Global Thesis Notes

Meeting 11/6/19

Optimisation

- Target dataset could be m_α
- Or could be rho optimisation
- 1 = integral, steady state - life histories evened out
  - solve for r - growth fitness
- Implicitly needs redefining what LH need to be optimised
- $l_x m_x$ = mortality*fecundity - resource supply not
- add in bucket shaped Z - use exponential decay with time
- Assume that very young and old ages have another mortality rate - so different trade-off scaling.
- Can do a sensitivity analysis
- Can use delta as a step function - i.e. hybrid function
- Once solved - can we potentially get data on age at maturation?
- It's easier to optimise exponent on cm term - keep energy intake fixed
  - optimise repro output
- scaling of Lt at any given age?
- At any given mass can numerically integrate reproductive output - cumulative integral from alpha to infinity
- Size-dependent fecundity equation
- scaling beyond age won't hold
- scaling equation fecundity - as function of mass - write-out optimisation parts

Method

- We can use a piece-wise approach
- Development rate equation
- a priori alpha size - integrating twice
- Juveniles/adults have different foraging strategies
- This offers rationale (?) for two-piece (but West argues α is relatively so low that you can just use the second equation)
- alpha at different times (intake rate as alpha at this point)
- juvenile scaling != adult scaling
- optimise scaling given supply?
- go as far as we can analytically

Meeting 23/7/19

- table for parameter values
- could use diego's data - could actually show hypo - lxmx curve. scaling of peak * fecundity?
- decline in fecundity after that is - scaling of fecundity relate to LH curve - which * part of their LH are we looking at here? Model output
- peak fecundity curve is a function
- emerges as consequence of survivorship
- master equation
- optimisation equation
- relate two together
- solved it by simultqneously doing numerical integration, and plugging back in
- check carefully for mistake by including mx in such a way - mx should be a curve which * peaks then declines
- fecundity curves with l_x curve
- dont worry about Van's solution on the board
- how is optimisation going to be done
- survivorship curve dominates -
- bounds on parameters in table
- conceptualise what we do/dont have data for - we know this doesnt do anything
- prioritise writing mathematical forumlation and dimensions

- master -> parameters -> dimensions
- scaling equations - no params needed

Van's Visit - 8/7/19

Day 1

1. Can keep $b = q \cdot c$
2. Hou *et al.* model - E_c assumed constant

- assume $B_0 m^{3/4}$ scaling
- portion of metabolism going to our process - B_{rest}
- $A(m) = B_{tot} + E_c \frac{dm}{dt} = fB_r + E_c \frac{B_r}{E_m}\left(1 - \left(\frac{m}{M}\right)^{1-\alpha}\right)$ where f is your "metabolic scope" i.e. active metabolism as a proportion of resting, $f = 1$ when you are resting
- $\therefore \frac{dm}{dt} = \frac{B_r}{E_m}\left(1 - \left(\frac{m}{M}\right)^{1-\alpha}\right)$
- $am^?$ during growth
- $\frac{dm}{dt}$ is combination of storage and biosynthesis term
- $\frac{dm}{dt} = \frac{A(m) - B_{tot}}{E_c}$ where $\frac{A(m)}{E_c} = B_0 m^{3/4}$
- across species $1 < f < 10$ - through growth within species does slope change?
- If active + restime have different mass scalings then as you grow, f **must** change
- *No* evidence for steeper scaling within organism
- Across species confound evolutionary effects (species + strategies)
- Hou *et al.* have $f + \gamma$
- f partially scales with mass
- Hou *et al.*: "equation 3 is general, indication of ow B_{rest}, B_{maint} and f scale with mass
- $B_{tot} = B_{maint} + B_{growth} + B_{rep}$
- $A(m) = B_{maint} + B_{act}(m) + B_{syn}(m) + S(m)$
- $A(m) = (f + \gamma)B_{rest}(m) - \gamma B_{maint}(m)$
- γ is amount going to storage (storage coefficient)
  - $fB_r + \gamma B_r \left(1 - \frac{m}{M}\right)^{1-\alpha}$
  - $(f + \gamma)B_r - \gamma B_r \left(1 - \frac{m}{M}\right)^{1-\alpha}$
- $(1 - \alpha)$ generates quarter power scaling
- If we assume $B_{rest} = B_0 m^\alpha$:
  - $A(m) = (f + \gamma)B_0 m^\alpha - \gamma B_0 m^\alpha \left(1 - \frac{m}{M}\right)^{1-\alpha}$
  - $A(m) = (f + \gamma)B_0 m^\alpha - \gamma B_0 \frac{m^1}{M^{1-\alpha}}$
  - $fB_r + \frac{E_c}{E_m}B_r \left(1 - \frac{m}{M}\right)^{1-\alpha}$
  - when $m = 1$, term $= 0$, as $m \to 0$, term $= 1$
- Diego and Andrew:
  - Let $\gamma = \frac{E_c}{E_m}$
    * $E_m =$ energy required to synthesise unit of biomass (energetic cost)
    * $E_c =$ structural cost
    * ATP vs actual use of molecules
- Tom: "framework doesn't simplift ATR problem"
- Samraat: "energy expended during growth is partitioned between energy content stored in newly synthesised biomass + energy expended in synthesising this biomass"
- Question is what are we trying to do here? Diego did this from perspective of understanding how much energy availble in fish community after growth
- $A(m)$ has relationship with all pieces - f, γ, B_0 - end up with $A(m)$ curve normalised
- Point of Hou *et al.* is that there exists a universal optima; assimilation rate (see figure) - we are not necessarily going for assimilation - we actually want to understand what would happen to dm/dt if we change $A(m)$ itself
- We wouldn't replace dm/dt - wouldn't express in terms of asymptotic mass - we want to establish asymptotic mass by $\int \frac{dm}{dt}$
- We wouldn't set $B_r = B_0 m^{3/4}$ (about creating mass)
- Van: In this model (Hou *et al.*) if you're fimishing growing and you reproduce, it would be outside scope of model $b/c \quad m = M$

