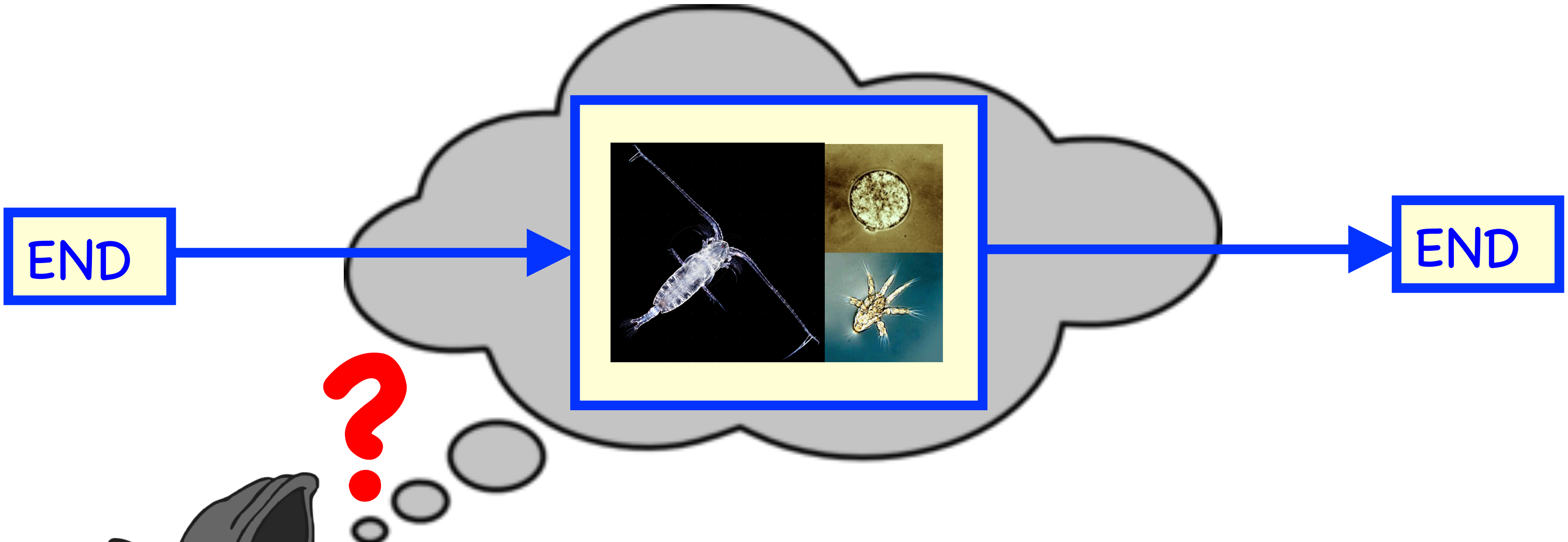
UNCERTAINTY IN COPEPOD MORTALITY RATES AND FATES: IMPLICATIONS FOR ECOLOGICAL LINKAGES



Wendy Gentleman

Erica Head
Tom Anderson

ICES/PICES Zooplankton Production Symposium: Workshop 5
May 2016

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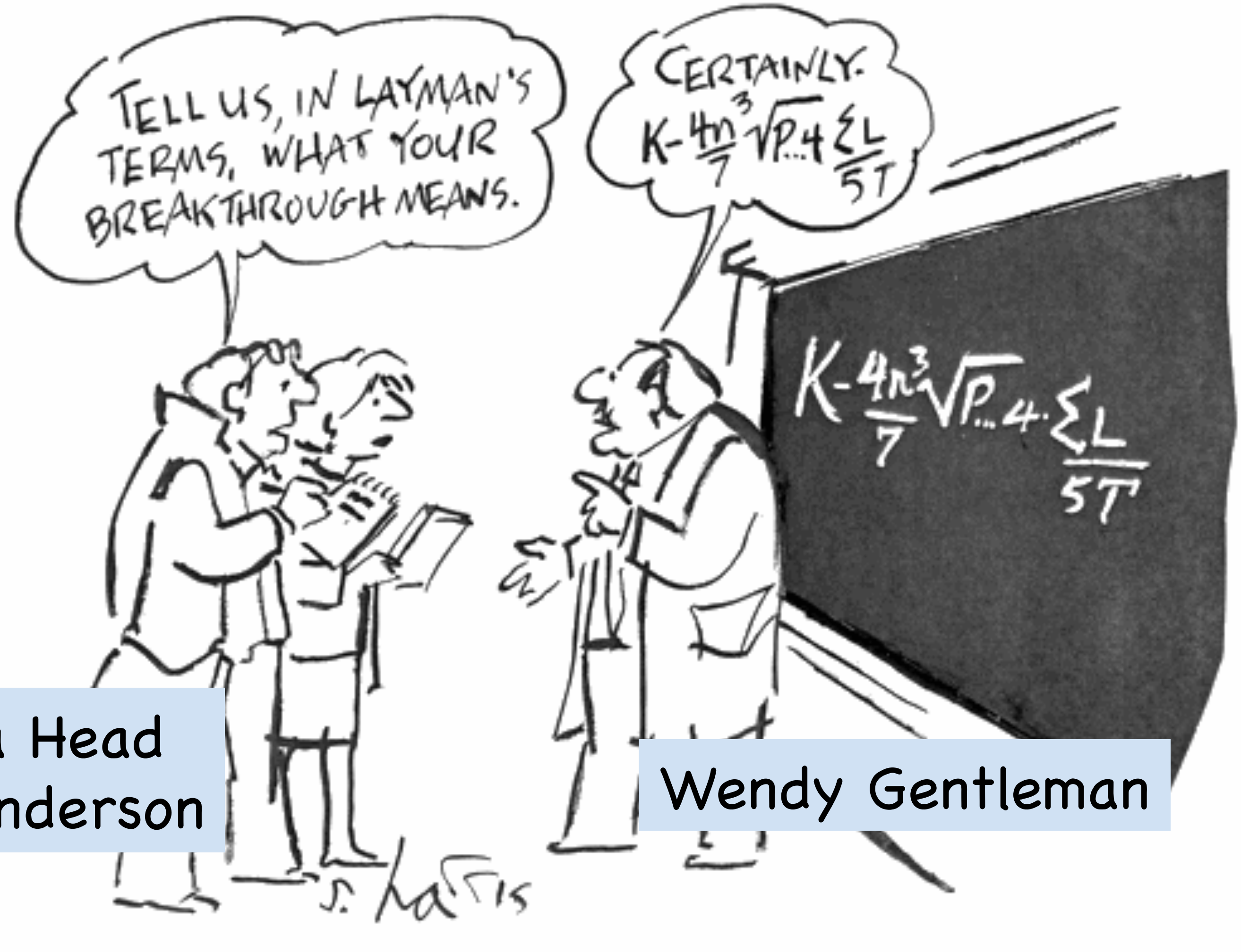

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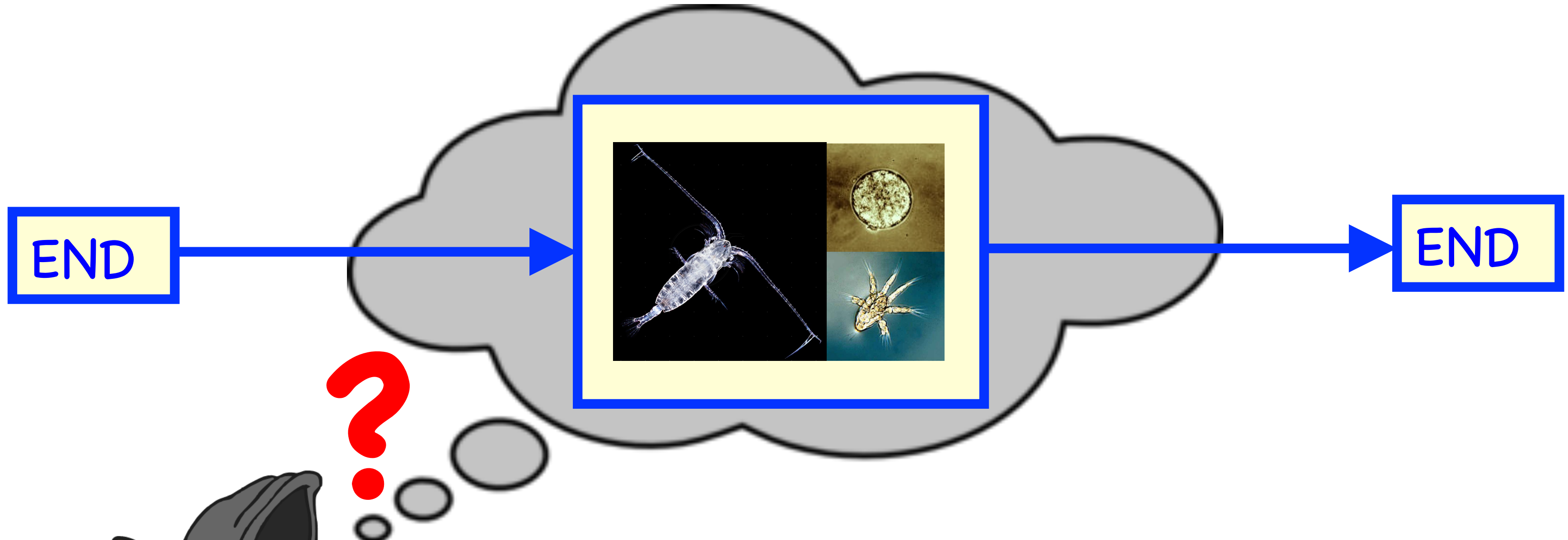

