Two-stanza growth for tropical tunas: Myth or reality?

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The Von Bertalanffy's growth model (1938)

Bioenergetics grounds

$$\underbrace{\frac{dW(t)}{dt}}_{\text{Changes in individual weight}} = \underbrace{\eta \times (W(t))^d}_{\text{Energy assimilation}} - \underbrace{\kappa \times (W(t))^n}_{\text{Energy losses}}$$

Where η and κ are constants of anabolism and catabolism, respectively.

Hypotheses

1. Energy density is constant
2. Energy assimilation is proportional to surface areas ($d = 2/3$)
3. Energy loss is proportional to body weight ($n = 1$)

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Assumption of isometric growth: $W(t) = a \times L(t)^3$

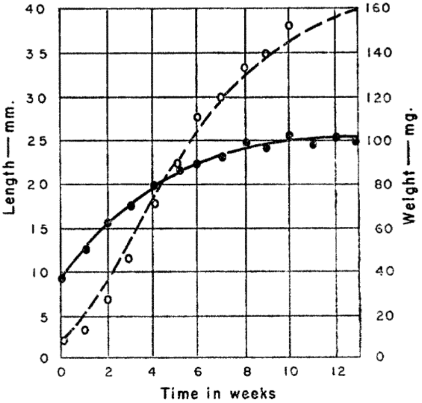
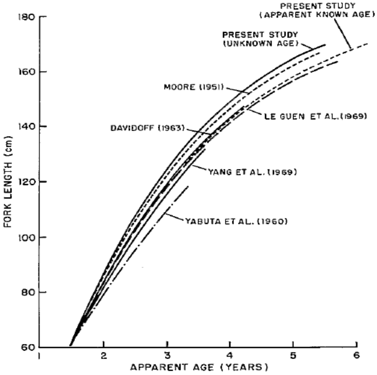
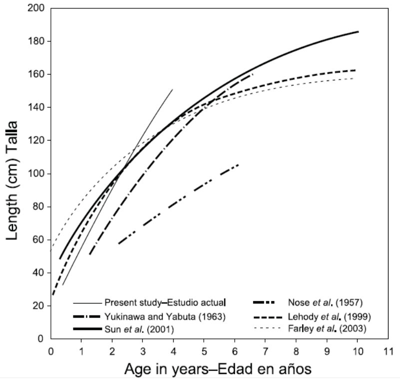


Figure: $L(t) = L_\infty \times (1 - \exp(-K \times (t - t_0)))$. Growth for females *Lebistes reticutatus* (von Bertalanffy & Müeller 1949)

von Bertalanffy growth initially used for tropical tunas



(a) Yellowfin in the Atlantic (Le Guen & Sakagawa 1972)



(b) Bigeye in the eastern Pacific (Schaefer & Fuller 2006)

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Tropical tunas question the use of VBGMs

Region	Size	Rate	Data	Source
E. Atlantic	40-70 cm	1.56 cm mo^{-1}	Catch & Tag	Fonteneau 1980
E. Atlantic	40-70 cm	1.48 cm mo^{-1}	Tag	Bard 1984
E. Atlantic	40-70 cm	1.62 cm mo^{-1}	Catch	Gascuel et al. 1992
W. Atlantic	40-70 cm	1.62 cm mo^{-1}	Catch	Gaertner & Pagavino 1992
W. Pacific	30-50 cm	1.3 cm mo^{-1}	Catch	Brouard et al. 1984

Table: Mean monthly growth rates estimated for different yellowfin populations derived from length-frequency and tagging data

Observations from the 3 oceans

Growth rates estimated for small yellowfin tuna stocks appear significantly lower than expected from a von Bertalanffy model

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2-stanza growth currently used for management advice

