

Modelling temperature impacts on fish growth using a growth model with reproductive costs: can we reproduce the temperature-size rule?

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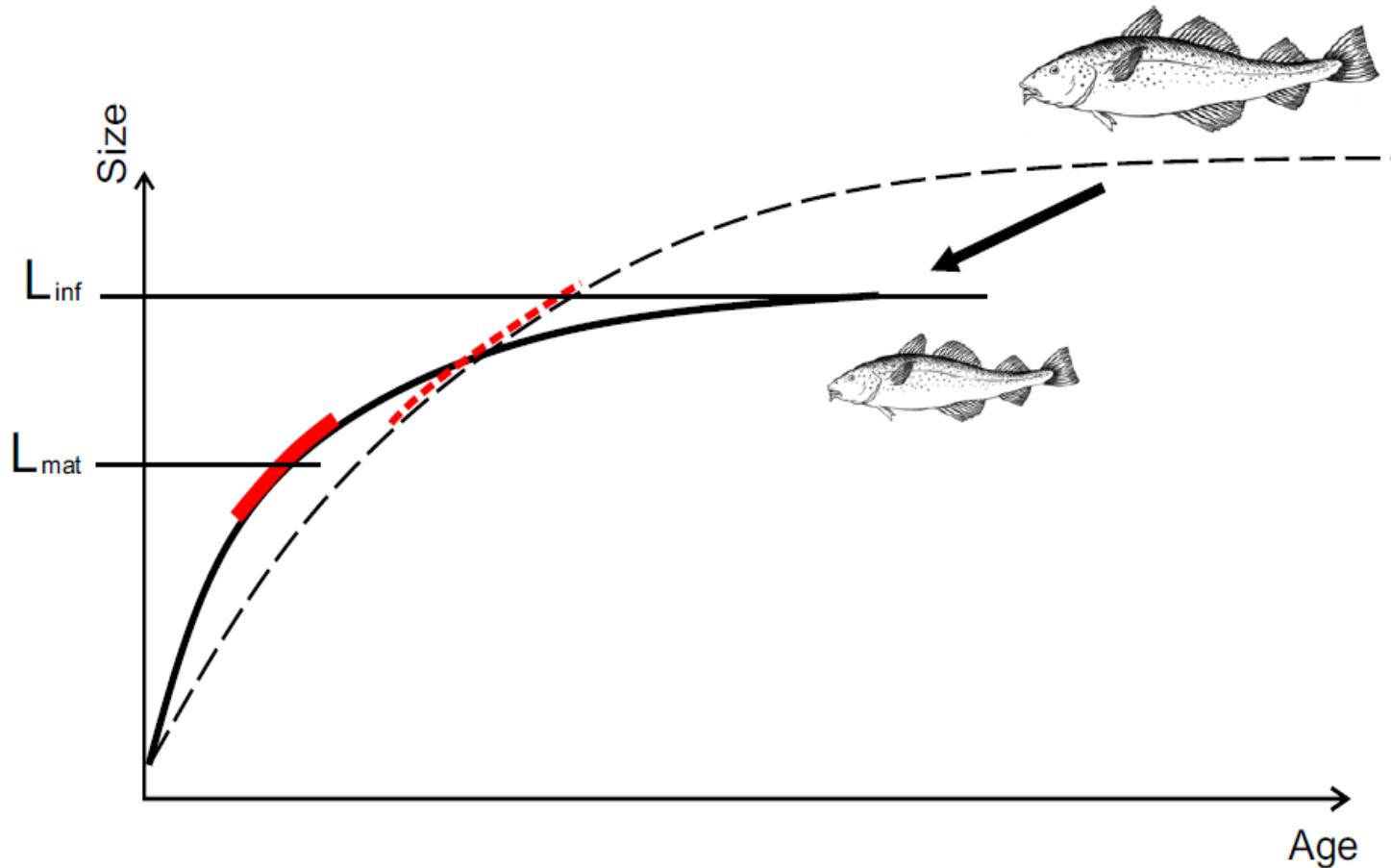
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2014-2020 Operational
Programme for the
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Can we explain temperature-size rule mechanistically?
Can we model it?

