a dynamic model for plankton

josé a. cuesta

Grupo Interdisciplinar de Sistemas Complejos
UC3M

collaborators

richard law

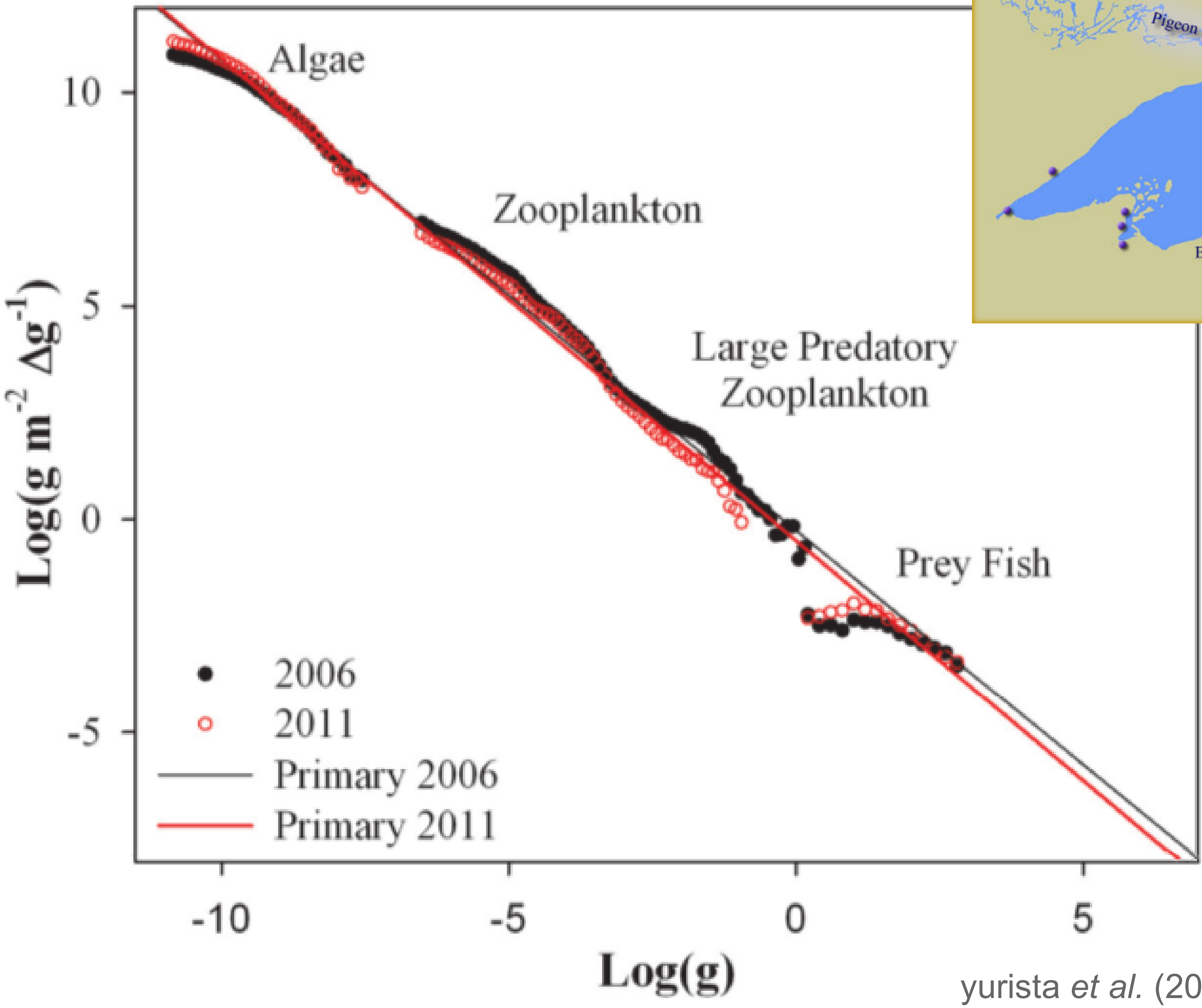
gustav delius

UNIVERSITY of York

YCCSA

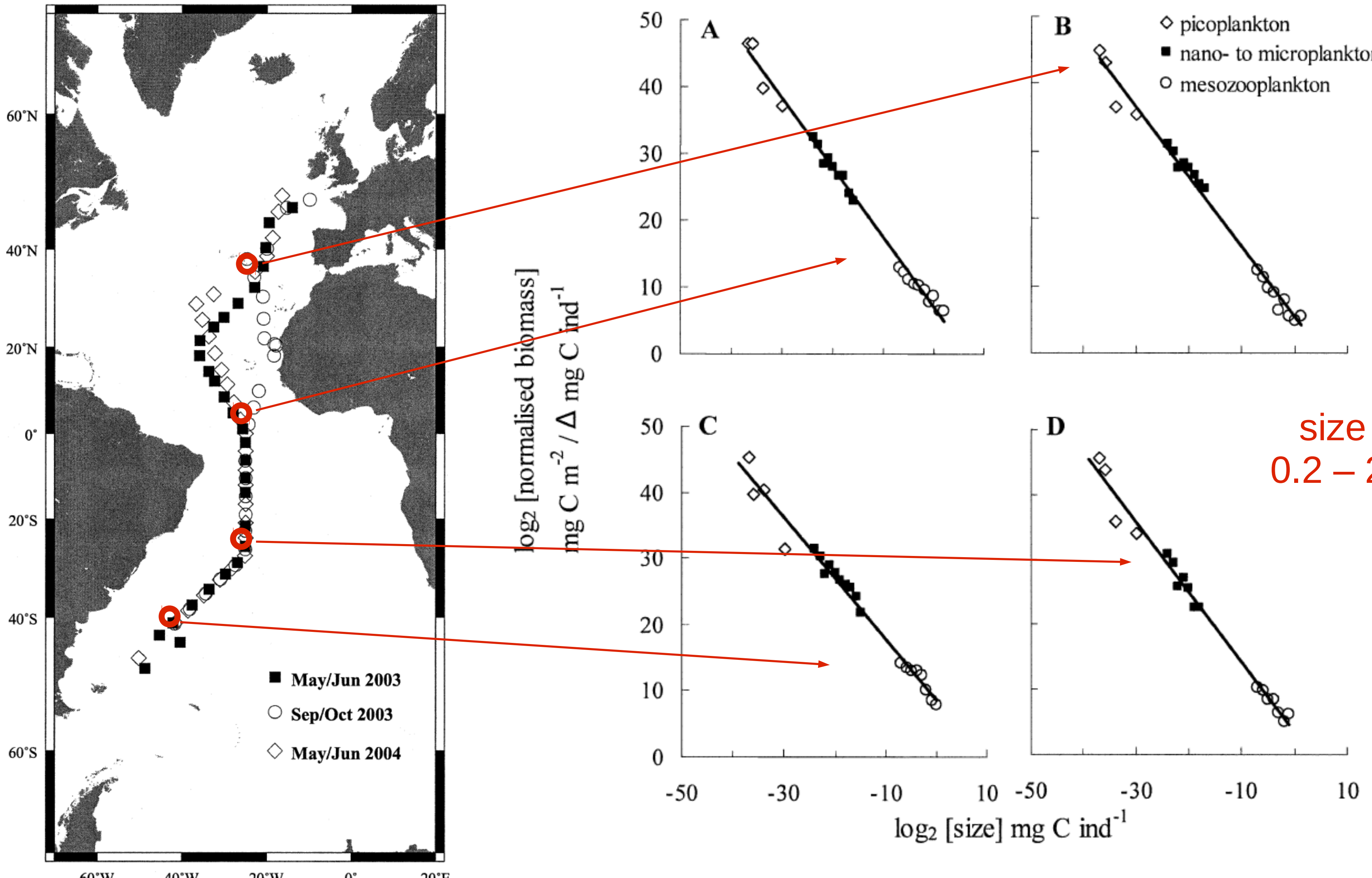
The University of York
York Centre for Complex Systems Analysis

