

Steep body mass scaling of biological rates in macrozooplankton supports a Surface Area dependent model

Martin Lilley, Andrew Hirst, Doug Glazier, David Atkinson



Metabolism

$$\text{Respiration} = a \text{ Mass}^b$$

- Respiration rate commonly related to organism size using a power function
- What determines the b power term has been a central question in ecology for over 100 years
- As organisms enlarge they commonly utilise less oxygen per unit mass ($b < 1$)
- Here we will focus on intra-specific scaling

Theories of Metabolic Scaling

Two groups of theories attempt to mechanistically describe metabolic scaling through resource supply:

Internal Transport Networks

1. Metabolic Theory of Ecology (West *et al.* 1999 Science)
2. Explosive Network Model (Banavar *et al.* 2010 PNAS)

$$R = a M^{3/4}$$

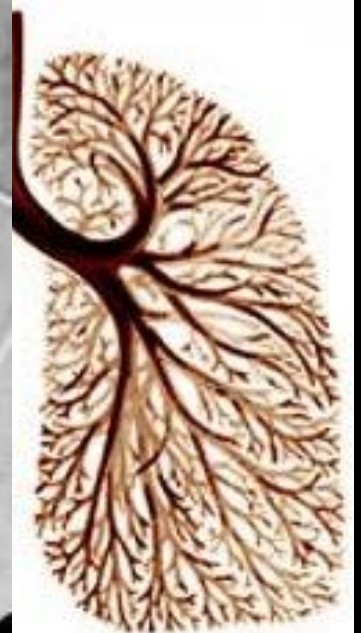
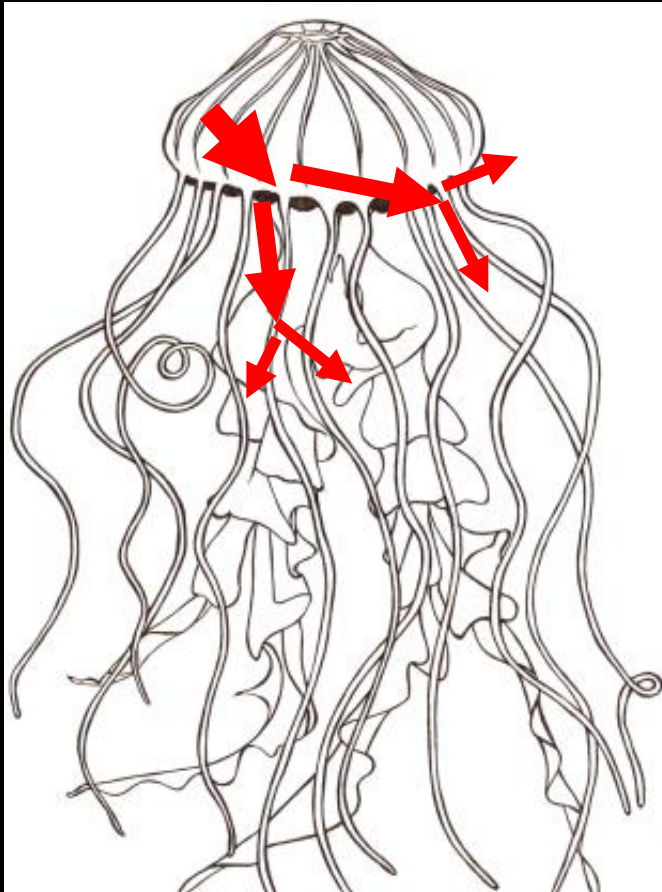
Surface Area Dependent Theory (originally used to describe heat loss in endotherms -Rubner 1883)

e.g. Dynamic Energy Budget (Kooijman 1986)

$$R = a M^{2/3}$$

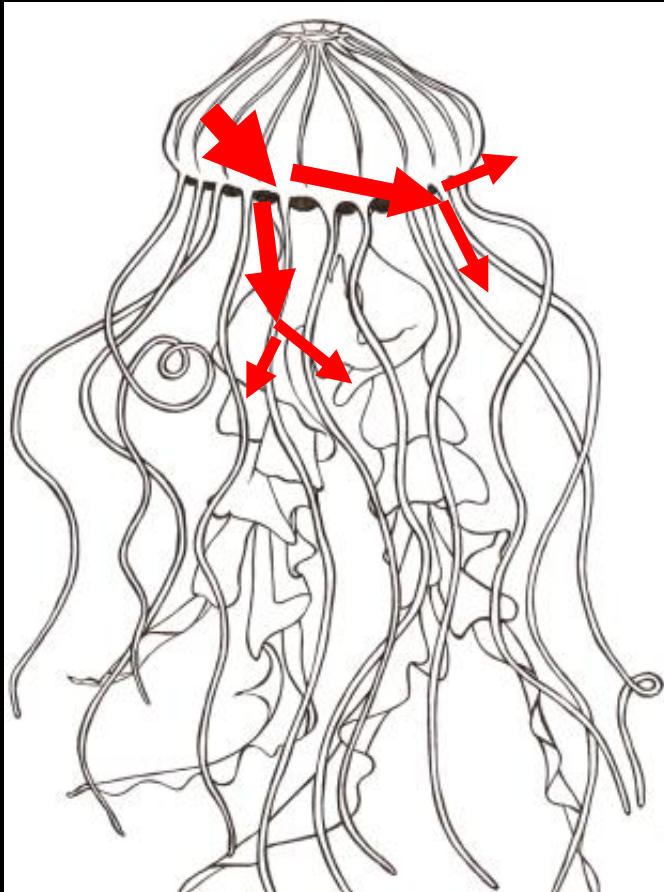
Internal Transport Networks

$$R = a M^{3/4}$$



Internal Transport Networks

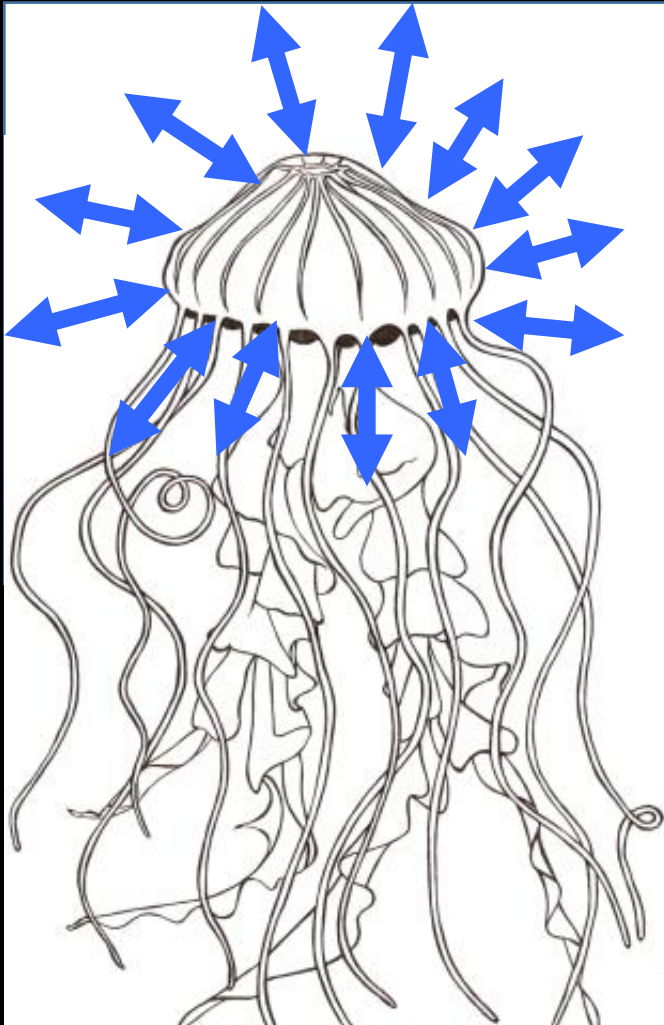
$$R = a M^{3/4}$$



- Based on resources passing through branching networks, observed in some animals and plants
- Deliver of nutrients and energy to body tissues takes longer for large organisms thus they have a slower metabolic rate
- Banavar *et al.* (2010) have developed a more general transport model with fewer assumptions

Surface Area Model

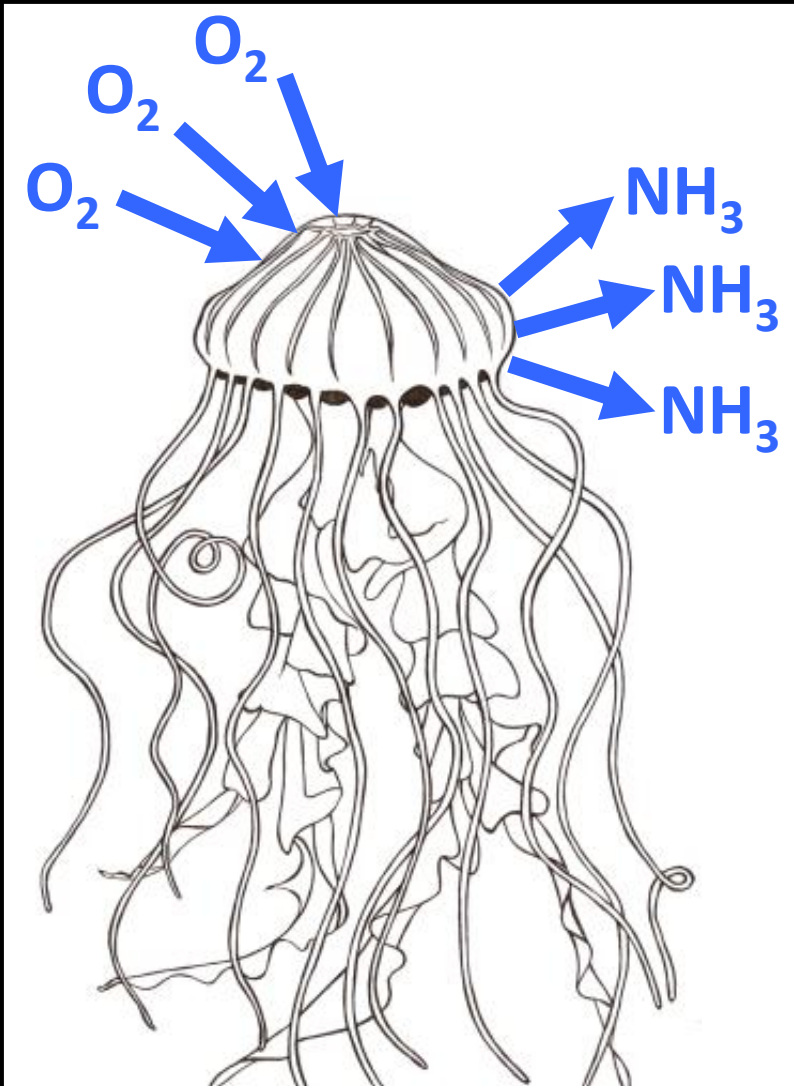
$$R = a M^{2/3}$$



Surface area constrains
rate of influx or efflux

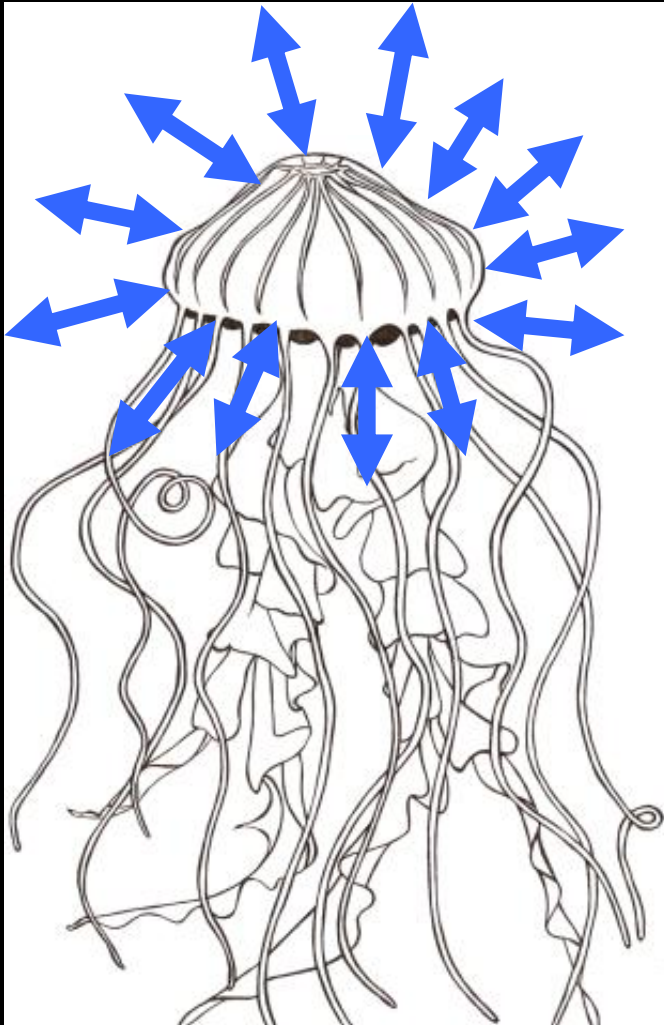
Surface Area Model

$$R = a M^{2/3}$$



Surface Area Model

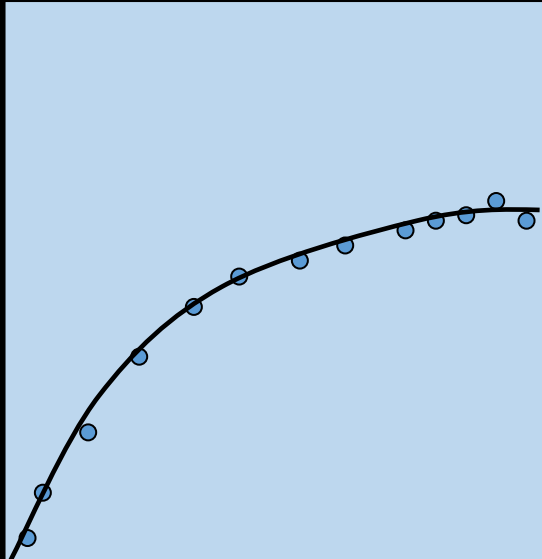
$$R = a M^{2/3}$$



Why a power of 2/3rds?

