Polychaetes experience metabolic acceleration as other Lophotrochozoans: inferences on the life cycle of *Arenicola marina* with a Dynamic Energy Budget model

Lola De Cubber[1*], Sébastien Lefebvre[1], Théo Lancelot[1], Lionel Denis[1] and Sylvie Gaudron[1, 2]

[1] Univ. Lille, ULCO, CNRS, UMR 8187 Laboratoire d'Océanologie et de Géosciences (LOG) – 62930 Wimereux, France

[2] Sorbonne Univ., UFR 918 & UFR 927 - 75005 Paris, France

* Corr. author : lola.decubber@gmail.com

De Cubber et al., *in revision*. Ecological Modelling

DEB2019 1-12 April 2019 / Brest (France)

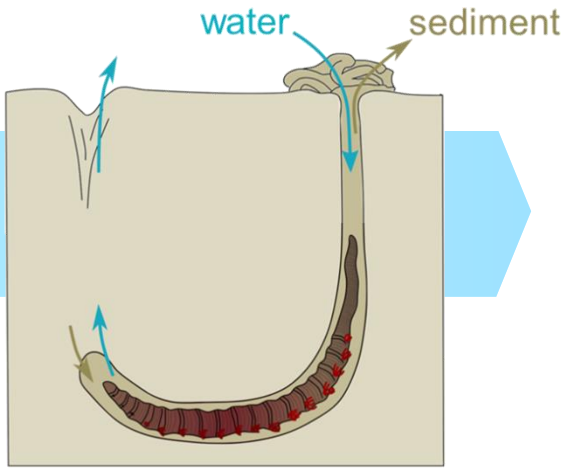
Sixth International Symposium and Thematic School on DEB theory for metabolic organization

Introduction

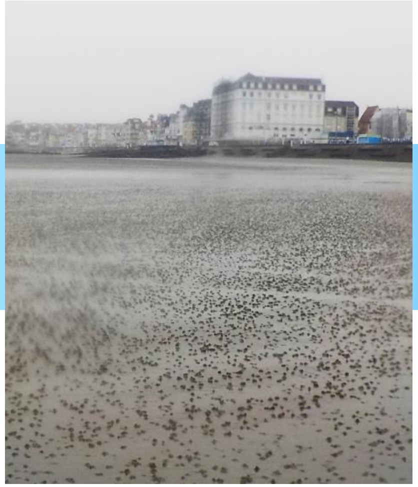
➢ Why *Arenicola marina* ?

Introduction

➢ Why *Arenicola marina* ?



Ecosystem engineer



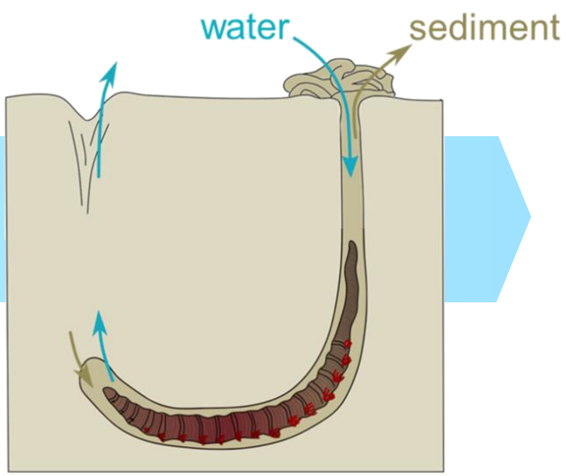
Trophic network

Future substitute to human blood ?

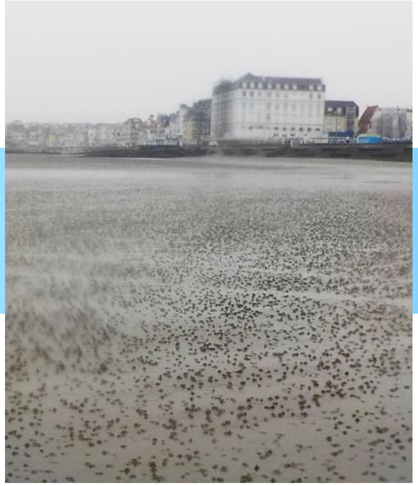
Fisheries

Introduction

➢ Why *Arenicola marina* ?



Ecosystem engineer



Trophic network

Future substitute to human blood ?

Fisheries

©Cardiff museum

Arenicola defodiens
Cadman & Nelson-Smith, 1993

→ The data relative to the species' life-cycle is anterior to 1993 and incomplete

Introduction

➢ A Dynamic Energy Budget adapted to *A. marina*'s life-cycle features ?

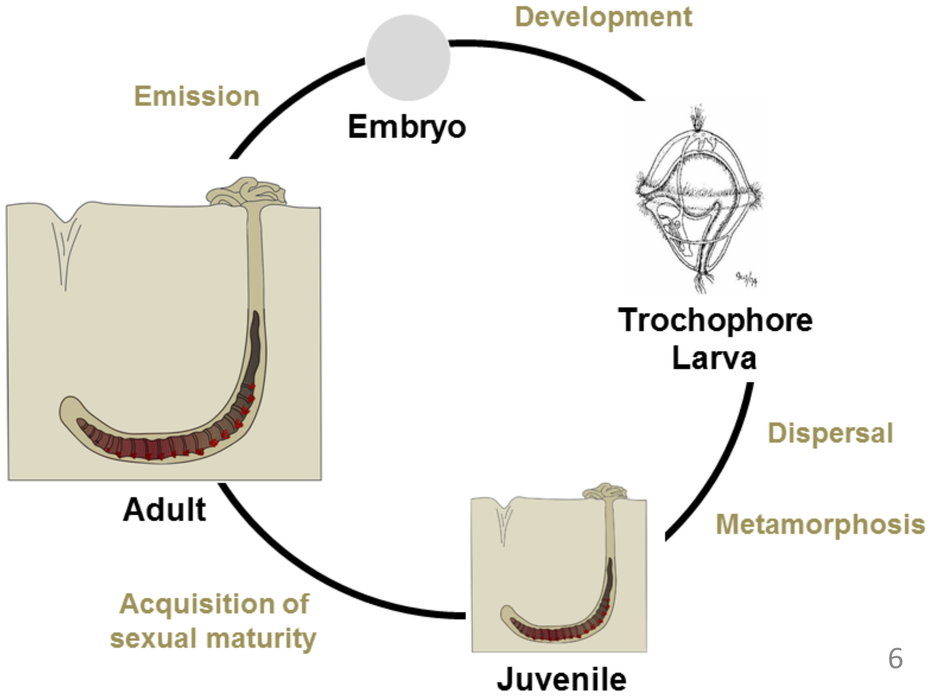
Standard (std-) DEB model

- **3 life stages: embryo, juvenile, adult**
- **isomorphism for all life stages**

Introduction

➢ A Dynamic Energy Budget adapted to *A. marina*'s life-cycle features ?

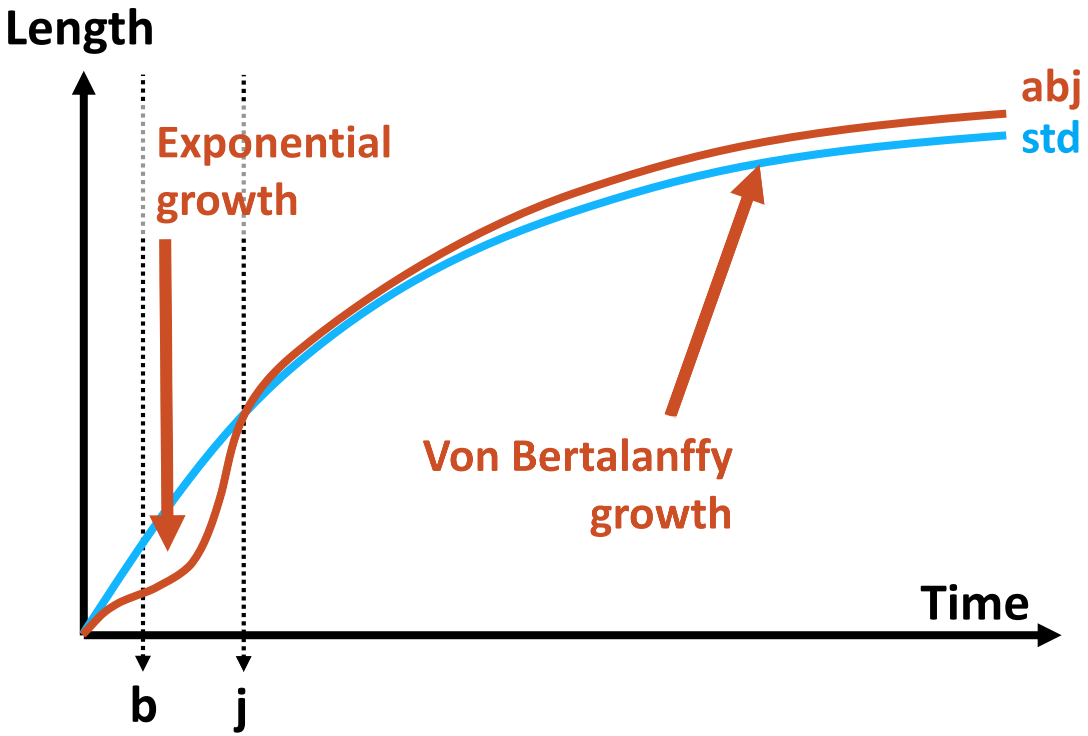
Standard (std-) DEB model	abj-DEB model
➢ 3 life stages: embryo, juvenile, adult ➢ isomorphism for all life stages	➢ acceleration between birth and metamorphosis (V1-morph) ➢ before and after acceleration: isomorphy

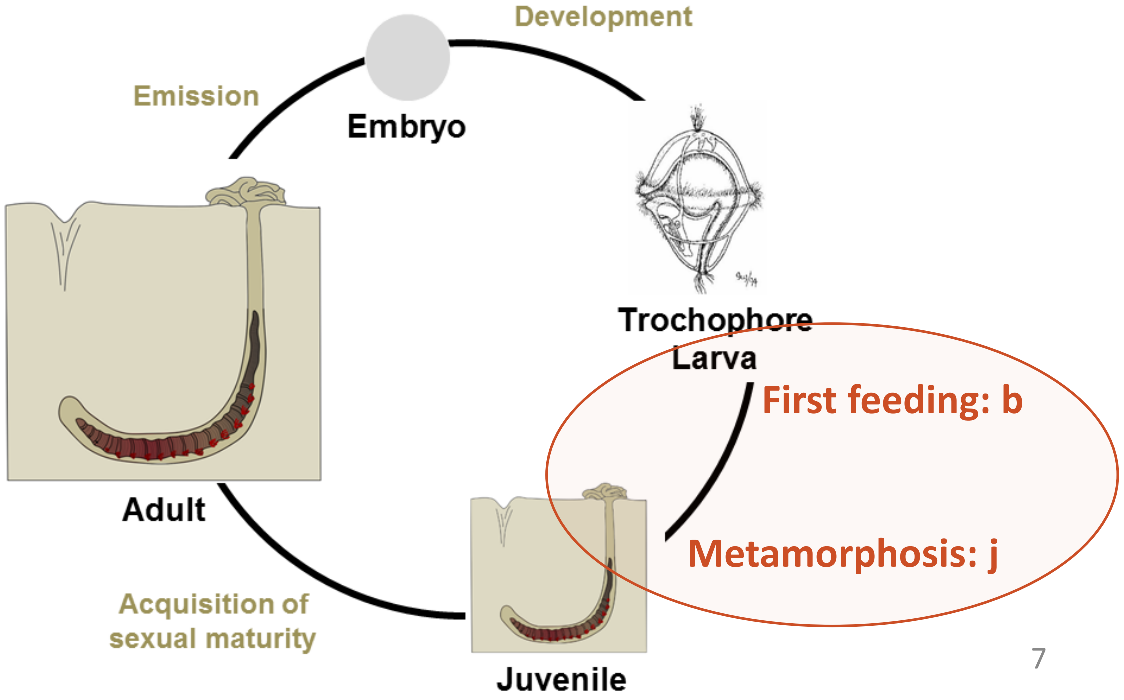


Introduction

➢ A Dynamic Energy Budget adapted to *A. marina*'s life-cycle features ?

Standard (std-) DEB model	abj-DEB model
➢ 3 life stages: embryo, juvenile, adult ➢ isomorphism for all life stages	➢ acceleration between birth and metamorphosis (V1-morph) ➢ before and after acceleration: isomorphy

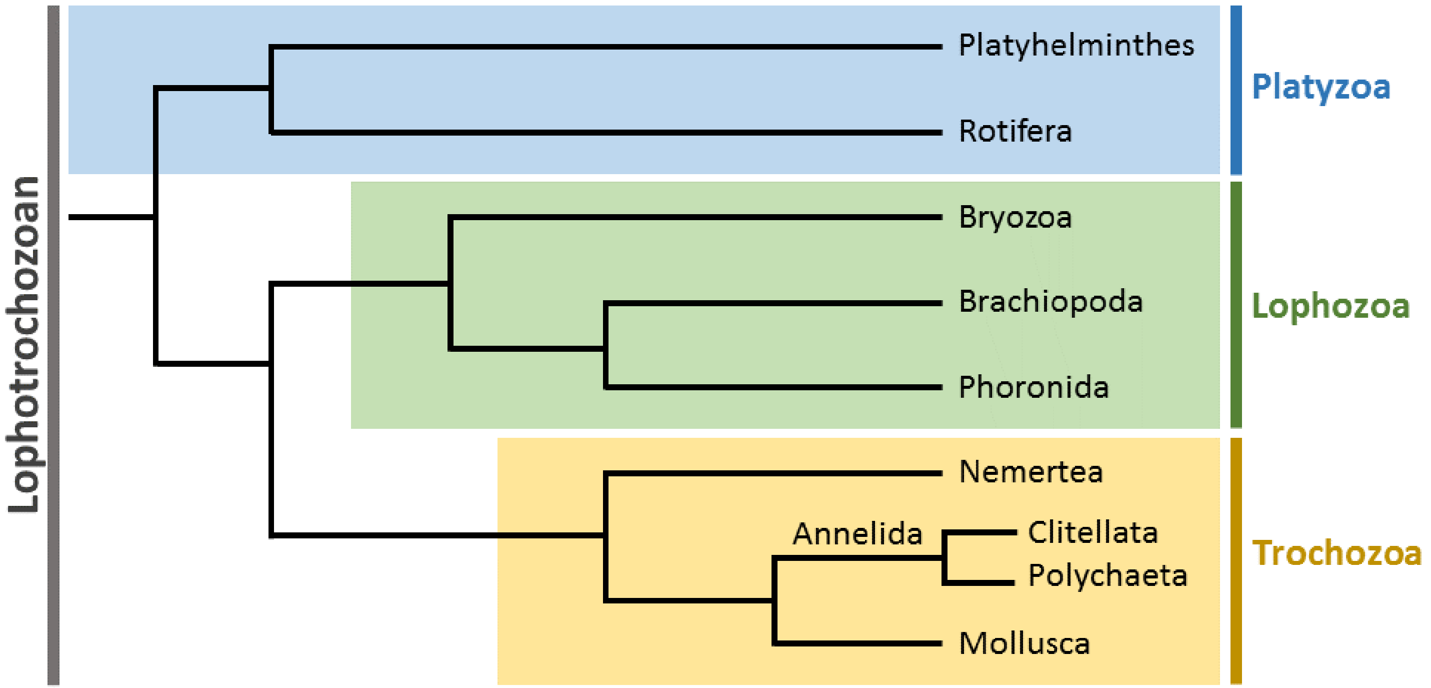




Introduction

➢ A Dynamic Energy Budget adapted to *A. marina*'s life-cycle features ?

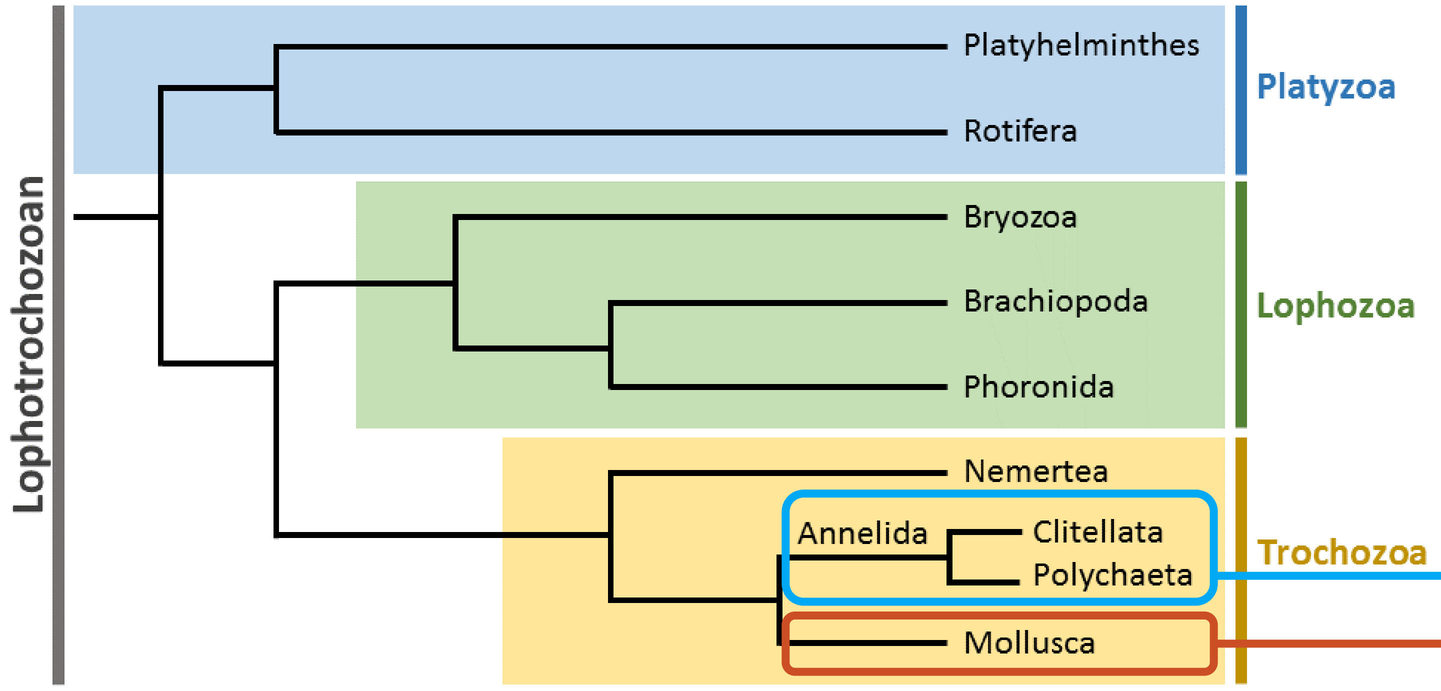
Standard (std-) DEB model	abj-DEB model
➢ 3 life stages: embryo, juvenile, adult ➢ isomorphism for all life stages	➢ acceleration between birth and metamorphosis (V1-morph) ➢ before and after acceleration: isomorphy



Introduction

➢ A Dynamic Energy Budget adapted to *A. marina*'s life-cycle features ?

Standard (std-) DEB model	abj-DEB model
➢ 3 life stages: embryo, juvenile, adult ➢ isomorphism for all life stages	➢ acceleration between birth and metamorphosis (V1-morph) ➢ before and after acceleration: isomorphy



In add-my-pet collection:

11 Annelida entries (std-model)

over 80 Mollusca entries (abj-model)

Objectives

(1) to calibrate a DEB model for *Arenicola marina* adapted to its life cycle features

(2) to make predictions about the chronology of the early life stages of *A. marina* and its growth potential according to *in situ* environmental conditions

(3) to compare the parameters with the other Lophotrochozoan species' parameters and discuss the advantages of the use of an abj-model for polychaetes

Material and Methods

Type of data	Data	abj
Zero-variate	Age at trochophore	X
	Age at birth	**X**
	Age at metamorphosis	**X**
	Age at puberty	X
	Lifespan	X
	Egg diameter	X
	Total length (L) of the trochophore larva	**X**
	Total length at birth	**X**
	Total length at metamorphosis	**X**
	Trunk length (TL) at puberty	X
	Total maximum length	X
	Wet weight (Ww) of an egg	X
Uni-variate	L-Ww	X
	TL-Ww	X
	TL-Wd	**X**
	t-TL	**X**
	T-Ww	X
	Ww-O_2	X
	TL-R	X

Dataset used for the parameter estimation

- **Data anterior to 1990 collected in the literature**

Material and Methods

Type of data	Data	abj
Zero-variate	**Age at trochophore**	**X**
	Age at birth	X
	Age at metamorphosis	X
	Age at puberty	**X**
	Lifespan	**X**
	Egg diameter	X
	Total length (L) of the trochophore larva	X
	Total length at birth	X
	Total length at metamorphosis	X
	Trunk length (TL) at puberty	**X**
	Total maximum length	**X**
	Wet weight (Ww) of an egg	X
Uni-variate	L-Ww	X
	TL-Ww	X
	TL-Wd	X
	t-TL	X
	T-Ww	**X**
	Ww-O_2	X
	TL-R	X

Dataset used for the parameter estimation

- **Data anterior to 1990 collected in the literature**
- **Data communicated by the authors or collected from literature published after 1990**

Material and Methods

Type of data	Data	abj
Zero-variate	Age at trochophore	X
	Age at birth	X
	Age at metamorphosis	X
	Age at puberty	X
	Lifespan	X
	Egg diameter	**X**
	Total length (L) of the trochophore larva	X
	Total length at birth	X
	Total length at metamorphosis	X
	Trunk length (TL) at puberty	X
	Total maximum length	X
	Wet weight (Ww) of an egg	**X**
Uni-variate	**L-Ww**	**X**
	TL-Ww	**X**
	TL-Wd	X
	t-TL	X
	T-Ww	X
	Ww-O_2	**X**
	TL-R	**X**

Dataset used for the parameter estimation

- **Data anterior to 1990 collected in the literature**
- **Data communicated by the authors or collected from literature published after 1990**
- **Data obtained in the laboratory or from field data and biometrics**
  - Oxygen consumption measurements at 3 temperatures

Material and Methods

Type of data	Data	abj
Zero-variate	Age at trochophore	X
	Age at birth	X
	Age at metamorphosis	X
	Age at puberty	X
	Lifespan	X
	Egg diameter	**X**
	Total length (L) of the trochophore larva	X
	Total length at birth	X
	Total length at metamorphosis	X
	Trunk length (TL) at puberty	X
	Total maximum length	X
	Wet weight (Ww) of an egg	**X**
Uni-variate	**L-Ww**	**X**
	TL-Ww	**X**
	TL-Wd	X
	t-TL	X
	T-Ww	X
	Ww-O_2	**X**
	TL-R	**X**

