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► To cite this version:

Eric Edeline, Nicolas Loeuille. Size-dependent eco-evolutionary feedback loops in harvested systems. Sféco2018: International conference on ecological sciences, Oct 2018, Rennes, France. hal-02958951

HAL Id: hal-02958951

<https://hal.inrae.fr/hal-02958951>

Submitted on 6 Oct 2020

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Size-dependent eco-evolutionary feedback loops in harvested systems

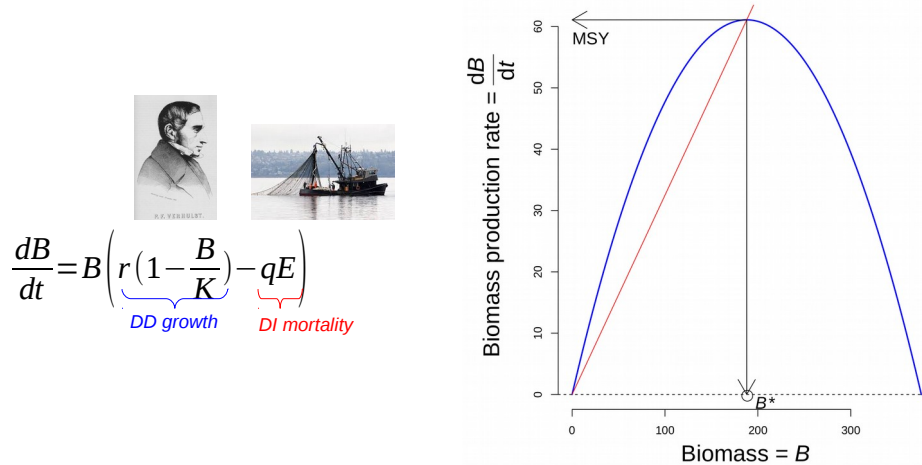


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Classical fisheries management



- The model assumes that *DD growth* is independent from *DI fisheries mortality*.
- **Problem:** this assumption is not always fulfilled.

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Classical fisheries management theory is based on the so-called Gordon Schaefer model in which population biomass dynamics are controlled by a density-dependent logistic growth term (blue) and a density-independent fisheries mortality term (red).



Graphically, we can visualize the equilibrium biomass as the intersection of the growth and mortality terms.

Managers usually seek to reach the effort that maximizes the equilibrium yield, the so-called maximum sustainable yield.

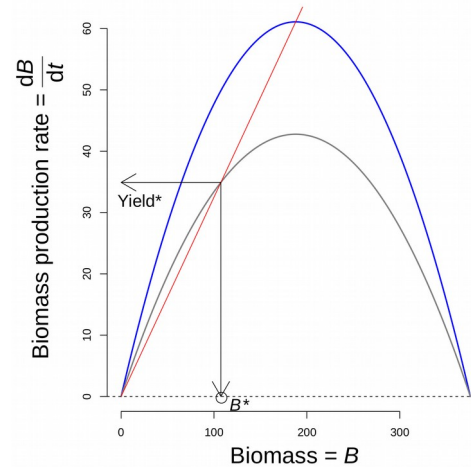
This very simple model assumes that the population growth function is independent from the density-independent fisheries mortality function.

However, this assumption is not always fulfilled.

Classical fisheries management

$$\frac{dB}{dt} = B \left(\underbrace{r \left(1 - \frac{B}{K} \right)}_{\text{DD growth}} - \underbrace{qE}_{\text{DI mortality}} \right)$$



- r decreases when E is sustained during several generations. Why?
- Harvesting generally selects against large-sized individuals which have higher fitnesses (Carlson et al. 2007, Olsen & Moland 2011).
- Exploitation drives average declines of almost 20% in body size-related traits (Darimont et al. 2009).
- Predicting yields requires accounting for population size structure and body size dynamics.

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In practise, the population growth rate r often decreases when the fishing effort is sustained over long time periods (grey curve).

