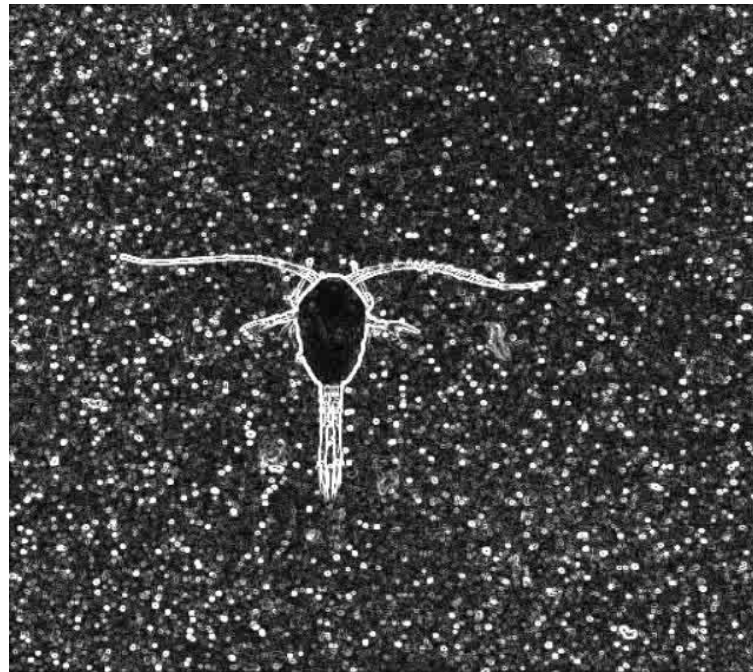


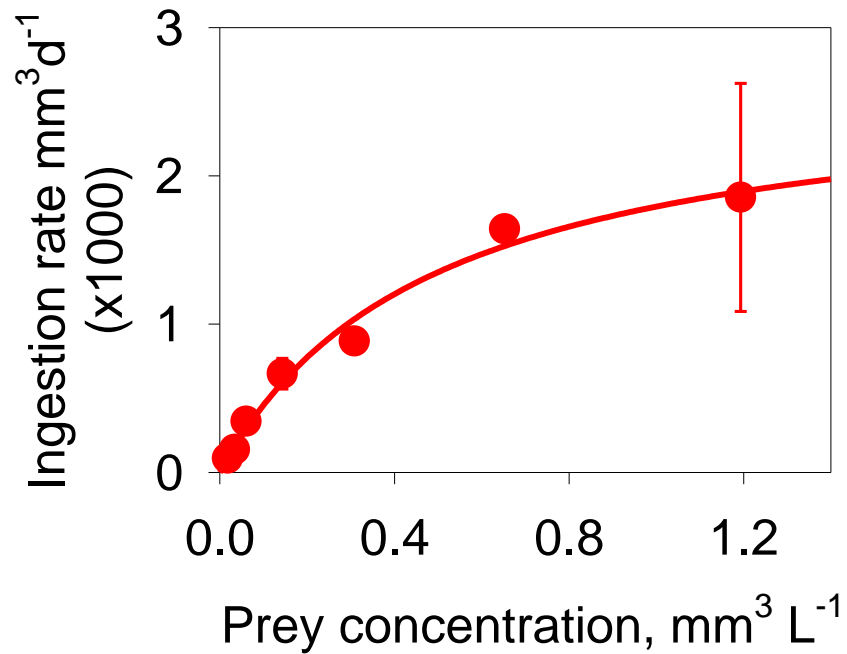
**The functional response in suspension
Mechanistic underpinning and implications
feeding copepods**



T Kiørboe, E Saiz, P Tiselius, P Brun, KH Andersen
Centre for Ocean Life, DTU Aqua

What is the functional response?

The change in feeding rate with prey concentration

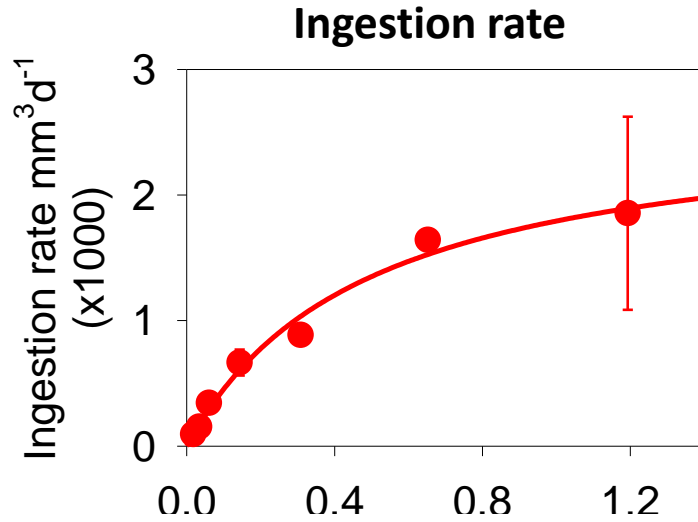


Oithona davisae

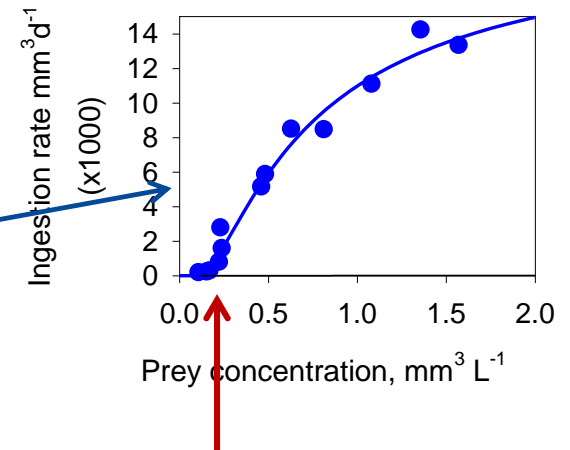
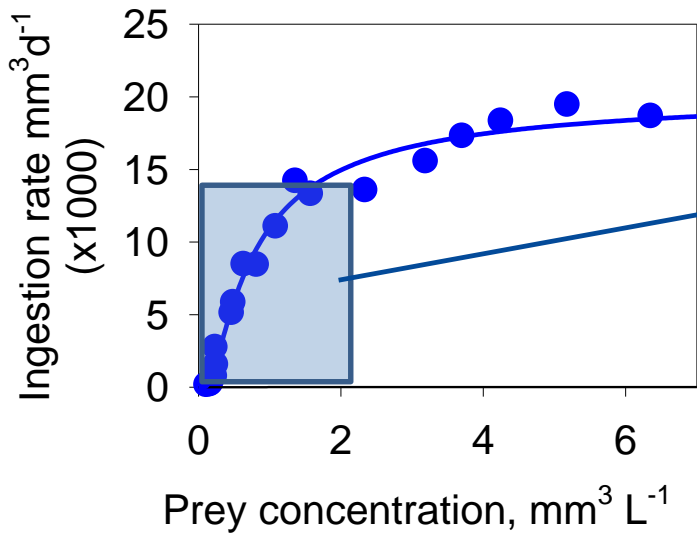
The functional response

Two types of responses

Type II



Type III

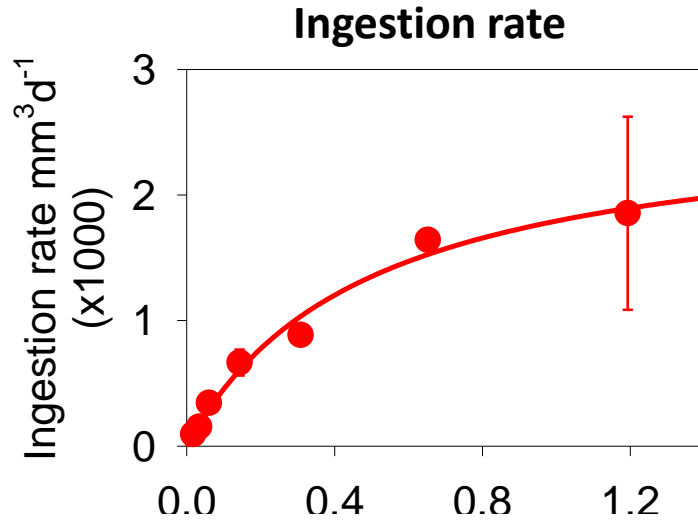


Threshold concentration

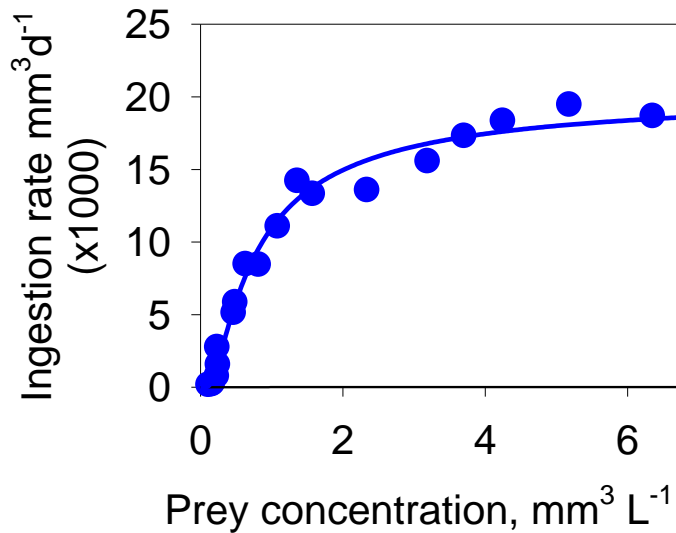
The functional response

Two types of responses

Type II



Type III



The functional response

Two types of responses

- Both types are found in pelagic copepods
 - Literature review: Type II: 88; Type III: 30



- Why different and what are the underlying mechanisms?
- What are the implications?