size spectrum in aquatic ecosystems



yurista *et al.* (2014) can. j. fish. aquat. sci. **71**, 1324-1333

size spectrum in aquatic ecosystems



size range:
0.2 – 2000 µm

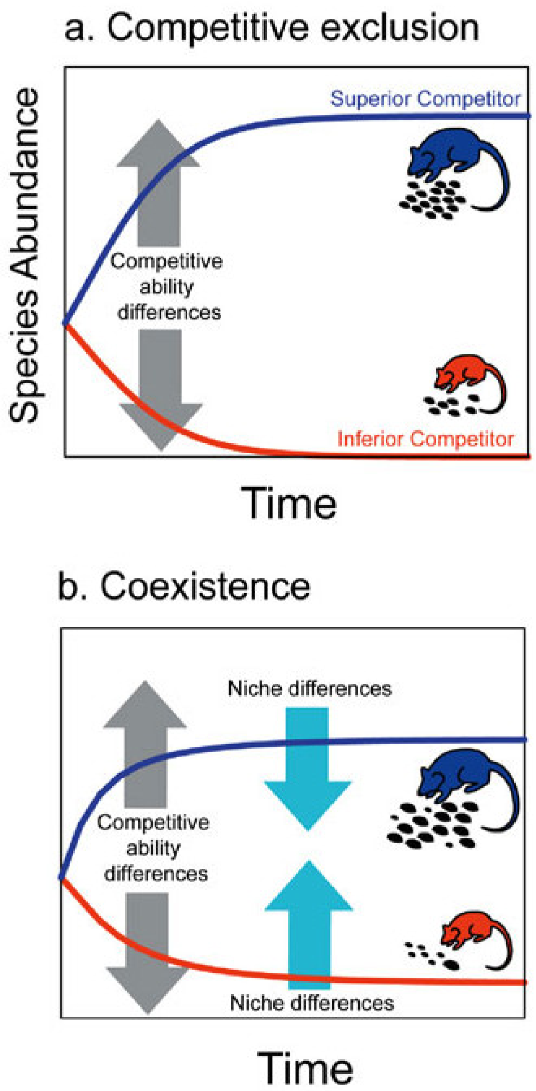
san martin *et al.* (2006) limnol. oceanogr. **51**, 2084-2091

