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Impact of metabolism on biocalcification processes: new tools to reconstruct environmental conditions and individual life histories from biogenic carbonates.

Keynote speaker

Laure Pecquerie

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Biogenic carbonates, biomineralization processes and DEB theory

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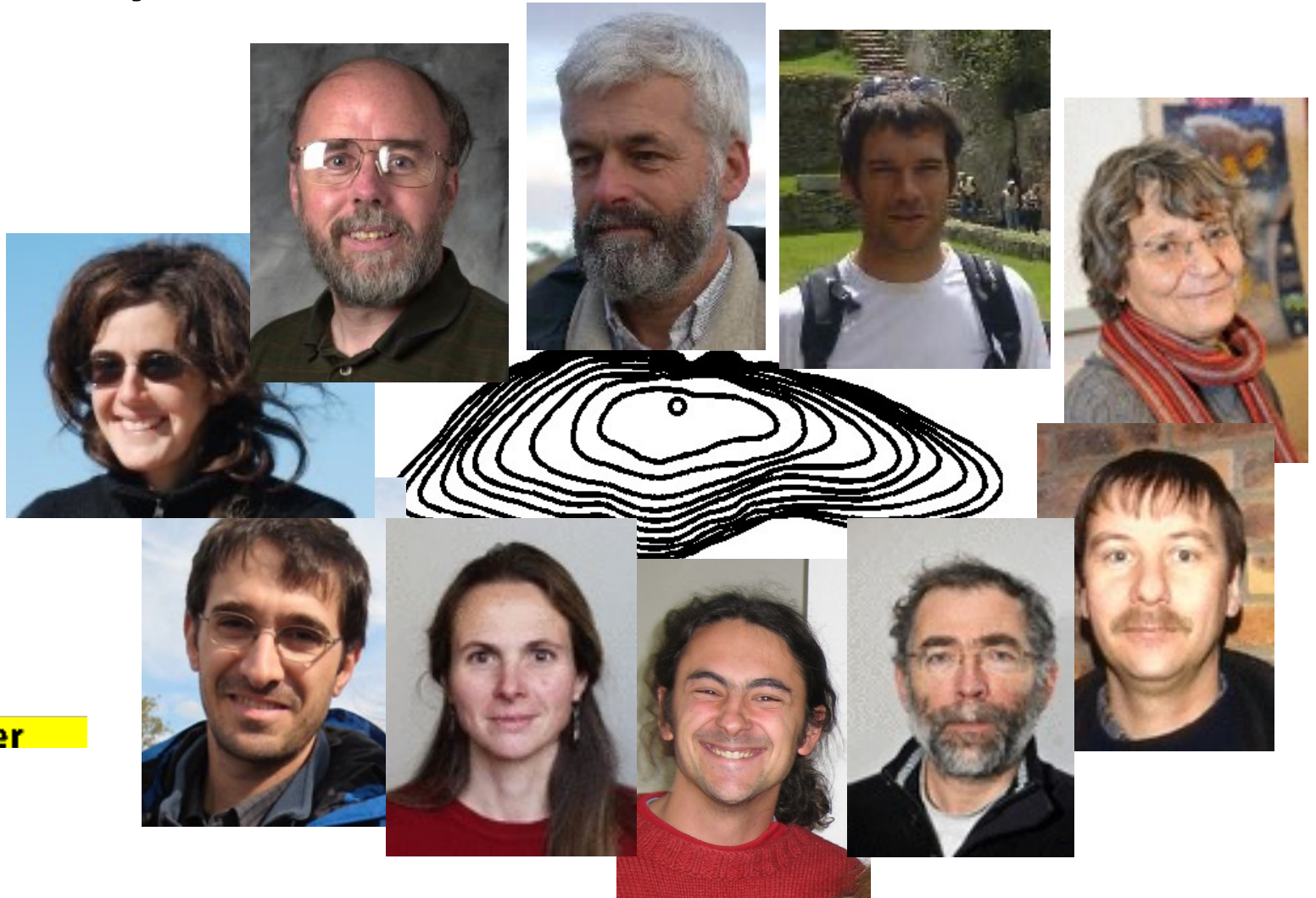
Annual growth bands in the umbo of an *Arctica islandica* shell (Alfred Wegener Institute)



Wed. 24th April,
DEB Symposium 2013, Texel

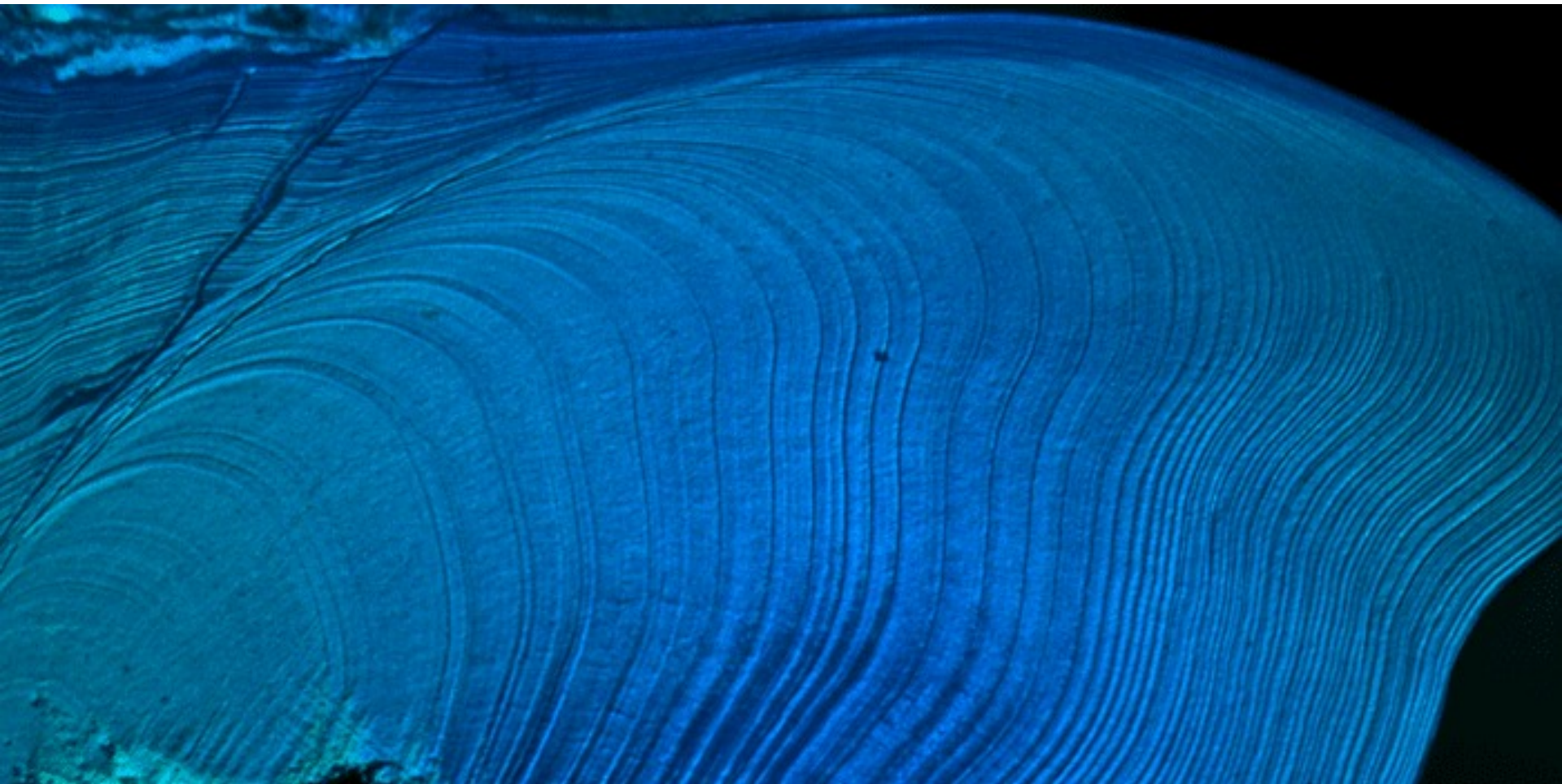


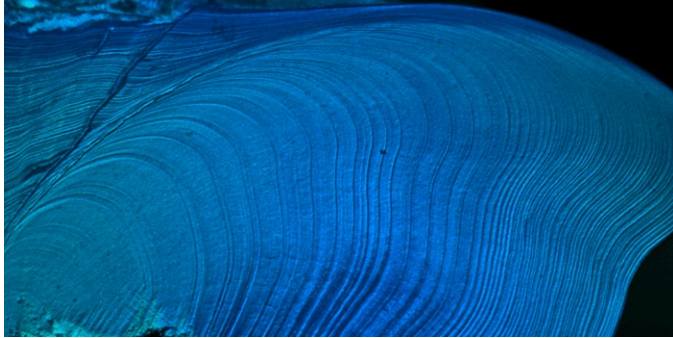
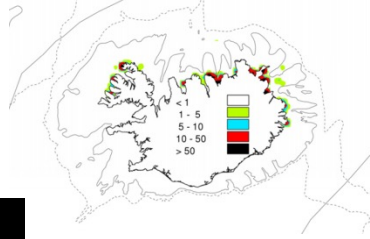
Many, many, thanks to :



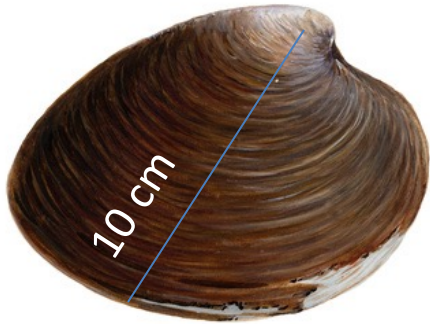
Bas Kooijman, Roger Nisbet, Ronan Fablet, H el ene de Pontual, Anne Lorrain, C edric Bacher, Pierre Petitgas,, Patrick Grellier, Sylvain Bonhommeau ,Jonathan Flye Sainte Marie, Fred Jean, Yves-Marie Paulet, Elise Dufour, David Gillikin, V eronique Loizeau







Annual growth bands in the umbo of an *Arctica islandica* shell (Alfred Wegener Institute)



(one of the) oldest non-clonal living animal : 507 years (Butler et al. 2013)

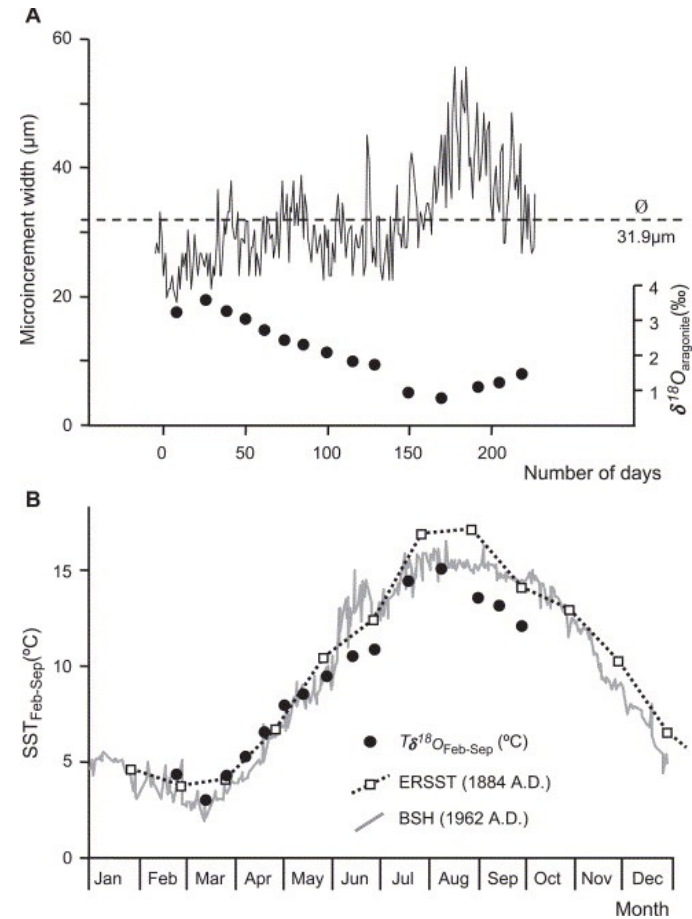
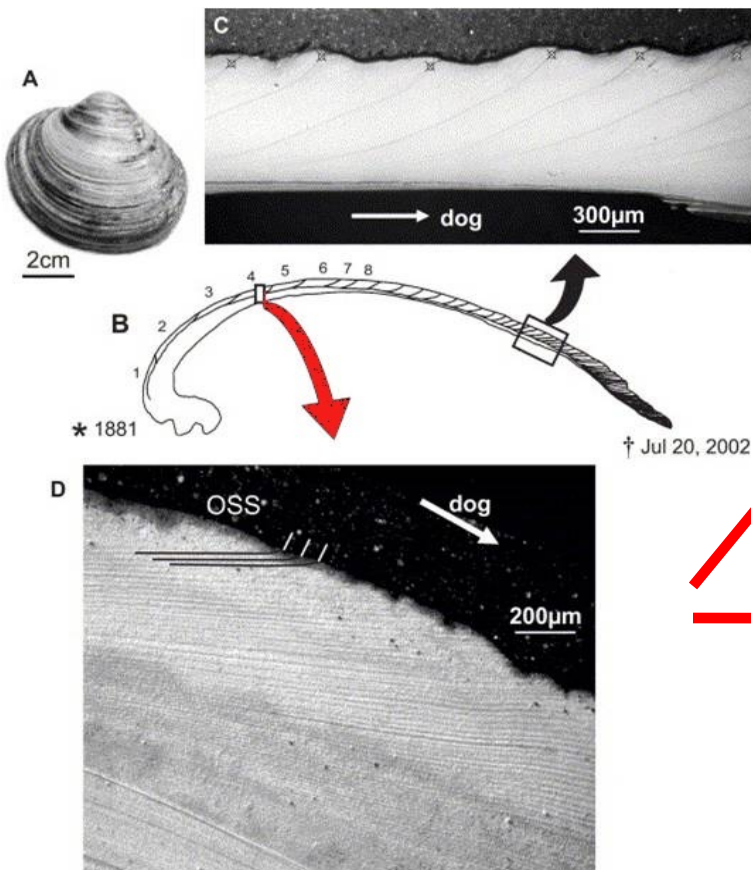
Ocean quahog
Arctica islandica (1499 – 2005)



The Republic of the Seven United Netherlands (1581 – 1795)

Isotopic composition of biogenic carbonates

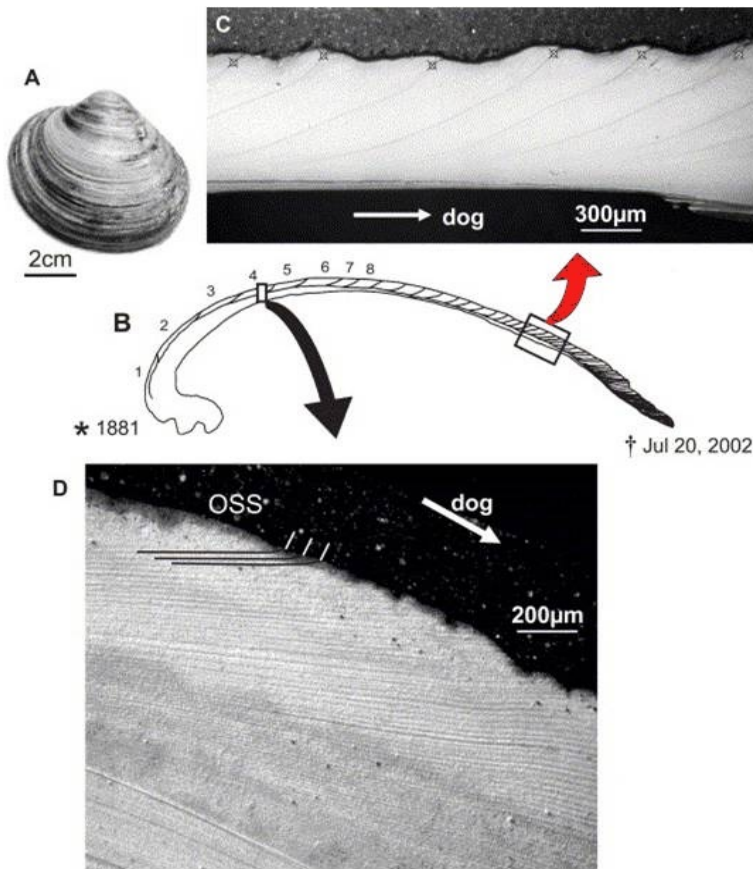
- Harold Urey (1948) \rightarrow $\delta^{18}\text{O}$ inversely correlated with temperature in limestone



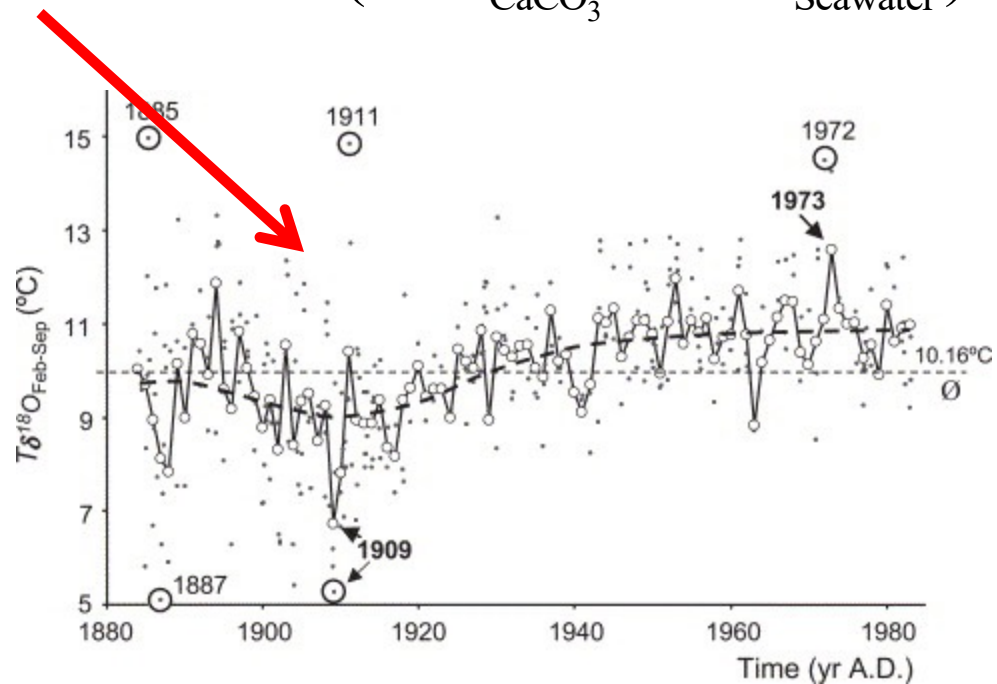
(Schöne et al. 2004)

Isotopic composition of biogenic carbonates

- Harold Urey (1948) \rightarrow $\delta^{18}\text{O}$ inversely correlated with temperature in limestone



$$+ T = a - b(\delta^{18}\text{O}_{\text{CaCO}_3} - \delta^{18}\text{O}_{\text{Seawater}})$$



(Schöne et al. 2004)

Why do we study biogenic carbonates?