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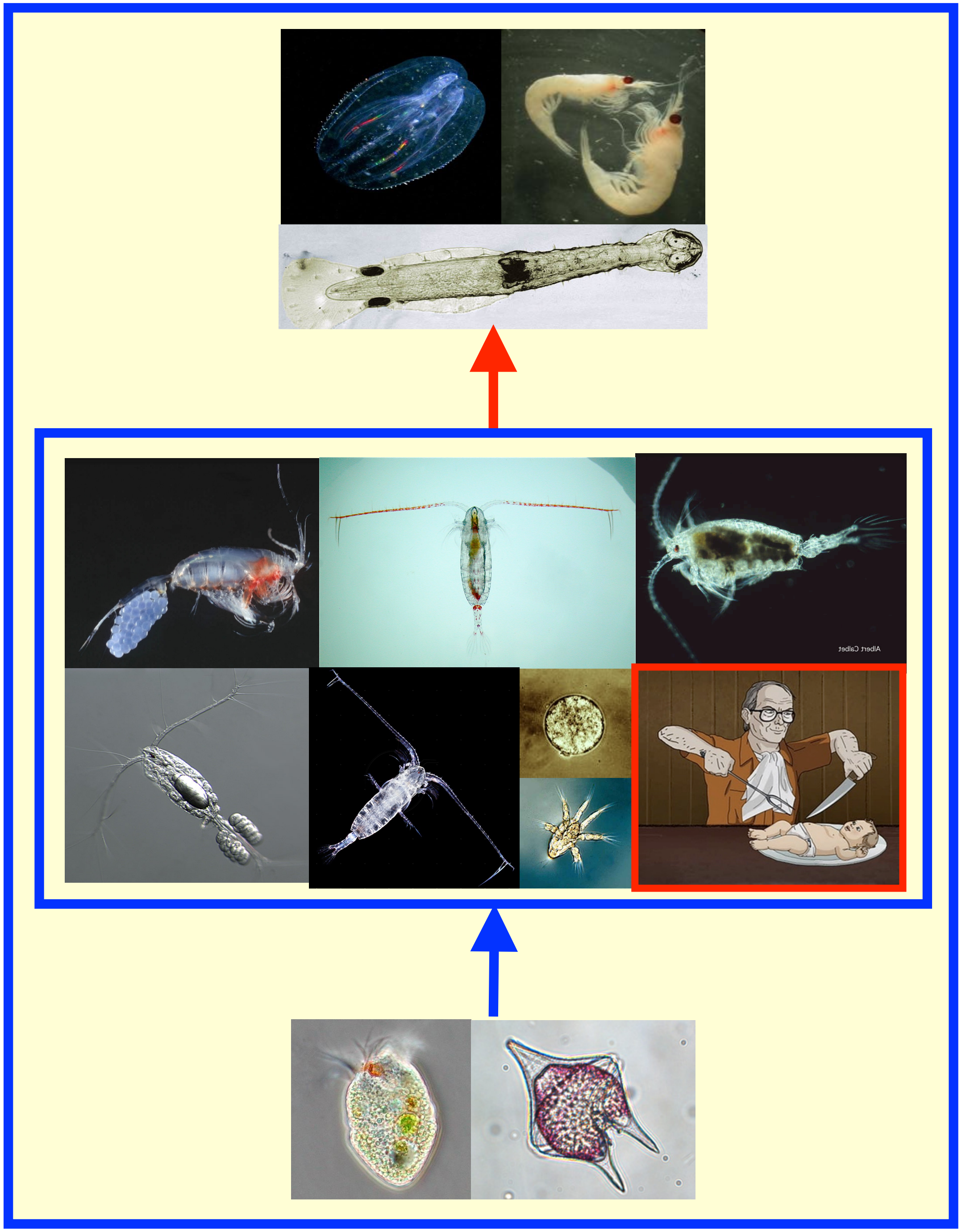
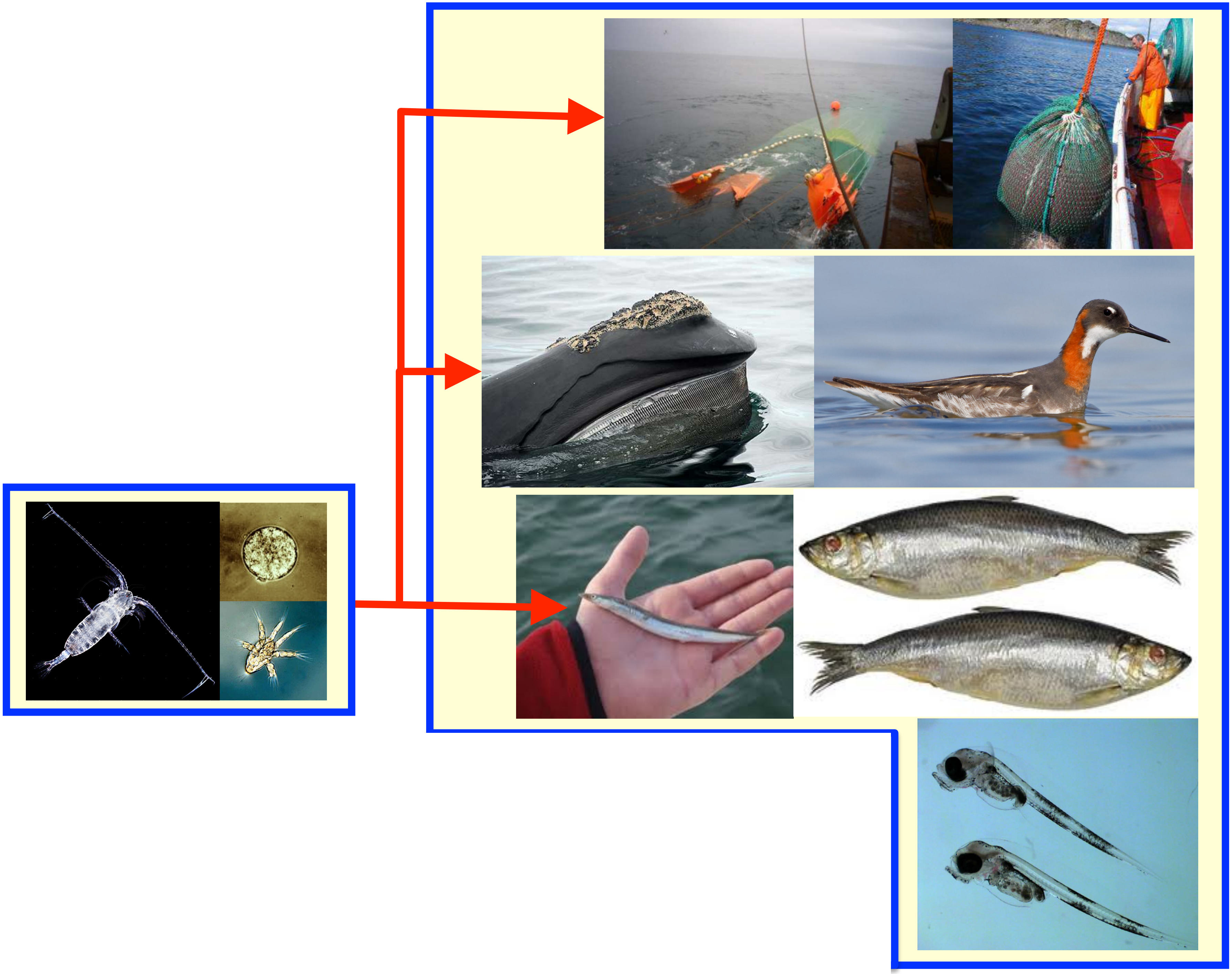
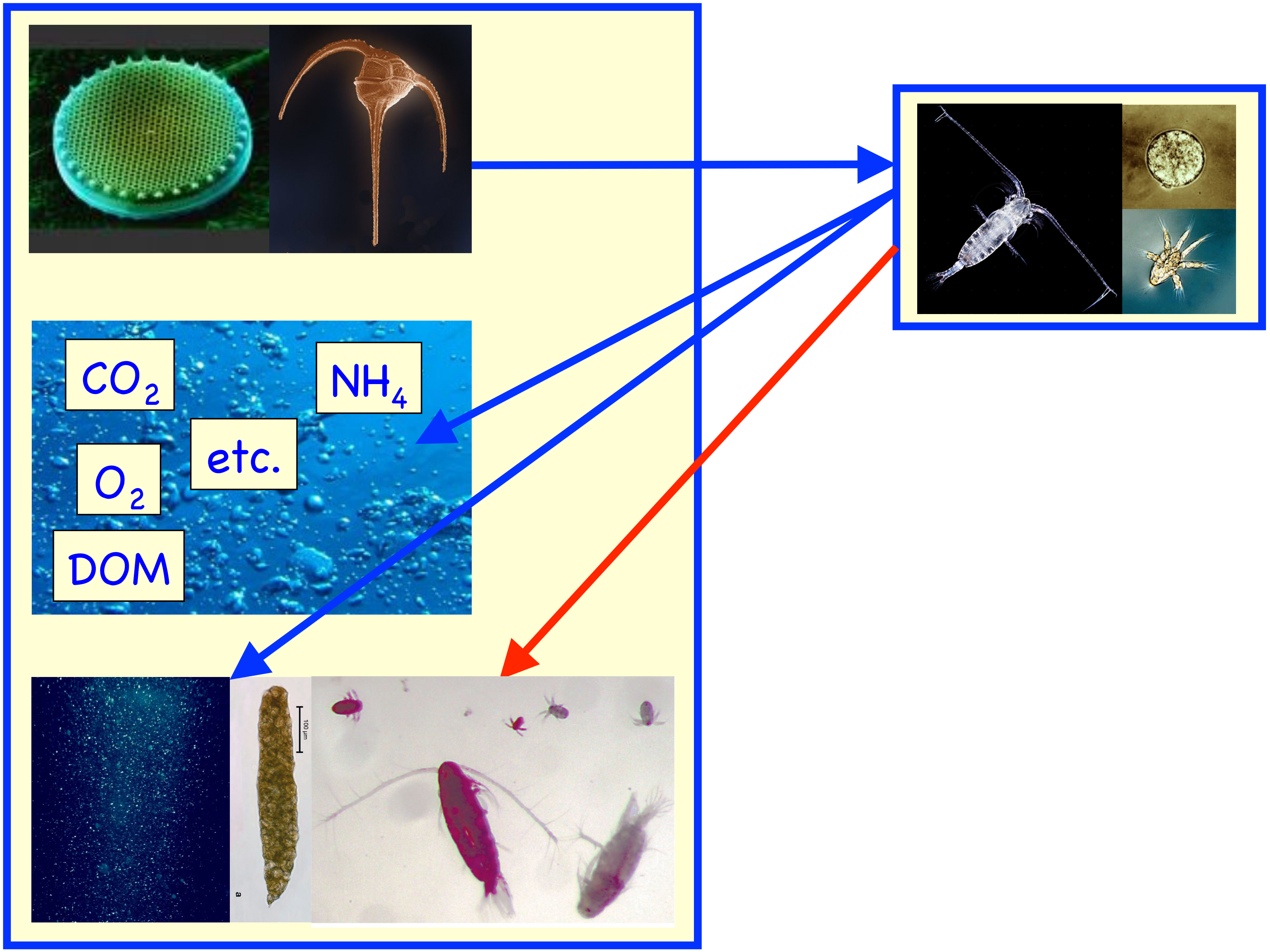
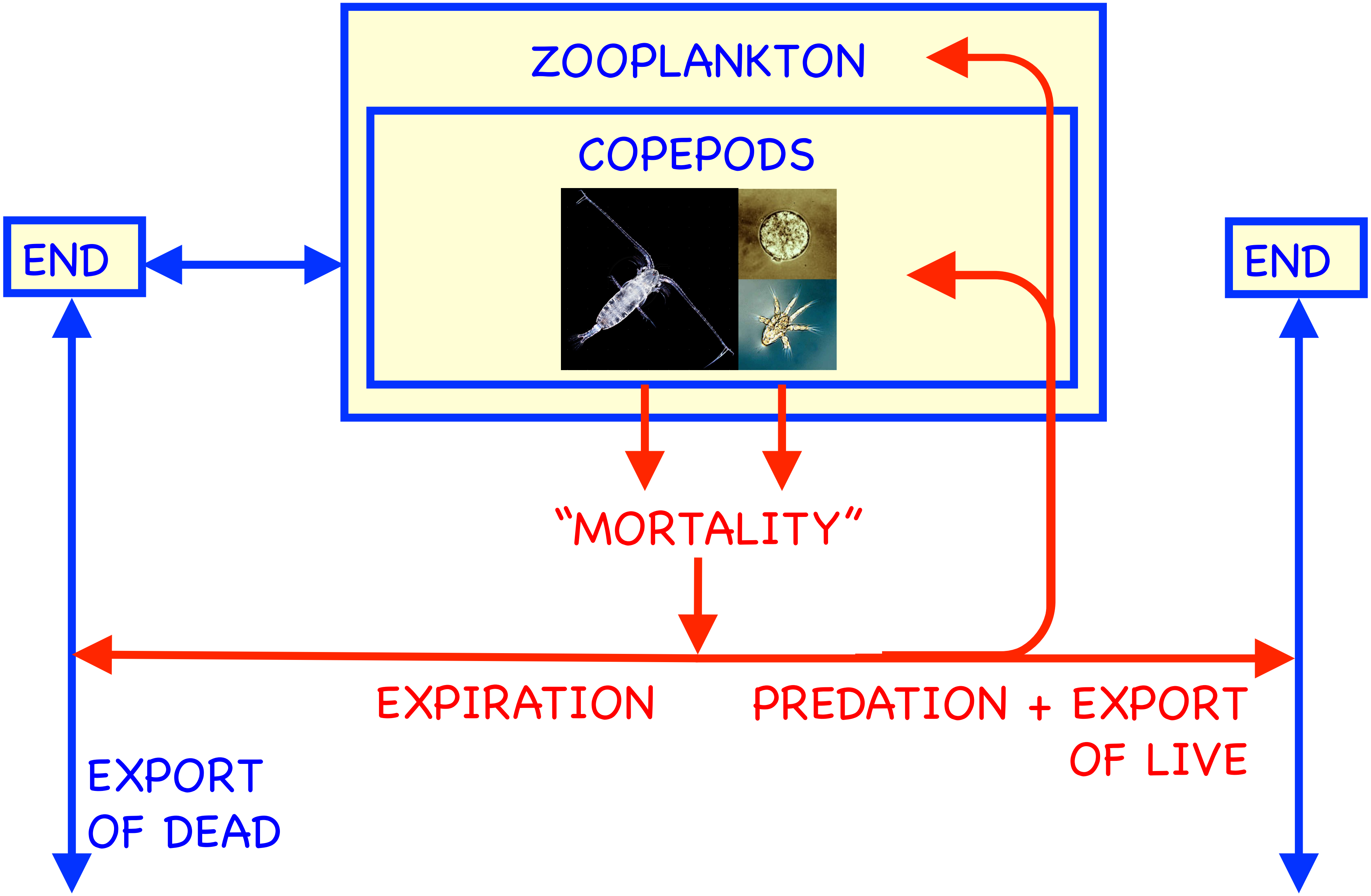
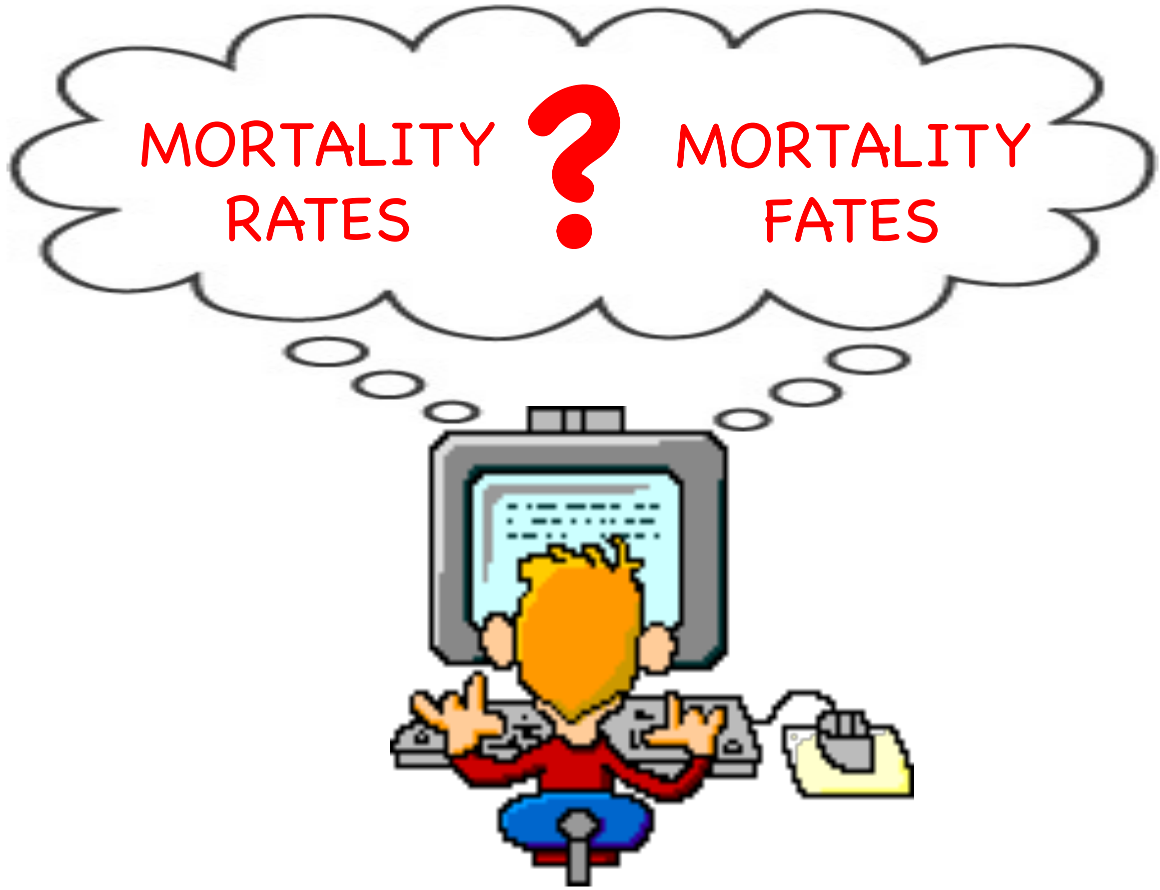