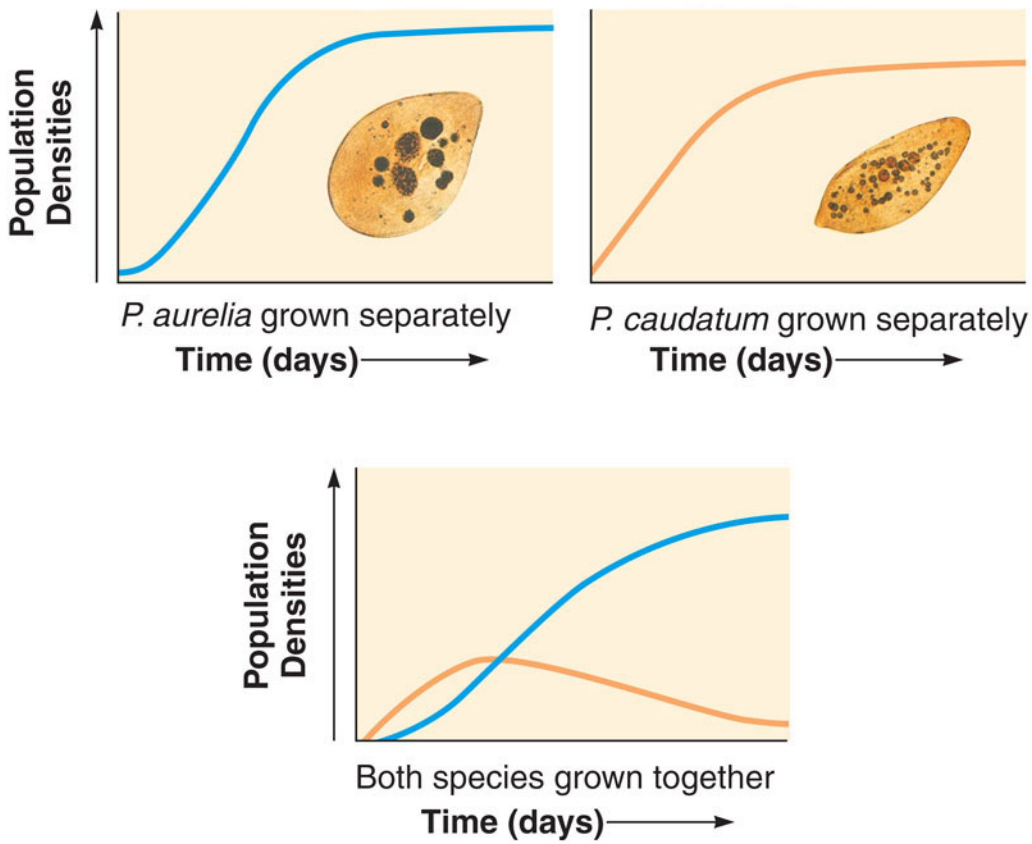
the paradox of the plankton

diatom algae

hutchinson (1961) am. nat. **95**, 137-145

competitive exclusion principle





gause (1934) *the struggle for existence*

the competitive exclusion theorem

$n_i \quad (i=1,\ldots,s)$ → populations

$R_j \quad (j=1,\ldots,r)$ → resources

$$\frac{\dot{n}_i}{n_i} = \sum_{j=1}^{r} b_{ij} R_j - \alpha_i \qquad R_j = R_j(n_1,\ldots,n_s)$$

$|n_i(t)| < \infty$ → resources *can be exhausted*

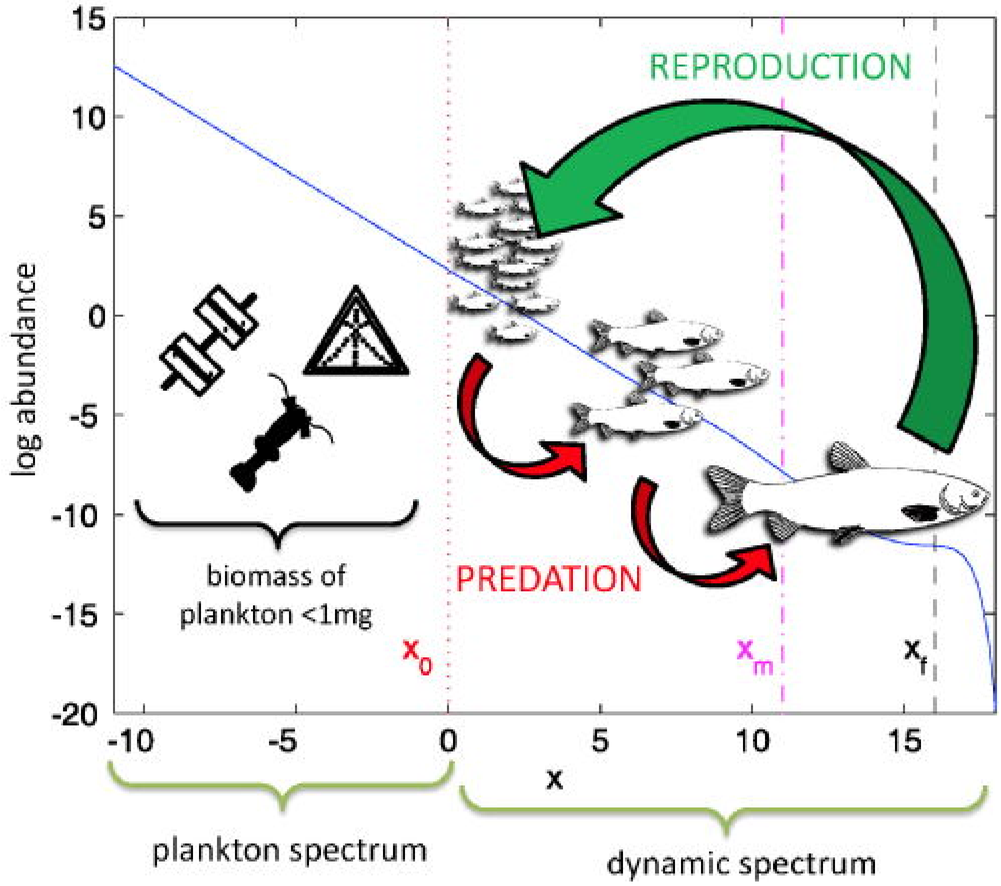
the competitive exclusion theorem

$$\text{if} \quad s > r \quad \text{then} \quad \sum_{i=1}^{s} c_i b_{ij} = 0 \quad \Rightarrow \quad \boldsymbol{c} = (c_1, \ldots, c_s) \neq \boldsymbol{0}$$

$$\sum_{i=1}^{s} c_i \frac{d}{dt} \log n_i = -a \qquad a = \sum_{i=1}^{s} c_i \alpha_i > 0$$

$$\prod_{i=1}^{s} n_i^{c_i} = e^{-at} \rightarrow 0$$

previous models



datta, (2011) *A mathematical analysis of marine size spectra* (ph.d. thesis)

population model of growing things

$$\frac{dw}{dt} = G(w)$$ → growth law

$p(w,t)\,dw$ → number of "things" between w and $w+dw$ at time t

$p(w,t)\,G(w)$ → flux of through w

$$\frac{\partial p(w,t)}{\partial t} dw = p(w-dw,t)\,G(w-dw) - p(w,t)\,G(w)$$

$$= -\frac{\partial}{\partial w}\left[p(w,t)\,G(w)\right] dw + o(dw)$$

population model of growing things

$$\frac{dw}{dt} = G(w) \longrightarrow$$ growth law

$$p(w,t)\,dw \longrightarrow$$ number of “things” between w and $w+dw$ at time t

$$p(w,t)\,G(w) \longrightarrow$$ flux of through w

$$\frac{\partial}{\partial t} p(w,t) + \frac{\partial}{\partial w}\left[p(w,t)\,G(w)\right] = 0$$