- Only makes indeterminate fish, in which case think of growth term being either growth or growth of eggs, but once stored them, not part of equation anymore
- Point of paper is discussing assimilation itself - not previously done - assumed to be 3/4
- Tom: "in terms of ATR there would be a way to include it at a cellular level and build up from that"
- Simplest function for growth to no growth
- Effective storage changing throughout lifetime since $\frac{m}{M}$ is proportion (Hou *et al.*)

Two-piece model

- $dm/dt = am^{3/4} - bm - cm^\rho \quad m > m_\alpha$
- $\rho = 1$ in Charnov model
- Maximise $\int_\alpha^\infty L_t b_t dt$ where b_t is fecundity output at time t NOT a rate.
- Fecundity at time t is subject to fecundity curve AND survivorship curve
- Diego's new frequency data is still within interval (e.g. a few bouts) - not lifetime growth
- Difficult to measure over time
- Diego accounts for egg size by taking energy content
- Luke: also if you are measuring across sizes which correlates with age, surely you are measuring across this fecundity curve
- Samraat: we won't worry about cm^ρ as parameter but optimise ρ given an intake rate
- Breeding is phenologically synced with food availability
- 20kg cod still reproducing so is $\alpha < 20kg$ or has α shifted?
- Multiple things to optimise, even c (GSI)
- We stick with 3/4 for assimilation - you could optimise it, but for basal MR data we quite reliably get 3/4 power scaling - assuming intake is fine
- Only limited by fractal architecture of capillaries
- Van: $am^{3/4}$ **is** assimilation but not just for basal.
- Maximal rate scales more steeply - you could be assimilating to be at maximal. Fractal limits basal (since it is an assumption of the West *et al.* model) not necessarily active.

Day 2

Right now, α will keep reducing and ρ will keep increasing in optimisation

- Need a constraint
- Need to make declining suvivorship relative to α thus t becomes $t - \alpha$
- Now survivorship starts at 1 for any α value
- don't optimise on α, optimise on c and ρ, using the αZ invariant
- α and β, could use male m to find b
- Then simulate fish with reproduction, growth trajectory would be different, and see what optimal c and ρ converge

Tom suggests using:

```
if m + dmdt < 0:
    dmdt = -m
```

Miscellaneous

Approach:

1. Gap in the literature - rationale
2. Our model - using intake
3. Results - figures (Hou *et al* figure)
4. cm^ρ

- Why superlinear fecundity emerges
- Resource supply AND questionable
- Sufficient resources not to shrink
- New way to quantify intake rate
- Life history traits at different timescales: α, ρ
- Could we fix α and optimise c and ρ?

- Figure I vs c, ρ

Diego's Visit

- $A(m) = B_{tot} + E_c \frac{dm}{dt}$
- $B_{tot} = B_{maint} + B_{growth}$ where B_{maint} is in W (J/S) and is part of B_{tot}
- $B_0 m^{3/4} = bm + E_c \frac{dm}{dt}$ where b_m is in $\frac{J}{s \cdot kg}$ b is $N_c B_{maint,c} = \frac{m}{m_c} B_{maint,c}$
- $dm/dt = am^{3/4} - bm$ where $a = \frac{B_0}{m_c}$ and if you take b/E_c units are $1/skg$
- Does your scope increase as you get bigger? within species
- $A(m) = fB_r + E_c \frac{B_r}{E_m}\left(1 - \left(\frac{m}{M}\right)^{1-\alpha}\right)$ where $f = \alpha m$?
- Diego's rate data is within a few bouts
- **NB:** Trade-off between ψ and I_0
- $t_f \to 0$ get back to basal
- if timescales align then $\psi + \gamma - \frac{1}{4} = \frac{3}{4} + \frac{1}{4} - \frac{1}{4} = \frac{3}{4}$ which is back to basal MR
- Reproduction intervals/frequency
- do Δt_R scale same as Δt_f? Do the two time scales come closer as $m \downarrow$, stretching long am timescale across cm^ρ timescale - right way round
- Mortality rate could change so that α changes
- endothermy evolved because of times of no supply
- Determinate growth is result of high maintenance? What is the mechanism here?
- Synchrony between reproductive timescale versus intake i.e. phytoplankton glut
- We need data supporting foraging timescales of $t = t_0 m^{3/4}$ and parameter values for every piece
- Models assume 100% ε and all Carbon is assimulated
- meaning egestion is purely N and P
- Carbon-loss not important at individual level
- Eating extra carbon to reach nitrogen target
- $I_{tot}\varepsilon = B_0 m^\alpha \left[f + \frac{E_c}{E_m}\left(1 - \left(\frac{m}{M}\right)^{1-\alpha}\right)\right]$
- $I_{tot}\varepsilon = B_0 m^\alpha f + E_c \frac{dm}{dt}$
- $\frac{dm}{dt} = \frac{I_{tot}\varepsilon - B_0 m^\alpha f}{E_c}$
- $\frac{dm}{dt} = \frac{a_0 m^{\gamma+\psi} - B_0 m^\alpha f}{E_c}$
- Expand notebook to include both derivations
  - come up with end result dm/dt
- $B_{tot} = fB_{rest}$ then follows Hou *et al.* approach.
- fB_{rest} then becomes cm term for reproduction
- For publication needs to be validated with data
- Outputs signature of intake rate on fecundity scaling
- Trade-off across species in egg size
- No trade-off within species for all 3 (Diego paper)
- Essentially we want a cohort + repeated measures - foraging timescale and growth timescale
- Maybe hyperallometry drops after fecundity peak
- Mortality: $e^{-\mu t}$ and $\mu(m)$ weak scaling with mass