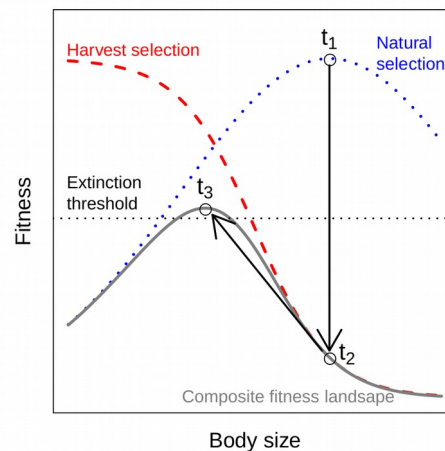
This decreased r results in decreased equilibrium biomass and yield.

Why should r decrease when E increases? Because not all individuals in the population are similar in terms of survival and reproduction as assumed by the Gordon Schaefer model.

Typically, fisheries favour smaller-sized individuals that reproduce at an earlier age, thus driving declines in size-related traits.

Predicting fisheries yields thus requires accounting for population size structure and body size dynamics.

Adaptive landscape perspective



- **Harvesting** immediately drives a t_1 to t_2 drop in fitness (and thus in biomass productivity dB/dt).
- Rapid evolution from t_2 to t_3 increases both productivity and sustainability (evolutionary rescue).
- The dynamics of **natural selection** are driven by **eco-evolutionary feedback loops (EEFLs)**.

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This goal can be achieved by adopting an adaptive landscape perspective on fisheries dynamics.

In a 2 dimensional landscape, where fitness is expressed as a function of body size, body size dynamics may be seen as following a 3-step sequence.

Initially, mean body size in the population resides at the naturally-selected fitness peak (Blue, t_1).

Adding harvest selection shifts the fitness peak down and leftward, such that the population mean body size now suddenly corresponds to low fitness values (t_2). Lower fitnesses mean lower fisheries productivity dB/dt .

A size-structured fisheries management model could capture this effect. However, often fisheries management models are age-structured at best.

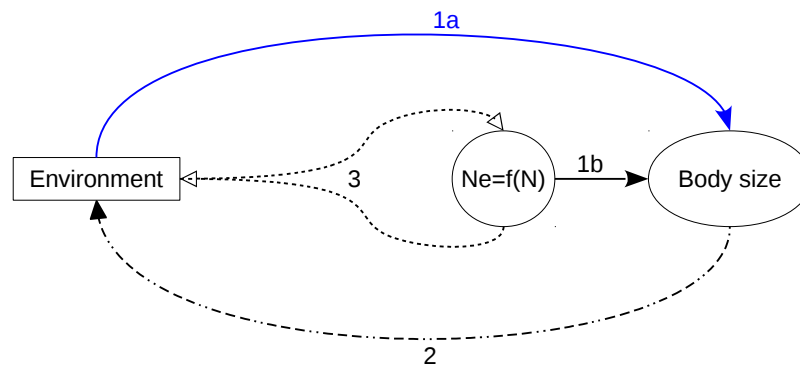
Rapid evolution to the new selective peak increases productivity and may allow the population to persist if an extinction threshold was crossed (a case of evolutionary rescue).

Hence, although mean body sizes decrease, which is undesirable from a commercial point of view, rapid evolution in fact increases both fisheries yields and sustainability.

Adopting this adaptive landscape perspective makes it clear that predicting fisheries yields requires accounting for the dynamics of both harvest selection and natural selection.

The dynamics of natural selection are controlled by the so-called EEFLs.

Size-dependent EEFL



1a: Natural selection (= 0 at the ESS).

2: Trait-dependent ecological interactions.

3: Density-dependent ecological interactions.

1b: Effective population size drives body size evolvability.