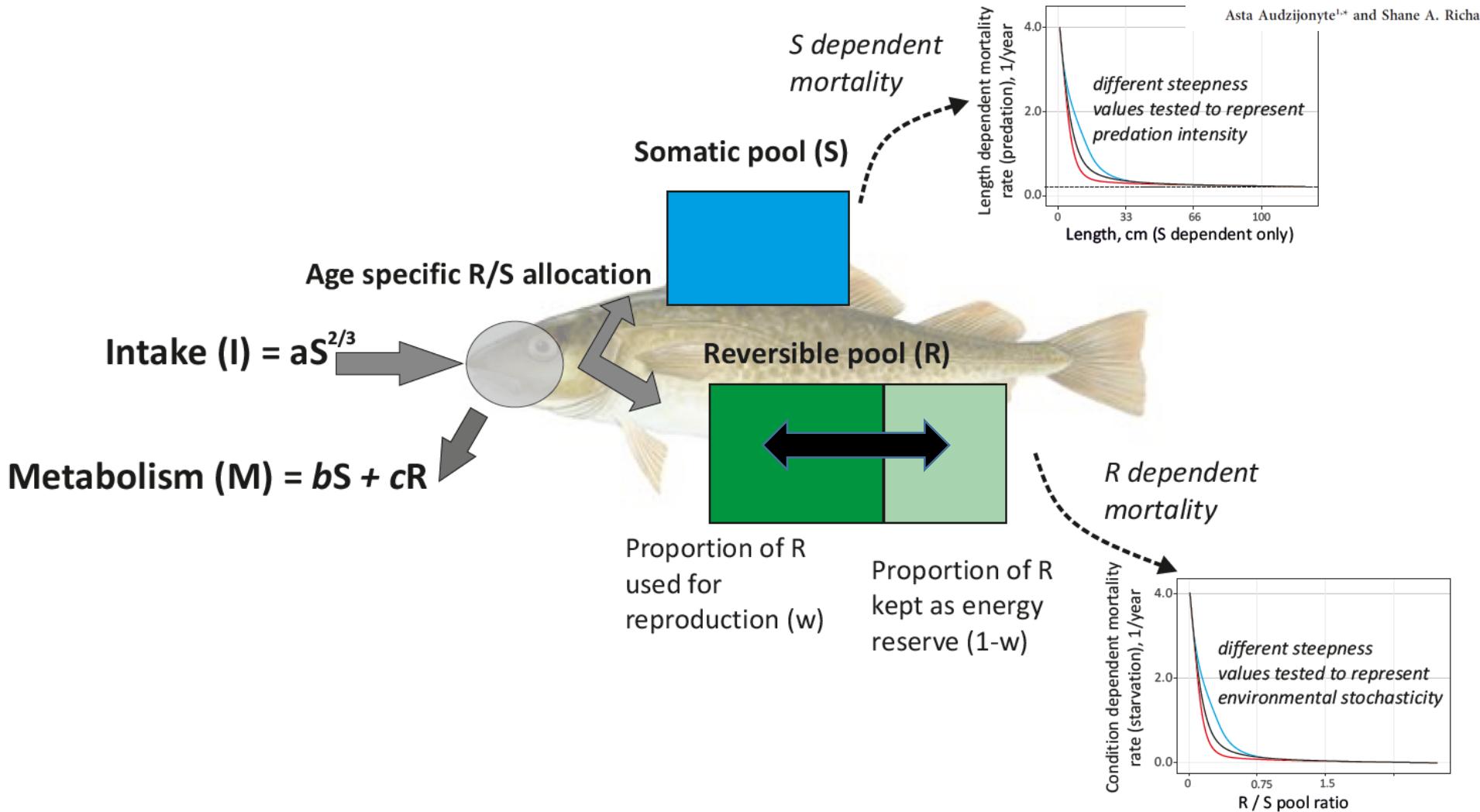


Model with EMERGENT maturation size and age

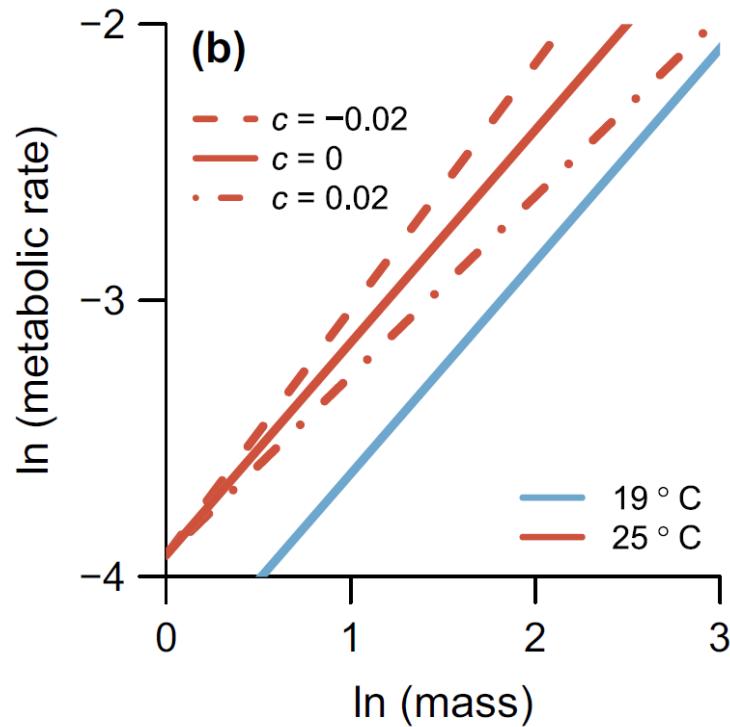
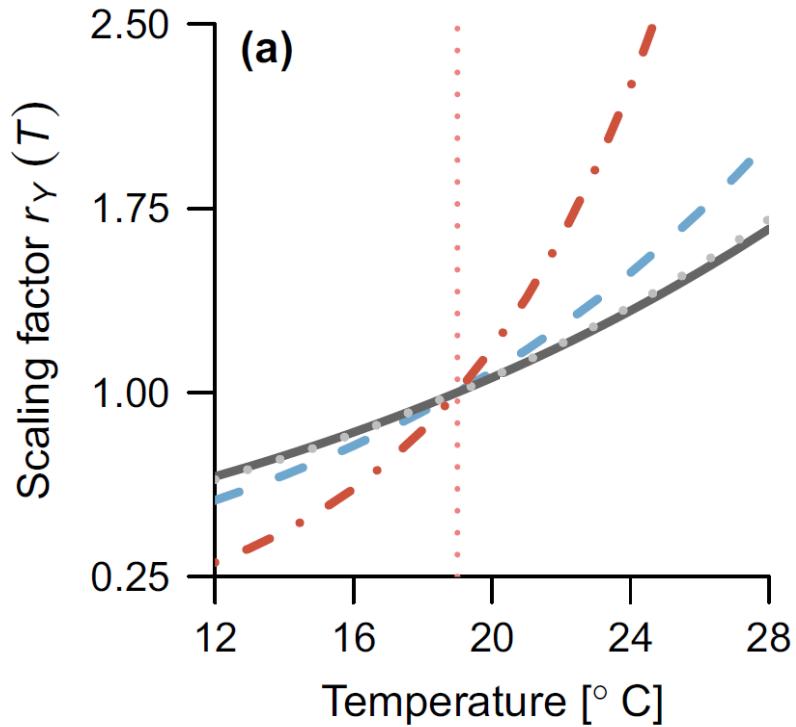
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E-ARTICLE

The Energetic Cost of Reproduction and Its Effect
on Optimal Life-History Strategies