Sclerochronology = study of the physical and chemical variations in calcified tissues of marine and freshwater organisms

Biogenic carbonates present an accretionary growth (by successive layers)

→ **Biological archives of the environment and the life history of marine and freshwater organisms**

- e.g. temperature, salinity, upwelling events, past CO₂ levels, contaminant concentration
- e.g. age, growth, migrations

Applications in marine and freshwater (paleo)ecology, fisheries sciences, paleoceanography, ...

BUT THEIR INTERPRETATION IS CHALLENGING, SOMETIMES ERRONEOUS

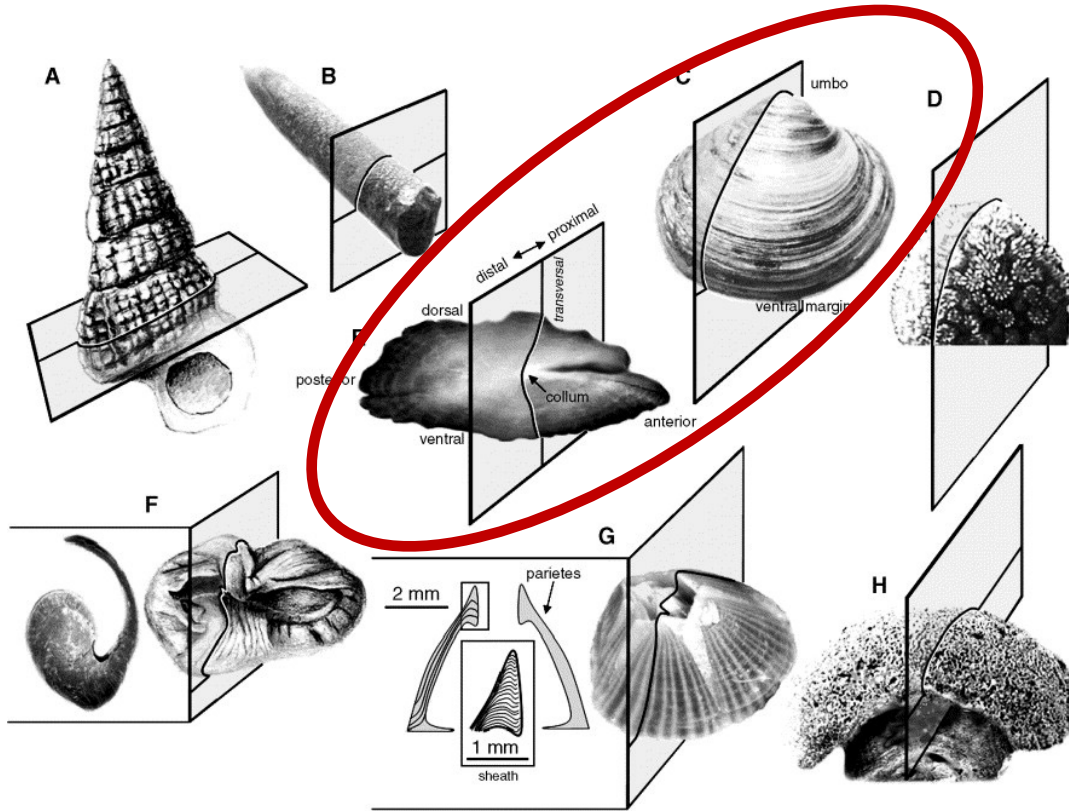
→ Striking examples of fish population overexploitation in New Zealand (Orange roughy, Andrews et al. 2009)

and in the Bering Sea (Walleye pollock, Beamish and McFarlane, 1996)

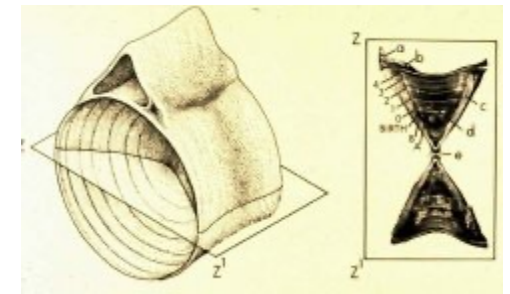
Outline

- Biogenic carbonates = biological archives, rich in information but difficult to interpret
- Physical properties: how DEB theory can help us better interpret fish ear bones (otoliths)?
- Chemical composition ($\delta^{13}\text{C}$): what can we learn from otoliths and shells comparison?
- Summary and perspectives
 - Annual \rightarrow Daily scale
 - Shell growth
 - Ocean acidification

Some biogenic carbonates

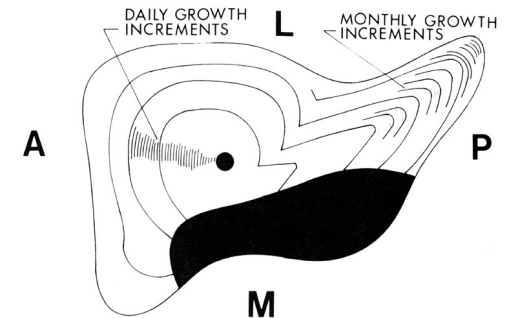


Some sampling position in biogenic skeletons (A) Gastropod, (B) belemnite, (C) bivalve mollusk, (D) coral, (E) sagitta (fish otolith), (F) whale's tympanic bulla, (G) barnacle, (H) sclerosponge. (Schöne et al. 2005)



Shark vertebrae

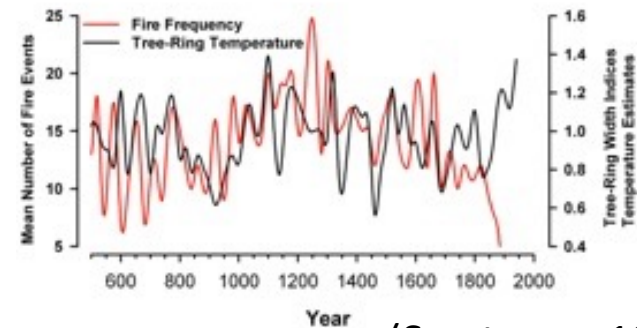
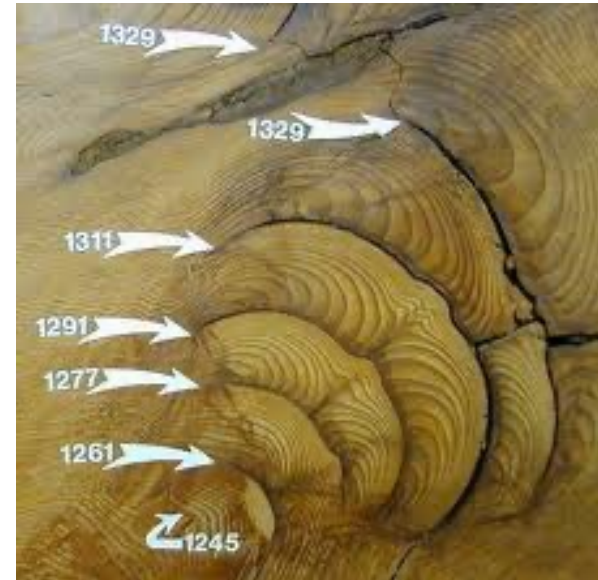
<http://na.nefsc.noaa.gov/sharks/age.html>



Squid statolith

(Recksiek and Frey, 1978)

Studying biogenic carbonates is a bit like...



(Swetnam, 1993)

Fire frequency reconstruction in California

→ more frequent between 800 and 1300 than in recent years



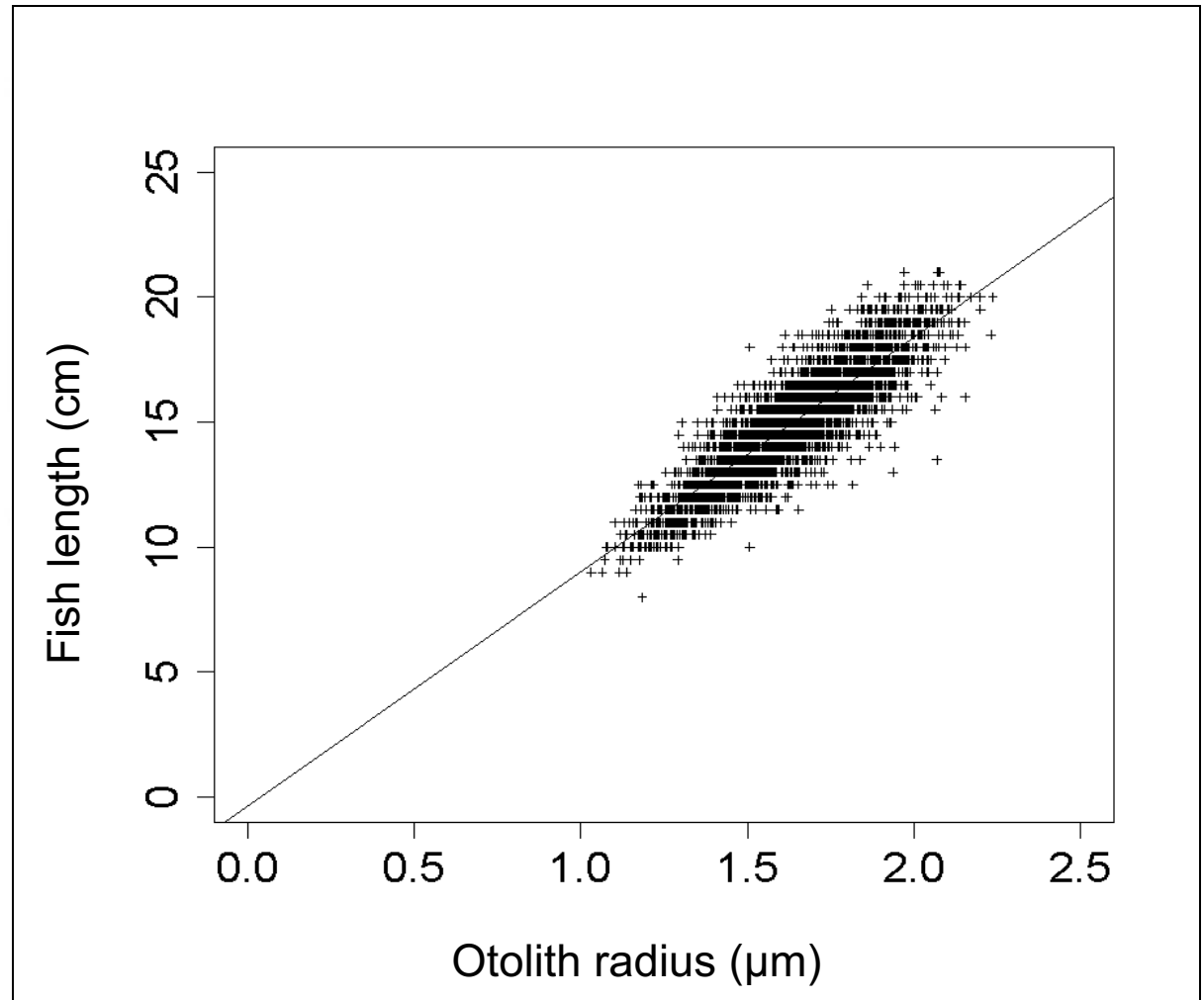
NATIONAL
GEOGRAPHIC
MAGAZINE



© Michael Nichols/National Geographic

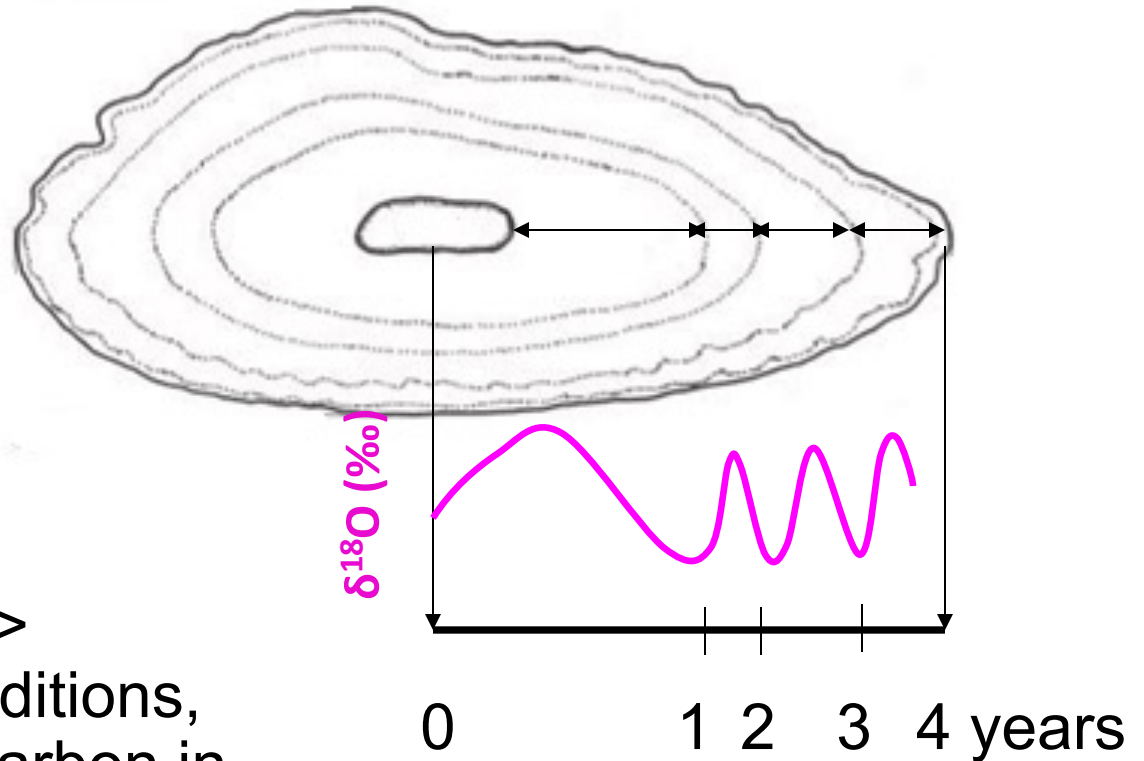
Fish otoliths = archives of individual life history

- Transect length
-> time
- Increment widths
-> growth



Fish otoliths = archives of individual life history

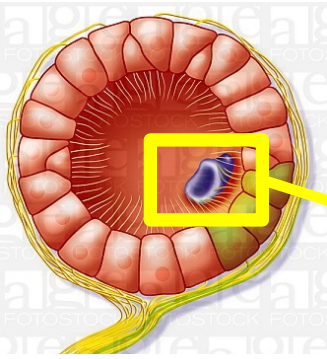
- Opacity pattern
-> time
- Increment widths
-> growth
- Isotopic composition ->
temperature, food conditions,
Dissolved Inorganic Carbon in
the water



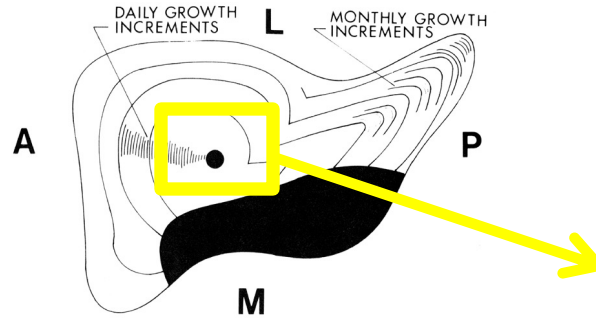
Getting the right age



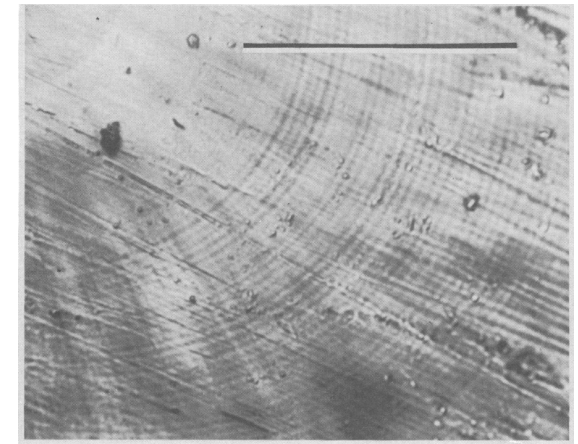
Market Squid, *Loligo Opalescens*



Statocyst in the central nervous system of squid



Squid statolith
(Recksiek and Frey, 1978)

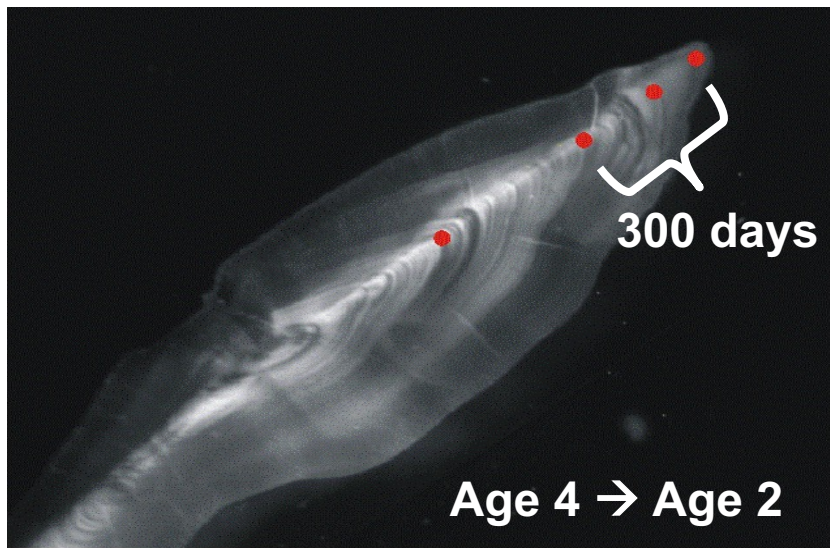


Growth rings

TABLE 2.
Number Growth Rings in Statoliths from Squid of Known Age.