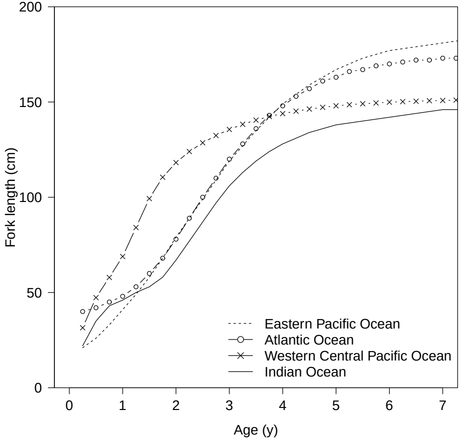

Figure: Growth curves used in yellowfin assessments within RFMOs

IOTTP data support a 2-stanza growth for yellowfin

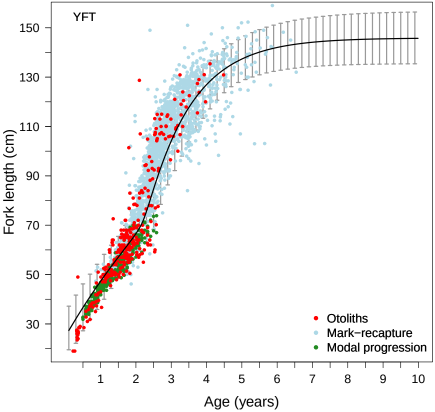

Figure: Bayesian integrated growth curve for yellowfin (Dortel et al. 2012)

IOTTP data support a 2-stanza growth for bigeye

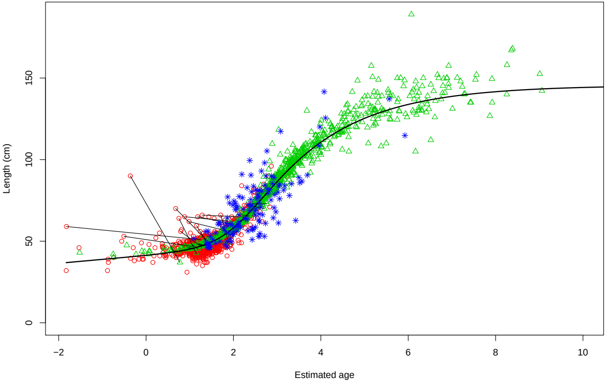

Figure: Integrated growth curve for bigeye (Eveson et al. 2012)

IOTTP data support a 2-stanza growth for skipjack

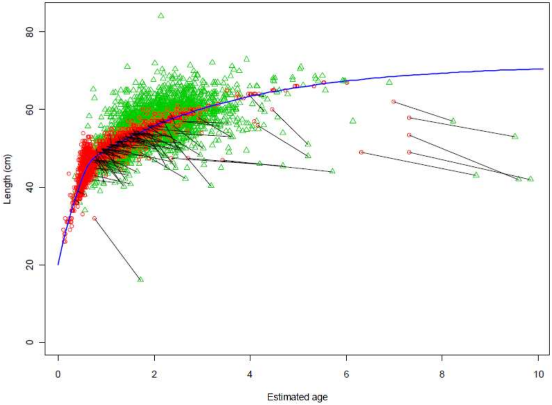

Figure: Integrated growth curve for skipjack (Eveson et al. 2012)

Methodological issues or bio-ecological reasons?

Potential sources of error

1. Modal progression analysis based on length-frequency data of the catch: Perhaps?
2. Age reading of otoliths due to interpretation (Cf. Sardenne et al.): Perhaps?
3. Fish selection at-tagging through pole and line gear: NO (Cf. Hallier et al.)
4. Fish selection at-recovery due to specific fishing grounds from recovery gears
5. Fish selection at-recovery due to size-based selectivity from recovery gears

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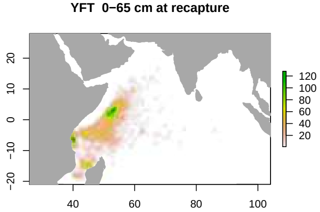
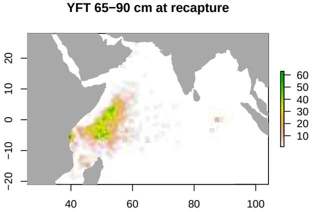
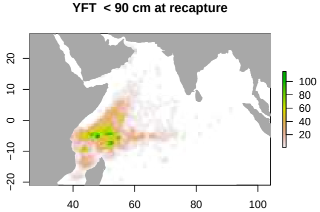
Yellowfin recaptures spread over the western Indian Ocean