Albert Calbet

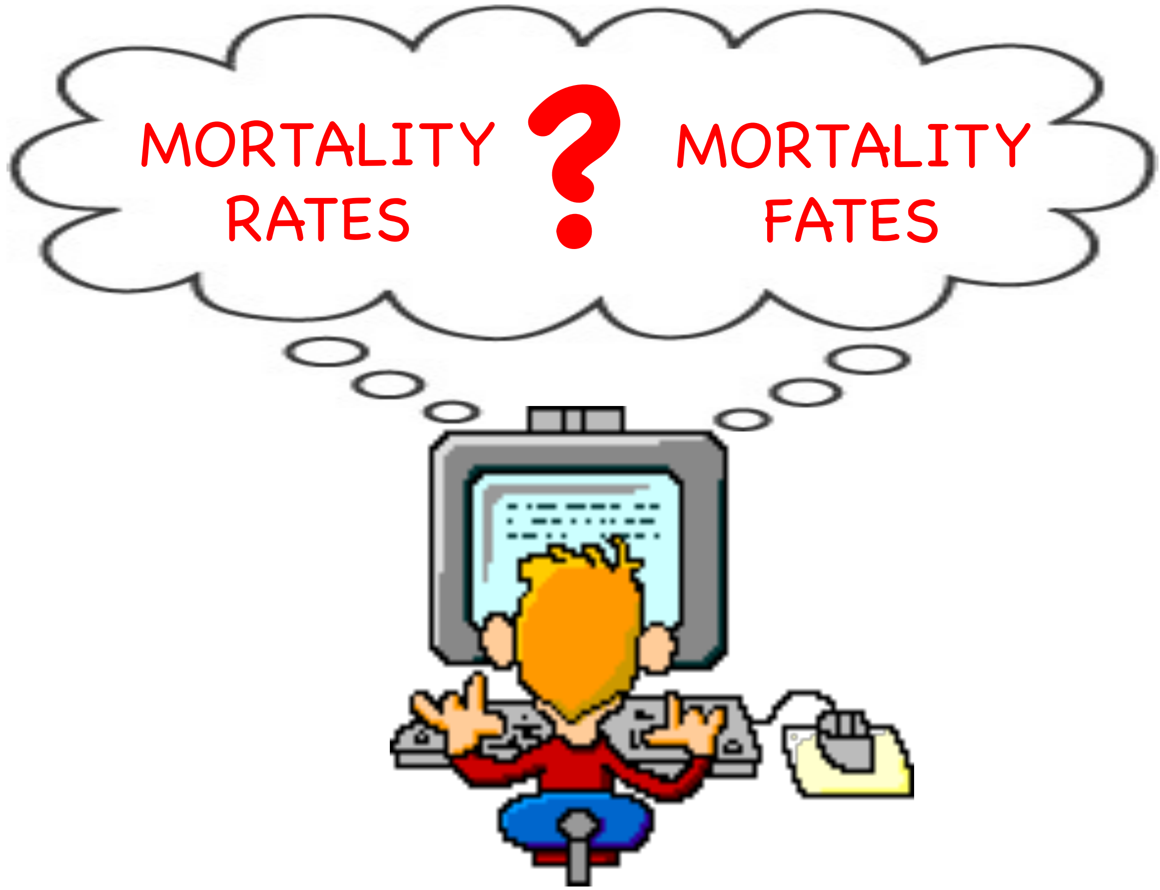




CO_2
NH_4
etc.
O_2
DOM

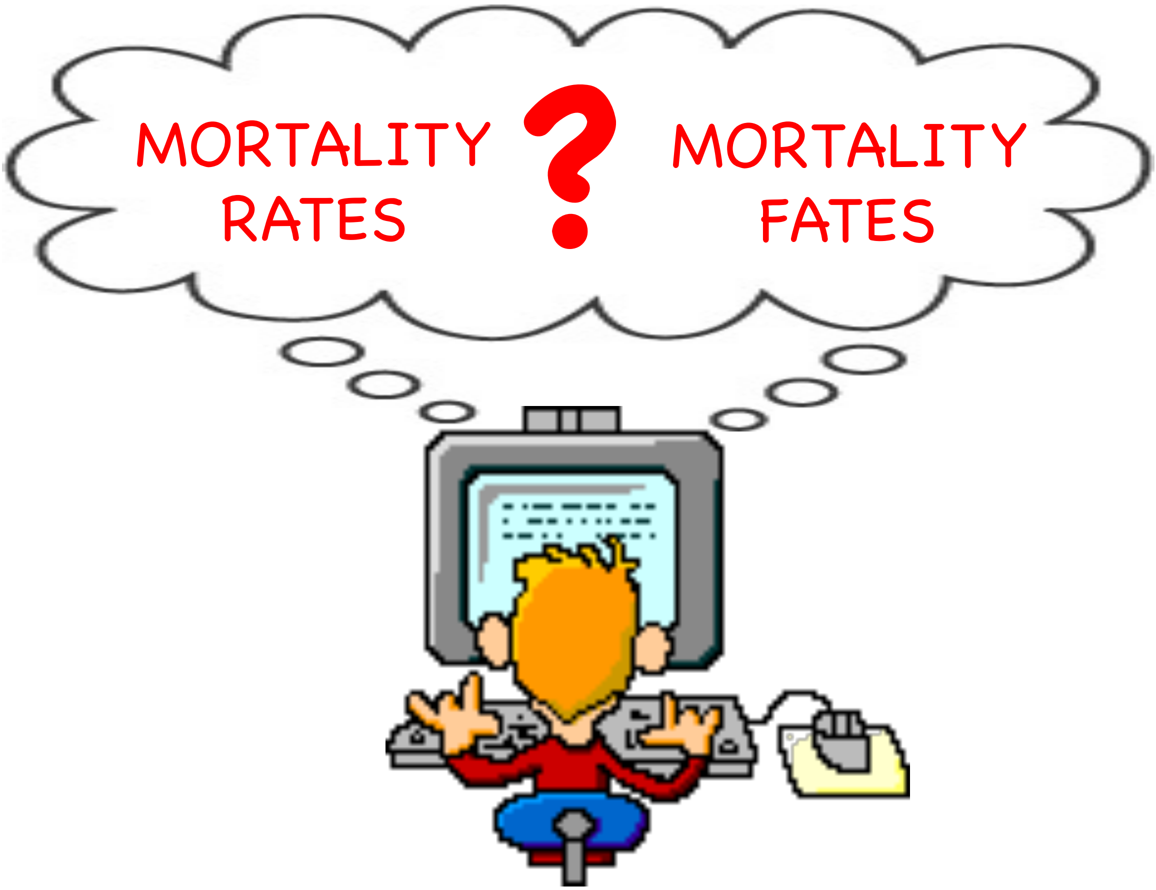

ZOOPLANKTON
COPEPODS
END
END
"MORTALITY"
EXPIRATION
PREDATION + EXPORT
OF LIVE
EXPORT
OF DEAD


MORTALITY RATES
?
MORTALITY FATES



Modeling choices matter!

Many previous studies: coefficients & closure



Modeling choices matter!

Many previous studies: coefficients & closure

Today: Two issues that are not as widely recognized, both relate to expiration

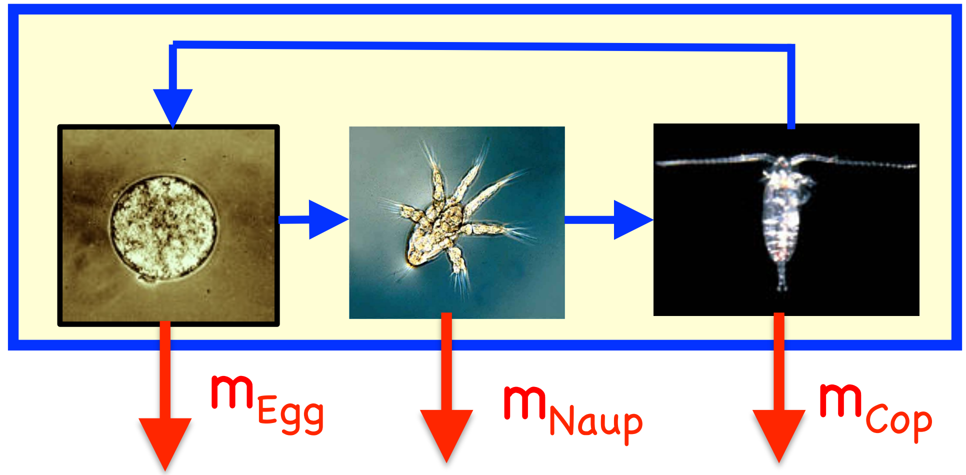
ISSUE I: INFLUENCE OF EXPIRATION ON EARLY STAGE MORTALITY ESTIMATION

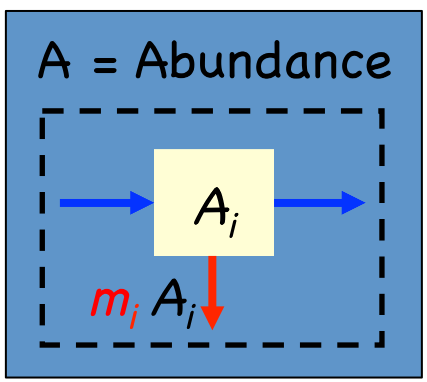
"MORTALITY"

EXPIRATION
(e.g. hatching failure, starvation, disease)

PREDATION + EXPORT OF LIVE

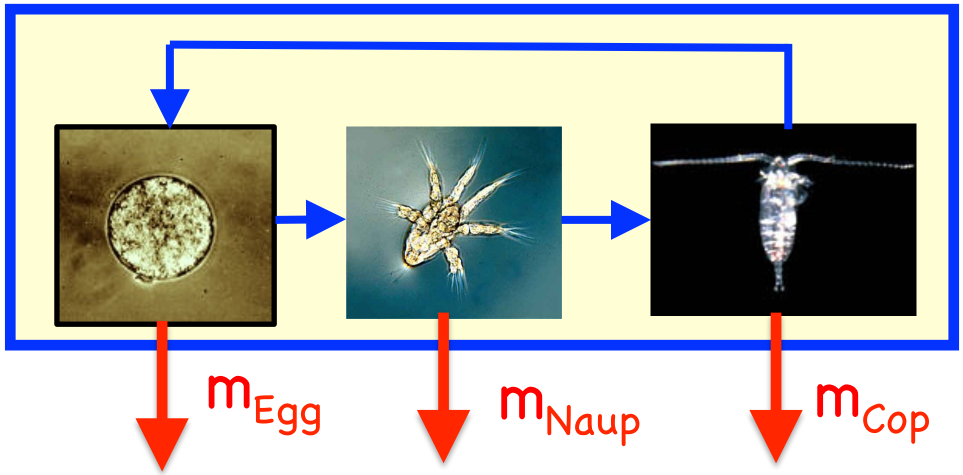
METHODS FOR ESTIMATING COPEPOD MORTALITY

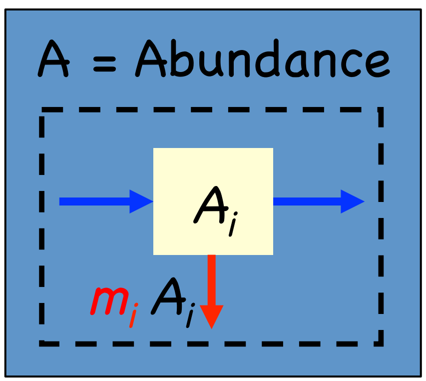




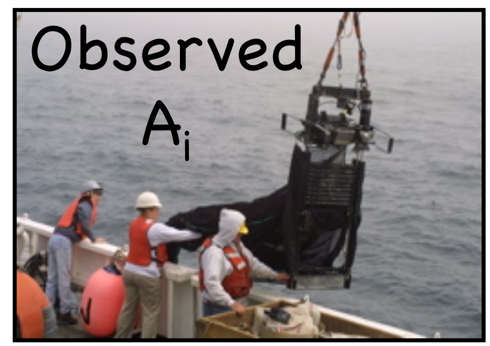
Founded on models of copepod population dynamics