Theoretical model

Feeding induced predation risk and metabolic costs reduces foraging effort

Theoretical model

Feeding induced predation risk and metabolic costs reduces foraging effort

Feeding rate (Holling II): $F = F_{max} \frac{\beta R}{\beta R + F_{max}}$

Foraging effort, p $F(p) = F_{max} \frac{p\beta R}{p\beta R + F_{max}}$

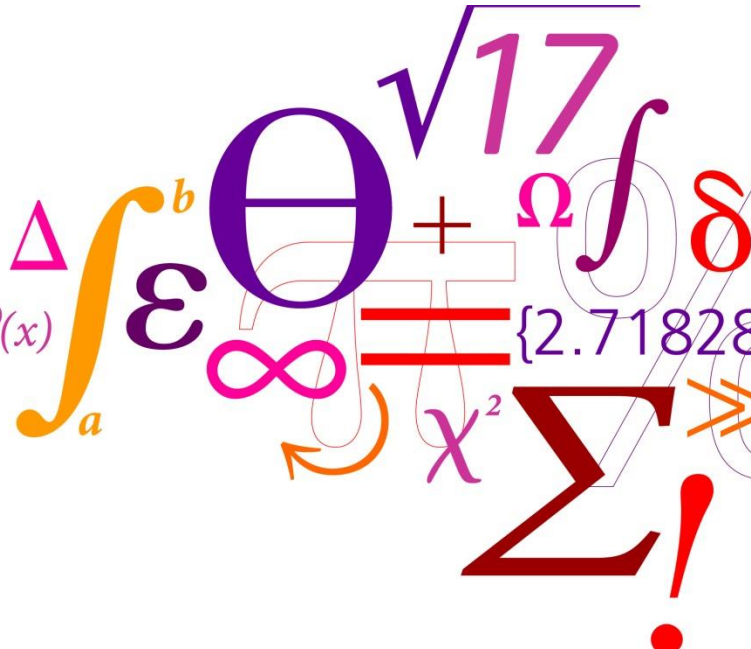
What foraging effort (p) optimizes the net energy gain?

Metabolism $M = m_0 + p m_f$ ← Metabolic cost of feeding

Mortality $\mu = \mu_0 + p \mu_f$ ← Predation risk of feeding

Theoretical model

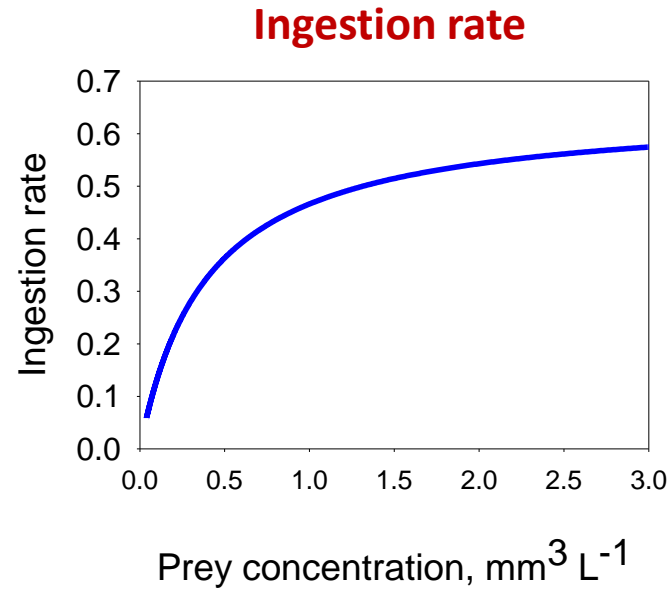
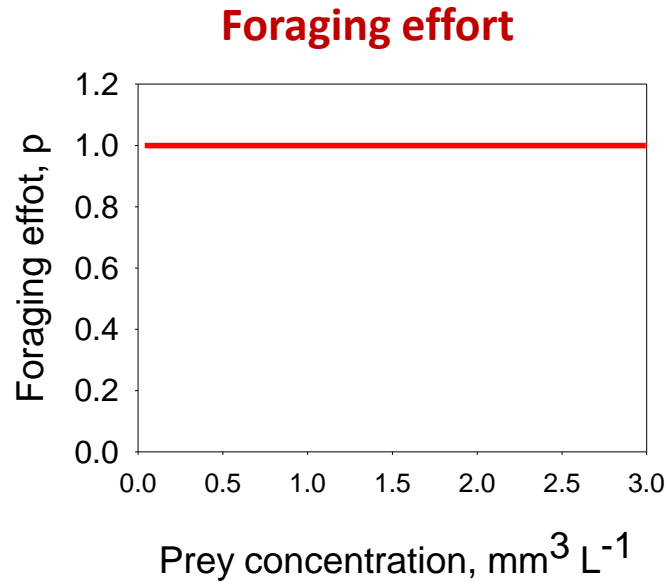
Solve the optimization (or have someone do it):

$$f(x+\Delta x) = \sum_{i=0}^{\infty} \frac{(\Delta x)^i}{i!} f^{(i)}(x)$$


The image features a central collage of mathematical symbols. On the left, a yellow integral symbol \int_a^b is shown. To its right is a purple Greek letter ϵ , followed by a large purple Θ . Further right is a pink infinity symbol ∞ , a purple χ^2 , and a large red Σ . A red exclamation mark $!$ is positioned at the bottom right. Other symbols include a purple Δ , a purple Ω , a purple δ , a purple $\sqrt{17}$, and a purple \int . A purple curly brace $\{2.71828$ is also present. The symbols are arranged in a somewhat chaotic but organized manner, suggesting a complex mathematical or optimization problem.