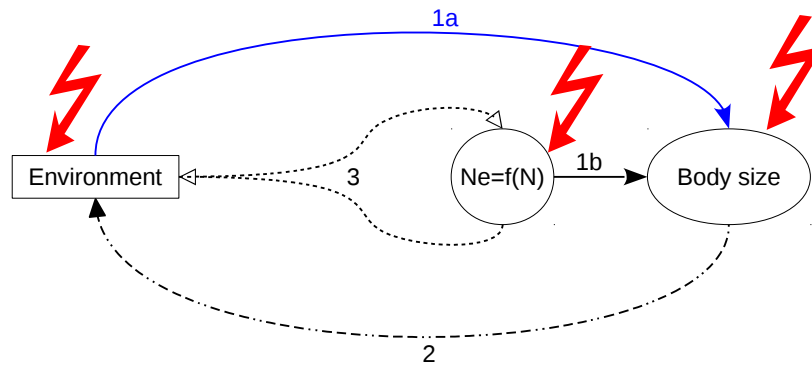
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This is a possible size-dependent EEFL in which we have a now-familiar feedback between the environment that sets natural selection (arrow 1a), and body size that controls the environment through size-dependent ecological processes (arrow 2).

Here, we add a third component, population size which, through the effective number of breeders (Ne), influences genetic diversity and thus the evolvability of body size (arrow 1b).

Finally, we have an ecological, density-dependent feedback loop between population numbers and the environment (loop 3).

Adaptive landscape perspective



- **Harvesting** potentially disrupts all nodes of the system.
- Body size is a pivotal ecological trait (Peters 1986).
- **Harvesting** has a high potential to trigger EEFLs (slowed down by lower Ne).
- How could harvest-induced, size-dependent EEFLs look like?

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All three nodes of the loop may be disrupted by harvesting.

Specifically, as shown before, harvesting directly selects for smaller body sizes (right lightning).

In parallel, harvesting directly reduced population numbers and Ne , thus potentially decreasing body size evolvability (central lightning).

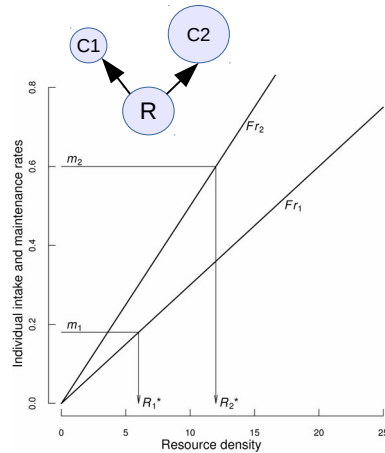
Finally, harvesting may alter the environment by impacting the habitats, predators or prey of the focal population (left lightning).

Because body-size is a key driver of ecological interactions, harvesting is a highly potent driver of EEFLs.

However, we know very few about whether such harvest-induced EEFLs exist and how they may look like.

Our aim here is to provide some first insights into these size-dependent EEFL and stimulate research on this topic.

Size-dependent selection from exploitative competition



$$Fr(R^*) = m$$

$$\alpha R^* = m$$

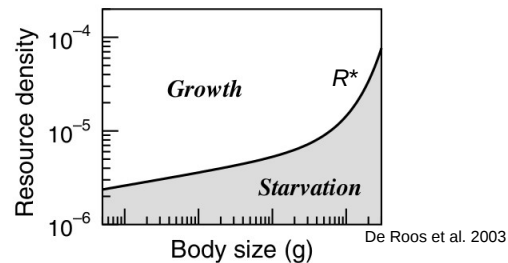
$$R^* = \frac{m}{\alpha}$$

$$m = c w^d$$

$$\alpha = a w^b$$

Peters 1986

$$R^* = \frac{c}{a} w^{d-b}$$



- Often, $d > b$. Then, R^* increases with body size (De Roos et al. 2003, Kooijman 2010).
- **Natural selection** from exploitative competition selects for smaller body-sizes.
- **Harvesting** decreases population density and relaxes intraspecific resource competition.
- **Harvesting** should change **natural selection** to **favour larger body sizes**.

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First, let us examine the effects of exploitative competition on body size.

Exploitative competition occurs when individuals strictly interact indirectly through the resource (scheme). In the scheme, we represent a small and large-sized consumer competing for the same resource.

On the graphic you can see that resource intake Fr (functional response) for each consumer increases with increasing resource density. In contrast, individual metabolism m (energy expenditure) is independent of resources.