population model of growing things

$$\frac{dw}{dt} = G(w)$$ → growth law

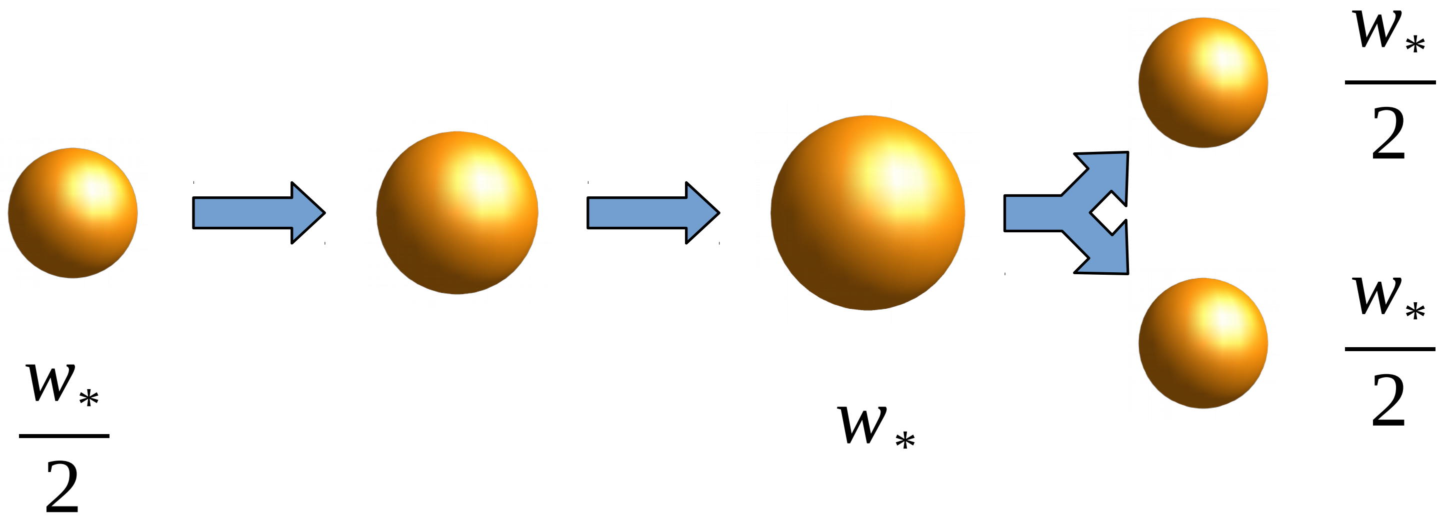
$$p(w,t)\,dw$$ → number of "things" between w and $w+dw$ at time t

$$p(w,t)G(w)$$ → flux of through w

$$\frac{\partial}{\partial t}p(w,t) + \frac{\partial}{\partial w}[p(w,t)G(w)] = S(w,t)$$

sources of population change

cell cycle



$$p(w_*/2,t)\,G(w_*/2) = 2\,p(w_*,t)\,G(w_*)$$

flux through smallest size — flux through largest size

population-growth model for cells

$p(w, w_*, t)\, dw\, dw_*$ → number of phytoplankton cells with size between w and w+dw from species with characteristic size between w_* and w_*+dw_* at time t

$$\frac{\partial}{\partial t} p(w, w_*, t) = -\frac{\partial}{\partial w}\left[p(w, w_*, t)\, G_p(w, w_*)\right] - M(w, w^*, t)\, p(w, w^*, t)$$

