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What can the shell tell about the scallop? Using growth trajectories along latitudinal and bathymetric gradients to reconstruct physiological history with DEB theory

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Abstract :

The great scallop, *Pecten maximus*, presents a strong variability of growth and reproductive patterns along its spatial distribution range. Such differences in life history traits result from complex interactions between organisms and environmental conditions that can be apprehended through the study of energy dynamics. As the determination of accurate food proxy can be a limitation for modeling bioenergetic, recent work by Lavaud et al. (accepted, this issue), based on the DEB theory, provided a new approach consisting of using temperature and growth time series to reconstruct the required assimilated energy to support observed growth. In this study we present an application of this method to growth trajectories of the great scallop *P. maximus* used to elucidate: (1) life history traits patterns and (2) the choice of food availability proxies. The inverted DEB model was used to reconstruct the functional response (f) for different age classes of *P. maximus* in 10 locations of its spatial distribution range. We especially explored the patterns of reconstructed f along latitudinal and bathymetric gradients. Average reconstructed f as well as its maximum value were found to increase with latitude. The variability of f , although increasing, did not show a significant relationship with the geographical position. Along the bathymetric gradient strong positive relationships were found between the mean f or its variability and depth. Ontogeny had low effect on the reconstructed f . Furthermore, as the inverted DEB model allows the reconstruction of physiological variables and energy fluxes, we explored the potential differences in reserve and maintenance fluxes dynamics from great scallops living in these contrasting environments. For one of the study sites, comparisons of f with field measurements of 11 food indicators (chlorophyll-*a* from the pelagic/benthic domains, phytoplankton cell counts, etc.) highlighted the complexity of the functional response and the diet of *P. maximus*. Pelagic or benthic phytoplankton biovolume, diatoms and dinoflagellates counts and chlorophyll-*a* were found to be the major contributors to the variability of f . Results suggest that although assimilation is best described by a combination of indicators, chlorophyll-*a* remains a good enough indicator of food availability for great scallops and bivalves in general.

Highlights

► We reconstructed food assimilation from growth in *P. maximus* using inverted an DEB model. ► Ten locations from France to Norway and along a bathymetric gradient were studied. ► Results showed an increase of mean functional response and its variations with latitude. ► Stronger positive relationships were found between reconstructed f and depth. ► Functional response was compared to various food indicators to identify food sources.

Keywords : Modeling, Dynamic Energy Budget, Environmental reconstruction, Latitudinal gradient, Bathymetric gradient, Growth, *Pecten maximus*, Sclerochronology

1. Introduction

Intraspecific variability in life history traits is a common feature of large spatial distribution range species. It has been widely described by biologists who first observed that populations, within a given species, could achieve significantly different patterns of life span, growth or reproductive activity. The study of the variability in life history patterns can be apprehended by the description and the understanding of the energy fluxes throughout the lifespan of organisms. Numerical modeling provides a useful tool to handle this question as it enables to test various hypotheses of metabolic organization and varying environment. The Dynamic Energy Budget (DEB) theory (Kooijman, 2010) quantitatively describes energy fluxes in a mechanistic framework given a set of species specific parameters and environmental forcing variables (temperature, food availability). While temperature data are usually easy to obtain in natural conditions, assessing food availability for wild organisms can be challenging. Marine bivalves, for instance, filter suspended particles from the surrounding water to retrieve food particles and are able of a complex pre-ingestive sorting depending on particle size and/or quality (see e.g. Ward et al. 1998). In addition to the important variability of seston quality and quantity, this makes the determination and quantification of relevant food proxies for these organisms a recurrent focus of bioenergetic modeling (Bayne, 1998; Bourlès et al., 2009; Alunno-Bruscia et al., 2011, Handà et al., 2011, Lavaud et al., 2014).

Recently, some studies tried to overturn this issue by inverting the model and reconstructed temporal assimilation time series from temperature and growth trajectories (Cardoso et al., 2006; Freitas et al., 2009; Troost et al., 2010; Pecquerie et al., 2012). The differences between the present approach and previous methods are discussed in Lavaud et al. (in review, this issue).

Valuable ecological information can be retrieved from present and past growth structures of organisms, namely to reveal intra- and inter-species interactions for food (Freitas et al., 2009, Troost et al., 2010), identify food limitations among different habitats (Cardoso et al., 2006) or provide a better understanding of population dynamics (Pecquerie et al., 2012). These patterns could even be refined in cases where high frequency growth data (trajectories) are available. Using theoretical growth trajectories of great scallops, Lavaud et al. (under review, this issue) showed that time series of food ingestion could be accurately reconstructed at a resolution of few days by using a single equation derived from DEB theory: the DEB Linear Equation (Rannou, 2009). Furthermore, this method allows for the reconstruction of the whole energy budget including somatic maintenance rate, flux of mobilized energy from reserve, reserve quantity, and reserve density (Kooijman, 2010).