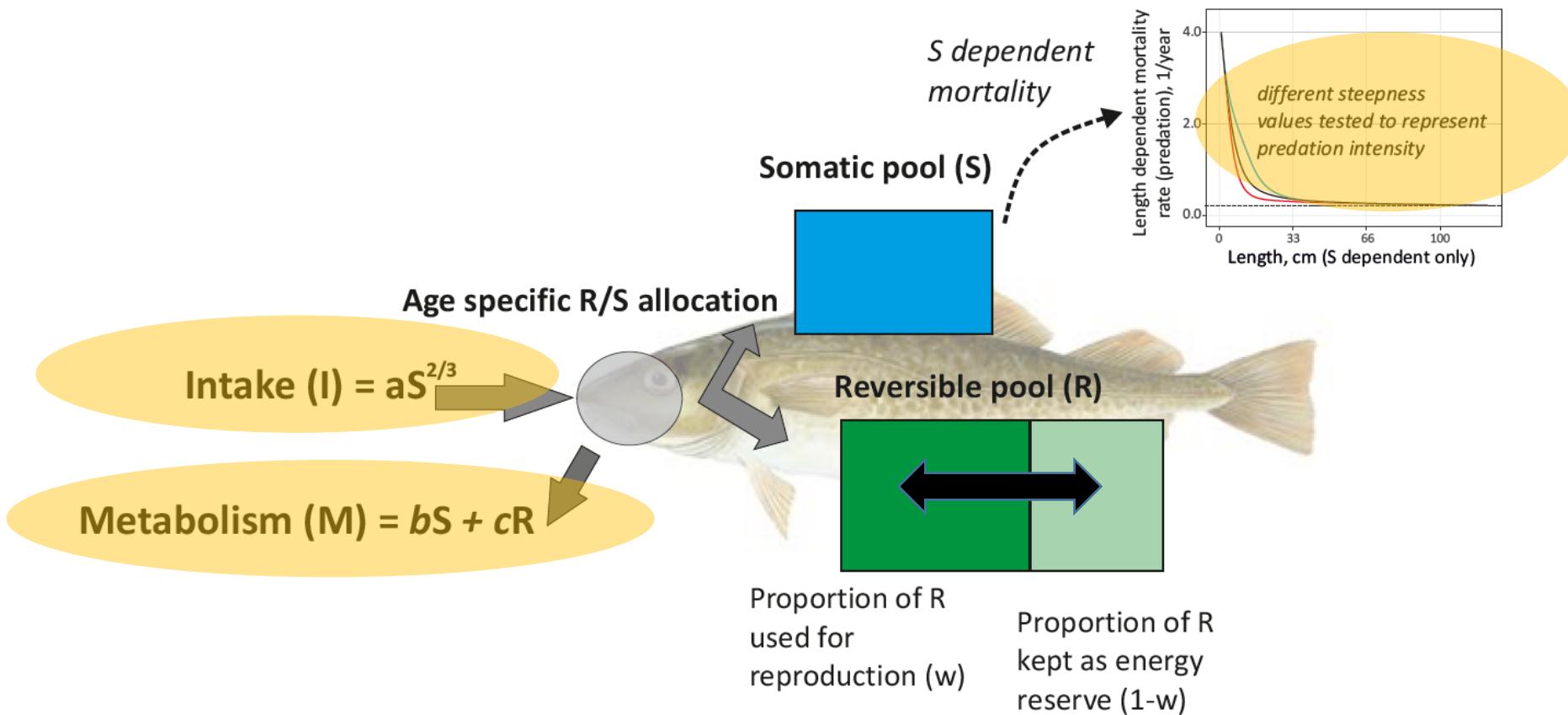


Adding temperature. Temperature speeds up life processes



This speeding up might
be size dependent

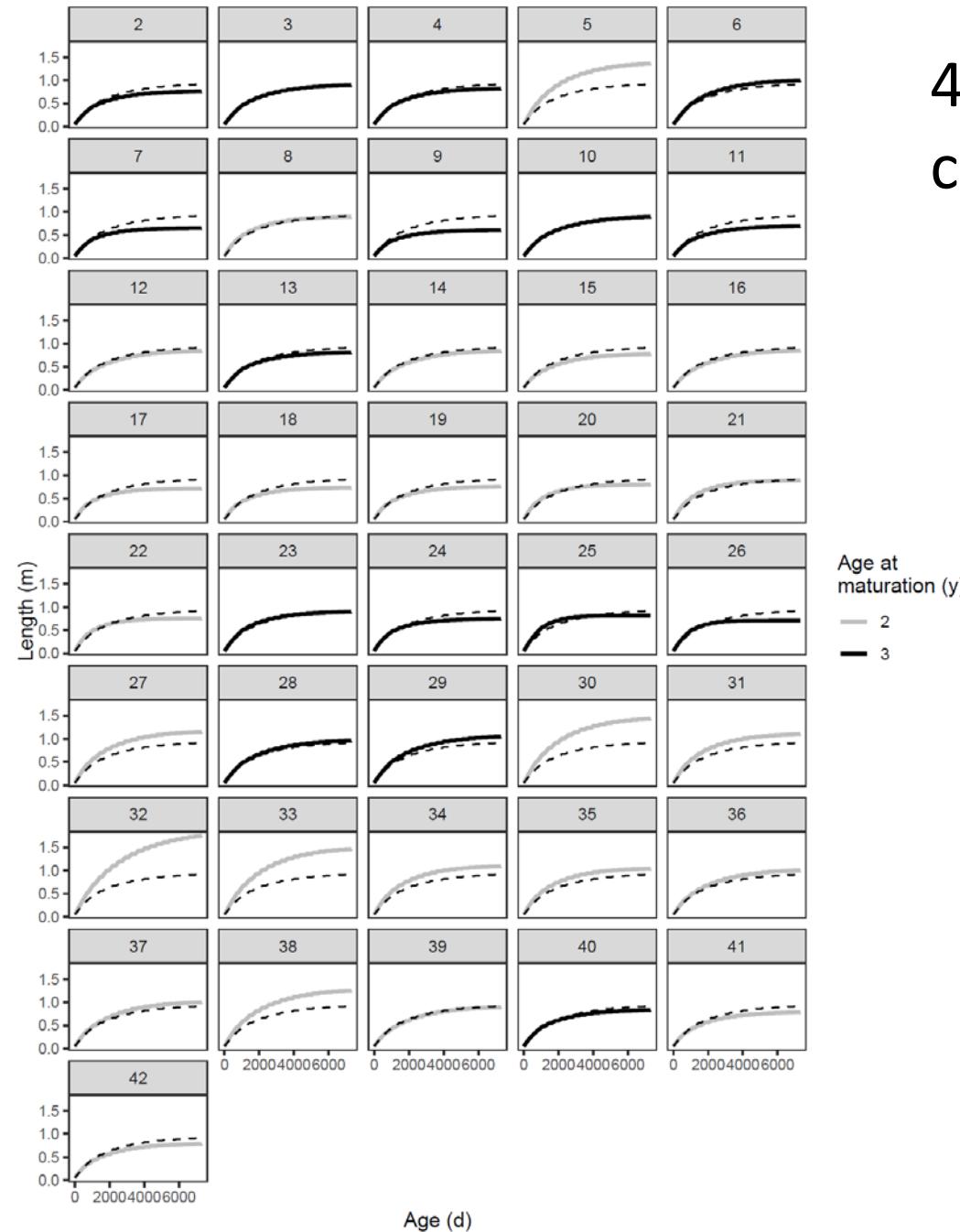
Temperature can affect intake, metabolism and mortality