$$\frac{w_*}{2} < w < w_*$$

death rate

$$p(w_*/2, w_*, t)\, G_p(w_*/2, w_*) = 2\, p(w_*, w_*, t)\, G_p(w_*, w_*)$$

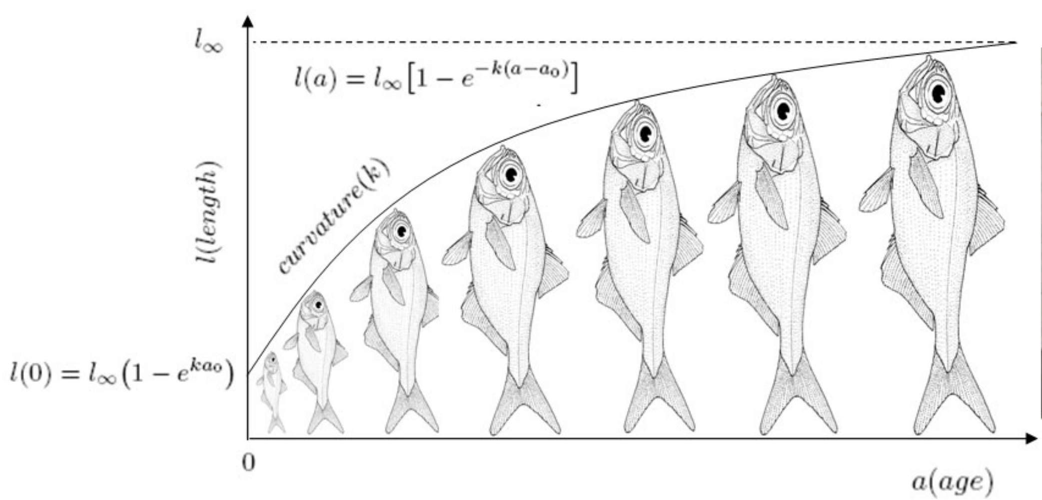
boundary condition

growth rate

$$\frac{dw}{dt} = A\,w^{2/3} - B\,w$$

nutrient uptake

metabolic rate

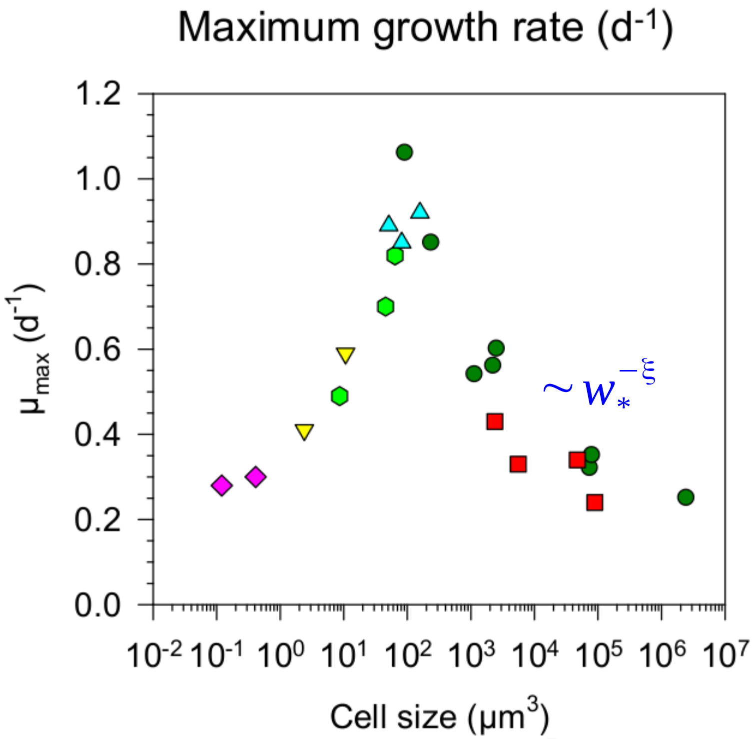


von bertalanffy

$k = B/3 \qquad l_\infty = A/B$

growth rate

$$\frac{dw}{dt} = G_p(w, w_*) = A(w_*)\,w^{\alpha} - B(w_*)\,w^{\beta} \qquad \alpha < \beta$$



$$T(w_*) = \int_{w_*/2}^{w_*} \frac{dw}{A(w_*)\,w^{\alpha} - B(w_*)\,w^{\beta}} \propto w_*^{\xi}$$

$$A(w_*) = a\,w_*^{1-\alpha-\xi} \qquad B(w_*) = b\,w_*^{1-\beta-\xi}$$

$$G_p(w, w_*) = w_*^{1-\xi}\left[a\left(\frac{w}{w_*}\right)^{\alpha} - b\left(\frac{w}{w_*}\right)^{\beta}\right]$$

marañón *et al.* (2013) ecol. lett. **16**, 371-379

common resource

$$a \longrightarrow a(N) = a_\infty \frac{N}{N+r}$$

monod's law

nutrient

$$\frac{dN}{dt} = \rho(N) - \sigma(N,[p])$$

$$\rho(N) = \rho_0\left(1 - \frac{N}{N_0}\right)$$

chemostat

$$\sigma(N,[p]) = \frac{a(N)}{\theta}\int_0^\infty dw_* \int_{w_*/2}^{w_*} dw\, w_*^{1-\xi}\left(\frac{w}{w_*}\right)^\alpha p(w, w_*, t)$$

yield (biomass created per unit resource)

nutrient consumption

steady state

$$p(w, w_*) = p(w_*, w_*) \frac{G_p(w_*, w_*, N_s)}{G_p(w, w_*, N_s)} \exp \int_{w}^{w_*} \frac{M(w, w_*)}{G_p(w, w_*, N_s)} dw$$

$$\int_{w_*/2}^{w_*} \frac{M(w, w_*)}{G_p(w, w_*, N_s)} dw = \log 2$$

boundary condition

- $p(w_*, w_*) \neq 0$ if w_* satisfies b.c.[*]
- $p(w_*, w_*) = 0$ otherwise

} competitive exclusion

[*] $\rho(N_s) = \sigma(N_s, [p])$ determines $p(w_*, w_*)$

coexistence (plankton paradox)

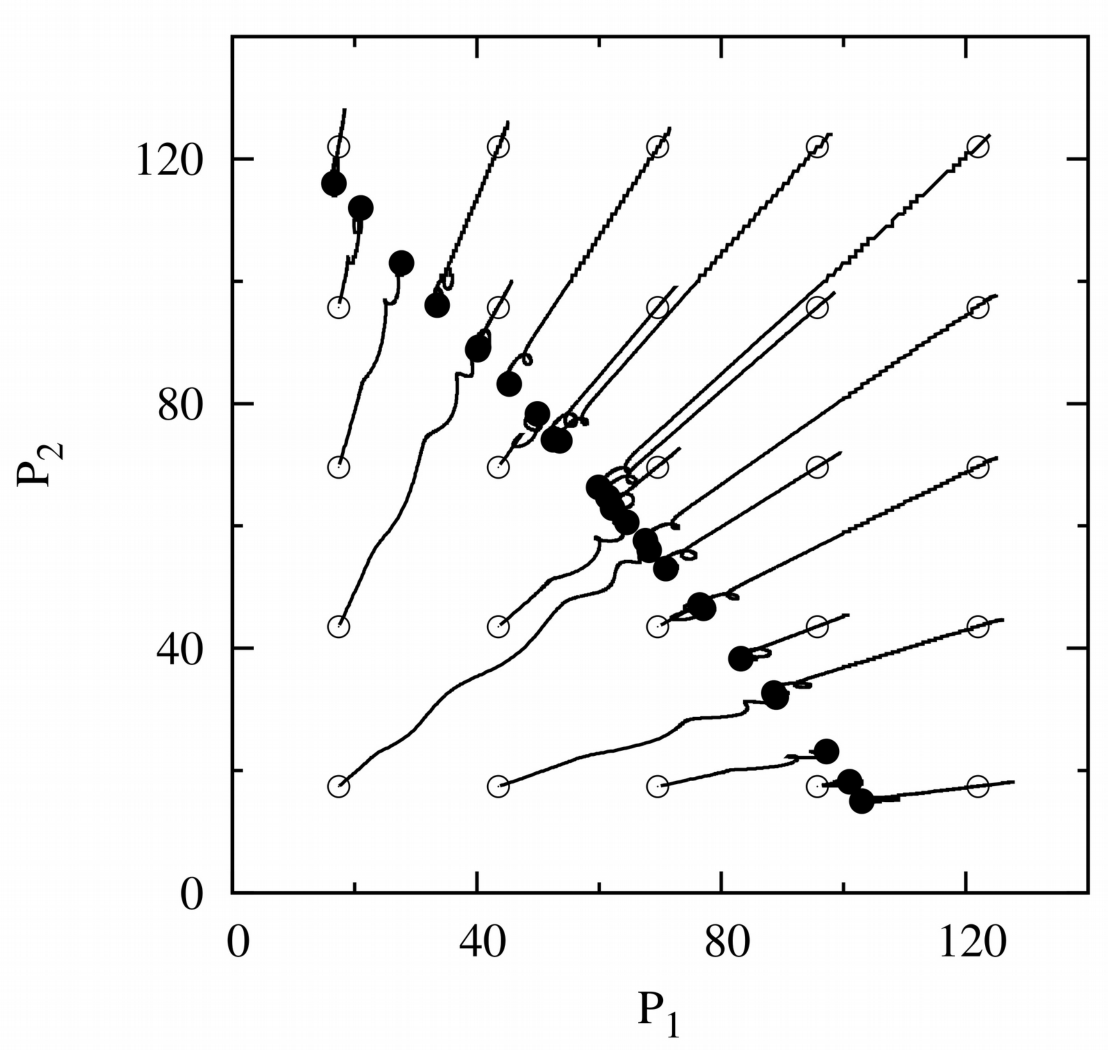
$$M(w,w_*) = w_*^{-\xi} m\left(\frac{w}{w_*}\right) \quad \Rightarrow \quad \int_{1/2}^{1} \frac{m(x)}{a(N_s)x^{\alpha} - b x^{\beta}} dx = \log 2$$