The great scallop (*Pecten maximus*) shell grows by sequential daily increments (Clark, 1968; Antoine, 1978; Chauvaud et al., 1998; Lorrain et al., 2000), producing growth striae on the shell surface that enable determining the age and the daily shell growth rate (DSGR) of an individual (Clark, 1968, Chauvaud et al., 1998; Lorrain et al 2000; Owen et al., 2002a), providing a high resolution record of its growth history. *P. maximus* is thus considered as a relevant and accurate biogenic archive used in paleo-environment reconstructions of seawater temperatures (Owen et al 2002b; Chauvaud et al., 2005; Jolivet et al., 2015), salinity (Chauvaud et al., 2005; Freitas et al., 2012), primary productivity (Barats et al., 2010; Thébault and Chauvaud, 2013). Great scallops have a large spatial distribution range, from northern Norway down to the Iberian Peninsula and from just below the water mark in coastal waters to the edge of the continental shelf, which corresponds to a depth gradient of about 200 m (Brand, 2006). This wide distribution results in highly contrasting environments, especially in terms of temperature and food availability, both in their dynamics and in the range of values encountered. These differential conditions have, thus, been hypothesized to be responsible for the observed variability and seasonality in growth and reproductive patterns of this species (Buestel et al., 1986; Strand and Nylund, 1991; Mackie and Ansell, 1993; Chauvaud et al., 2012).

In this study, we present an application of the method developed by Lavaud et al. (2018, this issue) for reconstructing physiological variables of great scallops from high frequency shell-derived growth trajectories. Data came from a collection of shells obtained from ten locations along a latitudinal and a bathymetric gradient. We tested the applicability of the method to different age classes and compared the reconstructed food assimilation trajectories to potential trophic sources whenever possible. In the end we evaluated whether the variability in life history traits could be explained by the functional response patterns in relation to environmental conditions for the different populations studied.

2. Material and Methods

2.1. Reconstruction of physiological history

The reconstruction procedure consists in the use of an inverted DEB model, described by Lavaud et al. (2018, this issue). This method allows one to reconstruct time series of the following physiological variables from temperature and growth trajectories: the scaled functional response f , the amount of reserve E , the reserve density $[E]$, the mobilization flux from reserve \dot{p}_C , and the flux of energy allocated to somatic maintenance \dot{p}_M . This approach relies on a reformulation of DEB state variables dynamics in a linear equation (Rannou, 2009) expressed in terms of structural growth. Here, daily shell growth rate (DSGR) was taken to be equal to structural growth rate. The time axis of the reconstructed variables was expressed in days (day of the year, DOY).

As growth trajectories can present strong high frequency variability (Chauvaud et al., 1998), growth rate time series were smoothed by applying the "DEB box" method (described in Lavaud et al., under review, this issue): at every time step (i.e. each day of recorded growth), the model calculates the possibilities of growth for the next day, for a maximum scaled functional response (1) and minimum one (0). When observed growth rate at the next day is to overshoot the expected values, outcomes are bound and corrected by a DSGR value corresponding to the maximum value that f can take at this time. The growth trajectory is therefore constrained to a time series compatible with DEB predictions. After

identifying issues linked to a low metabolic acceleration factor during first trials (metabolic acceleration results in an increase of \dot{v} and $\{\dot{p}_{Am}\}$ at metamorphosis, allowing faster development of juveniles; Kooijman, 2014), parameters for *P. maximus* published by Lavaud et al. (2014) were re-estimated using the same procedure (Lika et al., 2011).

2.2. Study sites and shell collection

Ten study sites were selected along a latitudinal gradient with regard to the contrasting growth patterns of *P. maximus* (Chauvaud et al., 2012) observed along its spatial distribution range and the availability of data (**Fig. 1**): Træna in mid-Norway (1), Austevoll in southern Norway (2), Holyhead in the Irish Sea (3), Plymouth in the English Channel (4), the Bay of Brest in west France (5), Quiberon in the northeast part of the Gulf of Biscay (6), and four sites along a bathymetric gradient off Brest in the Celtic Sea, at depth of 98 m (7), 109 m (8), 150 m (9), and 162 m (10).