<i>Specimen</i>	<i>MMAge in days</i>	<i>Growth rings in statoliths</i>
1	67-70	28
2	67-70	32
3	28-31	30
4	43-44	15
5	54-55	35
6	55-56	38

Getting the right time scale



Fish recovered 300 days after tagging

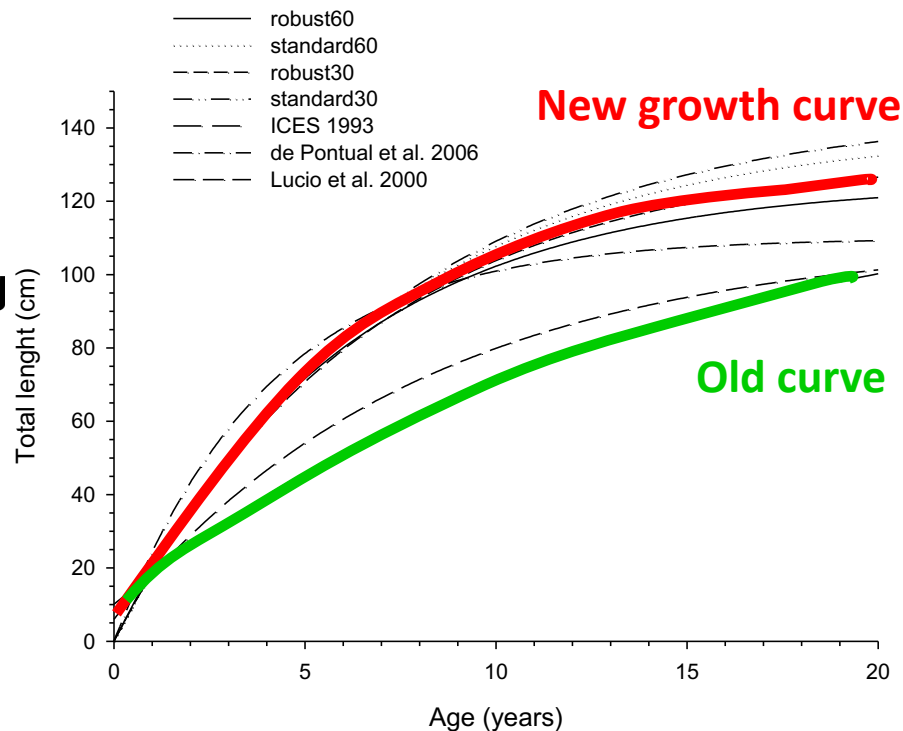
Winter ring (annulus)

● EU experts blind interpretation

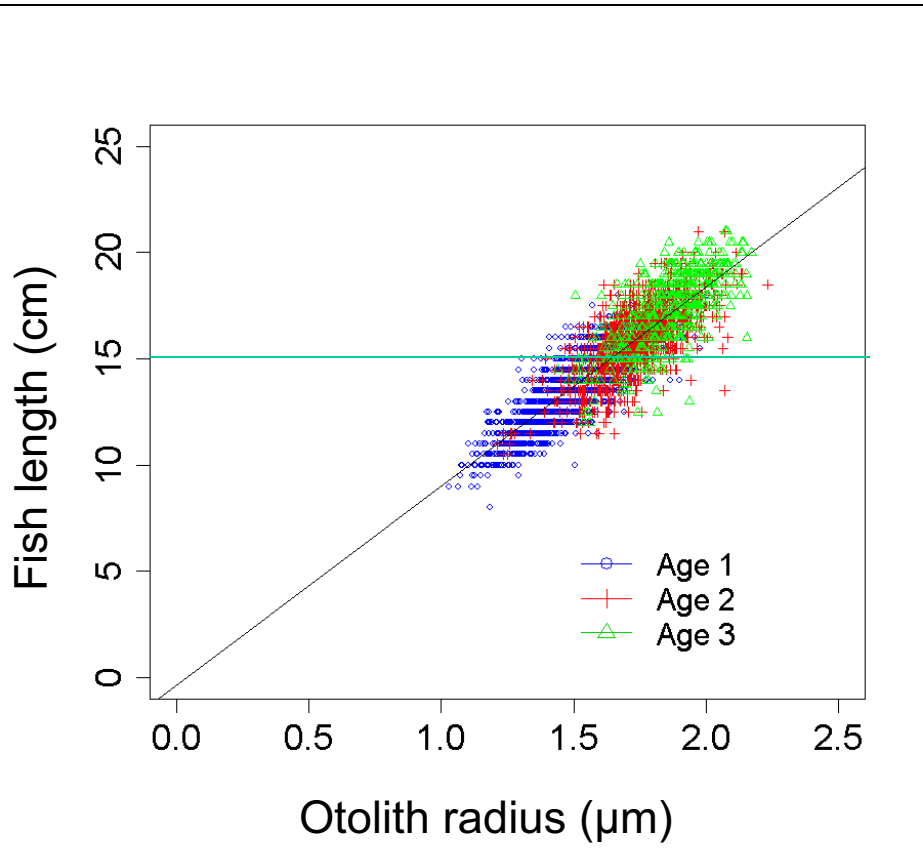
● Oxytetracycline mark



Hake (*Merluccius merluccius*)

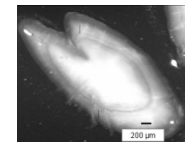


Getting the right length



- Linear otolith radius – fish length (OR-FL) relationship for adults
- Slow growing fish have larger otoliths

→ Biases in back-calculation of growth

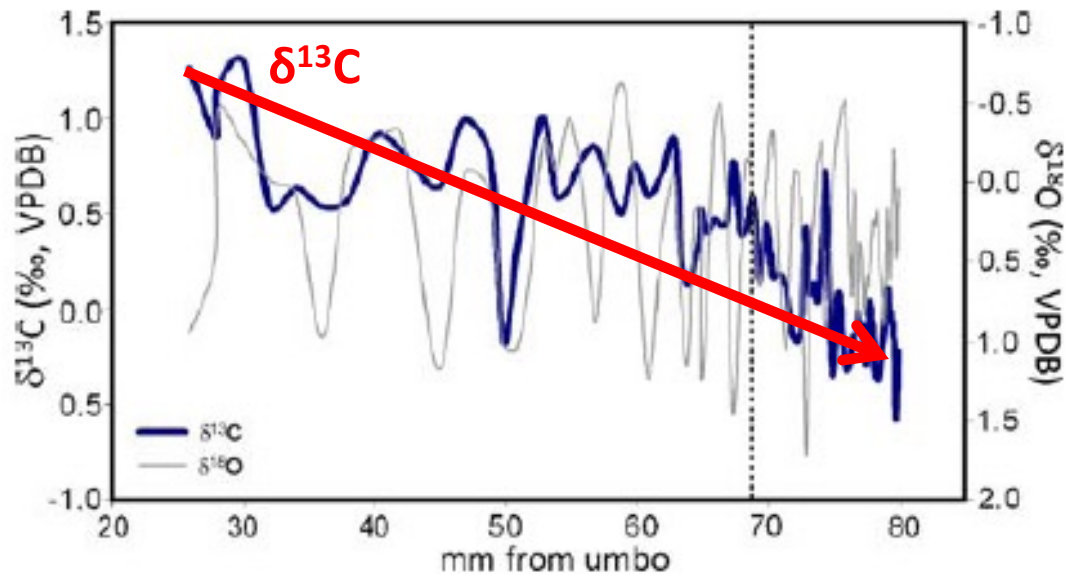


P. Oetler, IFREMER



Getting the right environmental proxy

- Harold Urey (1948) \rightarrow $\delta^{18}\text{O}$ inversely correlated with temperature in limestone
- $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ measured at the same time
but $\delta^{13}\text{C}$ is not used as an environmental proxy
e.g. $\delta^{13}\text{C}$ Shell \rightarrow $\delta^{13}\text{C}$ Dissolved Inorganic Carbon (DIC) \rightarrow Primary production



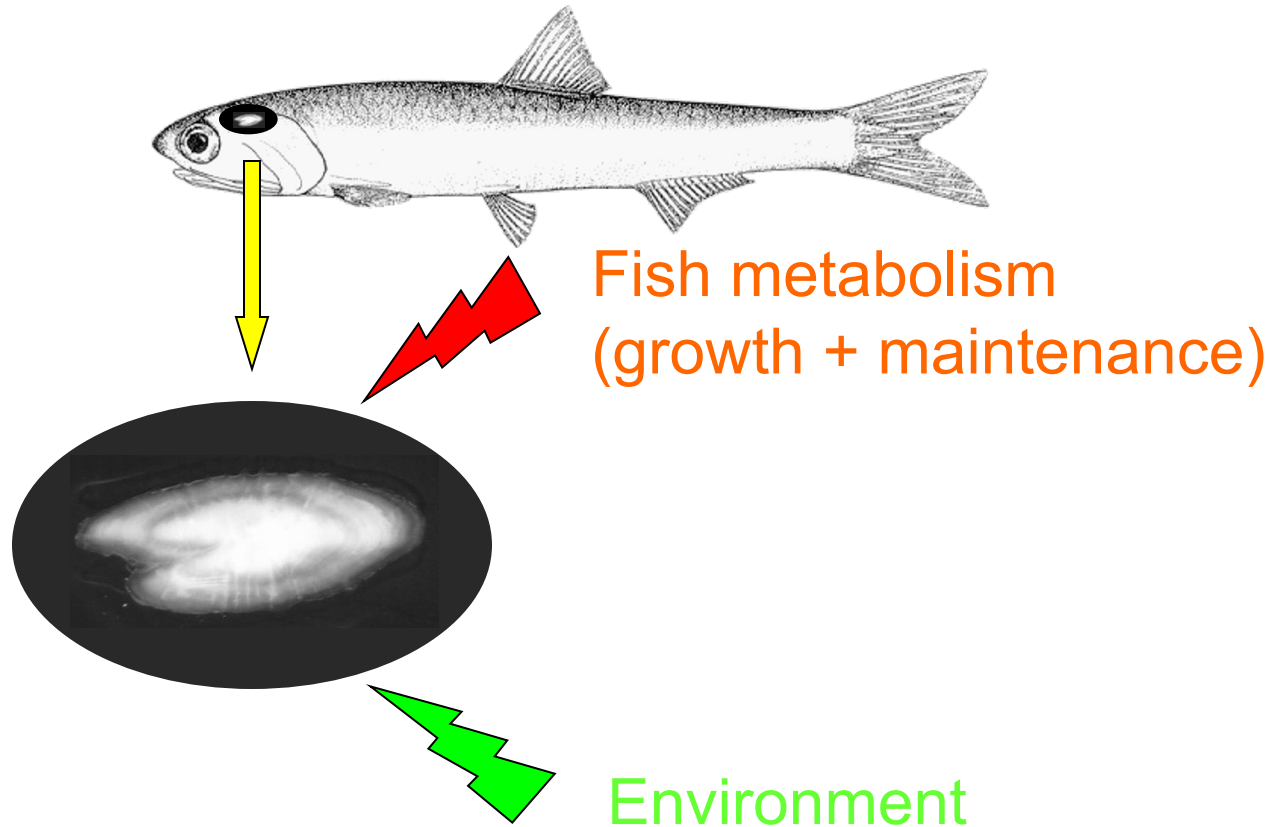
20 yr-old Butter clam
Saxidomus giganteus

(McConnaughey and Gillikin 2008)

Outline

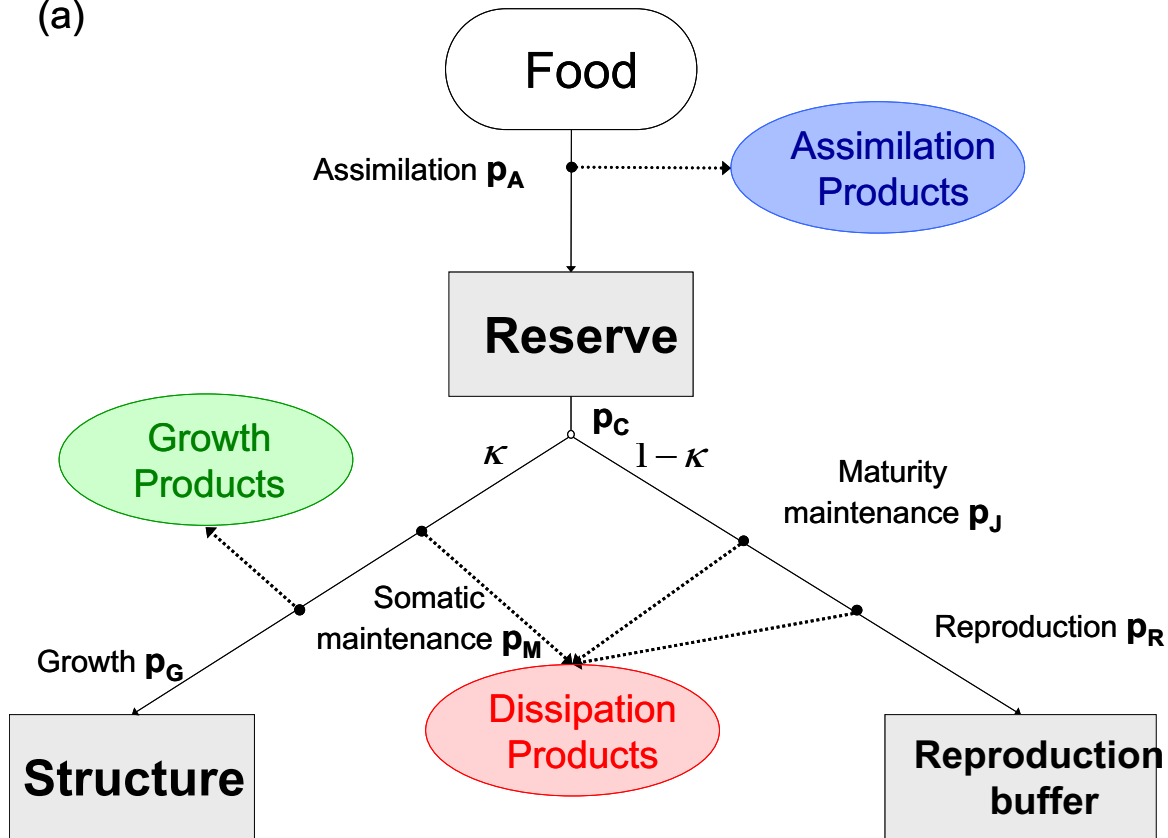
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Fish otoliths = bio-calcified structures

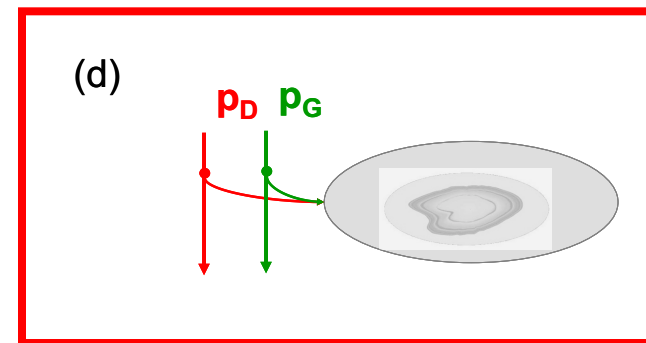
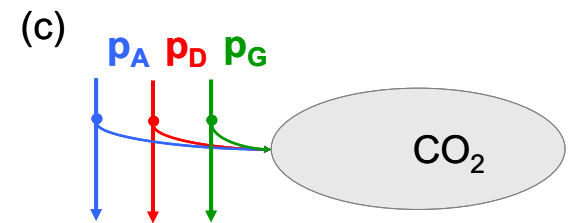
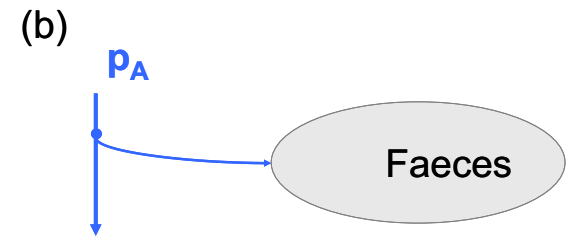
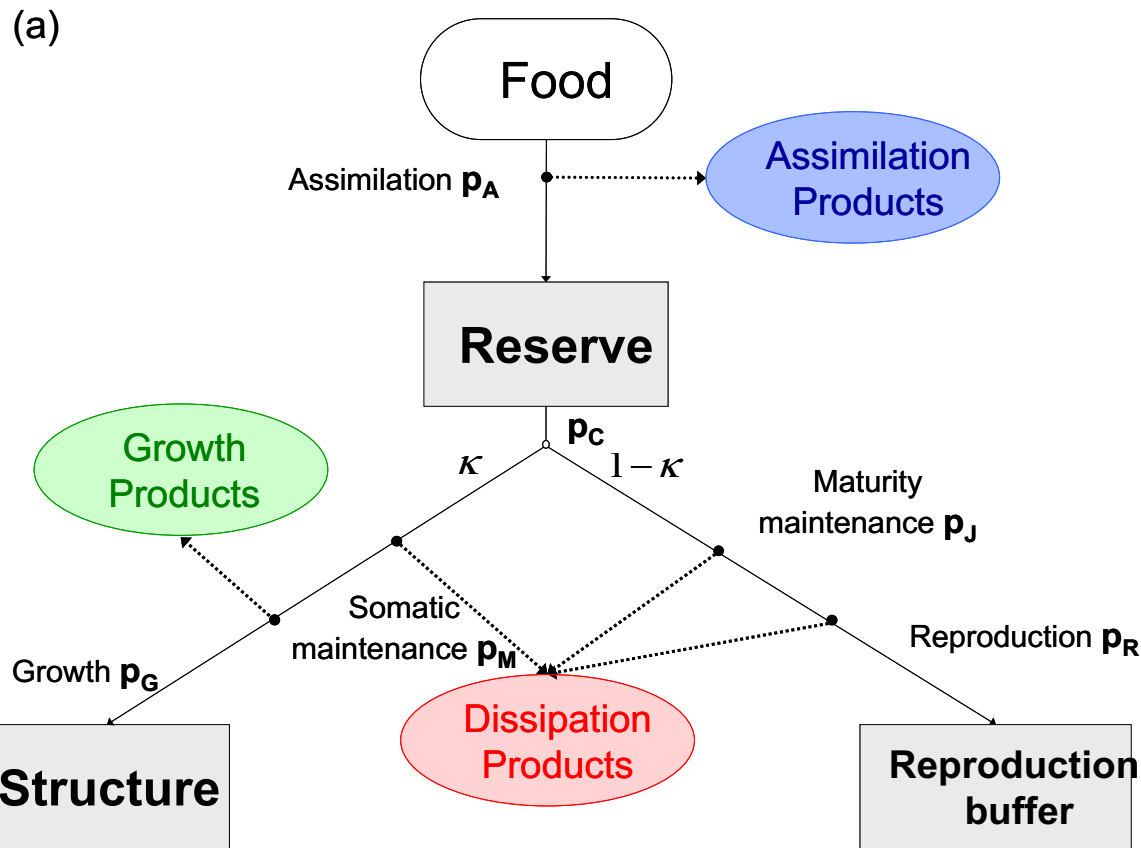