$$p(w,w_*) \quad = \quad p(w_*,w_*)\phi_{\alpha,\beta}\left(\frac{w}{w_*}, a(N_s)\right)$$

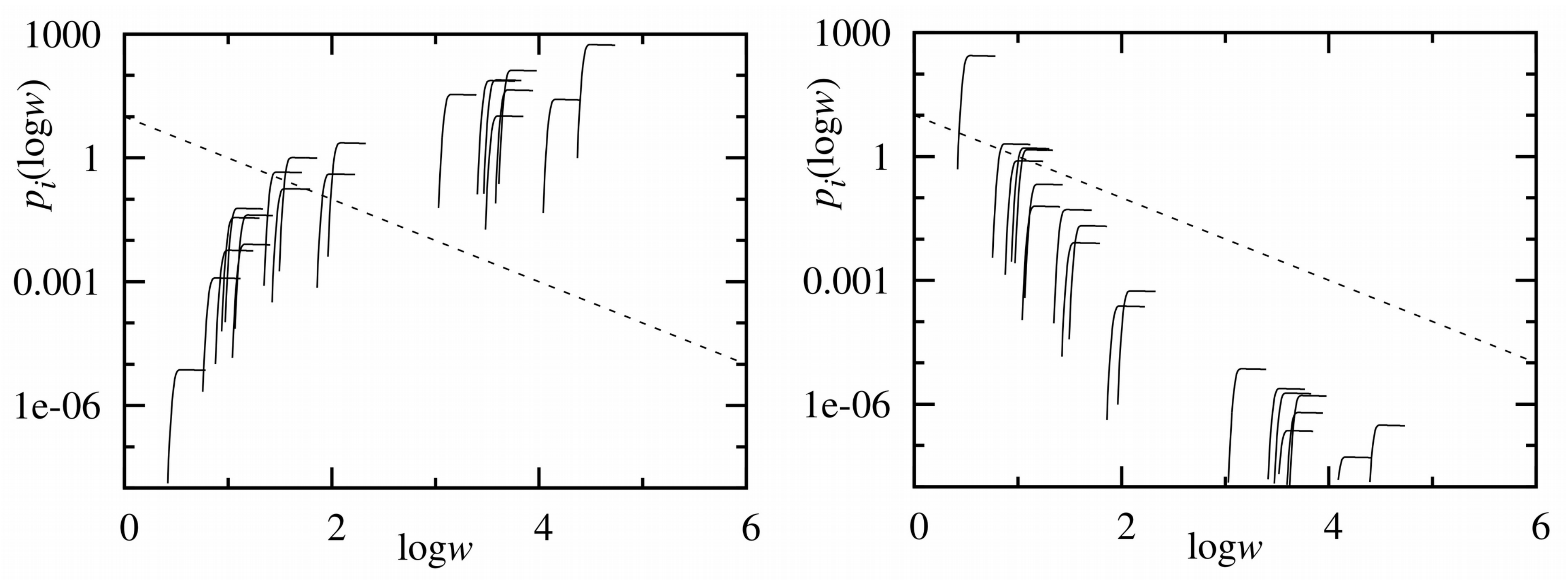
$$\phi_{\alpha,\beta}(x,a) \quad = \quad \frac{a-b}{a x^{\alpha} - b x^{\beta}} \exp \int_{x}^{1} \frac{m(y)}{a y^{\alpha} - b y^{\beta}} dy$$

$$\int_{0}^{\infty} w_*^{2-\xi} p(w_*,w_*) dw_* = \frac{\theta \rho(N_s)}{a(N_s)} \left(\int_{1/2}^{1} x^{\alpha} \phi_{\alpha,\beta}(x, a(N_s)) dx \right)^{-1}$$

coexistence (plankton paradox)