Theoretical model: predictions

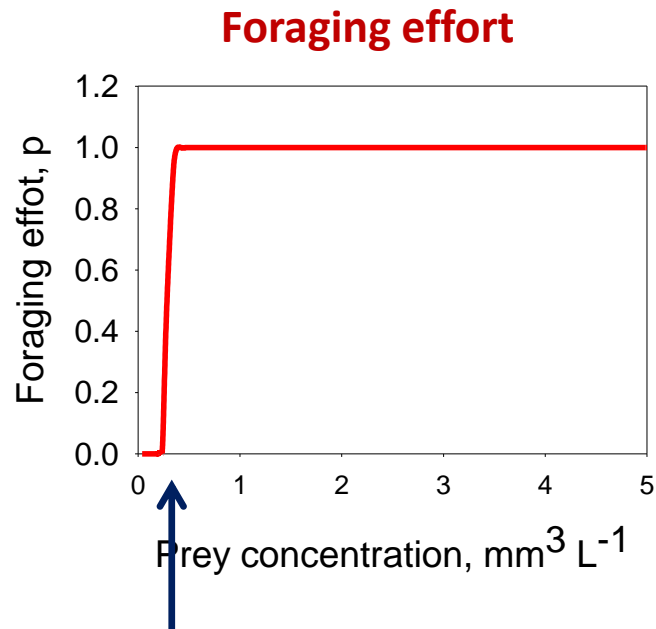
No risk, no cost



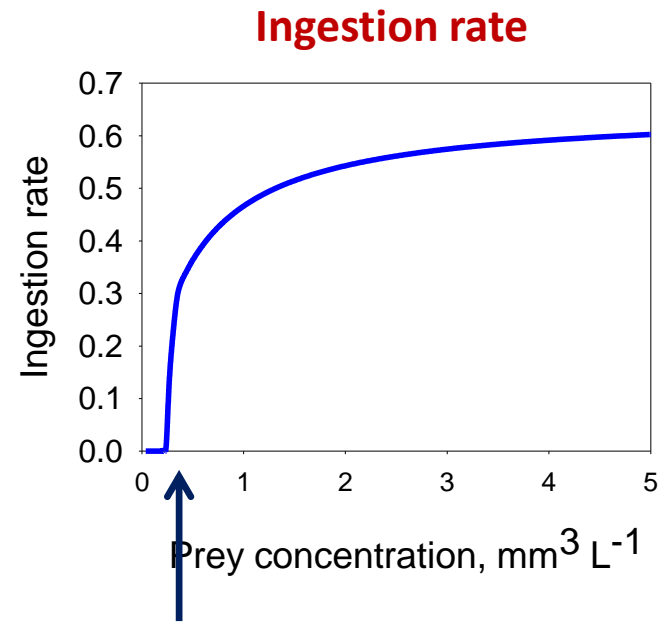
Type II response

Theoretical model: predictions

Metabolic cost



Feeding threshold

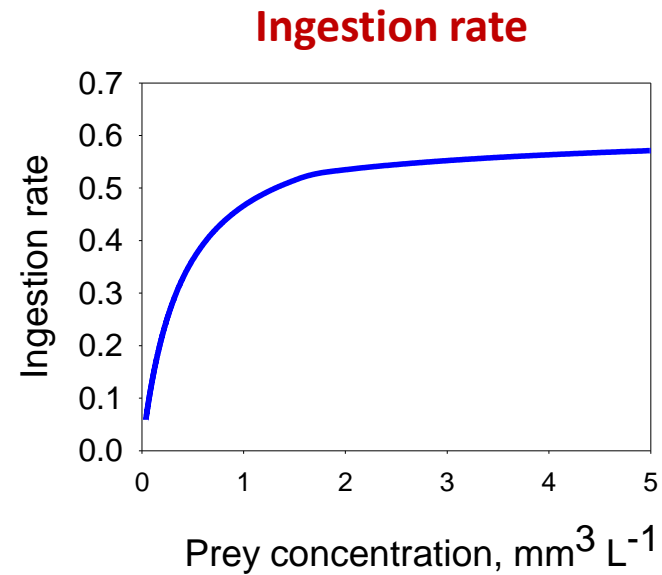
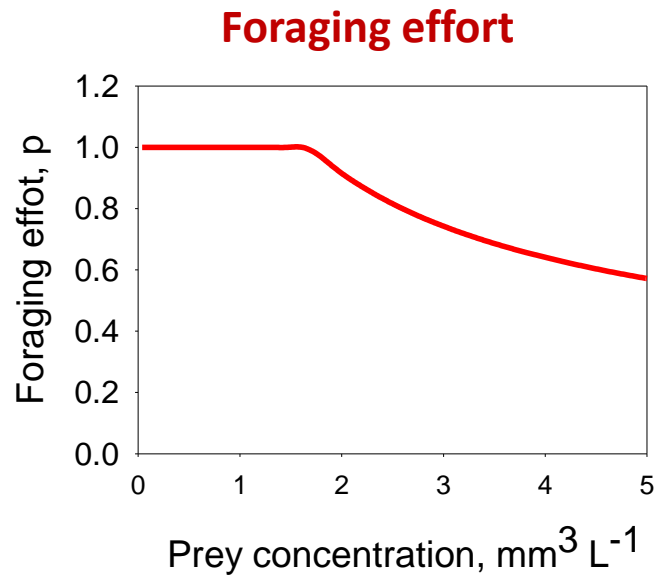


Feeding threshold

Type III response

Theoretical model: predictions

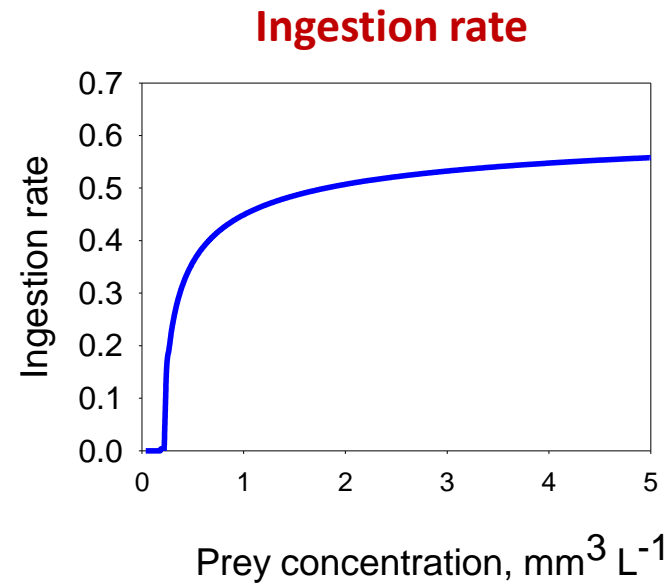
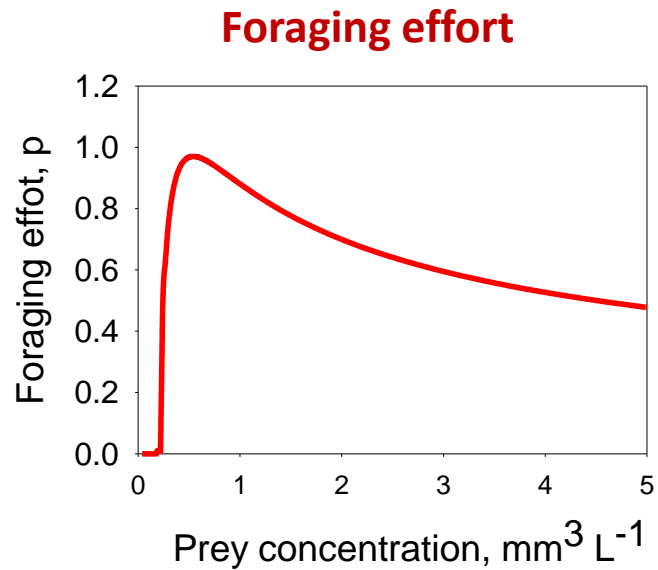
Predation risk



Type II response

Theoretical model: predictions

Predation risk + metabolic cost



Type III response

Theoretical model: summary of predictions

Feeding induced predation risk and metabolic costs reduces foraging effort

- Metabolic cost of feeding leads to feeding threshold and type III
- Predation risk leads to reduced foraging effort at high prey availability, but still a type II response
- **Question:** Are there differences in risk and cost between copepod species?

Two feeding modes

feeding current feeders

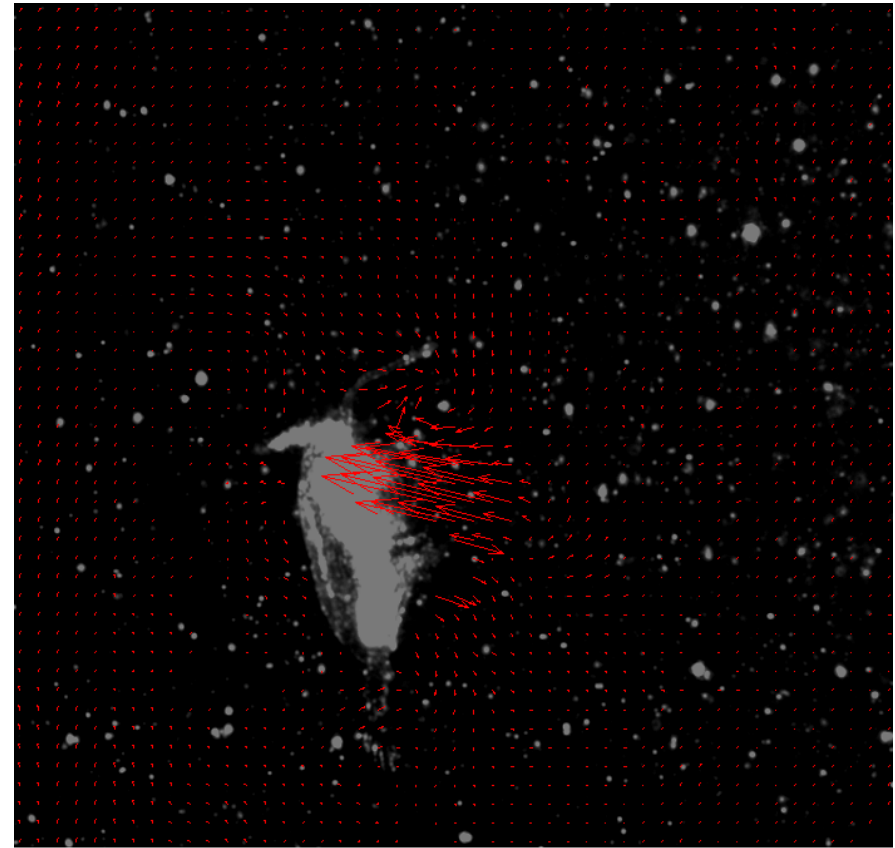
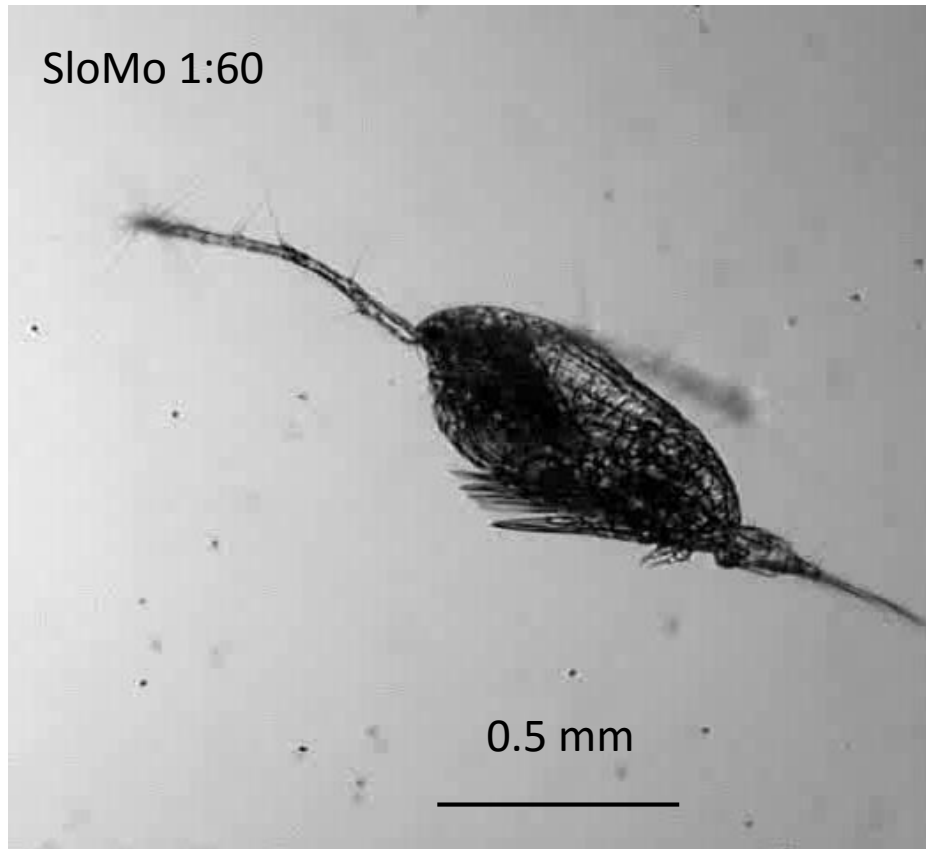
or

ambush feeders.

or both.

