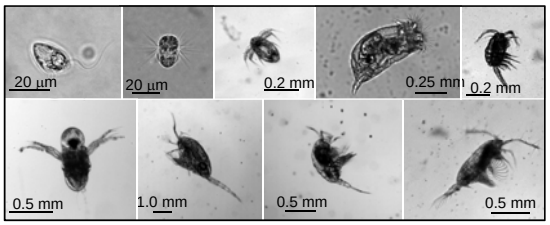
Ocean Life
Centre for Ocean Life
VKR Centre of Excellence

HOW TRAITS ARE INTERRELATED THROUGH TRADE-OFFS IN ZOOPLANKTON



Thomas Kiørboe
Centre for Ocean Life, DTU Aqua

What is a key trait ?

A property that is a main determinant of an individual's fitness

Commonly used fitness measures:

Net reproductive rate $R_0 = \int_0^\infty l_x m_x dx$

Survival

Fecundity

Survival and fecundity both depend on Feeding

Fundamental missions

The governing mission

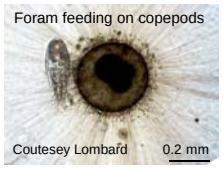
To eat

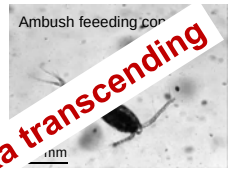
To survive

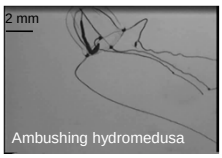
To reproduce

What is a usefull trait ?

What is common between these organisms?





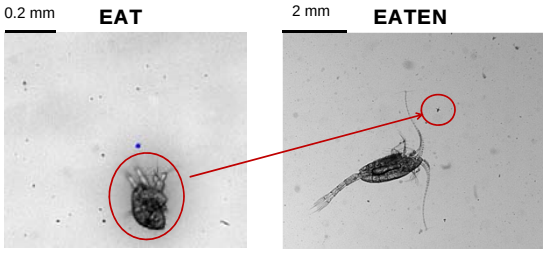


A useful trait is taxa transcending

Gilmer & harbison *Mar Biol* 1986; Kiørboe et al. *PNAS* 2009; Hansson & Kiørboe *LO* 2005

What is a trade off?

The costs and benefits of a certain trait



Copepod nauplius capturing a prey

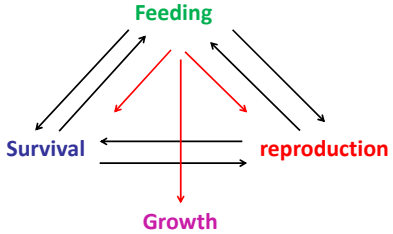
As it jumps, the **nauplius itself** is perceived by a predator

Bruno et al. *PlosOne* 2012,
Kjellerup & Kiørboe *Biol Lett* 2012

Both movies in SloMo

Traits are interrelated through trade-offs

Conflicts between missions



Behavioral interaction

Energy allocation

Litchman et al. *JPR* 2013

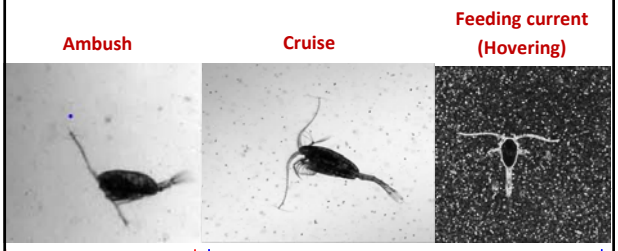
Outline

1. Taxa trascending feeding traits
2. Behavioral trade offs
   a. Survival (Predation risk)
   b. Reproduction
3. Energy allocation tradeoffs
   a. Maintenance (survival) vs. Growth & reproduction
4. Synthesis