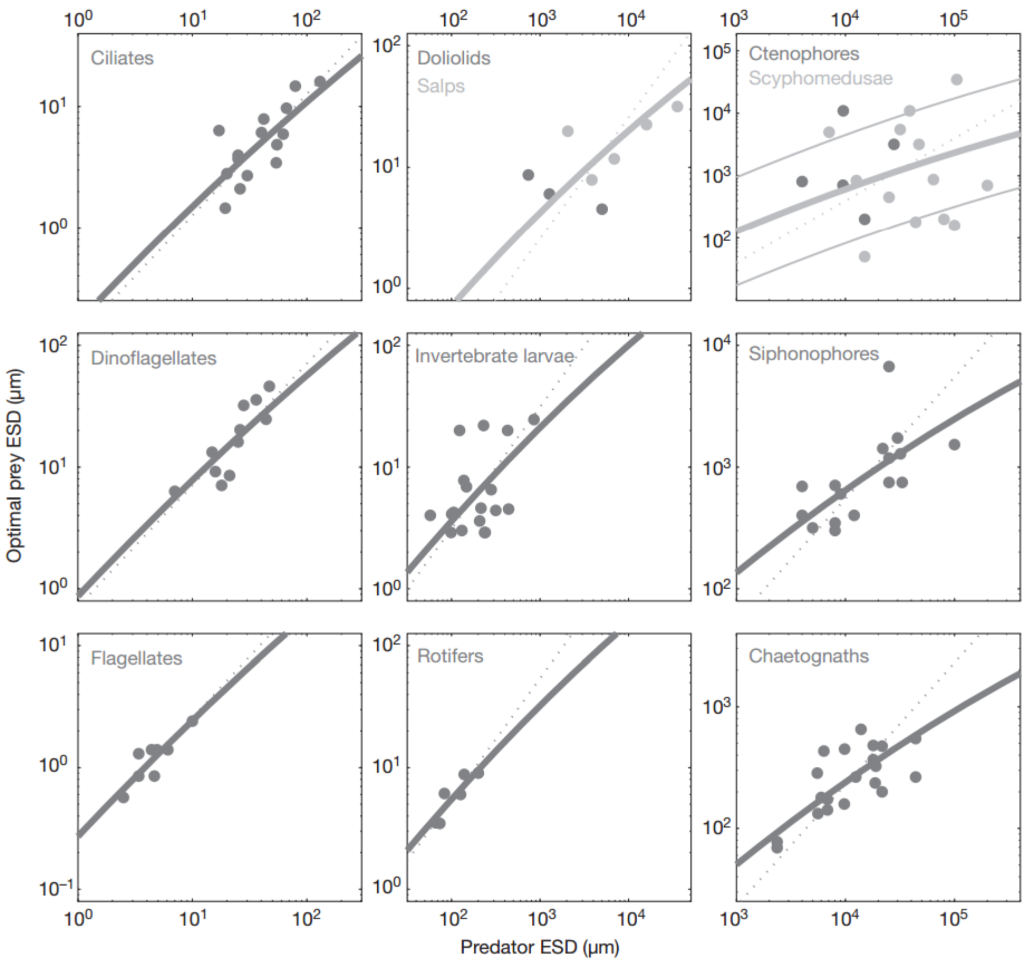


coexistence (plankton paradox)



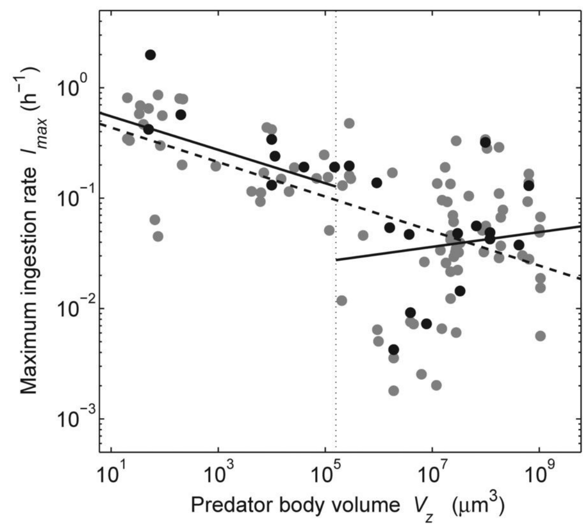
predation by zooplankton

optimal prey size



wirtz (2012) mar. ecol.-prog. ser. **445**, 1-12

allometric ingestion rate



wirtz (2013) j. plankton res. **35**, 33-48

$$S(w_{pd}, w_{py}) = w_{pd}^{\nu} \, s\left(\frac{w_{pd}}{w_{py}}\right)$$

predation kernel

death by zooplankton predation

$z(w, w_*, t)\,dw\,dw_*$ ⟶ number of zooplankton cells with size between w and $w+dw$ from species with characteristic size between w_* and w_*+dw_* at time t

$$p_c(w,t) = \int_0^\infty p(w, w_*, t)\,dw_*$$

$$z_c(w,t) = \int_0^\infty z(w, w_*, t)\,dw_*$$

} community size spectrum

- death is essentially caused by predation

$$M(w, w_*, t) = \int_0^\infty S(w', w)\,z_c(w', t)\,dw'$$

evolution equation for zooplankton

$$\frac{\partial}{\partial t} z(w, w_*, t) = -\frac{\partial}{\partial w}[z(w, w_*, t) G_z(w, w_*, t)] - M(w, w^*, t) z(w, w^*, t)$$

$$\frac{w_*}{2} < w < w_*$$

$$z(w_*/2, w_*, t) G_z(w_*/2, w_*, t) = 2 z(w_*, w_*, t) G_z(w_*, w_*, t)$$

boundary condition

$$G_z(w, w_*, t) = \int_0^\infty S(w, w') \epsilon w' [p_c(w', t) + z_c(w', t)] dw' - b w_*^{1-\xi} \left(\frac{w}{w_*}\right)^\beta$$

efficiency of biomass conversion

size spectrum ⇔ plankton paradox

$$G_p(\lambda w, \lambda w_*) = \lambda^{1-\xi} G_p(w, w_*)$$

Theorem: In the steady state, the scalings

$$G_z(\lambda w, \lambda w_*) = \lambda^{1-\xi} G_z(w, w_*)$$

$$M(\lambda w, \lambda w_*) = \lambda^{-\xi} M(w, w_*)$$

hold if and only if the scalings

$$p_c(\lambda w) = \lambda^{-\gamma} p_c(w) \qquad z_c(\lambda w) = \lambda^{-\gamma} z_c(w)$$

hold, with $\gamma = 1 + \xi + \nu$

steady state

$$p_c(w) = p_0 w^{-\gamma} \qquad z_c(w) = z_0 w^{-\gamma}$$

$$M(w, w_*) = m_0 w^{-\xi} \qquad m_0 \equiv z_0 \int_0^\infty y^{-1-\xi} s(y)\, dy$$