Dataset used for the parameter estimation

- **Data anterior to 1990 collected in the literature**
- **Data communicated by the authors or collected from literature published after 1990**
- **Data obtained in the laboratory or from field data and biometrics**
    - Oxygen consumption measurements at 3 temperatures
    - Collection of females during spawning period (between 2016 and 2018) and biometric measurements

Material and Methods

Type of data	Data	abj
Zero-variate	Age at trochophore	X
	Age at birth	X
	Age at metamorphosis	X
	Age at puberty	X
	Lifespan	X
	Egg diameter	**X**
	Total length (L) of the trochophore larva	X
	Total length at birth	X
	Total length at metamorphosis	X
	Trunk length (TL) at puberty	X
	Total maximum length	X
	Wet weight (Ww) of an egg	**X**
Uni-variate	**L-Ww**	**X**
	TL-Ww	**X**
	TL-Wd	X
	t-TL	X
	T-Ww	X
	Ww-O_2	**X**
	TL-R	**X**

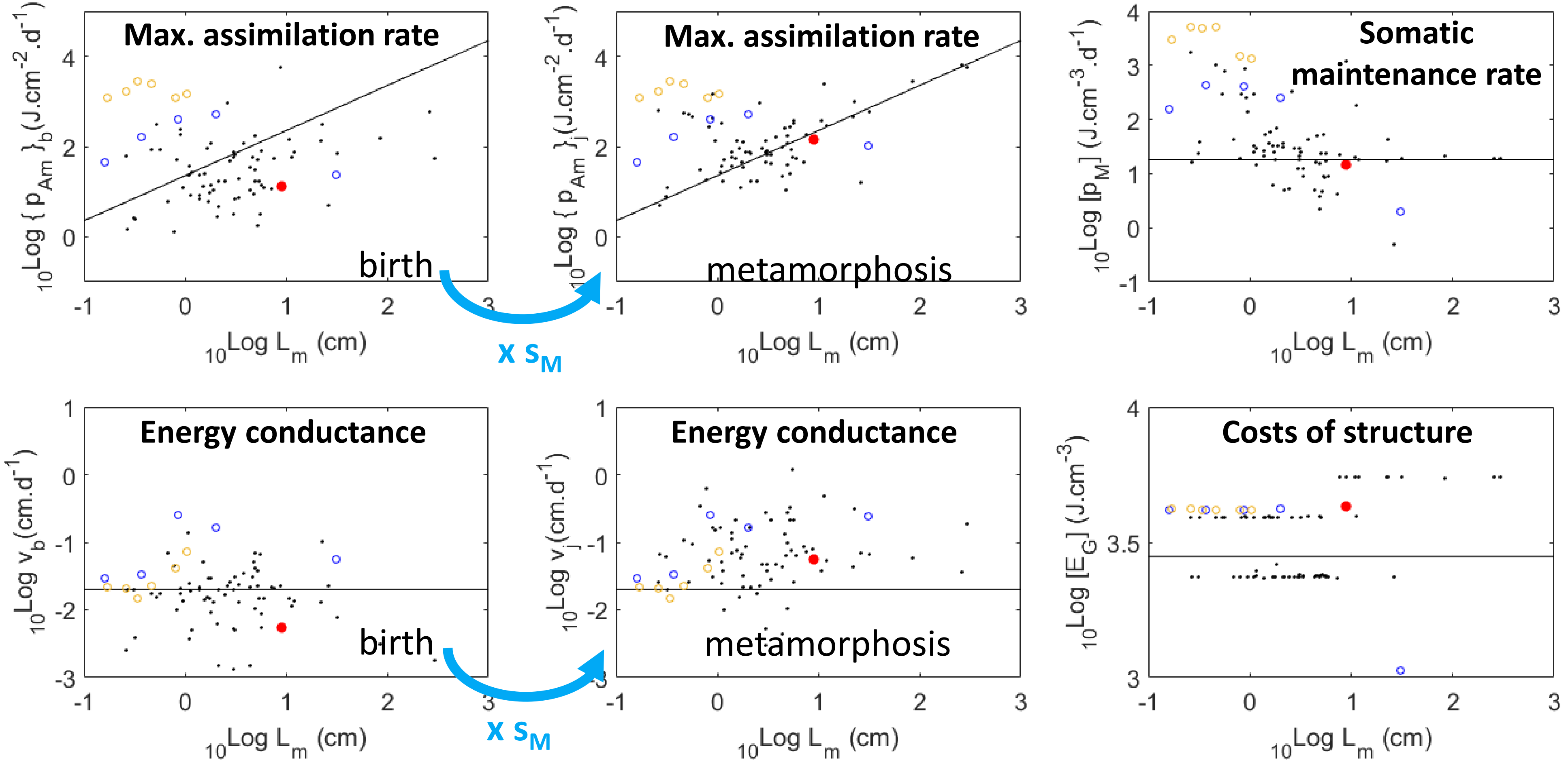
Dataset used for the parameter estimation

- **Data anterior to 1990 collected in the literature**
- **Data communicated by the authors or collected from literature published after 1990**
- **Data obtained in the laboratory or from field data and biometrics**
  - Oxygen consumption measurements at 3 temperatures
  - Collection of females during spawning period (between 2016 and 2018) and biometric measurements
  - Biometric measurements on lugworms collected in July 2017

Results

➢ Parameter estimation

- ➢ Good fit : MRE 0.22 /SMSE 0.24
- ➢ Acceleration rate s_M ~ 10

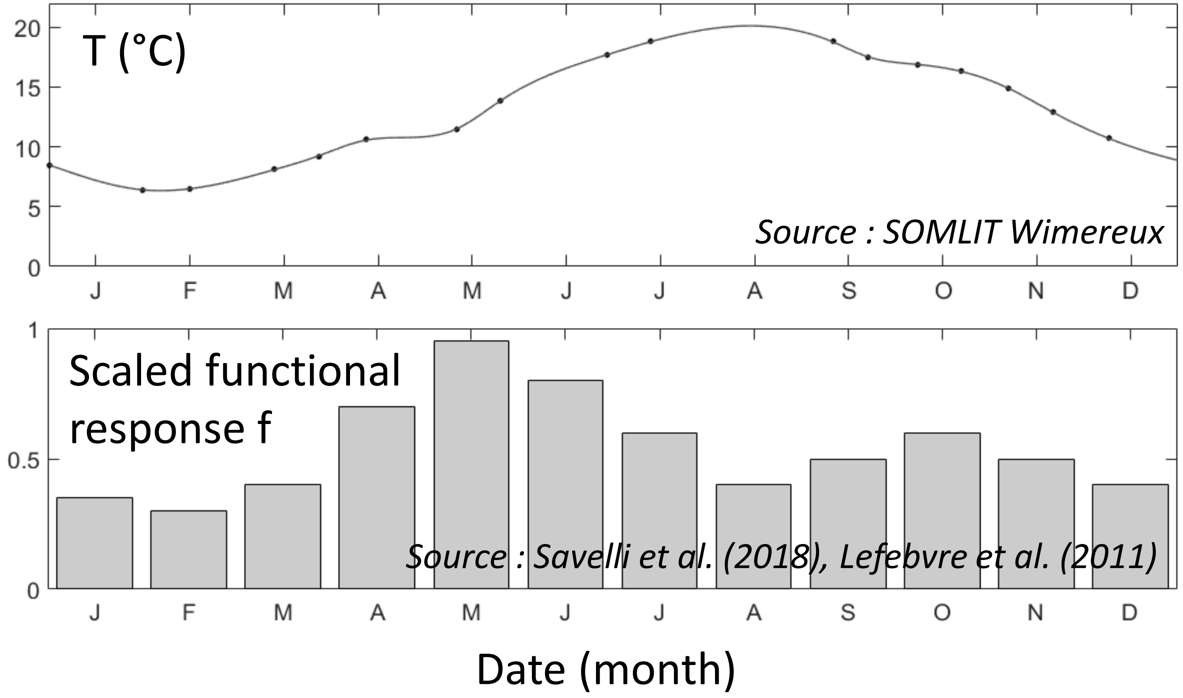


→ Parameters generally closer to the mollusks' values

Results

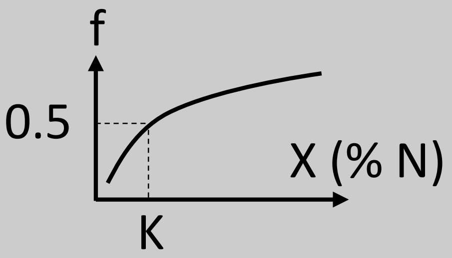
➢ Predicted *in situ* chronology of the first life stages

In situ environmental conditions



$$f = \frac{X}{X + K}$$

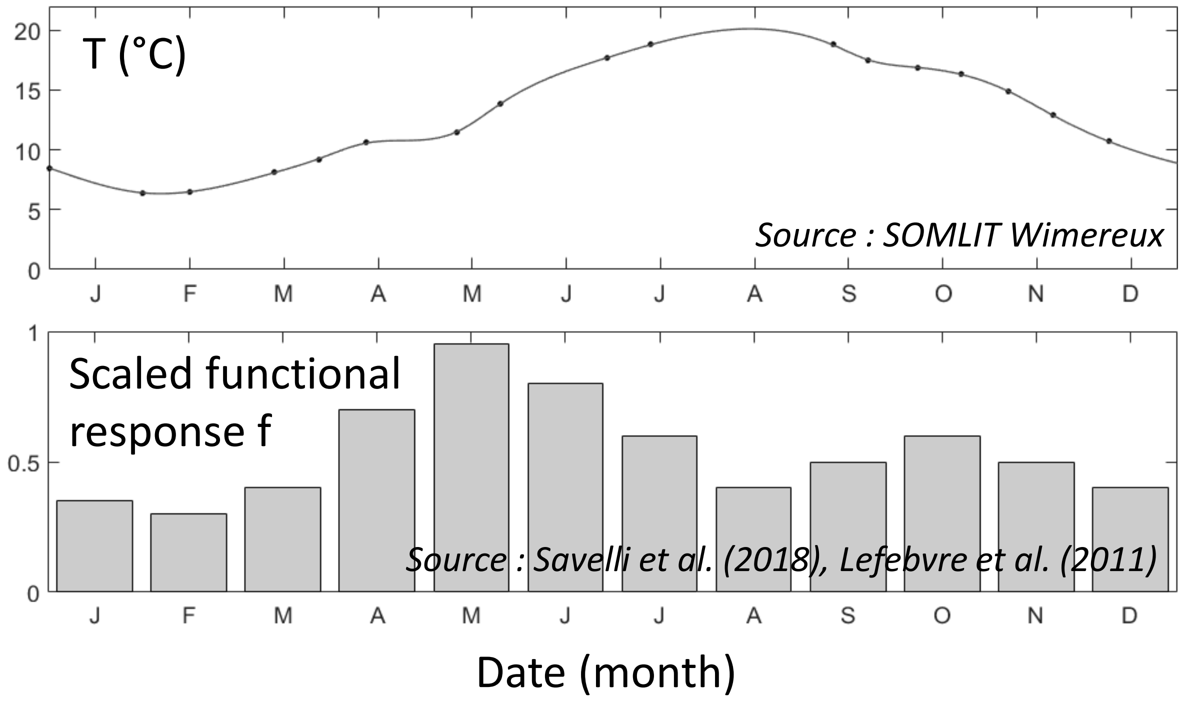
- X → Food
- K → Half saturation coefficient