METHODS FOR ESTIMATING COPEPOD MORTALITY





Estimated m_i = rate for which model fits data



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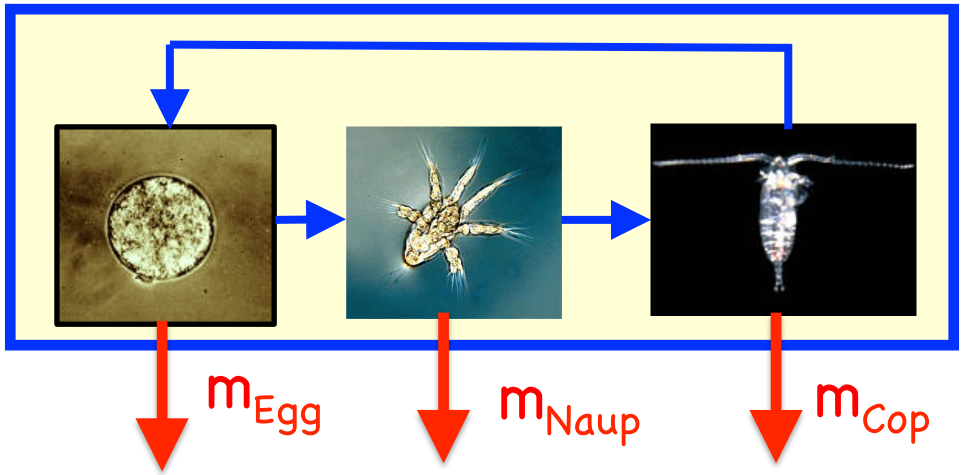

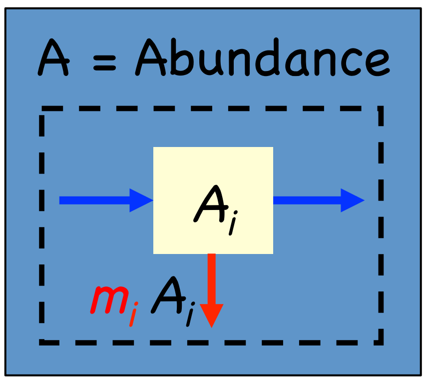

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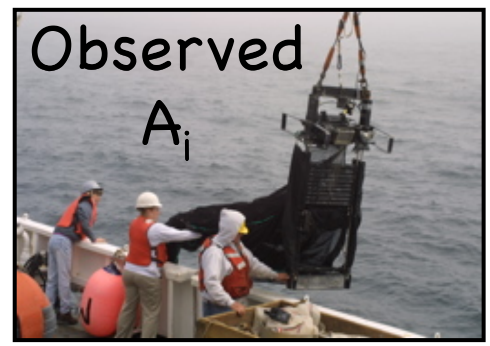
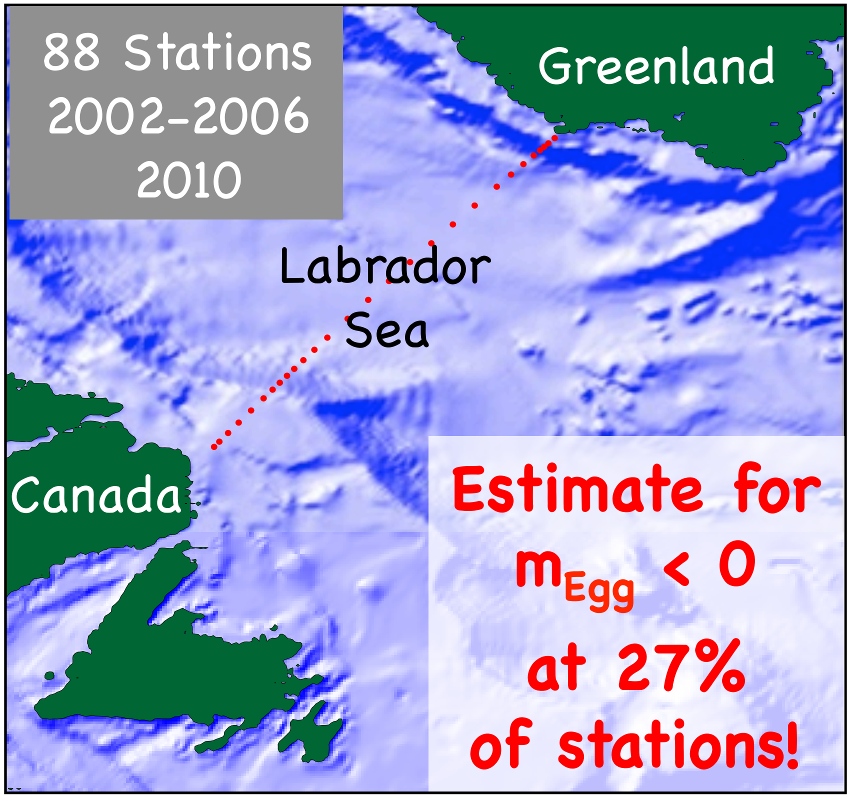


Most common

= "vertical" methods = simple formulae from simplified model
(Mullin & Brooks, 1970; Aksnes & Ohman, 1996; Gentleman et al., 2012)

= use of aggregate "stages"

ESTIMATES OF MORTALITY RATES for *C. finmarchicus* EARLY LIFE STAGES IN THE LABRADOR SEA



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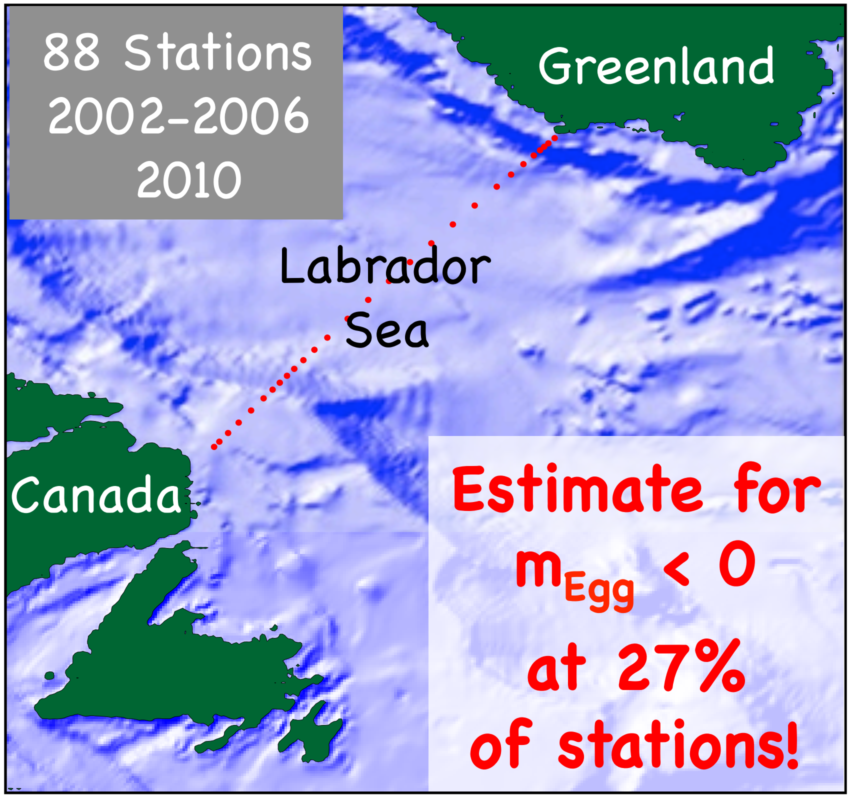

Sensitivity studies demonstrated that negative egg mortalities were not explained by commonly recognized source of error

Head et al., 2015

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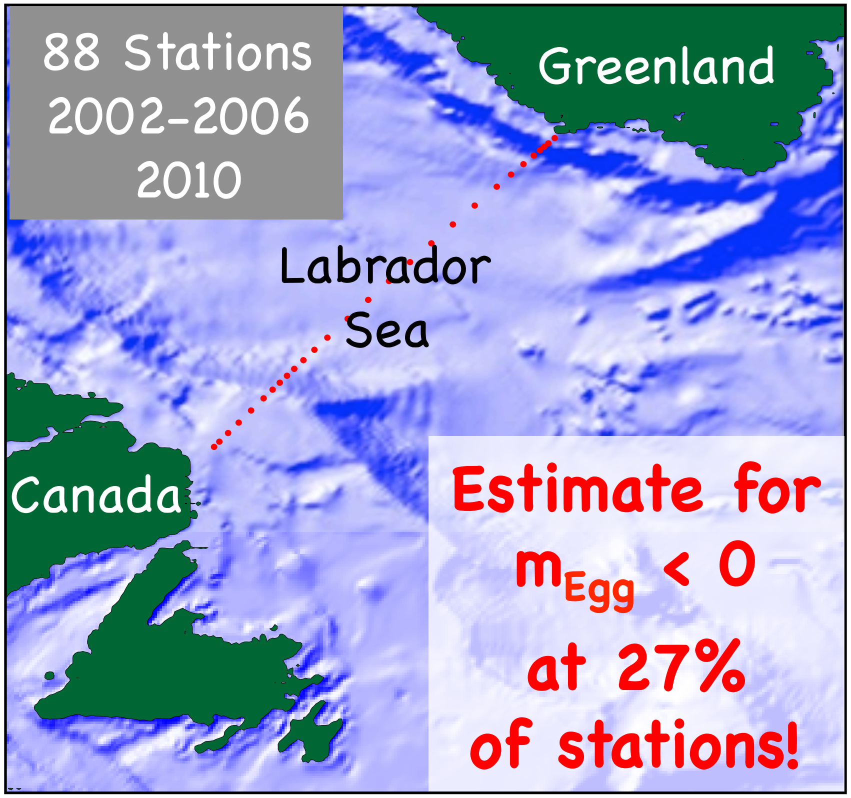

Sensitivity studies demonstrated that negative egg mortalities were not explained by commonly recognized source of error

Head et al., 2015

Hirst et al., 2007 showed standard methods are biased when egg viability (i.e. hatching success) < 100%

EXPIRATION-RELATED ISSUES WITH STANDARD ESTIMATION METHODS

(Hirst et al., 2007; Elliott & Tang, 2011; Gentleman & Head, under revision)

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e.g. Basic method for "stage" 1 (1 = Eggs or Eggs + Nauplii)

Survivorship:

$$S_1 = e^{-m_1 D_1}$$

$$\frac{A_1}{A_F} = \frac{\varepsilon\left(1 - S_1\right)}{m_1}$$

EXPIRATION-RELATED ISSUES WITH STANDARD ESTIMATION METHODS

(Hirst et al., 2007; Elliott & Tang, 2011; Gentleman & Head, under revision)

e.g. Basic method for "stage" 1 (1 = Eggs or Eggs + Nauplii)