Our Intake Rate Model

- Intake rate $= I_0 m^\gamma$
- Total intake $= I_0 m^\gamma * t$
- Total intake $= I_0 m^\gamma t_0 m^\psi$
- Total intake, $I_{tot} = I_0 t_0 m^{\gamma+\psi}$

Which in effect is "mass-specific intrinsic distribution of resources"

- $\frac{dm}{dt} = I_{tot}\epsilon\left(am^{-\frac{1}{4}}\right) - bm - cm^\rho$
- $\frac{dm}{dt} = I_0 t_0 m^{\gamma+\psi}\epsilon\left(am^{-\frac{1}{4}}\right) - bm - cm^\rho$
- $\frac{dm}{dt} = I_0 t_0 \epsilon am^{\gamma+\psi}\left(m^{-\frac{1}{4}}\right) - bm - cm^\rho$
- let $a_0 = I_0 t_0 \epsilon a$
- $\frac{dm}{dt} = a_0 m^{\gamma+\psi-\frac{1}{4}} - bm - cm^\rho$

- 2D Saturated $->$ Intake $= a\varepsilon I_0 t_0 m^{\frac{3}{4}+\beta-\frac{1}{4}}$
- 3D depleted $->$ Intake $= a\varepsilon I_0 t_0 m^{1.06+\beta-\frac{1}{4}}$
- If the foraging time scales as $3/4$ then $3/4 + 3/4 - 1/4 = 5/4 = 1.25$
- Cod - total length max 80cm $\therefore$ weight $= 0.00624(80)^{3.126} = 5549.372$
- a and b are calculated from fundamental cellular properties
- Energy content of mammalian tissue $\approx 7e6 J kg^{-1}$
- $m_c \approx 3e - 9g$
- $\therefore$ energy to create cell $E_c \approx 2.1e - 5J$ (in vivo)
- $B_0 \approx 1.9e - 2W$
- $\therefore a \equiv B_0 m_c/E_c \approx 0.25 g^{1/4} day^{-1}$
- $E_g = \int E_c \frac{dN_c}{dt} dt = \frac{E_c}{m_c} \int \frac{dm}{dt} dt = \frac{E_c}{m_c}(m_M - m_0)$
- West *et al.* say add egg term but this increases maintenace only
- also t estimated to be so small that only 1 equation matters - skip optimisation o α since time period prior to α is negligible
- $B = \sum_c \left[N_c B_c + E_c \frac{dN_c}{dt} + E_e \frac{dN_e}{dt} \right]$
- During spawn, mass of clutch, $m_K = m_e \Delta N_e =$ constant fraction of mass i.e. $= \lambda m$
- $\therefore E_e \frac{dN_e}{dt} \approx E_e \frac{\Delta N_e}{\Delta t} \approx \frac{\lambda E_e m}{m_e t_s}$
- energy density is similar s.t. $\frac{E_e}{m_e} \approx \frac{E_c}{m_c}$
- $\therefore \frac{E_e dN_e}{dt} \approx \lambda \left(\frac{E_c}{t_s} \right) N_c$
- so B_c becomes $\left(B_c + \lambda \frac{E_c}{t_s} \right)$ and maintenance goes up i.e. same as Charnov's trade-off but with first principles logic
- Charnov says GSI $= c$ and GSI/Z invariant ≈ 0.6 - tie this to West *et al.*'s comment on short immaturity period

