Modelling the evolution of the size-distribution in aquatic ecosystems

Laura Kanzler

CNRS &
Laboratoire Jacques-Louis Lions - Sorbonne Université

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CIMPA School on "Mathematical models in biology and related applications of partial differential "

Joint work with *B. Sarels* (LJLL), *B. Perthame* (LJLL), *E. Thebault* (iEES)

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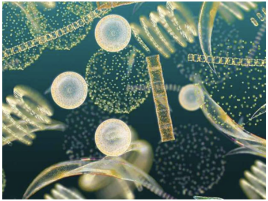
Main Motivations to Study the Size-structure in Aquatic Ecosystems

- Gain **insights** into impacts of human- and environment driven changes on the aquatic ecosystem
  - Fishing, changes in nutrient levels
  - Pollution, change in temperature
- Understanding the **internal ecosystem functioning**
  - Collective life activities of its organisims
  - Giving rise rise to **emergent distributions of biomass**, **abundance** and **production of organisms**
- Understanding the direct and indirect **influence organisms of different trophic positions** have on each other



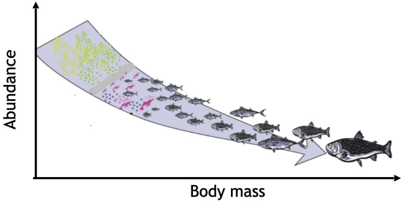


Figure: Blanchard et.al, Journal of Animal Ecology, 2008

- **Body size** as 'master trait' (Elton, Animal Ecology, 1927)
- Treating individuals as **particles** with states given by their size
- **Sheldon's conjecture** (Sheldon et al., Liminology Oceanography, 1972]): $\int_{w_1}^{w_2} wf \, \mathrm{d}w = \ln\left(\frac{w_2}{w_1}\right)$, implying $f(w) \approx w^{-2}$

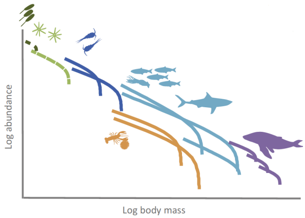


Figure: Blanchard et. al, Journal of Animal Ecology, Trends Ecol Evol., 2017

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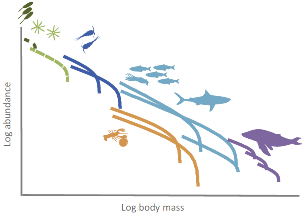
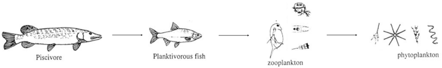


Figure: Blanchard et. al, Journal of Animal Ecology, Trends Ecol Evol., 2017

Development of size-spectrum models (SSMs):

- Age-Structured (McKendrick-von Foerster type):
  - Benoît, Rochet, J. Theor. Biol., 2003
  - Andersen, Beyer, Fish & Fisheries, 2015
  - Blanchard et. al, Journal of Animal Ecology, Trends Ecol Evol., 2017
- Jump-growth/'collisional' -type:
  - Datta, Delius, Law, Bulletin of Mathematical Biology, 2010



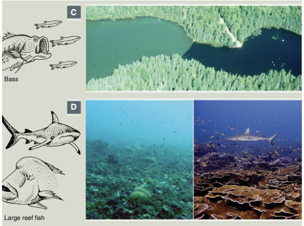


Figure: Estes et. al., Science, 2011

- **Cascade effect**, describes the suppression of specific trophic levels in the ecosystem as result of an indirect influence from one trophic level to the second next lower or higher
- Top-down or bottom-up effects
- (Hairston et al., The American Naturalist, 1960), (Estes et. al., Science, 2011), (Rossberg, Gaedke, Kratina, Nat Commun 10, 2019)

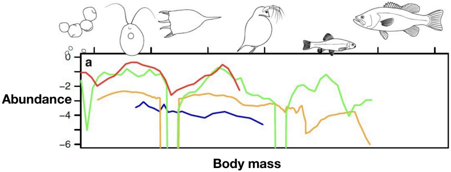


Figure: Rossberg, Gaedke, Kratina, Nat. Commun., 2019

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Modelling

Microscopic dynamics:

- Each individual is characterized by its **body-weight/-size** $w \in \mathbb{R}_+$ at time $t > 0$
- $f = f(w,t)$ denotes the **size-spectrum distribution** function of the ecosystem
- We assume **binary predation events** between two individuals
- Predation event: $(0 < K, K' \ll 1)$

$$(w, w_*) \to \left(w + K w_*, \frac{1-K}{K'} K' w_* \right),$$

- K . . . **assimilation constant**
- K' . . . **'offspring' production** constant

Phase space: $w \in \mathbb{R}_+$, time $t > 0$

$$\partial_t f(w) = \int_0^{\frac{w}{K}} k(w - Kw_*, w_*) f(w - Kw_*) f(w_*) \, \mathrm{d}w_* + \frac{1-K}{K'^2} \int_0^\infty k\left(w_*, \frac{w}{K'}\right) f\left(\frac{w}{K'}\right) f(w_*) \, \mathrm{d}w_* - \int_0^\infty \Big(k(w, w_*) + k(w_*, w)\Big) f(w_*) f(w) \, \mathrm{d}w_*,$$

$$f(w, 0) = f_0(w)$$

- Smoluchowski equation (Phys. Z., 1916)
- Collision-induced breakage equation (Giri, Laurençot, JDE, 2021)

Phase space: $w \in \mathbb{R}_+$, time $t > 0$

$$\begin{aligned}\partial_t f(w) &= \int_0^{\frac{w}{K}} k(w - Kw_*, w_*) f(w - Kw_*) f(w_*)\, \mathrm{d}w_* \\ &+ \frac{1-K}{K'^2} \int_0^\infty k\left(w_*, \frac{w}{K'}\right) f\left(\frac{w}{K'}\right) f(w_*)\, \mathrm{d}w_* \\ &- \int_0^\infty \Big(k(w, w_*) + k(w_*, w)\Big) f(w_*) f(w)\, \mathrm{d}w_*,\end{aligned}$$

$$f(w, 0) = f_0(w)$$

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Feeding kernel: (asymmetric!)

$k(w, w_*)$ ... rate at which an organism of size w feeds on a prey with weight w_*

Strong dependence on the **ratio** between the weights of predator and prey (following Ware, J. Fish. Res. Board Can., 1978, Benoît & Rochet, J. Theor. Biol., 2004):

$$k(w, w_*) = Aw^{\alpha} s\left(\frac{w}{w_*}\right)$$

- Aw^{α} ... volume searched per unit time by an individual with size w, modelled as **allometric function** of the animal's weight (Kleiber, 1932, Brown, Ecology 2004)
- $s : \mathbb{R}_+ \to \mathbb{R}_+$ ... **feeding preference function**

$$s(r) = \begin{cases} \frac{1}{\sigma\sqrt{2\pi}} \exp\left(-\frac{(r-B)^2}{2\sigma^2}\right) =: s_G(r) \\ \\ \frac{1}{\sigma^2} \exp\left(\frac{\sigma^2}{(r-B)^2-\sigma^2}\right) \mathbb{1}_{[B-\sigma, B+\sigma]}(r) =: s_C(r) \end{cases}$$

- B ... preferred feeding ratio
- σ ... variance

Size-spectrum Model for Aquatic Ecosystems

$$
\begin{aligned}
\partial_t f(w) = Q(f,f) &= G_1(f,f) + G_2(f,f) - L_1(f,f) - L_2(f,f) \\
&:= A \int_0^{\frac{w}{K}} (w - Kw_*)^\alpha \, s\left(\frac{w - Kw_*}{w_*}\right) f(w - Kw_*) f(w_*) \, \mathrm{d}w_* \\
&\quad + A \frac{1-K}{K'^2} \int_0^\infty w_*^\alpha s\left(\frac{w_* K'}{w}\right) f\left(\frac{w}{K'}\right) f(w_*) \, \mathrm{d}w_* \\
&\quad - A \int_0^\infty \left(w^\alpha s\left(\frac{w}{w_*}\right) + w_*^\alpha s\left(\frac{w_*}{w}\right)\right) f(w_*) f(w) \, \mathrm{d}w_*,
\end{aligned}
\tag{1}
$$

$$f(w,0) = f_0(w)$$

- Existence of solutions?
- Equilibria?
- Asymptotic behaviour: $f(\cdot,t) \to ?$ as $t \to \infty$?