Feeding current feeding

Metabolic cost of beating appendages; fluid signal = predation risk.



Acartia tonsa beating its feeding appendages to generate a feeding current

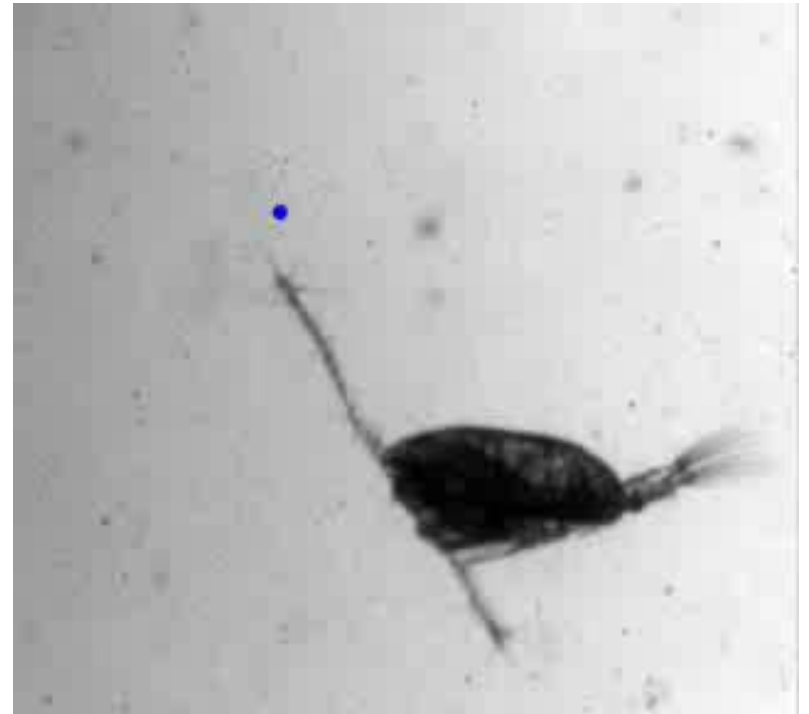
SloMo 1:40

Ambush feeding

Sit-wait-and attack: no foraging effort; no feeding-induce risk



Real time



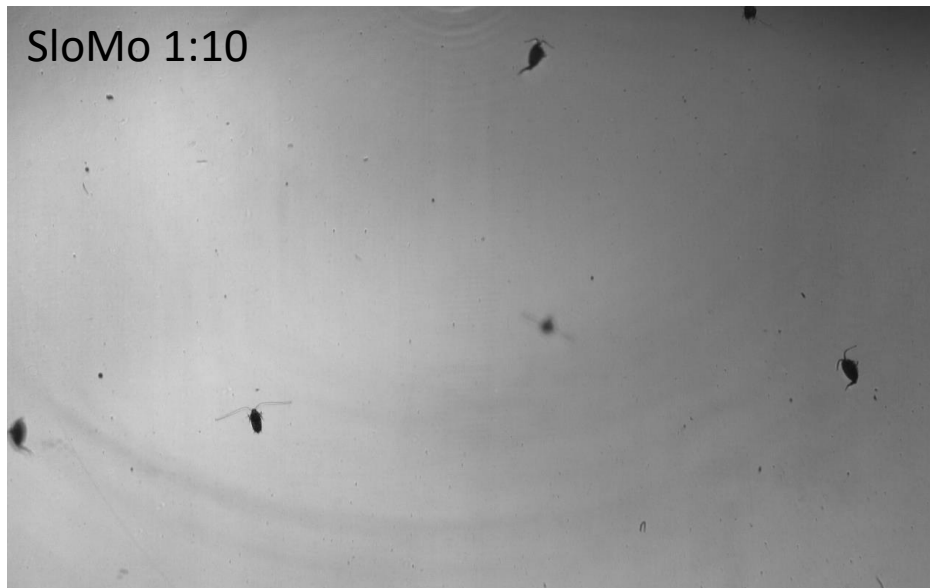
SloMo 1:270

Hypotheses

- **Feeding current feeders:**
 - Reduce foraging at low prey concentration; type III response
 - Reduced foraging effort in the presence of predator (cue)
- **Ambush feeders:**
 - Type II response
 - No effect of predator (cue)

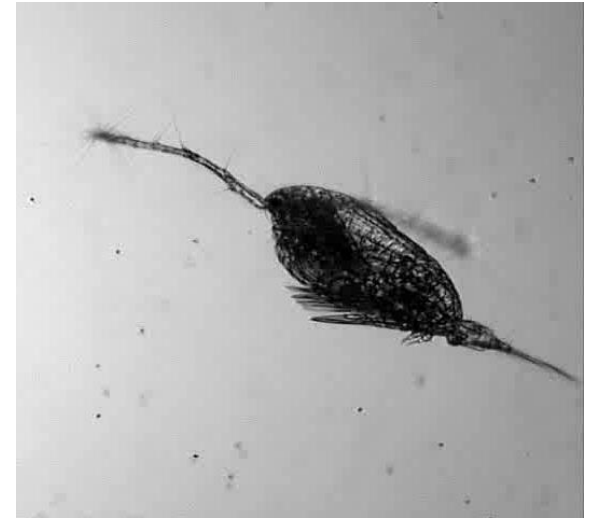
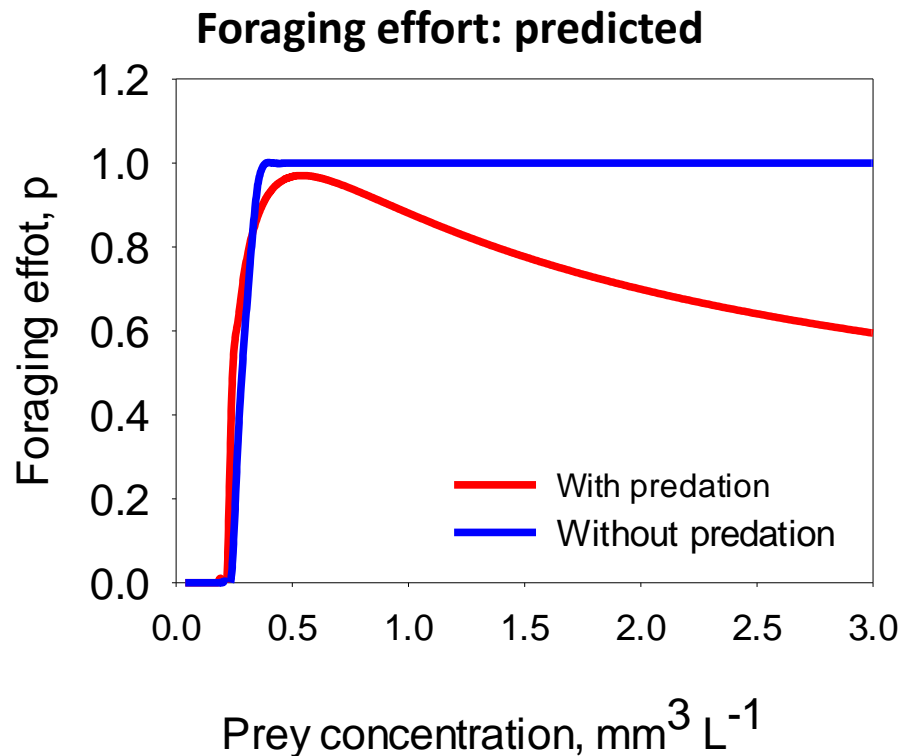
Experiments

- **Observe behavior of free-swimming copepods**
 - Quantify foraging effort (appendage beating)
 - At different prey concentrations
 - In absence and presence of predator cue (fish smell)
 - For ambush and feeding current feeders
- **Measure functional response** (incubation experiments)



