Discussion items for MPM errors paper

# Introduction

1. [LGF:] I like this Intro, reasonably short and to the point!

# Section 2, Challenges in MPM construction

1. “did Caswell coin this phrase?]” [“birth-pulse”]
   1. [LGF:] I guess, Hal will hardly be offended if you ask him about it.
   2. [BK:] This actually appears to be Caughly (1967) – ms has been updated.
2. "we will focus on this case [birth-pulse] in our analysis"
   1. [MF:] We just do not deal with the "birth-pulse" and "birth-flow" issues in this paper. For example, the lionfish is clearly a birth flow population. I suspect many of the examples in the database exhibit birth flow.
   2. BK: I agree that we don’t deal with birth-flow. I think I introduced it in the context of explaining some of the sources of confusion. We can move it to the Discussion where we discuss the sources of the errors.
   3. BK: Should we also add a Discussion section on “other MPM construction errors?” What else, besides innapropriate birth-pulse, should we include? BTW, does your paper from last year have anything to say about the effects of such an error?
   4. MF: The paper published last year focuses on the conversion of age structured model into stage structured model. It deals with the error in calculating transition rate (our issue #2.3). We basically ignored the error associated with fertility because we decided to focus on it in the next paper.
3. "This requires a variety of mathematical approximations to suitably transform continuous-time processes into a discrete-time representation, and gives a different view of the identity of individuals in a particular age or stage class. "
   1. [MF:] I think this is a bit ambiguous. Do you want to say different "age-identity" of individuals in a particular class? First, I thought you are talking about the identity as in a longitudinal study.
   2. [LGF] different from what ?
   3. [BK:] I think this whole sentence will disappear when we move the birth-flow issue to the discussion.
4. "MPMs assume that the population at time $t$ is a snapshot at a particular "census date." "
   1. [MF:] I think this is the most important sentence. I prefer beginning the section with this sentence. A population vector is equivalent to a static life table.
   2. [BK:] It might be worth starting with the cohort life table (e.g., Table 1), and then talking about how the MPM attempts to represent the life table, as a simple overview to MPM construction. In a sense, this may be all that we need in the intro to section 2.
   3. [BK:] The term “static life table” seems to have two meanings. In ecology it refers to a snapshot of the population distribution at a particular time. But in human demography, it is used as a synonym to the period life table, the age-specific survival probabilities at a given moment in time (<https://en.wikipedia.org/wiki/Life_table>), which doesn’t include information on age-specific relative abundances. Note that the period life table and the cohort life table will have identical age-specific survival rates if the environment is constant.
   4. [MF:] I think it makes sense. The “static life table” and “period life table” are equivalent in a sense that they are based on the survivorship estimated from the snapshot of the population distribution. It is also what we incorporate into MPM.
5. [MF:]I think the paragraphs before 2.1 will need to be simplified in the final version. It is a bit heavy to begin with. Perhaps, it is ok for now.
   1. [BK:] I think that moving some of the sources of errors to the discussion will help. And see my reply to the previous comment.
6. 2.1. Ensuring that the fertility transition spans a full timestep
   1. [LGF:] As I (and other non-English readers) can understand English grammar, the *fertility transition* is equivalent to the *transition of fertility,* which is absolutely wrong in this context.
   2. [BK:] Perhaps the solution (following Caswell) is to call the matrix elements “coefficients”.
7. [RSG:] Include lx in discussion of life table
   1. [BK:] I am not averse to this, although the lx terms are only used to construct the Px terms. I’m also not sure that lx is meaningful in a stage structured representation. Masami, do you have thoughts? If we do this, then my preferences would be to define Px = l\_{x+1}/l\_x for both pre- and post-breeding census models (contra Caswell eq. 2.40), so that we use P\_0 for newborn survival. (and yes, we are using sigma rather than P) [MF:] I think this is fine with me.
   2. [BK:] Regarding notation: I noticed that in your recent paper you used s\_x (for age structure) and S\_x (for stage structure) to denote survival. Should we use that instead? I only used sigma because that’s what Caswell uses in the stage-structured models.
   3. [MF:] I do NOT suggest following my notation. My choice of symbols is not consistent with anything because I quit following symbols in any particular subjects. My papers get reviewed by statistician, theoretical ecologists, fishery biologists, etc. No matter what symbol I use, I am criticized!
8. “survival (often denoted $P\_x$ (most common, but has a different meaning in stage-structured models), $s\_x$, or $\sigma\_x$, where $x$ is the age or stage; we will use $\sigma\_x$)”
   1. [LGF:] This [“age or stage”] is a bit confusing after contrasting these two formalisms in the previous paragraphs. May be, it's a right place to articulate that *stage* can be understood in a *generalised sense*, so that the *age* is a particular case of *stage* ?
   2. [LGF:] Could you please avoid the hierarchical brackets ?
   3. [BK:] I’m thinking that we may want to use different notation for age and stage structure, as in F&D-L. Masami, do you have an opinion on this (I assume you’d be in favor)?
   4. [MF:] I am fine whatever you decide to do. Perhaps, we could use sigma and s are survival probability for age and stage structured model, and P and G for elements of stage structured population matrices. Again, this is just a suggestion, and I do not have any strong preference.
9. "the first age class represents all individuals between zero and one timestep old at time $t$"
   1. [MF:] Before we begin talking about "age", we need to define it. We just need to state that the age in this paper begins when parent produces their offspring, which could be egg or live birth.
   2. I think you are just thinking about terrestrial vertebrate studies here. In other discipline, age may be defined differently. For example, in fisheries, age can be age from the recruitment. For salmon, there could be two ages (river age and ocean age). For egg-laying organisms, age could be from hatching (not from the time of parents laying eggs).
   3. I believe one of the major confusion among fish biologists is that age in MPM and age in recruitment models are defined differently.
   4. [BK:] I’m happy to define age as counting from egg laying [or hatching] or birth. And this will be easy if we skip the discussion of birth-flow models.
10. "Age-structured models follow a convention that makes sense for a continuously breeding species"
    1. [MF:]I think the main issue is that researchers mistakenly think the subscript in the Leslie matrix is an age. Numbers used in subscripts are simply showing the location in a matrix and vector. Because there is no 0th element, there is no "0" in subscript. I think it may be easier for researchers dissociate age and subscript rather than think about how age and subscript are associated.
    2. [BK:] Sure, and by moving all this to the discussion it will be easier to deal with there. But my general philosophy is that it is less confusing to use subscripts that have biological meaning (actual age, or an abbreviation of the stage name) rather than indices, for the quantities inside the matrix or vector. Thus I’m happy to say for a post-breeding census model. I admit that this is trickier for age-structured vectors, as “n\_1” could represent the first element of the vector or the number of one-year-olds (which won’t be the same in a post-breeding census model). But since we don’t actually use the population vector in the present paper I don’t think we need to solve that problem.
    3. [MF:] As long as we clearly define age and subscript, I do not have any objection.