Keyword:
Taxa-transeding;
Mechanistic;
Rationalize & Generalize

Zooplankton feeding traits

Three principal feeding modes



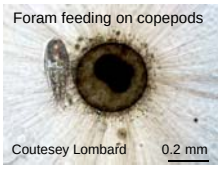
Passive feeding modes

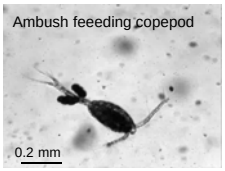
Active feeding modes

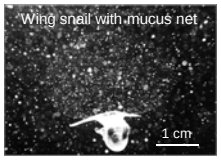
All movies in SloMo
1:100-1:300

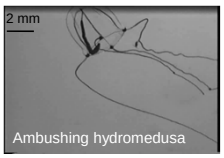
Kiørboe *Biol Rev* 2011

Diversity of ambush feeders: Taxa transcending



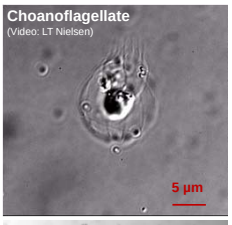


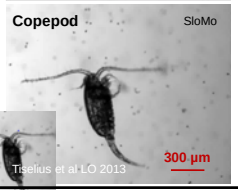




Gilmer & harbison *Mar Biol* 1986; Kiørboe et al. *PNAS* 2009; Hansson & Kiørboe *LO* 2005

Diversity of current feeders: taxa transcending





Trade-offs: Feeding efficiency

All movies in SloMo
1:10 -1:300

The 3 principal feeding modes differ in efficiency

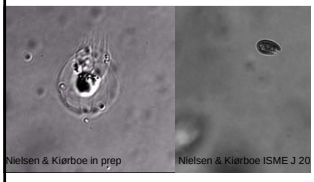
LOW — Volume of water scanned per unit time — HIGH

Kiørboe *Biol Rev* 2011

Feeding efficiency

The basis for the conclusion and generalisation:

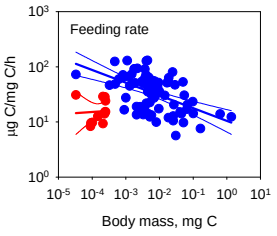
1. Mechanistic understanding of encounter mechanisms



2. Theoretical analysis of corresponding encounter models
3. Experimental tesgting of predictions

Ambush

Hover & Cruise

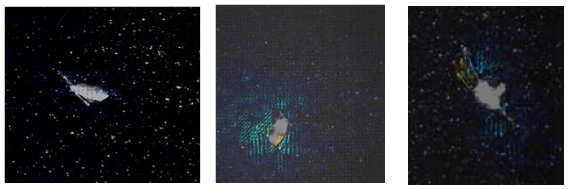


Kiørboe ICB 2013

All in SloMo ~ x 50

Trade-offs: Risk and cost of feeding

Feeding behavior and fluid signals



Ambush (reposition jump) | Cruise | Feeding current (hovering)

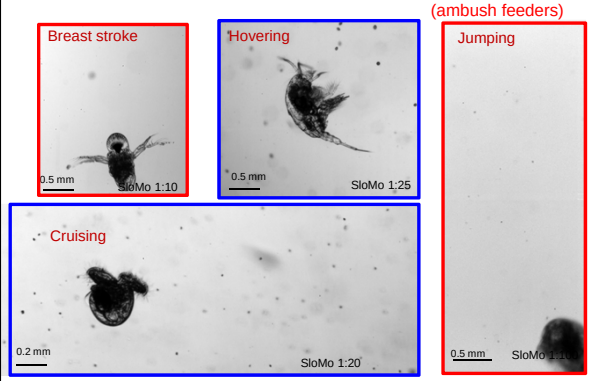
LOW — HIGH

Kiørboe et al. *Proc. Roy Soc B* 2010; Kiørboe & Jiang *J Roy Soc Interface* 2011