Intersection of Fr and m defines equilibrium resource density R^* . Above R^* the individual grows, below R^* the individual starves to death.

R^* is given by the ratio of metabolic to intake rates, and is thus a function of body mass w .

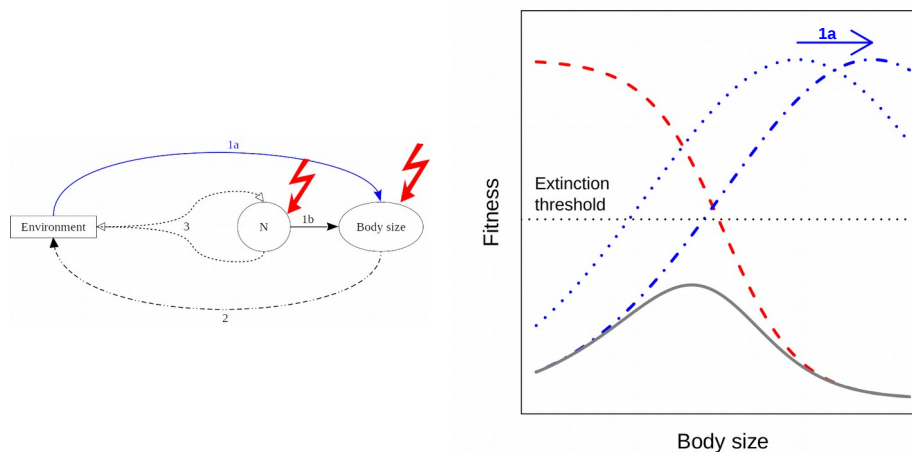
Allometric scaling exponents d and b determine whether R^* increases or decreases with body size, i.e., whether a large-sized individuals dominate or are dominated in exploitative competition.

Often, $d > b$, such that the metabolism increases faster than intake with body size (left graph) and thus R^* increases with body size (right-hand graph).

In this case, natural selection from exploitative competition selects for smaller body sizes.

Harvesting, by decreasing population density and exploitative competition thus relaxes a natural selection component for smaller body sizes.

Size-dependent selection from exploitative competition



- Opposition between **natural selection** and **harvest selection** is magnified
- Evolutionary change in mean trait value is dampened → decreased probability for a loop through trait-dependent processes (arrow 2).
- BUT the new fitness peak shifts below the extinction threshold → decreased evolvability and persistence probability.
- Evolutionary trapping (*sensu* Dieckmann & Ferrière 2004).

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Here in the loop we figure the double effect of harvesting on body sizes and population density.

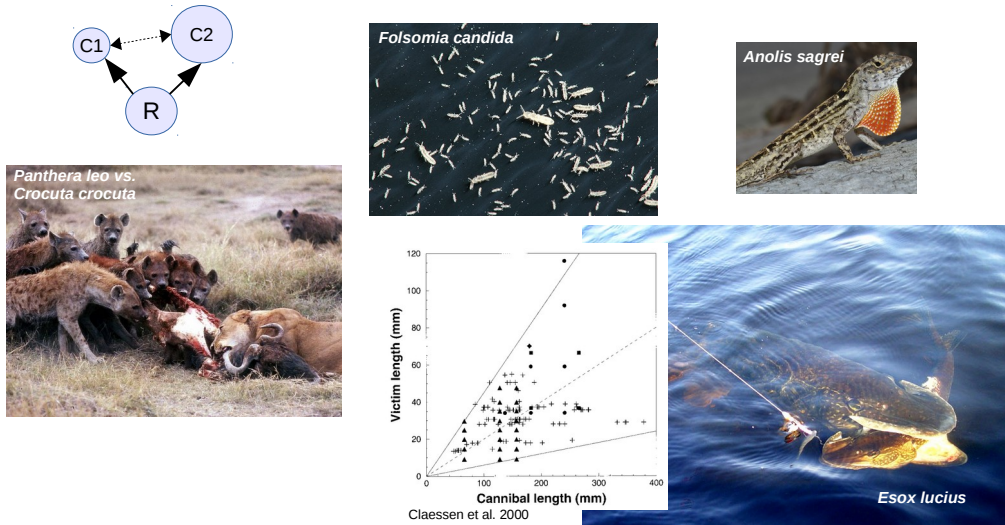
By decreasing population density, harvesting makes the environment less competitive, and thus favours a shift of the naturally-selected fitness peak to the right (arrow 1a). The opposition between harvest selection and natural selection is thus magnified.