Biocarbonate = metabolic product

(a)



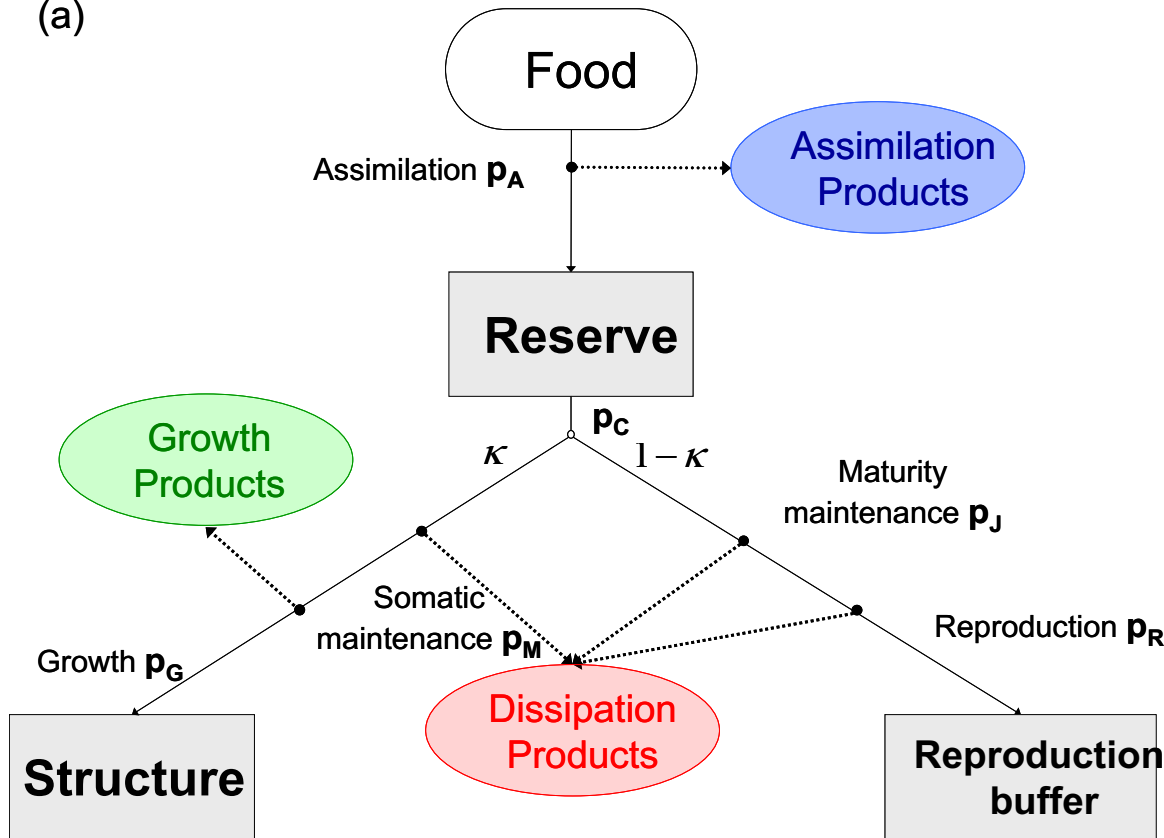
Biocarbonate = metabolic product



Assumption: biocarbonate formation coupled to growth + maintenance fluxes

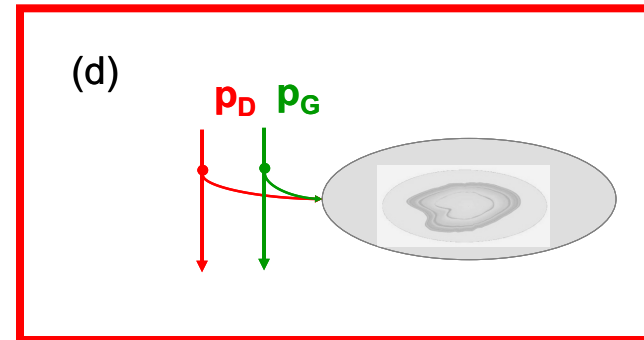
Biocarbonate = metabolic product

(a)



$$\frac{dV_o}{dt} = \alpha \dot{p}_G + \beta \dot{p}_D$$

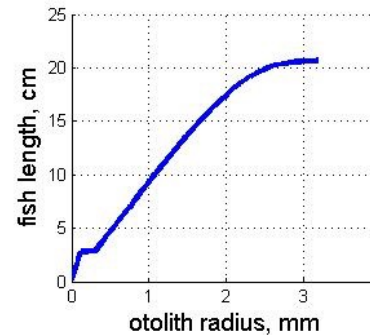
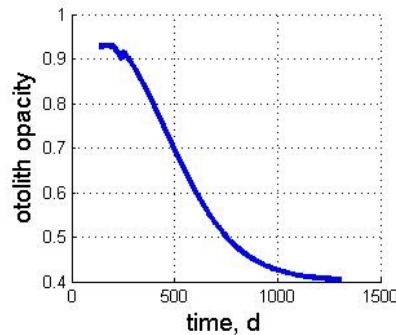
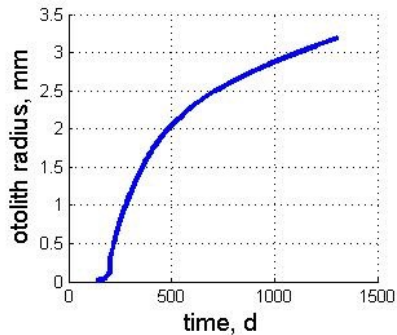
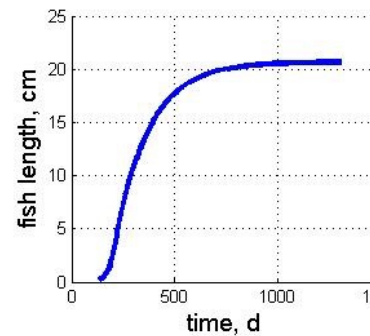
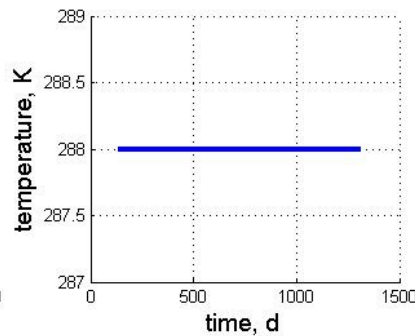
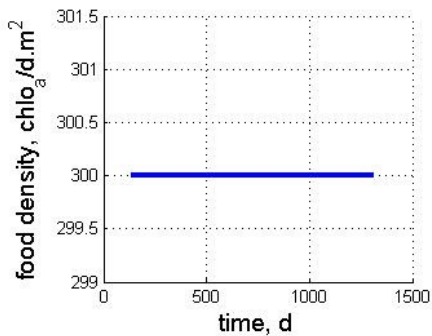
$$0 = \frac{\alpha \dot{p}_G}{\alpha \dot{p}_G + \beta \dot{p}_D}$$



Assumption: biocarbonate formation coupled to growth + maintenance fluxes

Biocarbonate = metabolic product

Simulation for a constant environment

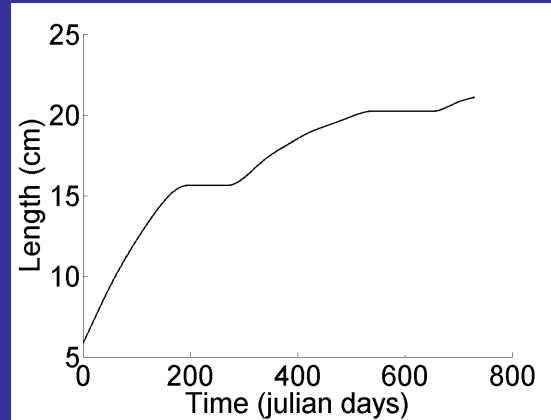
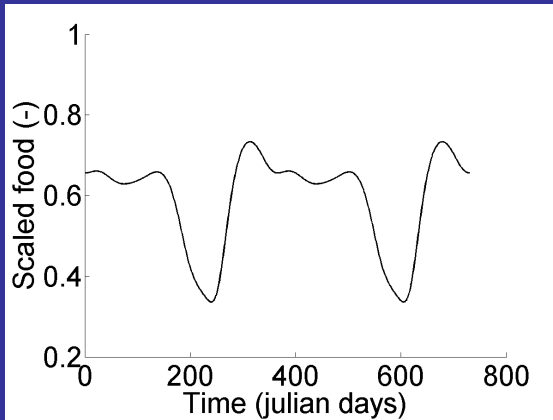
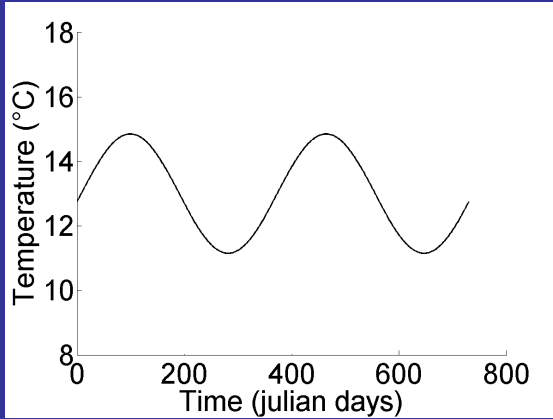


$$\frac{dV_o}{dt} = \alpha \dot{p}_G + \beta \dot{p}_D$$

$$O = \frac{\alpha \dot{p}_G}{\alpha \dot{p}_G + \beta \dot{p}_D}$$

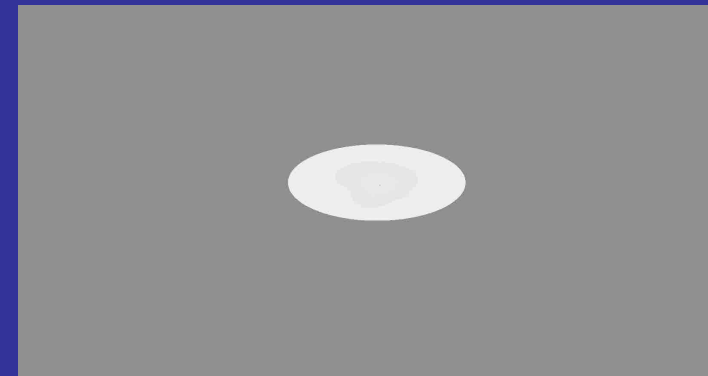
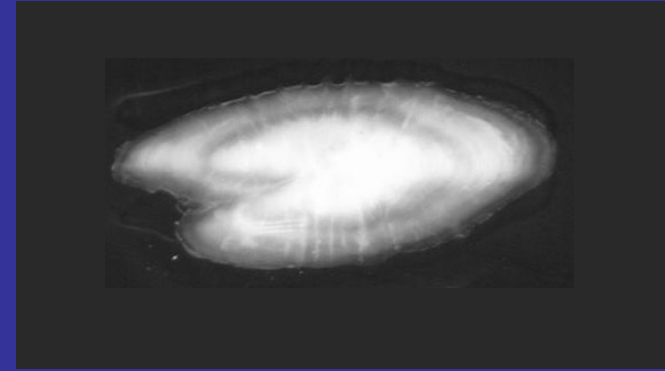
Assumption: biocarbonate formation coupled to growth + maintenance fluxes

Otolith modeling : individual history



Otolith growth and opacity

Data



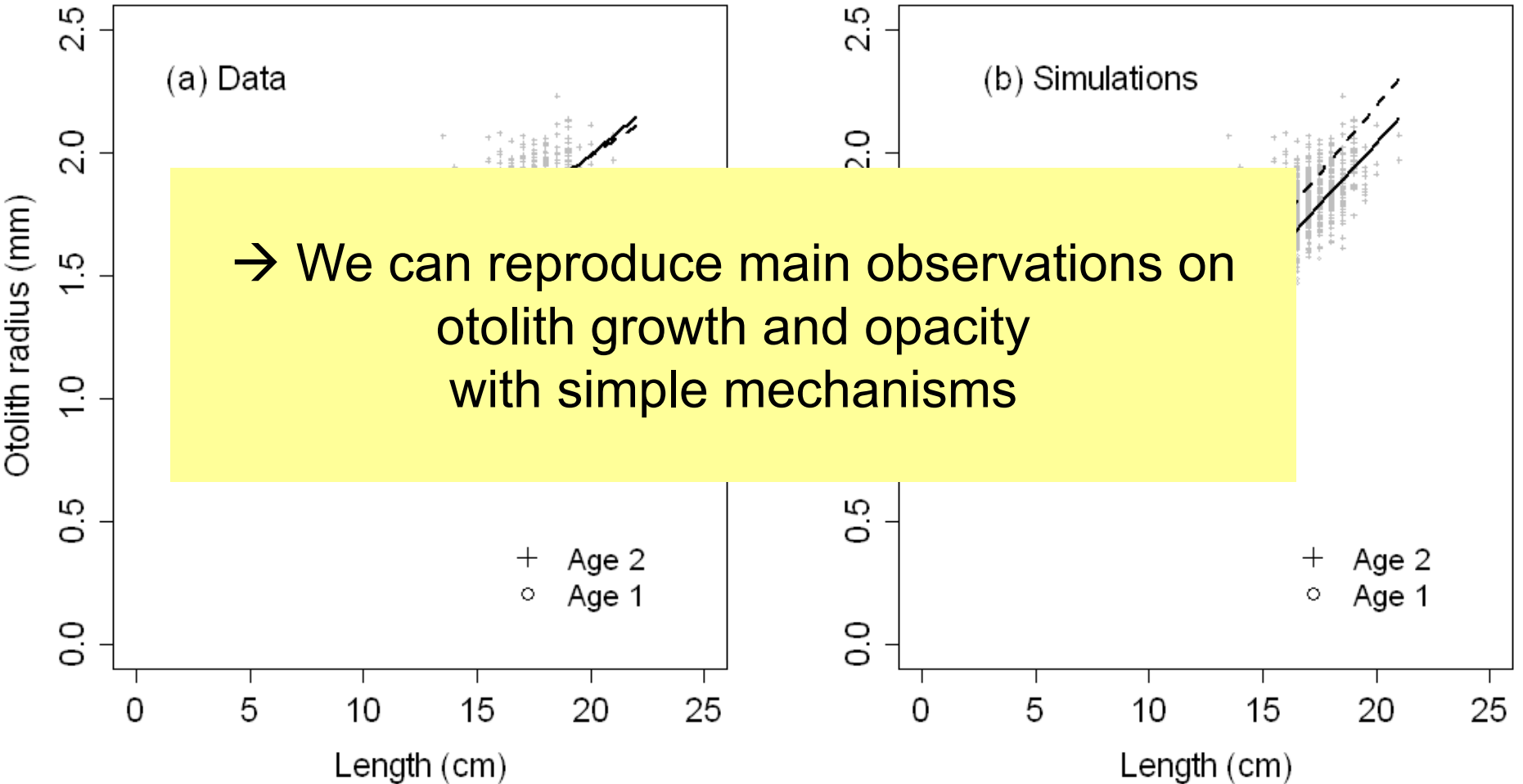
Environment \longrightarrow Length

\uparrow
DEB model

Simulation

Otolith modeling : individual history

Slow growing fish have larger otoliths



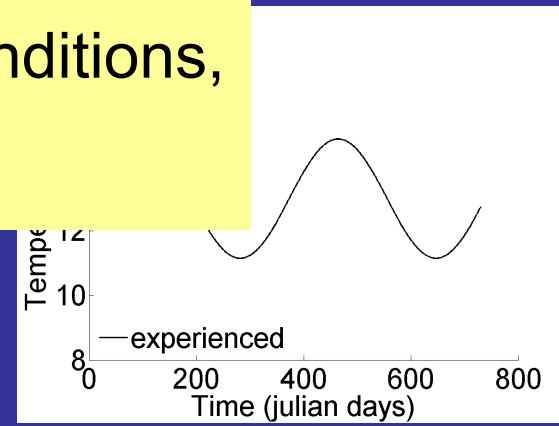
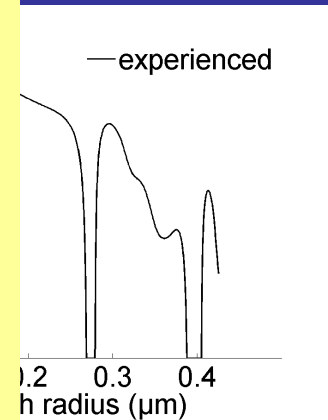
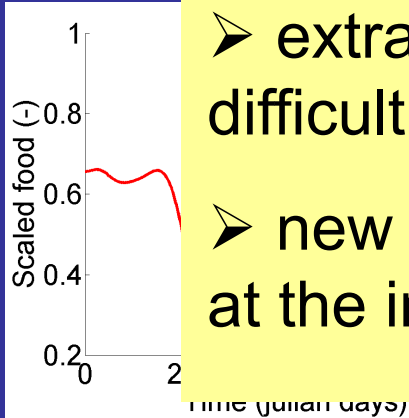
Food history reconstruction from otolith



DEB model

We can theoretically reconstruct both growth and assimilated food from temperature and otolith data

- extraction of new information from data difficult to obtain
- new information = food in natural conditions, at the individual scale



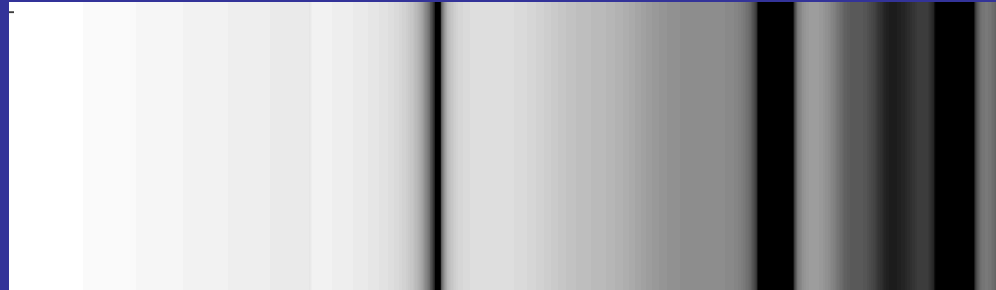
Assimilated food

+

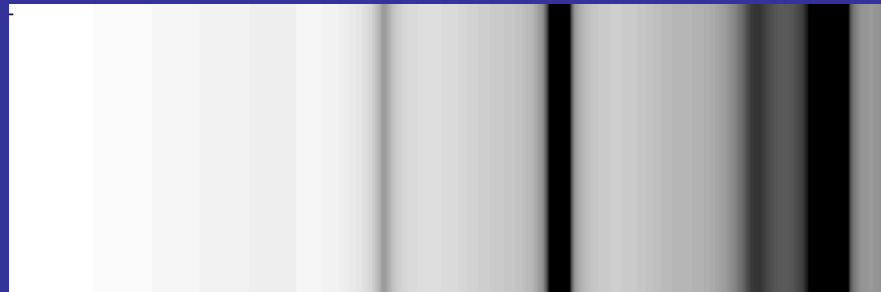
Reconstruction of length

Two age-3 individuals ?