Total egg production

≠ viable egg production

Survivorship:

$$S_1 = e^{-m_1 D_1}$$

Mortality

≠ death

$$\frac{A_1}{A_F} = \frac{\varepsilon\left(1 - S_1\right)}{m_1}$$

"Stage" Duration

≠ period of expiration

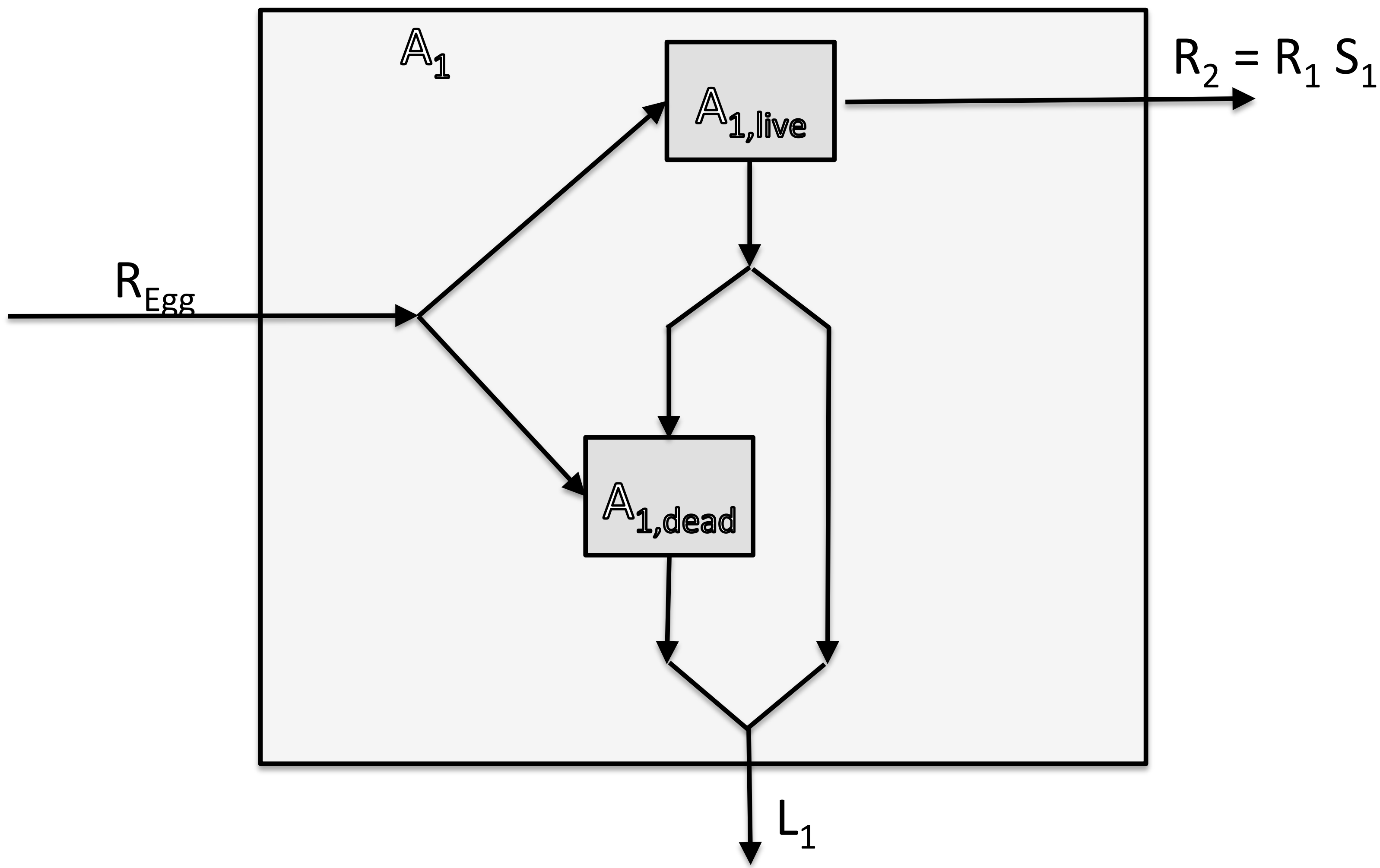
Observed ratio of stage abundances

may include dead individuals

Mortality = $\ell_1 \neq m_1$

NEW METHODS ACCOUNTING FOR VIABILITY <= 100%

(Gentleman & Head, under revision)



Based on model that considers expiration of "stage" 1

(1 = Eggs or Eggs+Nauplii, R = Recruitment, S = Survivorship, L = Loss)

NEW METHODS ACCOUNTING FOR VIABILITY <= 100%

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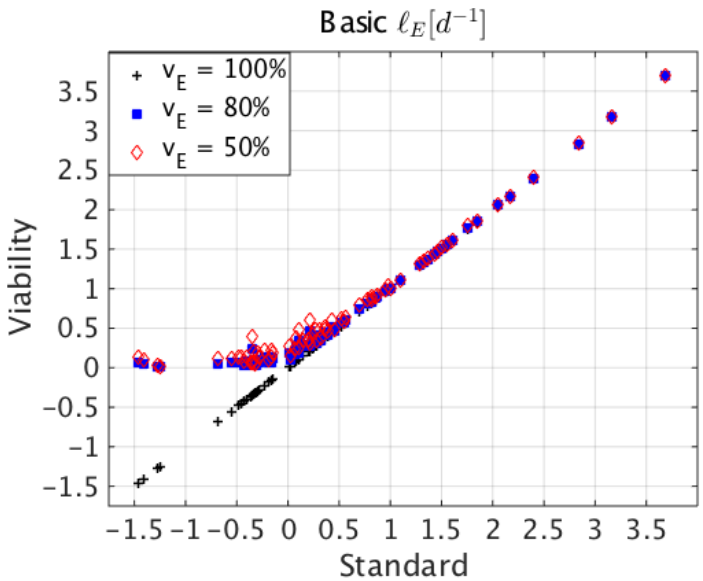

- Previous negatives now all positive

NEW METHODS ACCOUNTING FOR VIABILITY <= 100%

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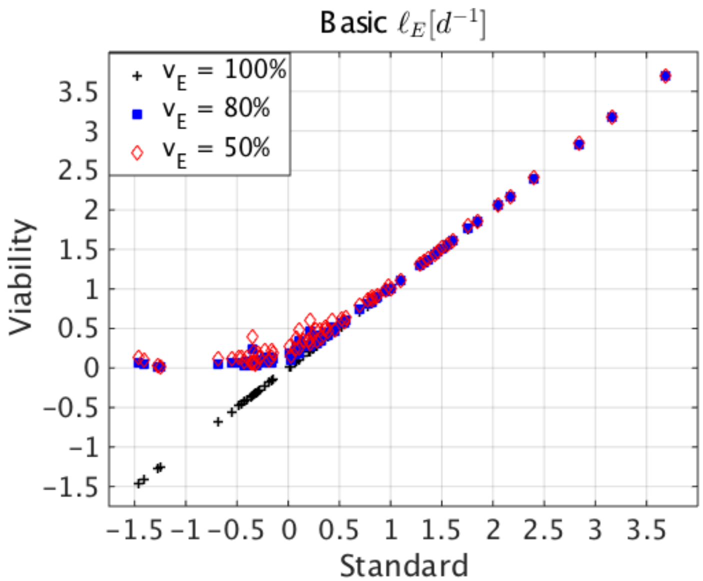

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- Changes regional means by >20%

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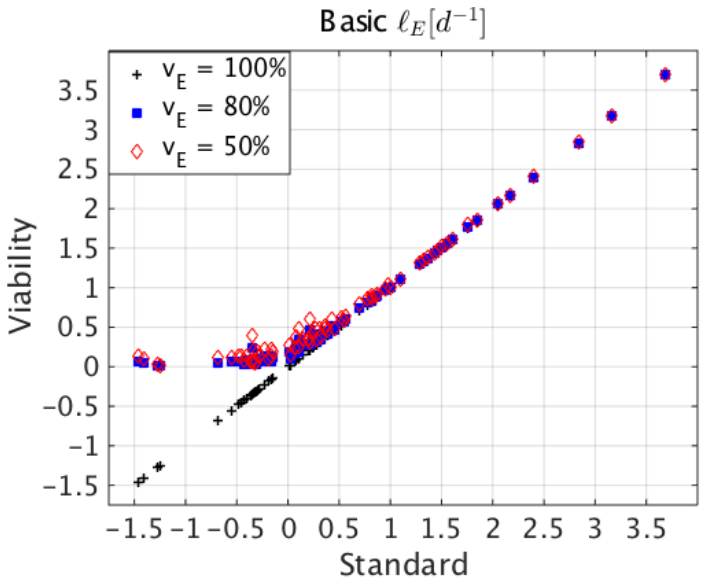
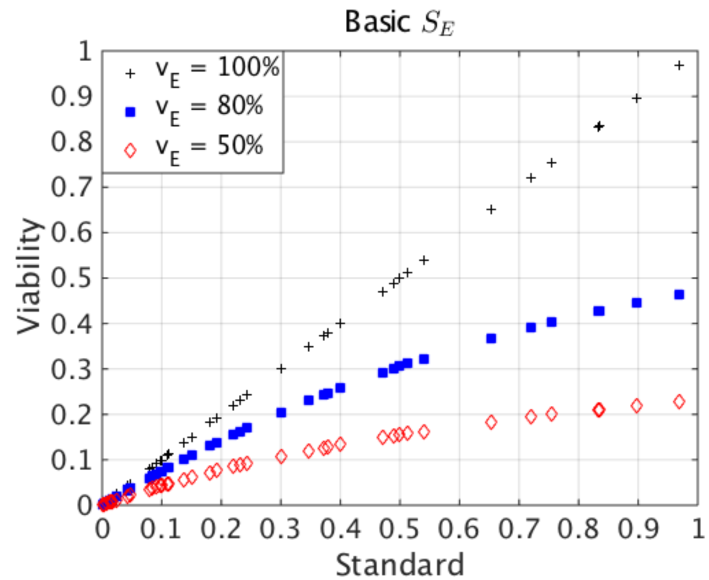


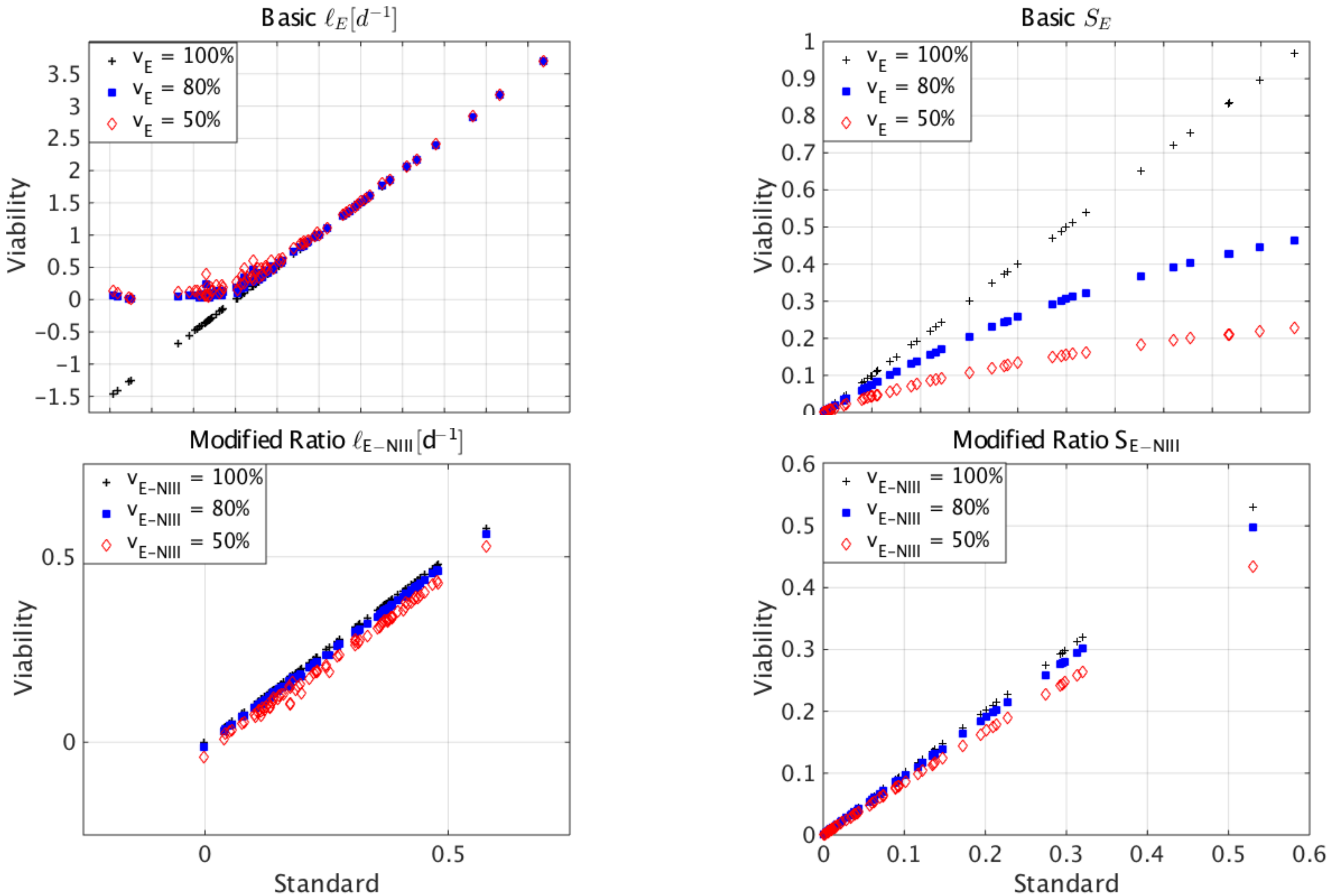


- Previous negatives now all positive
- Changes regional means by >20%
  (Head et al., 2015)
- Biggest effect at lowest "mortality"

- Biggest effect for highest survivorship
- Minimizing egg expiration key for recruitment

METHODS ACCOUNTING FOR VIABILITY <= 100%

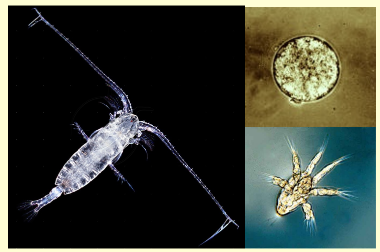
(Gentleman & Head, under revision)



Aggregating stages masks significance of expiration

ISSUE II: INFLUENCE OF EXPIRATION ON ECOLOGICAL FATE OF MORTALITY

ZOOPLANKTON



END

END

"MORTALITY"

