change $\sqrt{z} \rightarrow z$ in a very cumbersome way. The solution is terrifying when the initial conditions are included; it covers several pages.

Since $\frac{d}{dx} {}_0F_1(\cdot, a, x) = {}_0F_1(\cdot, a + 1, x)$, obviously there is some structure in the pair of hypergeometric functions for each constant.

The problem remains to be tough, to say the least, since it is necessary to calculate F_0 from $F_0 + \int_0^\infty \frac{B(\sqrt{z})}{\kappa\sqrt{z}} e^{-\mu z} dz = 1$.

An approximate way of moving forward is to write

$$f_0(x) = b_0 \kappa^{-1} x^{-1/2} e^{-\mu x}$$

and to continue with

$$f_i(x) = \left(\sum_{k=0}^{i-1} b_k x^{k/2} \right) \kappa^{-1} x^{-1/2} e^{-\mu x}$$

which would give quite simple formulas for the normalization of F_0 ! Since $\int_0^\infty x^{n/2} e^{-\mu x} dx = \mu^{-(1+n/2)} \Gamma(n/2 + 1)$ and using the standard formulas for the Gamma-function.

F.3.3 Deterministic meal size

Another possibility to get through would be to find the solution for the deterministic meal size. Using the Picard iteration one finds that:

$$\begin{aligned} g_0(x) &= 0 \\ g_1(x) &= \lambda V_0 (1 - \Theta(x - x_s)) \\ g_2(x) &= \lambda V_0 \left(1 + \frac{2\lambda}{\kappa} \sqrt{x} \right) (1 - \Theta(x - x_s)) \\ &\quad + \frac{2\lambda^2 V_0}{\kappa} (\sqrt{x_s} - \sqrt{x - x_s}) (\Theta(x - x_s) - \Theta(x - 2x_s)) \\ g_3(x) &= \lambda V_0 \left(1 + \frac{2\lambda}{\kappa} \sqrt{x} + \frac{2\lambda^2}{\kappa^2} x \right) (1 - \Theta(x - x_s)) \\ &\quad + \frac{2\lambda^2 V_0}{\kappa} (\sqrt{x_s} - \sqrt{x - x_s} + \frac{\lambda}{\kappa} (2x_s - x)) (\Theta(x - x_s) - \Theta(x - 2x_s)) \\ g_4(x) &= \lambda V_0 \left(1 + \frac{2\lambda}{\kappa} \sqrt{x} + \frac{2\lambda^2}{\kappa^2} x + \frac{4\lambda^3}{3\kappa^3} x^{3/2} \right) (1 - \Theta(x - x_s)) \end{aligned}$$

If one tries to differentiate the integral equation one finds that:

$$\frac{d}{dx} f(x) = -\lambda V_0 \delta(x - x_s) + \frac{\lambda}{r(x)} f(x) - \frac{\lambda}{r(x - x_s)} f(x - x_s)$$

A delay-differential equation; these are more tricky to solve than ODEs, but this one has a structure that $f(x) = 0$ when $x < 0$. It is easy to solve for $0 \leq x \leq x_s$ but then in the next period one finds an integral $\int_{x_s}^x \frac{\lambda}{\kappa \sqrt{y-x_s}} e^{\frac{2\lambda}{\kappa}(\sqrt{y-x_s}-\sqrt{y})} dy$ which seems to be analytically unsolvable.

The solution for the first period is $\lambda V_0 e^{\frac{2\lambda}{\kappa}\sqrt{x}}$ which has the series expansion seen in the Picard iteration above.

The attempt to solve:

$$r'(x)v(x) + r(x)v'(x) = -\lambda V_0 \delta(x - x_s) + \lambda v(x) - \lambda v(x - x_s)$$

gave the solution $v(x) = \frac{\lambda V_0}{\kappa} x^{-\frac{1}{2}} e^{\frac{2\lambda}{\kappa}\sqrt{x}}$ for $0 \leq x \leq x_s$. But in the next step one gets the same type of integral to solve as in the $f(x)$ formulation.