Our model's Life History

Survivorship

- $R_0 = \int_\alpha^\infty l_x b_x dx$
- let $l_x = l_\alpha e^{-Z(x-\alpha)}$
- and $l_\alpha = \int_0^\alpha e^{-Z_J \alpha} dx = e^{-Z_J \alpha}$
- $\therefore R_0 = \int_\alpha^\infty e^{-Z_J \alpha} e^{-Z(x-\alpha)} bx dx$
- $R_0 = e^{-Z_J \alpha} \int_\alpha^\infty e^{-Z(x-\alpha)} bx dx$
- l_α effectively becomes a scaling term - how many juveniles make it to the α timepoint - height of fecundity*survivorship curve
- We explore b_x using a decay rate parameter κ
- $b_x = b_{pk} e^{-\kappa(x-\alpha)}$

Recent notes - Objectives

- Discuss resource supply problem right from outset - context of master equation
- Problem with resource supply
- might explain recent finding. . .
- Write units in-line
- $Z(x)$ is a constant factor
- Easiest option: assume within survivorship, fecundity is constant (not decaying) - increasing output with no trade-off
- fix $\kappa = 0$ and output optimisation surfaces for c and ρ

Fecundity function

- $R_0 = \int_\alpha^\infty cm^\rho e^{-\kappa(x-\alpha)} \cdot L_t dt$
- $b_x = cm^\rho h(t)$ where $h(t)$ is like an efficiency term
- $b_x = cm^\rho e^{-\kappa(t-\alpha)}$
- $\alpha \cdot Z$ invariant
- $0 < \kappa < 0.1$
- $dm/dt = am^x - bm - (cm^\rho)h(t)$ - **BUT** is this correct? Mathematically you are still losing **less** energy as you get older, allowing more for growth
- $R_0 = \int cm^\rho h(t) \cdot L_t dt$

- $R_0 = \int cm^\rho(t)^\rho e^{-\kappa(t-\alpha)} \cdot l_\alpha e^{-Z(t-\alpha)} dt$
- $R_0 = c \cdot l_\alpha \int m(t)^\rho e^{-\kappa(t-\alpha)} \cdot {}^{-Z(t-\alpha)} dt$
- $R_0 = c \cdot l_\alpha \int m(t)^\rho e^{-(\kappa+Z)(t-\alpha)} dt$
- $R_0 = c \cdot \int_0^\alpha e^{-Z(t)} dt \int_\alpha^\infty m(t)^\rho e^{-(\kappa+Z)(t-\alpha)} dt$
- Define two new constants
    - $q_1 = \alpha \cdot Z$
    - $q_2 = \frac{\int_\alpha^\infty b(t) dt}{L}$ "lifetime fecundity output as a proportion of lifespan"

Alex's help with rearranging West *et al.* sum

- $B = \sum_c \left[N_c B_c + E_c \frac{dN_c}{dt} \right]$
- $B = \sum_c \left[N_c B_c \right] + \sum_c \left[E_c \frac{dN_c}{dt} \right]$
- $B - \sum_c \left[N_c B_c \right] = \sum_c E_c * \sum_c \frac{dN_c}{dt}$
- $\sum_c \frac{dN_c}{dt} \geq \frac{B - \sum_c \left[N_c B_c \right]}{\sum_c E_c}$
- $\because a_1 b_1 + a_2 b_2 \leq (a_1 a_2)(b_1 b_2)$

Presentation feedback

- Superlinear scaling possible
- Growth dependent on component
- LH in methods not intro - means to an end
- Intro: people have ignored resource supply
- Not *too* much emphasis
- Diego's result is a two-line mention at most... "which means that if we ignore.... we get shrinking fish" - consequence vs rationale
- Less focus on the specific results of Pawar *et al.* - focus is on energy supply and Pawar *et al.* is a good example
- Results: Max fitness $\rightarrow$ Measure R_0 $\rightarrow$ equations

Lyon poster notes

- $M = \left(\frac{a}{b+c} \right)^4$
- Equation is always finite, m won't go $\rightarrow \infty$ in finite time
- Gonzalez-Forereo PLoS comp. He says do a phase portrait since high ρ value may cause bifurcation
- Fisher (1950) - size of offspring/size of population rule

Charnov (2001)

- Develops new evolutionary model for life histories by combining new production-growth model with some general constraints on reproductive allocation
- invariance across fish species of dimensionless numbers made up from reproductive & timing variables: age at maturity/average lifespan and proportion of mass to repro X E
- these invariants apply within closely related taxons
- i.e. after removing absolute scale (age) then life histories of elephants and squirrels look much more alike than elephants versus fish
- Disagreement over how well E correlates with α such that claiming $\frac{E}{\alpha}$ is invariant is true, but $R^2 > 0.8$ usually.
- Evolutionary LHT can be used to predict when such dimensionless invariance is expected
- Model allows natural selection to adjust age of first breeding and metabolic production - growth - capacity of cells
- Optimal LHT correctly predicts numeric value of dimensionless numbers which combine maturation age (size), mortality & reproductive allocation
- LH prediction yields new model & predicts fastest growth rate to be near the size of first reproduction
- Charnov says West *et al.* equation excludes reproduction which changes the asymptotic size to $\left(\frac{a}{b+c} \right)^4$
- Notes that gonad mass in fish is commonly proportional to body mass, thus after age α, growth $= dm/dt = am^{.75} - (b+c)m$