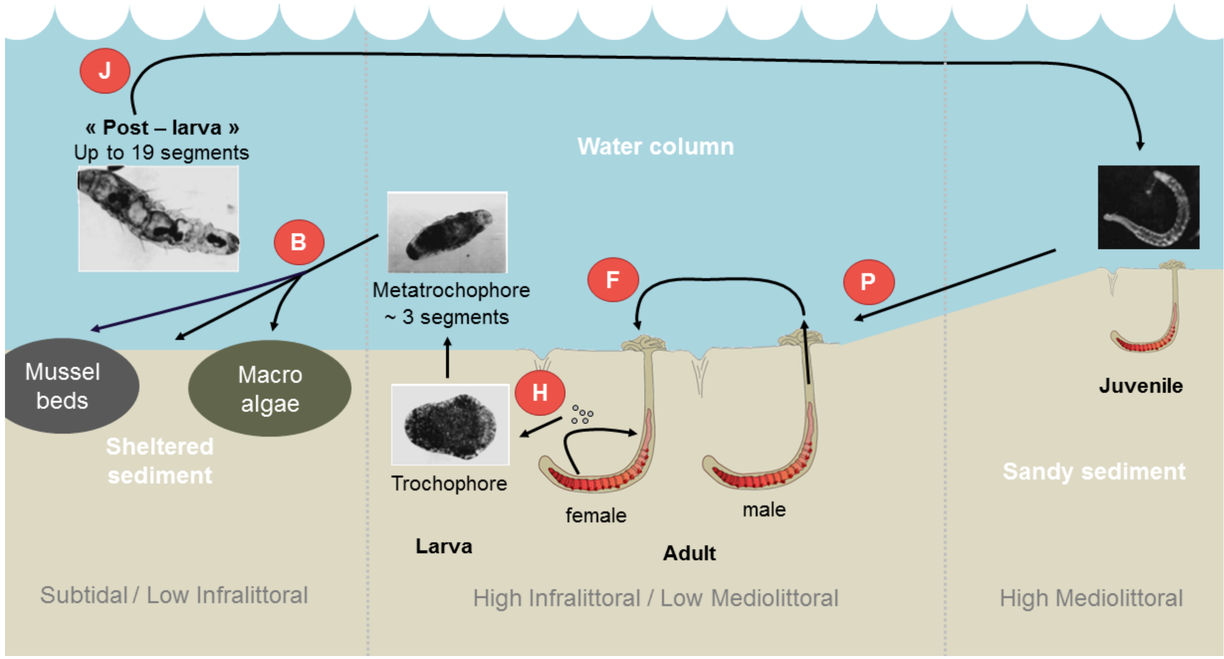


Results

➢ Predicted *in situ* chronology of the first life stages

In situ environmental conditions

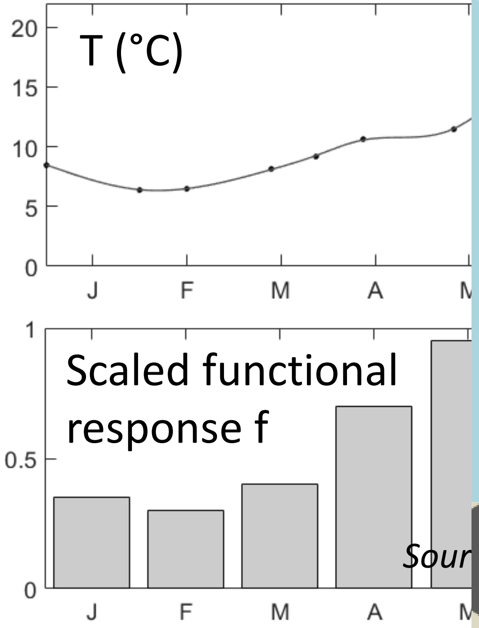


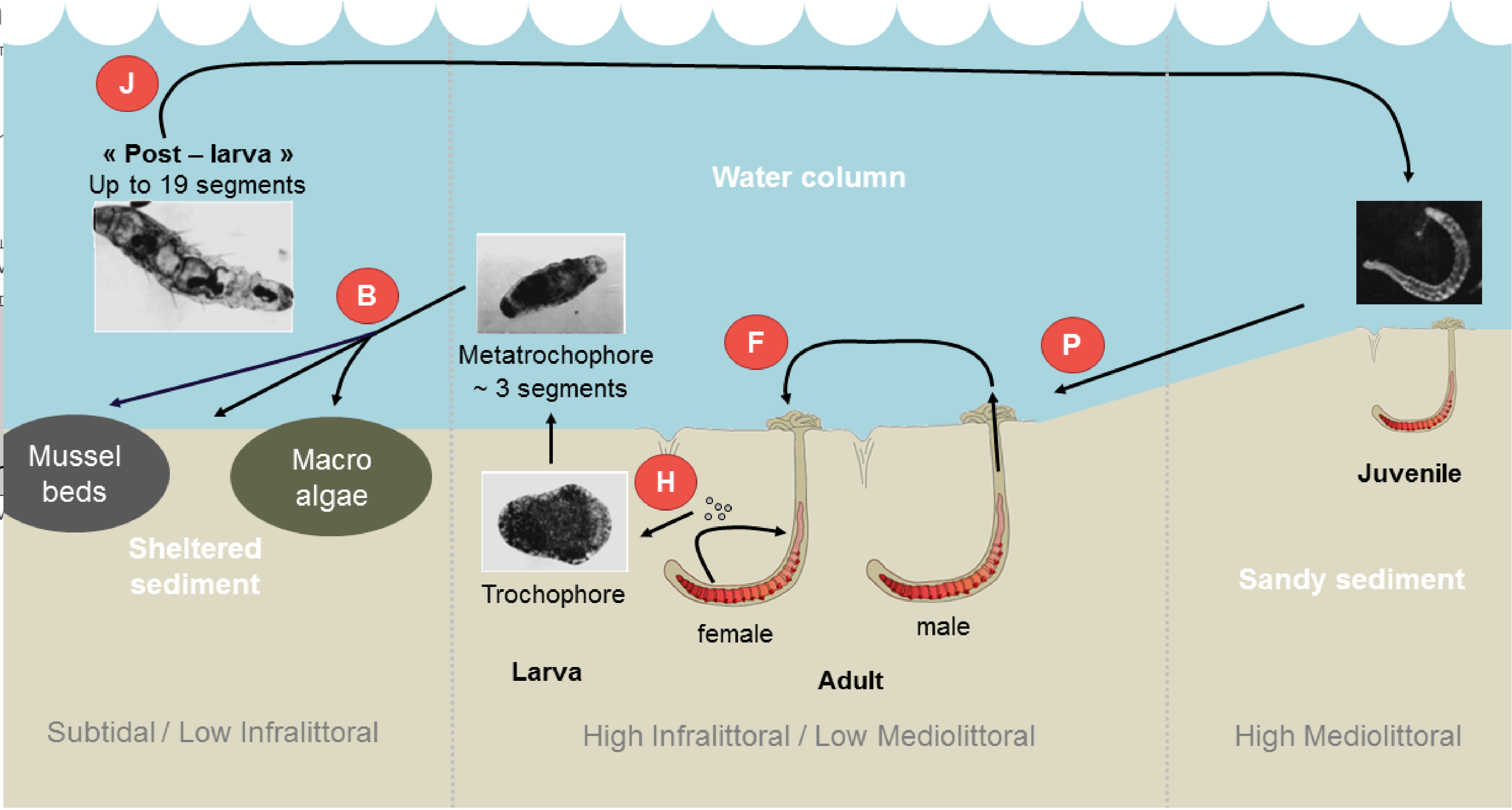


Results

➢ Predicted *in situ* chronology of the first life stages

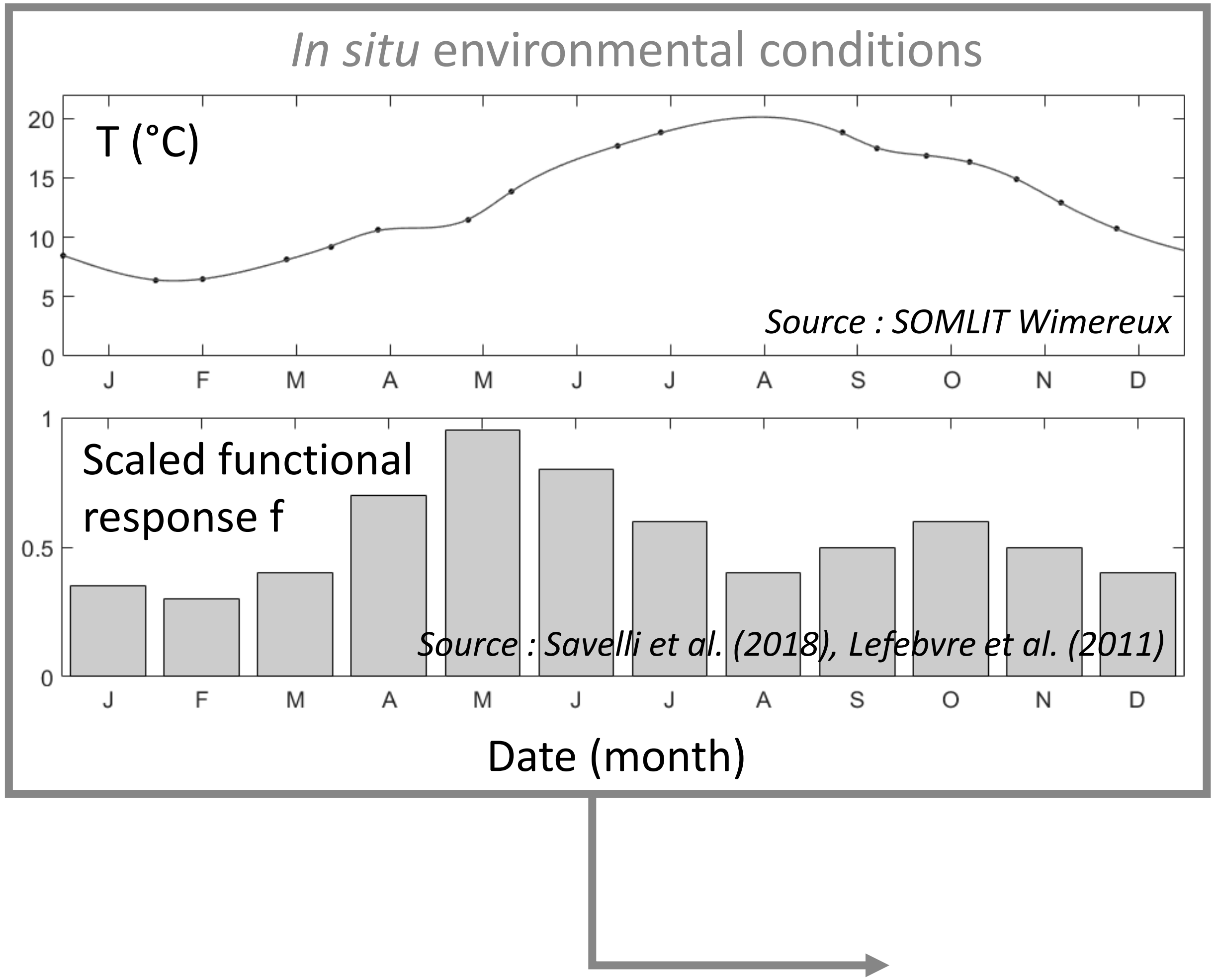
In situ en

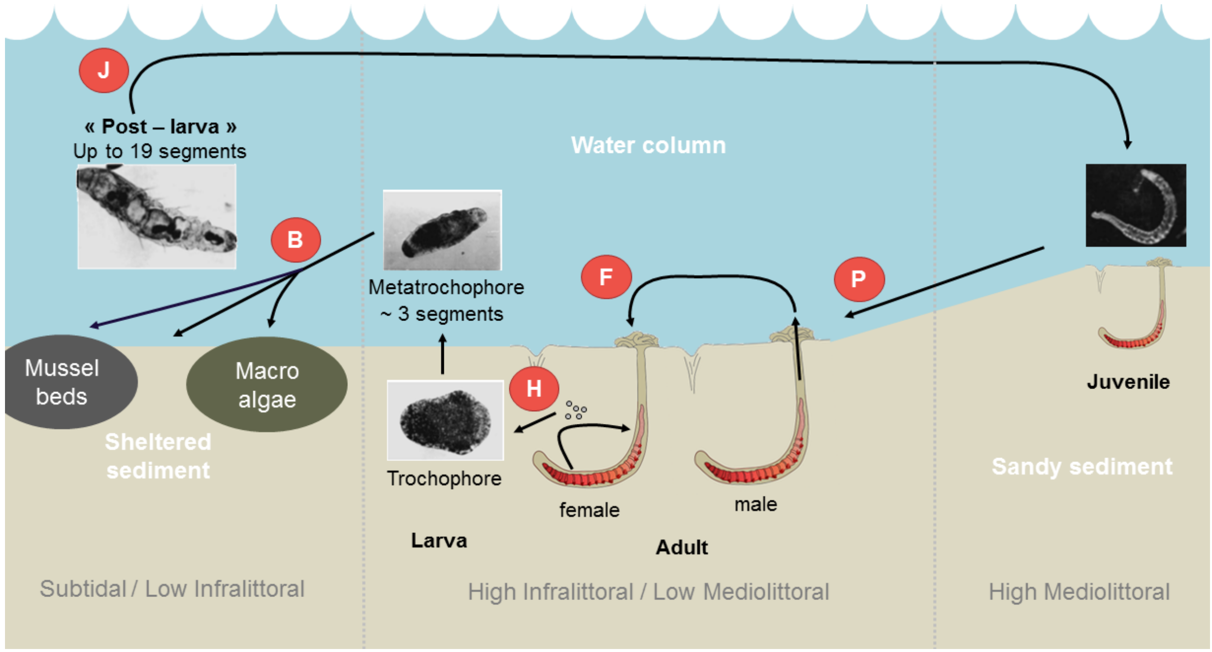




Results

➢ Predicted *in situ* chronology of the first life stages





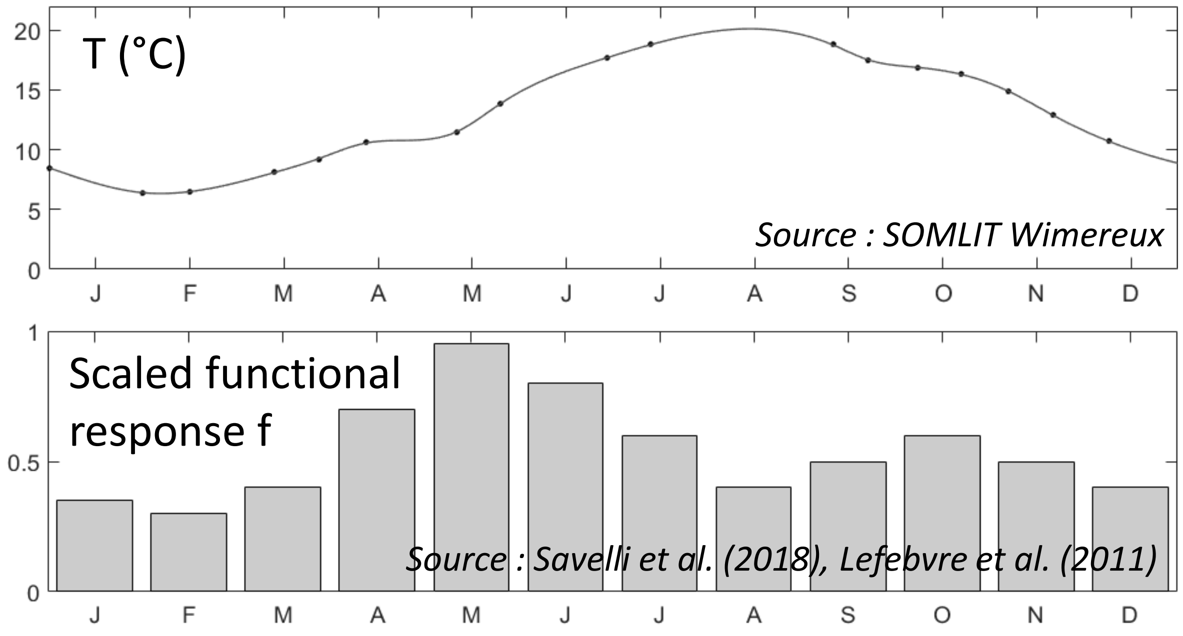
Life-cycle predictions of the abj-DEB model

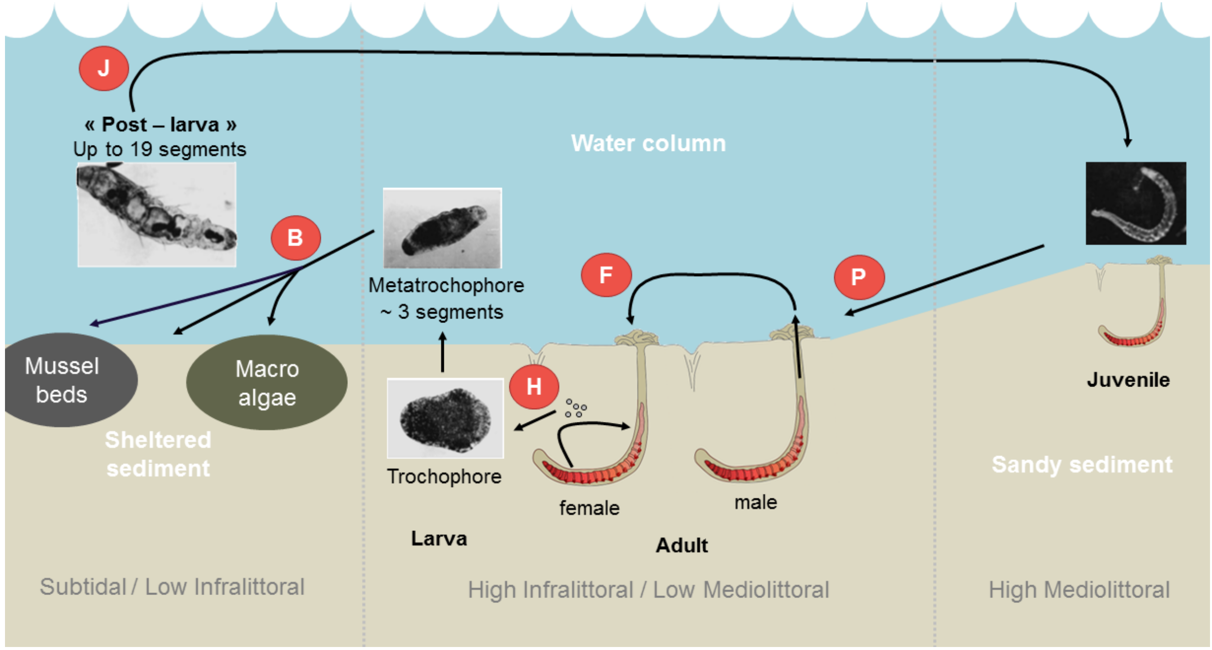
H	0.022 (cm)	5.8 (d)

Results

➢ Predicted *in situ* chronology of the first life stages

In situ environmental conditions



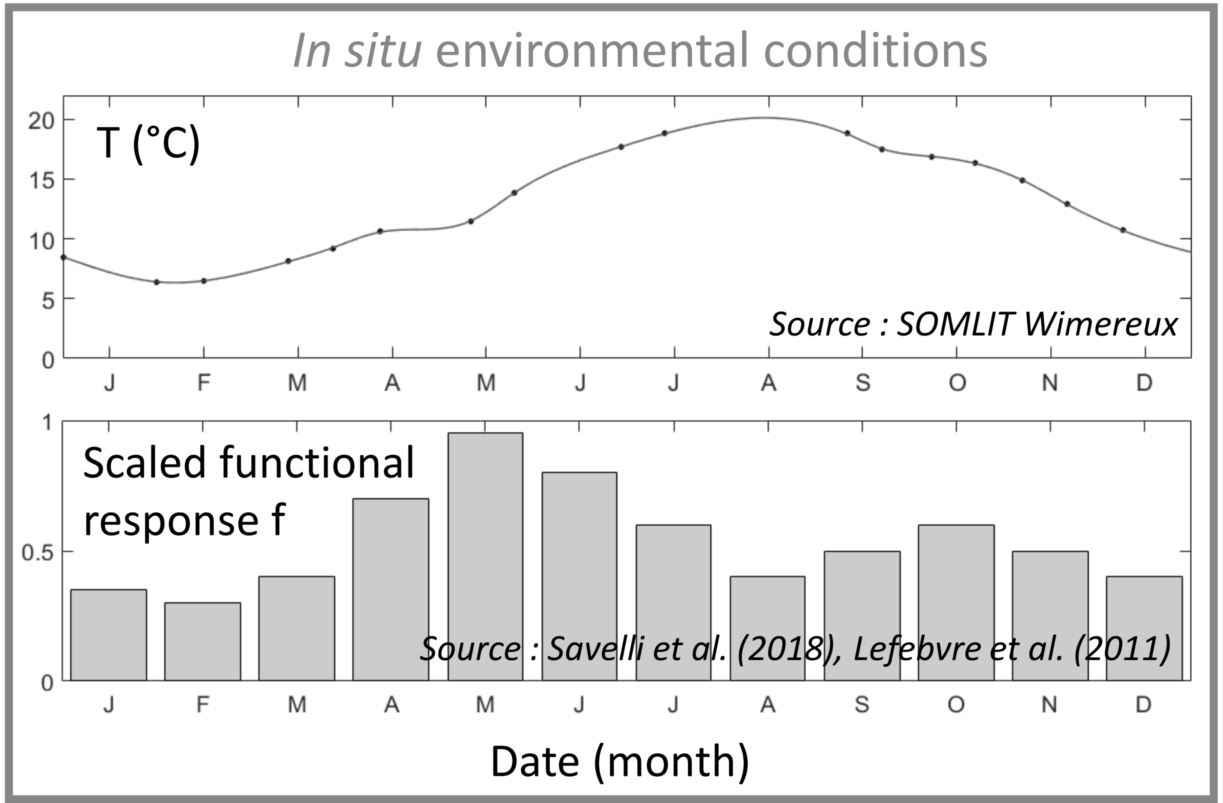


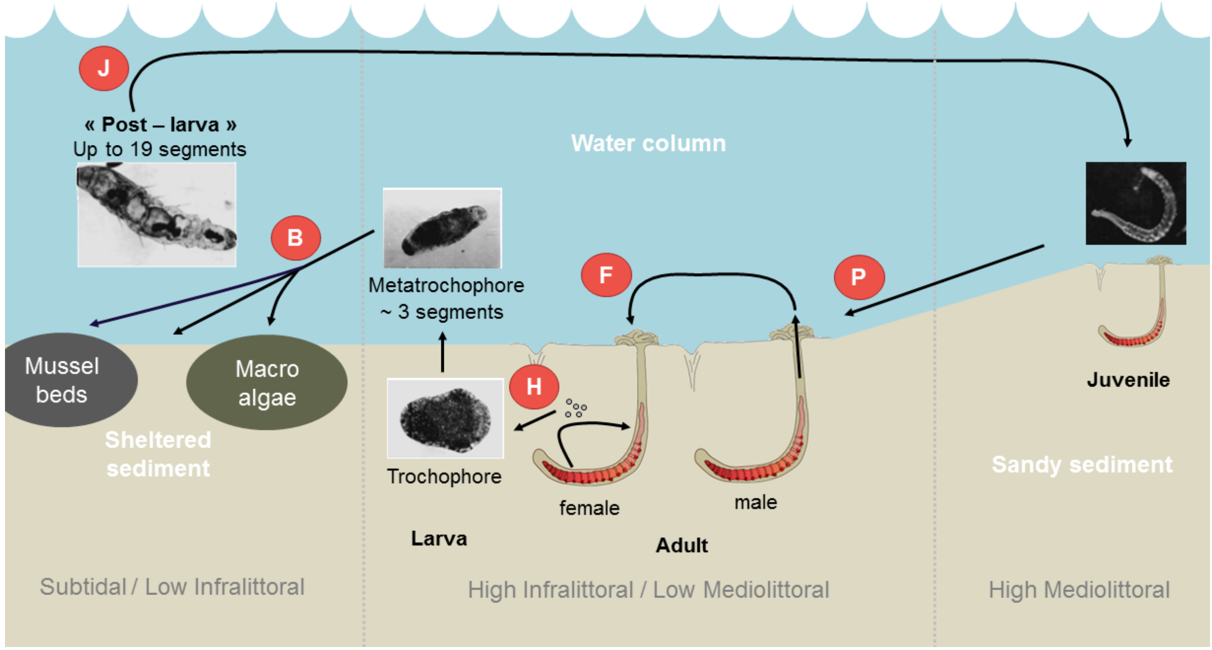
Life-cycle predictions of the abj-DEB model

H	0.022 (cm)	5.8 (d)
B	0.037	13.5

Results

➢ Predicted *in situ* chronology of the first life stages



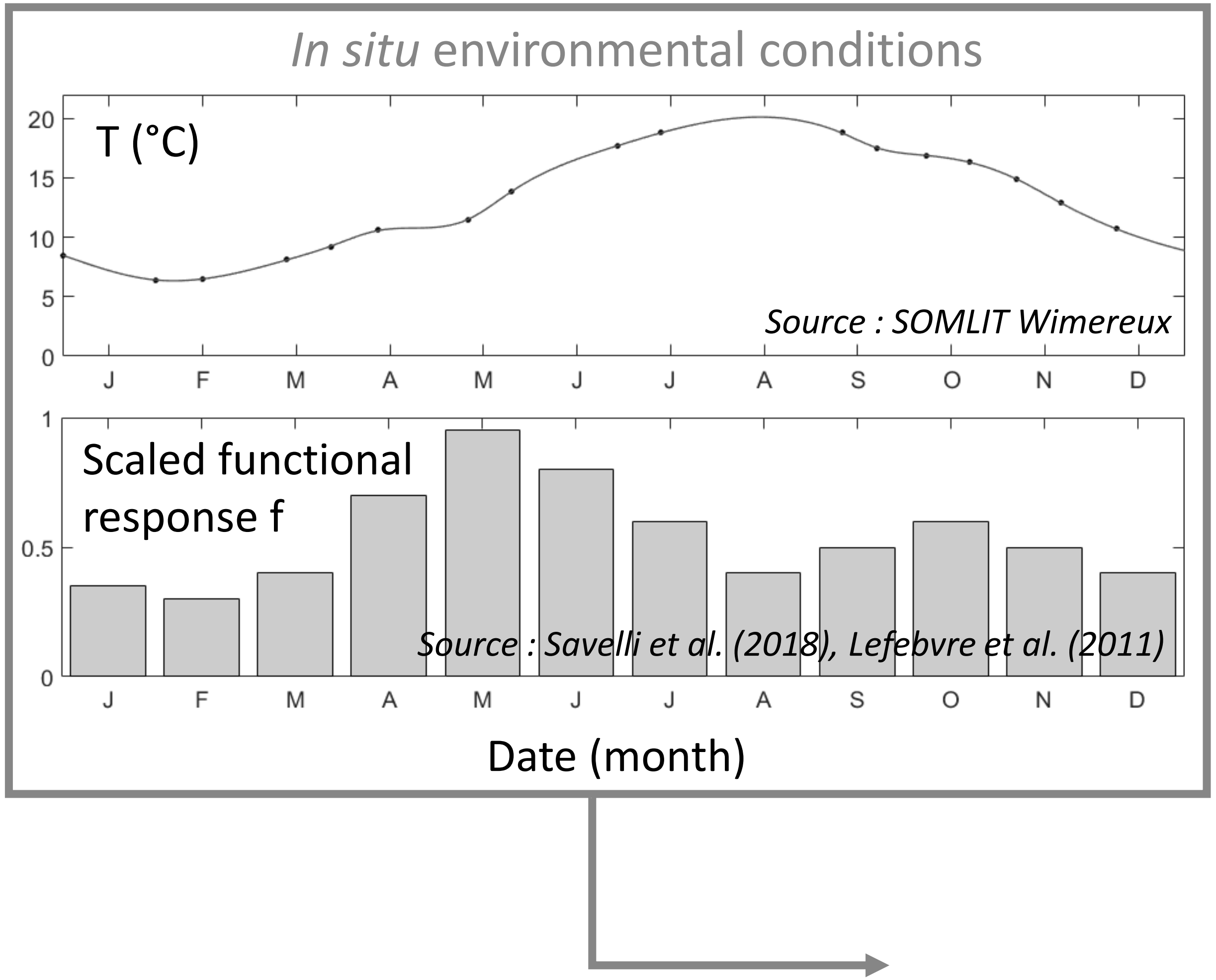


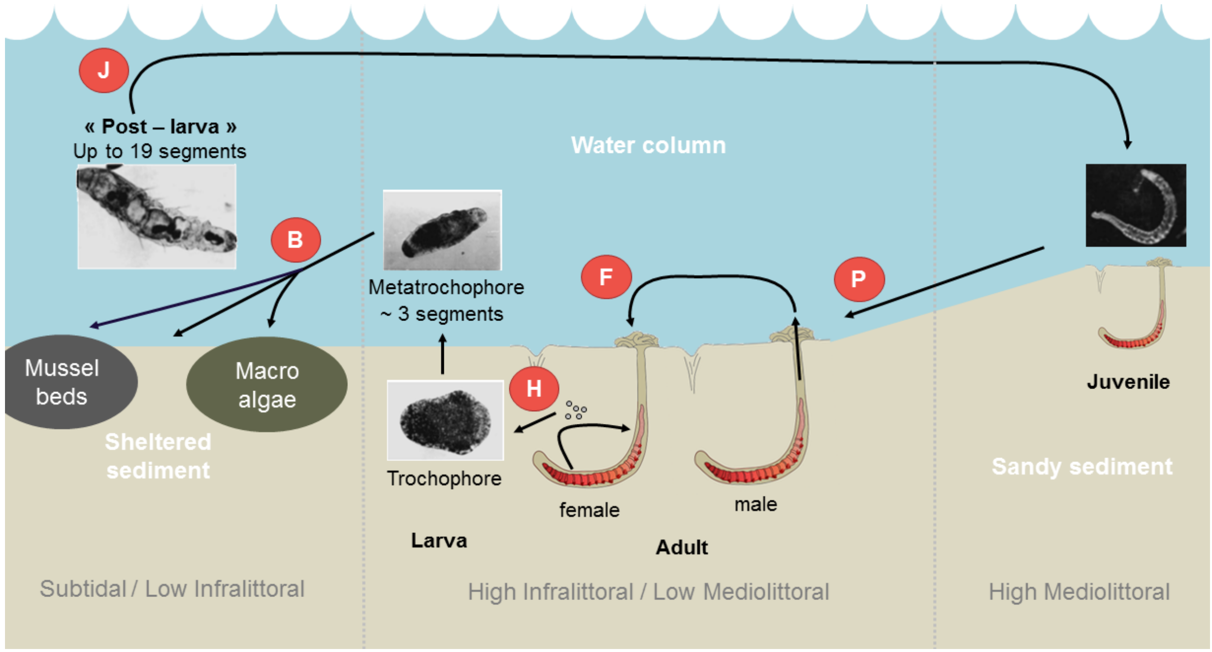
Life-cycle predictions of the abj-DEB model