F.3.4 New version

Using the ansatz $g(x) = \lambda V_0 e^{\frac{2\lambda\sqrt{x}}{\kappa}} (1 - \Theta(x - x_s) + \sum_{i=0}^{\infty} a_i x^i (\Theta(x - x_s) + \Theta(x - 2x_s) + b(x)(\Theta(x - 2x_s) - \Theta(x - 3x_s)) + \dots$ gives for $x_s \leq x < 2x_s$ that

$$a(x) = \lambda V_0 (e^{\frac{2\lambda}{\kappa}\sqrt{x}} - e^{\frac{2\lambda\sqrt{x-x_s}}{\kappa}}) + a_0 \cdot (\sqrt{x} - \sqrt{x-x_s}) + a_1 (x^{3/2} - (x-x_s)^{3/2}) + \dots$$

which does not conform to the basis (easily, could perhaps do some matching with Taylor expansions, but looks intractable). Using the basis $a(x) = \sum_i a_i x^{\frac{i}{2}}$ gives arcsinh functions. Thus does not seem to be an alternative since the basis is not closed. The only value of this attempt is that it shows that the solution at x_s^+ is $\lambda V_0 (e^{\frac{2\lambda\sqrt{x_s}}{\kappa}} - 1)$.

F.4 Numerical issues

F.4.1 The time-dependent problem

Thygesen et al. (2005) used a regular (in squared coordinates to remove the weak singularity at 0 (see Press et al., 1992)) finite-volume discretization in stomach content, and then a “method of lines”-solution; a time-dependent problem only $\dot{p}(t) = A(t)p(t)$, where $p(t)$ is a vector of probabilities of being in a node and $A(t)$ a updating matrix, which corresponded to a Markov model in their first approximation. They reported problems with numerical accuracy and stiffness. The order of the numerical scheme was estimated using refined meshes. They solved the problems using higher order approximations (non-Markovian) in stomach content, solving the time-dependent problem with a Runge-Kutta integrator until a periodic solution was obtained (since the encounter rate with prey was periodic).

In a review Shaw and Whiteman (1997) advocated the use of adaptive Galerkin methods for classes of similar partial integro-differential equations. Galerkin methods have the benefit of being able to provide a priori error estimates that tells us whether the present grid-size is sufficient for the solution to meet our requirements. Sometimes it is possible to obtain a posteriori error estimates, which tells us how close the numerical approximation is to the true solution. The latter can be used for adaptive mesh generation, using the equidistribution property of error, i.e. the mesh is refined at those points where the error is largest (see Johnson).

There are a number of developments (for more advanced IDEs) that could be useful in the optimization of numerical solution schemes. In some cases using Richardson interpolation it is possible to obtain super-convergence to the solution even for Galerkin methods (Lin et al., 2000).

There is a lot of additional structure, in particular to the cdf-formulation of the finite stomach problem that one could benefit from. Since one knows that the $F(x, t) \leq 1$ for all t and x . Since there is only a finite stomach there is an x_{max} which limits the x domain. Furthermore, $F(x, t)$ is non-decreasing, and one knows from the stationary analysis of (Bekker et al., 2004) when to expect an atom at 0. Choudhury et al. (1994) solved the time-dependent workload evolution for the $M/G/1$ queue using Laplace transforms; these techniques could possibly be used in this context too.

A probabilistic equivalent to the adaptive grid problem would be to distribute the grid points such that the probability of being in any such point would be equal, except for the grid-point that denotes the atom. The equidistribution of error would in this case be equidistribution of probability mass.

F.4.2 The time-stationary problem

For this class of problems there is both the standard Volterra integral technique in the case of an atom in zero where the solution can be found using Picard iteration techniques, i.e. one starts with $v_0(x) = 0$. Then $v_1 = \lambda(x)V_0G(x)$, then inserting one finds $v_2(x) = \lambda V_0G(x) + \int_0^x \lambda(y)G(x-y)v_1(y) dy$.¹ I tried a numerical variation of this, an example is shown for the deterministic meal size times the evacuation rate $f(x)r(x)$ with a comparison of the exact second Picard iteration in red see fig(F.2). Another possibility is to use ODE-solvers that include options for Volterra IE (Press et al., 1992). A third option is to solve an approximate Markov chain for the stationary distribution see fig(F.3) for the deterministic case.

For time-stationary problems that do not have an atom in 0, singular Volterra

¹A Maple script for solving the Volterra IE of the second kind written by Thomas Schramm is available at <http://www.adeptscience.co.uk/maplearticles/f298.html>

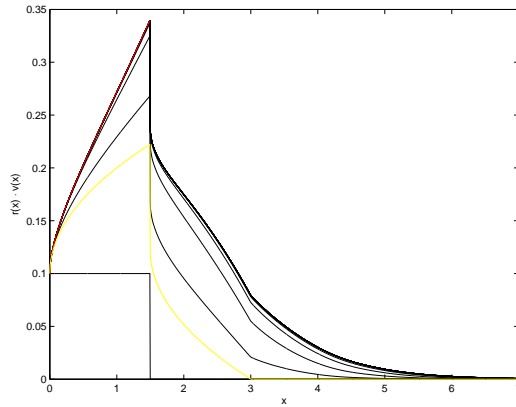


Figure F.2: The stationary distribution of stomach contents times evacuation rate for a stomach model with deterministic meal size with mean 1.5 and $\kappa = 2$, $\lambda = 1$. The analytic solution to the second Picard iteration and the exact solution for the interval $[0, x_s]$ are shown in yellow respectively red. Based on 20 iterations and continuous linear basis functions.