Isomorphic Increase

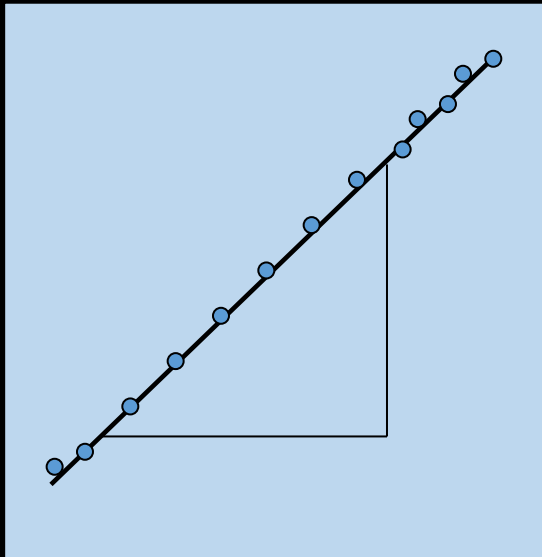
Surface Area



Body Mass



Log₁₀ Surface Area



Log₁₀ Body Mass

$$\text{Surface Area} = a \text{ Mass}^{2/3}$$

so, SA Model predicts:

$$\text{Respiration} = a \text{ Mass}^{2/3}$$

Predicting Surface Area

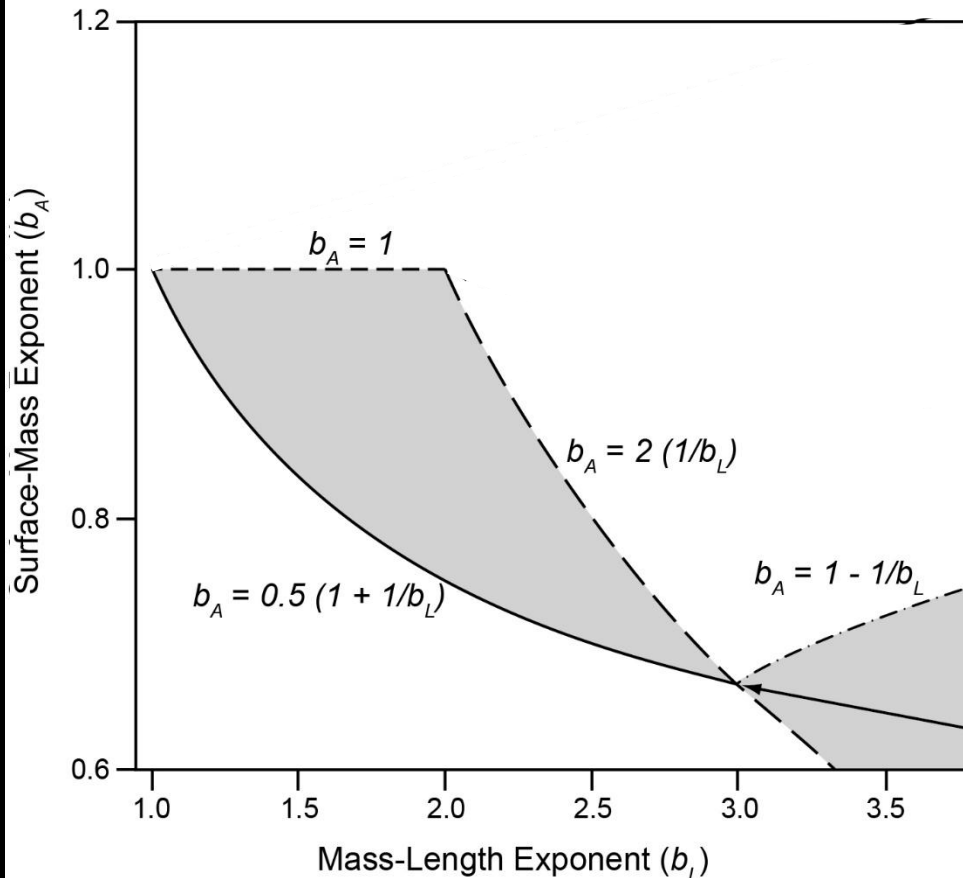
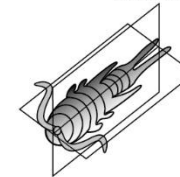
Length relations: $l_2 \propto l_1^\theta$; $l_3 \propto l_1^\beta$

Mass-length relation: $M \propto V \propto l_1 l_2 l_3 \propto l_1^{(\theta + \beta + 1)}$

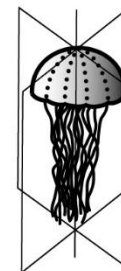
Area-Mass relation: $A \propto M^{(\theta + 1) / (\theta + \beta + 1)}$



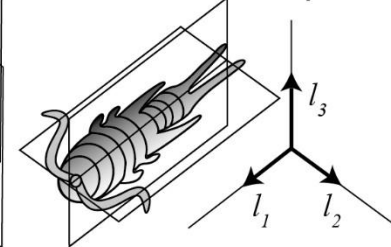
Initial shape



Smooth 3D surface
Volume \propto Mass^{2/3}



Isomorphic



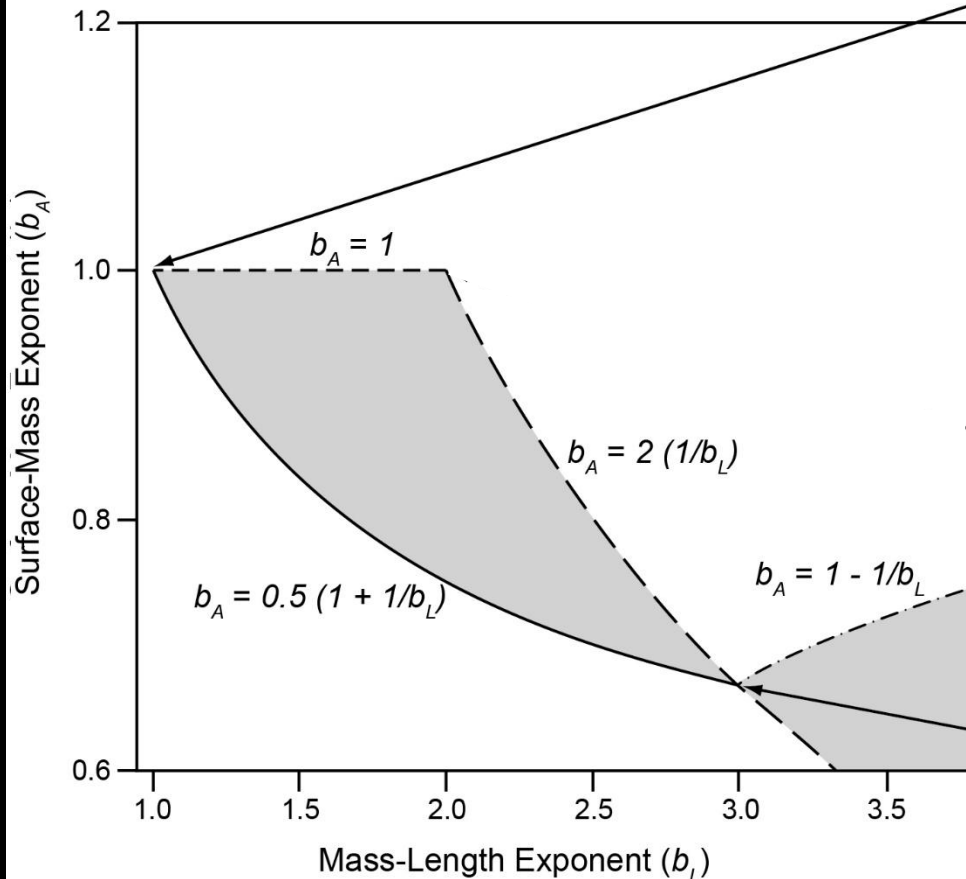
$b_L = 3$

Predicting Surface Area

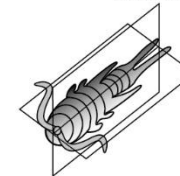
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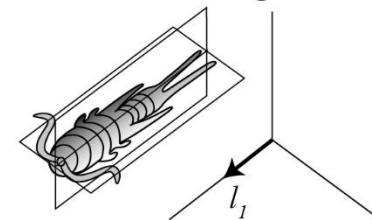
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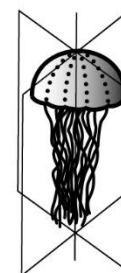
Initial shape



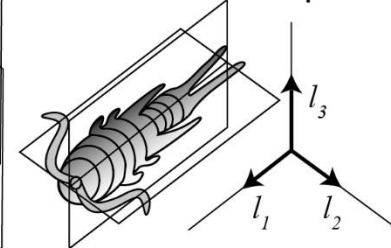
Pure elongation



$b_L = 1$



Isomorphic



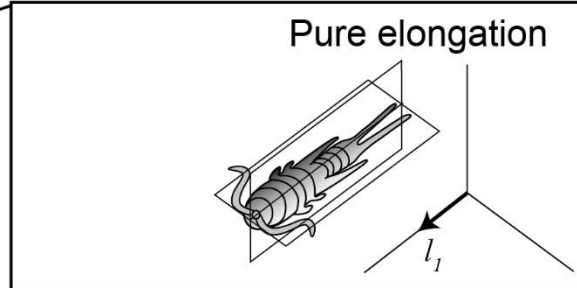
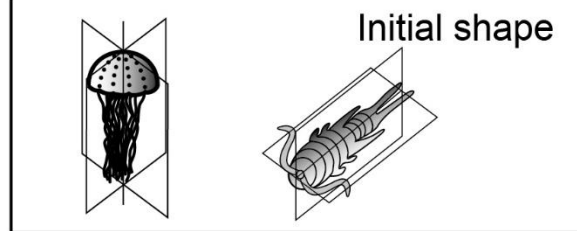
$b_L = 3$