- Thus, lifetime growth reflects production & timing (α) & magnitude ($c \cdot m$) of reproduction
- If population size is fixed (i.e. not growing) then can calculate $c \cdot m$
- Evolutionary optimisation argument: α and c chosen to maximise a quantity proportional to lifetime production of offspring in the face of a mortality rate Z which is externally imposed
- "Under the same growth rate, a larger size requires longer development time, which comes at a cost: delayed reproduction" (p238)

Optimising

- Proportion of energy to growth - determines body size, determinant of production rate
- Proportion of energy to repro - allocation throughout life defines fitness
- age at maturity α
- size at maturity m_α
- $R_0 \propto \int_\alpha^\infty L(x)m(x)dx$
- Optimising Life history sets $\frac{\partial R_0}{\partial \alpha} = 0$ and $\frac{\partial R_0}{\partial c} = 0$
- cm can be optimised wrt Z but no trade-off between the two i.e. high $cm \neq$ high Z
- it's actually the reverse causality, shorter lifespan (high Z) selects for greater per unit time ATR (high c)
- $c \cdot E$ is average proportion of body mass ATR over average adult lifetime
- GSI/Z ratio is invariant $\approx 60\%$ on average
- Almost always optimal to give 100% growth to repro at age α i.e. $c = a \cdot m_\alpha^{-0.25} - b$ (determinate growth schedule)
- Because c/b is a fixed value, assumption leads to lower value for c (than 100) meaning there could be surplus for growth after α (i.e. indeterminate) hence why Charnov believes determinate is unlikely?

Misc

- Production rate is mediated by mortality + size dependence
- Implied that size shapes allometries througjh design constraints
- It was realised that interspecific allometries can be phylogeny-dependent
- cost of being big - delayed reproduction (under same growth rate) and increased risk of dying having not reproduced
- Conversely, larger organisms usually benefit from better reproductive capacity (more energy channeled)
- Growth considered an investment in future reproductive success
- Strictly dominating strategy - extra calorie dedicated to growth yields >1 calorie of reproductive allocation
- Expected future reproduction weighted by probability of surviving to a given age, which is set by mortality rate
- Heavy mortality = investment in future repro is lost
- Production rate also comes into play since growing faster means you can be large quicker
- Energy may be limited by **resource supply** or t_h
- Optimal proportions of surplus energy going to different sinks can chance throughout life
- Reproductive allocation throughout life defines fitness
- Growth changes size which is determinant of production rate

Charnov (2004)

- $R_0 = \int_\alpha^\infty L_t b_t dt$
- $R_0 = \int_\alpha^\infty L_t cm_t dt$
- R_t = net reproductive rate (mean offspring over lifespan)
- L_t = chance of being alive at age/time t
- f_t = offspring produced at age t
- Fixed offspring (egg) size (I)
- $f_t = \frac{cm_t}{I}$ or $f_t \propto cm_t$ $\because$ egg size is fixed so number produced must be proportional to mass allocated
- b = maintenance MR per cell/Cost of building new cell
- $\frac{c}{b} = q$ high c requires high b - multiplier
- $c = bq$ and $\frac{c}{Z}$ quantity
- Optimising Life history sets $\frac{\partial R_0}{\partial \alpha} = 0$ and $\frac{\partial R_0}{\partial c} = 0$
- Instantaneous mortality rate Z high at low t (i.e. high when young) but drops to a constant Z as $t \to \alpha$

Kozlowski (1987)

- Assume a 2-year lifespan
- Fitness measured as lifetime energy allocation to reproduction (or no. offspring produced) for species living at most 2 years and reproducing in both years:
- $L(x) = \mathbb{P}(\text{surviving to age } x)$
- $m(x)$ = rate of energy allocation to reproduction (or rate of offspring production)
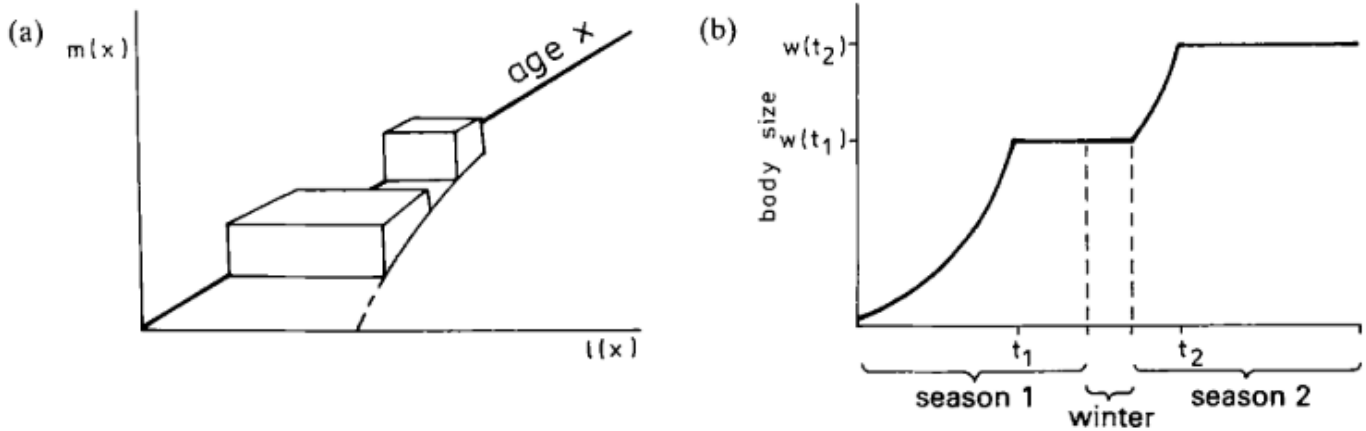- Measure of fitness is equivalent to the volume of two solids, $V_1 + V_2$