$$G_z(w, w_*, t) = w_*^{1-\xi} \left[a_{pz} \left(\frac{w}{w_*} \right)^{1-\xi} - b \left(\frac{w}{w_*} \right)^{\beta} \right]$$

$$a_{pz} \equiv \varepsilon (p_0 + z_0) \int_0^\infty y^{\gamma-3} s(y)\, dy$$

steady state

$$p(w,w_*)=\frac{p_0}{I_{\alpha,\beta}\left(\gamma-1,a(N_s)\right)}\phi_{\alpha,\beta}\left(\frac{w}{w_*},a(N_s)\right)$$

$$z(w,w_*)=\frac{z_0}{I_{1-\xi,\beta}\left(\gamma-1,a_{pz}\right)}\phi_{1-\xi,\beta}\left(\frac{w}{w_*},a_{pz}\right)$$

$$I_{\alpha,\beta}(\eta,a)=\int_0^\infty y^\eta\phi_{\alpha,\beta}(y,a)\,dy$$

- $a(N_s)$ and a_{pz} are determined by the boundary conditions
- p_0 and z_0 are determined by a_{pz} and the equation for the resource

discussion

- according to the literature $\xi \approx 0.15$ and $\nu \approx 0.7–1.5$, hence $\gamma \approx 1.85–2.65$
- introducing a predation kernel is too *ad hoc* a modelling; adaptive predation would be more appropriate
- we can't assess the stability of the steady state
- the model is too ideal: it assumes an infinite spectrum as well as a continuum of species
- the paradox of the plankton and the size spectrum are “two sides of a single coin”

finitely many species (numerics)

- unstable, unless predation is modified as

$$S(w_{\text{pd}}, w_{\text{py}}) = w_{\text{pd}}^{\nu}\, s\left(\frac{w_{\text{pd}}}{w_{\text{py}}}\right) P_{py}^{\chi}$$

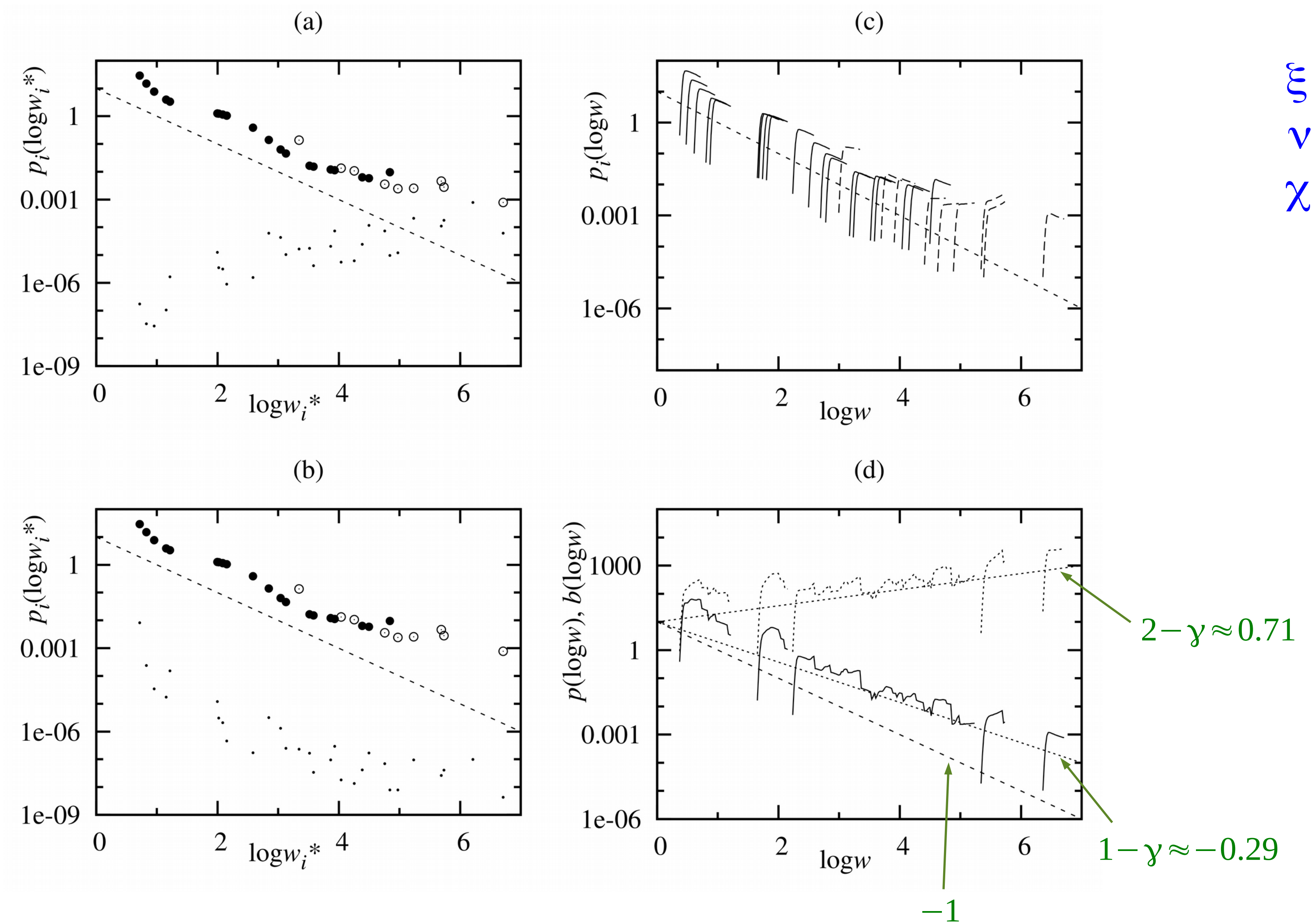
$\chi > 0$

total abundance of predated species

- the scaling of the size spectrum changes to

$$\gamma = 1 + \frac{\xi + \nu}{1 + \chi}$$

finitely many species (numerics)



$\xi = 0.15$
$\nu = 0.85$
$\chi = 0.4$