Four propulsion modes

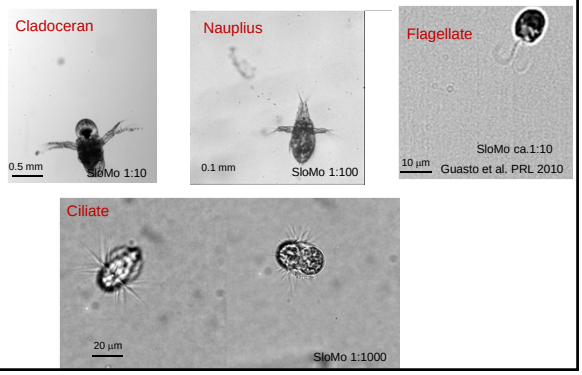
Propulsion and feeding are partly related

Feeding and swimming (active feeders)
Swimming (ambush feeders)



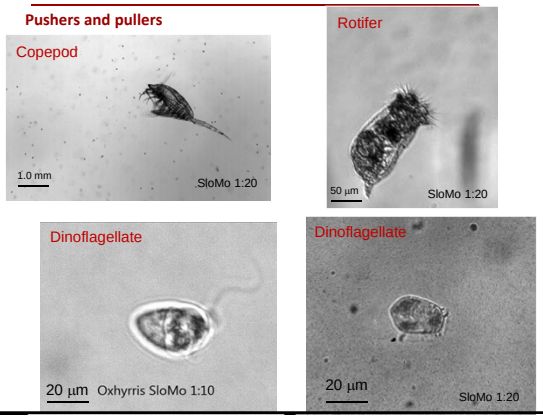
Diversity of breast strokers: Taxa transcending

Diverse organisms and diverse machineries



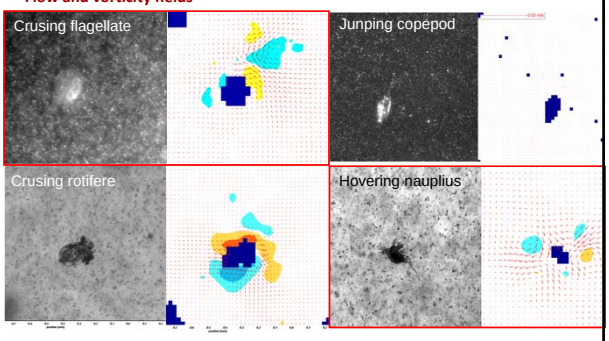
Diversity of cruisers: Taxa transcending

Pushers and pullers



Fluid disturbances

Flow and vorticity fields



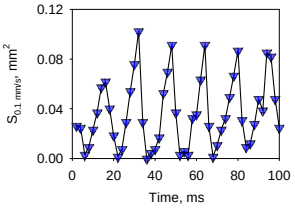
SloMo 1:40

Kiørboe et al. *PNAS* 2014

Extension of flow field: temporal variation

Area with imposed velocities > U* (= Predator encounter cross section)

Oxyrrhis marina

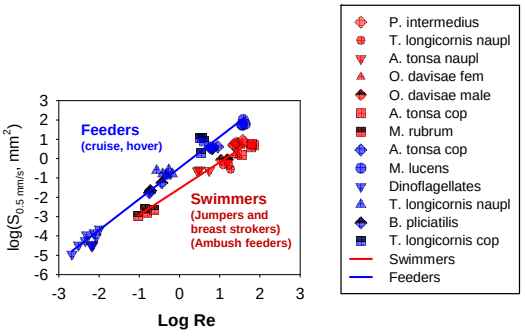


U* = 0.08 mm/s
SloMo1:40

Kiørboe et al. *PNAS* 2014

Peak extension of flow field

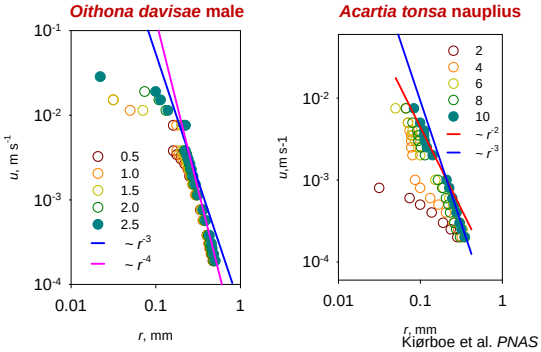
Feeders generate larger flow fields than swimmers