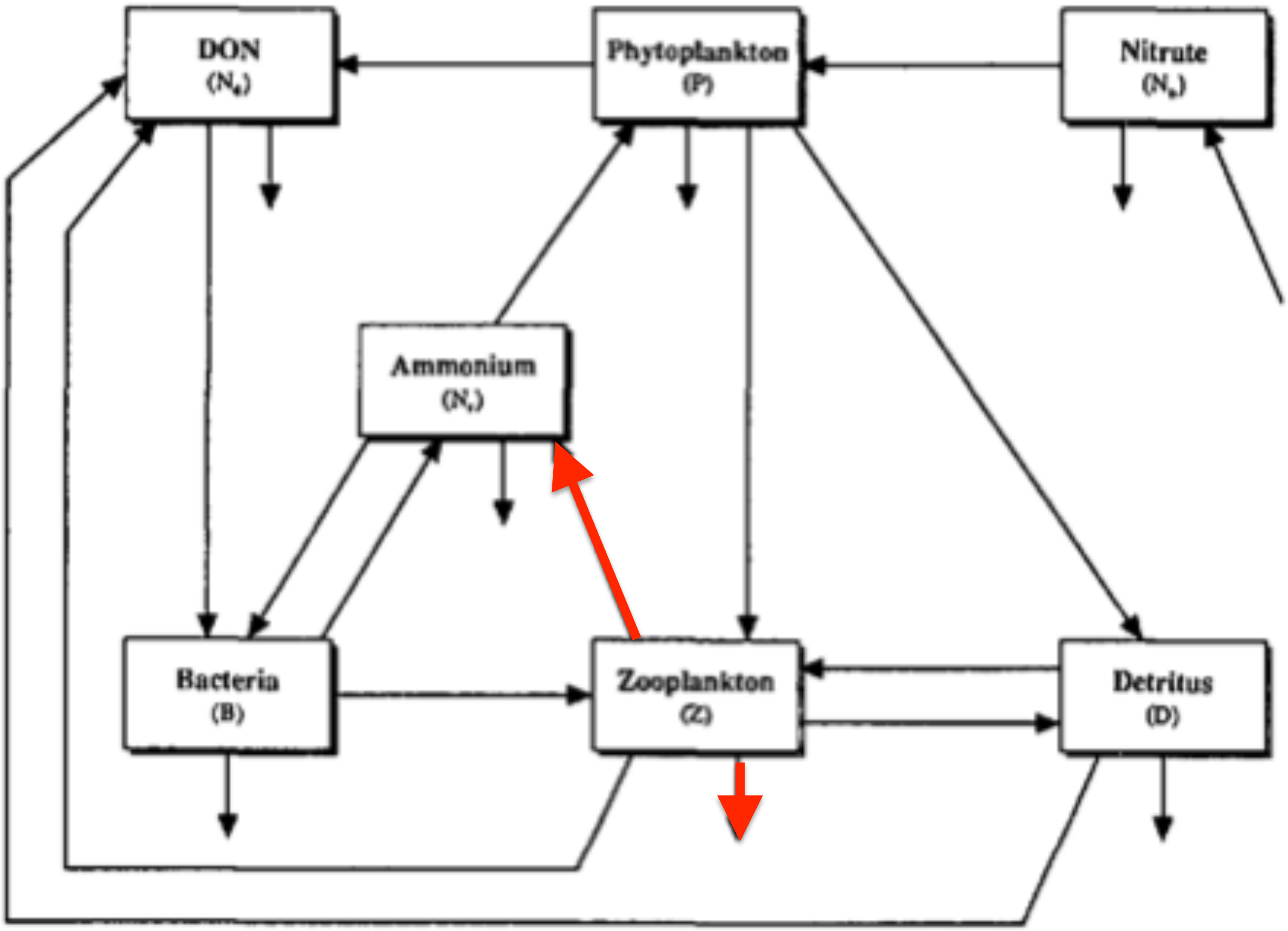
EXPIRATION

PREDATION + EXPORT OF LIVE

EXPORT OF DEAD

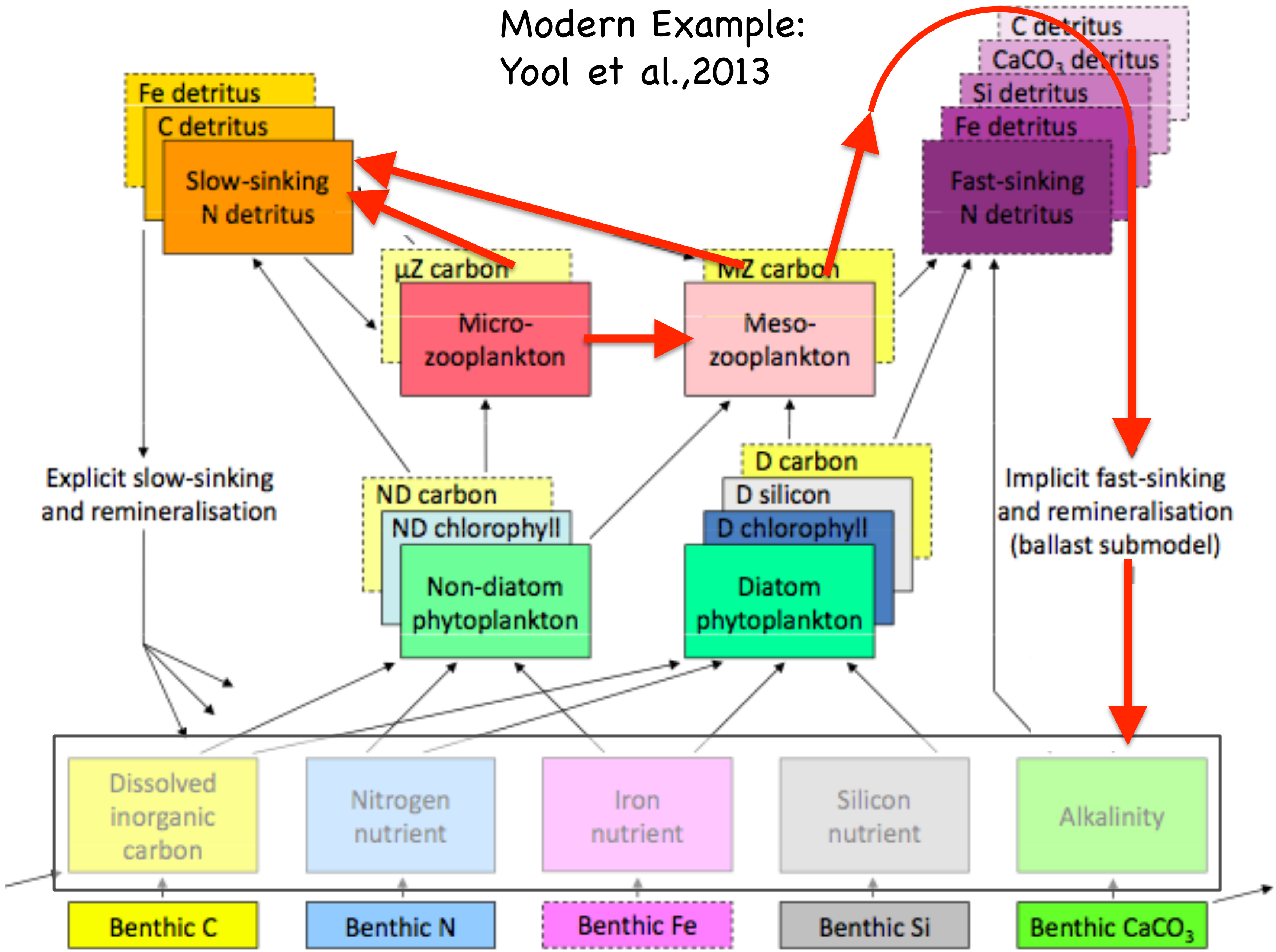
PARTITIONING MODELED ZOOPLANKTON MORTALITY

Classic Example: Fasham et al., 1990



PARTITIONING MODELED ZOOPLANKTON MORTALITY

Modern Example:
Yool et al.,2013



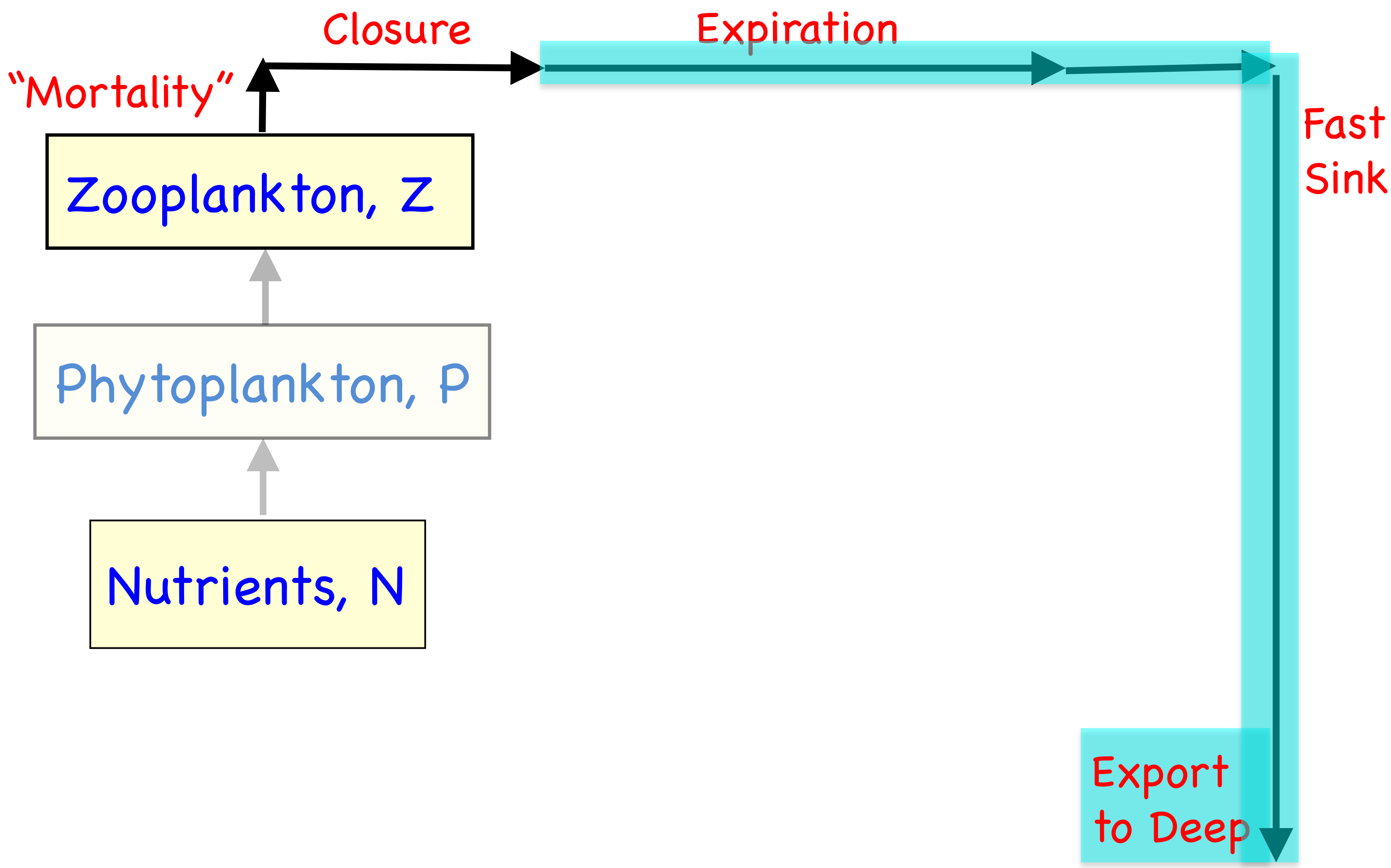
SENSITIVITY OF ECOSYSTEM DYNAMICS TO PARTITIONING ZOOPLANKTON MORTALITY

(Gentleman & Anderson, in prep)