# Section 2.2. Matching the age at first reproduction to the species’ life history

1. “age at [reproductive] maturity."
   1. [MF:]I think maturity is not necessarily equivalent to reproduction. we could define maturity as the state of individuals that potentially allow them to reproduce in the next reproductive season. We can simply reduce the duration in the pre-mature stage especially if survival rate changes one time-step before the first reproduction.
   2. [BK:] Regardless of how we define the term “maturity,” we still have the issue that in many post-breeding census models the age of first reproduction in the model is one timestep later than in the described life history. This occurs even in Leslie models. That is, if x is the lowest age with a non-zero mx, which I would interpret as first reproduction just on their x birthday (which is what the continuous age m(x) would mean), then using F\_{x-1} = 0 and F\_x = s\_x \* m\_x gives first reproduction at age “almost x+1” rather than age x
   3. [MF:] This is an issue of how organisms change survival relative to when organisms start reproducing. If organisms change survival one time step before reproduction, then we can simply reduce the time step of pre-mature stage by one from your model. Then, the first reproduction is still at age x without letting pre-mature stage to reproduce. The model you described is needed if the survival rate changes immediately after the reproduction. However, we probably do not have to get into this issue in this paper. The main point of the paper is to make sure that the duration between the birth and the average time to the first reproduction needs to be incorporated correctly, and we present one way to do it.
2. " Embracing this transition [to assigning age to beginning of timestep]"
   1. [MF:]This is one way (common way) of handling the problem. However, another way is to reduce the duration of juvenile stage. The reduction in the duration has a problem that the last juvenile stage has the same survival as adults. But it is a reasonable assumption in many cases (I would argue a majority of cases). The problem with letting juveniles to reproduce is that it will effectively decrease the time to reproduction. I expect it to have an impact (e.g. damping ratio and generation time) on organisms with delayed maturation. You may decide whether we discuss these issues or not, but I prefer writing in a way that the model with juvenile reproducing is ONE of the ways to handle the problem of adjusting the time of first reproduction.
   2. [BK:] Your alternative works, and for things like fish it goes a little bit of the way toward ameliorating the problem of non-constant demography within a stage. But I don’t think it is *better* than the standard solution at solving the non-intuitiveness of post-breeding models, it just creates a different set of challenges, as I describe in the comments below. I prefer the standard solution, in part because it is standard and is in the textbooks, and in part because it can be explained as an accounting trick rather than relying on a potentially deep philosophical discussion of the differences between models and “reality” (the latter is of course important, but I think it would be a distraction in this paper).
   3. [BK:] So my preference would be to stick with the standard approach in the main text (but can mention that there are others). If you like we can add a paragraph about your preferred approach in the discussion. Do you have experience suggesting that your approach is more easily understood than the standard one?
   4. [BK:] There are actually two issues here. The first is the appropriateness of assigning the same survival to all individuals in a stage, which as you have shown is problematic in fish and other species where the demography is really size-structured. The other issue is whether having a non-zero fertility coefficient for juveniles gives the wrong time to reproduction. I would argue that the latter issue is not actually due to the juvenile fertility coefficient, but to the exponential distribution of residence times: the pre-breeding census model (which does have a zero fertility coefficient for juveniles) gives exactly the same minimum time to first reproduction and mean time to reproduction as the post-breeding census model as is standardly constructed. The non-zero juvenile fecundity is required to ensure the pre- and post-breeding models are equivalent (which they should be—the only difference being the time of census). To maintain equivalency with your suggested solution, the pre-breeding census model would also need to have a one-year “pre-adult” class split off. This could be justified, e.g., by virtue of the higher survival of such individuals, and the desire to increase the minimum age of first reproduction by a year, but those are solving separate issues from the intuitively disturbing notion of having nonzero juvenile fertility coefficient.