H	0.022 (cm)	5.8 (d)
B	0.037	13.5
J	0.98	148.4

Results

Predicted *in situ* chronology of the first life stages





Life-cycle predictions of the abj-DEB model

H	0.022 (cm)	5.8 (d)
B	0.037	13.5
J	0.98	148.4
P	3.79	489.7

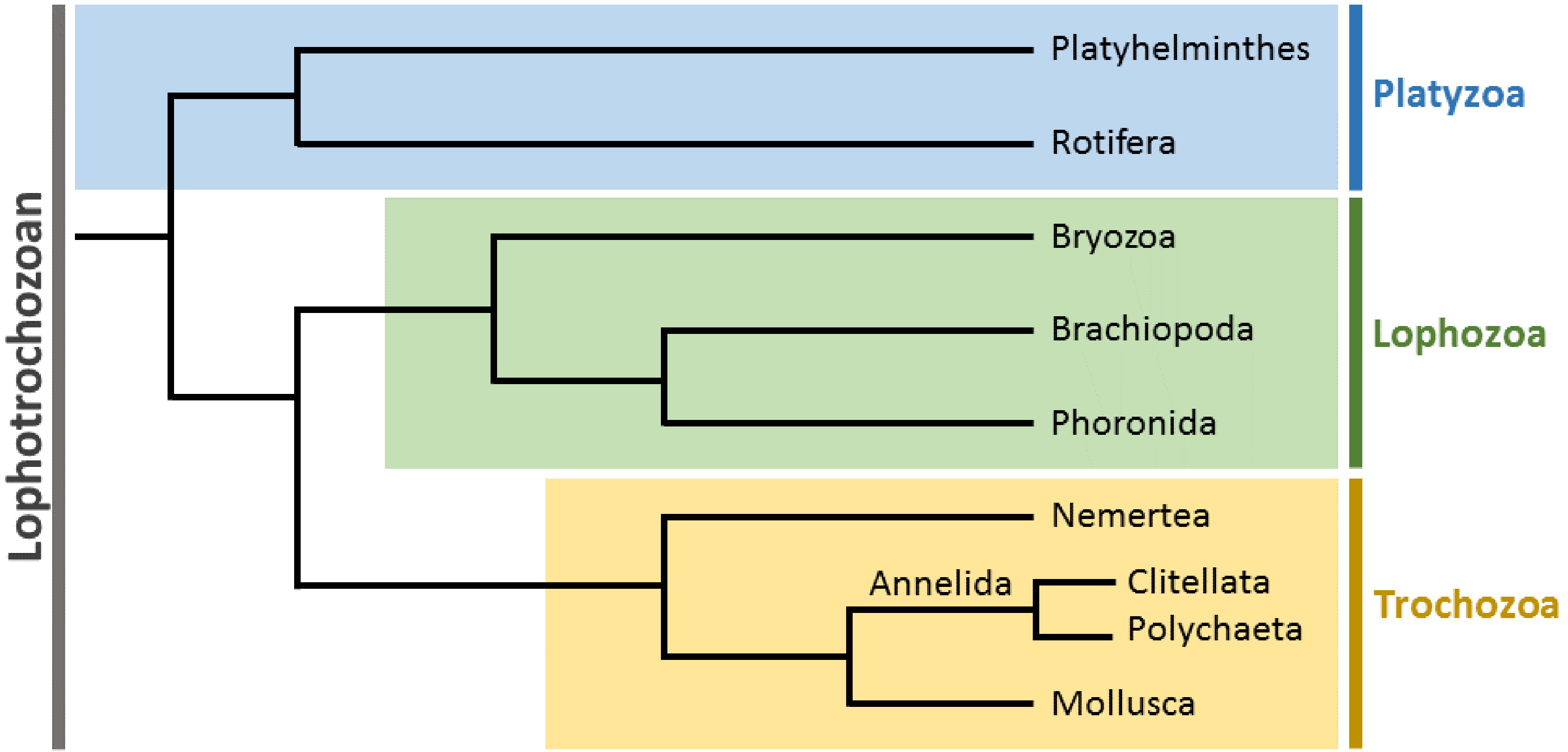
Conclusions

- **Try to use abj models for polychaetes !**

Conclusions

- **Try to use abj models for polychaete species !**

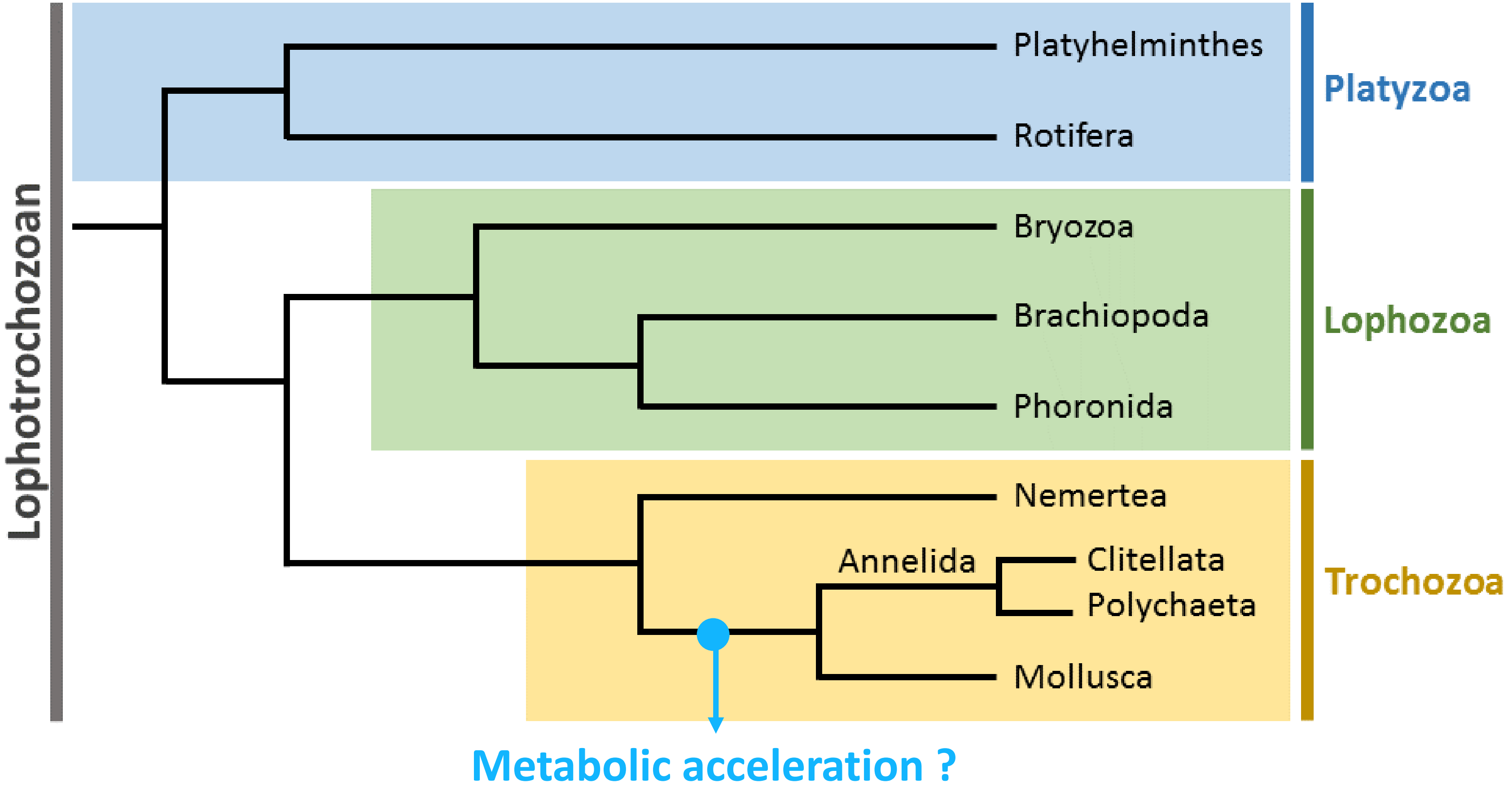
- **Phylogenetic prospect**



Conclusions

- **Try to use abj models for polychaete species !**

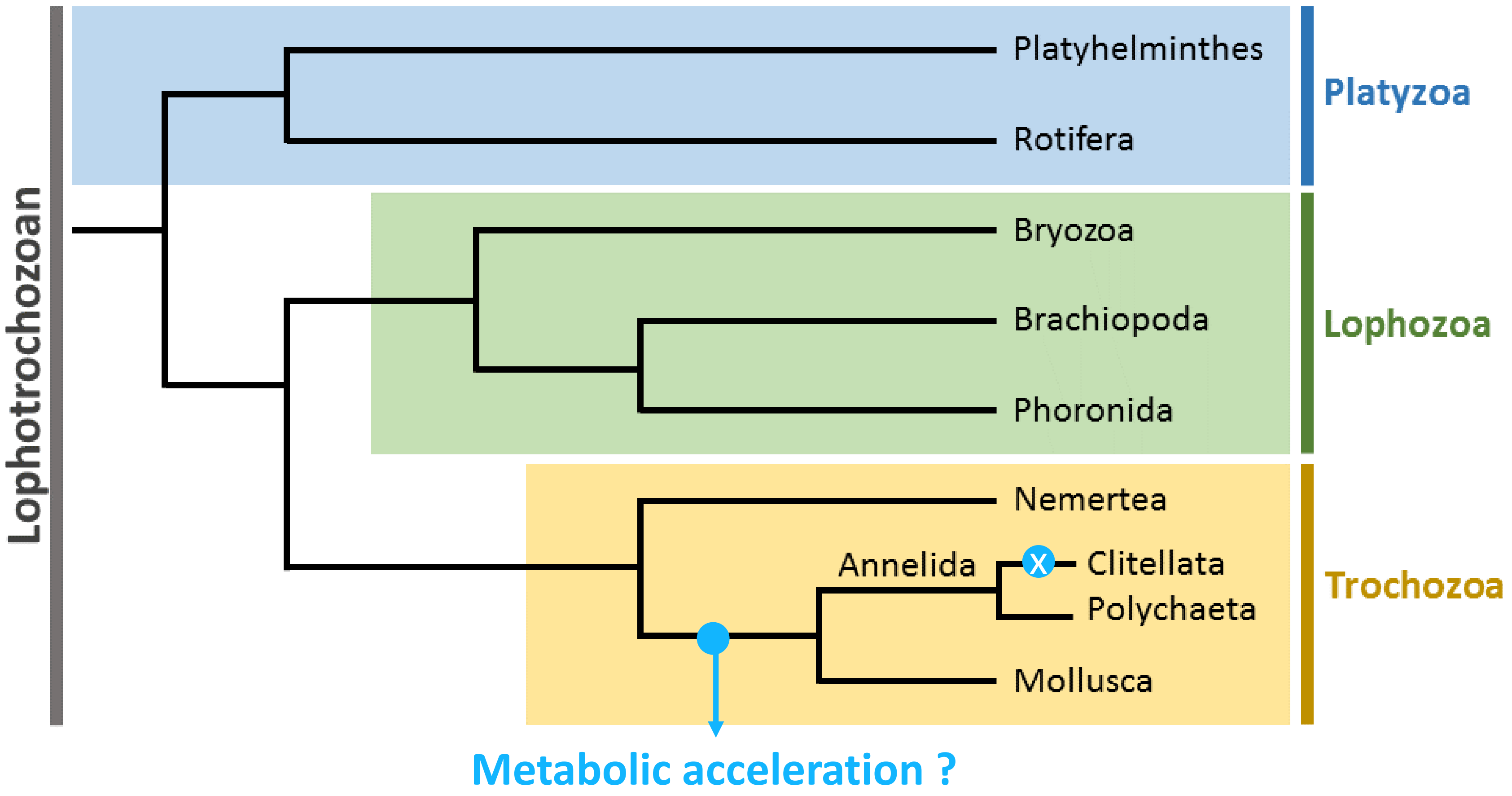
- **Phylogenetic prospect**



Conclusions

- **Try to use abj models for polychaetes !**

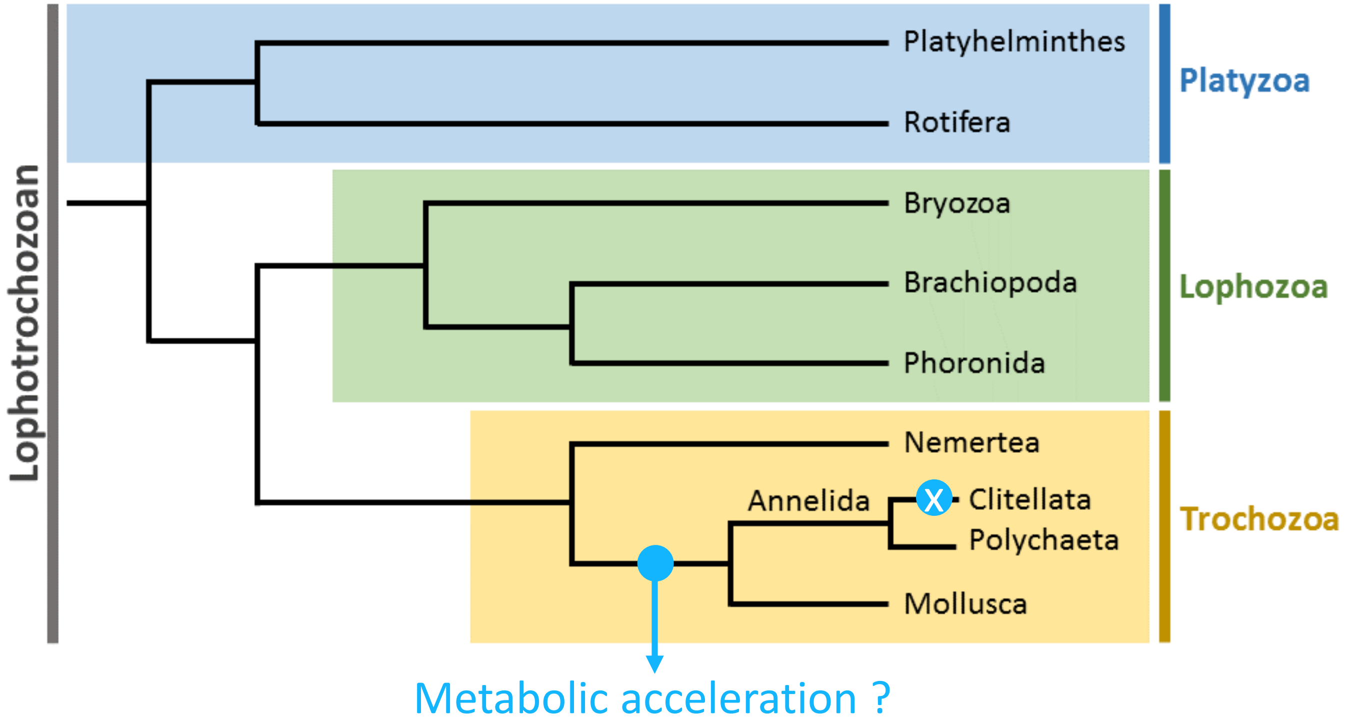
- **Phylogenetic prospect**



Conclusions

- **Try to use abj models for polychaete species !**

- **Phylogenetic prospect**



- **First step towards population modeling and population connectivity studies for management purposes**

References

Beukema, J.J., De Vlas, J., 1979. Population parameters of the lugworm *Arenicola marina* living on tidal flats in the Dutch Wadden Sea. Netherlands J. Sea Res. 13, 331–353. https://doi.org/10.1016/0077-7579(79)90010-3

De Cubber, L., Lefebvre, S., Fisseau, C., Cornille, V., Gaudron, S.M., 2018. Linking life-history traits, spatial distribution and abundance of two species of lugworms to bait collection: A case study for sustainable management plan. Mar. Environ. Res. 140. https://doi.org/10.1016/j.marenvres.2018.07.009

De Wilde, P.A.W.J., Berghuis, E.M., 1979. Laboratory experiments on growth of juvenile lugworms, *Arenicola marina*. Netherlands J. Sea Res. 13, 487–502. https://doi.org/10.1016/0077-7579(79)90020-6

Farke, H., Berghuis, E.M., 1979a. Spawning, larval development and migration behaviour of *Arenicola marina* in the laboratory. Netherlands J. Sea Res. 13, 512–528.

Farke, H., Berghuis, E.M., 1979b. Spawning, larval development and migration of *Arenicola marina* under field conditions in the western Wadden sea. Netherlands J. Sea Res. 13, 529–535.

Kooijman, S.A.L.M., 2010. Dynamic energy budget theory for metabolic organisation. Cambridge University Press.

Kooijman, S.A.L.M., 2014. Metabolic acceleration in animal ontogeny: An evolutionary perspective. J. Sea Res. 94, 128–137. https://doi.org/10.1016/j.seares.2014.06.005

Lefebvre, A., Guiselin, N., Barbet, F., Artigas, F.L., 2011. Long-term hydrological and phytoplankton monitoring (1992 – 2007) of three potentially eutrophic systems in the eastern English Channel and the Southern Bight of the North Sea. ICES J. Mar. Sci. 68, 2029–2043.

Marques, G.M., Augustine, S., Lika, K., Pecquerie, L., Domingos, T., Kooijman, S.A.L.M., 2018. The AmP project: Comparing species on the basis of dynamic energy budget parameters. PLoS Comput. Biol. 14, 1–23. https://doi.org/10.1371/journal.pcbi.1006100

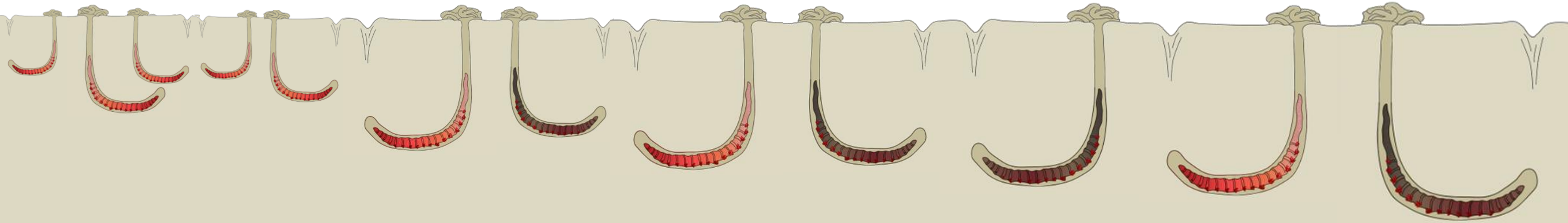
Olive, P.J.W., Craig, S., Cowin, P.B.D., 2006. Aquaculture of marine worms. US 7,004,109 B2.

Reise, K., 1985. Tidal flat ecology - An experimental approach to species interactions, Ecological Studies.

Reise, K., Simon, M., Herre, E., 2001. Density-dependent recruitment after winter disturbance on tidal flats by the lugworm *Arenicola marina*. Helgol. Mar. Res. 55, 161–165. https://doi.org/10.1007/s101520100076

Savelli, R., Dupuy, C., Barillé, L., Lerouxel, A., Guizien, K., Philippe, A., Bocher, P., Polsenaere, P., Le Fouest, V., 2018. On biotic and abiotic drivers of the microphytobenthos seasonal cycle in a temperate intertidal mudflat: a modelling study. Biogeosciences 15, 7243–7271. https://doi.org/10.5194/bg-15-7243-2018

Thank you !



A special thank to D. Menu and to V. Cornille for their technical support.

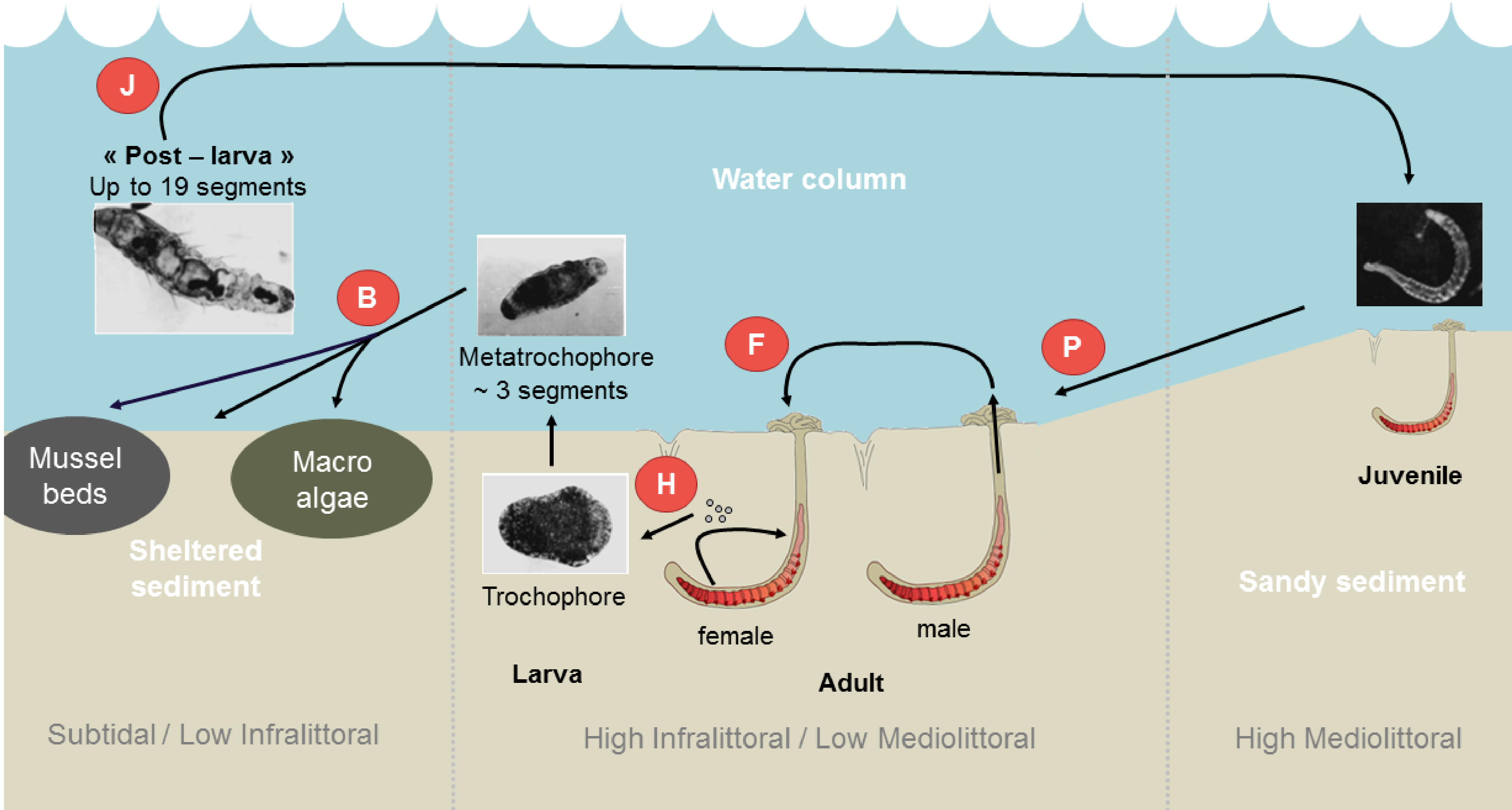
Supplementary Material

- DEB Equations

State variables	Reserve	$\frac{dE}{dt} = \dot{p}_A - \dot{p}_C$
	Structure	$\frac{dV}{dt} = \frac{\dot{p}_G}{[E_G]}$
	Offsprings or Maturity	$\frac{dE_R}{dt} = \kappa_R \cdot \dot{p}_R$ or $\frac{dE_H}{dt} = \dot{p}_H$
Fuxes	Ingestion	$\dot{p}_X = \{\dot{p}_{Xm}\} \cdot f \cdot V^{2/3}$
	Assimilation	$\dot{p}_A = \{\dot{p}_{Am}\} \cdot f \cdot V^{2/3}$
	Mobilisation	$\dot{p}_C = E \cdot \frac{\dot{v} \cdot V^{2/3} \cdot [E_G] + \dot{p}_S}{\kappa \cdot E + [E_G]}$
	Somatic maintenance costs	$\dot{p}_S = [\dot{p}_M] \cdot V$
	Maturity maintenance costs	$\dot{p}_J = \dot{k}_J \cdot E_H$
	Growth	$\dot{p}_G = \kappa \cdot \dot{p}_C - \dot{p}_S$
	Reproduction	$\dot{p}_R = (1 - \kappa) \cdot \dot{p}_C - \dot{p}_J$
	Maturity	$\dot{p}_H = (1 - \kappa) \cdot \dot{p}_C - \dot{p}_J$

Material and Methods

➢ A Dynamic Energy Budget adapted to *A. marina*'s life-cycle features ?



b → j

$$\{\dot{p}_{Am}\}_{btoj} = \{\dot{p}_{Am}\}_b \times \frac{L}{L_b}$$

$$\dot{v}_{btoj} = \dot{v}_b \times \frac{L}{L_b}$$

$$\dot{p}_A = \{\dot{p}_{Am}\} \times f \times V^{2/3}$$

$$\delta_{Me} \geq \delta \geq \delta_M$$

j → p

$$\{\dot{p}_{Am}\}_j = \{\dot{p}_{Am}\}_b \times \dot{s}_M$$

$$\dot{v}_j = \dot{v}_b \times \dot{s}_M$$

$$\delta = \delta_M$$

Adapted from Farke and Berghuis (1979a, 1979b), Reise (1985) and Reise et al. (2001). Pictures of the different life stages of *A. marina* are taken from Farke and Berghuis (1979a)