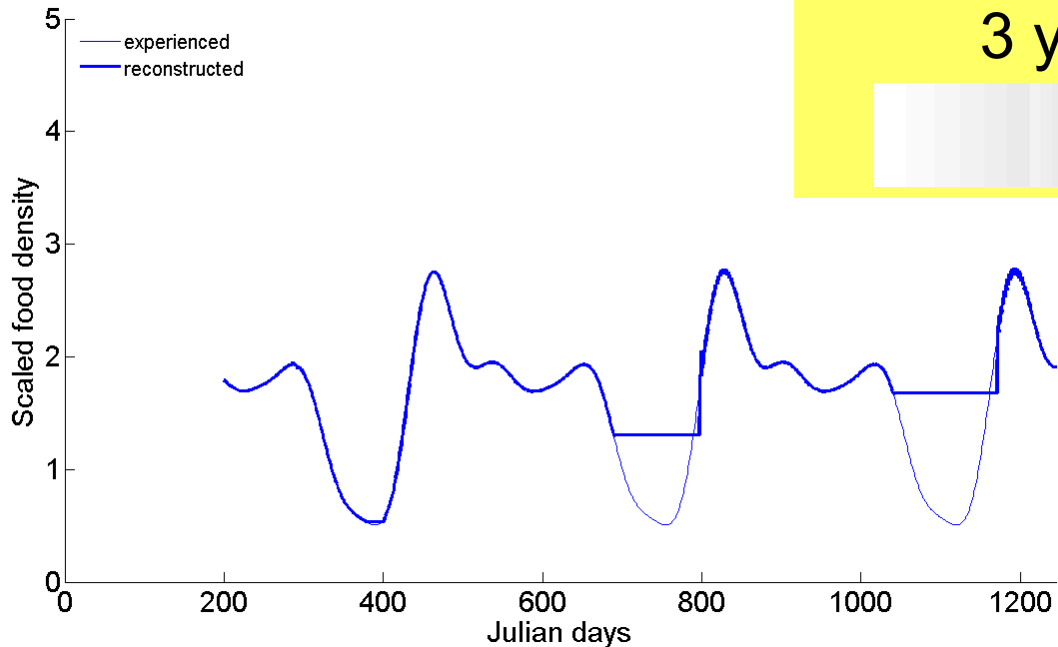
Individual 1



Individual 2



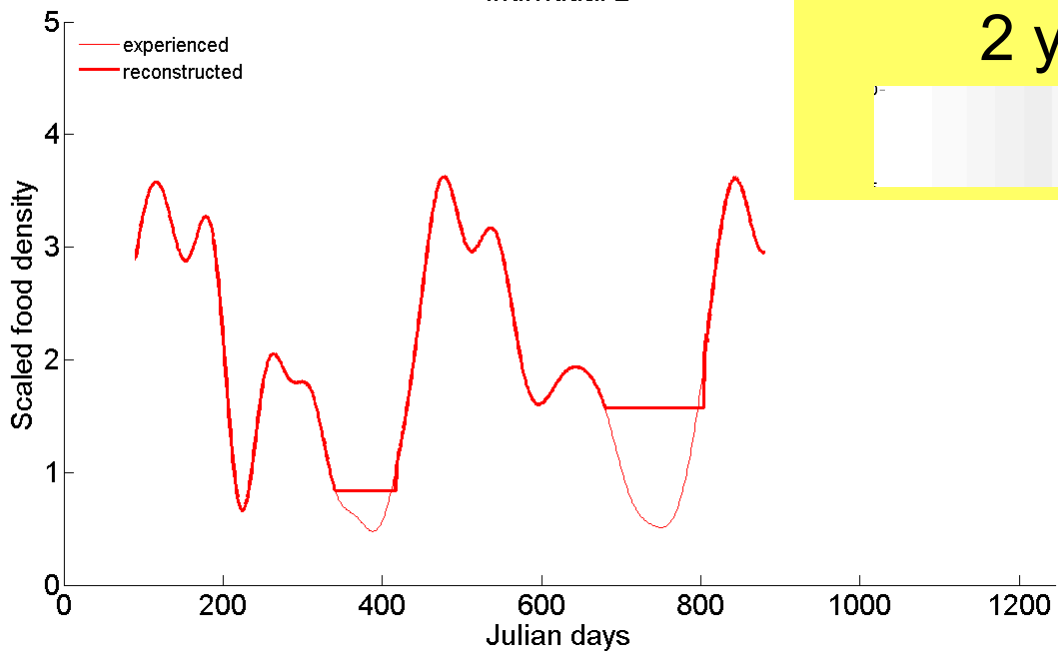
Individual 1



3 years-old



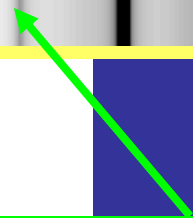
Individual 2



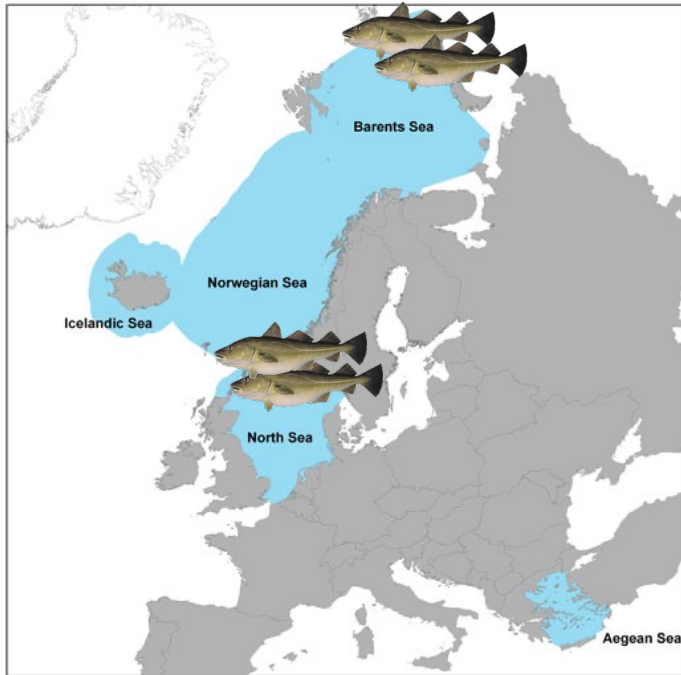
2 years-old



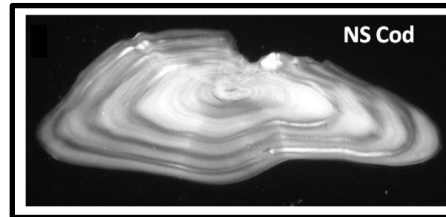
False check



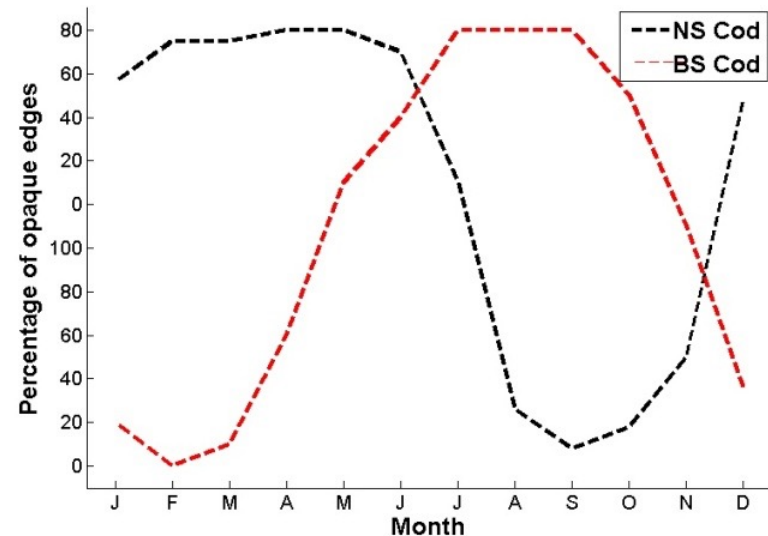
Application: North Sea (NS) cod otoliths at odds with Barents sea (BS) cod otoliths



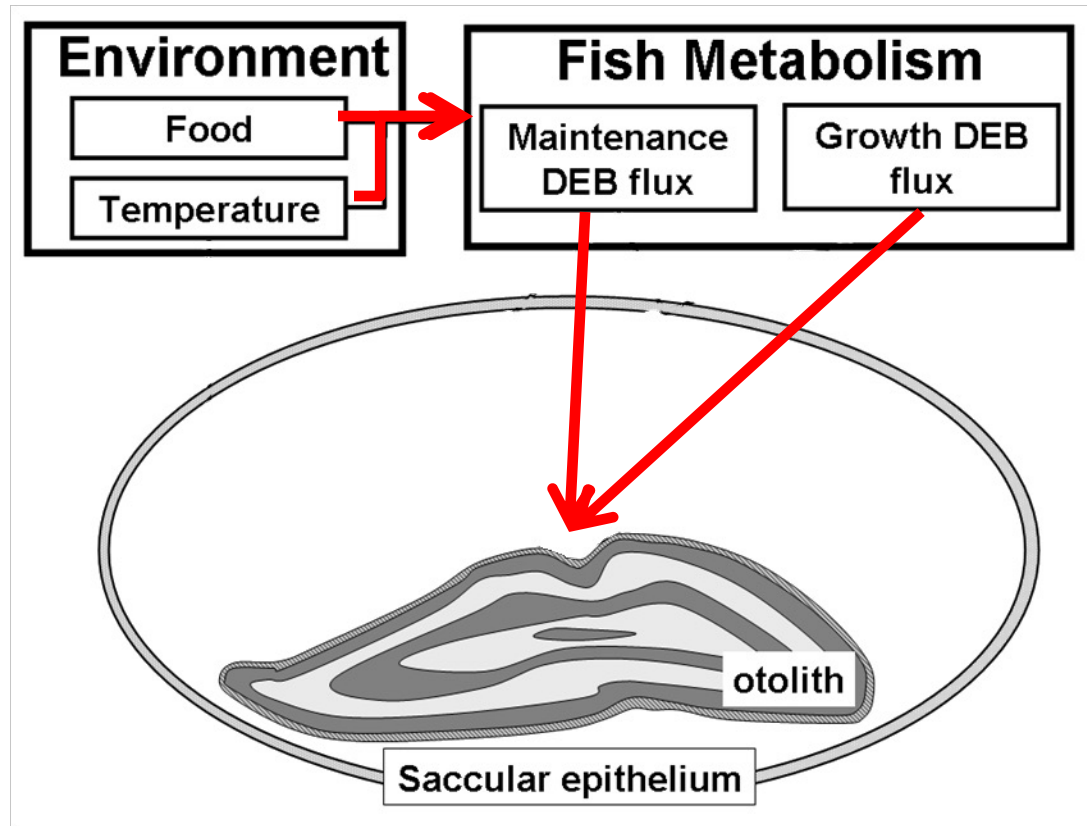
Classic pattern:
translucent edge in winter
→ Slow growth in winter



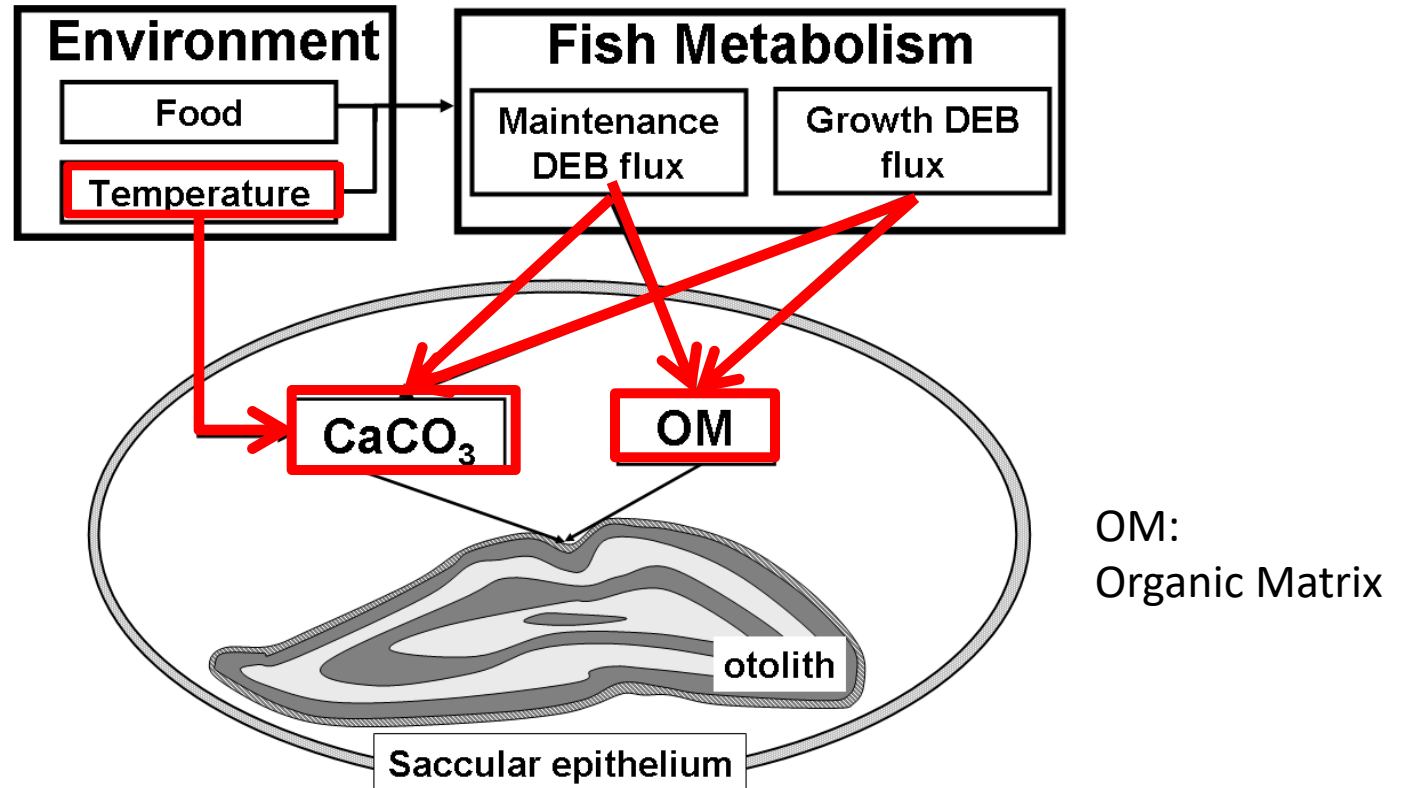
Opposite pattern:
translucent edge in summer
→ Slow growth in summer ?