Predicting Surface Area

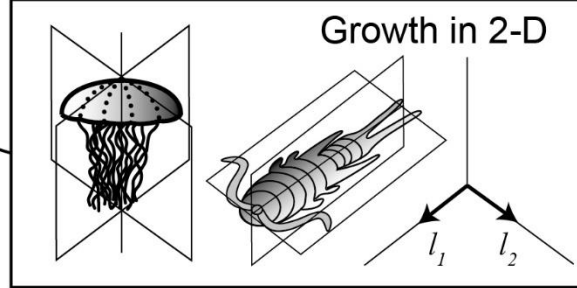
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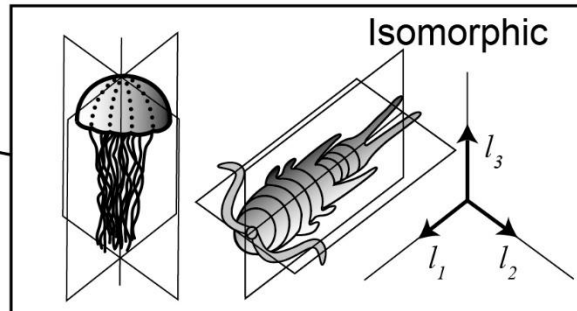
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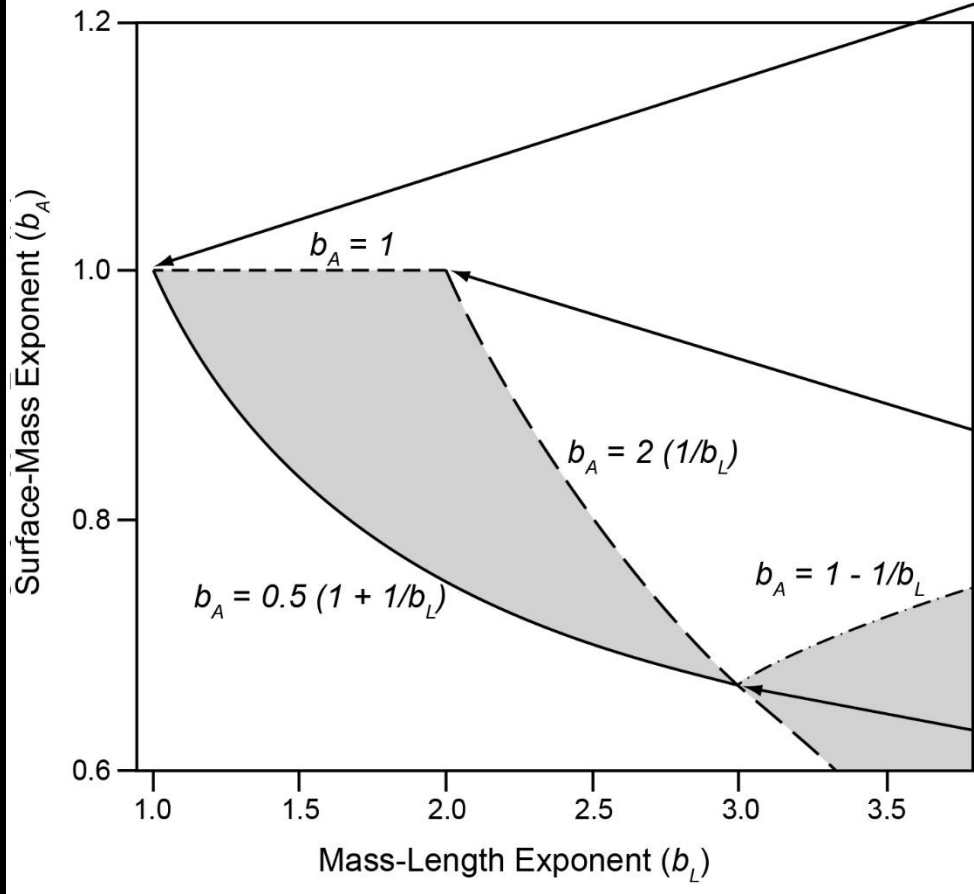
$b_L = 1$



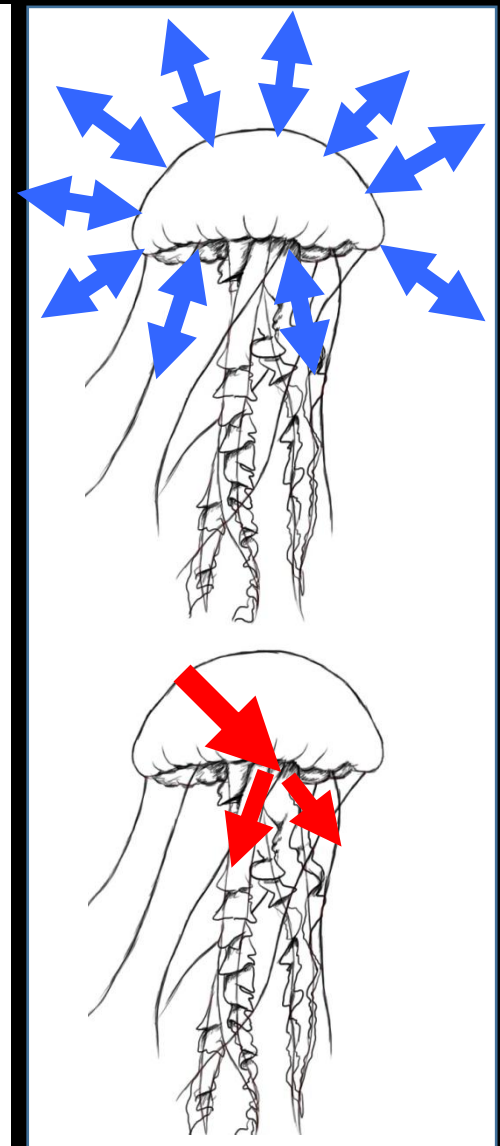
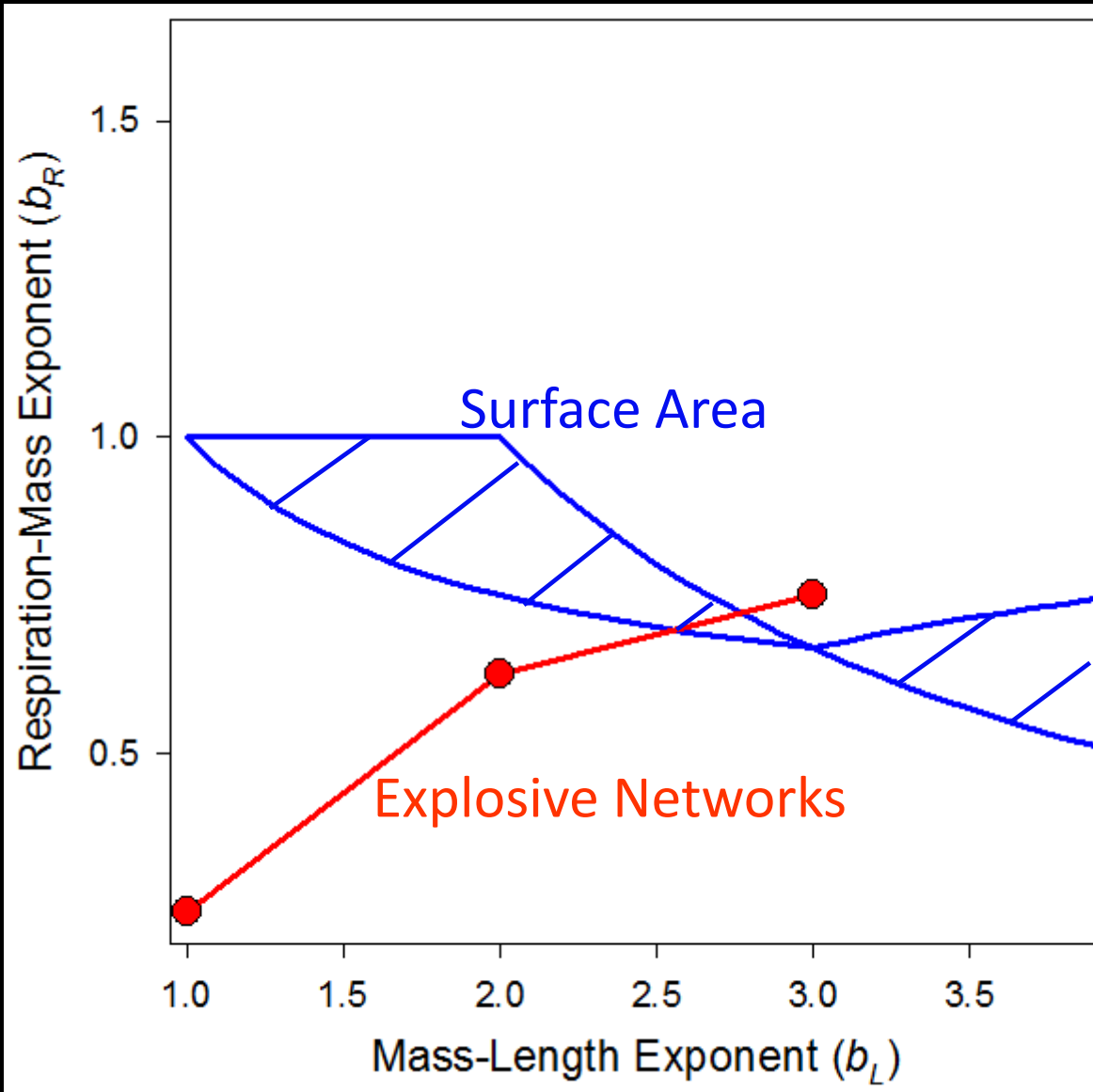
$b_L = 2$



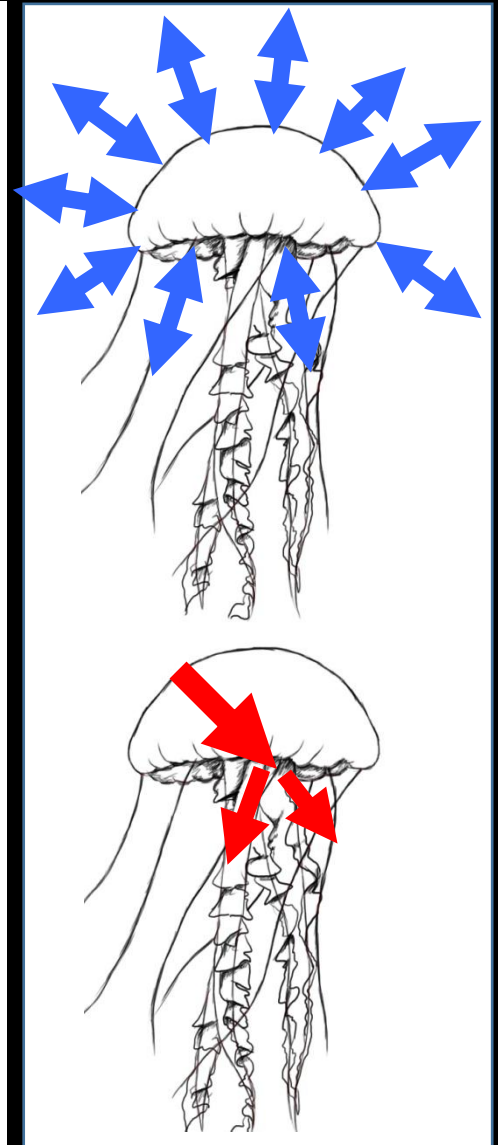
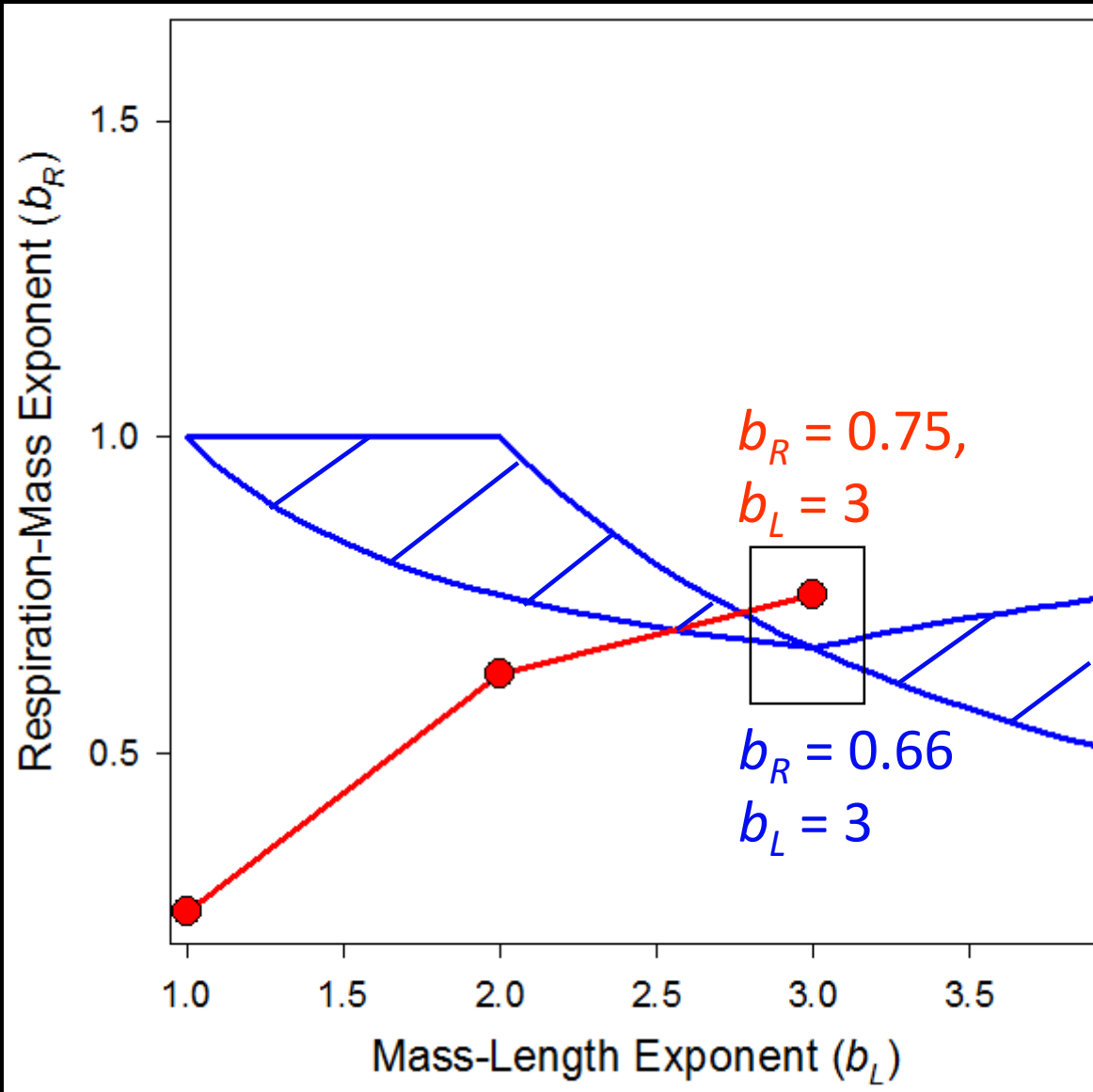
$b_L = 3$