Kiørboe et al. *PNAS* 2014

Spatial attenuation of flow fields

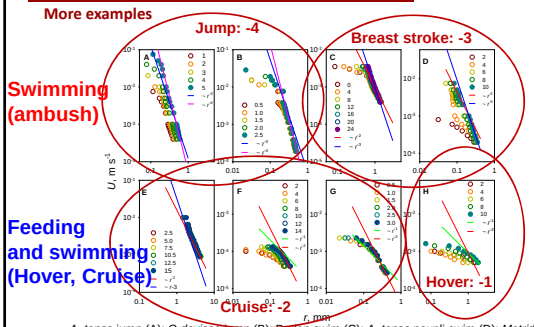
During peak of power stroke (closed symbols)



Kiørboe et al. *PNAS* 2014

Spatial attenuation

More examples



A. tonsa jump (A); *O.davisae* jump (B); Podon swim (C); *A. tonsa* naupli swim (D); *Metridia* cruising (E); Dinoflagellate cruising (F), *Temora* nauplius feeding current; *Temora* copepodit hovering

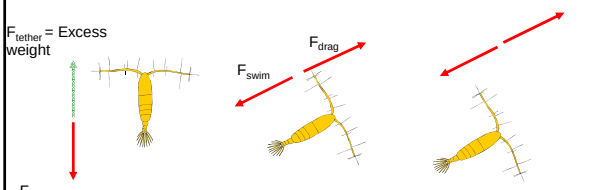
Kiørboe et al. *PNAS* 2014

Idealized models

R-1 Hovering (feeding current) (negatively boyant)

R-2 Crusing (Neutrally boyant)

R-4 Jumping (Jump)



Ffeeding current — **STOKESLET**

Fdrag = Fswim — **STRESSLET**

Fdrag = Fswim — **IMPULSIVE STRESSLET**

Only red forces act on the water

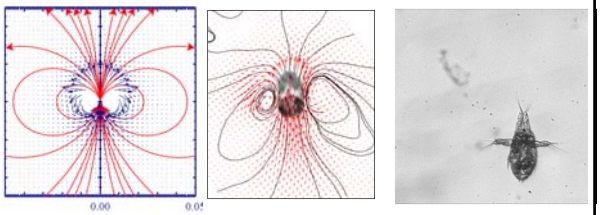
Kiørboe et al. *PRSB* 2010

Breast stroke: Quadropole

R-3

Breast stroke swimming: appendages follow streamlines of a potential dipole (quadropole)

Predicted streamlines | observed streamlines | Breast swimming nauplius



Kiørboe et al. *PNAS* 2014; Andersen et al. *PRE* 2015

Bulk properties of flow

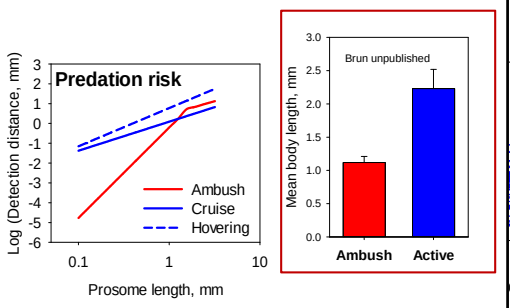
Spatial flow attenuation from idealized , taxa-transcending models