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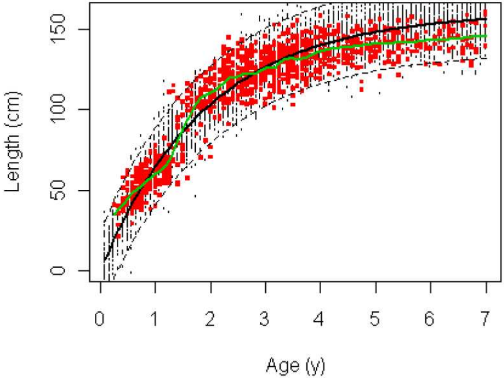

Figure: Simulations suggest that a 2-stanza growth might result from size-based selectivity of the purse seine fishery (Kolody 2011)

Rationale

Simulation approaches have been conducted during IOTC working groups (Hampton 2008, Anganuzzi 2008, Kolody 2011) but they yielded contradictory results

Objectives

Develop a simulation framework modelling tuna growth estimation from mark-recapture experiments:

1. To investigate the effects of individual variability and size-dependent natural mortality,
2. To test the hypothesis that size-based selectivity of some fishing gears might modify our perception of the functional form of tuna growth
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Simulating a mark-recapture experiment

Principles

1. Fish tagged and released with age assumed known at-tagging
2. They grow over time following a von Bertalanffy growth model with individual variability
3. Natural mortality derived from stock assessment
4. At each time step: (i) they die naturally, or (ii) they are caught by the fishery with size-based selectivity, or (iii) they survive
5. VB and VB-logK models are fitted to the age-length data
6. Models are compared using loglikelihood ratios

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Case study of the Indian Ocean yellowfin

Tagging

- 50,911 fishes tagged: 46,845 from the RTTP and 4,066 from small-scale tagging operations
- Size-frequency histograms-at-tagging similar to the IOTTP

Biology

- VB growth with μ_K=0.4 y^{-1} and μ_{L_∞}=160 cm
- Individual variability through normal distribution on L_∞ and K with standard deviation of 10 cm and 0.1 y^{-1}, respectively
- Size-based natural mortality

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Recaptures

- Assumption of separability of gear-specific fishing mortality
- Fishing mortality constant over the period analysed: F=0.2
- Size-based selectivity constant over the period analysed

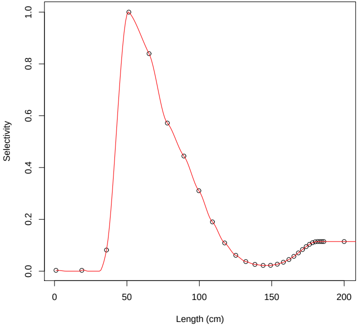

Figure: Size-based selectivity for pole and liners

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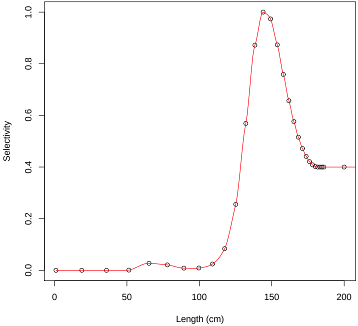

Figure: Size-based selectivity for longliners

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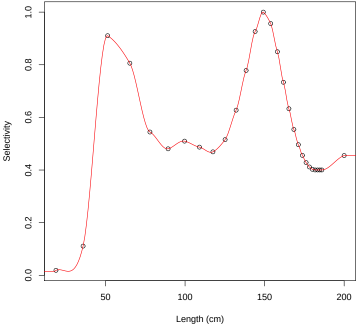

Figure: Size-based selectivity for purse seiners

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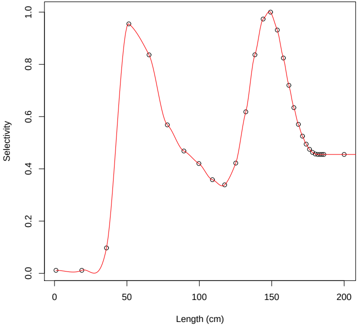

Figure: Size-based selectivity for all fishing gears

Scenario runs

- Gear-specific size-based selectivity
- With and without sexual dimorphism in growth with sex-ratio at-tagging of 0.5:
  - Males: $\mu_{L\infty}$=160 cm and μ_K=0.4
  - Females: $\mu_{L\infty}$=140 cm and μ_K=0.6
- Sensitivity to levels of individual variability
- Sensitivity to natural mortality: U-shaped (Hampton 2000)