Supplementary Material

- abj and std-DEB parameters

Parameter	Symbol	Value std-model	Value abj-model	Unit
Reference temperature	T_{ref}	293.15	293.15	K
Searching rate[1]	$\{\dot{F}_m\}$	6.50	6.50	$d^{-1}.cm^{-2}$
fraction of food energy fixed in reserve[1]	κ_X	0.80	0.80	-
Arrhenius temperature	T_A	4927	3590	K
Zoom factor	z	5.66	0.87	-
Energy conductance[2]	$\dot{v}_b$	2.3e^{-02}	5.4e^{-03}	$cm.d^{-1}$
	$\dot{v}_j$	-	5.6e^{-02}	$cm.d^{-1}$
Allocation fraction to soma	K	0.95	0.95	-
Reproduction fraction fixed in eggs[1]	K_R	0.95	0.95	-
Volume specific costs of structure	$[E_G]$	4294	4282	$J.cm^{-3}$
Maturation threshold for the trochophore larva	E_H^h	3.33e^{-04}	1.55e^{-04}	J
Maturation threshold for birth	E_H^b	3.33e^{-04}	6.98e^{-04}	J
Maturation threshold for metamorphosis	E_H^j	-	0.77	J
Maturation threshold for puberty	E_H^p	248.07	300.70	J
Weibull ageing acceleration	$\ddot{h}_a$	4.99e^{-07}	2.11e^{-07}	d^{-2}
Gompertz stress coefficient	s_G	4.26e^{-05}	7.73e^{-05}	-
Acceleration rate	s_M	-	10.29	-
Maximum assimilation rate[2]	$\{\dot{p}_{Am}\}_b$	233.76	13.47	$J.cm^{-2}.d^{-1}$
	$\{\dot{p}_{Am}\}_j$	-	138.61	$J.cm^{-2}.d^{-1}$
Specific somatic maintenance rate	$[\dot{p}_M]$	39.11	14.70	$J.cm^{-3}.d^{-1}$
Maturity maintenance rate	$\dot{k}_J$	2.00e^{-03}	2.00e^{-03}	d^{-1}

[1] The values were taken from the generalized animal (Kooijman, 2010)
[2] $\dot{v}_b = \dot{v}_j$ and $\{\dot{p}_{Am}\}_b = \{\dot{p}_{Am}\}_j$ for std-model and $\dot{v}_j = s_M \cdot \dot{v}_b$ and $\{\dot{p}_{Am}\}_j = s_M \cdot \{\dot{p}_{Am}\}_b$ for the abj-model

Results

Parameter estimation

- Good fit : MRE 0.22 /SMSE 0.24
- Acceleration rate ~ 10
- Zero-variate predictions: globally well fitted, **except for some of the least reliable observations**
- Uni-variate predictions globally well fitted to the observations

Data	Symbol (unit)	Observation	Prediction (RE)	Reference
Age at hatching	a_h (d)	7 (10°C)	7.85 (0.12)	Pers. comm. from S. Gaudron
Age at birth	**a_b (d)**	**30 (12°C)**	**14.63 (0.51)**	**Guessed from Farke and Berghuis (1979)**
Age at metamorphosis	a_j (d)	78 (12°C)	90.9 (0.17)	Guessed from Farke and Berghuis (1979)
Egg diameter	L_0 (cm)	0.02 (13°C)	0.023 (0.13)	De Cubber et al. (2018)
Total length of the trochophore larva	L_h (cm)	0.025 (12°C)	0.022 (0.11)	Farke and Berghuis (1979)
Total length at birth	**L_b (cm)**	**0.08 (12°C)**	**0.037 (0.54)**	**Guessed from Farke and Berghuis (1979)**
Total length at metamorphosis	L_j (cm)	0.89 (12°C)	0.98 (0.10)	Farke and Berghuis (1979)
Wet weight of an egg	Ww_0 (g)	4.78^{e-6} (13°C)	6.04^{e-6} (0.26)	This study

Supplementary Material

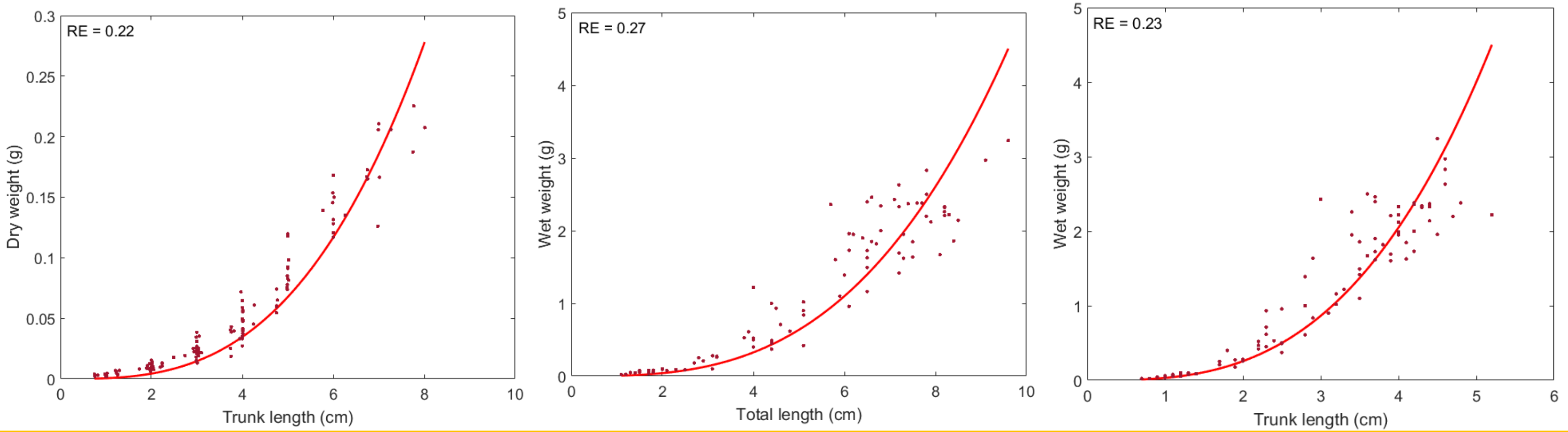
➢ Zero-variate observations vs predictions

Data	Symbol	Value	Predictions (RE)		Unit	Reference
			std-model	abj-model		
age at hatching	a_h	7	2.912 (0.58)	7.845 (0.12)	d	Pers. comm. from S. Gaudron
age at birth	a_b	30	2.582 (0.91)	14.63 (0.51)	d	Farke and Berghuis (1979)
age at metamorphosis	a_j	78	-	90.9 (0.17)	d	Farke and Berghuis (1979)
age at puberty	a_p	548	287.3 (0.48)	292.5 (0.47)	d	De Cubber et al. (2018)
lifespan	a_m	2190	2190 (0.00)	2184 (0.00)	d	Beukema and De Vlas (1979), De Cubber et al. (2018)
egg diameter	L_0	0.02	0.022 (0.10)	0.023 (0.13)	cm	Watson et al. (1998), De Cubber et al. (2018)
total length of the trochophore larva	L_h	0.025	0.028 (0.12)	0.022 (0.11)	cm	Farke and Berghuis (1979)
total length at birth	L_b	0.08	0.028 (0.65)	0.037 (0.54)	cm	Farke and Berghuis (1979)
total length at metamorphosis	L_j	0.89	-	0.98 (0.10)	cm	Farke and Berghuis (1979)
trunk length at puberty	TL_p	2.5	4.03 (0.61)	3.84 (0.54)	cm	De Cubber et al. (2018)
maximum trunk length	TL_i	34	24.73 (0.27)	31.64 (0.07)	cm	Pers. comm. from S. Gaudron (Sorbonne Univ.)
wet weight of an egg	Ww_0	4.78 e^{-6}	5.62 e^{-6} (0.17)	6.036 e^{-6} (0.26)	g	This study

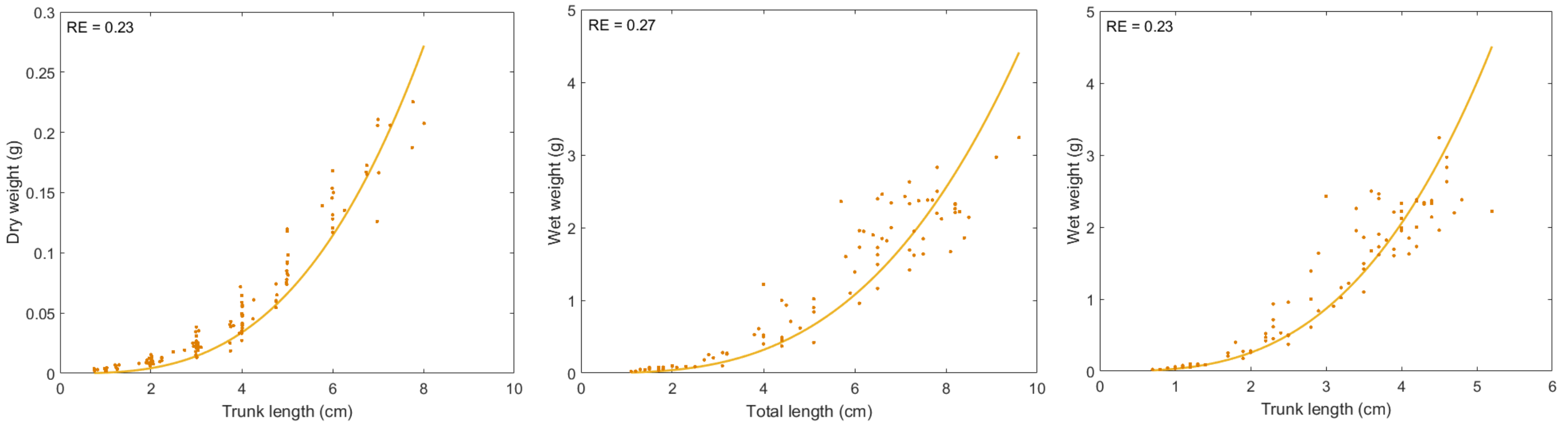
Supplementary Material

Uni-variate observations vs predictions : shape

abj

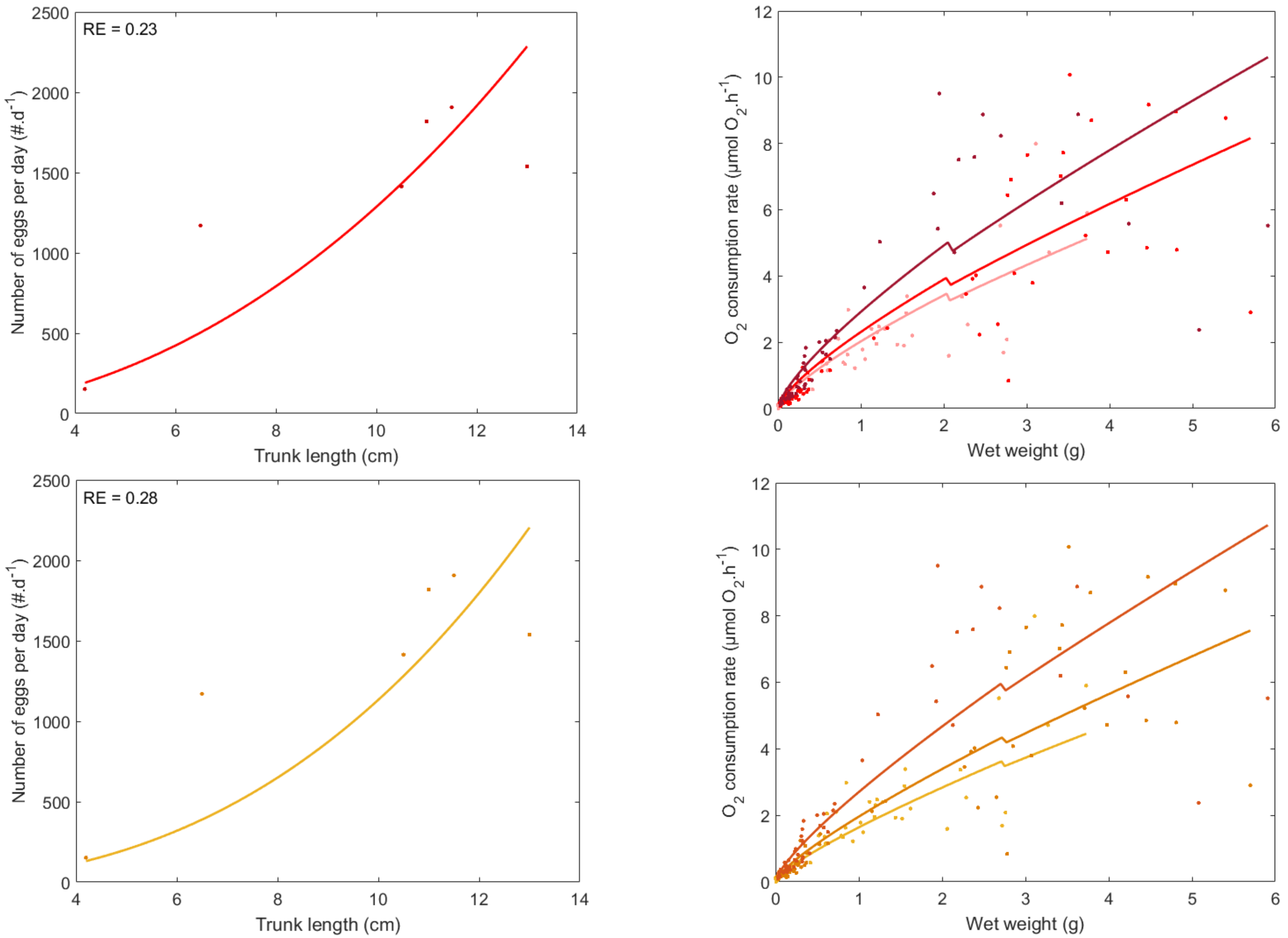


std



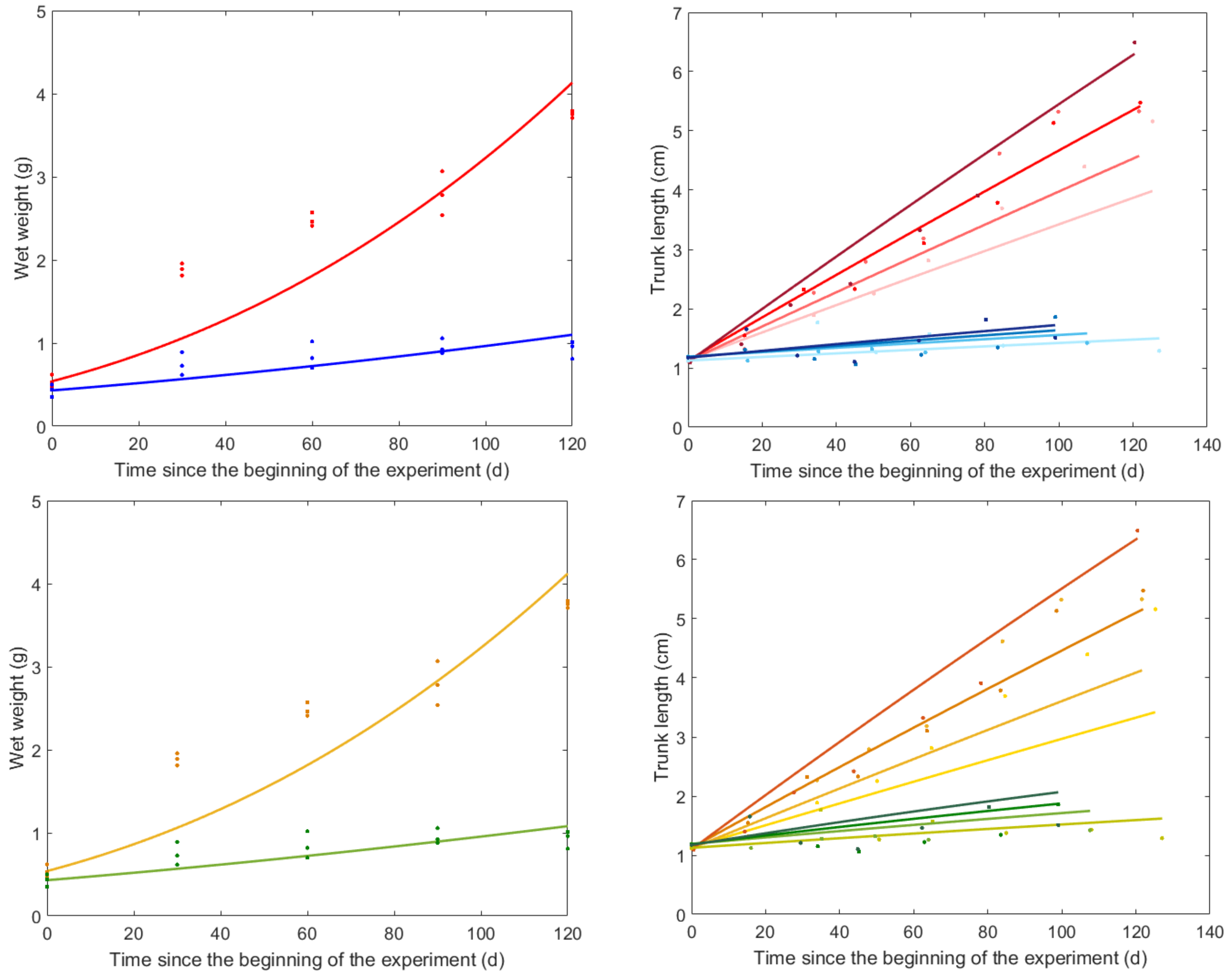
Supplementary Material

➢ Uni-variate observations vs predictions



Supplementary Material

➢ Uni-variate observations vs predictions : Growth

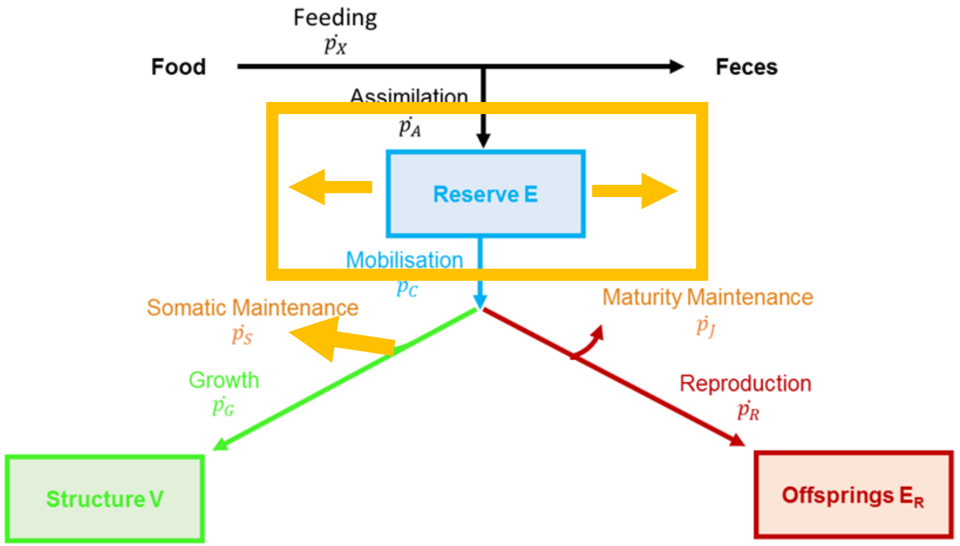


Results

➤ The abj-model gives better fit results

- Parameters values : 2 types of organisms

Parameter	Symbol	Std-	Abj-	Unit
Maximum assimilation rate	$\{\dot{p}_{Am}\}_b$	233.76	13.47	$J.cm^{-2}.d^{-1}$
	$\{\dot{p}_{Am}\}_j$	-	138.61	$J.cm^{-2}.d^{-1}$
Energy conductance	$\dot{v}_b$	$2.3e^{-2}$	$5.4e^{-3}$	$cm.d^{-1}$
	$\dot{v}_j$	-	$5.6e^{-2}$	$cm.d^{-1}$
Specificsomatic rate	$[\dot{p}_M]$	39.11	14.70	$J.cm^{-3}.d^{-1}$
Reserve capacity	$[E_m]$	10 164	2 494	$J.cm^{-3}$



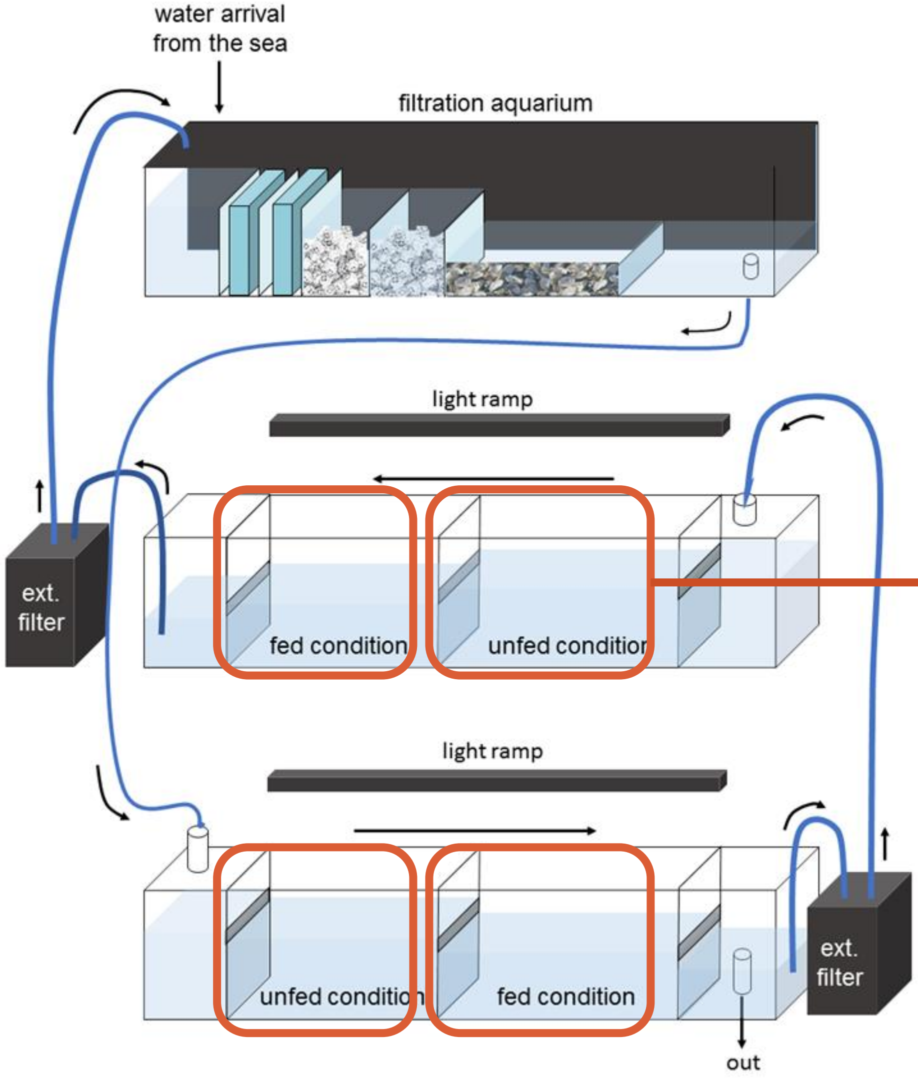
- MRE/SMSE 0.28/0.34 (std)
  0.22/0.24 (abj) ➡ acceleration rate ~ 10