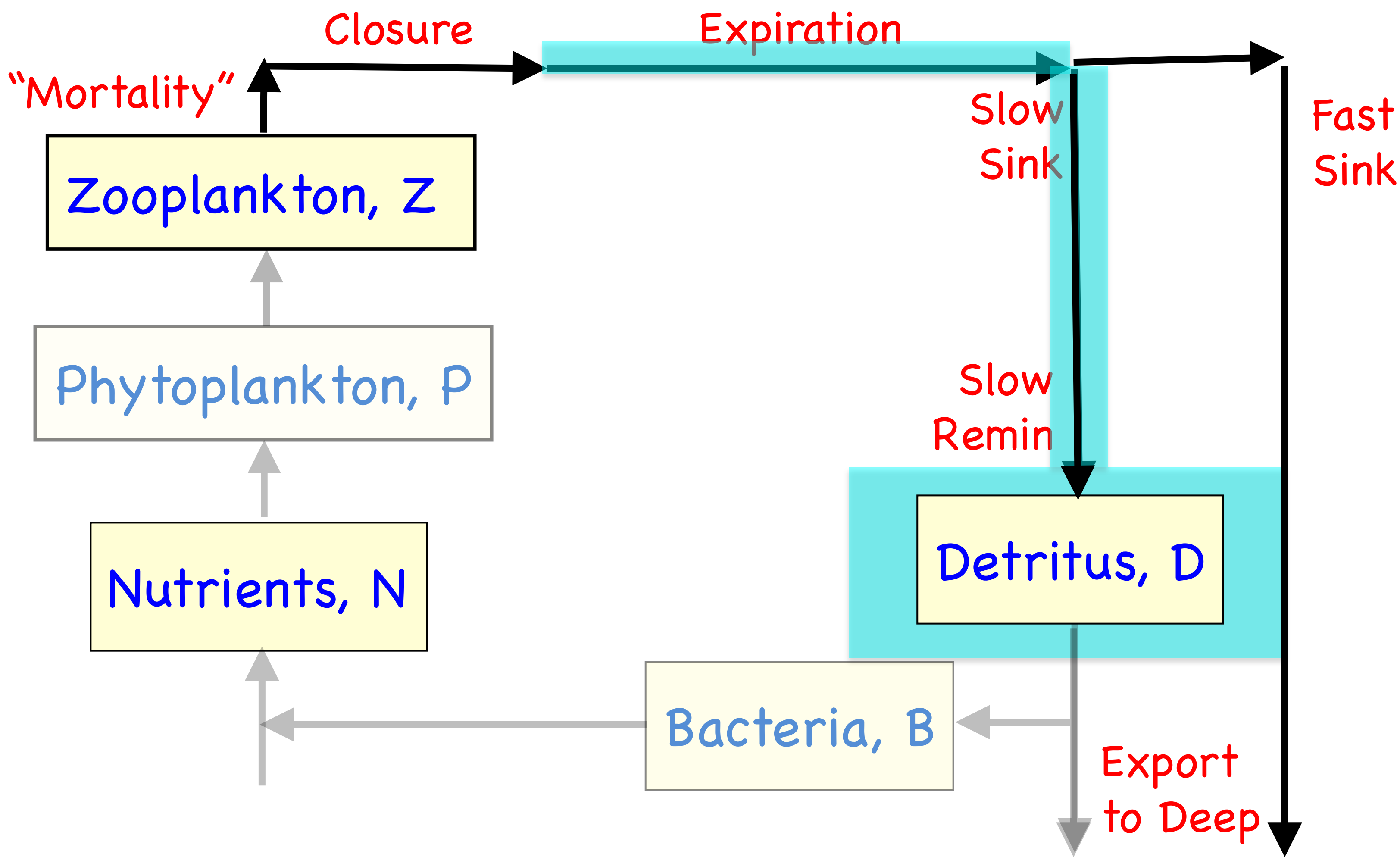
- Generic NPZD (Anderson et al., 2015)
- Forced with Seasonal Temp, Light, MLD & deep NO_3 for Station India

First set of simulations look at fate of expiration:
Contrast 3 extreme cases

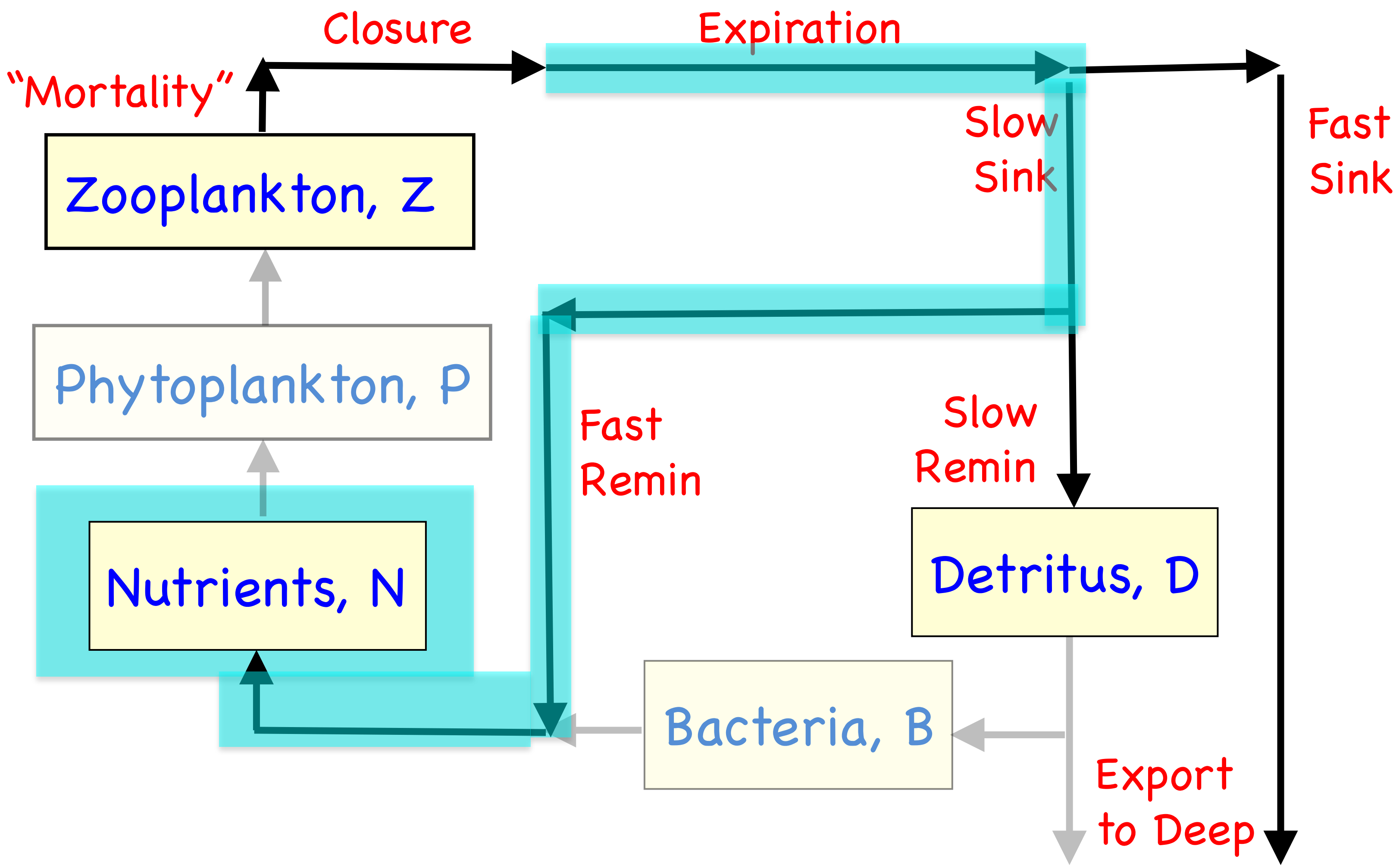
CASE 1: ALL TO EXPORT



CASE 2: ALL TO DETRITUS



CASE 3: ALL TO NUTRIENTS



SENSITIVITY OF ECOSYSTEM DYNAMICS TO PARTITIONING ZOOPLANKTON MORTALITY

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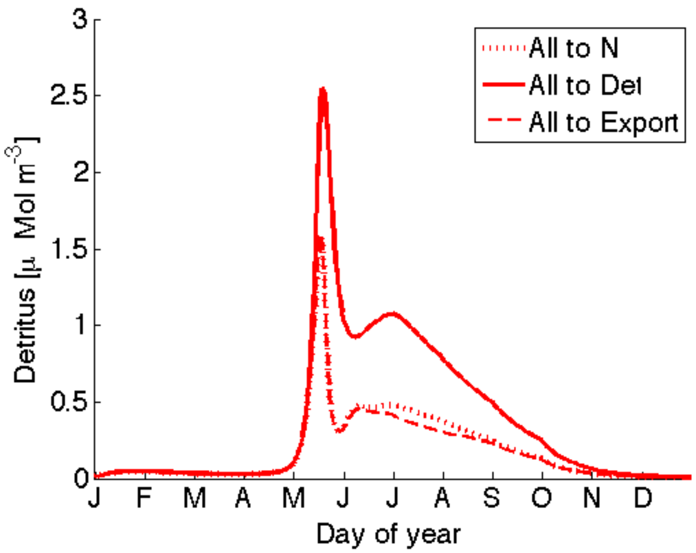
1. Fate of expiration: Contrast 3 extreme cases



- Fast remin = Fast sink
- Expiration related to zoo mortality ≈ total from phyto death + zoo physiological loss

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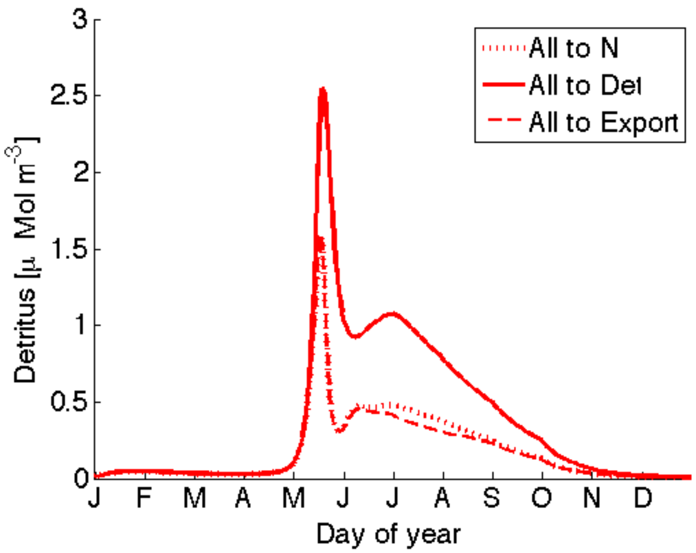
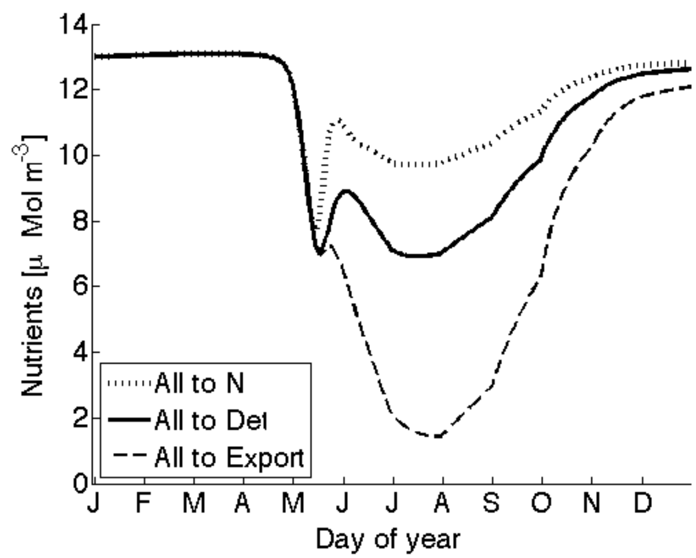




- Fast remin = Fast sink
- Expiration related to zoo mortality ≈ total from phyto death + zoo physiological loss

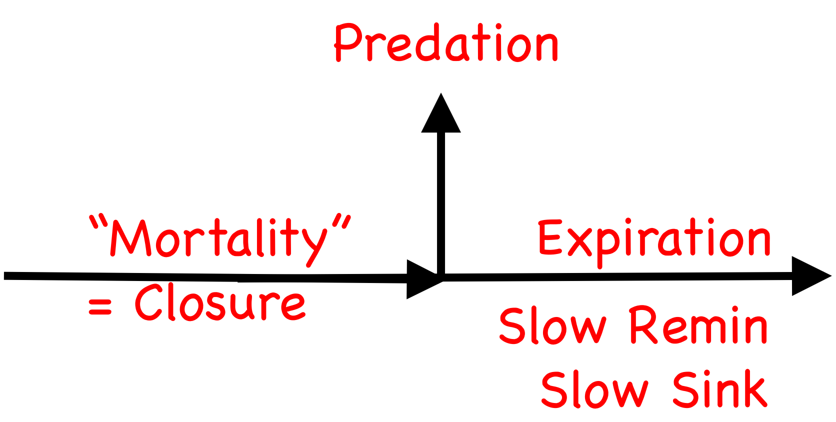
- Fast remin ≠ Fast sink
- Size and nature of dead key for local nutrient regen (bottom up)

SENSITIVITY OF ECOSYSTEM DYNAMICS TO PARTITIONING ZOOPLANKTON MORTALITY

(Gentleman & Anderson, in prep)