   5. [MF:] Let’s stick with the way we have now. I agree that the discussion can be a bit confusing. For the type of the audience we are targeting, we do not want to introduce too many problems to digest.
3. "we impose a constraint that individuals in the last year of the juvenile stage have the same survival as adults"
   1. [MF:]I am not sure. For example, if we are dealing with size dependent mortality (a large number of species), the survival should become closer to adults as they reach closer to maturity.
   2. [BK:] To me, privileging the final age within the stage to get the next stage’s survival seems somewhat arbitrary (why not break the class up further? Or just go all the way to the Leslie model?), and if adults also grow, such that the actual first-year adults are smaller and thus have lower survival than the adult mean, then the mean adult survival might not be any better a representation of last-year juvenile survival than is the mean juvenile survival.
   3. [MF:] Yes, I agree with you. I think I just commented that in many situations, imposing the constraint is not necessarily a problem. For the readers who do not see the constraint is a problem, the statement may be felt strange.
4. "failing to have the reproductive transition out of the last juvenile class in post-breeding census models will lead to a one-year delay in the age at first breeding"
   1. [MF]"can" or "may" or conditional statement like "unless the duration in juvenile stage is reduced" [this is related to the "embracing this approach" comment above]
   2. [BK:] I am not yet convinced that your proposed alternative solves the cognitive dissonance problem. Your proposed approach still introduces an apparent discrepancy between the actual stage duration and the modeled stage duration (i.e., if the actual juvenile duration is 3 years, we would set the transitions to give a mean stage duration of 2 years, and call the third year “adult”). Furthermore, this approach makes it harder to move between pre-breeding and post-breeding models. In effect, your solution creates a (virtual) one-year “pre-adult” stage to replace the last year of the juvenile stage. You would implement that by lumping it with the adults, as it has adult demography. But when moving to the pre-breeding formulation, that stage has to be explicitly modeled, as it has the adult survival but still has a zero fertility coefficient. This seems likely to create more problems than it solves. Also note that the overall issue (last juvenile class has a non-zero fertility coefficient in post-breeding census) also applies in age structured models as well—if the target age at first reproduction is 5, then in a post-breeding census model the 4-year-olds still need to be given a non-zero fertility term, so under your proposal you will have to define 4-year-olds as “adults” which will likely result in as much confusion from the biologists as would the standard solution.
   3. [MF:] We probably do not want to get into this issue in the paper. Assignment of “stage” in a stage-structured model should be done by grouping them based on survival rate and/or reproductive rate. We can just focus on the cases in which both can change only at the same time in this paper. Then, everything you described makes sense.

# Section 2.3. Ensuring that the mean time in each developmental stage matches the species' life history

1. “With longitudinal data on individuals”
   1. [LGF:] "longitudinal" is ambiguous here as it may have both the *time* and *space* meanings, the latter confusing with the size-structured models. Perhaps use “time-series data”
   2. [BK:] I propose to use “repeated observations of marked individuals”
   3. [MF:] It is a good solution although I do not see the problem with “longitudinal” either. I think most population ecologists dealing with data would understand.
2. “Check Caswell's actual wording” [for 1/T model]
   1. [LGF:] and note that the "identified individuals" kind of data (p. 134) eliminates this problem at all.
   2. [BEK:] Actually the “identified individuals” data does **not** solve the problem; this is the “longitudinal data” mentioned above. Maybe we need to explicitly include this approach here?
   3. [BEK:] Regarding what Caswell says about the 1/T model (which he calls the “geometric distribution” (section 6.4.1):
      1. It is the first solution he offers
      2. He calls it “the simplest approximation”
      3. He closes by saying “Intuitively, if the average duration of the stage is Tbar\_i, then during each time interval a fraction Tbar\_i^{-1} of the individuals must grow to the next stage.” Of course, that “intuition” is correct only if S/lambda=1, but he doesn’t say that!

[MF:] We should state that 1/T model is derived by setting S/lambda=1. It will clarify why 1/T is not always a good approximation.