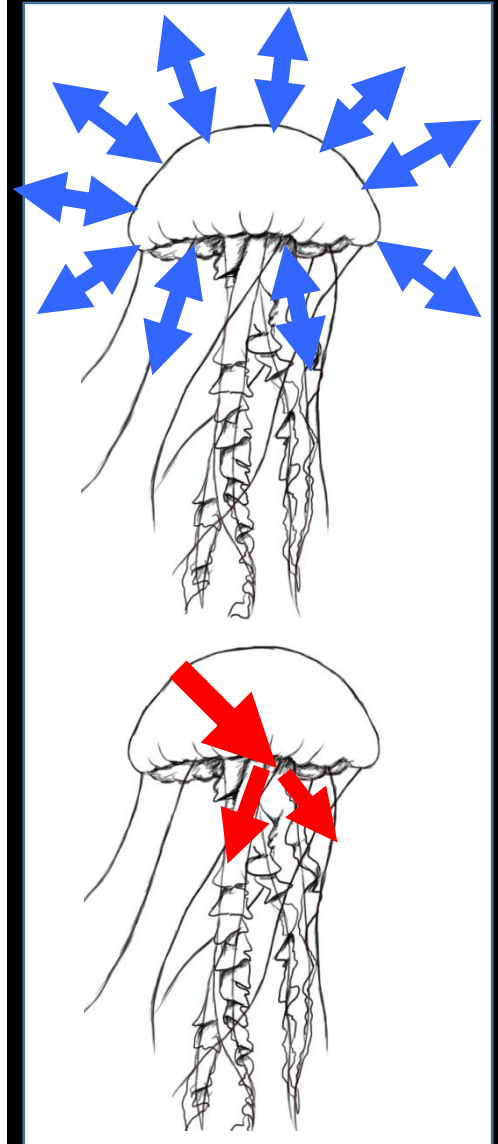
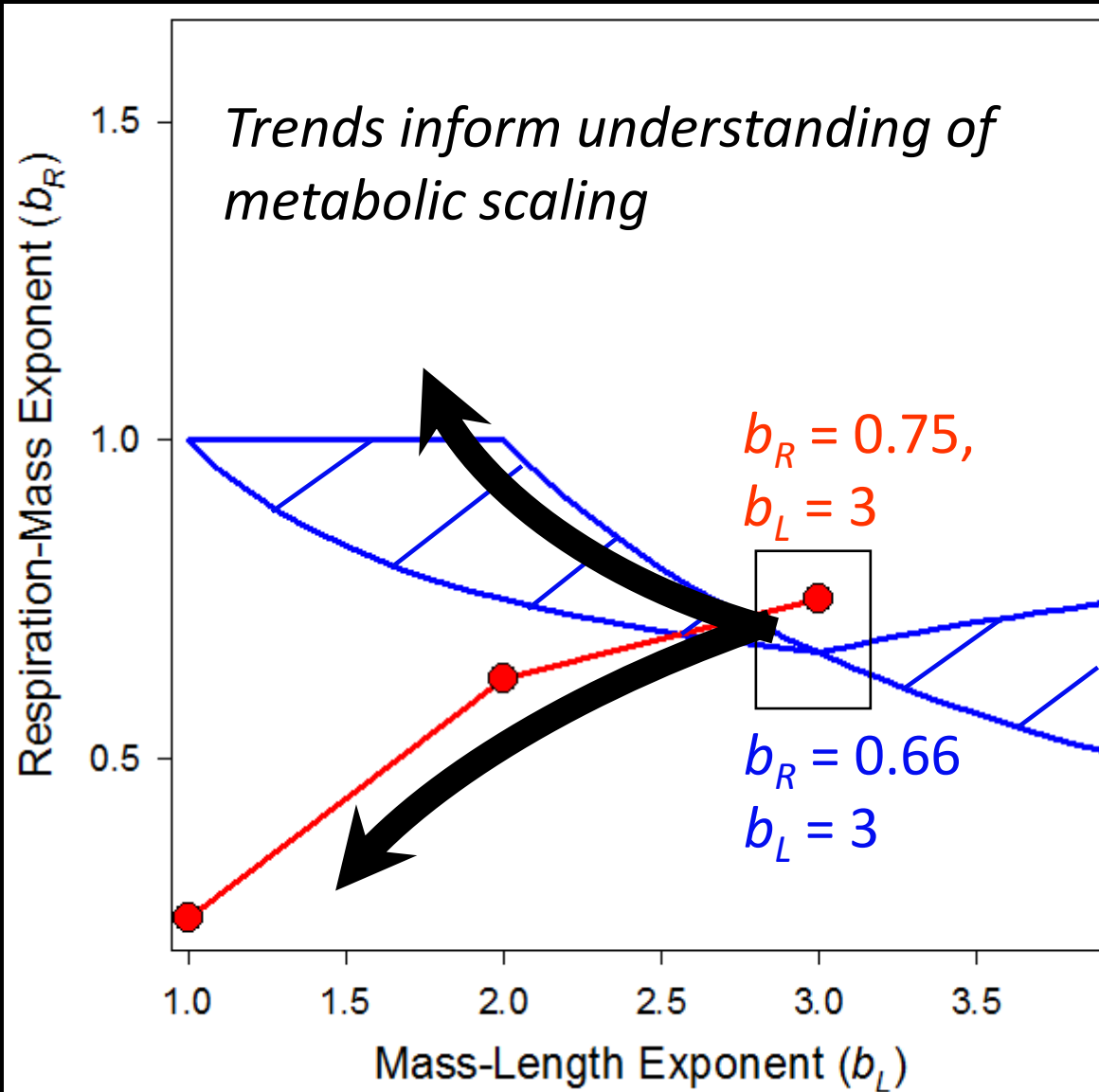
Divergent Predictions



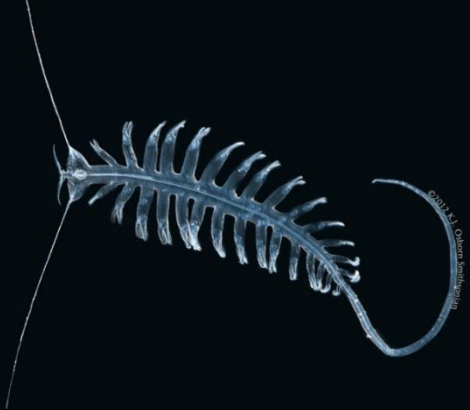
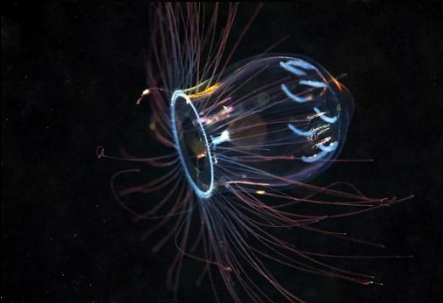
Divergent Predictions



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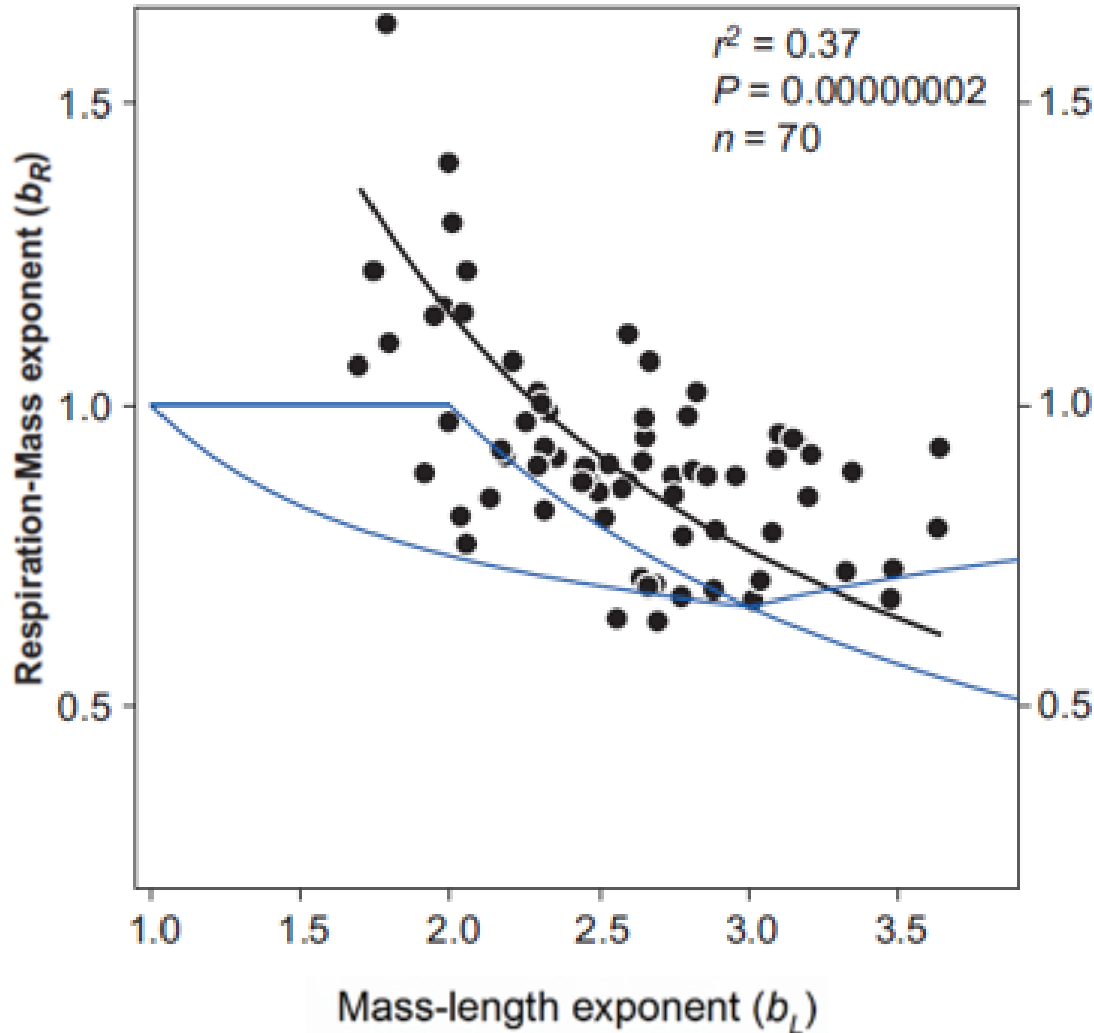