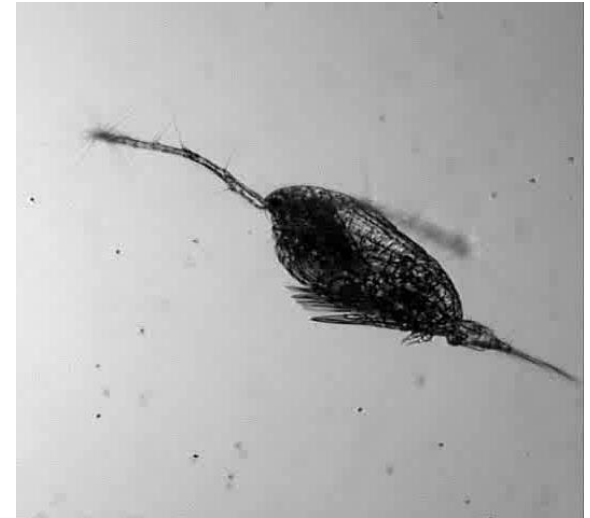
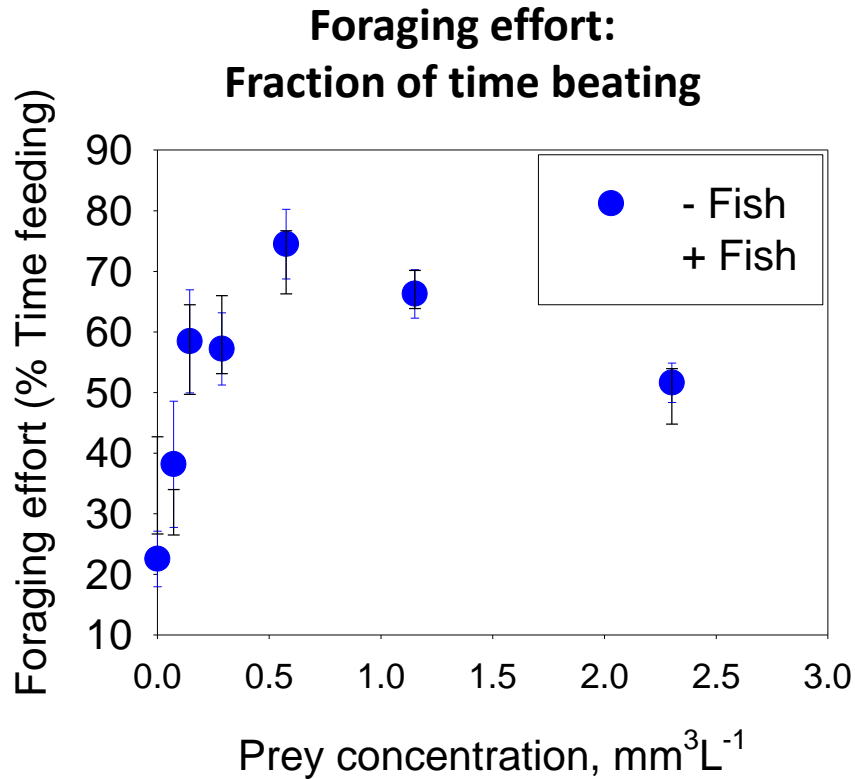
Observed behavior: feeding current feeder

Acartia feeding on a small (~non-motile) phytoplankton



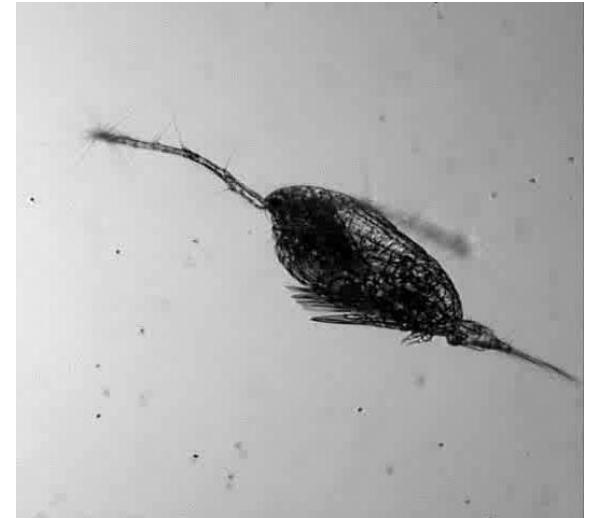
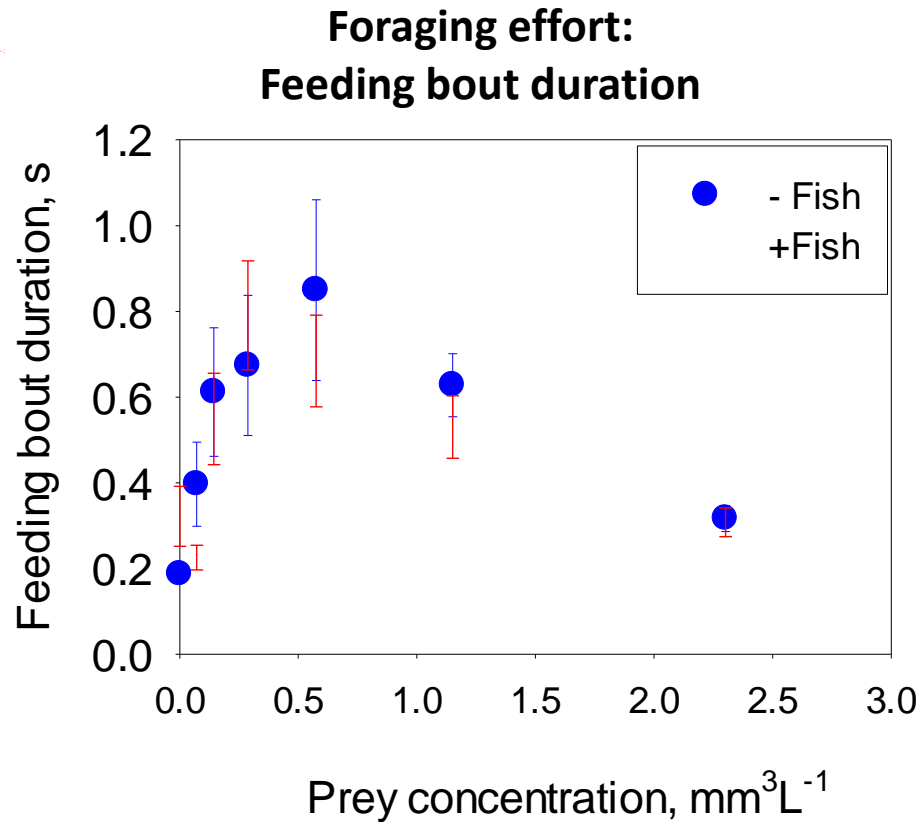
Observed behavior

Acartia feeding on a small (~non-motile) phytoplankton



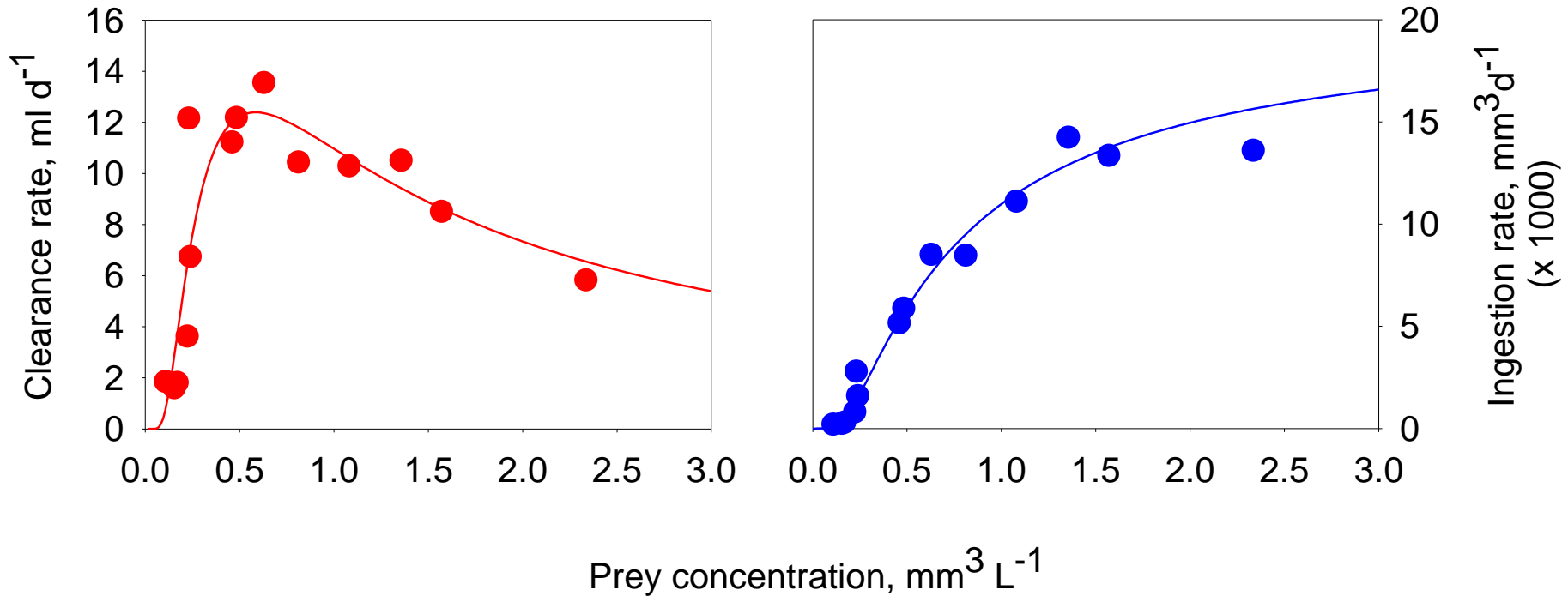
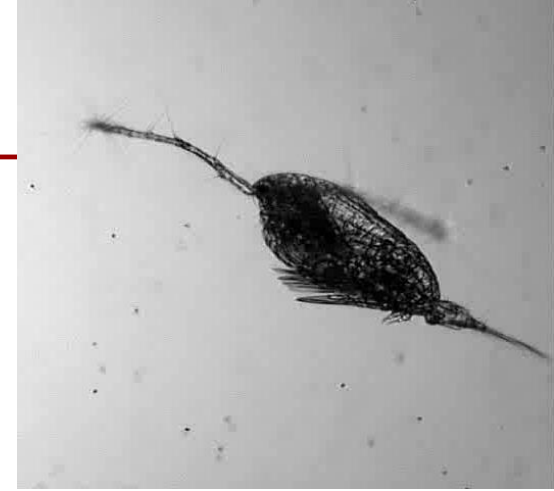
Observed behavior