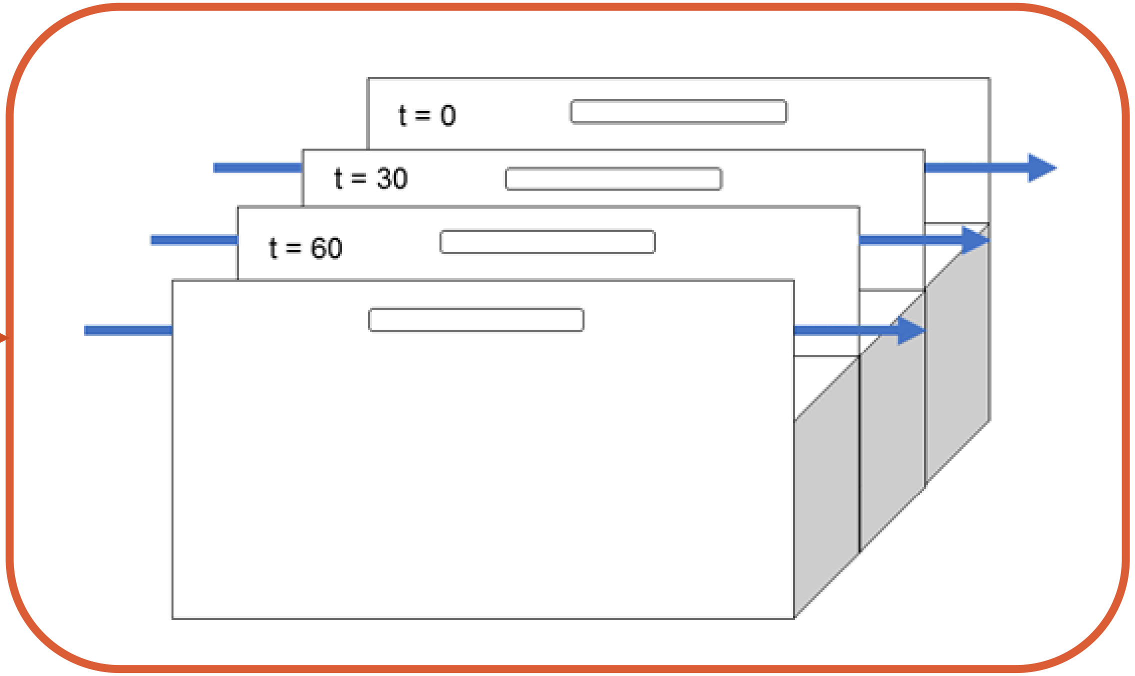
- Better zero-variate predictions for the early life-stages with the abj-DEB model

- The uni-variate predictions of both models are close after puberty

Results

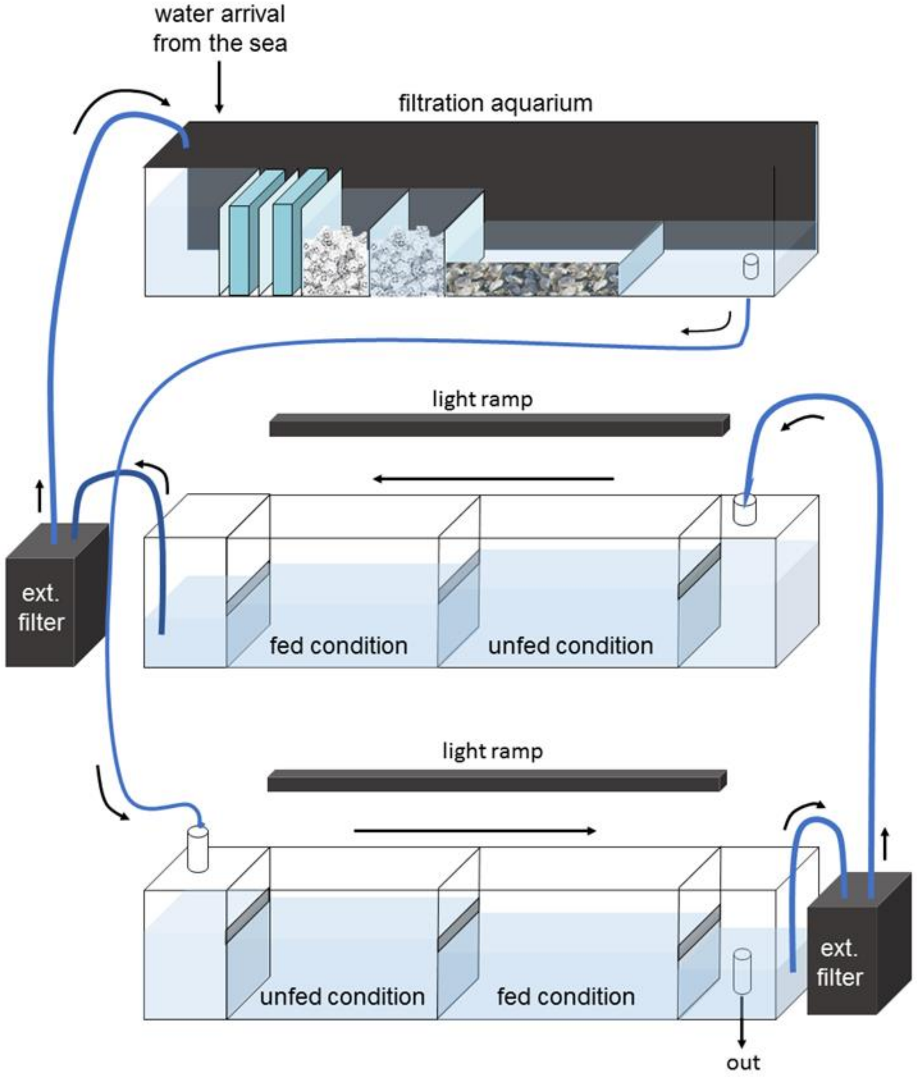
➢ Inferences on the scaled functional response f : experimental data

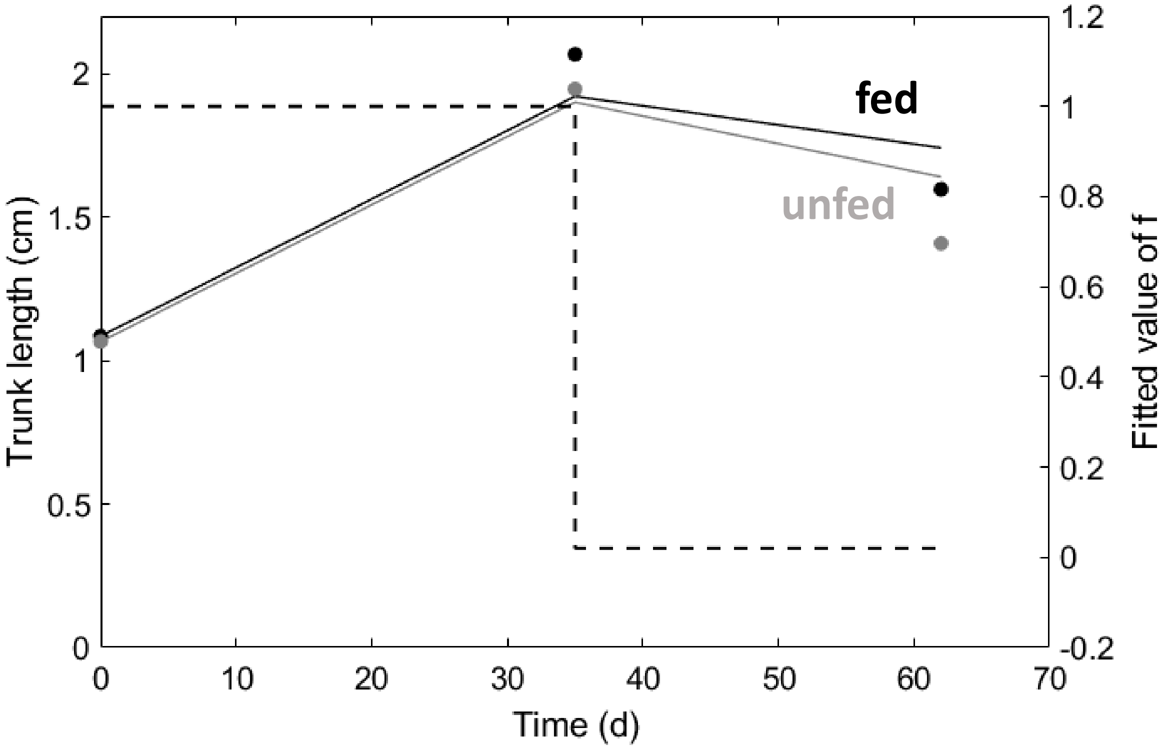




Results

➢ Inferences on the scaled functional response f : experimental data



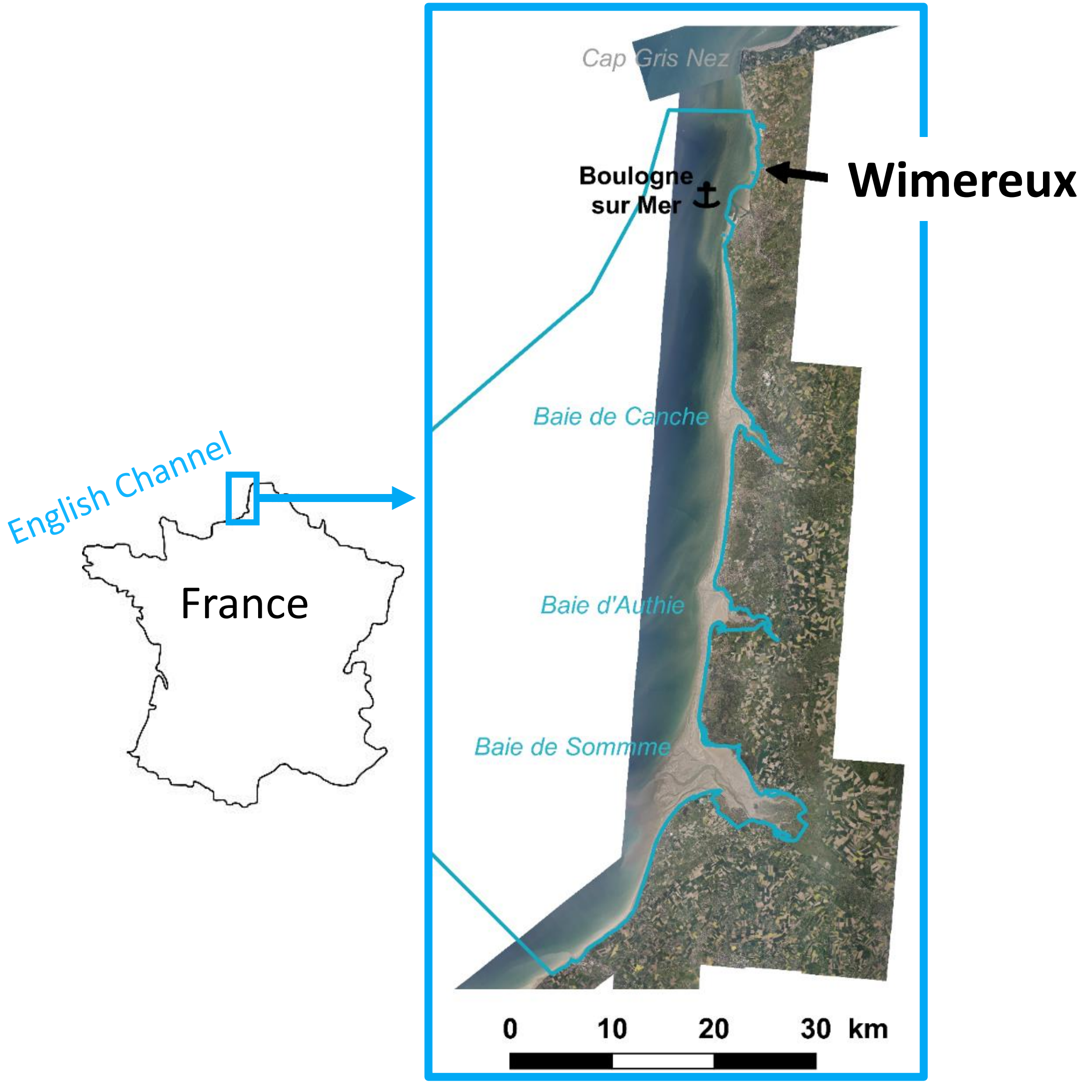


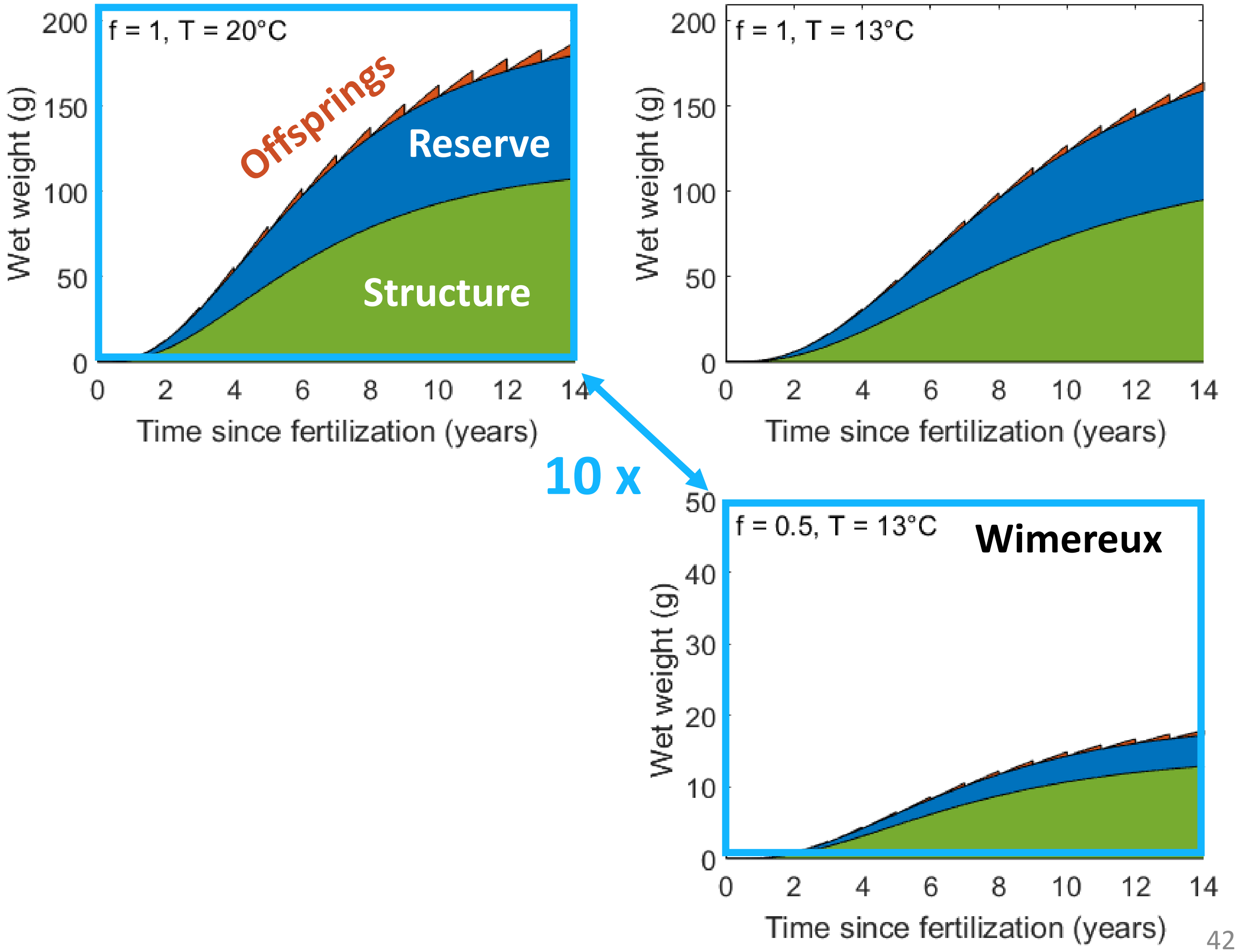
→ Good fit to the data for the first 35 days

→ Food quality/quantity issue

Results

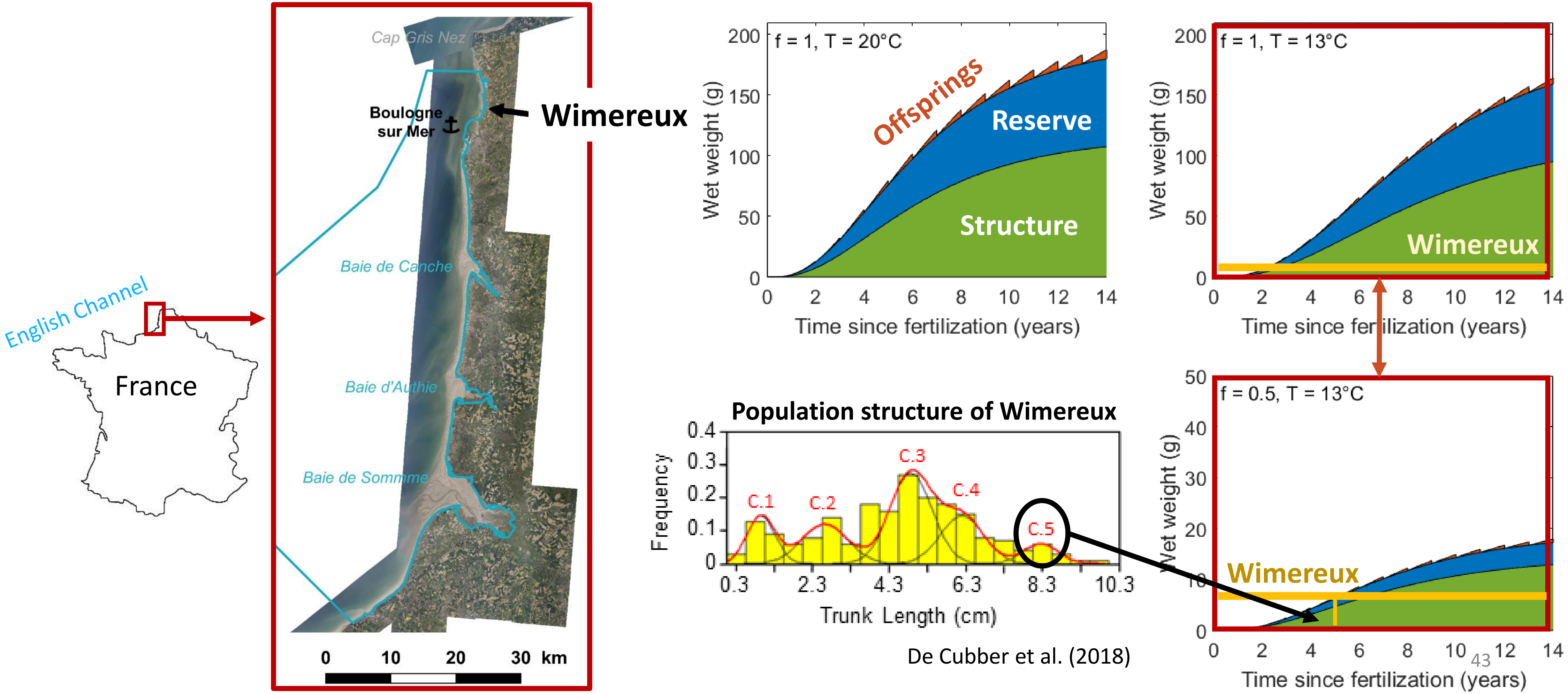
➢ Predicted growth under *in situ* environmental conditions





Results

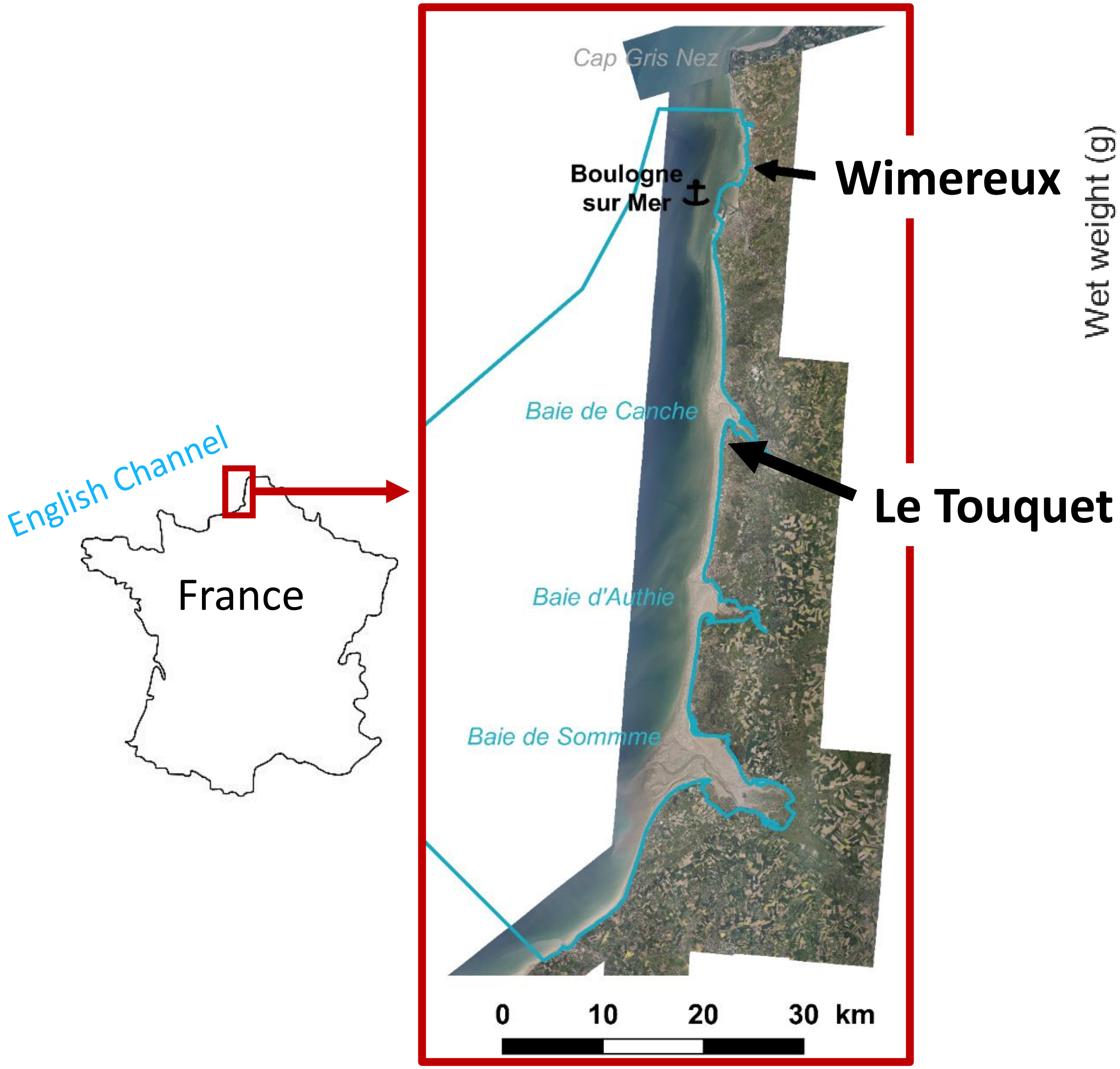
➢ Predicted growth under *in situ* environmental conditions