Figure 1: Kozlowski's Volume Representation

- V_1 = reproductive success in first season
- $R_0 \propto \int_\alpha^\infty L(x)m(x)dx$
- V takes maximum for times t_1, t_2
- $\frac{dV_1}{dt_1} + \frac{\partial V_2}{\partial t_1} = 0$ and simultaneously $\frac{\partial V_2}{\partial t_2} = 0$

1. $m(x) = 0$ when immature
2. onset of reproduction at age t, size w, to the end of the first reproduction with reproductive rate $H(w_1)$ (assume size-dependency of reproduction not age)
3. then again $m(x) = 0$ throughout winter and part of growing season 2 prior to switch back to reproduction at age t_2, size w_2
4. t_2 to end of 2nd season, $H(w_2)$

- $V(t_1, t_2) = v_1(t_1) + v_2(t_1, t_2)$
- Volume of first solid depends only on t_1, age at maturity second solid depends on age at maturity, t_1 and time of switch from growth to reproduction in second year, t_2 $\therefore$ body size in year 2 depends on sum of growth periods in both years

Kozlowski Notes

- Does Kozlowksi assume that growth and repro cannot occur simultaneously?

- Charnov: he suggests that because Z is different for different species, times for switch from growth to repro should also change. Heavy mortality makes lower α more optimal

- Charnov's crucial assumption is that animals share the same productivity

  – differences scatter the point around allometry lines but don't change the slope
  – Kozlowski & Wiener show otherwise - changing parameters of productivity changes allometry slope
  – $\therefore$ optimal size depends not only on Z but on $p(m)$ - function describing dependence of productivity rate on body size

- Tus, species with higher production have larger optimal size even if no difference in productivity

- Charnov is heuristically optimistic: everything depends on distribution of Z alone $\therefore$ interspecific allometries he describes have some explanatory meaning

- $P(w) = aw^b$ where a, b are species-specific. Function describes a size-dependent production rate

- Optimal to stop growing + start allocating to reproduction when $\frac{dP(w)}{dw} = m$, m = constant mortality rate

- Optimal size, $w = \left(\frac{m}{ab}\right)^{\frac{1}{b-1}}$

- Optimal age at maturity, $\alpha = \frac{1}{a(1-b)}(w^{1-b} - w_0^{1-b})$

- $\frac{dP(w)}{dw} = baw^{b-1}$

- $baw^{b-1} = m$

- $w^{b-1} = \frac{m}{ab}$

- $w = \sqrt[b-1]{\frac{m}{ab}}$

Misc Notes

- How do we find how many eggs produced in a lifetime?
- We know age (x), and energy allocation as function of age $m(x)$
- If stop growing at α, then would assume that you're just allocating to repro?
- But this assumes that you are always surviving (no Z) so α always low
- But Z exists, which introduces $\mathbb{P}$(survival to age x) as a third dimension
- Allocation is now height of volume (see Kozlowski figure) - fraction ATR after α is constant
- Given the likelihood you'll survive to age x and that at that age you'll have ATR of η, the volume is how much you'll reproduce - now what α maximises this volume?
- If $\mathbb{P}$(survival) was 100% then you would omit the $L(x)$ axis
- If energetic cost of producing offspring is constant, then $m(x)$ expressed as rate of production or rate of ATR
- Fecundity gain hypothesis - larger size at maturity (delaying repro) = more offspring - so constant fraction once you have reached terminal size
- $V = H \cdot D \cot W = \alpha \cdot L(x) \cdot age$
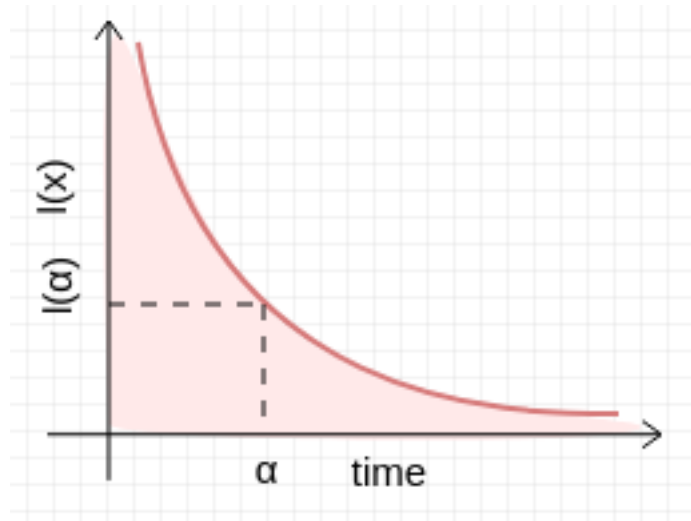- $\frac{dV}{d\alpha} = \frac{dH}{d\alpha}S + H\frac{dS}{d\alpha}$ (product rule $u'v + v'u$)