Acartia feeding on a small (~non-motile) phytoplankton



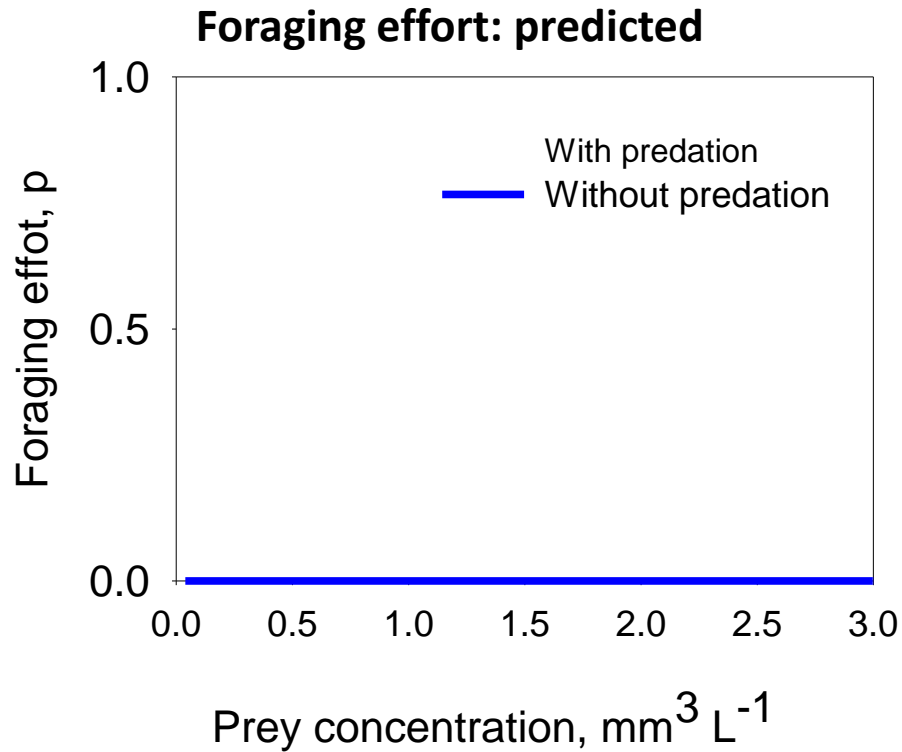
Resulting functional response

Acartia feeding on a small (~non-motile) phytoplankton



Observed behavior ambush feeder

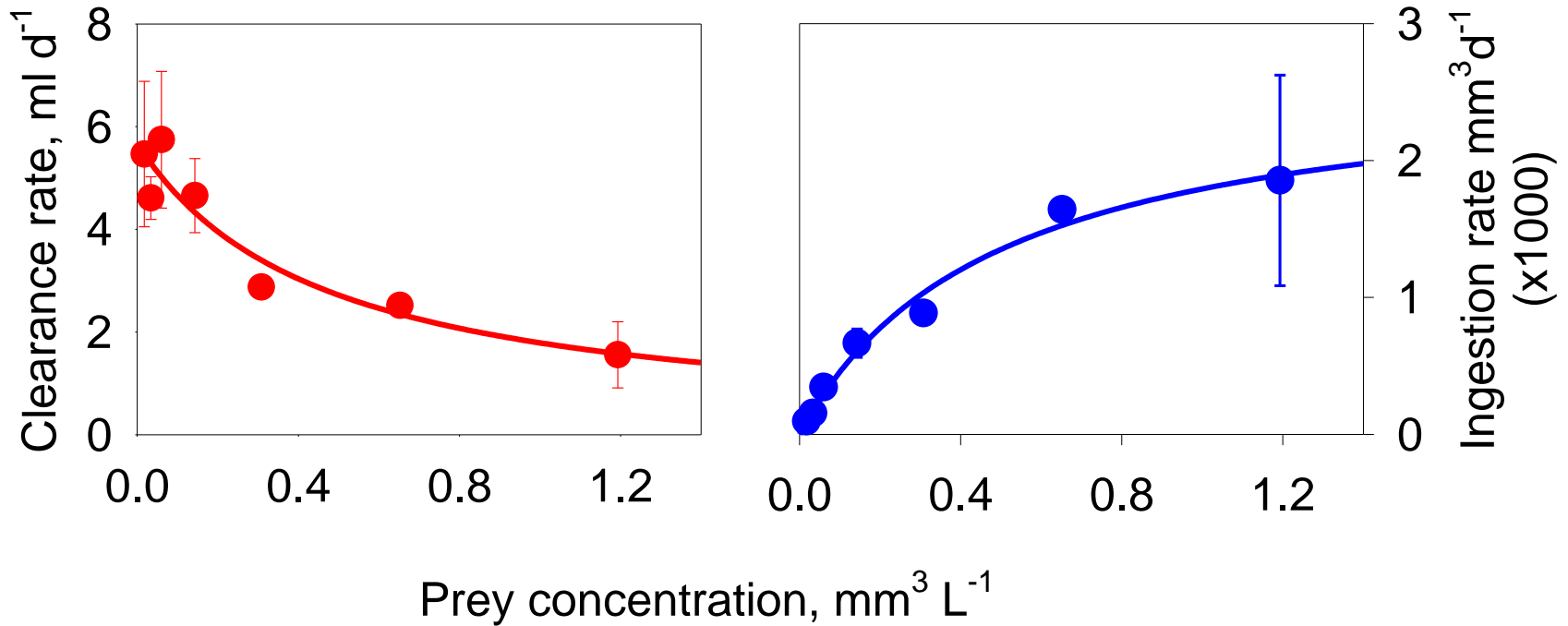
Oithona davisae feeding on Oxyrrhis marina
(No cost, no risk – no effort)