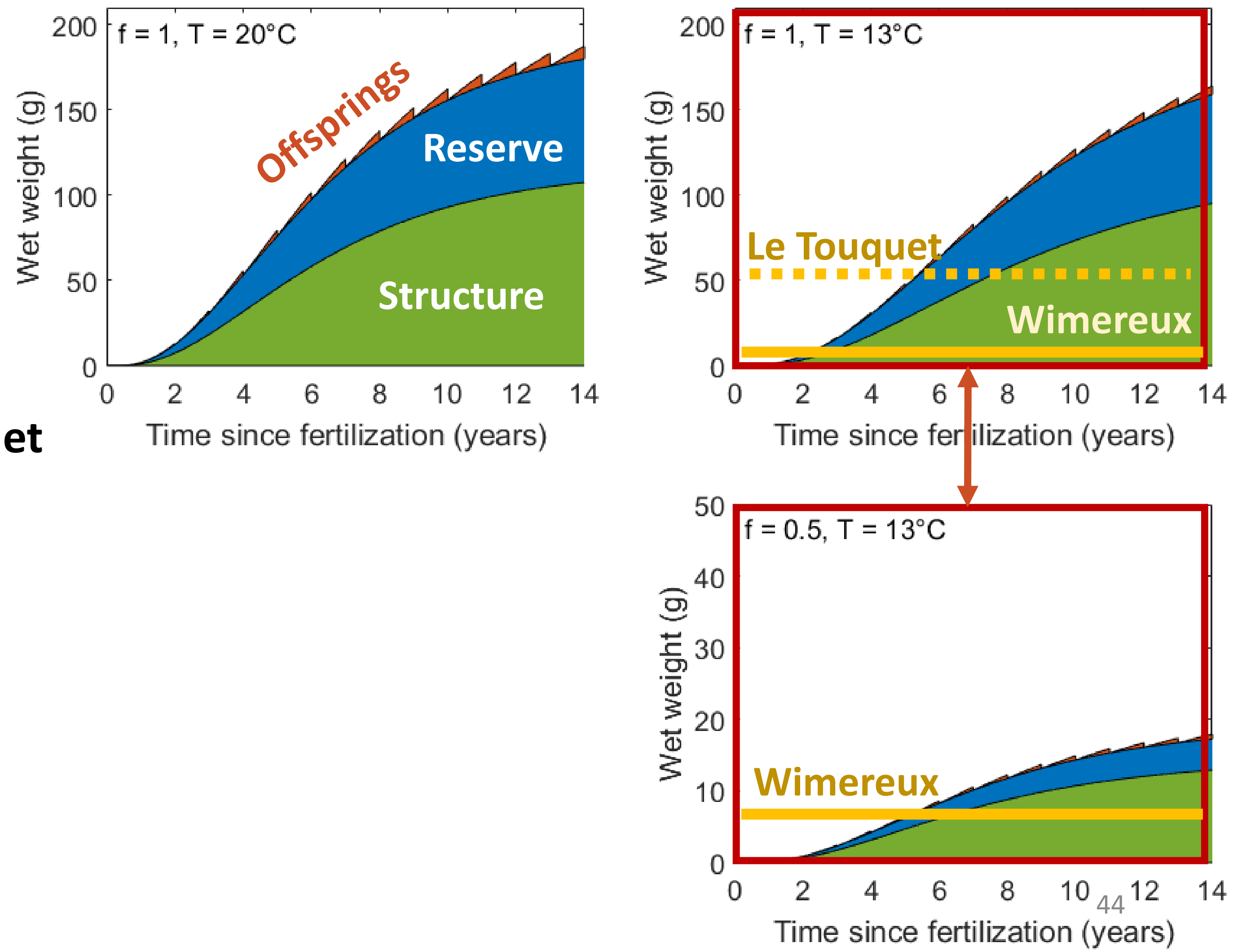


De Cubber et al. (2018)

Results

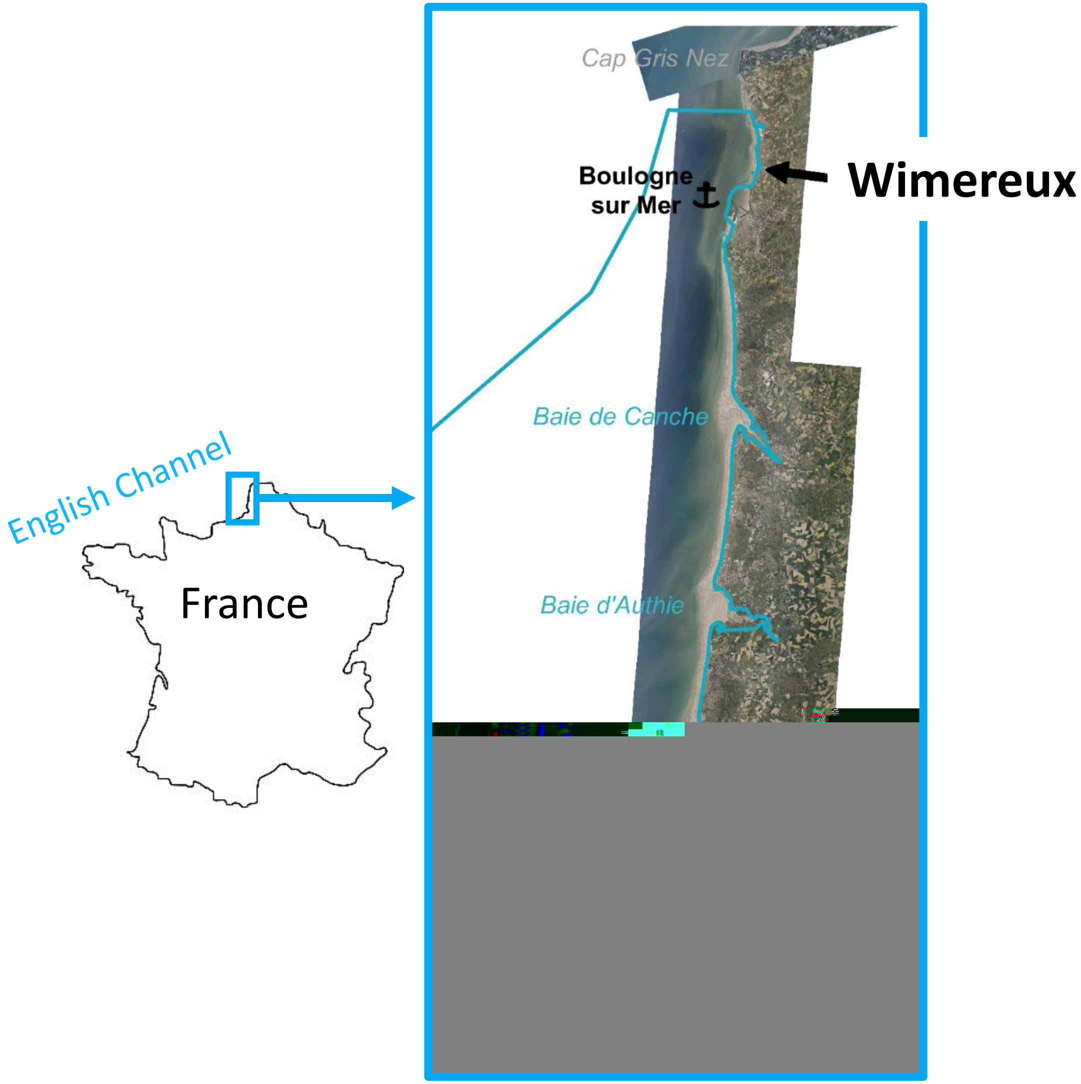
➢ Predicted growth under *in situ* environmental conditions

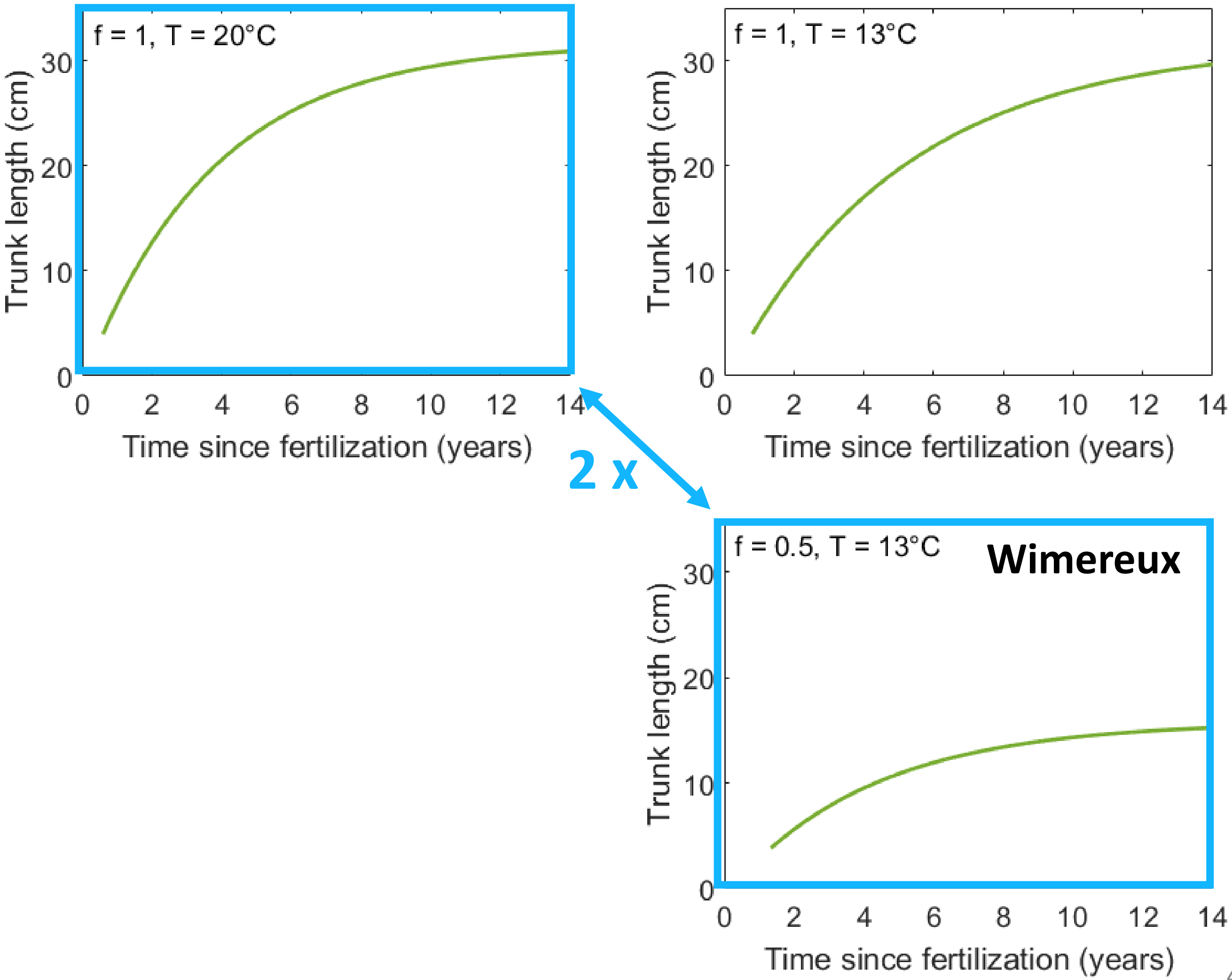




Results

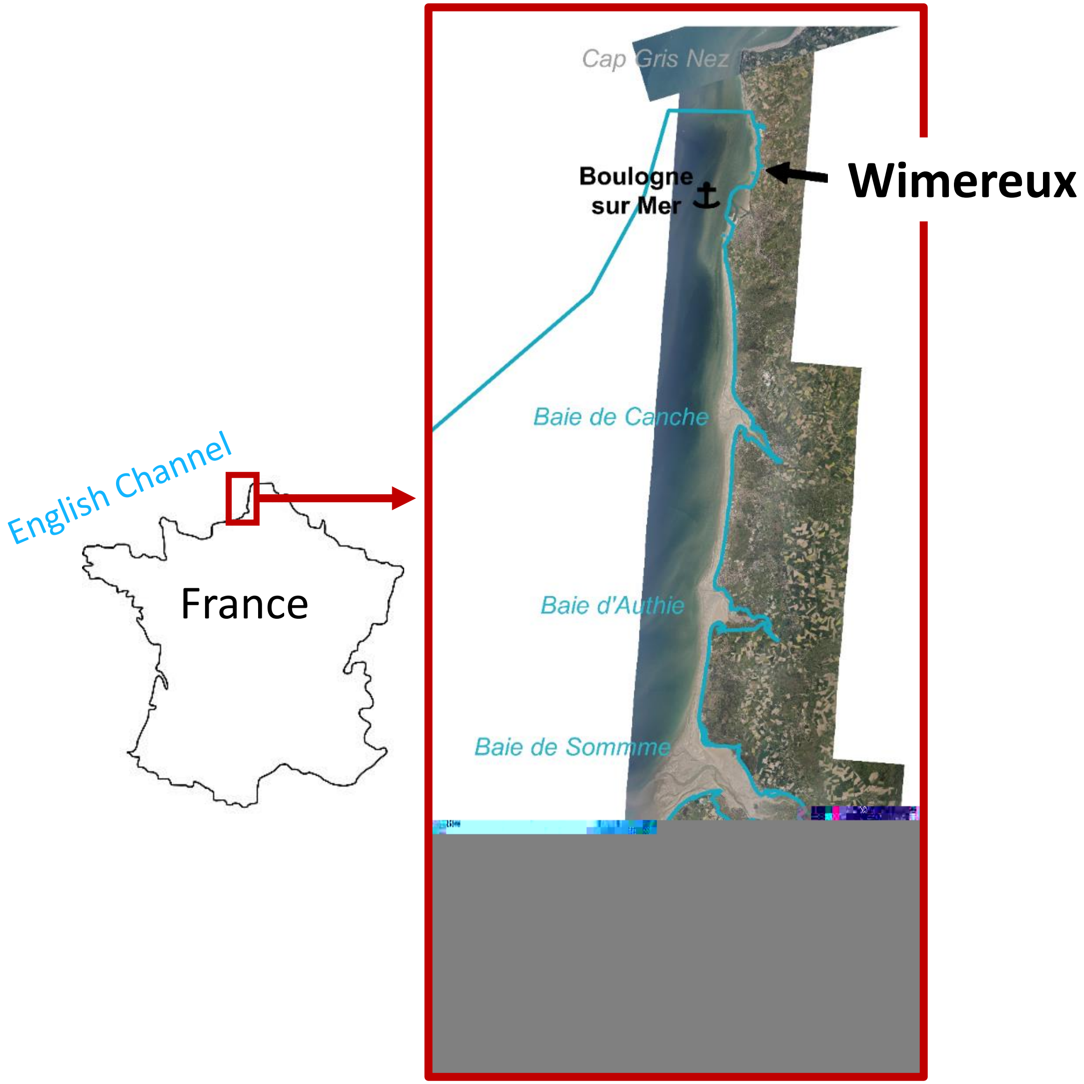
➢ Predicted growth under *in situ* environmental conditions

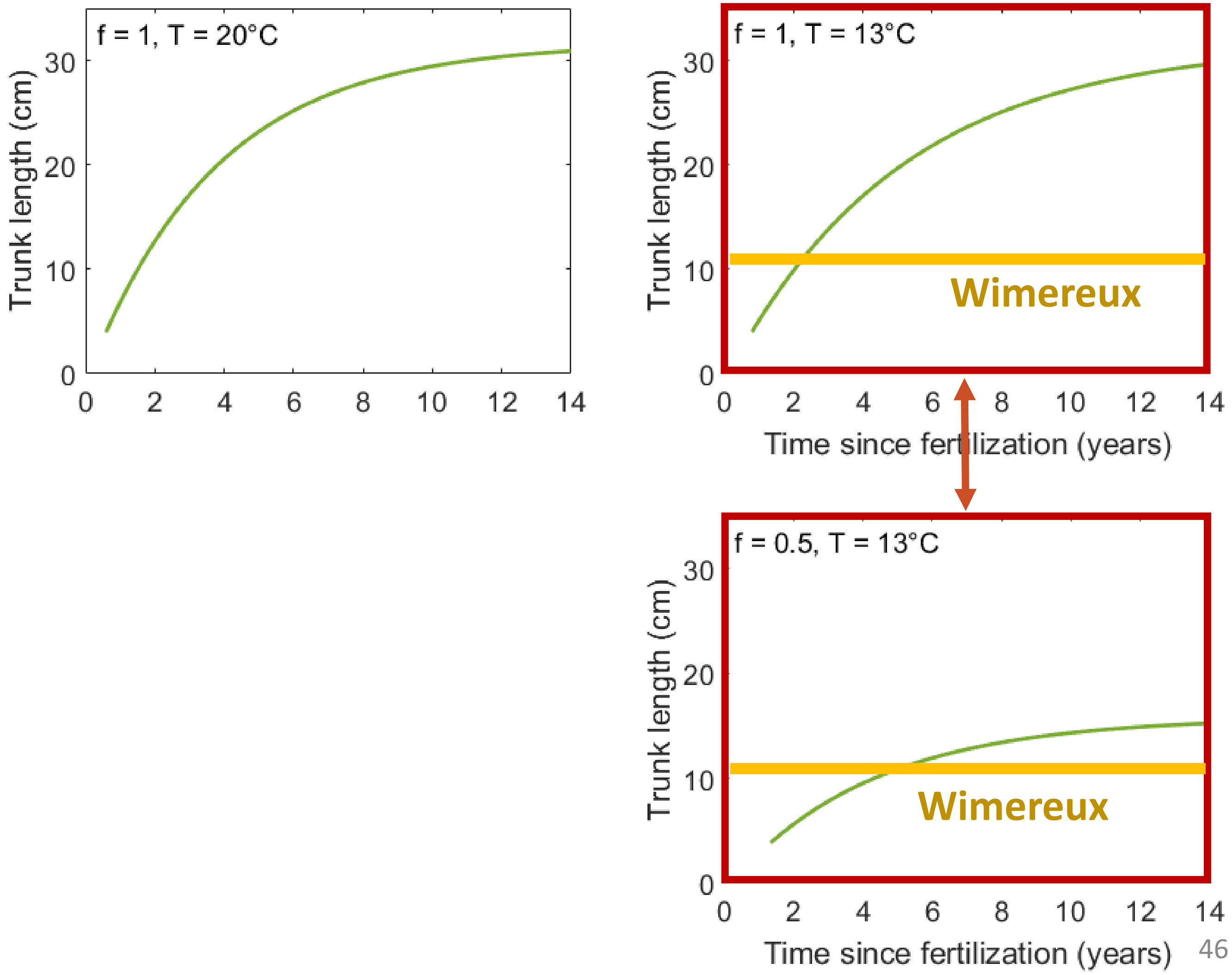




Results

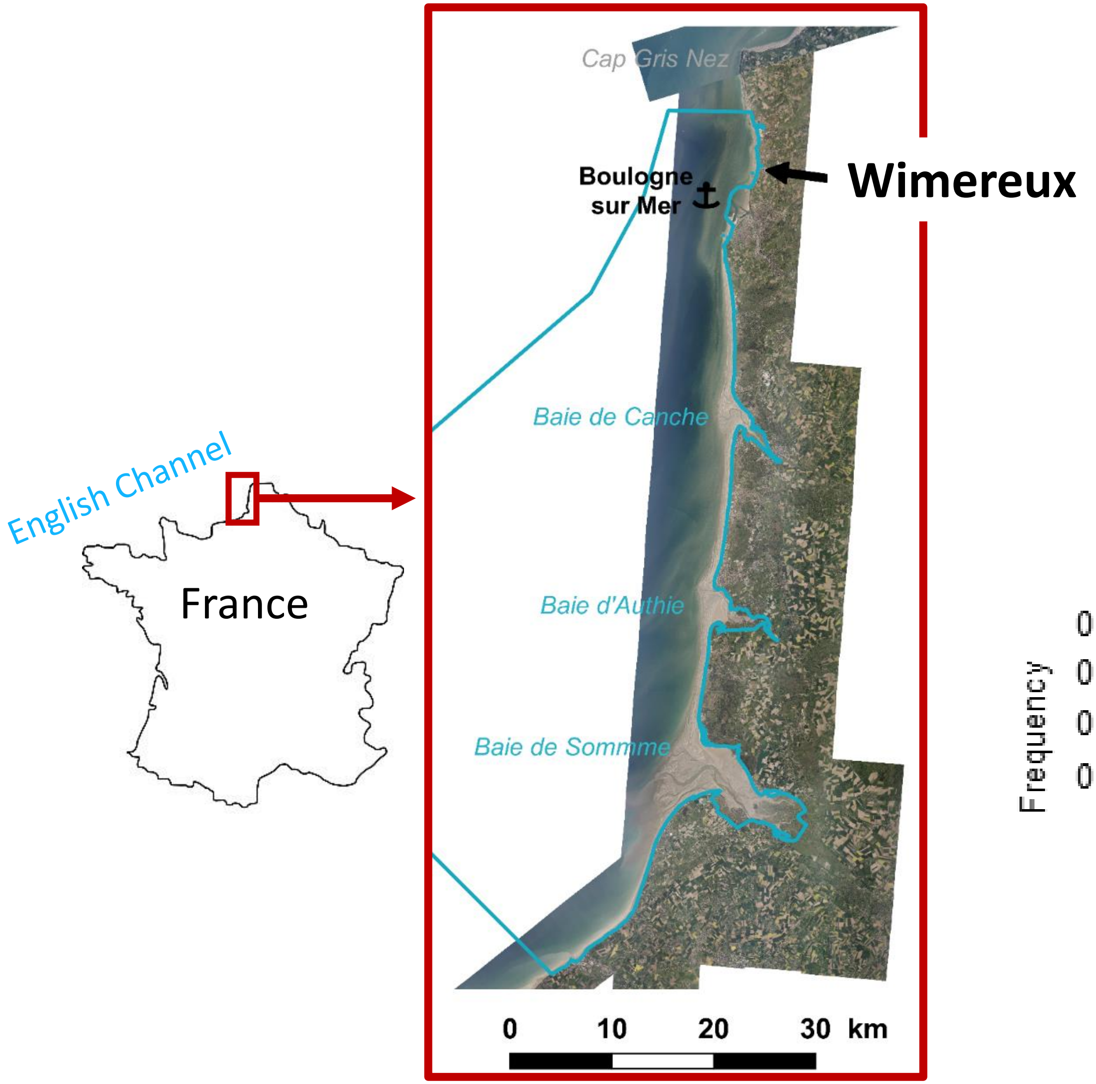
➢ Predicted growth under *in situ* environmental conditions