Figure 2: Survivorship curve

Samraat Dimensionality Paper

Stages:

- Detection
- Capture
- Subjugation

Paper models the biomechanics of searching and attacking
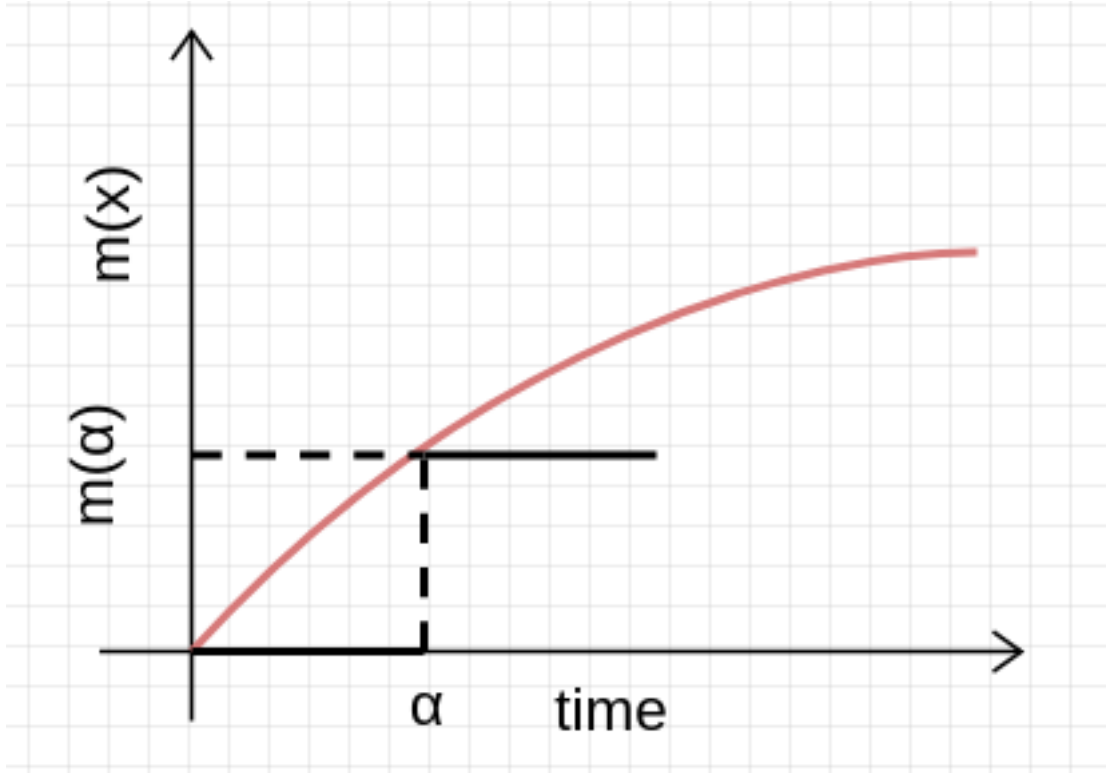
- $v_R, v_C \propto m_C^{P_V}$

Figure 3: ATR lifetime curve

- P_V = scaling exponent for consumer or resource velocity
- $d \propto (m_R m_c)^{P_d}$
- P_d = scaling exponent for consumer-resource reaction distance
- $t_h \propto m_C^{-\beta}$ - exponent for handling time
- $K_{RC} = \frac{m_R}{m_C}$ = Body mass ratio
- $\alpha = s_D v_R d^{D-1}$
- α = search rate
- s_D is 2 in 2D and π in 3D
- v_R = relative velocity - rate at which c-r pairs converge $v_R = \sqrt{v_R^2 + v_C^2}$
- d = radius of search space
- Power for movement is product of body velocity v and force f applied by locomotory appendages onto medium. Assume MR devoted to locomotion is constant proportion of B:
- $v \propto \frac{B_0 m^\beta}{F}$
- Force proportional to cross-sectional area of muscle - scales with mass
- $v = v_0 m^{\beta - \beta_F}$
- v_0 is a constant which depends on locomotory mode and metabolic scaling exponent
- $f(x_R) = \frac{\alpha(m_R x_R)^{q+1}}{1 + t_h \alpha(m_R x_R)^{q+1}}$
- Pursue, subdue, ingest 1 resource unit
- Delay between encounter + completion of ingestion prevents consumers exploiting resource in direct proprotion to availability
- Type II functional response
- as $x_R \to 0$ consumption $\to \alpha m_R x_R$ because the 1 in denominator dominates, since second term is multiplied by 0
- as $x_R \to \infty$, consumption $\to \frac{1}{t_h}$ because 1 becomes negligible so can remove, then the $\alpha m_R x_R$ terms cancel out, leaving $\frac{1}{t_h}$
- where $\frac{1}{t_h}$ = per-capita handling time/resource mass

Dimensionality and Growth

- B assumes constant rate of energy flow
- If define B as f(energy supply in env) (type II functional response)