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$$\mathcal{M}_m[f](t) := \int_0^\infty w^m f(w,t)\,\mathrm{d}w,$$
$$\dot{\mathcal{M}}_m[f](t) = \int_0^\infty \int_0^\infty F\left(\frac{w}{w_*}, m\right) w^\alpha w'^m s\left(\frac{w}{w_*}\right) f(w) f(w_*)\,\mathrm{d}w_*\,\mathrm{d}w$$

$$\dot{\mathcal{M}}_1[f](t) = \int_0^\infty \int_0^\infty ((w + w_*) - (w + w_*))\, w^\alpha s\left(\frac{w}{w_*}\right) f(w) f(w_*)\,\mathrm{d}w_*\,\mathrm{d}w$$

- Conservation of total biomass **provided that the involved integrals are finite**!
- *"Dust formation"*

- For $s = s_C$ we have existence of constants $0 < m_* < 1$ and $1 < \tilde{m} < \infty$ only depending on B, σ, K, K' s.t.
  - $F\left(\frac{w}{w'}, m\right) > 0, \ \forall m \in (\tilde{m}, 1)$
  - $F\left(\frac{w}{w'}, m\right) < 0, \ \forall m \in (1, m_*)$
- Conservation of biomass $\dot{\mathcal{M}}_1[f](t) = 0$ for $\alpha \in (1, m_*)$

Theorem (L. K., B. Perthame, B. Sarels, Global existence)

Let $s = s_C$, such that $\inf \operatorname{supp}(s) = B - \sigma > 0$ and K and K' small enough. We further assume that for the search-volume exponent it holds $\alpha \in (1, m_*)$ and $f_0 \in L^1_+(\mathbb{R}_+, w)$ such that

$$\mathcal{M}_\alpha^0 := \int_0^\infty w^\alpha f_0(w) \, \mathrm{d}w < \infty.$$

Then there exists a unique solution $f \in C^1\left([0,\infty), L^1_+(\mathbb{R}_+, w)\right)$ to (1) and $\mathcal{M}_\alpha(t) := \int_0^\infty w^\alpha f(w,t) \, \mathrm{d}w \leq \mathcal{M}_\alpha^0$.

- For $s = s_C$ we have existence of constants $0 < m_* < 1$ and $1 < \tilde{m} < \infty$ only depending on B, σ, K, K' s.t.
  - $F\left(\frac{w}{w'}, m\right) > 0, \ \forall m \in (\tilde{m}, 1)$
  - $F\left(\frac{w}{w'}, m\right) < 0, \ \forall m \in (1, m_*)$

- Conservation of biomass $\dot{\mathcal{M}}_1[f](t) = 0$ for $\alpha \in (1, m_*)$

Theorem (Local existence)

Let $s = s_C$, such that $\inf \operatorname{supp}(s) = B - \sigma > 0$ and K and K' small enough. Moreover, let $\alpha \in (\tilde{m}, 1)$ and assume $f_0 \in L^1_+(\mathbb{R}_+, w)$ such that

$$\mathcal{M}^0_\alpha := \int_0^\infty w^\alpha f_0(w) \, \mathrm{d}w < \infty.$$

Then there exists a unique solution $f \in C^1\left(\left[0, \bar{T}\right), L^1_+(\mathbb{R}_+, w)\right)$ to (1), where $\bar{T} = \bar{T}(B, \sigma, K, K')$.

Blow-up of $\mathcal{M}_\alpha$ in finite time is possible:

$$\mathcal{M}_\alpha(t) \leq \frac{\mathcal{M}_\alpha(0)}{1 - tC(B, \sigma, K, K')\mathcal{M}_\alpha(0)}.$$

Trivial equilibrium: $\bar{f}_0(w) = \frac{\mathcal{M}}{w}\delta_0(w)$

Lemma (Extinction of all species)

Let f be a solution to (1) with feeding preference function $s = s_C$ and parameters fulfilling $B - \sigma < 1 < B + \sigma$. Further, assume initial conditions f_0 satisfying $\int_0^\infty w^m f_0 \,\mathrm{d}w < \infty$, for at least one $m \in (1, m_*)$ with $m < 2$. Then f satisfies

$$\lim_{t\to\infty} f(t) = \bar{f}_0,$$

in the sense of distributions.