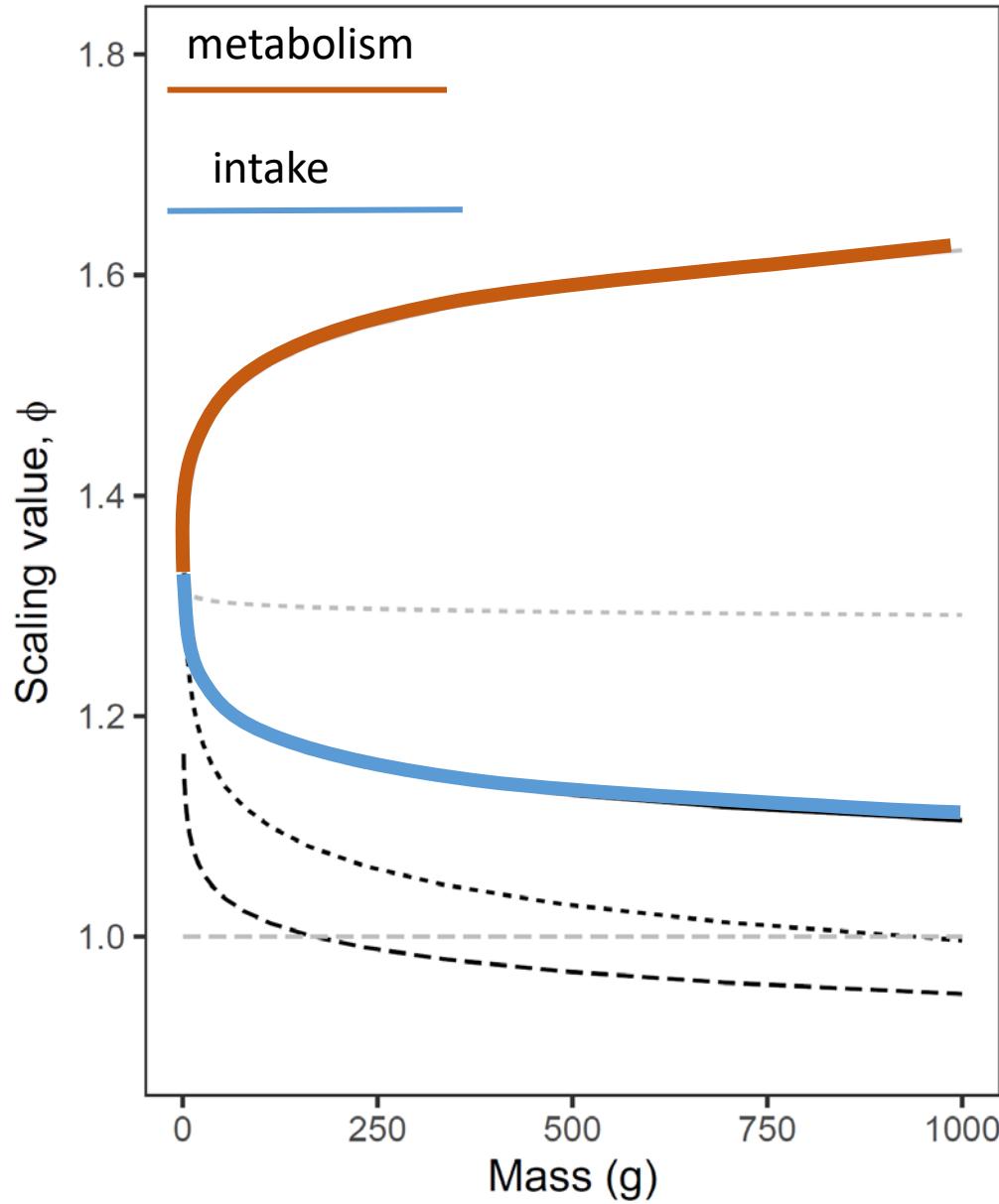
42 scenarios of different parameter combinations