Macroplankton Diversity



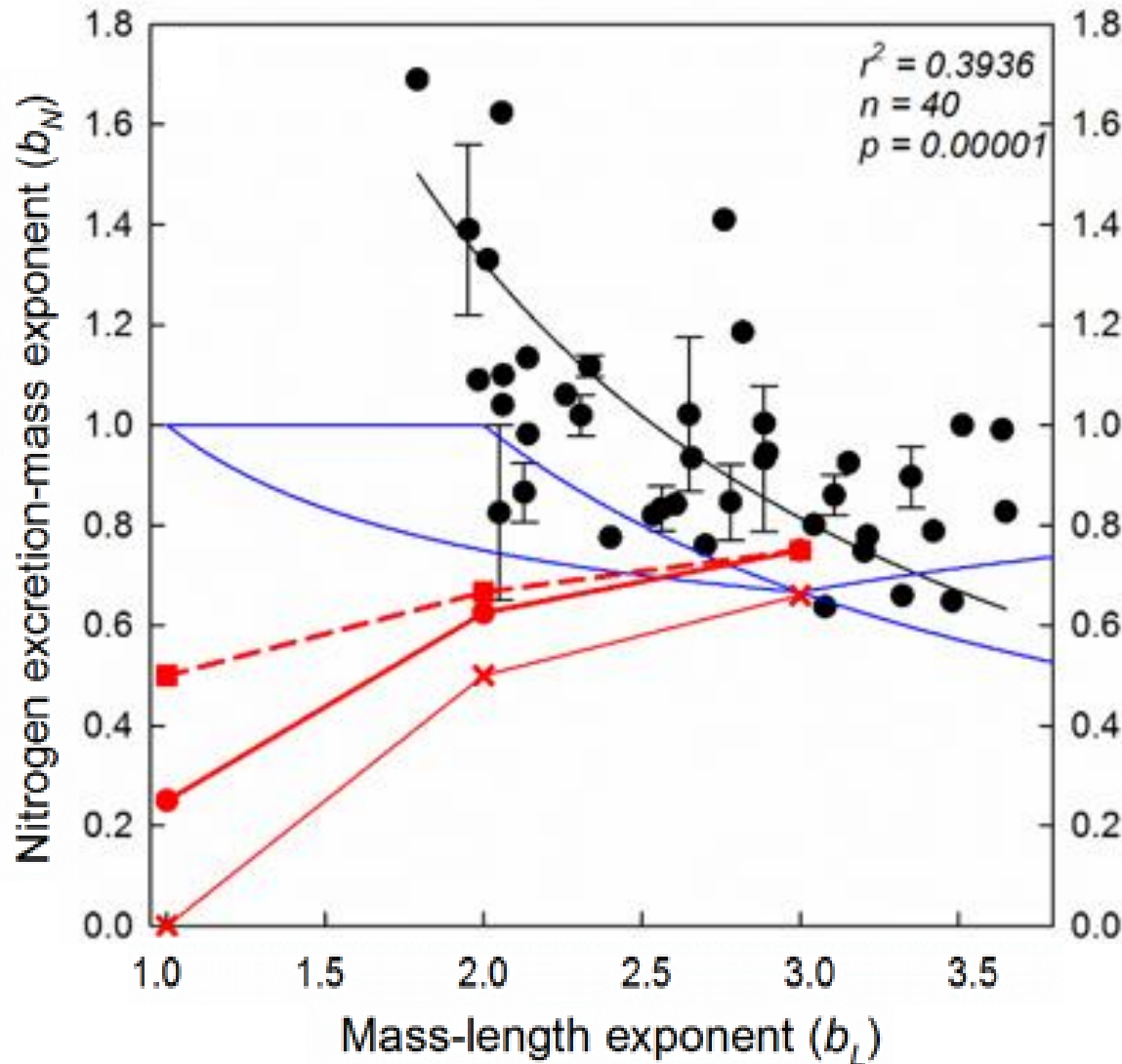
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Pelagic Invertebrate Respiration



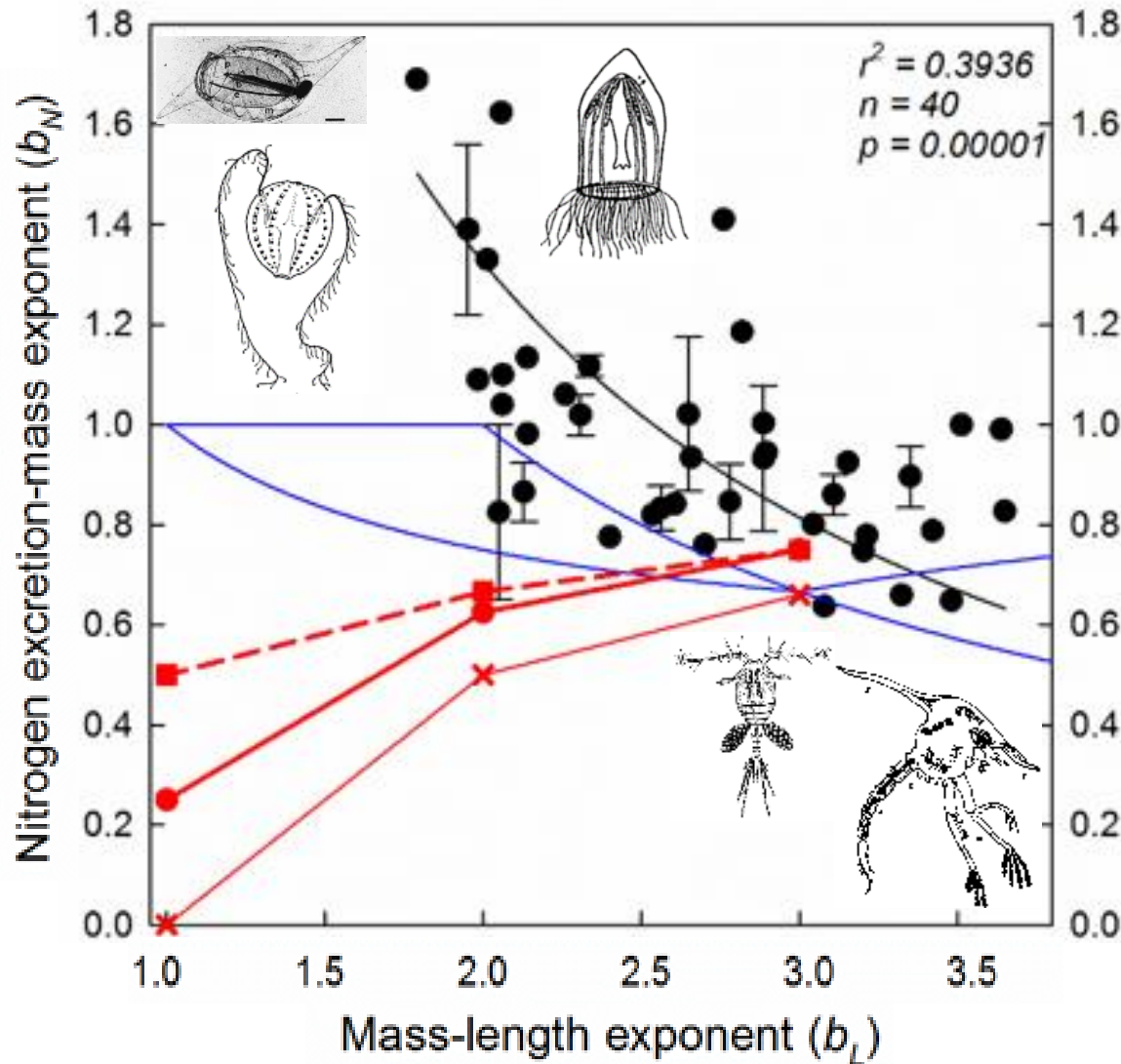
- Across 70 species there is wide variation in Respiration-scaling.
- Body forms are diverse
- Scaling follows the Surface-Area theory
- Steeper scaling is observed in species growing in 1D, compared to 2D or 3D growth.

Pelagic Nitrogen Excretion



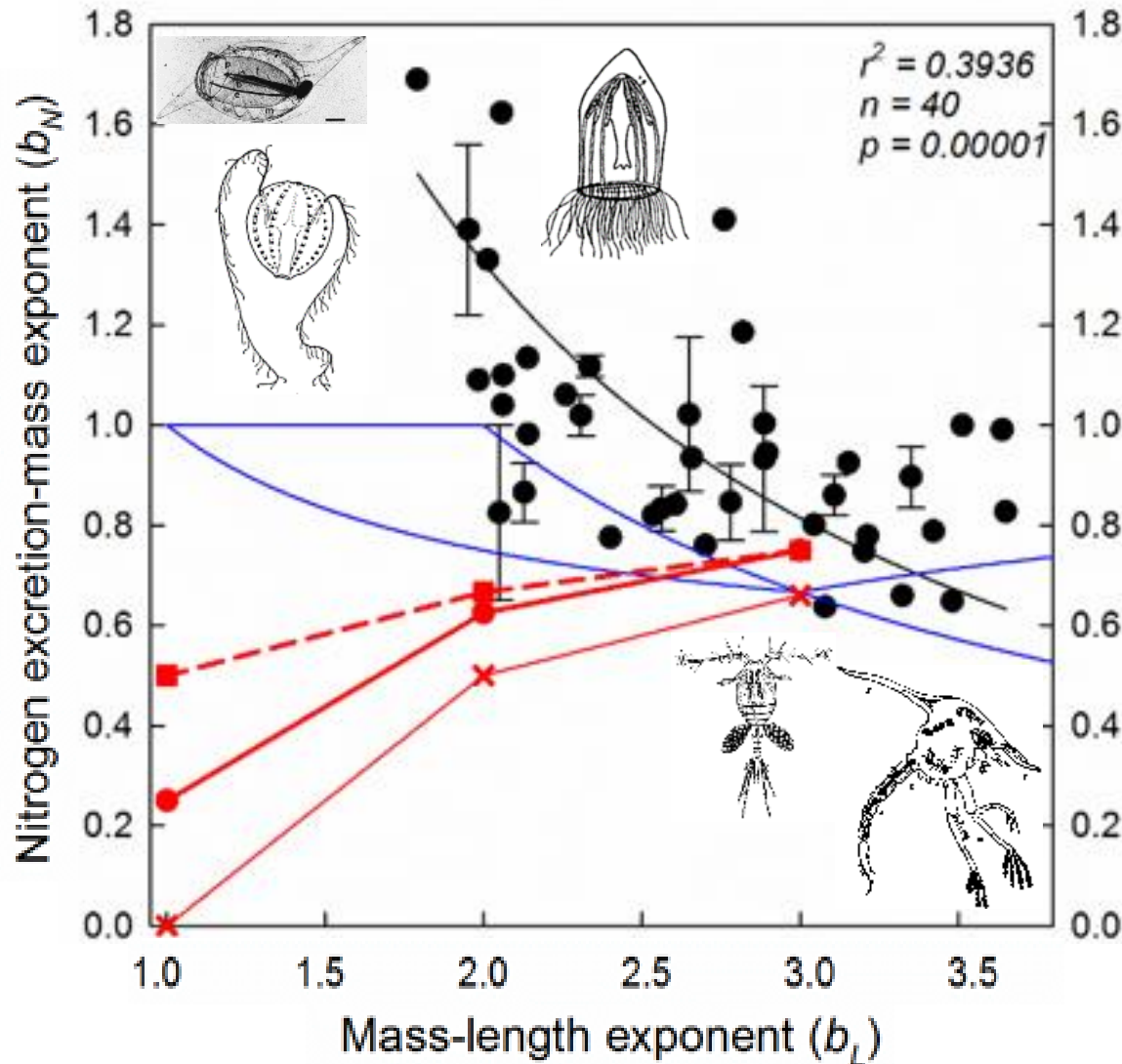
- N-excretion scaling parallels Respiration scaling
- Higher variation, due to different N-products and fewer data.