Model extension to take into account temperature effect on CaCO_3 precipitation



Model extension to take into account temperature effect on CaCO_3 precipitation

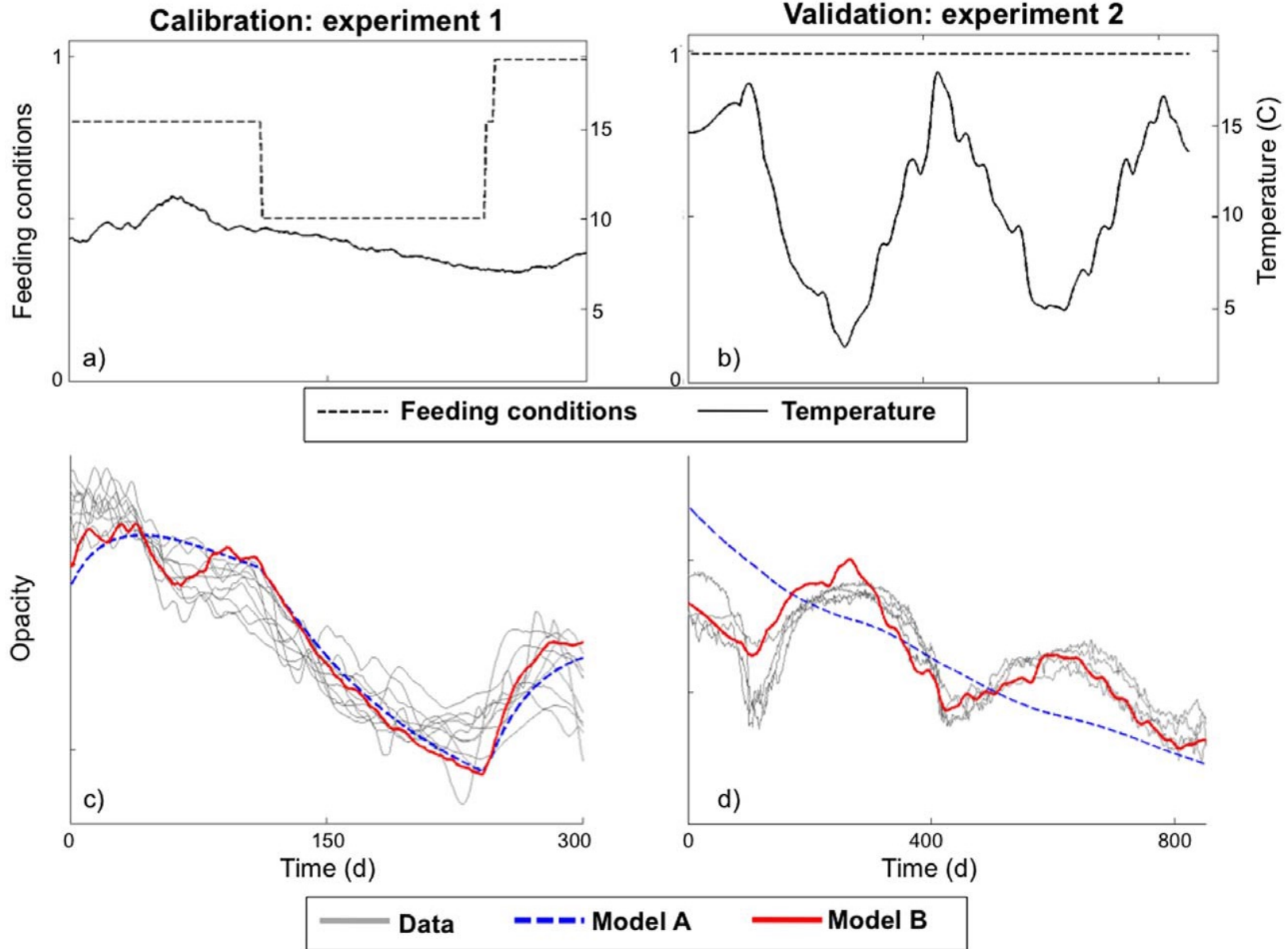


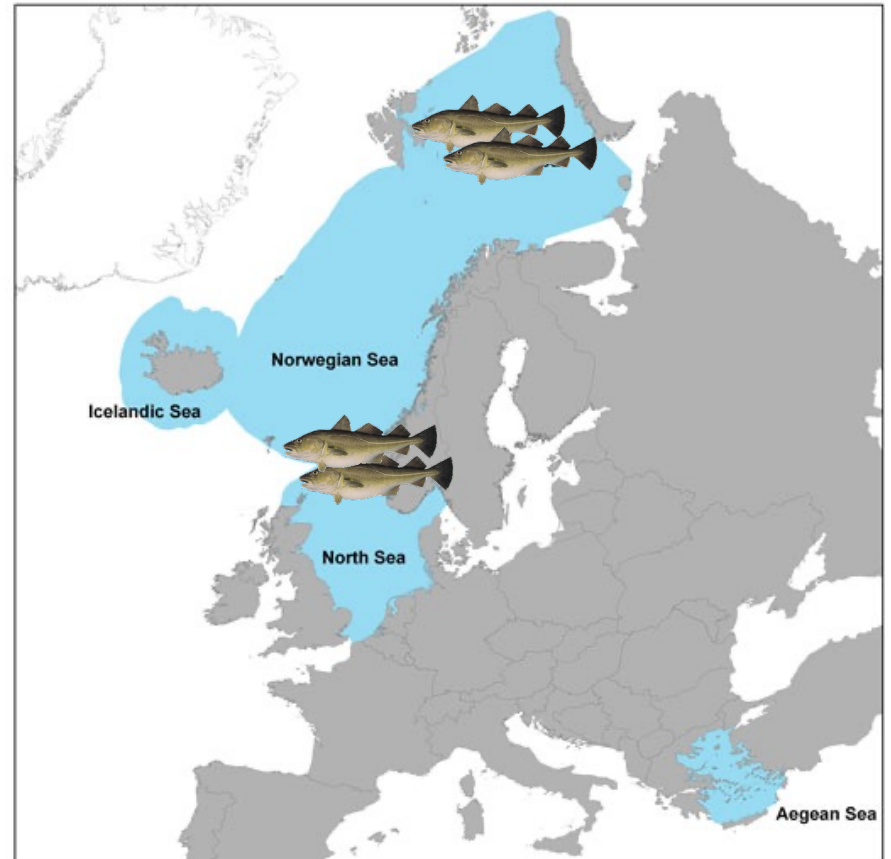
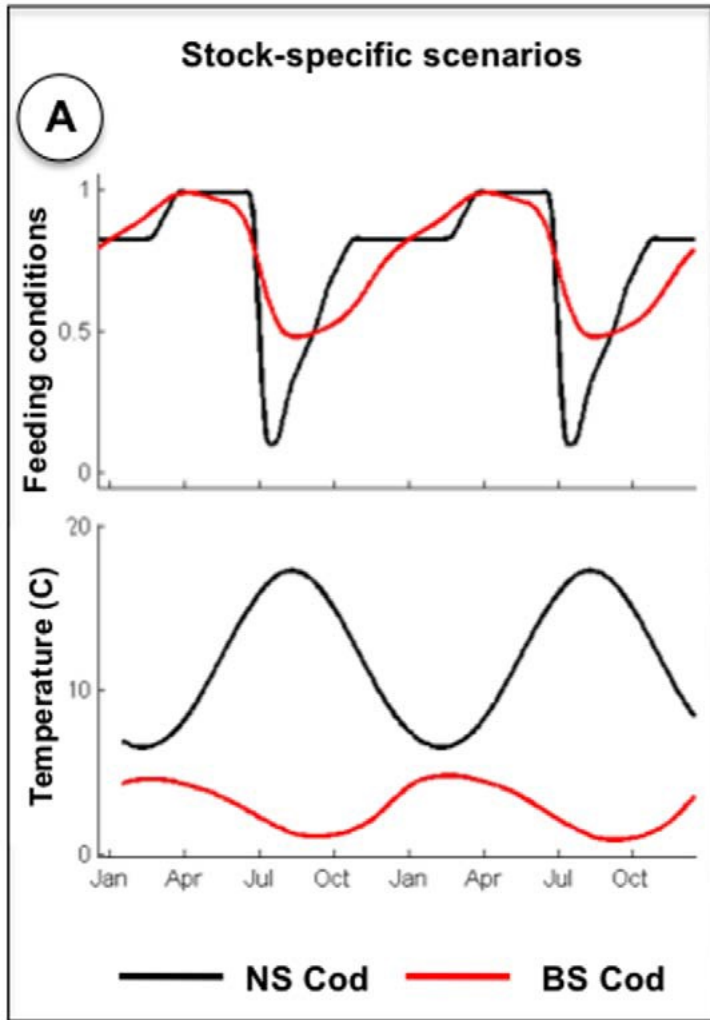
Model extension to take into account temperature effect on CaCO₃ precipitation

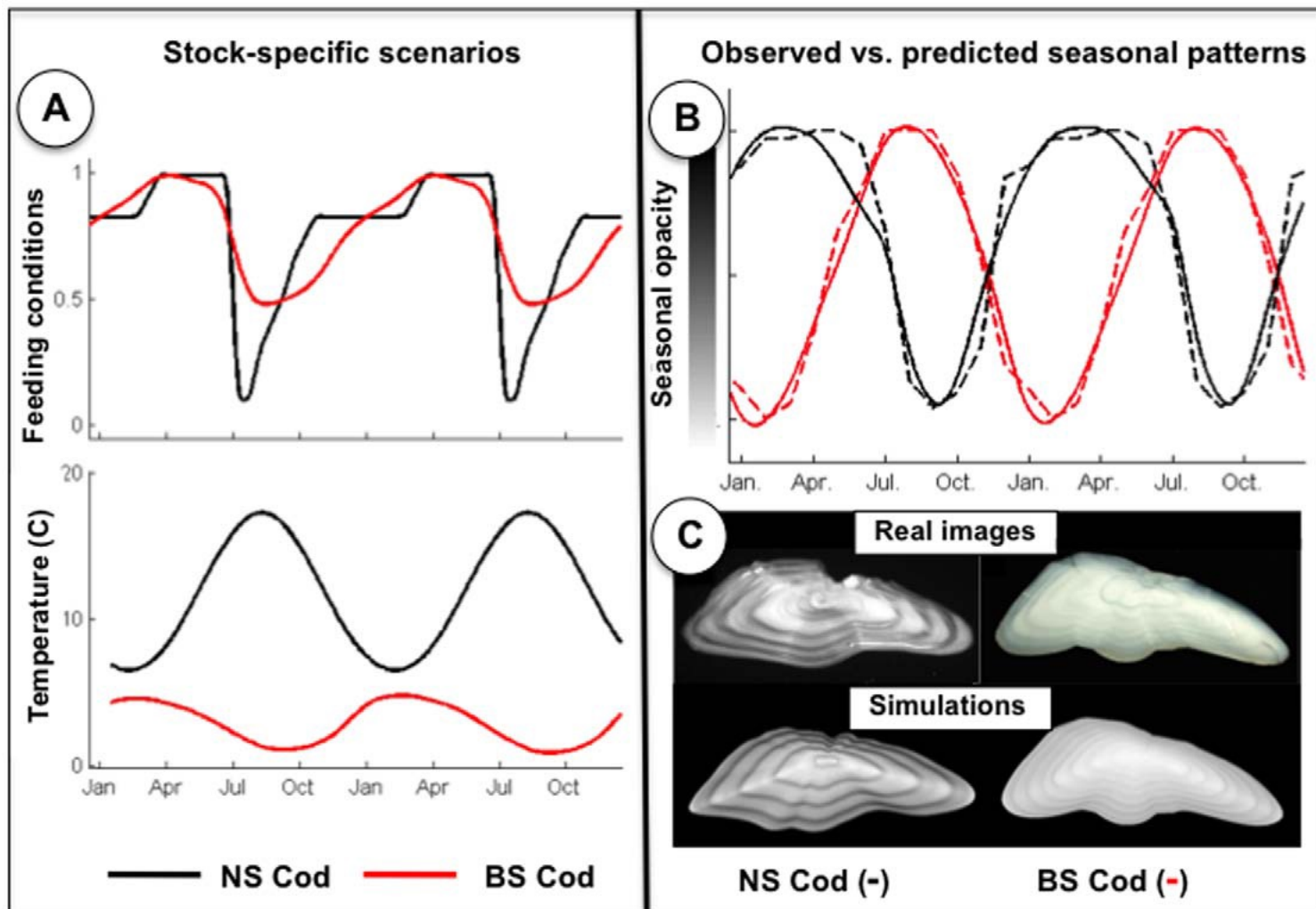
Otolith accretion = CaCO₃ (V_C) flux + OM (V_P) flux
Specific temperature effect on dV_C/dt

$$\frac{dV_C}{dt} = c_C(T) \cdot [\alpha_C p_G + \beta_C p_M]$$
$$L_O = \frac{V_C^{1/3}}{\delta_O}$$
$$O = \frac{\Delta V_P}{\Delta V_C} \approx \frac{dV_P/dt}{dV_C/dt} = \frac{1}{c_C(T)} \cdot \frac{\alpha_P p_G + \beta_P p_M}{\alpha_C p_G + \beta_C p_M}$$

Model calibration and validation with long-term experimental data







Summary

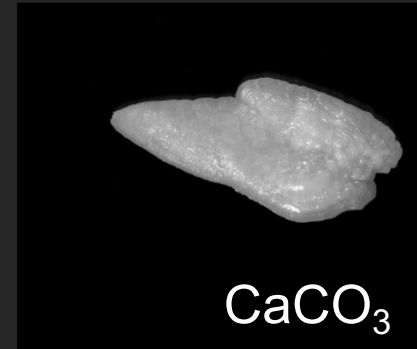
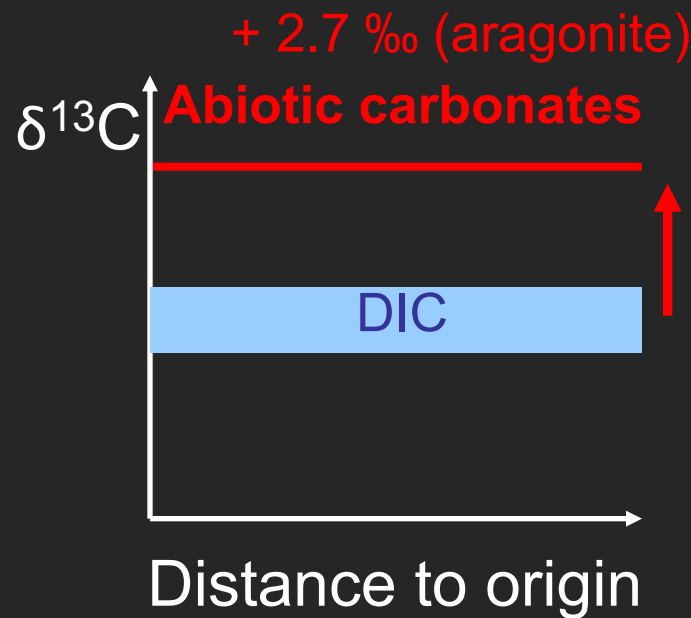
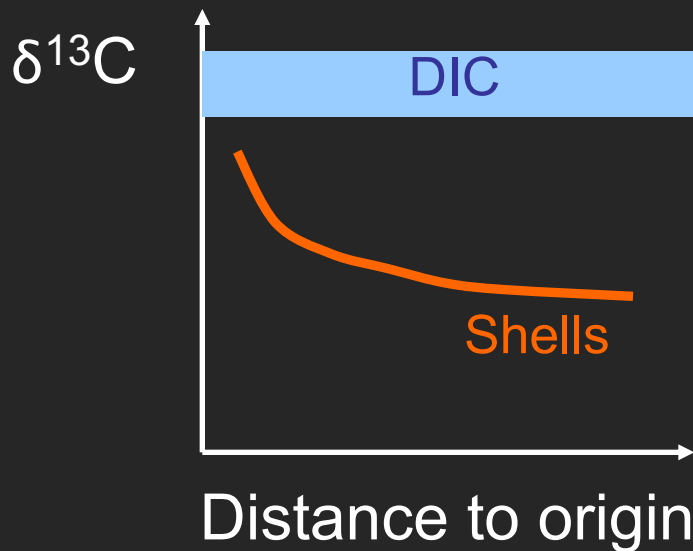
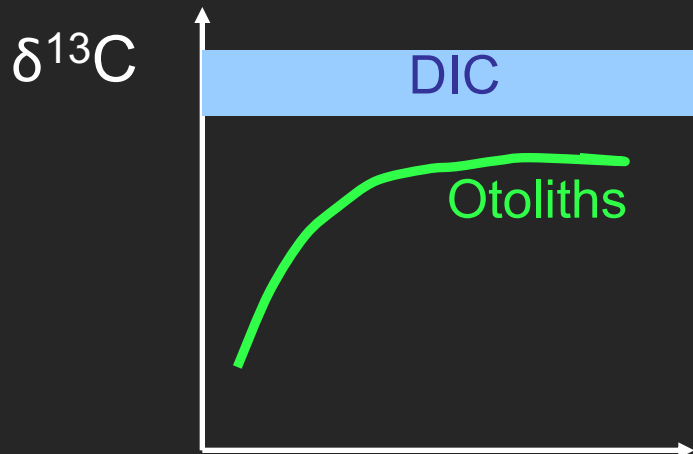
Biogenic carbonates physical properties

- DEB theory = new approach to study biomineralization processes at the individual scale
- First step: Annual scale, ontogeny --> macro-structures
Experimental validation
- New information, new interpretation by taking into account the interactions between environmental and physiological drivers
- Step-wise approach from simple → more complex model to reproduce the different patterns (temperature effect on CaCO_3 precipitation)

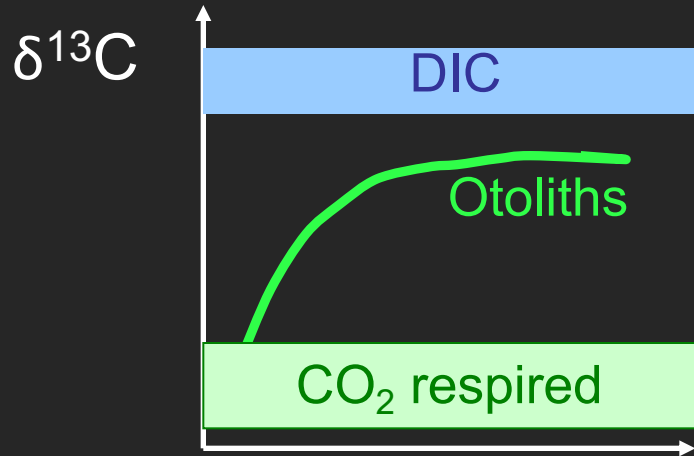
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- Chemical composition ($\delta^{13}\text{C}$): what can we learn from otoliths and shells comparison?
- Summary and perspectives
 - Annual \rightarrow Daily scale
 - Shell growth
 - Ocean acidification

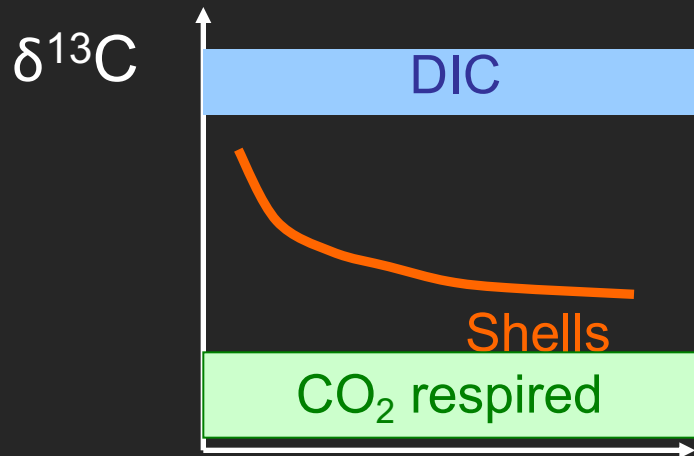
$\delta^{13}\text{C}$ in otoliths and shells differ in ontogenic patterns