| Name | Mat age | Mat wgt | Wgt 1y | Wgt 5y | Wgt 10y | Wgt 15y | Spawn 3y | Fitness | E_M | E_I | A_M | A_I | z_p | $M_{P,min}$ |
|---|------------|------------|-----------|-----------|------------|------------|-------------|---------|-------|-------|-------|--------|-------|-------------|
| Life-history responses in baseline scenario | | | | | | | | | | | | | | |
| Base (1) | 3 | 632 | 99 | 3026 | 6860 | 9063 | 150 | 314 | 0 | 0 | 0 | 0 | 8 | 0.2 |
| Scenario group I: Original TSR explanation – metabolism activation energy is higher: $E_M > E_I$ | | | | | | | | | | | | | | |
| I-1 (2) | 3 | 0.83 | 0.94 | 0.77 | 0.66 | 0.61 | 0.91 | 0.58 | 0.7 | 0 | 0 | 0 | 8 | 0.2 |
| I-2 (3) | 3 | 1.02 | 1.04 | 1.01 | 0.98 | 0.97 | 1.09 | 1.03 | 0.15 | 0.05 | 0 | 0 | 8 | 0.2 |
| I-3 (4) | 3 | 0.96 | 1.05 | 0.91 | 0.80 | 0.75 | 1.13 | 0.84 | 0.6 | 0.1 | 0 | 0 | 8 | 0.2 |
| Group Ia: Metabolism activation energy is higher, combined with different temperature-size interactions | | | | | | | | | | | | | | |
| I-4 (5) | 2 | 1.12 | 2.34 | 2.93 | 3.22 | 3.30 | 4.28 | 7.41 | 0.7 | 0.63 | 0 | 0.01 | 8 | 0.2 |
| I-5 (6) | 3 | 1.28 | 1.14 | 1.33 | 1.34 | 1.32 | 1.56 | 1.66 | 0.7 | 0.01 | 0 | 0.01 | 8 | 0.2 |
| I-6 (7) | 3 | 0.73 | 0.93 | 0.62 | 0.46 | 0.39 | 0.95 | 0.38 | 0.7 | 0.01 | 0.01 | 0 | 8 | 0.2 |
| I-7 (8) | 2 | 0.64 | 1.67 | 1.22 | 1.07 | 0.99 | 1.88 | 1.74 | 0.7 | 0.63 | 0 | -0.005 | 8 | 0.2 |
| I-8 (9) | 3 | 0.58 | 0.81 | 0.48 | 0.36 | 0.32 | 0.64 | 0.22 | 0.7 | 0.01 | 0 | -0.01 | 8 | 0.2 |
| I-9 (10) | 3 | 0.95 | 0.97 | 0.94 | 0.94 | 0.95 | 0.90 | 0.89 | 0.7 | 0.01 | -0.01 | 0 | 8 | 0.2 |
| I-10 (11) | 3 | 0.65 | 0.82 | 0.58 | 0.50 | 0.46 | 0.58 | 0.32 | 0.7 | 0.01 | -0.01 | -0.01 | 8 | 0.2 |
| Group Ib: Metabolism activation energy is higher, combined with increased mortality | | | | | | | | | | | | | | |
| I-11 (12) | 2 | 0.41 | 1.06 | 0.85 | 0.83 | 0.81 | 1.53 | 0.23 | 0.15 | 0.05 | 0 | 0 | 8 | 0.4 |
| I-12 (13) | 3 | 0.97 | 1.05 | 0.90 | 0.78 | 0.72 | 1.24 | 0.21 | 0.6 | 0.1 | 0 | 0 | 8 | 0.4 |
| Scenario group II: Life-history explanation - increased mortality only | | | | | | | | | | | | | | |
| II-1 (14) | 2 | 0.42 | 1.02 | 0.86 | 0.82 | 0.80 | 1.49 | 0.02 | 0 | 0 | 0 | 0 | 4 | 0.2 |