Behaviour	Purpose	Model	Attenuation
Hovering	Feeding	Stokeslet	R-1
Cruising	Feeding & locomotion	Stresslet	R-2
Ambush (Jumping)	Locomotion	Impulsive stresslet	R-4
Ambush (Breast stroking)	Locomotion	Quadropole (potential dipole)	R-3

we can rationalize and – therefore – generalize the observed fluid disturbances

Feeding tradeoffs

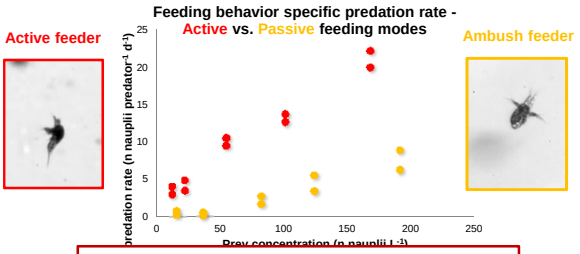
Predation risk estimated from simple generic fluid mechanical models



Kiørboe et al. *Proc Roy Soc B* 2010

Feeding tradeoff: Experimental testing

Rheotactic predator feeding on active and passively feeding nauplii

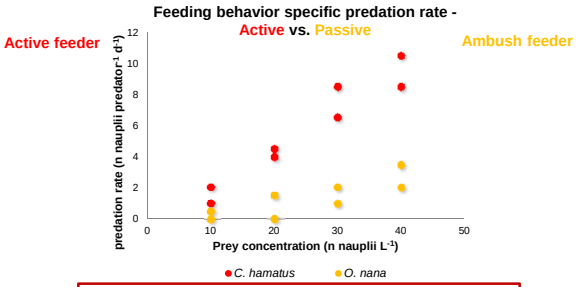


THE MORTALITY RISK OF THE ACTIVE FEEDER IS MUSCH HIGHER THAN THAT OF THE PASIVE FEEDER

Someren Gréve and Almeda unpublished

Feeding, swimming, and predation risk

Experimental testing: Large copepod feeding on nauplii



SAME RESULT FOR DIFFERENT SET OF PREY

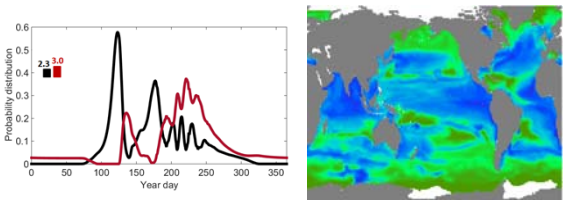
Someren Gréve et al unpublished

Trait based models

Examples of trait based models of zooplankton

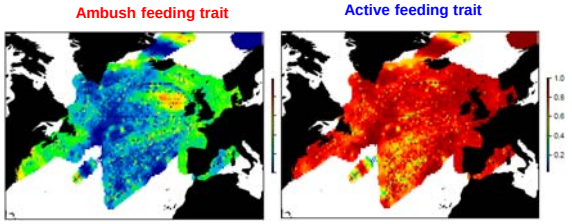
Kaisia Kenitz: Seasonal succssion of zooplankton feeding traits