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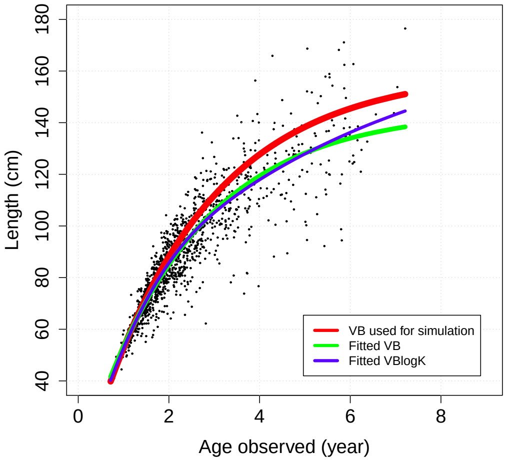

Figure: **Pole and liners**: Underestimation of growth for large sized fishes & no significant difference between VB and VB-logK models

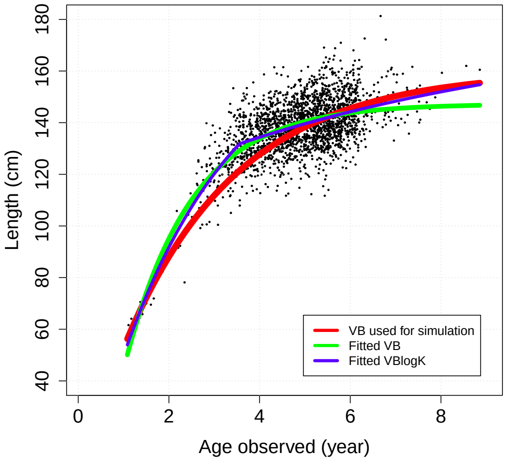

Figure: **Longliners**: Overestimation of growth for small sized fishes & significant difference between VB and VB-logK models

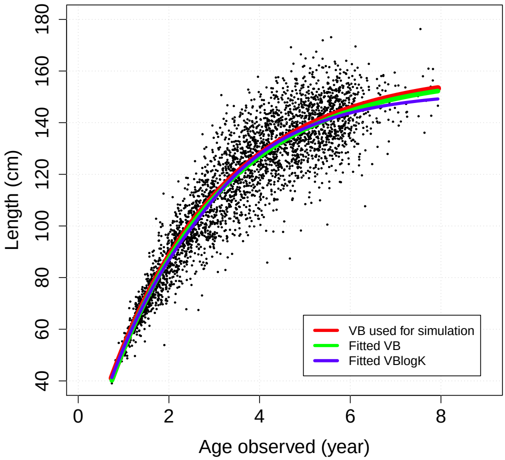

Figure: **Purse seiners**: No bias in growth & no difference between VB and VB-logK models

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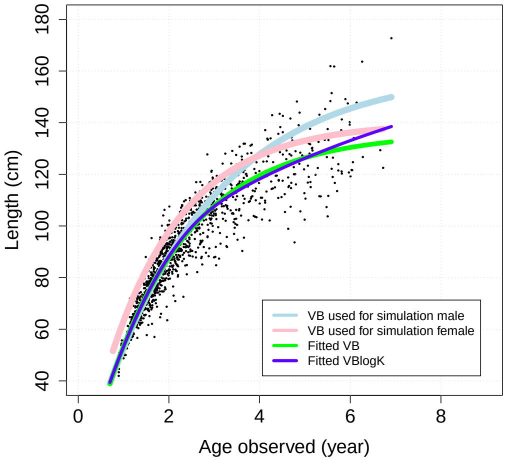

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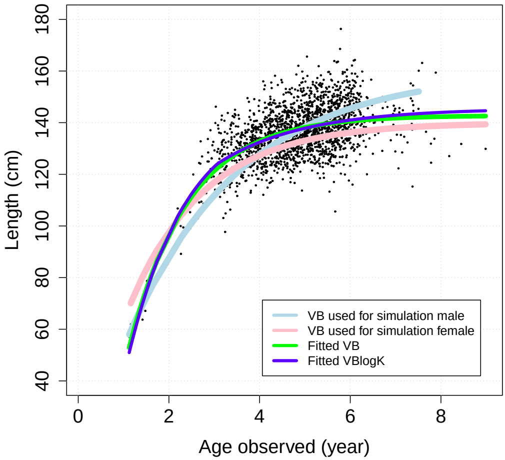