Observed:
Fraction of time active: 0

Resulting functional response

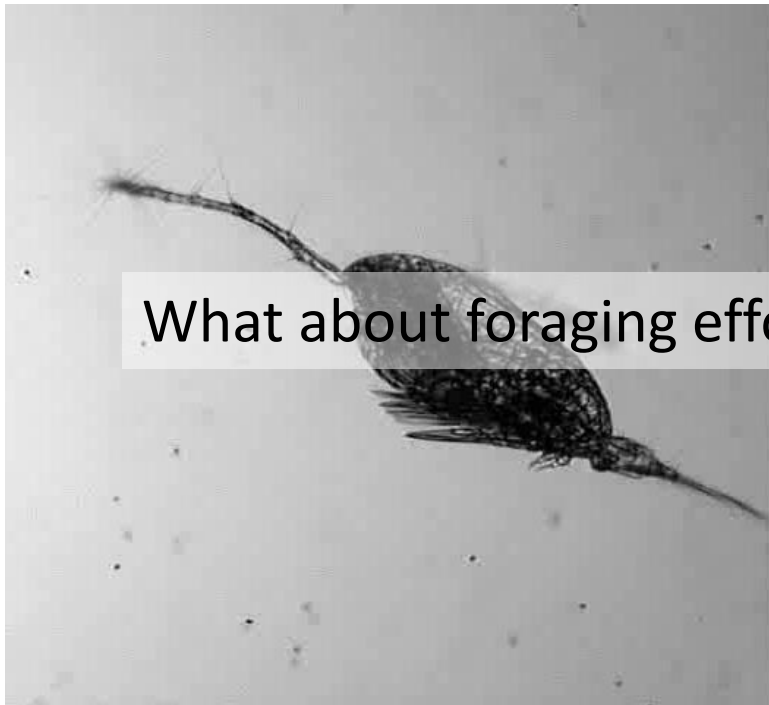
Oithona davisae feeding on *O. marina*



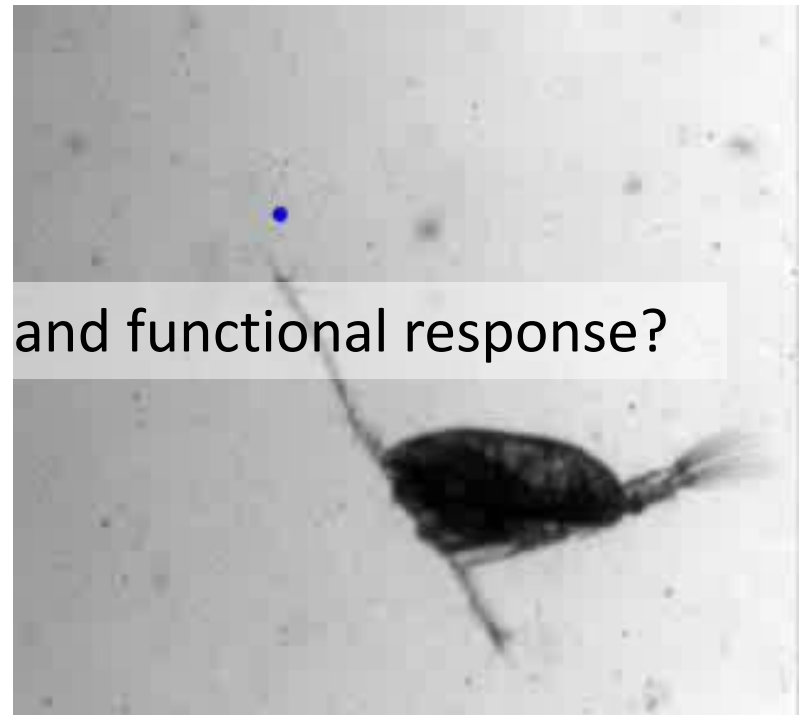
Acartia has two foraging modes

Acartia can be both a feeding current and an ambush feeder

Feeding current feeding when offered small non-motile prey



Ambush feeding when offered large motile prey

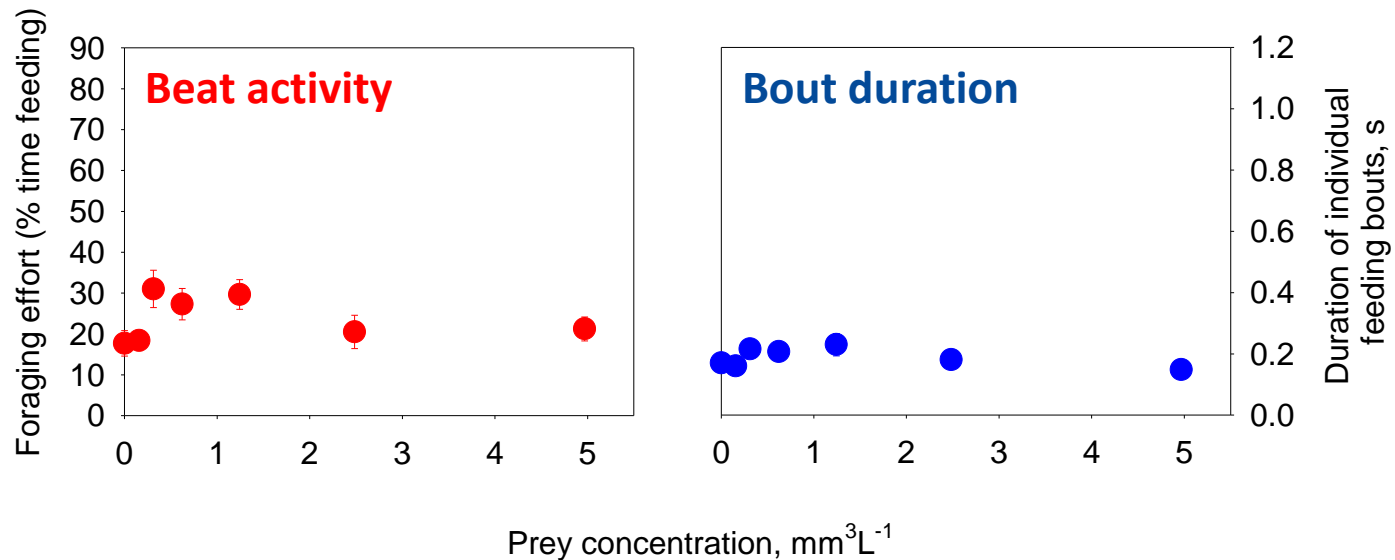


What about foraging effort and functional response?

Acartia as an ambush feeder

Acartia offered large, motile prey

Foraging effort

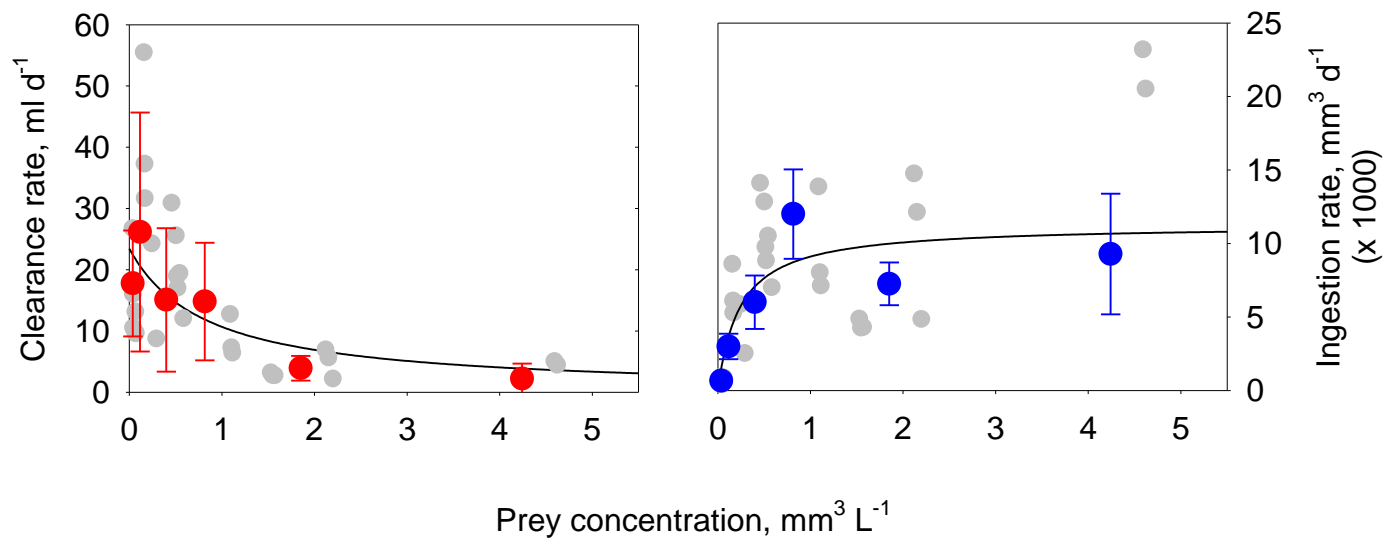


Low, constant foraging effort: Type II

Acartia as an ambush feeder

Acartia offered large, motile prey

Resulting functional response

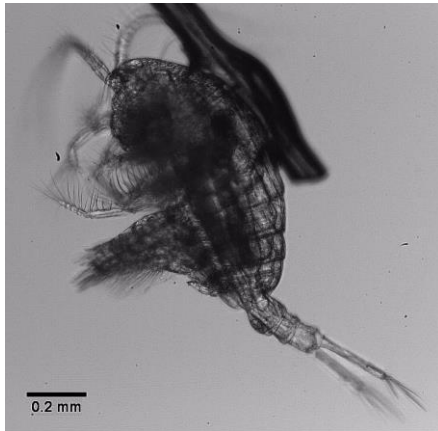


Type II functional response

Unpredicted results

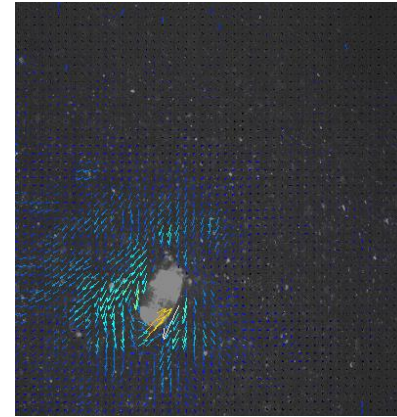
Temora longicornis and *Centropages typicus* are active feeders but have type II responses

Temora



1. ~100 % foraging effort **independent of prey concentration**
2. **Type II response**
3. No effect of **predator cue**

Centropages



1. ~50 % foraging effort **independent of prey concentration**
2. **Type II response**
3. No effect of **predator cue**

Consistency between behavioral observations and resulting functional response

Summary

Conclusions so far

1. **Mechanistic underpinning:** There is consistency between individual behavioural responses and resulting functional response
2. **Type II and III responses** only partly follow the prediction of the optimization

Literature review # papers	Type II	Type III
Ambush	43	0
Feeding current	30	25 (+20)

3. **Predator responses** (if any) wired into the genes

The functional response

Two types of responses

- Both types are found in pelagic copepods
 - Literature review: Type II: 88; Type III: 30
- What are the underlying mechanisms?
- • What are the implications?

Feeding and maintenance thresholds

The optimization model predicts two thresholds.

The two thresholds depend on the relative prey size:

The smaller the prey, the higher the concentration needed to maintain a population

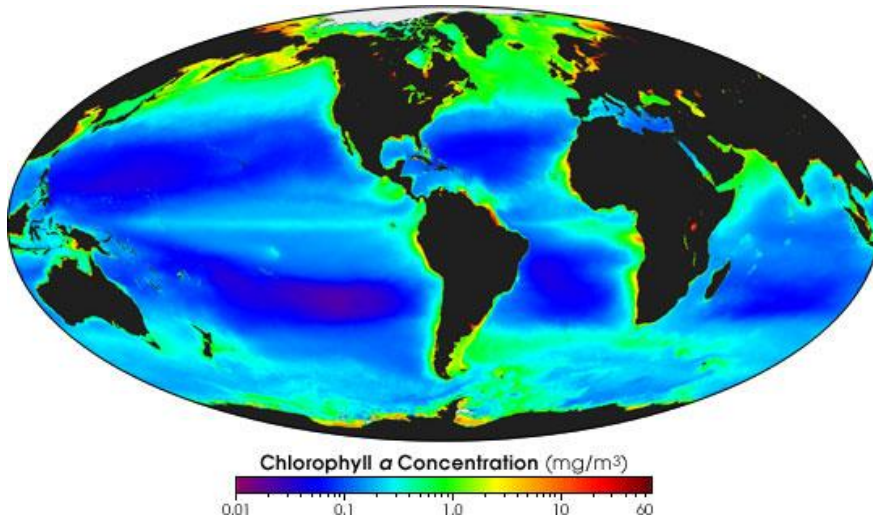
The feeding threshold is the prey concentration at which foraging stops (only type III)