Fi Prowe: Global distribution of zooplankton feeding traits



Trait biogeography

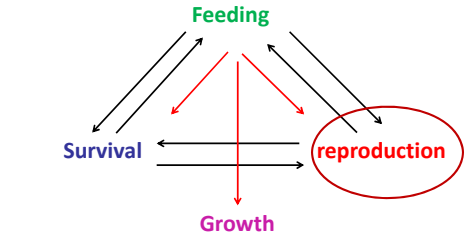
Field data that allow testing of models



Brun et al in prep

Traits are interrelated through trade-offs

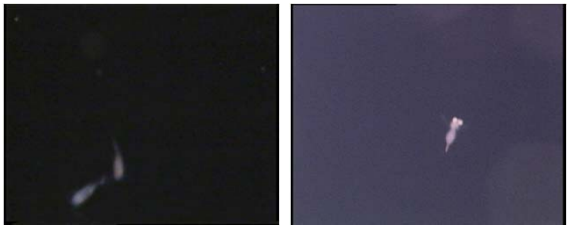
Conflicts between missions



Litchman et al. *JPR* 2013

Reproduction

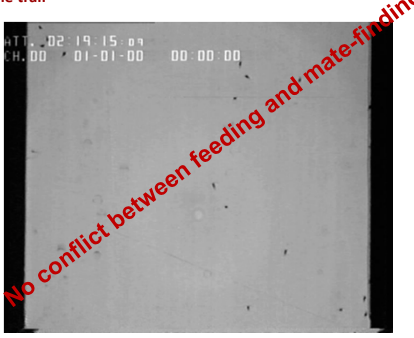
How do they find one another?



I will show that mate finding strategies depend on feeding behavior

Blind dating: Cruise feeder

Pheromone trail



Bagøien & Kiørboe *MEPS* 2005

Blind dating: Feeding current feeder

Pheromone cloud

Kiørboe & Bagøien *MEPS* 2005

Blind dating: Feeding current feeder

Pheromone cloud

Kiørboe & Bagøien *MEPS* 2005

How can an ambush feeder ever find a mate?

Males compromises both feeding and survival
STRONG CONFLICT

The males sacrifices feeding for part of their time to search for females.
When searching they also run elevated predation risk

Kiørboe *LO* 2007

Sex, food and death

Feeding-mortality-reproduction tradeoffs

Mate finding compromises survival and feeding in males

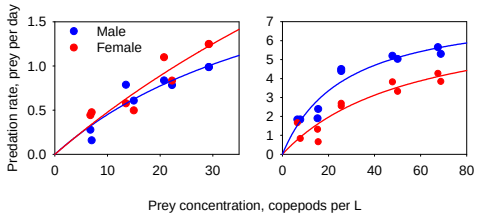
differently for different feeding bahaviors

Mate finding and predation risk

Experimental test: Different predation mortality risks between sexes

CRUISE FEEDER: no difference

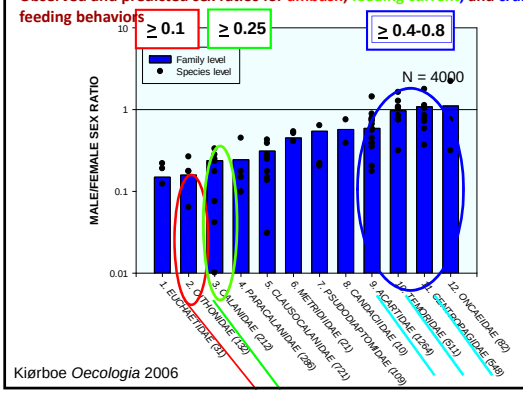
AMBUSH FEEDER: Higher mortality risk in males



Someren Gréve and Almeda unpublished

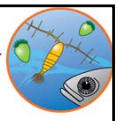
Differential mortality and biased sex ratios

Observed and predicted sex ratios for ambush, feeding current, and cruiser feeding behaviors



Kiørboe *Oecologia* 2006

Energy allocation tradeoffs



Evolution of ageing

Disposable soma theory:

1. Investment in survival (maintenance) is traded off against investment in growth and reproduction
2. Large external mortality (relative to total mortality) may push the tradeoff against low investment in maintenance

Application to zooplankton:

1. High risk (feeding, mate finding) behaviors lead to early aging and short life spans, even in the absence of predators, and high fecundity – and vice versa

Predictions:

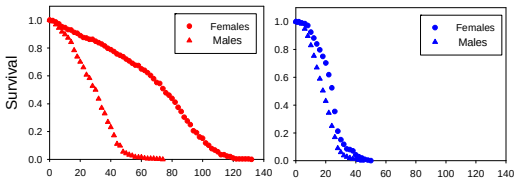
1. *Ambush feeders*: Long lifespan, low fecundity, large male/female difference in lifespan
2. *Active feeders*: the opposite