This results in a dampened evolutionary change in mean body size, and thus decreases probability for a feedback loop through trait-dependent processes (arrow 2).

However, the fitness peak is severely lowered, this increasing probability for population collapse.

This is a case akin to evolutionary trapping: the evolutionary attractor corresponds to trait values where extinction occurs.

Size-dependent selection from interference competition and cannibalism



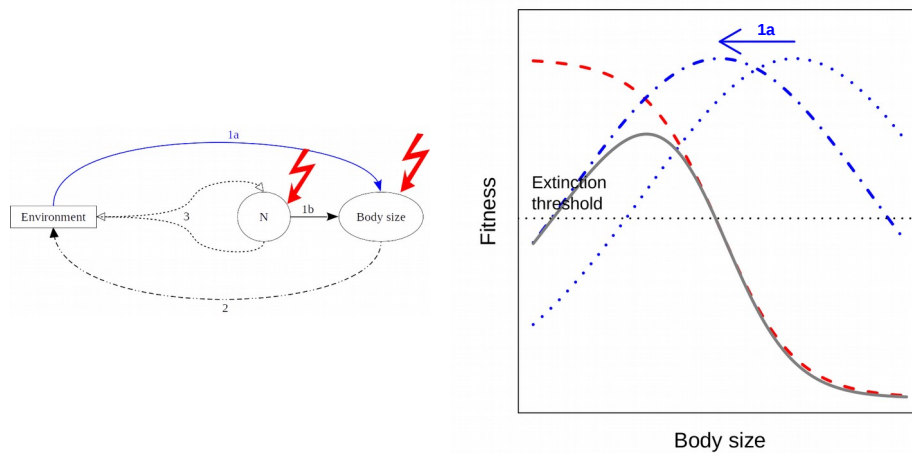
- In interference competition, large-sized individuals dominate by suppress access to food by smaller-sized individuals (Calsbeek & Smith 2007, Le Boulrot et al. 2014).
- Cannibalism is an extreme case of interference that also favours large-sized individuals (Claessen et al 2000).

Now let us consider interference competition, in which individuals interact directly to gain access to resources.

In this case, large individuals may simply suppress access to food by smaller sized individuals.

At its extreme, interference leads to cannibalism, in which large individuals are also dominant.

Size-dependent selection from interference competition and cannibalism



- **Harvest**-relaxed intraspecific resource competition should **change natural selection** to **favour smaller body sizes**.
- Evolutionary change in mean trait value is magnified by changing **natural selection**.
- Increased body size evolvability and probability for evolutionary rescue.
- Potential for evolutionary rebound after exploitation is enhanced: e.g. Windermere pike (*Esox lucius*).

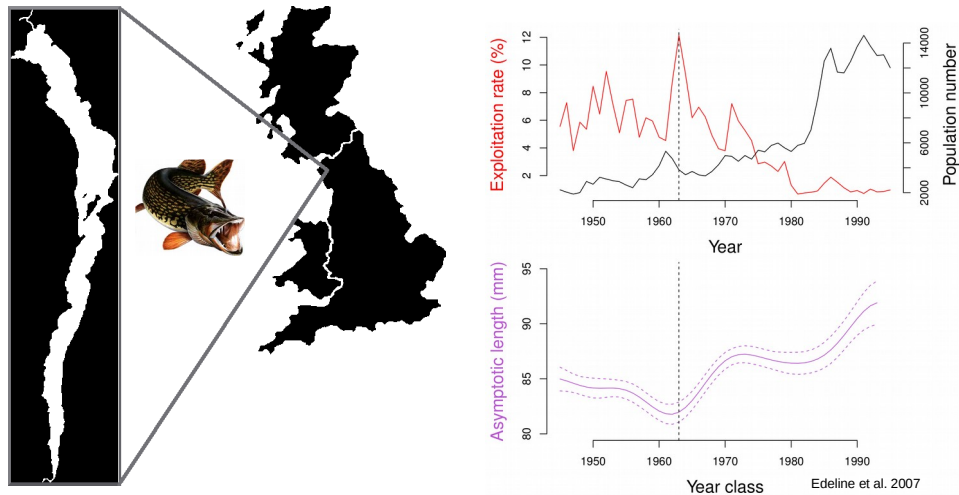
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Here, harvest-relaxed competition favours a leftward shift in the naturally-selected adaptive peak.