(Frequency distribution of thresholds estimated from ~200 functional response experiments)

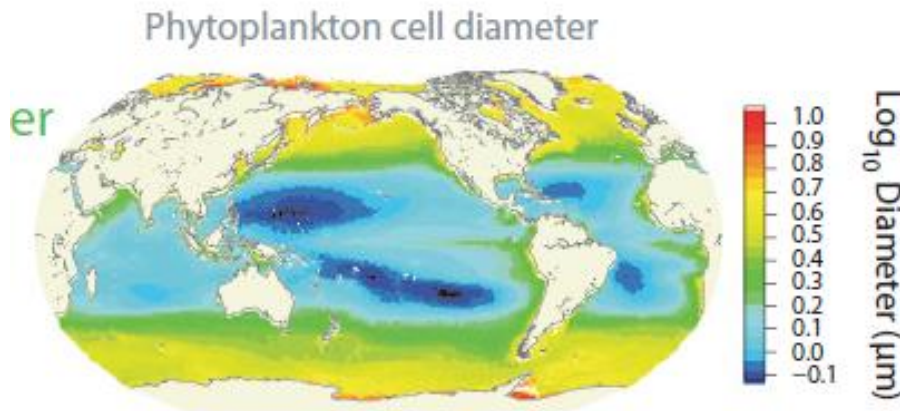
If we know the **biomass** and **size** of phytoplankton in the ocean, we can estimate the **maximum possible size of the (copepod) grazers**

Global distribution of phytoplankton biomass and size

Biomass and size estimated from satellite



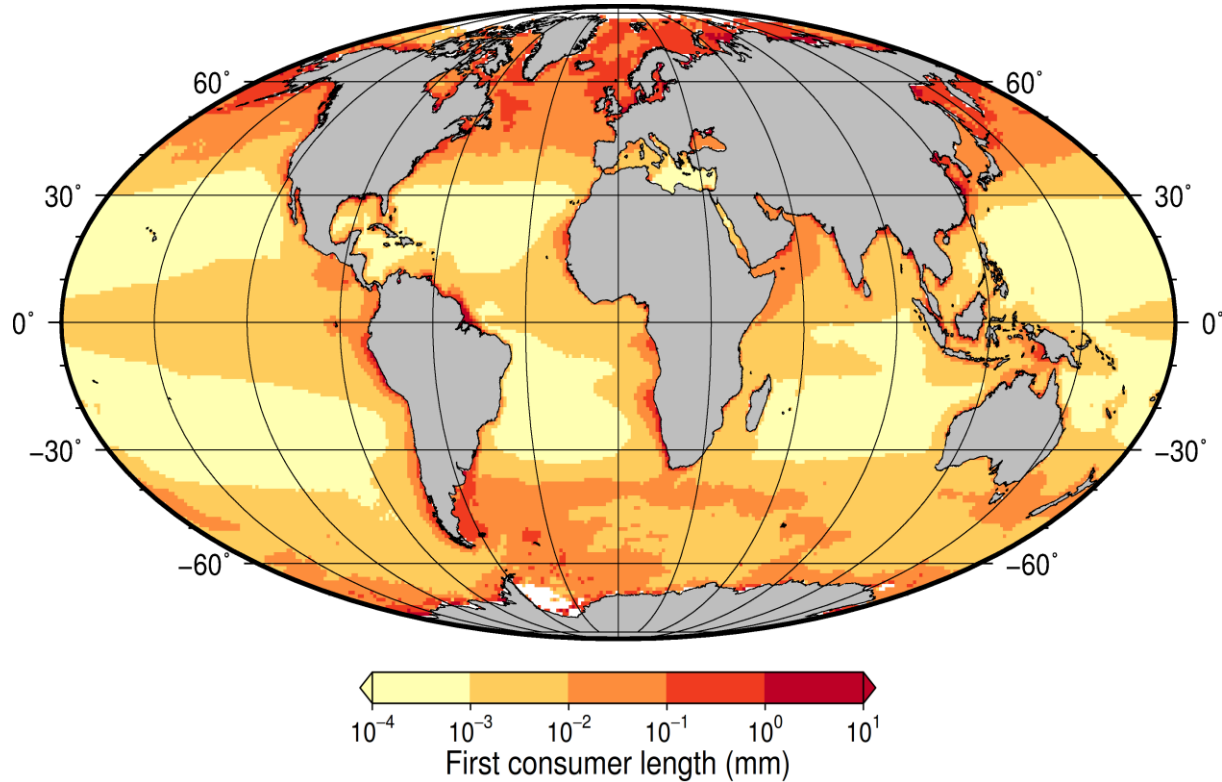
Biomass (NaSA)



Phytoplankton median diameter (based on Barnes et al. 2011)

Copepod trait biogeography: Size

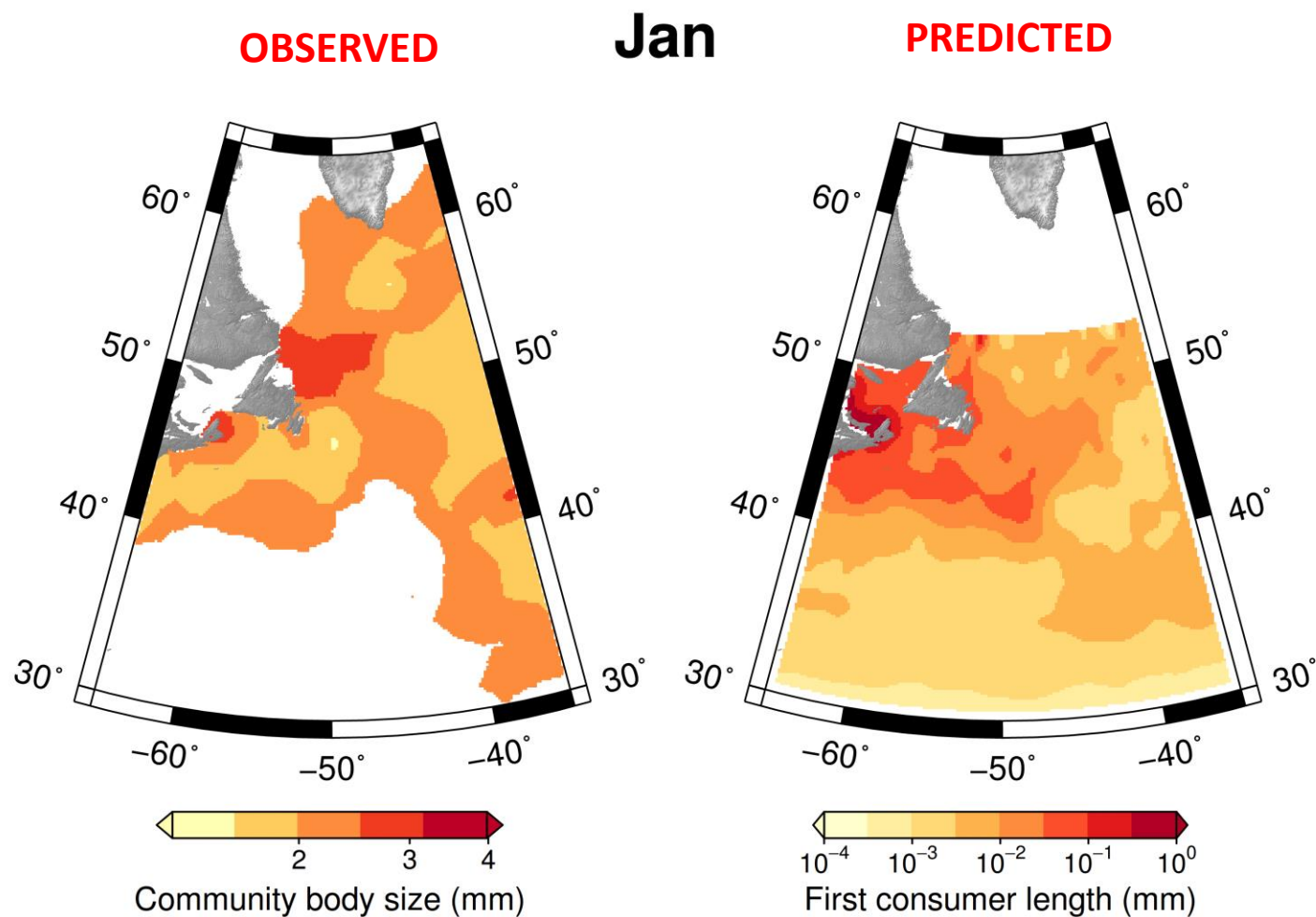
Copepod (first consumer) maximum size



Is this phantasy?

Copepod trait biogeography: Size

Observed and predicted spatio-temporal pattern in copepod size in NW Atlantic



Conclusions

Conclusions

1. Mechanistic underpinning: There is consistency between individual behavioural responses and resulting functional response
2. Type II and III responses only partly follow the prediction of the optimization

Literature review	Type II	Type III
Ambush	43	0
Feeding current	30	25 (+20)

3. Predator responses (if any) wired into the genes
4. **The functional response is a fundamental property of a zooplankter that impacts population dynamics, trophic structure and transfer efficiencies, as well as biogeography**