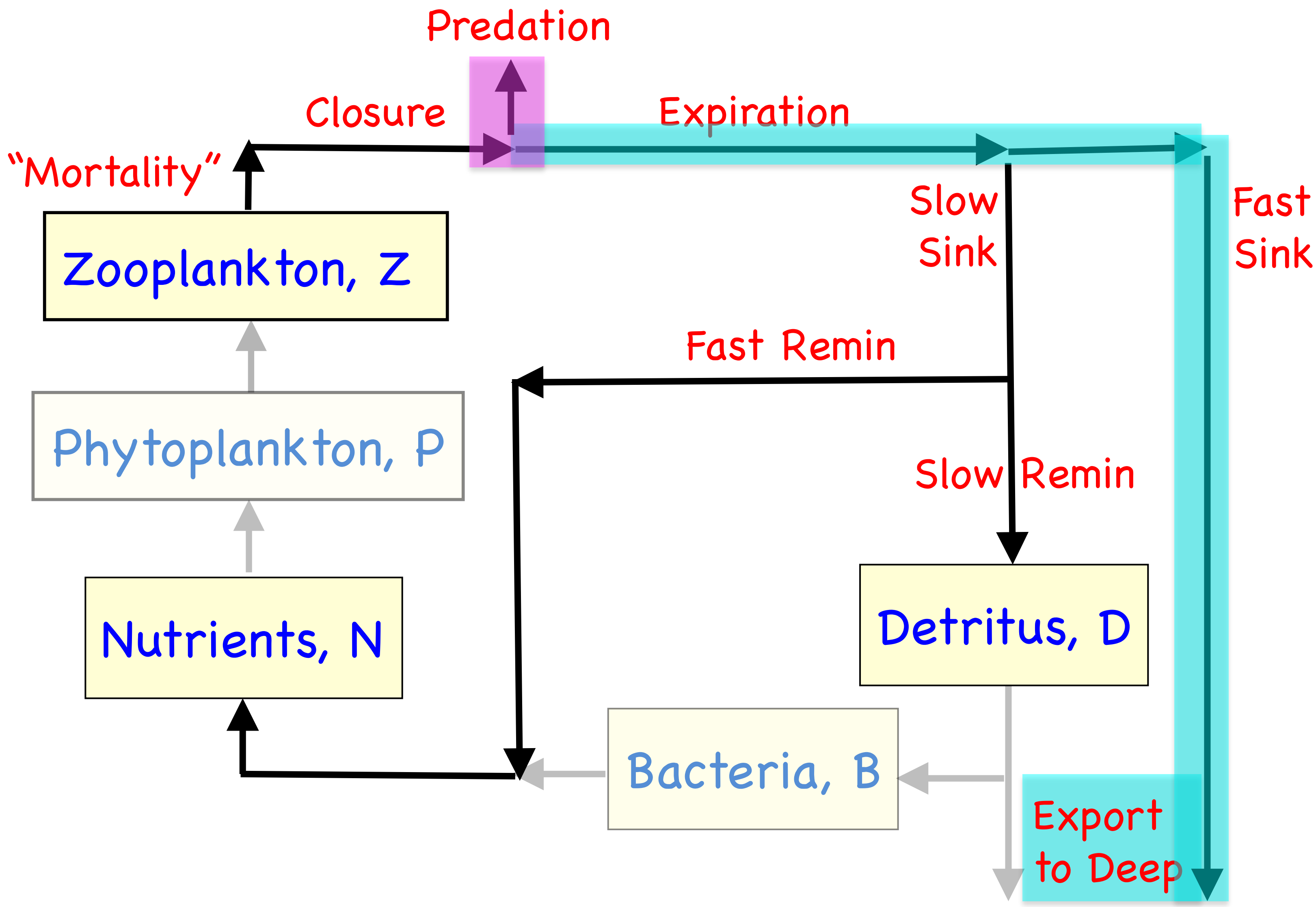
- Generic NPZD (Anderson et al., 2015)
- Forced with Seasonal Temp, Light, MLD & deep NO_3 for Station India

Second set of simulations looks at expiration-related fraction of total mortality: Contrasts 4 cases



Case 1: None

CASE 1: NONE = SAME LAST CASE 1: ALL TO EXPORT



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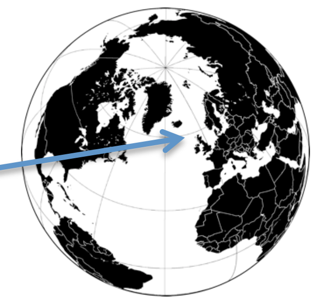
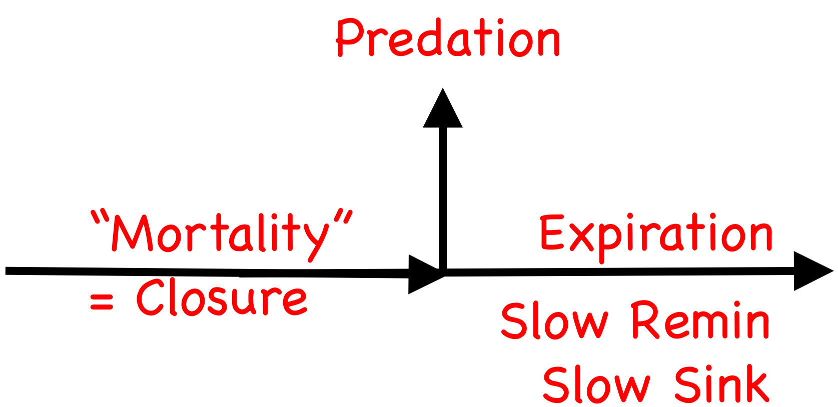
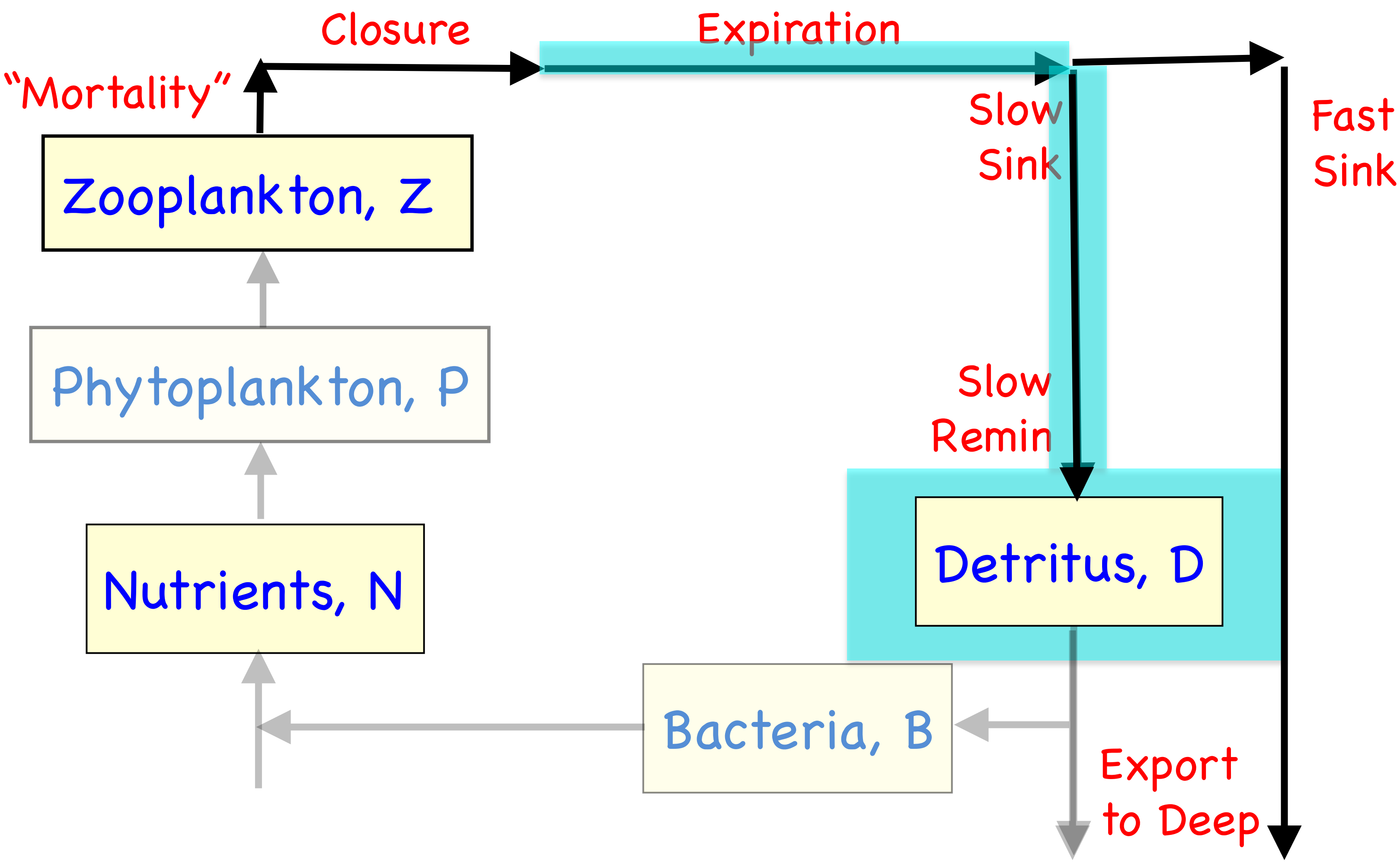


Second set of simulations contrast predation vs. expiration



Case 1: None
Case 2: All to Exp

CASE 2: ALL = SAME AS LAST CASE 2: ALL TO DETRITUS



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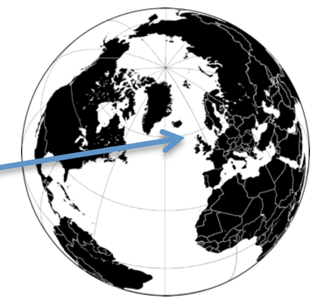
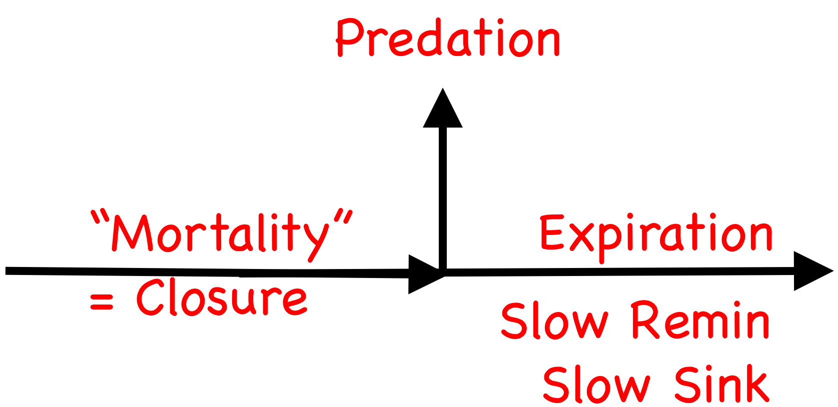


Second set of simulations contrasts expiration fraction of total mortality: Contrasts 4 cases



Case 1: None
Case 2: All
Case 3: Half
Case 4: Exp = Linear
Pred = Quadratic

SENSITIVITY OF ECOSYSTEM DYNAMICS TO PARTITIONING ZOOPLANKTON MORTALITY

(Gentleman & Anderson, in prep)

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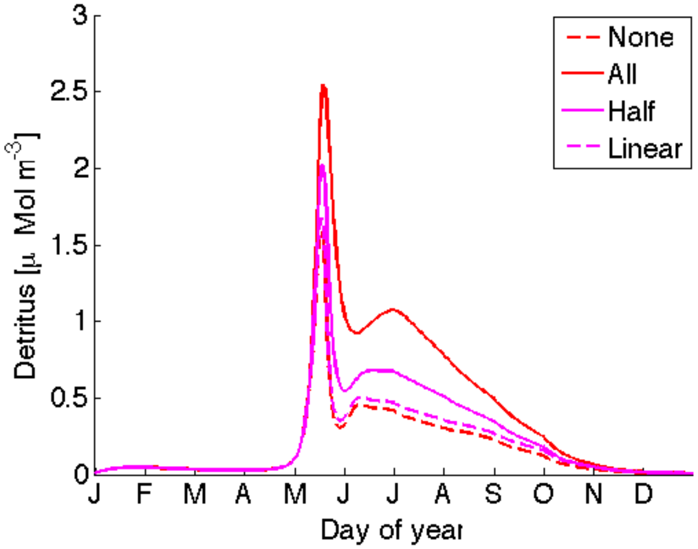
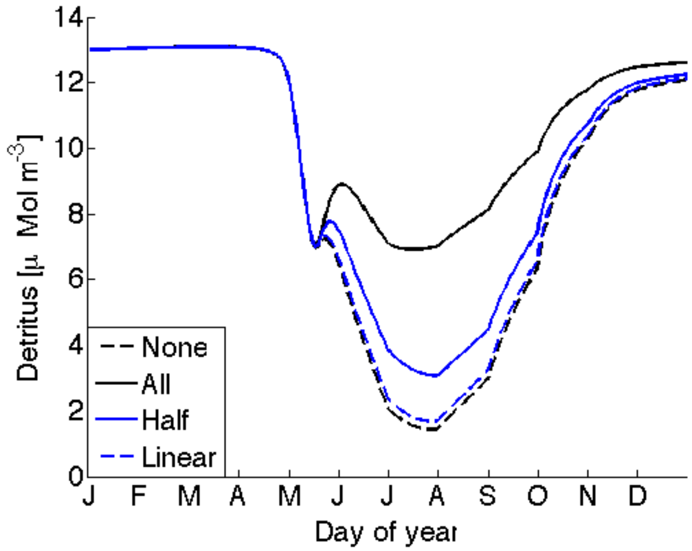
2. Expiration fraction of total mortality: Contrasts 4 cases





- Pred vs. Exp affects ecosystem structure & function
- Here: Linear ≈ "None", i.e. Total Mort ≈ Pred

SUMMARY & DISCUSSION POINTS

Uncertainty in copepod mortality rates and fates limits our understanding and prediction of Zooplankton Community Structure, Zooplankton Ecological Linkages, and Export

Today: Importance of Expiration

- Expiration biases estimation of early stage mortality rates
- New methods show egg viability is a significant factor for survivorship, which is masked by aggregating early stages
- The size and composition of dead individuals impacts local nutrient regeneration vs. export
- The relative importance of local predation vs. expiration affects ecosystem structure & function

Ecological implications include copepod recruitment, food for copepod predators and pathways for the biological pump. More consideration needs to be given to the ecological role of expiration, and its relative importance to other loss processes (e.g. predation & physiology as well as transport & migrations).