As a result, change in mean trait value is eased by changing natural selection, probability for evolutionary rescue increases, and thus evolutionary rebound after relaxation of the fishing pressure is eased.

This is presumably an EFFL that occurred in Windermere pike due to cannibalism, which is notoriously intense in pike.

Size-dependent selection from interference competition and cannibalism



- Decreased fishing pressure increased both population density and body size.
- BUT, increased probability for trait-dependent processes (arrow 2) through trophic interactions.

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Windermere is the largest natural lake in England. Pike in Windermere were scientifically exploited since the early 1940s, such that the fishing effort, densities and body size values were accurately recorded.

Time series show that the exploitation rate (red) tended to decrease through time, while in parallel population density and presumably cannibalism increased (black).

Body size decreased during an initial period when fishing was high and population density was low.

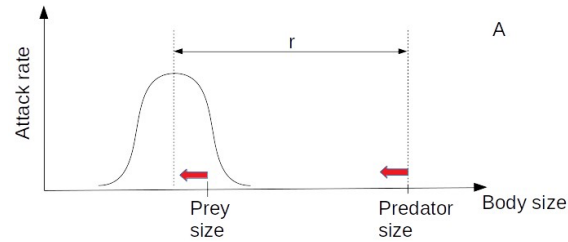
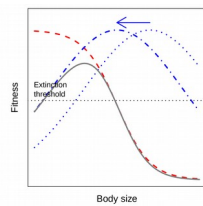
However, after the fishing effort decreased pike body size increased very rapidly in parallel with population density and, presumably, cannibalism.

Therefore, Windermere pike might provide a case of a size-dependent EEFL that favoured population resilience.

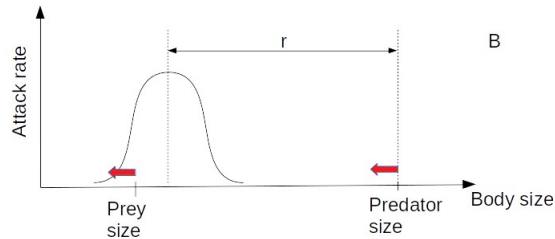
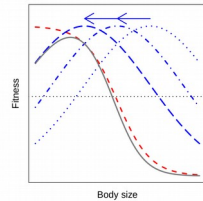
However, such an EEFL magnifies body size changes and thus increases probability of trait-dependent feedbacks through arrow 2.

A major potential pathway is through trophic interactions, which are highly size-dependent.

Size-dependent selection from interspecific trophic interactions



- Predator-prey interactions oppose further change in natural selection



- Predator-prey interactions favour further change in natural selection.
- Runaway EEFs may potentially lead to evolutionary suicide if functional constraints (*sensu* Arnold 1992) are reached.
- Alternatively, co-evolutionary arms race cycles may emerge (Abrams & Matsuda 1997).

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Here we have sketched how these feedbacks may look like.

In A, we illustrate a case where prey body size is larger than optimal prey size for the predator.

In this case, harvest-induced decrease in predator body size will decrease its efficiency on the prey, while harvest-induced decrease in prey body size will increase its mortality through predation.

Hence, the feedback loop will make natural selection to stabilize.

In B, we illustrate an inverse case where prey body size is smaller than optimal prey size for the predator.