Dashed line is baseline, solid line is scenario

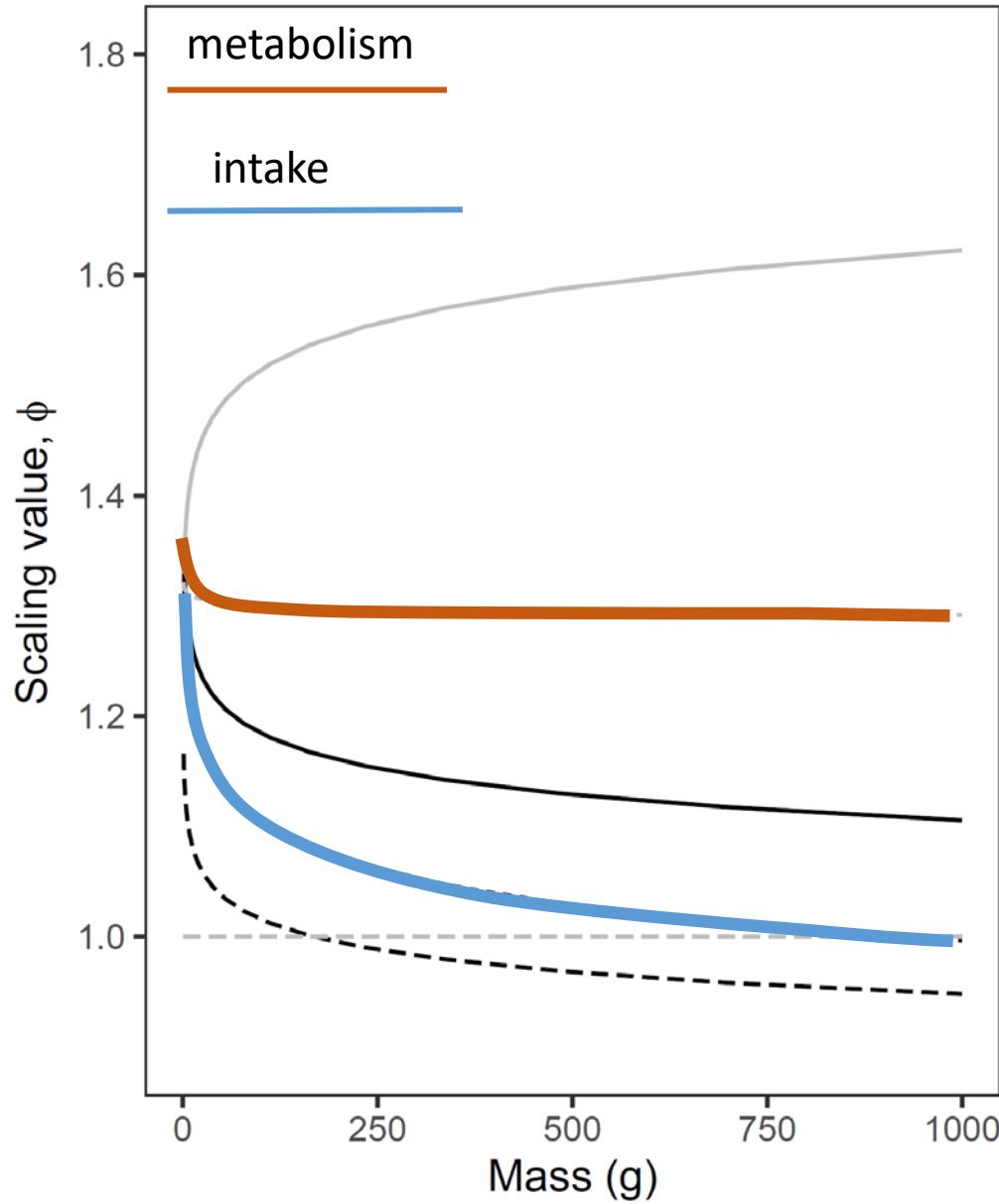


42 emergent growth and maturation curves



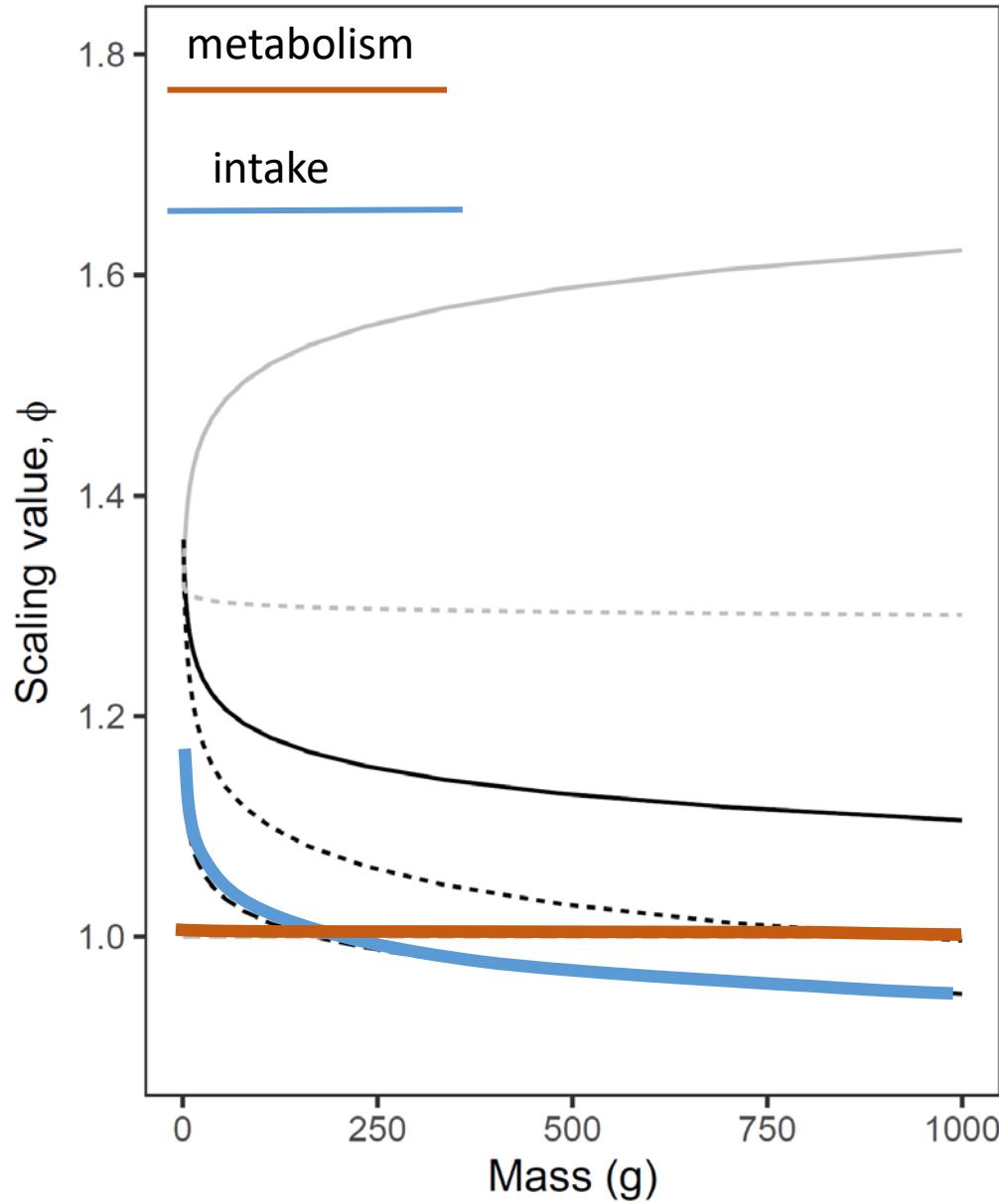
Two main ways how TSR can emerge

- 1. Metabolism increases more with size than intake*



Two main ways how TSR can emerge

1. *Or at least metabolism decreases with size slower than intake*

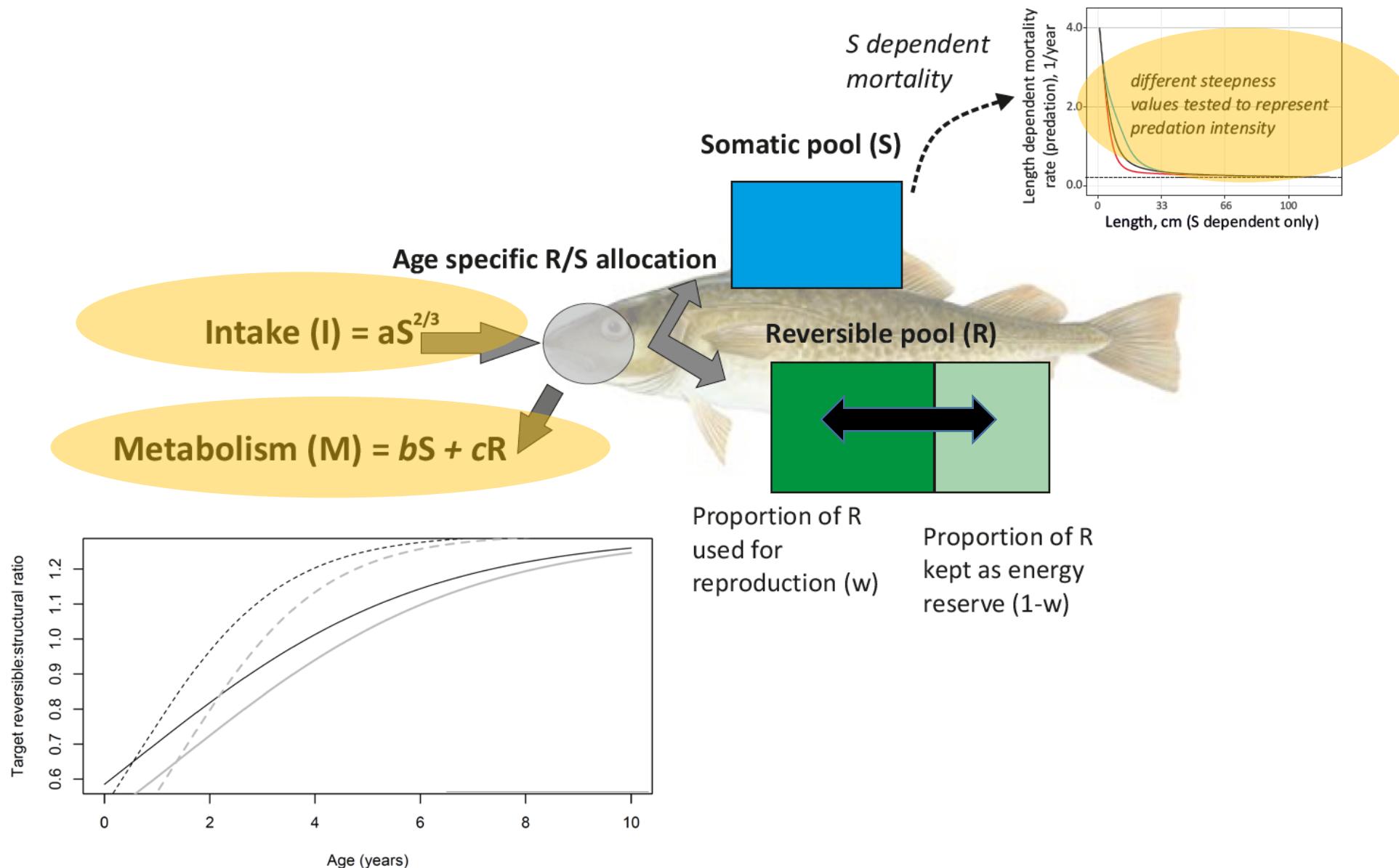


Two main ways how TSR can emerge

2. *Metabolism does not increase, but relative intake rate decreases in large fish + mortality increases*

Wootton et al. 2022, Ecol. Letters – TSR observed without increased baseline metabolic rate

In each case life-history optimisation is important



Take home & significance

Temperature – size rule growth is likely to be caused by a combination of **physiological processes related to food or oxygen intake and use**

AND

life-history optimisation of energy allocation between growth, reproduction and other processes

To understand how it works we need cross-disciplinary research and dialogue

Publication accepted in The Biological Bulletin special issue “An oxygen perspective on climate change”

Play with the model yourself!

github.com/astaaudzi/TSRmodel

Supplementary Material to Audzinyte & Richards: "The energetic cost of reproduction and its effect on optimal life-history strategies"

To run the model optimisation the Excel add-in "Solver" is required. The optimized parameters are shown in orange (r, abar and w). To explore optimal allocation and emergent life-history, modify blue parameter and run optimization using Solver (Data -> Solver).

Solver should maximise the fitness by changing r, abar and w and adhering to the condition that of $0.01 > w > 0.99$. Further explanations on parameters are given in Table 1 of the manuscript. NOTE - mortality is expressed in daily (not yearly) values

NOTE - the **r** and **abar** values given below are multiplied by 1000 and 0.01 respectively to improve Solver efficiency, because optimised values should be around 1. In the equation 1 of the manuscript abar is reflected in days at which allocation to R is half the maximum

To find the optimal solution multiple starting points of w must be tested. In particular for higher fishing rates, higher w values ($w > 0.8$) might need to be used as initial starting points!