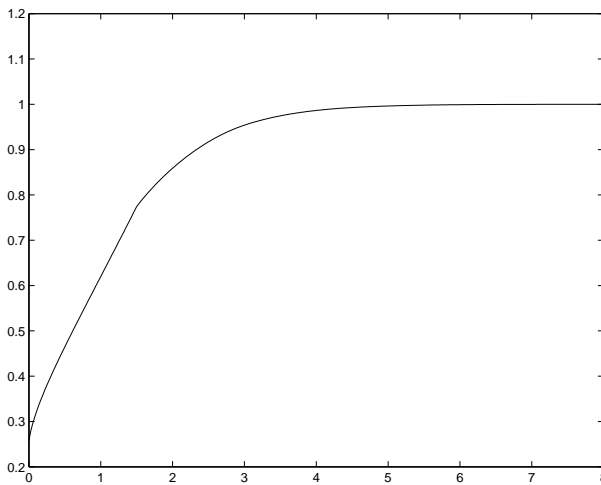


Figure F.3: The stationary cumulative distribution of stomach contents times evacuation rate for a stomach model with deterministic meal size with mean 1.5 and $\kappa = 2$, $\lambda = 1$.

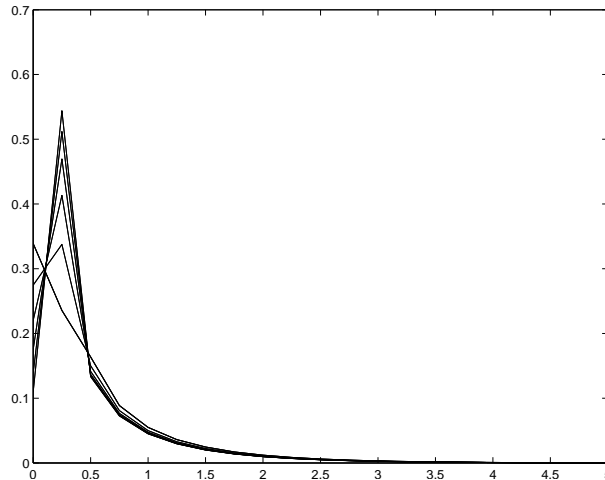


Figure F.4: The stationary distribution of stomach contents for a stomach model with $r(x) = 2x$, $\lambda = 0.7$ and $Exp(1)$ distributed meals; the solutions are for 20, 40, 80, 160, 320, 640 grid-points, but the probabilities are lumped for comparison.

equations may occur, these are much more difficult to solve (see Bekker et al., 2004). But from a queueing perspective this should not be too difficult, it is just to simulate and estimate the stationary distribution here the domain is $(0, x_{max}]$. For instance the infinite dam with constant arrival rate and a release rate, $r(x)$ that is κx is not solvable using the Neumann kernel. Using a non-transformed uniform grid the solution seems to converge, see fig(F.4). Using the simple discretization scheme in Thygesen et al. (2005) is possible to verify the solution for the square-root queue (using a non-transformed coordinate system; transforming will probably improve solutions since a uniform grid in transformed system will give more weight to positions close to 0), see Figure F.5.

F.4.3 The inverse problem

Given that we know the stomach size-distribution $f(x)$ what can we say about the meal size distribution?

For a simple example where the answer is known: Suppose that the emptying rate was constant with rate 1 and that the workload density where $v(x) = (1 - \rho)\delta(t) + \rho(\mu - \lambda)e^{-(\mu - \lambda)x}$, where $\rho = \frac{\lambda}{\mu} < 1$. Then we would like to find

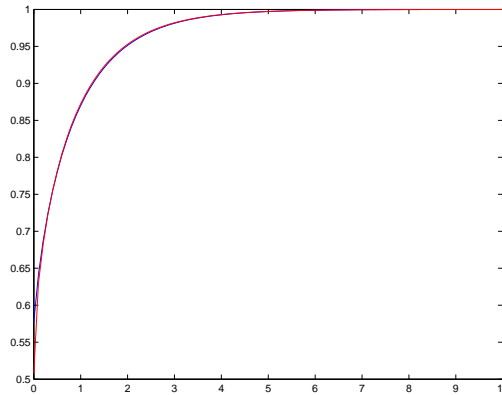


Figure F.5: The stationary cumulative probability distribution of stomach contents for a square-root-stomach model with exponential meal size with mean 1 and arrival rate of 0.7, κ is equal to 2. Red is the true distribution and blue is numerical; 100 grid points were used. Note the initial discrepancy, the Markov chain estimate of empty queue is 0.578 whereas the true value is 0.508.