Figure: **Longliners**: Bias in growth estimation & no significant difference between VB and VB-logK models

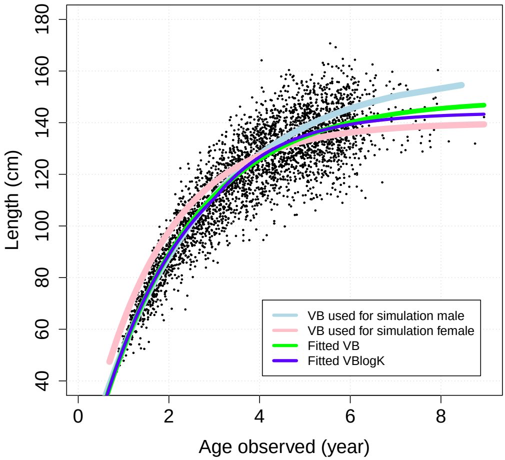

Figure: **Purse seiners**: Growth model in between male and female growth & no significant difference between VB and VB-logK models

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Key points

- Size-based selectivity might result in biases in growth estimation from mark-recapture experiments
- Purse-seine selectivity does not result in biases in "unisex" growth due to the large size-range of fishes harvested
- Recaptures limited to longline or pole and line fishing would result in strong biases in growth
- The absence of small sized tunas in longline fisheries might result in apparent 2-stanza growth
- Simulating sexual dimorphism in growth (i) results in similar patterns in estimation bias and (ii) does not indicate the emergence of 2-stanza growth from gear selectivity

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What eco-physiological factors might explain the 2 stanzas?

Changes in metabolism

- For yellowfin, shift in growth at about 73 cm ($\pm$ 7 cm) seems to match with period of acquistion of sexual maturity (Zudaire et al. 2010)
- Reduction in energy costs linked to change in aggregative behaviour and associated decrease in inter-specific competition
- Development of swim bladder, subcutaneous heat exchangers, deep red muscle, ram jet ventilation and anal and pectoral fins and associated reduction in energy costs as well as changes in utilisation of the vertical habitat

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Going back to von Bertalanffy's studies

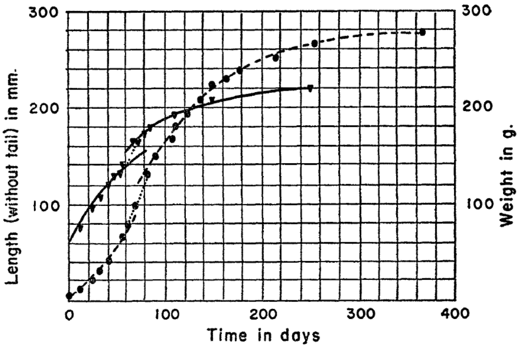

Figure: Growth of the albino rat with shift in mechanisms of energy allocation at maturity: 2 growth cycles must be distinguished (von Bertalanffy 1941)

What we call growth of even a simple organism is a tremendously complex phenomenon from the biochemical, physiological, cytological, and morphological viewpoints

Ludwig von Bertalanffy, 1957

The VB model is nested in the VB-logK model

Assumption of lognormal distribution of observed sizes

$$\begin{aligned}
\log \ell_i^* &\sim \mathcal{N}\left(\log L_{VB}(t_i|\theta_{VB}) - \sigma_2^2/2, \sigma_1^2\right), \\
\log \ell_i^* &\sim \mathcal{N}\left(\log L_{VB\log K}(t_i|\theta_{VB\log K}) - \sigma_2^2/2, \sigma_2^2\right).
\end{aligned}$$

On obtient donc deux vraisemblances lognormales $L_{VB}(D|\theta_{VB})$ et $L_{VB\log K}(D|\theta_{VB\log K})$ où D indique les données

$$R = 2\log\frac{L_{VB\log K}(\hat{\theta}_{VB\log K})}{L_{VB}(\hat{\theta}_{VB})} \sim \frac{1}{2}\delta_0 + \frac{1}{2}\chi_1^2$$