| Parameter | Value | Age | Breed | Lambda | Structure | Reserve | Total | FishLength | Lambda observed | FishMort | NatMort | StarvMort | MortRate | MortProb | StillAlive | Assimilated Intake | Maintenanc e cost | Net Intake | Rneed | Sneed | Intake Rmax | Reserves Rmax | Intake reserves Smax | Reserves reserves used | Intake structure used | Net intake remaining | | |
|---------------------------------------|------------------|-------------------------|-------|--------|-----------|-------------|------------|------------|-----------------|------------|---------|------------|------------|------------|------------|--------------------|-------------------|------------|------------|------------|-------------|---------------|----------------------|------------------------|-----------------------|----------------------|------------|---|
| weight at age 0 | 1 | 1 | F | 1000 | | | | | | | | | | | | | | | | | | | | | | | | |
| Structure/reserve allocation strategy | lambda min | 0 | 2 | F | 900 | | | | | | | | | | | | | | | | | | | | | | | |
| | lambda_max | 1.3 | 3 | F | 900 | | | | | | | | | | | | | | | | | | | | | | | |
| Intake scaling | I0 | 0.1 | 4 | F | 800 | | | | | | | | | | | | | | | | | | | | | | | |
| | I1 | 0.66667 | 5 | F | 700 | | | | | | | | | | | | | | | | | | | | | | | |
| Structure maintenance | cS | 0.003 | 6 | F | 600 | | | | | | | | | | | | | | | | | | | | | | | |
| Reserve maintenance | cR | 0.0003 | 7 | F | 600 | | | | | | | | | | | | | | | | | | | | | | | |
| Efficiency of structure sys | eS | 0.33333 | 8 | F | 500 | | | | | | | | | | | | | | | | | | | | | | | |
| Efficiency of reserve sys | eR | 0.9 | 9 | F | 500 | | | | | | | | | | | | | | | | | | | | | | | |
| Reproduction cost | r0 | 6 | 10 | F | 400 | | | | | | | | | | | | | | | | | | | | | | | |
| | r1 | 0.6 | 11 | F | 300 | | | | | | | | | | | | | | | | | | | | | | | |
| Shape parameter for len | l | 5787 | 12 | F | 200 | | | | | | | | | | | | | | | | | | | | | | | |
| Natural mortality | MPmin | 0.00137 Daily rate | 13 | F | 100 | | | | | | | | | | | | | | | | | | | | | | | |
| | MPmax | 0.01644 Daily rate | 14 | F | 100 | | | | | | | | | | | | | | | | | | | | | | | |
| | zp | 8 | 15 | F | 0 | | | | | | | | | | | | | | | | | | | | | | | |
| Starvation mortality | MCmax | 0.01096 Daily rate | 16 | F | 0 | | | | | | | | | | | | | | | | | | | | | | | |
| | zC | 6 | 17 | F | 0 | | | | | | | | | | | | | | | | | | | | | | | |
| Fishing morality | MFmax | 0 Daily rate | 18 | F | 0 | | | | | | | | | | | | | | | | | | | | | | | |
| | Lbar | 0.3 | 19 | F | 12000 | | | | | | | | | | | | | | | | | | | | | | | |
| | zf | 20 | 20 | F | 0 | | | | | | | | | | | | | | | | | | | | | | | |
| | r (optimized) | 3.41 multiplied by 1000 | 21 | F | 10000 | | | | | | | | | | | | | | | | | | | | | | | |
| | abar (optimized) | 2.48 multiplied by 0.01 | 22 | F | 0 | | | | | | | | | | | | | | | | | | | | | | | |
| | w (optimized) | 0.821 | 23 | F | 8000 | | | | | | | | | | | | | | | | | | | | | | | |
| Fitness | 35.0358 | maximise this | 24 | F | 0 | | | | | | | | | | | | | | | | | | | | | | | |
| | Mean age | 0.34 | 25 | F | 6000 | | | | | | | | | | | | | | | | | | | | | | | |
| | Age first rep | 2 | 26 | F | 4000 | | | | | | | | | | | | | | | | | | | | | | | |
| | Mass at F R | 776.26 | 27 | F | 0 | | | | | | | | | | | | | | | | | | | | | | | |
| | Mass at 1 y | 154.57 | 28 | F | 0 | | | | | | | | | | | | | | | | | | | | | | | |
| | Mass at 5 y | 3685.07 | 29 | F | 0 | | | | | | | | | | | | | | | | | | | | | | | |
| | Mass at 10 | 7896.61 | 30 | F | 0 | | | | | | | | | | | | | | | | | | | | | | | |
| | Mean weight | 889.38 | 31 | F | 0 | | | | | | | | | | | | | | | | | | | | | | | |
| Ambient temperature | Temp | 285 | 32 | F | 0 | | | | | | | | | | | | | | | | | | | | | | | |
| reference temp, in Kelvin | Tref | 283 | 33 | FALSE | 0.4221 | 1.93937091 | 0.81671544 | 2.75608635 | 0.06946016 | 0.4211239 | 0.01 | 2500 | 0 | 2000 | 0 | 1500 | 0 | 1000 | 0 | 500 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| metabolism activation er | ea_met | 0.55 | 34 | FALSE | 0.42307 | 1.99046001 | 0.84016385 | 2.83062395 | 0.07006482 | 0.4220953 | 0 | 0.005 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| intake activation energy | ea_int | 0.63 | 35 | FALSE | 0.42404 | 0.024420204 | 0.86407461 | 2.9064767 | 0.07066905 | 0.42306786 | 0 | 0.005 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| botzman constant | k_boltz | 8.62e-05 | 36 | FALSE | 0.42502 | 0.095202404 | 0.88485295 | 2.98365538 | 0.07127286 | 0.42404158 | 0 | 0.005 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| emergent metabolism scalar | met_scalar | 1.17 | 37 | FALSE | 0.42599 | 2.14886695 | 0.91330382 | 3.06217077 | 0.07187624 | 0.42501646 | 0 | 0.005 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| emergent intake scalar | intake_scalar | 1.20 | 38 | FALSE | 0.42697 | 2.20340124 | 0.93863238 | 3.14203362 | 0.0724792 | 0.42599249 | 0 | 0.005 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| size dependency of met | ca_met | 0 | 39 | FALSE | 0.42795 | 2.25881093 | 0.96444376 | 3.22324568 | 0.07308173 | 0.42699666 | 0 | 0.00976752 | 0.00084564 | 0.01061315 | 0.01055703 | 0.644403 | 0.2063725 | 0.00827739 | 0.19809511 | 0.00202984 | 0 | 0.1782856 | 0.86799937 | 0.00630104 | 0.00202984 | 0 | 0.19563979 | |
| size dependency of intal | ca_int | 0 | 40 | FALSE | 0.42893 | 2.31510158 | 0.99074306 | 3.30584644 | 0.07368383 | 0.42794798 | 0 | 0.00972716 | 0.00084069 | 0.01056785 | 0.01051221 | 0.6376 | 0.20978071 | 0.00848446 | 0.20130255 | 0.00226755 | 0 | 0.1811273 | 0.89166875 | 0.00710018 | 0.00226755 | 0 | 0.19878305 | |
| | | | 41 | FALSE | 0.42991 | 2.37227875 | 1.01753546 | 3.38991421 | 0.07428555 | 0.42829744 | 0 | 0.00968703 | 0.00083576 | 0.01052279 | 0.01046762 | 0.630897 | 0.21322707 | 0.00869842 | 0.20453227 | 0.00232625 | 0 | 0.1840790 | 0.91578192 | 0.00817674 | 0.00232625 | 0 | 0.20194774 | |
| | | | 42 | FALSE | 0.43089 | 2.43034794 | 1.04482612 | 3.47517406 | 0.07488675 | 0.42990804 | 0 | 0.00964712 | 0.00083086 | 0.01047798 | 0.01042328 | 0.624293 | 0.21669266 | 0.00809085 | 0.20778417 | 0.00238594 | 0 | 0.18700575 | 0.94034531 | 0.00962607 | 0.00238594 | 0 | 0.20513319 | |
| | | | 43 | FALSE | 0.43187 | 2.48931463 | 1.07260213 | 3.56193484 | 0.07548575 | 0.43088977 | 0 | 0.00960743 | 0.00082598 | 0.01034341 | 0.01037917 | 0.617786 | 0.22018366 | 0.0091255 | 0.20730202 | 0.00244664 | 0 | 0.18950325 | 0.96535819 | 0.00705320 | 0.00244664 | 0 | 0.20833967 | |
| | | | 44 | FALSE | 0.43286 | 2.54918427 | 1.10092291 | 3.65010719 | 0.07608799 | 0.43187263 | 0 | 0.00956798 | 0.00082112 | 0.01038908 | 0.01035354 | 0.611374 | 0.22370008 | 0.00934585 | 0.21435418 | 0.00205836 | 0 | 0.19291874 | 0.90903062 | 0.007415068 | 0.00205836 | 0 | 0.21156793 | |

Reproductive cost versus R and S weight

Fish length (m)

Reserve:Structure ratio

Daily probability of mortality

Mortality components

Survivorship

Spawning mass (g)

Expected fitness components (g)



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