Pelagic Nitrogen Excretion



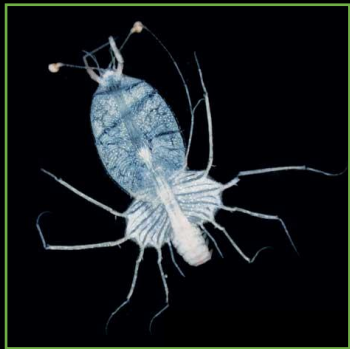
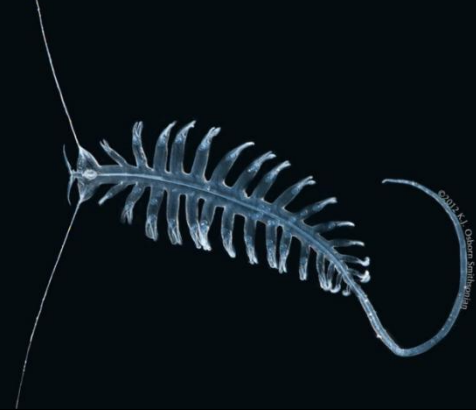
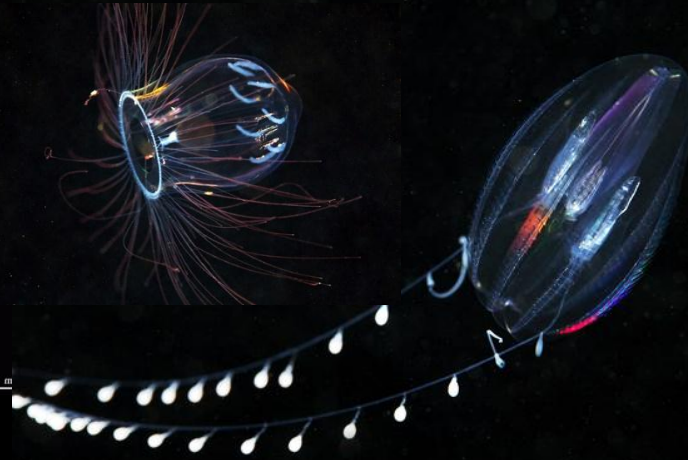
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- Macrozooplankton still conform to the SA model – with variability and body structure differences

Pelagic Nitrogen Excretion



- N-excretion scaling parallels Respiration scaling
- Higher variation, due to different N-products and fewer data.
- Macrozooplankton still conform to the SA model – with variability and body structure differences
- Steeper scaling at 2D v 3D growth.

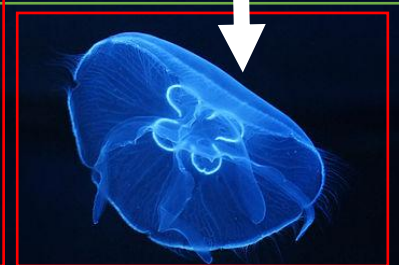
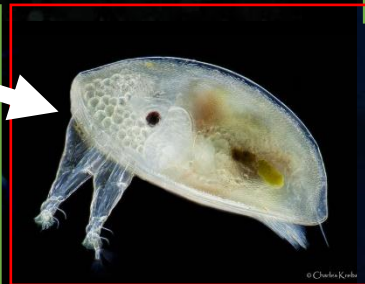
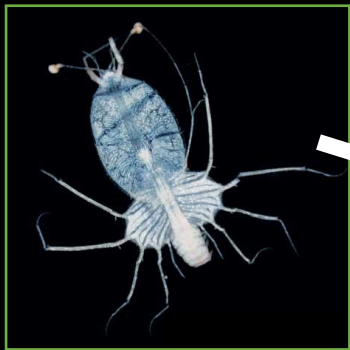
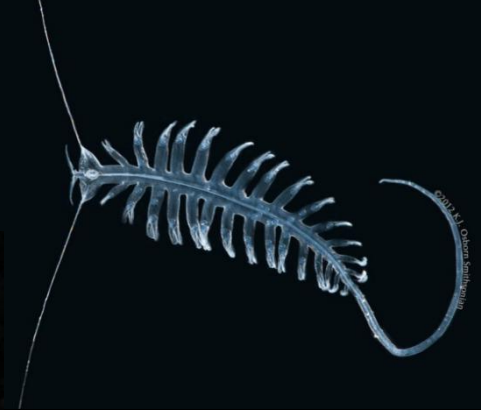
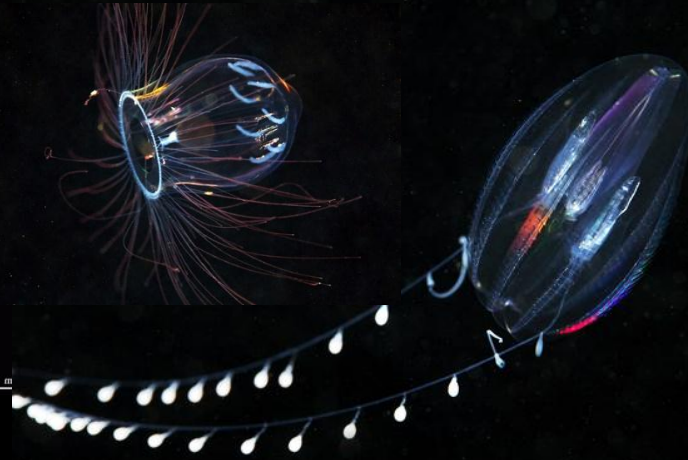
Macroplankton Diversity Shape-shifting



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Macroplankton Diversity

Shape-shifting

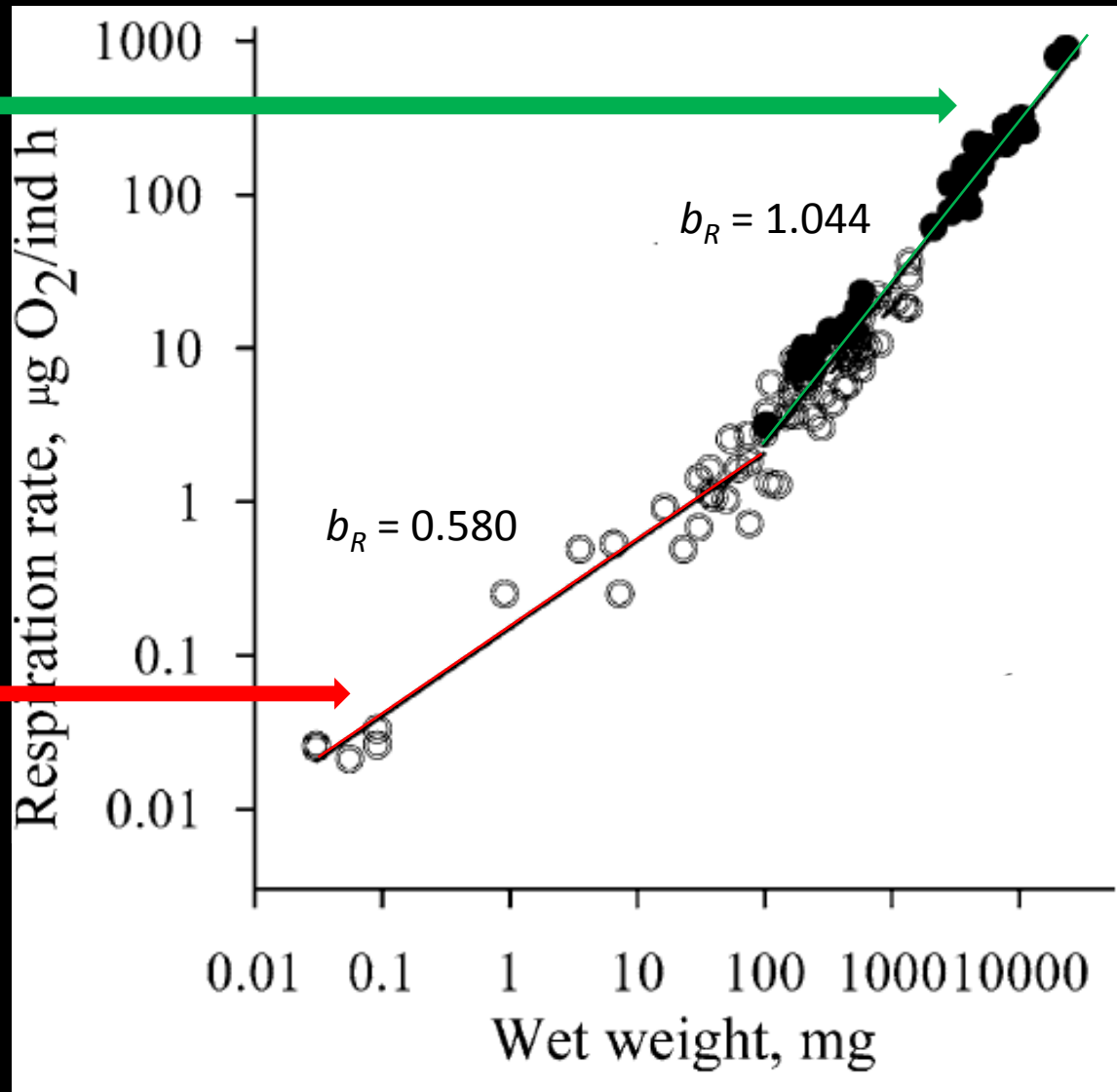


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Organisms With Biphasic Growth

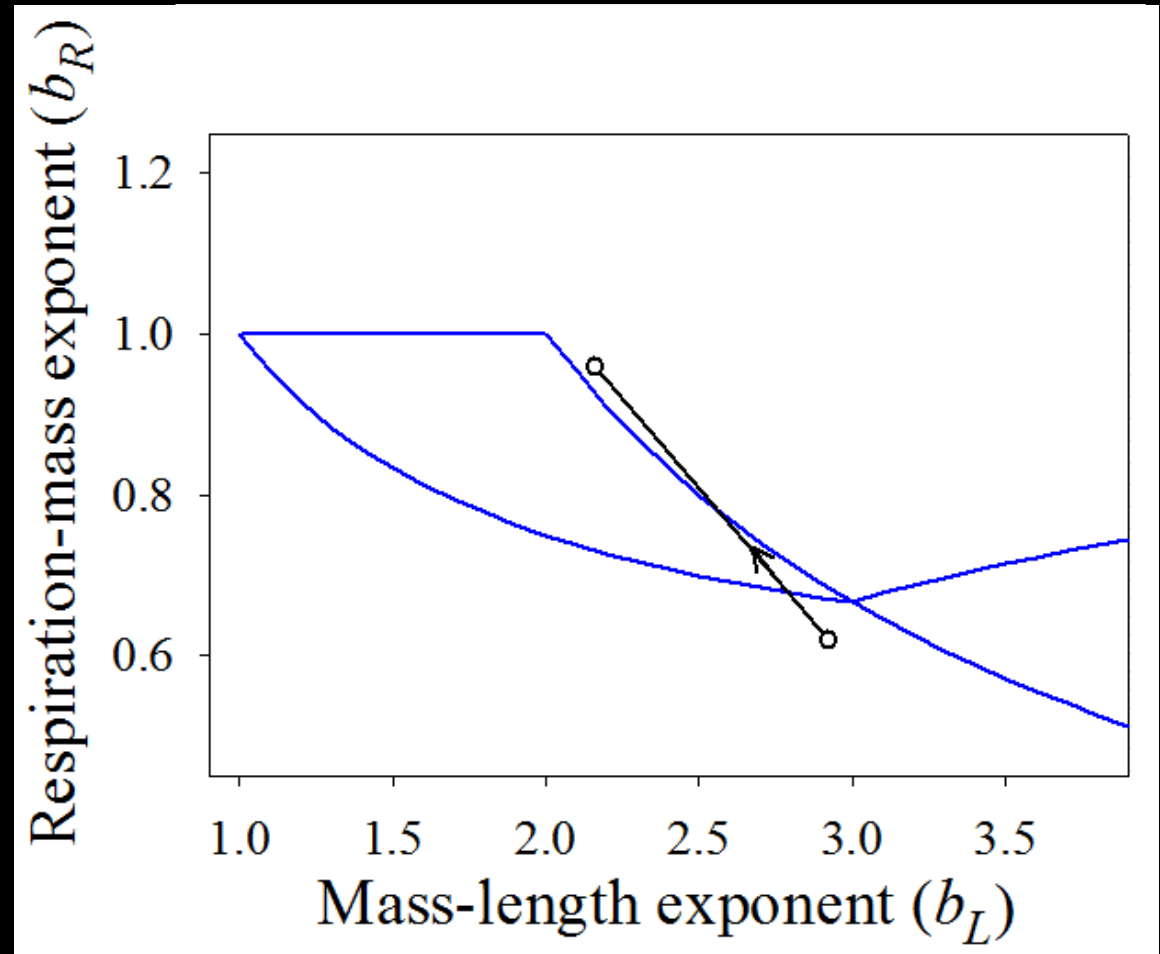


Beroe ovata



From Svetlichny *et al.* (2004)