Feeding tradeoffs

Empirical support: Differences in survivorship

AMBUSH FEEDER
Oithona davisae

CRUISE FEEDER
Centropages typicus

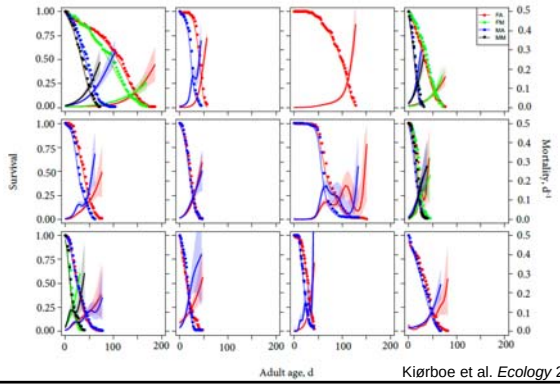


Survivorship measured in lab in absence of predation

Kiørboe et al. *Ecology* 2015

Variation in survivorship

12 species of copepods: Longevity varies by factor 10 between species



Kiørboe et al. *Ecology* 2015

Results

Feeding behavior and gender are the main determinants of longevity and ageing

Log (T) = a + b Mixed + c Sex....

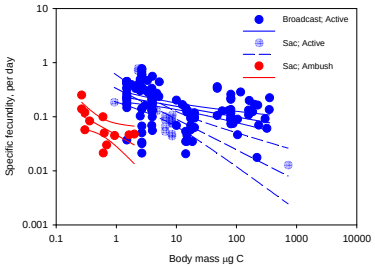
Dependent variable					
Mean longevity		Intercept	Sex Mixed vs separate	**Gender** Male vs female	**Feeding behaviour** Passive vs active
	Coefficient	3.37 (29 d)	-0.23 (-21 %)	-0.26 (-23 %)	0.58 (+79 %)
	p-value		0.062	0.013	0.032
Ageing shape		Intercept	**Feeding behaviour** Passive vs active	**Gender** Male vs female	
	Coefficient	1.17 (3.2)	0.55 (73 %)	-0.24 (-21 %)	
	p-value		0.018	0.005	

Kiørboe et al. *Ecology* 2015

Energy allocation

The maintenance vs fecundity trade-off?

Active feeding modes (cruise, hover)
Passive feeding modes (ambush)



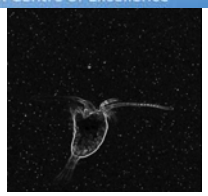
Kiørboe et al. *Ecology* 2015

Ocean Life
Centre for Ocean Life
VKR Centre of Excellence

TAKE HOME:

1. Energy acquisition (feeding) is the '**governing mission**' from which **key traits** and **tradeoffs** should be defined
2. In zooplankton, **mate finding**, **predation risk**, **propulsion mode**, **longevity**, **ageing**, **fecundity**, and **energy allocation** are all defined by the **feeding behavior**
3. A mechanistic understanding of **feeding traits** in zooplankton allows us
   - to rationalize and generalize observations and hence to define key **taxa-transcending** traits
   - to **quantify tradeoffs**
4. This provides a solid, mechanistic basis for the development of trait-based models

Ocean Life
Centre for Ocean Life
VKR Centre of Excellence



ACKNOWLEDGEMENTS:

Collaborators:
Hoshuo Jiang
Rodrigo Almeda
Hans Sommeren Greve
Philipp Brun
Espen Bagøien
Fi Prowe
Lasse Tor Nielsen
Peter Tiselius
Uffe H Thygesen
And others from the Ocean Life teams

Funding:
Centre for Ocean Life is funded by
- The Villum Foundation
- Danish Research Council for Fundamental Research
- HC Ørsted Foundation
- Niels Bohr Foundation
- EU (Marie Curie)