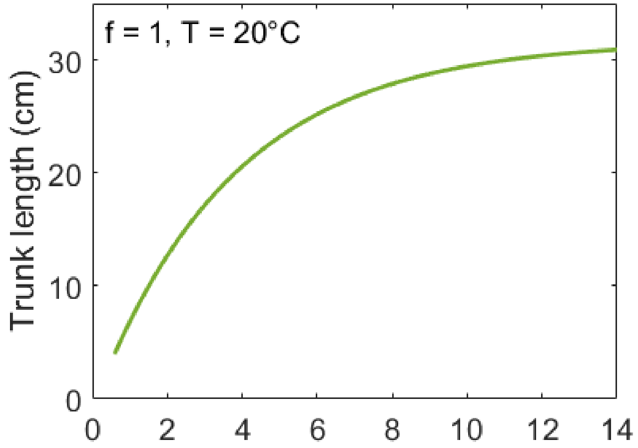


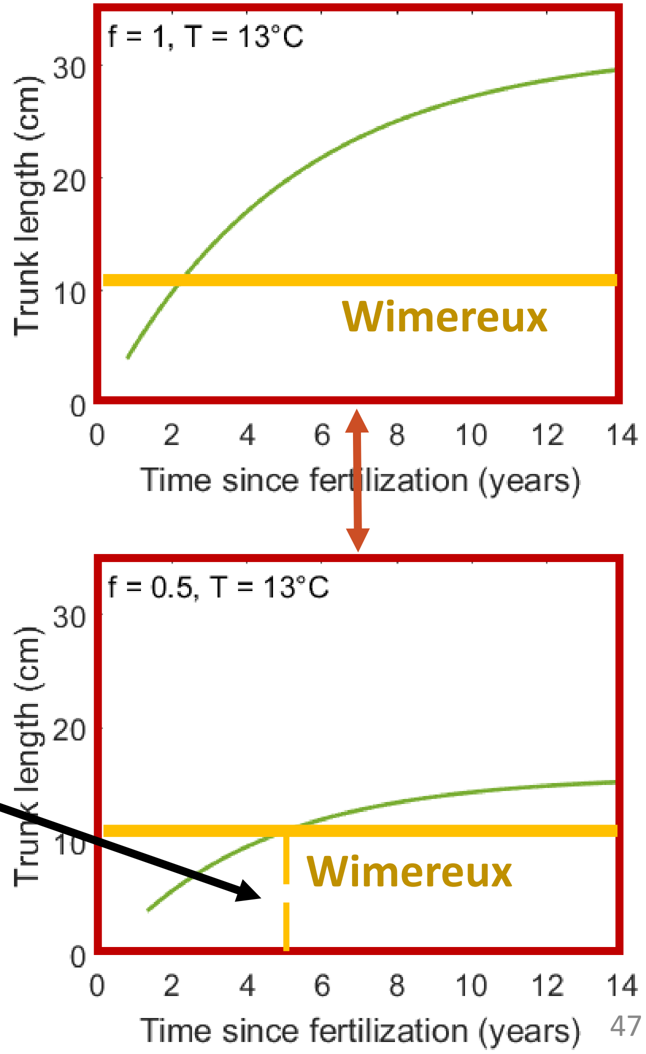


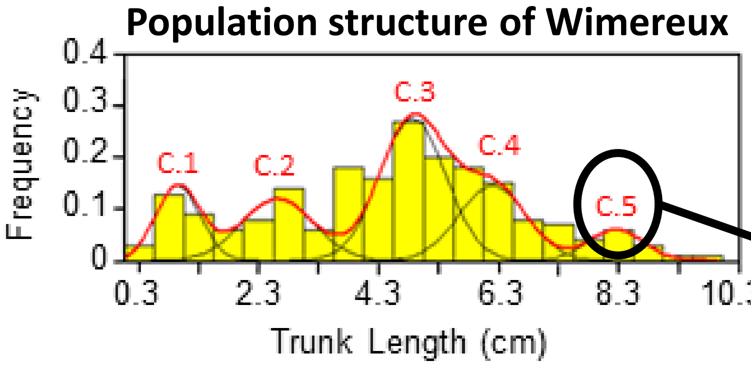
Results

➢ Predicted growth under *in situ* environmental conditions





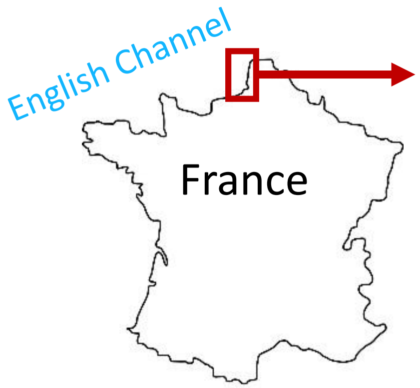


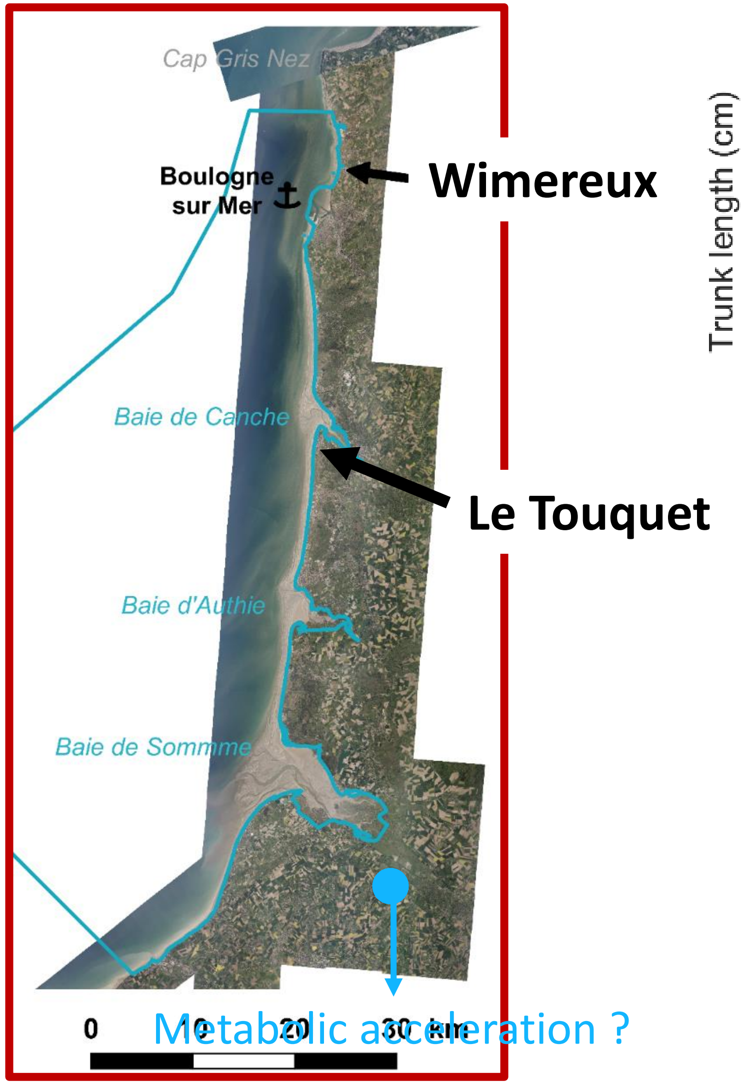


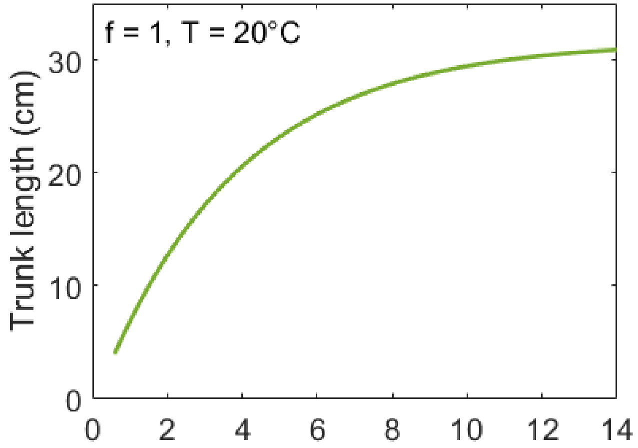
De Cubber et al. (2018)

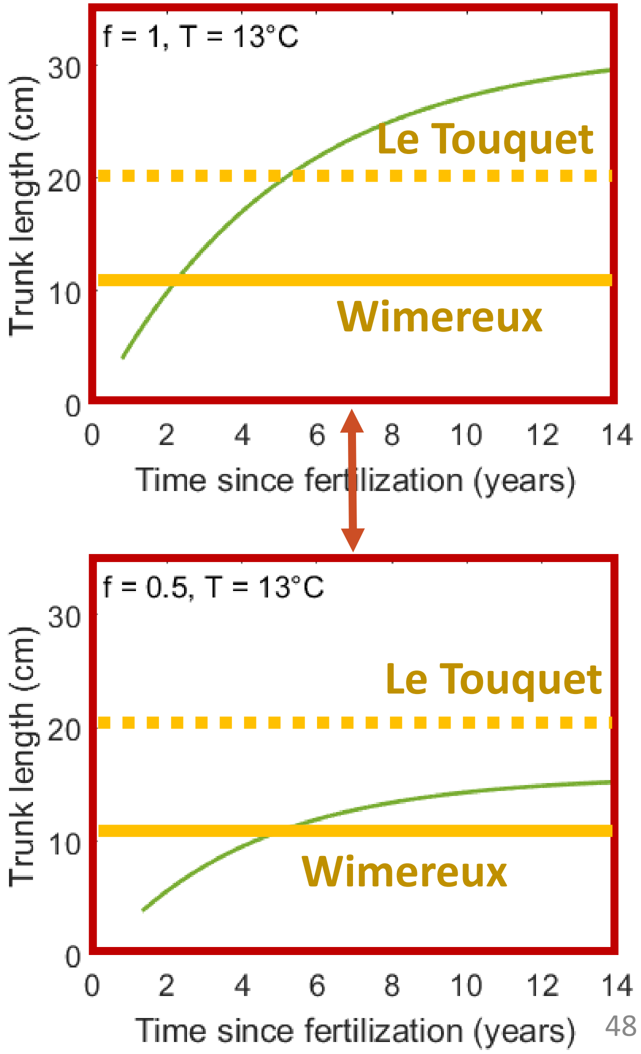
Results

➢ Predicted growth under *in situ* environmental conditions



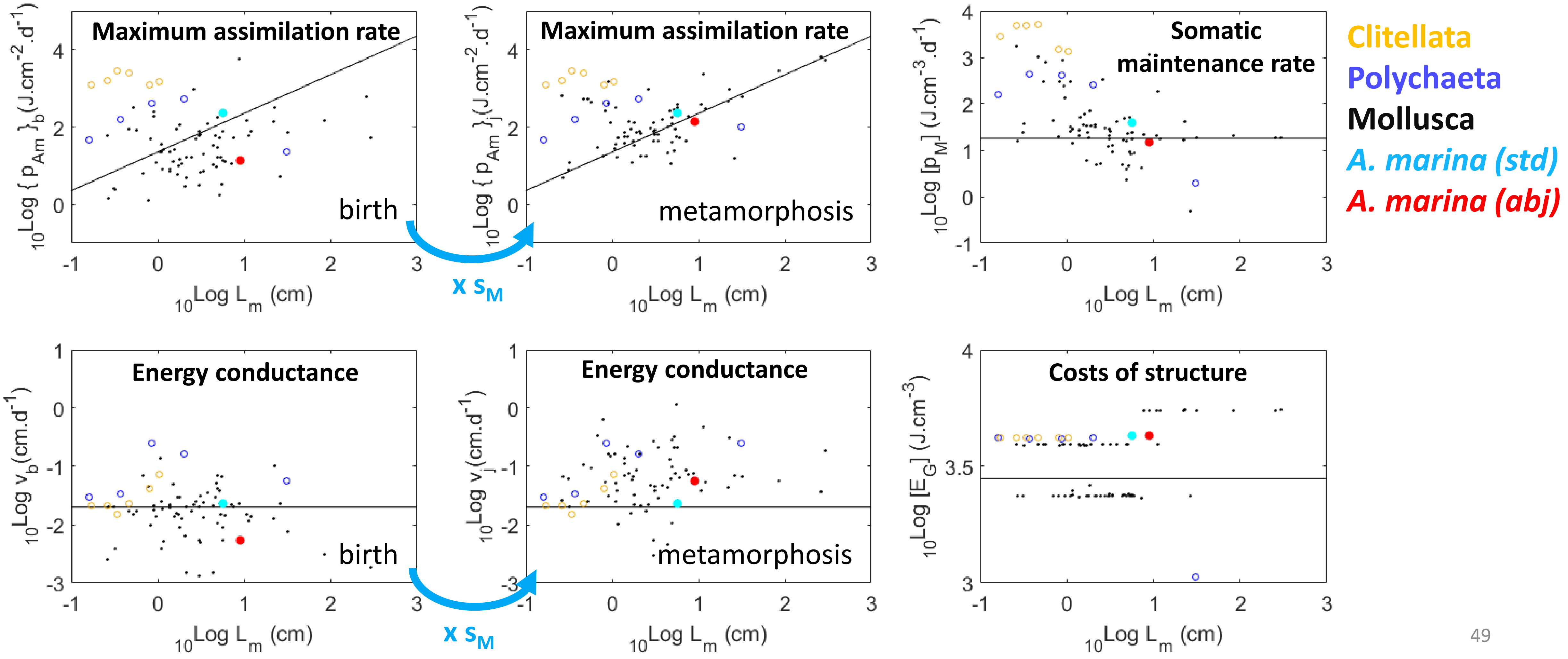






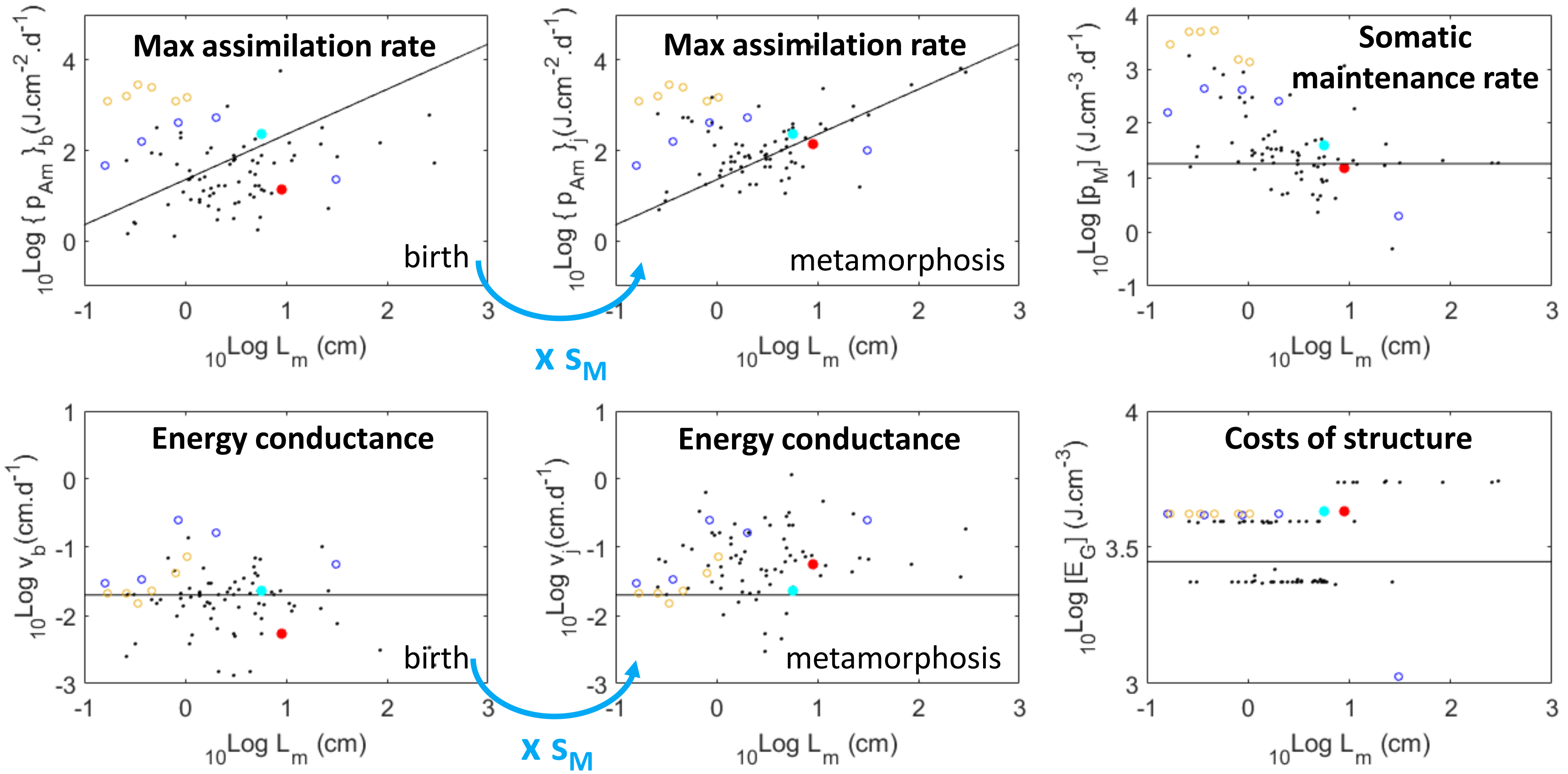
Results

➢ Comparison of DEB parameters among Lophotrocozoans



Results

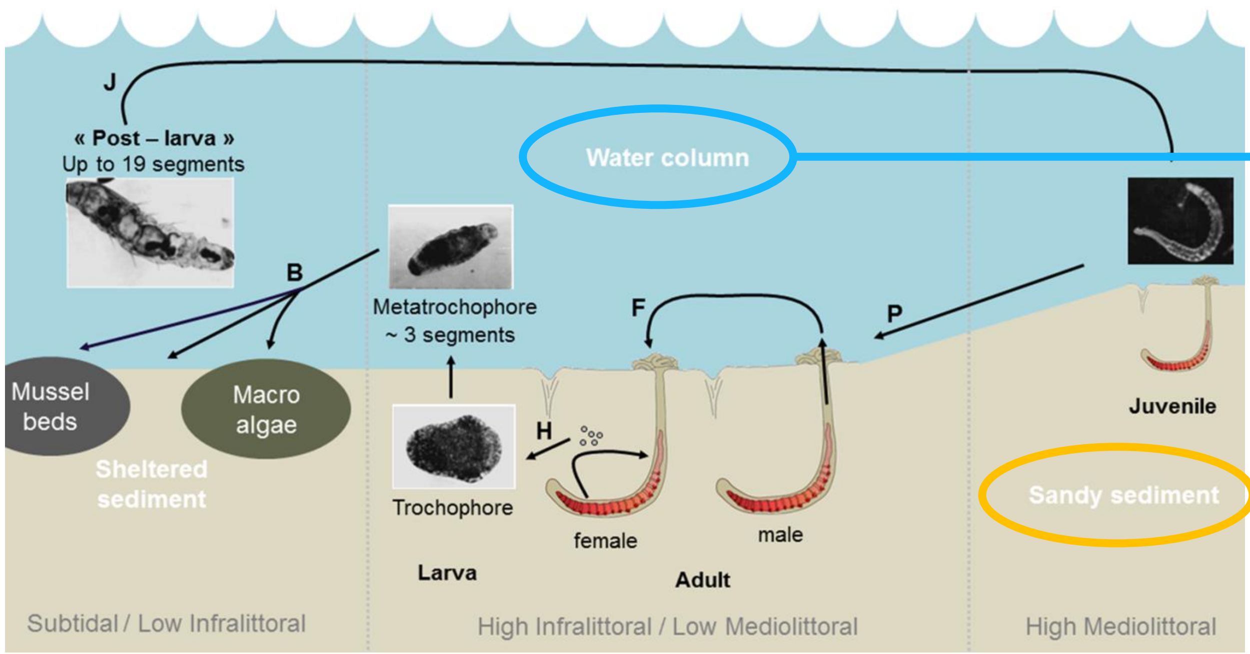
➢ Comparison of DEB parameters among Lophotrocozoans



Clitellata
Polychaeta
Mollusca
A. marina (std)
A. marina (abj)

- For *A. marina*, main differences abj/std before metamorphosis
- abj/std values of *A. marina* closer to the mollusks' values
- Polychaetes' parameters were assessed without considering the early stages and are probably closer to the mollusks' values too

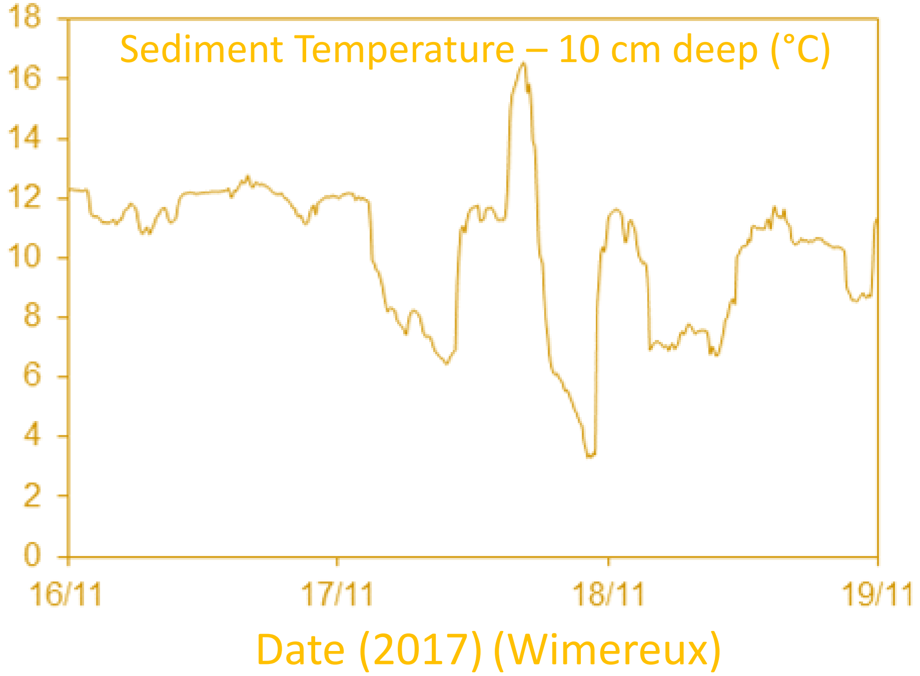
Model improvements



- ➢ Arrhenius temperature along the life-cycle ?

Rather constant variations → High T_A

Large and fast temperature variations → Low T_A



- ➢ Aerial exposure correction term

Gradual migration

Higher shore (juveniles) → aerial exposure +++

Middle shore → aerial exposure ++

Lower shore (adults) → aerial exposure +