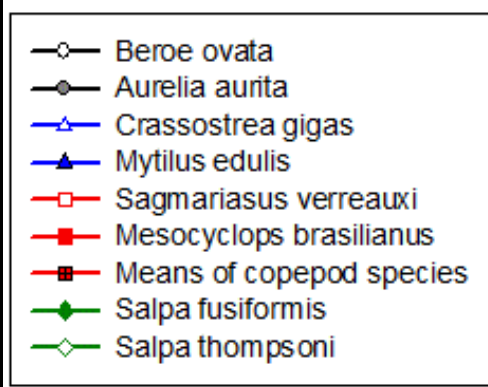
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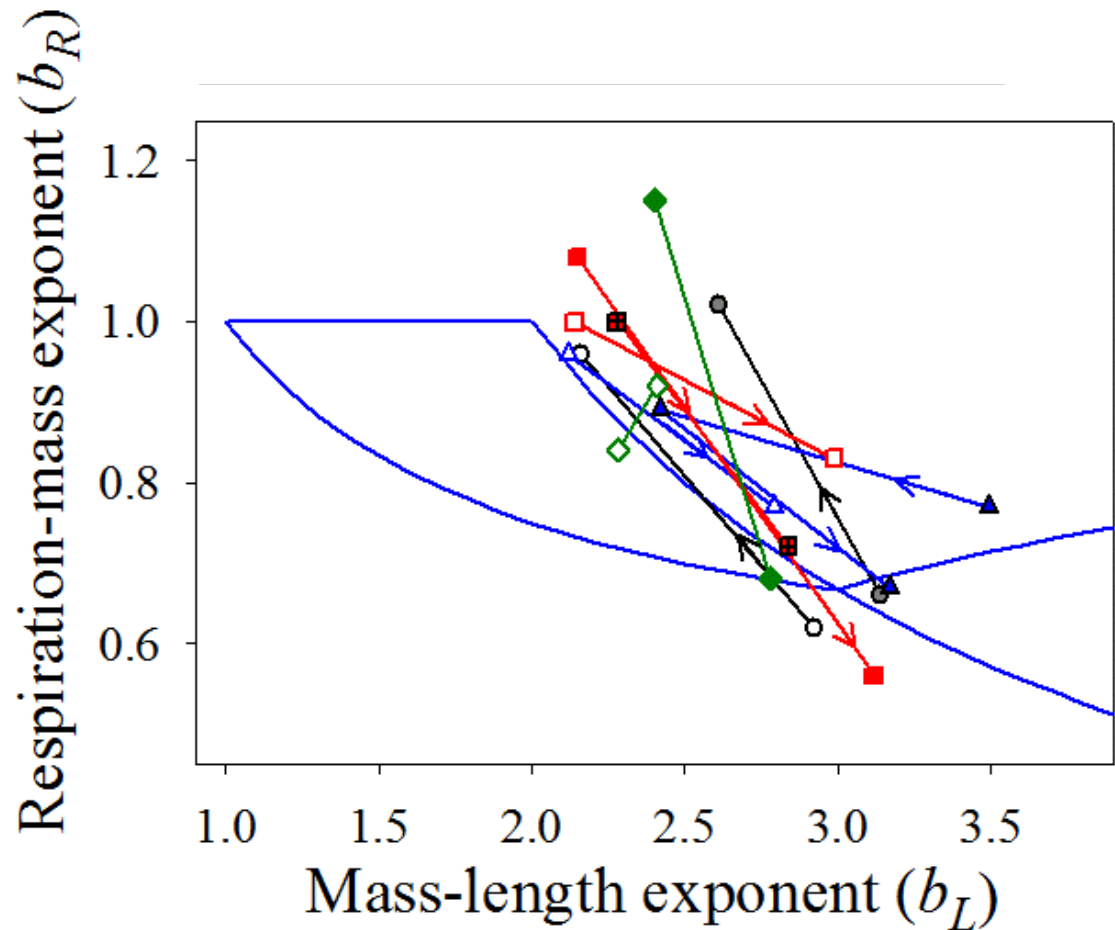
Beroe ovata

Glazier et al (2015)

Organisms With Distinct Life Phases



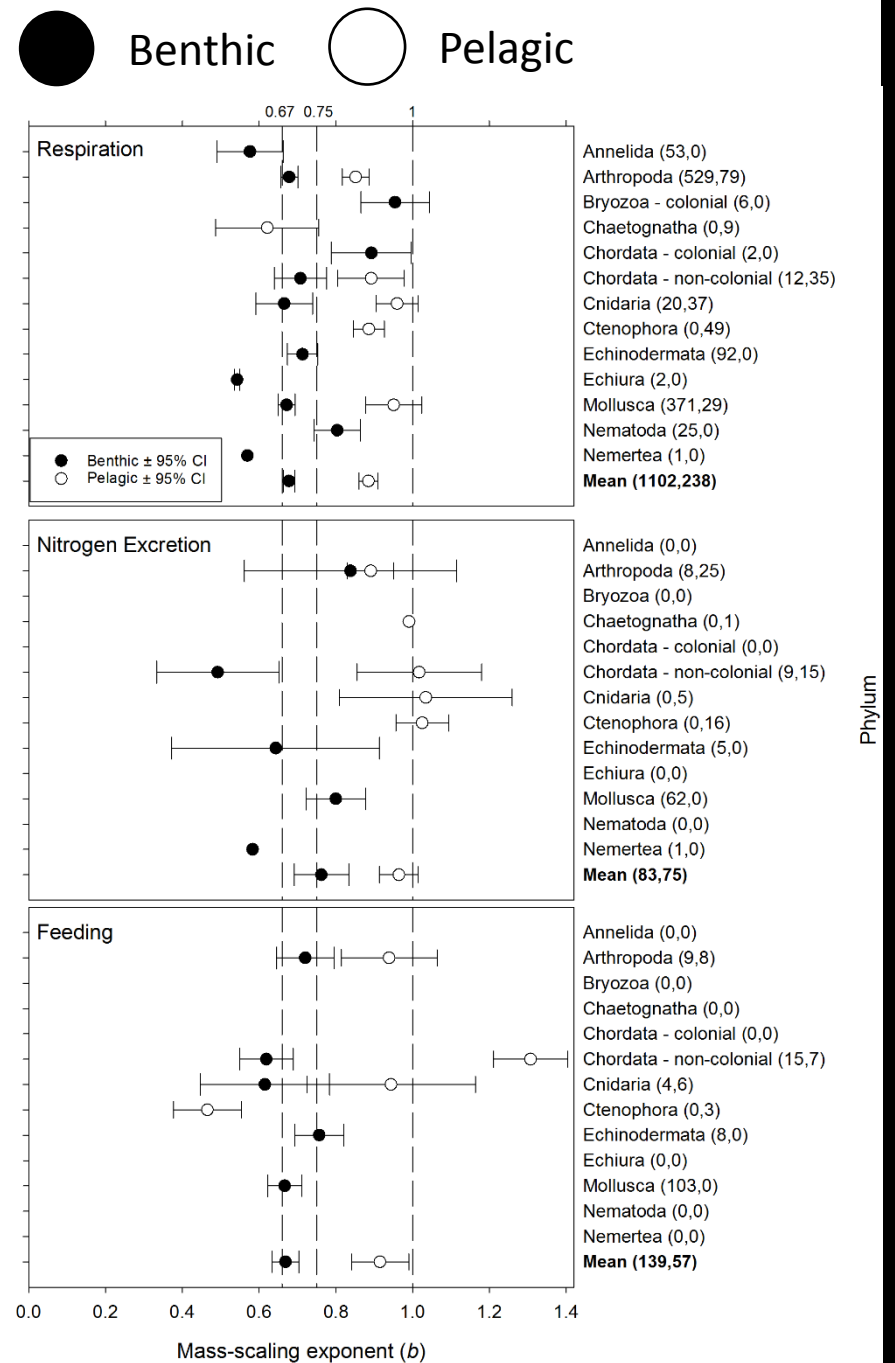
9 of the 10 shifts follow trends predicted by Surface Dependent Model



Benthic/Pelagic scaling

Do marine benthic invertebrates show the same patterns as pelagic species?

$$\text{Metabolism (Rate/ind/time)} = a * \text{Mass of the individual}^b$$

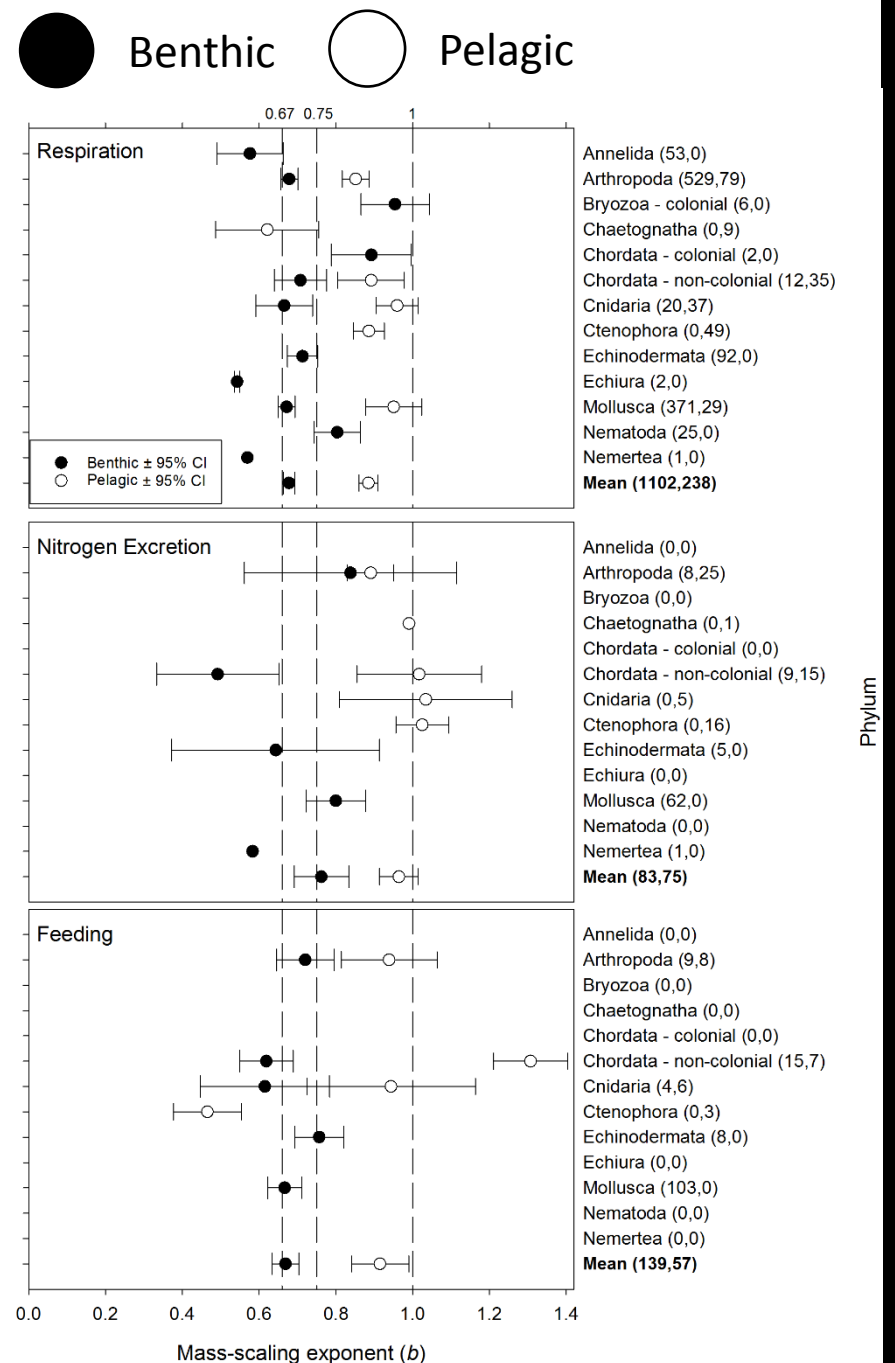


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- Metabolism-mass scaling
Benthic species < pelagic species.
- Increased scaling:
 - increased activity?
 - feeding method?
 - trophic position?