- Suspicion that West **et al.** cherry picked their growth data from lab with idealised conditions
- If energy flow is consumption then $B = C = am_R x_R f(\cdot)$
- a = search
- m_R = mass of resource
- x_R = abundance of resource - Damuth's law
- $f(\cdot) = \frac{1}{1+at_h x_R}$ note there is no mass term here - only in terms of individuals - second term units: $\text{Individual} \cdot \frac{\text{Area}}{\text{Time}} \cdot Time \cdot \frac{\text{Individual}}{\text{Area}}$ so dimensionless
- But consumption also a function of time which can vary - because organisms move between resource depleted and saturated environments and 2D and 3D
- Thus is type 2 but abundance of resource can actually fluctute through time (abundance of resource is a function of time)
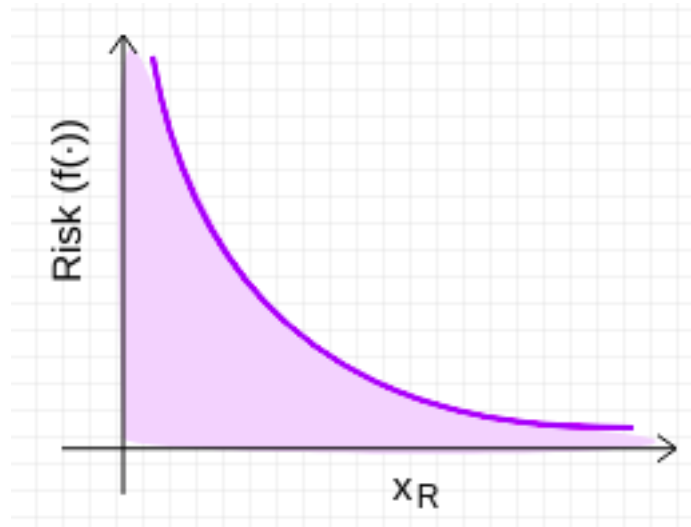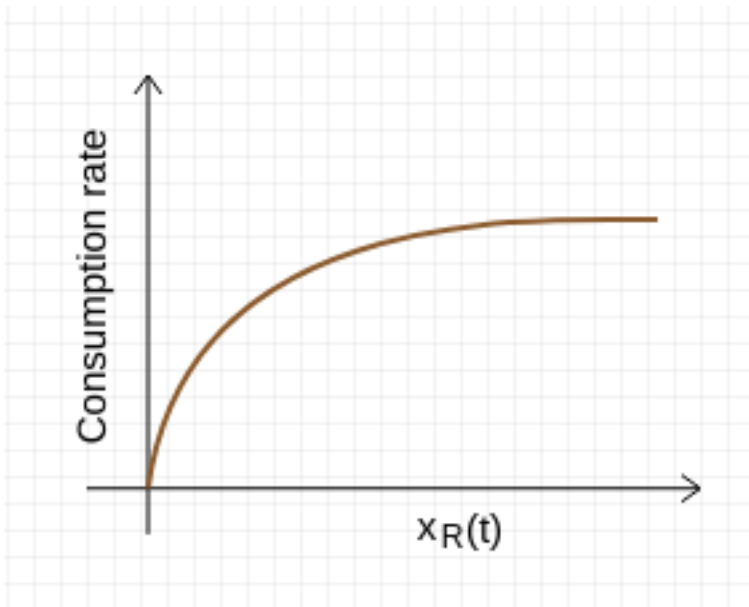

Figure 4: Risk vs resource abundance

Numpy meshgrid

- Creates a matrix of repeated x values in y plane and repeated y values in x plane

Thesis notes: meeting with Dr Samraat Pawar - 2/4/2019 14:00 - 15:00

Modelling Fish Growth

- Thus far, energy supply is treated as an implicit assumption in growth/fecundity models. Incorporate as an explicit assumption.
- What do we need to change in the West & Brown model?
- Check forward citations of Chernov paper to see other models people have come up with.
- Problem of resource supply:
  - governing equations
  - master equation energy balance
- Useful to specify master equation in more meaningful way.
- Diego's results suggest lifehistory must be getting enough resource supply

Thesis notes: meeting with Dr Samraat Pawar

Option 1: Carbon Flux

- Stability or volume of carbon efflux from ecosystem
- Relation to species interactions/does it matter?
- More focus on microbial networks
- Talk to Tom Clegg, it involves modelling dynamical systems - interactions effecting dynamics - ODEs
- individual $\rightarrow$ multiple pops competing with each other for same resource

Option 2: Modelling Fish Growth

- Find the growth model which is worth pursuing
- Reproduction in fish $\rightarrow$ understanding growth in fish.
- Use symbolic regression to identify what combo works best/explains best
- Population growth - mass conservation equation
- Brown equist model - universal model which predicts ecto/endotherm growth rates.
- Diego's post-doc advisor - carbon economy of the individual
- Optimisation - write equation for carbon economy to maximise fitness (growth strategy or size)
- Equation which maximises reproductive output of an individual, energy-balance - maximise remaining energy in organism, left over for reproduction
- Richer dataset - more ready things, provide empirical data