Trivial equilibrium: $\bar{f}_0(w) = \frac{\mathcal{M}}{w}\delta_0(w)$

Lemma (Extinction of all species)

Let f be a solution to (1) with feeding preference function $s = s_C$ and parameters fulfilling $B - \sigma < 1 < B + \sigma$. Further, assume initial conditions f_0 satisfying $\int_0^\infty w^m f_0 \, \mathrm{d}w < \infty$, for at least one $m \in (1, m_*)$ with $m < 2$. Then f satisfies

$$\lim_{t \to \infty} f(t) = \bar{f}_0,$$

in the sense of distributions.

$$\dot{\mathcal{M}}_m[f](t) = \int_0^\infty \int_0^\infty F\left(\frac{w}{w'}, m\right) w^\alpha w_*^m s_C\left(\frac{w}{w_*}\right) f(w) f(w_*) \, \mathrm{d}w_* \, \mathrm{d}w \le 0$$

and

$$\dot{\mathcal{M}}_m[f](t) = 0 \quad \Leftrightarrow \quad f(w) \equiv 0, \; \forall w > 0.$$

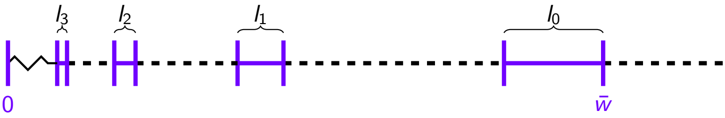
- After the coordinate change $w_* \to r := w_{predator}/w_{prey}$ in (1) with $s = s_C$, i.e. $r \in [B-\sigma, B+\sigma]$ one obtains

$$0 = r^{\alpha}(r+K)^{-\alpha-2} f\left(\frac{wr}{r+K}\right) f\left(\frac{w}{r+K}\right) + (1-K)K'^{-3-\alpha} f\left(\frac{w}{K'}\right) f\left(\frac{wr}{K'}\right) - r^{-2} f(w) f\left(\frac{w}{r}\right) - r^{\alpha} f(w) f(rw), \quad \text{for a.e. } w \in \mathbb{R}_+ \tag{2}$$

as sufficient equilibrium condition.

- $\bar{f}(w) \neq 0 \Rightarrow \bar{f}(w_*) = 0$ for $w_* \in \left[\frac{w}{B+\sigma}, \frac{w}{B-\sigma}\right]$
- **Non-trivial steady state** $\bar{f}$ with gaps in the size-spectrum (cascade-effect):

$$\operatorname{supp}(\bar{f}) \subset \bigcup_{i \in \mathbb{Z}} \left[\frac{\bar{w}}{(B-\sigma)^{i+1}(B+\sigma)^{i}}, \frac{\bar{w}}{(B-\sigma)^{i}(B+\sigma)^{i}}\right], \ 1 \notin [B-\sigma, B+\sigma], \ \bar{w} > 0.$$



Also the **Power-law** $\tilde{f}(w) = w^{-\frac{3+\alpha}{2}}$ fulfills the sufficient equilibrium condition (2), but does not have finite first moment!

- Not expected in a small ecosystem, rather observed by investigating a large quantity of data from huge ecosystems (Sheldon et al., Liminology Oceanography, 1972)
- (Datta et al., JMBO, 2011) proved for several similar models **instability** of the power-law equilibrium