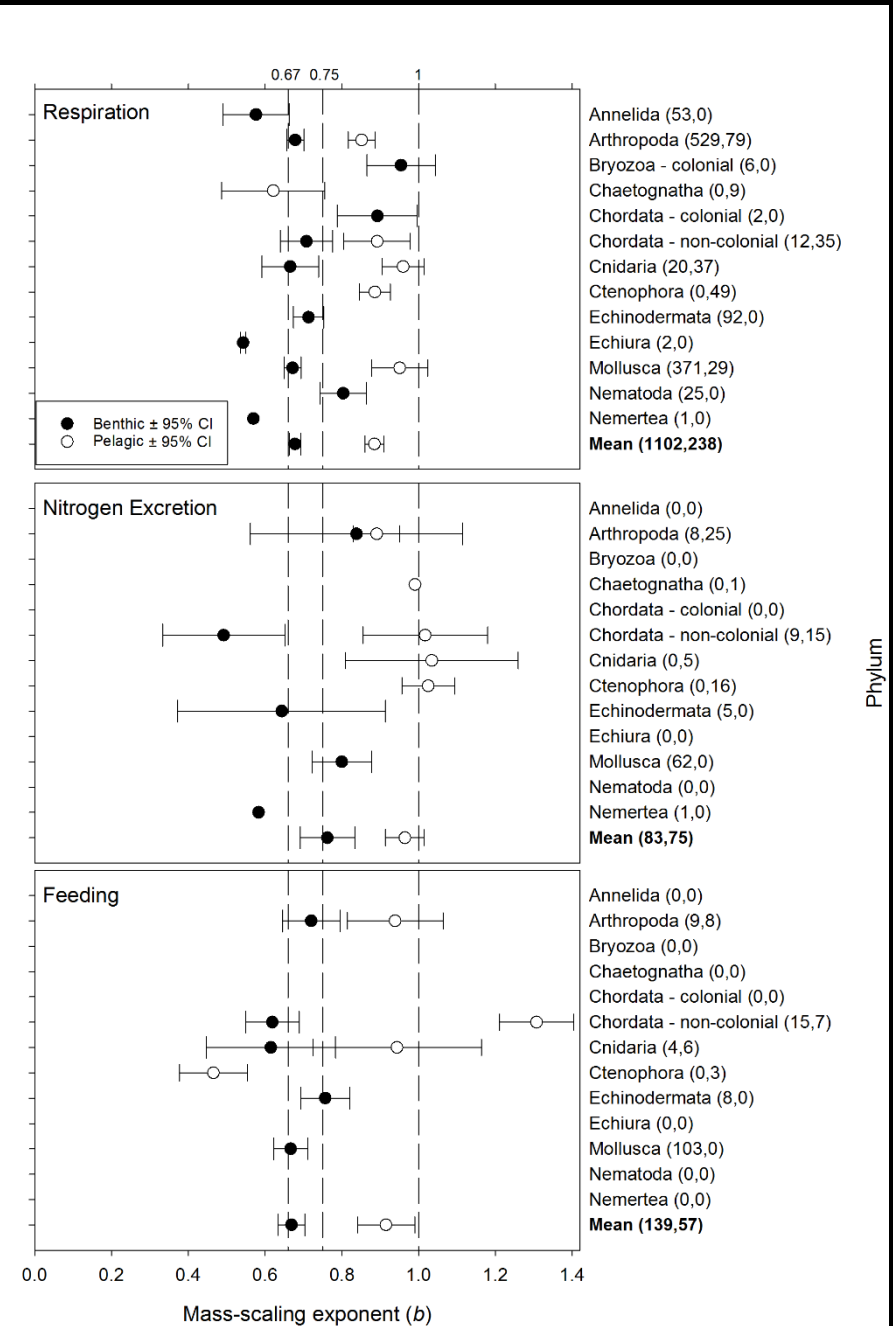
Phylum

Benthic/Pelagic scaling

Scaling of metabolic rates with body mass of an individual.

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○ Benthic ● Pelagic



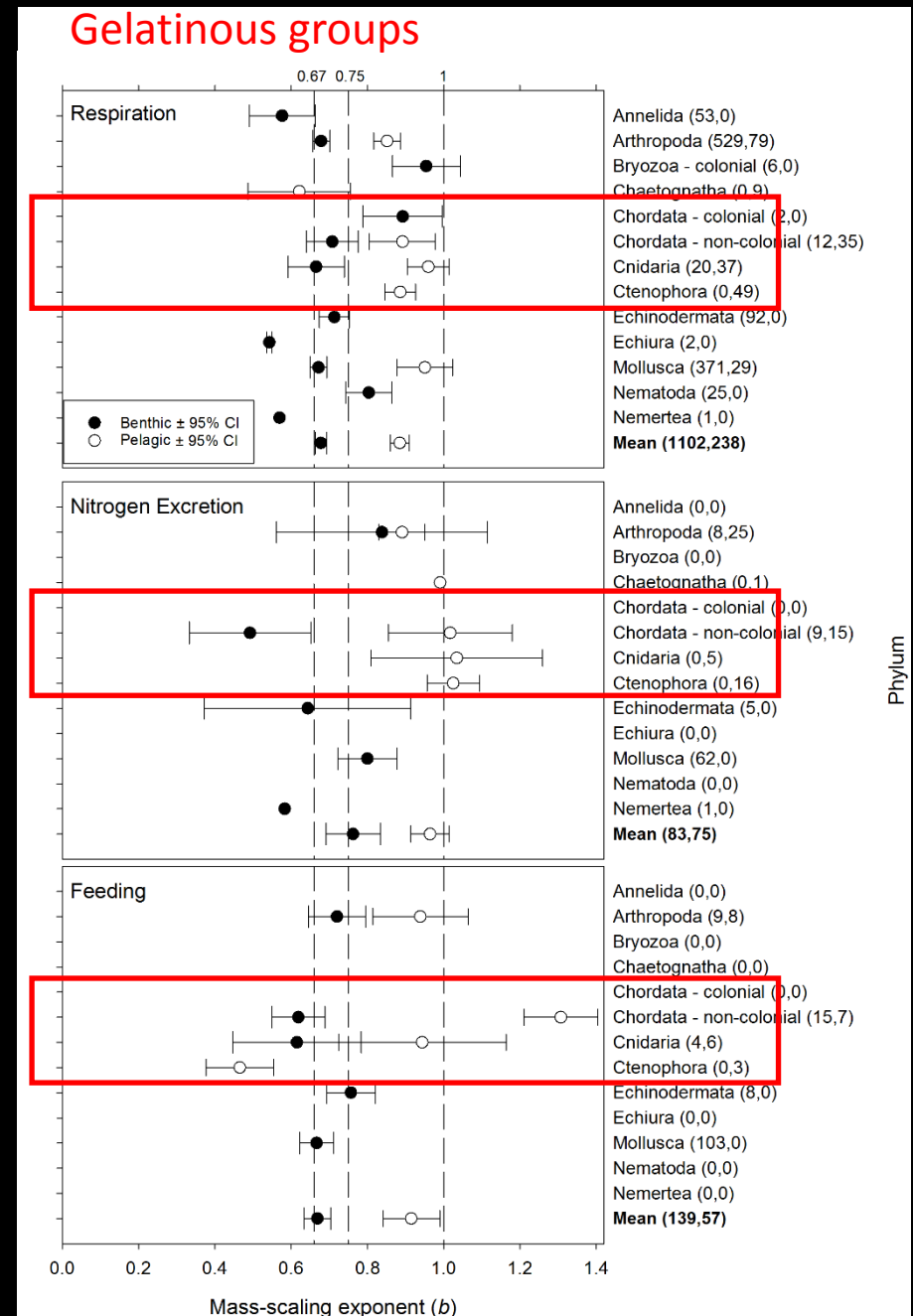
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- Consistently steeper scaling:
 - Respiration - Pelagic > Benthic
 - N-excretion - Pelagic > Benthic
 - Feeding rates – similar trends
- Mechanism:
 - Activity levels typically cause slower metabolic rates in benthic species.

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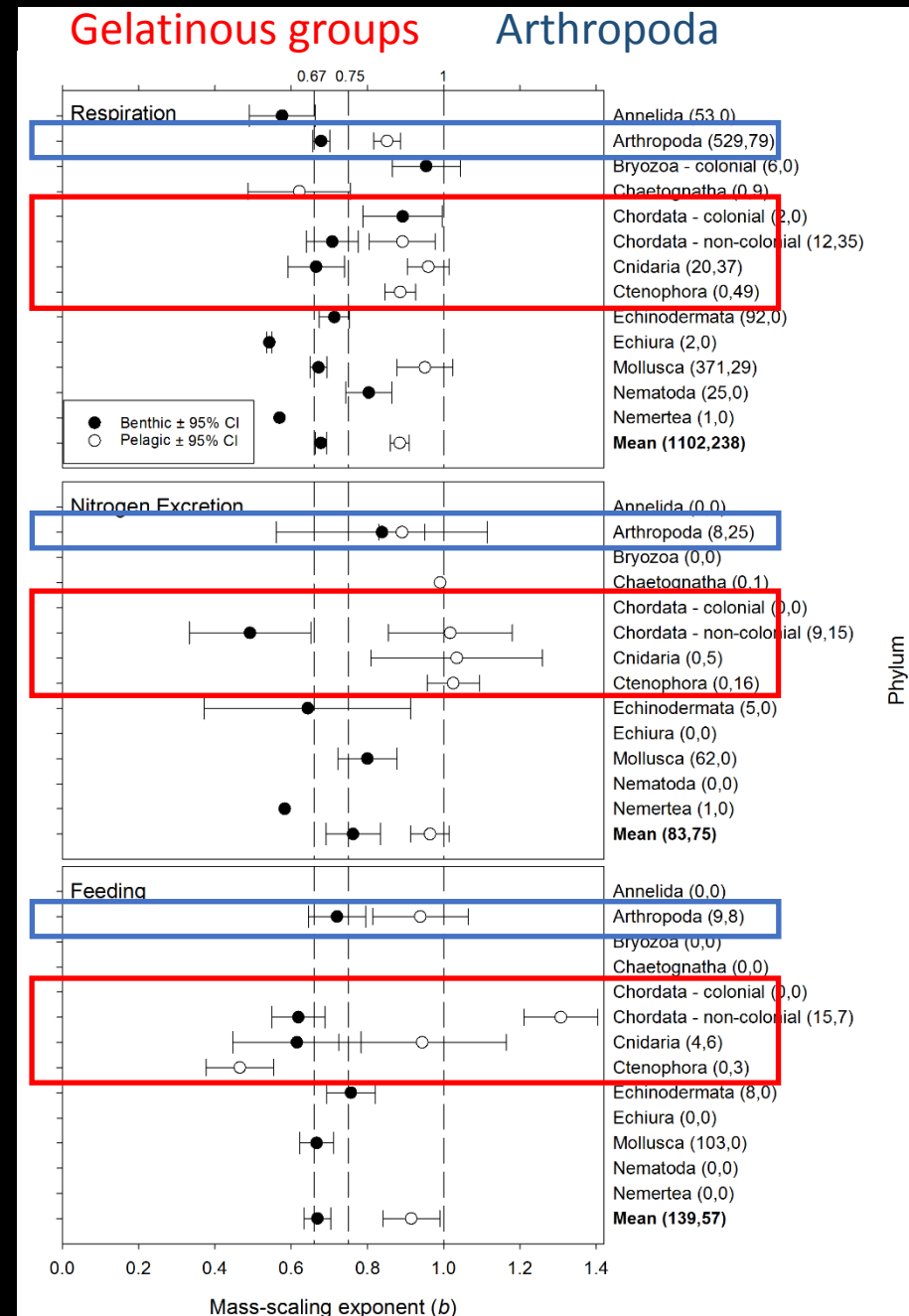
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- Arthropoda integuments change the surface area available, but there are still scaling differences between larvae and adult.

○ Benthic ● Pelagic



Phylum

Conclusions

Body size is known to influence metabolic rates, but the scaling factors have been debated for years.

Recent analyses provide support for the Surface Area model in planktonic invertebrates by linking mass-length to metabolism.

Taxonomic differences may be due to habitat and activity levels.

Some species change their metabolic scaling through their development

Benthic invertebrates lower activity levels reduce metabolic scaling compared to pelagic species.

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References

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Contact

m.lilley@qmul.ac.uk
a.g.hirst@qmul.ac.uk