Carbon in biogenic carbonates also originates from CO_2 respired



CO_2

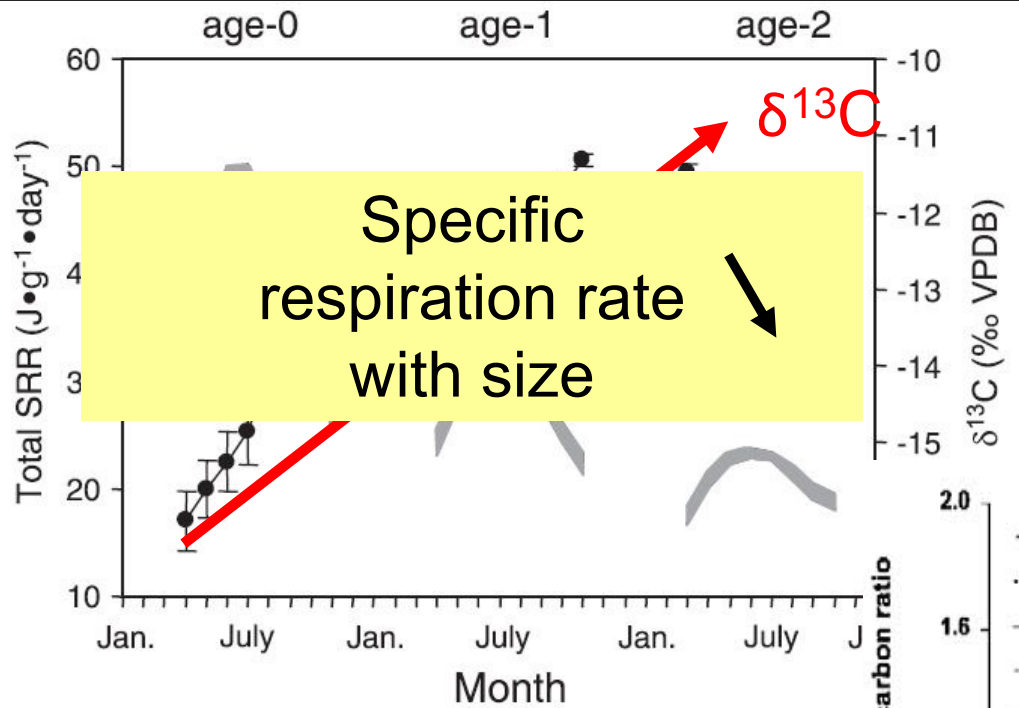


CO_2



Distance to origin

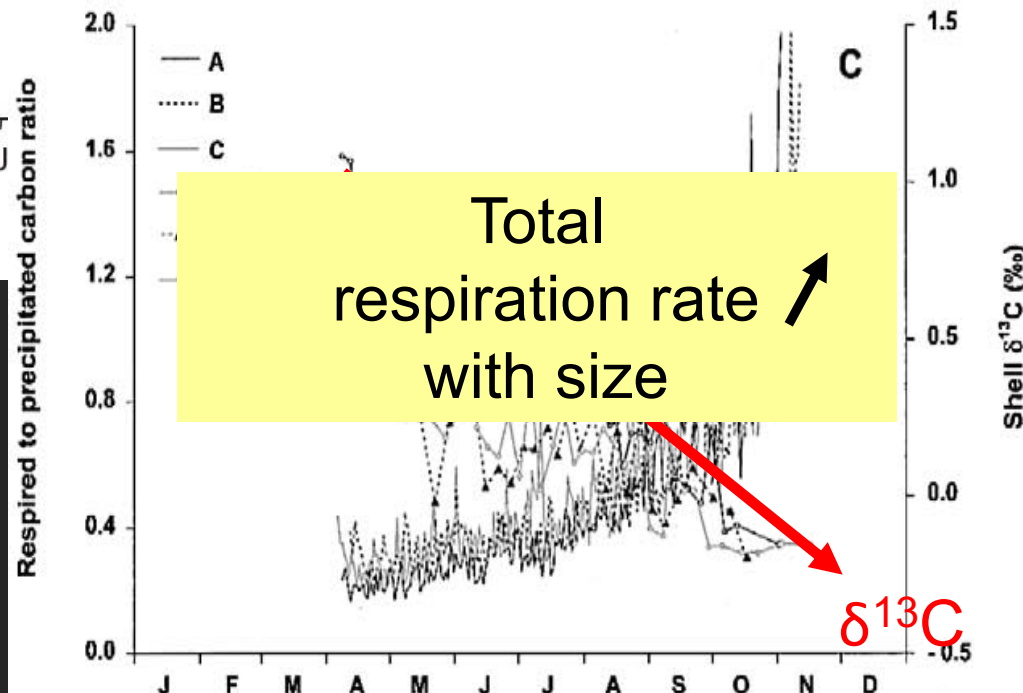
Different interpretations of the ontogenic patterns in otoliths and bivalves



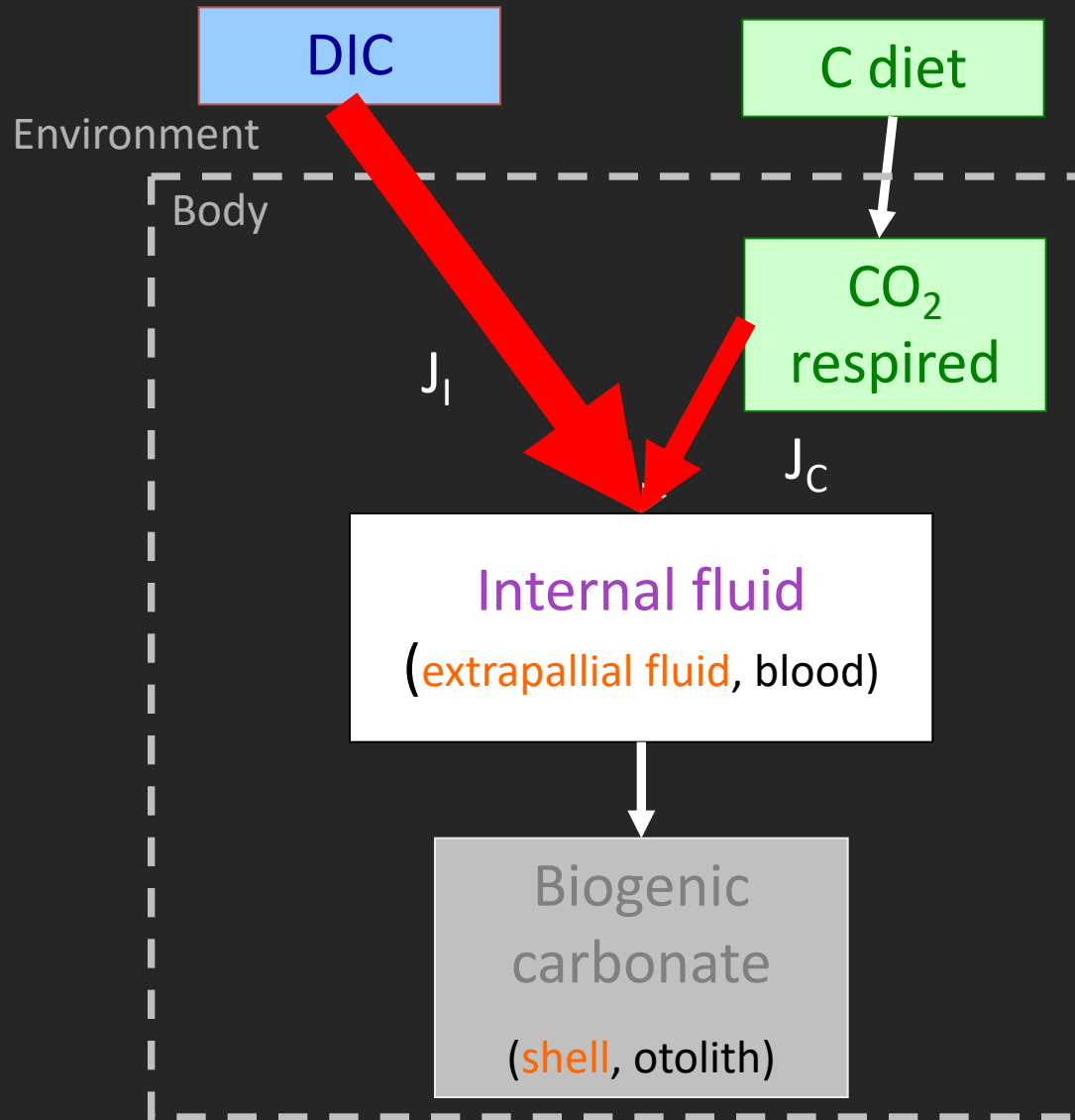
(Dufour et al. 2007)



(Lorrain et al. 2004)



Proposed definition for the proportion of metabolic carbon that precipitates



Proposed definition for the proportion of metabolic carbon that precipitates

- We define $M = \frac{J_C}{J_C + J_I}$

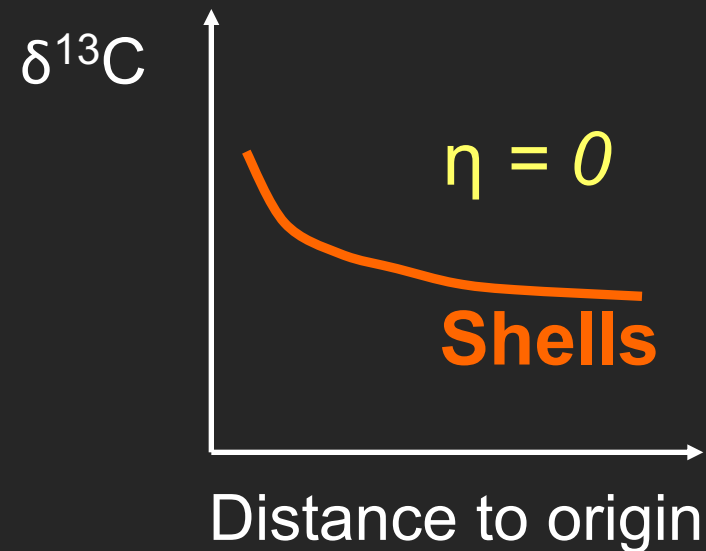
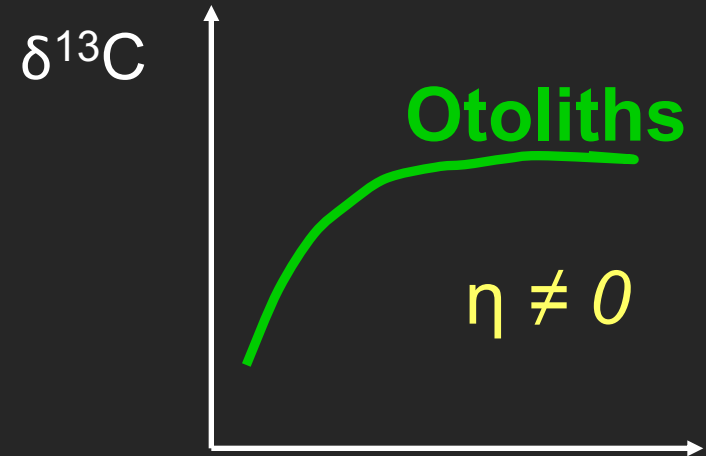
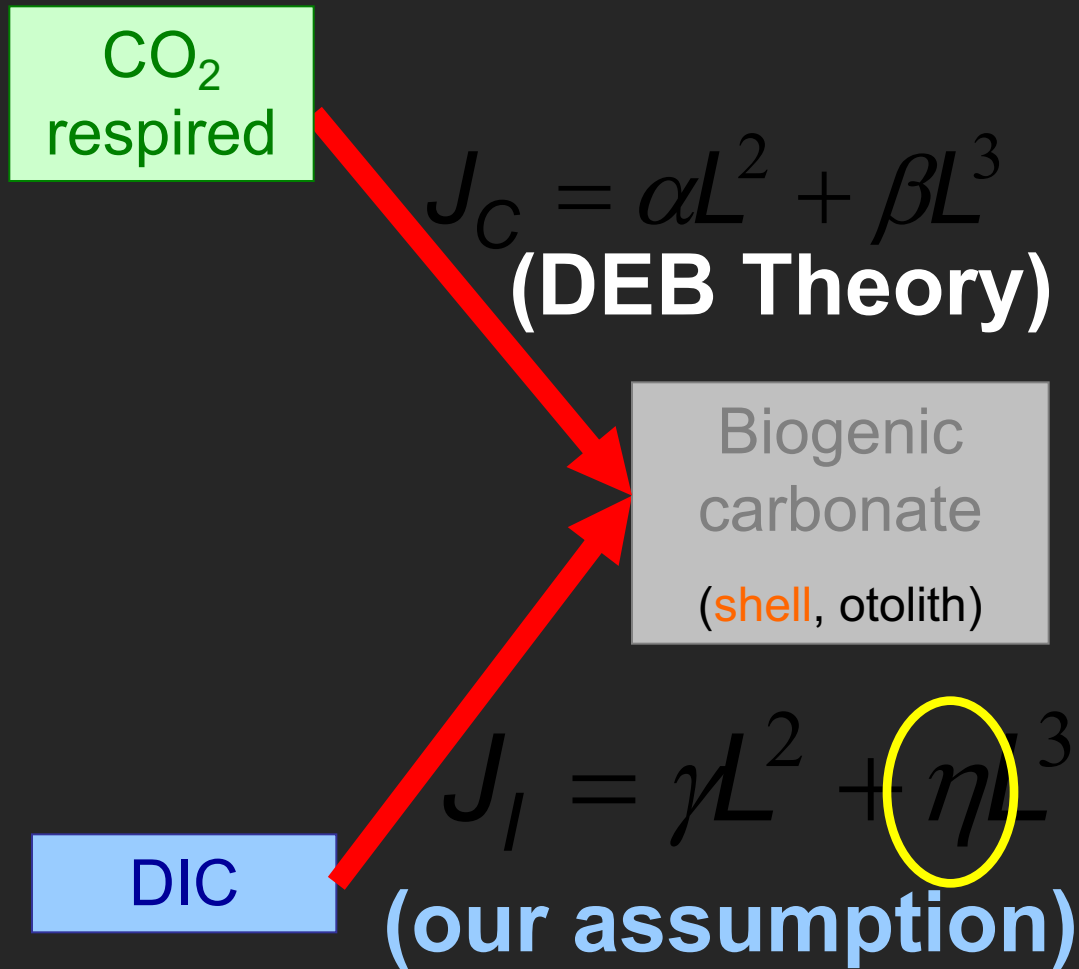
J_C flux of metabolic carbon (Cmoles d⁻¹)

J_I flux of inorganic carbon (Cmoles d⁻¹)

- $$\delta^{13}C_{carb} = M \delta^{13}C_m + (1 - M) \delta^{13}C_i$$
$$= \delta^{13}C_i + M (\delta^{13}C_m - \delta^{13}C_i)$$

→ If the difference is large, small variations of M will generate large variations of $\delta^{13}C_{carb}$

Proposed mechanism for the variation of the proportion of metabolic carbon that precipitates



Ontogeny pattern: DIC entrance flux scales differently with structure in fish and bivalves

Otoliths

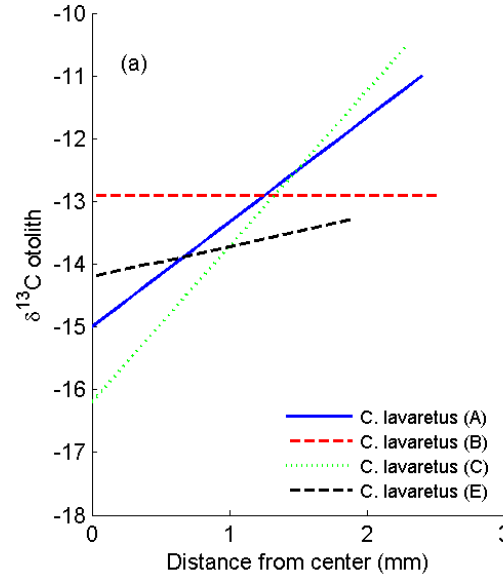


Whitefish
Coregonus lavaretus
(Dufour et al, 2007)

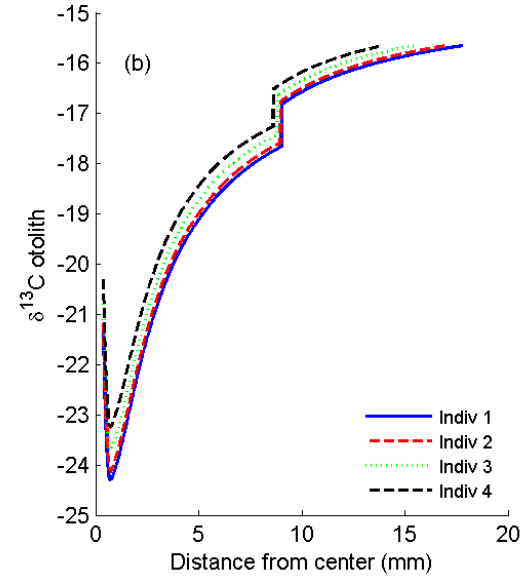
$$J_l = \gamma L^2 + \eta L^3$$

$$\eta \neq 0$$

Data



Simulations



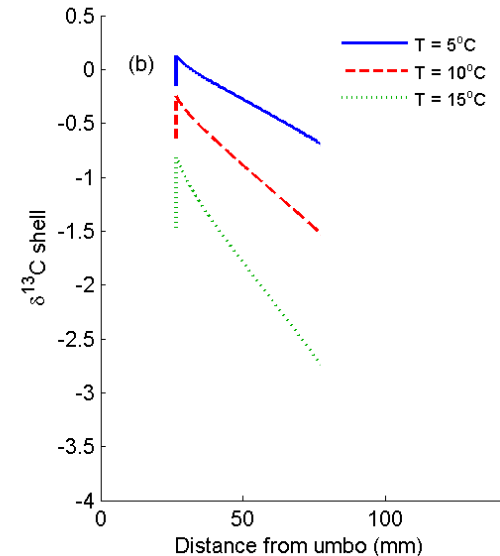
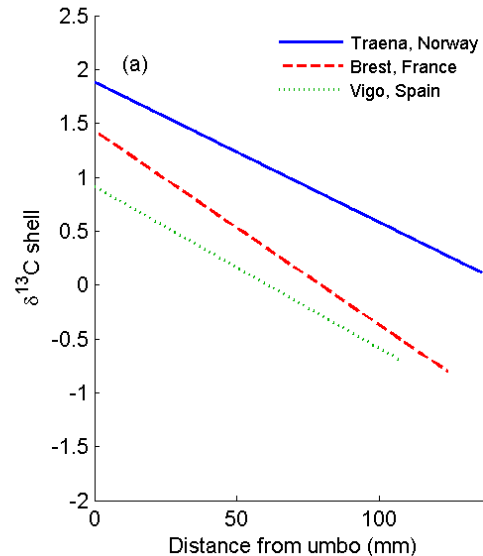
Shells