the meal size distribution. We have for $x > 0$:

$$v(x) = \lambda V_0 G(x) + \lambda \int_{0+}^x G(x-y)v(y) dy \quad (\text{F.3})$$

Denote the Laplace transform for $v(x) : x > 0$ with $V^+(s)$. Laplace transforming Equation F.3 gives

$$\begin{aligned} V^+(s) &= \lambda(1-\rho)G(s) + \lambda G(s)V^+(s) \\ \frac{\mu-\lambda}{s+\mu-\lambda} &= \lambda \left((1-\rho) + \rho \frac{\mu-\lambda}{s+\mu-\lambda} \right) G(s) \end{aligned}$$

Solving for $G(s)$ gives $G(s) = \frac{1}{s+\mu}$ which correspond to an exponential $G(x) = e^{-\mu x}$ in the time-domain. This is natural this is the survival function of an exponential distribution; it is the $M/M/1$ -queue.

F.4.3.1 The square-root problem

Taking the Laplace transforms we find that:

$$R(s) * F^+(s) = \lambda F(0)G(s) + \lambda G(s)F^+(s)$$

in principle it should be possible to invert $G(s) = \frac{R * F^+}{\lambda(F(0) + F^+)}$ using the techniques reviewed in Abate et al. (1999). Here $R * F^+(s) = \frac{1}{2\pi} \int_{-\infty}^{\infty} R(\zeta) F^+(s - \zeta) d\zeta$ is the convolution in the Laplace plane. When the stomach distribution is estimated it may be a much more difficult problem. Interestingly, the technique of Choudhury et al. (1994) may work for the time-dependent problem too, since they were able to solve the time-dependent behaviour of a $M/G/1$ queue.

F.5 Discussion

It may be necessary to distinguish between digestion and gut evacuation. For instance, Thygesen et al. (2005) assume that the stomach fullness determines the satiation. The subsequent fate of the food in the lower digestive tract may have an effect on satiation. This would be quite easy to include with the addition another dam in sequence. Jeschke et al. (2002) have argued, based on empirical evidence, that most animals are digestion limited. Hence their functional response includes a rudimentary stomach model as a controlling process. Clearly satiation or digestion is important in shaping the predator-prey interaction.

In Rindorf and Lewy (2004) it is stated (with reference to Andersen (2001)) that the energy contents of prey determine how fast they are evacuated. Fat fish are evacuated more slowly than lean fish, crabs are slower than other invertebrates (non-shelled presumably). These considerations are of course important and it would be interesting to study a fluid-queue or dam that includes different types of food. Also, if there are interactions between food types such that a cod that have eaten a particular prey type, such as crabs, will tend to continue to eat crab due to physiological constraints or not. The physiological processes that determine this could be the lack of specific nutrients, activation of enzyme systems or that the presence of shell in the digestive apparatus will make pursuit of fish impossible for long.

Possible developments could be to include patchiness in food encounter which would increase the variability. If the encounter process were an IPP instead of a Poisson process, it would be quite simple to formulate this as a dam. The sampling programmes may have to be very extensive in order to ensure the identifiability of the parameters. The details of enzyme excretion are also worth to mention as a complication. If a whiting contains a herring that has digested for some time and it consumes yet another herring then the former herring will digest faster than the square-root model and the later will digest slower than the square-root model (Beyer, pers. comm.). But the digestion rate of food matter in the stomach will follow the square-root model. Thus it is more difficult than expected to back-calculate the food ingestion time on the level of food items. From an optimal perspective it is also interesting to know the cost of enzyme production and its mechanisms. Could one understand the distribution of empty

stomachs using optimal foraging theory?

This article assumes that there are no satiation effects. In practice this may not be a problem, since it is possible to include a cut-off in the encounter rate as a function of stomach contents. Another possibility is to use a finite dam. Finite dams of water have long been modelled. Here, the event of a too big rain will just lead to overflow of excess water. This is probably not a good model for fish—if there is no room in the stomach then the chewing apparatus may not be able to just ingest what fills the stomach. Hall et al. (1995) have an interesting solution, they specify the arrival process as the arrival rate of items of a certain size. Could one make this work in a backwards sense to estimate the arrival rate of the prey spectrum this would be very interesting biologically to compare with the expected encounter rate based on the estimated densities of prey and some model for their movement speed.

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