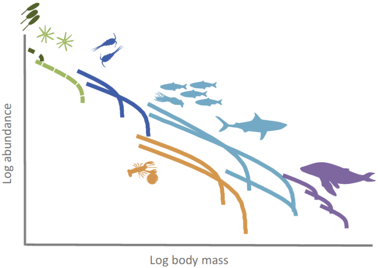


Figure: Blanchard et. al, Journal of Animal Ecology, Trends Ecol Evol., 2017

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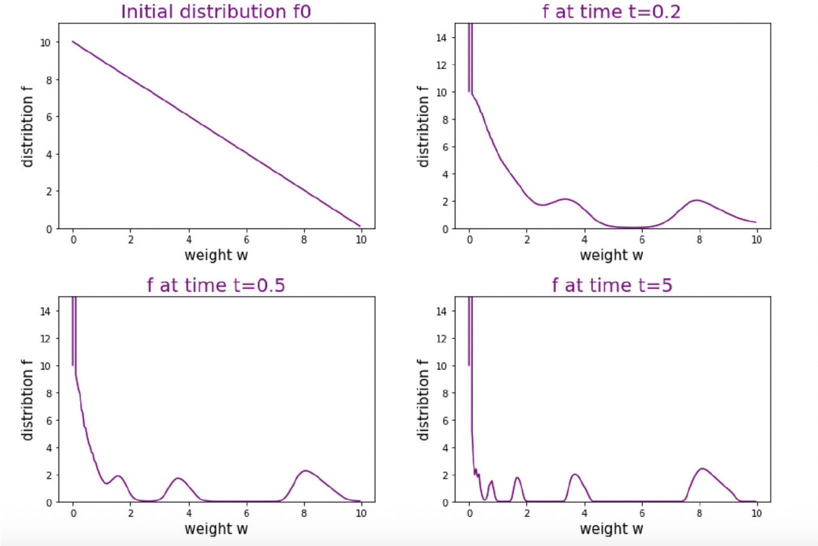
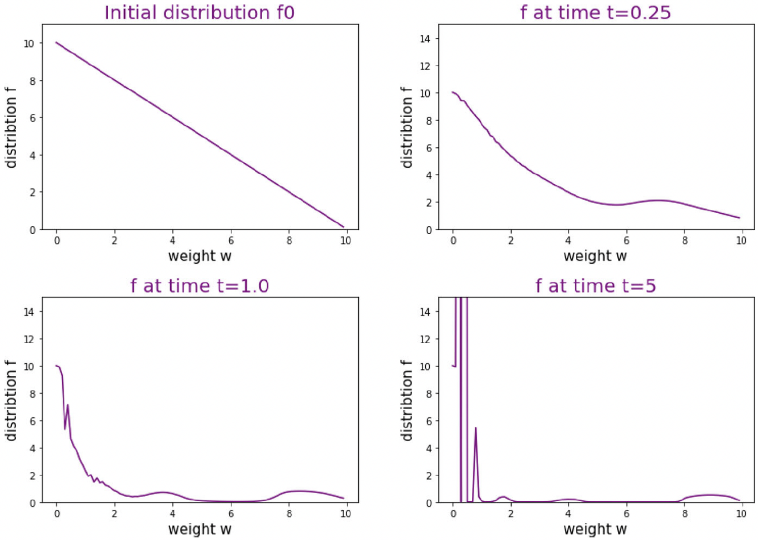
Cascade effect I



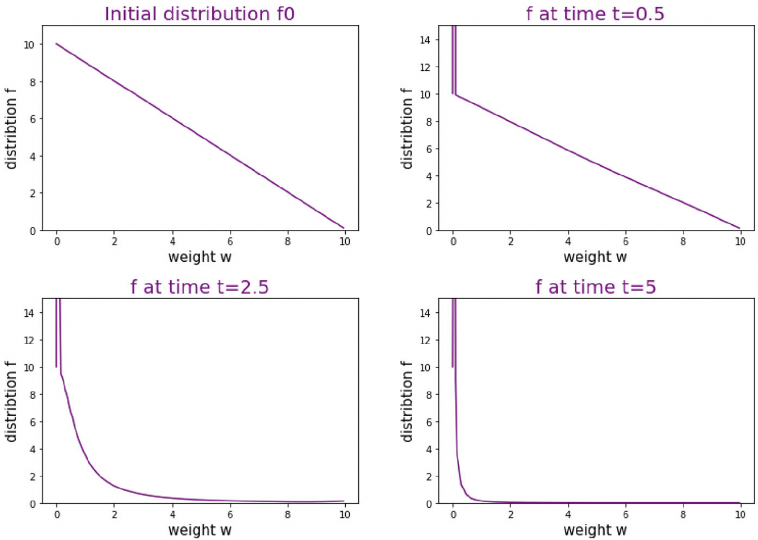
Cascade-effect: $s = s_c, \ \alpha = 0.9, \ B = 1.5, \ \sigma = 0.3, \ K = 0.1, \ K' = 0.01$

Cascade effect II



Cascade-effect: $s = s_c$, $\alpha = 0.9$, $B = 1.5$, $\sigma = 0.3$, $K = 0.4$, $K' = 0.01$

Cascade effect II



Cascade-effect: $s = s_c$, $\alpha = 0.9$, $B = 1.1$, $\sigma = 0.3$, $K = 0.1$, $K' = 0.01$

Thank you for your attention!