# Physiological ecology meets the ideal-free distribution: predicting the distribution of size-structured fish populations across temperature gradients 

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## Synopsis

We describe a habitat selection model that predicts the distribution of size-structured groups of fish in a habitat where food availability and water temperature vary spatially. This model is formed by combining a physiological model of fish growth with the logic of ideal free distribution (IFD) theory. In this model we assume that individuals scramble compete for resources, that relative competitive abilities of fish vary with body size, and that individuals select patches that maximize their growth rate. This model overcomes limitations in currently existing physiological and IFD-based models of habitat selection. This is because existing physiological models do not take into account the fact that the amount of food consumed by a fish in a patch will depend on the number of competitors there (something that IFD theory addresses), while traditional IFD models do not take into account the fact that fish are likely to choose patches based on potential growth rate rather than gross food intake (something that physiological models address). Our model takes advantage of the complementary strengths of these two approaches to overcome these weaknesses. Reassuringly, our model reproduces the predictions of its two constituent models under the simple conditions where they apply. When there is no competition for resources it mimics the physiological model of habitat selection, and when there is competition but no temperature variation between patches it mimics either the simple IFD model or the IFD model for unequal competitors. However, when there are both competition and temperature differences between patches our model makes different predictions. It predicts that input-matching between the resource renewal rate and the number of fish (or competitive units) in a patch, the hallmark of IFD models, will be the exception rather than the rule. It also makes the novel prediction that temperature based size-segregation will be common, and that the strength and direction of this segregation will depend on per capita resource renewal rates and the manner in which competitive weight scales with body size. Size-segregation should become more pronounced as per capita resource abundance falls. A larger fish/cooler water pattern is predicted when competitive ability increases more slowly than maximum ration with body size, and a smaller fish/cooler water pattern is predicted when competitive ability increases more rapidly than maximum ration with body size.

## Physiological vs Ideal Free Distribution Models

- Physiological Models (i.e. bioenergetics)
- Choose habitats to maximize growth rates
- Choose based on temperature and food availability
- When hungry prefer cooler habitats
- Does not consider the influence of competitors
- Ideal Free Distribution
- Predicts how animals distribute when habitat patches contain different resource availability
- Individuals have "ideal"(perfect) knowledge of distribution of resources and competitors
- They are "free" to move from patch to patch
- At equilibrium fitness equal among individuals (equal competitors)
- Ideal despotic distribution is for unequal competitors
- Does not consider the influence of temperature and size dependent physiology

Food availability $=750 \mathrm{mg} / \mathrm{d}$

| $750 \mathrm{mg} / \mathrm{d}$ | $\square$ | $\square \square$ |
| :---: | :---: | :---: |
| $1500 \mathrm{mg} / \mathrm{d}$ | $\square$ |  |
|  | $\square$ | $\square$ |




Food availability $=750 \mathrm{mg} / \mathrm{d}$
$750 \mathrm{mg} / \mathrm{d}$


$1500 \mathrm{mg} / \mathrm{d}$
$\square \square \square$



Food availability $=1500 \mathrm{mg} / \mathrm{d}$

| $750 \mathrm{mg} / \mathrm{d}$ | $\square$ | $\square$ |
| :---: | :---: | :---: |
| $1500 \mathrm{mg} / \mathrm{d}$ | $\square$ |  |
|  | $\square$ |  |




Food availability $=3000 \mathrm{mg} / \mathrm{d}$
$750 \mathrm{mg} / \mathrm{d}$

$1500 \mathrm{mg} / \mathrm{d}$
$\square \square]$


300 g fish
Max ration
@14 ${ }^{\circ} \mathrm{C}=2010 \mathrm{mg} /$ day
$14^{\circ} \mathrm{C}$
$14^{\circ} \mathrm{C}$

300 g fish
Max ration
$@ 14{ }^{\circ} \mathrm{C}=2760 \mathrm{mg} /$ day
$14^{\circ} \mathrm{C} \quad 14^{\circ} \mathrm{C}$

300 g fish
Max ration
$@ 14{ }^{\circ} \mathrm{C}=2760 \mathrm{mg} /$ day
100g fish
Max ration
@ $14{ }^{\circ} \mathrm{C}=620 \mathrm{mg} /$ day

$14^{\circ} \mathrm{C}$
$14^{\circ} \mathrm{C}$


300 g fish
Max ration
@14 ${ }^{\circ} \mathrm{C}=2760 \mathrm{mg} /$ day

300g fish Max ration $@ 6^{\circ} \mathrm{C}=620 \mathrm{mg} /$ day


| $5000 \mathrm{mg} / \mathrm{d}$ | $5000 \mathrm{mg} / \mathrm{d}$ |
| :--- | :--- |
|  |  |


$6^{\circ} \mathrm{C}$
$14^{\circ} \mathrm{C}$