Great scallop
Pecten maximus
(Chauvaud et al., 2011)

$$J_l = \gamma L^2 + \eta L^3$$

$$\eta = 0$$

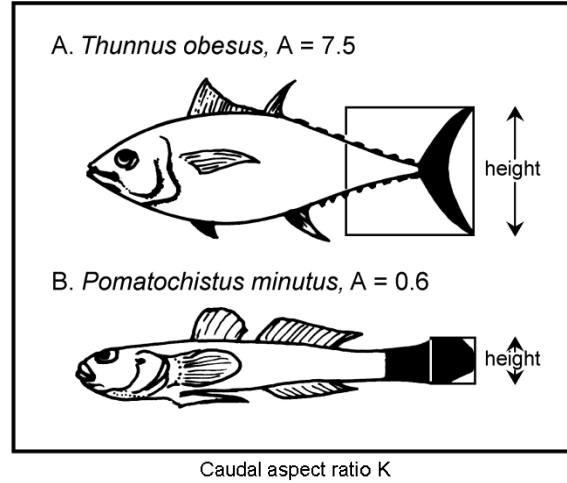
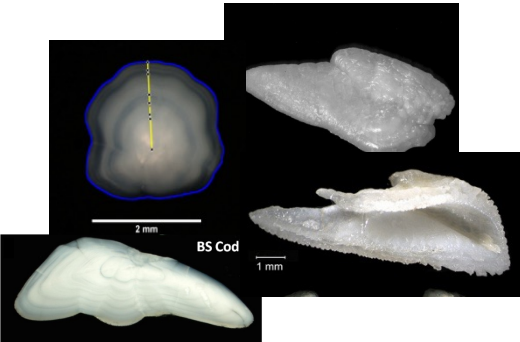


Inter-species comparison

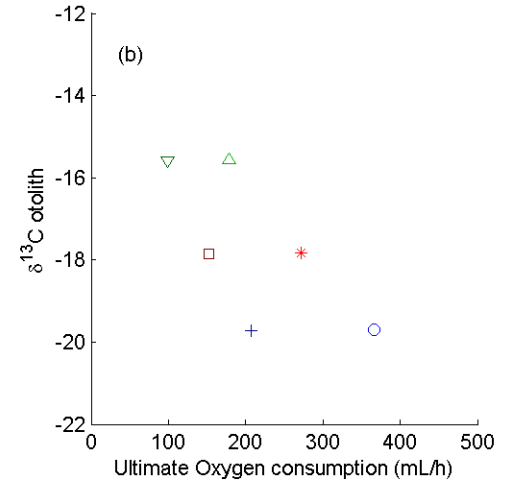
Data

Simulations

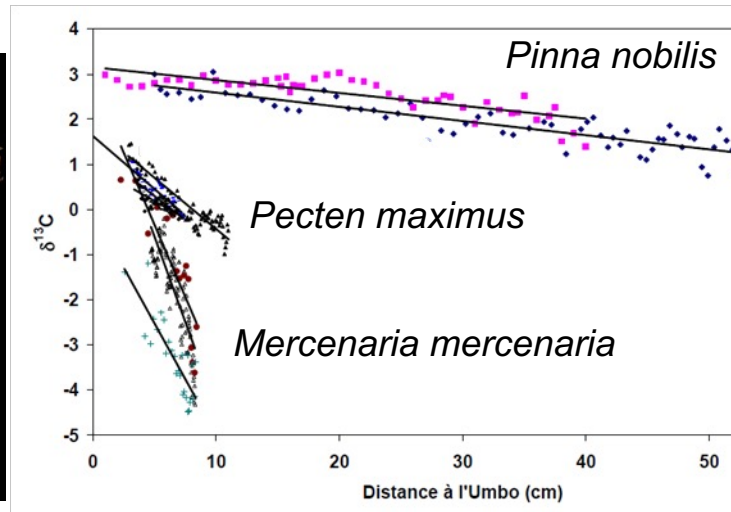
Otoliths



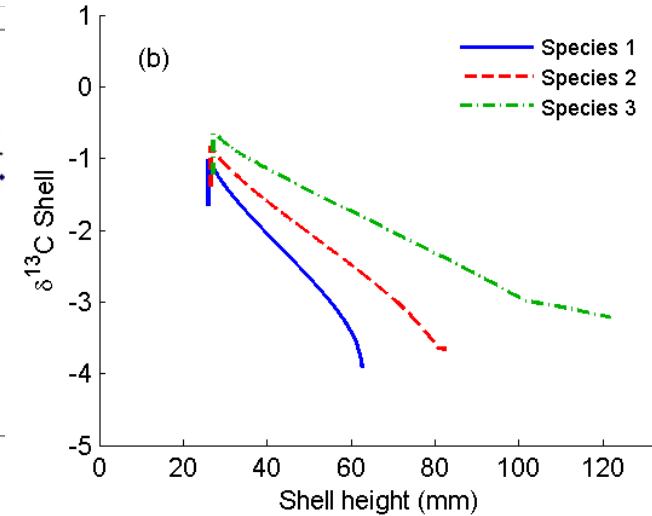
(Sherwood and Rose, 2003)



Shells



(Y.-M. Paulet, 2005, data from: Freitqs et al. 2005, Lorrain et al. 2004, Gillikin 2005))



Seasonal pattern: Simplest assumption → No specific temperature on DIC entrance flux

Data

Simulations

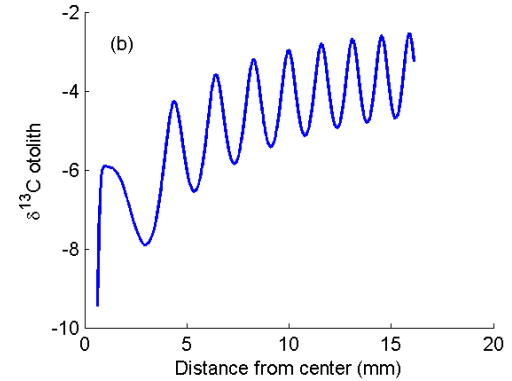
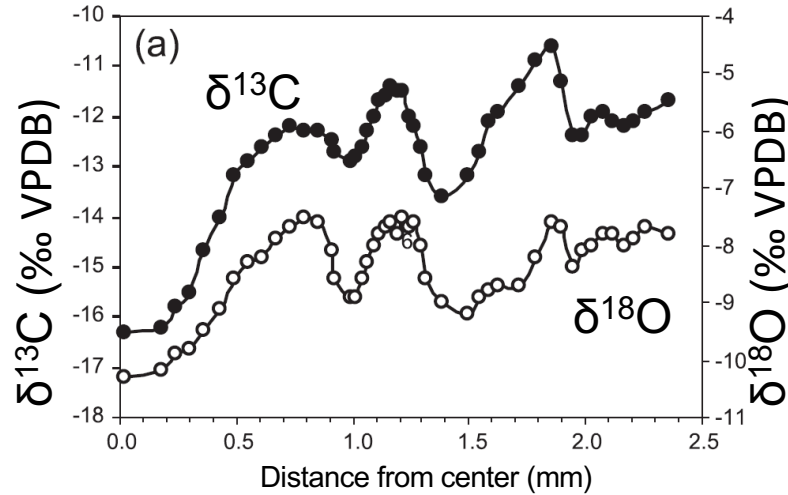
Otoliths



Whitefish
Coregonus lavaretus
(Dufour et al, 2007)

$$J_I = \gamma L^2 + \eta L^3$$

$$C_T = 1$$



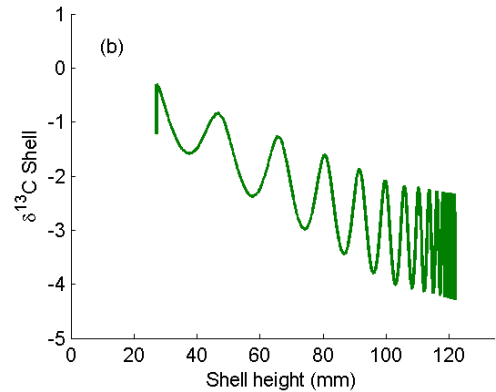
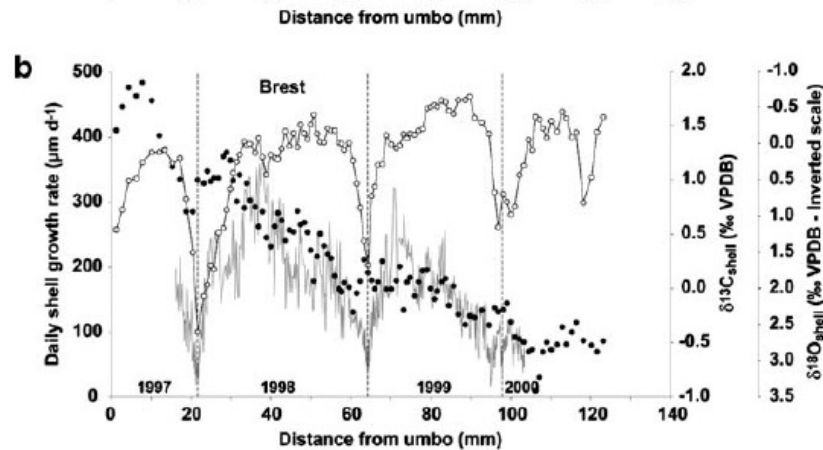
Shells



Great scallop
Pecten maximus
(Chauvaud et al., 2011)

$$J_I = \gamma L^2 + \eta L^3$$

$$C_T = 1$$



Summary

Biogenic carbonates chemical composition

- Potential mechanism explaining ontogenic patterns in both shells and otoliths: processes controlling the entrance of Dissolved Inorganic Carbon (DIC)
- New questions!
 - Which mechanism could explain that DIC entrance flux scales with a weighted sum of L2 and L3 processes?
 - Which temperature dependence?
- ^{14}C experiments?

Perspectives



- Otoliths: daily scale, other species, experimental validation

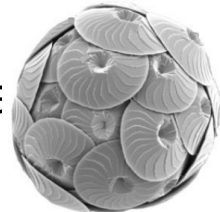
October 24, 2012

Two million fish ear bones contain new environmental insights

- Shells: shell growth movie premiere for DEB 2015! with J. Flye Sainte Marie
shell color variation, length and thickness + isotopic composition (oxygen, carbon)



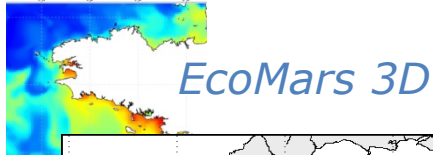
- Ocean Acidification
→ Talk on Friday morning: Modeling the impact of ocean acidification on marine calcifiers. E.B. Muller, R.M. Nisbet



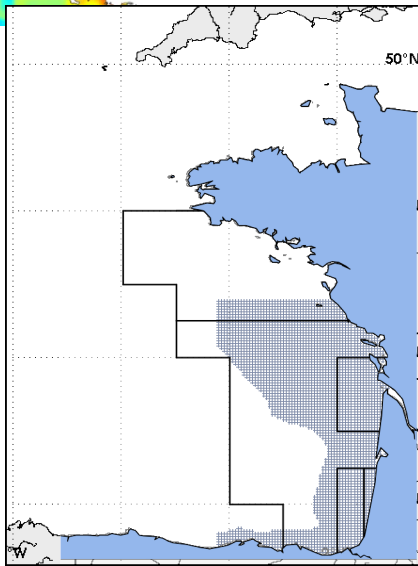
Coccolithophorid *Emiliana huxleyi*

Perspectives: Connectivity, Larval dispersal

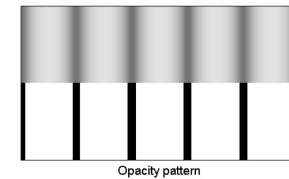
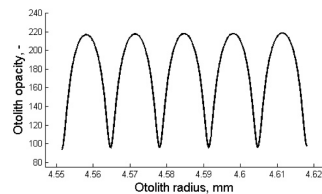
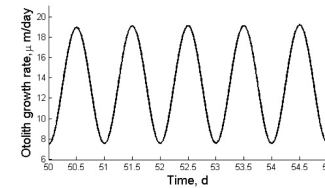
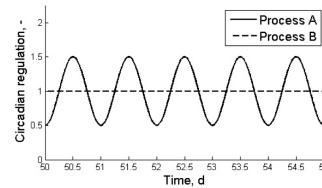
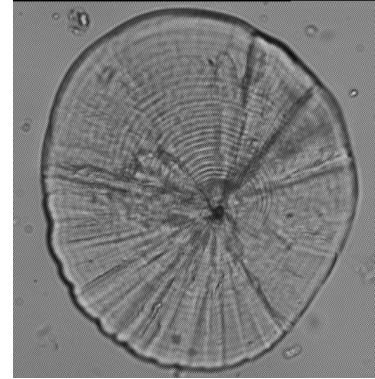
Validation of larval dispersal simulations



EcoMars 3D



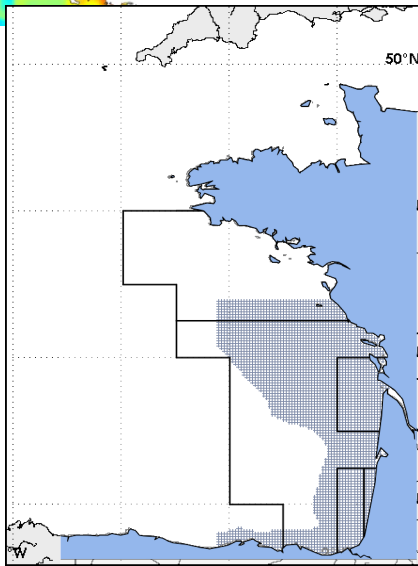
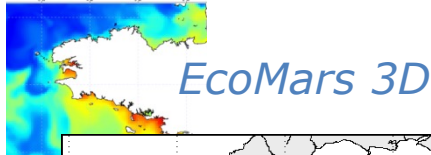
M. Huret, Ifremer



Microstructure pattern
R. Fablet, H. de Pontual

Perspectives: Connectivity, Larval dispersal and migrations?

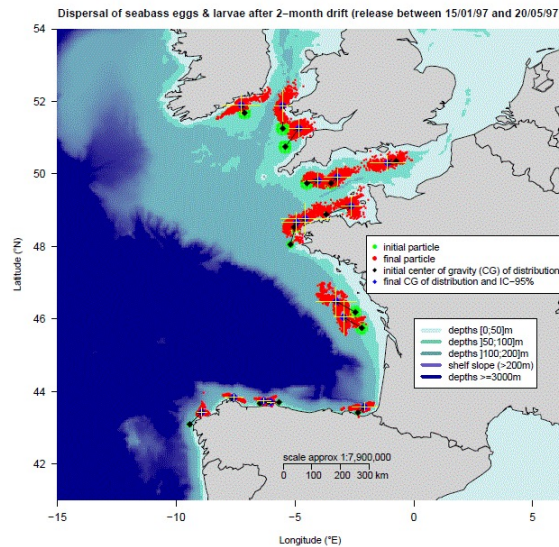
Validation of larval dispersal simulations and migrations



M. Huret, Ifremer



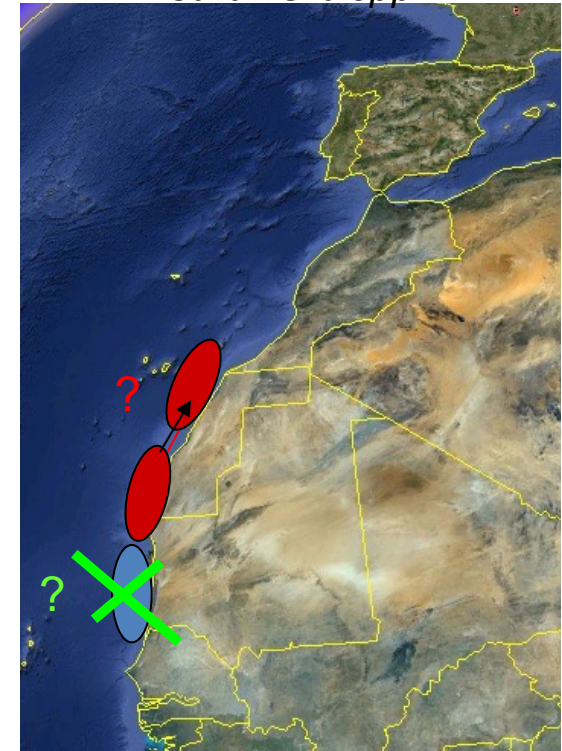
Seabass,
Dicentrarchus labrax



R. Lopez, M. Huret, H de Pontual,
Ifremer, France



Round Sardinella
Sardinella spp.



T. Brochier, C. Lett,
P. Verley (ICHTHYOP, IRD)

Summary

Biogenic carbonates = Treasure of information *when* we can decipher them

Challenging but often the only way to reconstruct individual trajectories in natural environments (\neq from trajectories obtained from sample averages) and past environmental conditions

Biomineralization processes and DEB theory = Conceptual and quantitative framework to better understand the interaction between (dynamic) environmental and physiological drivers controlling biomineralization at the individual scale

Summary

Biogenic carbonates = Treasure of information *when* we can decipher them

Challenging but often the only way to reconstruct individual trajectories in natural environments (\neq from trajectories obtained from sample averages) and past environmental conditions

Biom mineralization processes and DEB theory = Conceptual and quantitative framework to better understand the interaction between (dynamic) environmental and physiological drivers controlling biom mineralization at the individual scale

Added value of this approach: **quality** of the data, **new data**, virtual lab to test assumptions, complementary to the experimental approach

Auxiliary theory under development: growth, opacity, carbon isotopic composition, two types of biogenic carbonates: fish otoliths and bivalve shells

Current/Future challenges:

Experimental calibration/validation

Trajectory reconstructions constrained by multiple proxies

Other types of biogenic carbonates (scales, vertebrae, statoliths, cuttle bones,...)

(Paleo-) ecology, oceanography, climate applications, Ocean acidification

References for biogenic carbonate formation and growth and food reconstruction

- **Kooijman 2010 – DEB book**
 - 4.3 Mass aspects of univariate deb models (4.3.1, 4.3.2, pp.134-138)
 - 4.4 Respiration + 4.5 Nitrogen balance + 4.6 Water balance (pp. 143-150)
 - 4.9 Products (pp.159-160)
- **Kooijman 2010 – Comments DEB book (Kooy2010_c.pdf)**
 - Some elements of section 4.3 (Mass fluxes), 4.4 (Respiration), 4.9 (Otoliths), 4.11 (Trajectory reconstruction)
- **DEBtool routines: o2f.m**
- **Pecquerie, L. 2008.** Bioenergetic modelling of the growth, development and reproduction of a small pelagic fish: the Bay of Biscay anchovy, Vrije Universiteit.
<http://dare.uvu.vu.nl/handle/1871/11716>
- **Fablet, R., et al. 2011.** Shedding Light on Fish Otolith Biomineralization Using a Bioenergetic Approach. **PLoS ONE** 6:e27055.
- **Pecquerie, L., et al. 2012.** Reconstructing individual food and growth histories from biogenic carbonates. **Marine Ecology Progress Series** 447:151-164.