In this inverse case, harvest-induced decrease in predator body size will increase its efficiency on the prey, while harvest-induced decrease in prey body size will decrease its mortality through predation.

Hence, trophic interactions favour further change in natural selection and lead potentially to evolutionary suicide if functional constraints are reached, or alternatively to co-evolutionary arms-race cycles.

Conclusions and prospects



- Theoretical tools are available to make qualitative predictions on the direction of size-dependent EEFLs.
- Key questions remain to be answered if we are to make progress towards a new synthesis (Schoener 2011).
- **Are EEFL important at all to understanding real-world functioning?**
 - Experimental and empirical measures of fitness-surface dynamics under contrasted harvest and ecological (competition, predation) regimes are critically needed.
- **How does ecological complexity influence the flexibility of adaptive landscapes?**
 - In trophic networks, when should we expect the multiplicity of direct and indirect effects to freeze adaptive landscapes or instead to make them highly flexible?
 - Is landscape flexibility dependent upon trophic levels?
- **How free are traits to move on fitness surfaces?**
 - Is the speed of (body size) evolution set by population numbers?
 - Is the direction of (body size) evolution constrained by phenotypic complexity?
 - Body size is correlated to multiple traits,
 - Selection often acts on multiple traits in parallel.
- Fisheries and size-dependent EEFLs provide a fruitful and stimulating framework to explore these questions.

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To conclude, we already have tools at hand to make some qualitative predictions on the direction of size-dependent EEFLs.

We identify 3 key questions that remain to be answered if we are to make progress towards a new synthesis.

Maybe the most important is to provide experimental and empirical proofs that EEFLs are important or unimportant to understand the real-world functioning. This requires, we believe, strong research efforts to measure fitness surfaces and their dynamics.

Second, and this is maybe more a question for theoreticians, how does ecological complexity influence the flexibility of adaptive landscapes? In particular, should we expect the multiplicity of direct and indirect trophic interactions to freeze adaptive landscapes or instead to make them more flexible? Is landscape flexibility dependent upon trophic levels?

Third, and this is a long-standing question in evolutionary ecology but still highly relevant to EEFLs: how do traits are constrained by evolvability? In particular, we are still in need of informations on whether the speed of evolution is effectively constrained by population number (mutation-limited theory), and whether phenotypic complexity constrains the direction of evolution.

We believe that fisheries and size-dependent EEFLs provide a fruitful and stimulating framework to explore these questions.

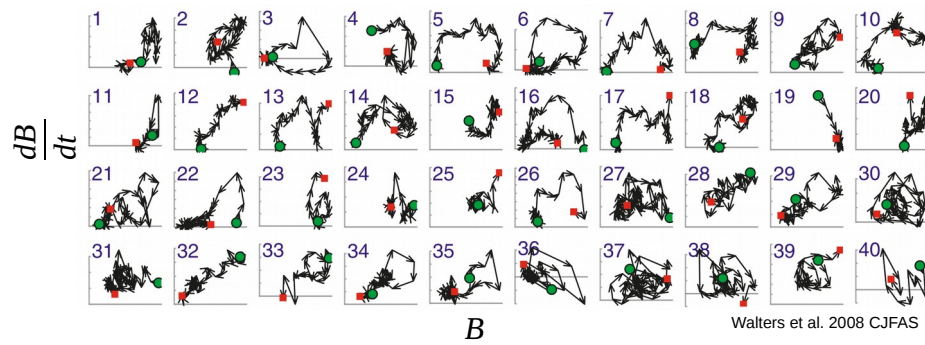
I feel that this symposium and the very interesting talks we have heard today demonstrate that we are progressing in the right direction!

I thank you for your attention.

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Density-dependent stock production in real-world fisheries



- Often, negative density-dependence of stock production is hard to detect.
- Positive temporal autocorrelation ("recruitment anomalies") generates cyclicity (Walters et al. 2008 CJFAS).
- Environmental stochasticity may blur negative density-dependent signals.
- **The rapid evolution hypothesis:** average declines of almost 20% in size-related traits in commercially exploited systems (Darimont et al. 2009).