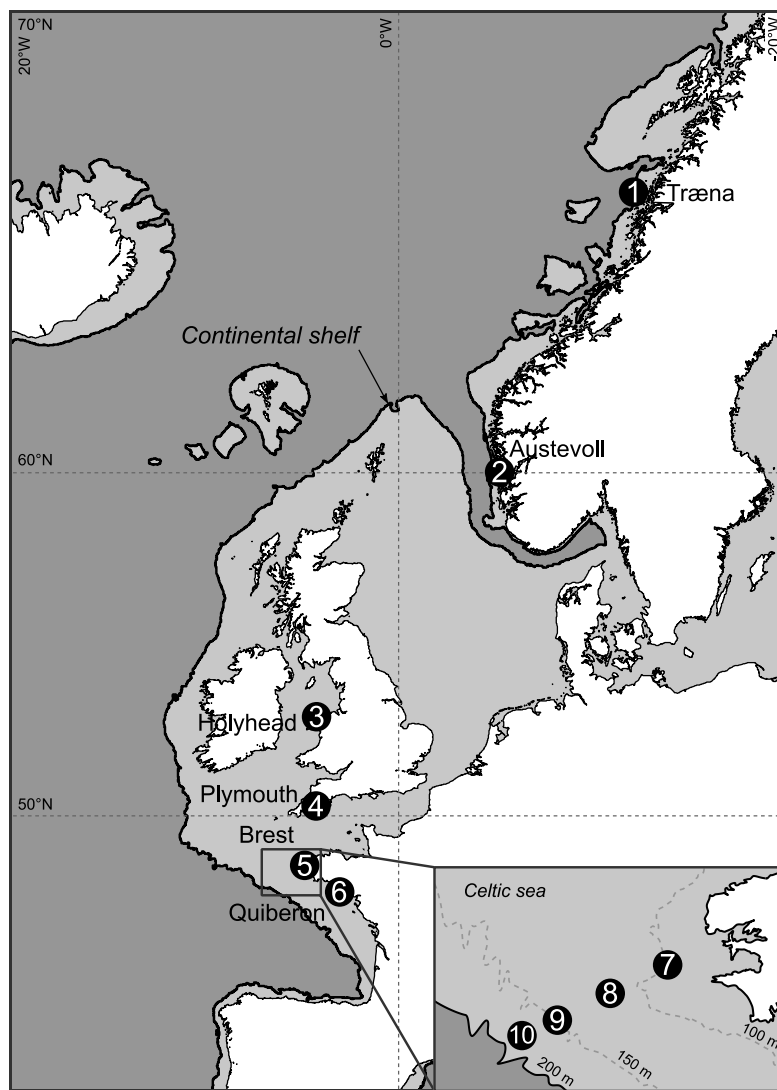


Fig. 1. Geographic location of the 10 locations from which shells of *Pecten maximus* and temperature data were collected: (1) Træna, (2) Austevoll, (3) Holyhead, (4) Plymouth, (5) Brest, (6) Quiberon and four deep sites in the Celtic Sea, at (7) 98 m, (8) 109 m, (9) 150 m and (10) 162 m depth.

Great scallop shells came from the multi-decadal archives of the EVECOS time series (maintained by the observatory of coastal domain in the University of Brest), gathering shells from all around the distribution range of the great scallop. Depending on the site and their accessibility, individuals have been collected by scuba diving or dredging. The number of shells used and their age at the time of collection are presented in **Table 1**.

Table 1. Geographical position of the 10 locations along a latitudinal and a bathymetric gradient where scallops were collected and number and age classes of individuals used.

Site	Latitude	Depth	Age classes	N
Træna	66°30'N	18	3 and 6	15
Austevoll	60°06'N	15	3 to 5	37
Holyhead	53°03'N	46	3 to 6	13
Plymouth	50°20'N	12	2 to 5	25
Brest	48°23'N	20	1 and 3	271
Quiberon	47°48'N	15	1 and 2	55
Celtic Sea 98 m	48°36'N	98	4 to 6	11
Celtic Sea 109 m	48°19'N	109	4 and 5	11
Celtic Sea 150 m	47°55'N	150	4 to 8	11
Celtic Sea 162 m	47°53'N	162	4 to 6	8

Seawater temperature time series were obtained from various scientific institutions: SOMLIT (Service d'Observation en Milieu Littoral, INSU-CNRS, Brest) for the French locations, CEFAS (Centre for Environment, Fisheries and Aquaculture Science; Joyce, 2006) for the English locations. In the Norwegian locations, data were provided by Ø. Strand and L. Chauvaud (unpublished data). All these measurements corresponded to periods of growth of the studied animals. In the deepest locations, a monitoring of deep sea temperatures (ASPEX mooring equipped with Microcat T/S/P recorder, Laboratory of Physical and Spatial Oceanography, Ifremer, France) at 150 m over one year in 2010–2011 in the area where scallop shells were collected (47°12'643 N, 5°15'963 W; Le Boyer et al., 2013; L. Marié, unpublished data) and hydrological models (Lazure et al., 2009) have shown that temperature only varies of 0.5 to 1 °C during the year, for an average of 12 °C. Therefore, a constant temperature of 12 °C was chosen for the reconstructions carried out in the deep Celtic Sea locations.

2.3. Measurement of growth trajectories

The daily shell growth rate of *P. maximus* at the different locations was determined by measuring the distance between two successive daily growth striae on the external surface of the left valve (Chauvaud et al., 2005; Chauvaud et al., 2012), from the ventral margin toward the umbo. Different cohorts were studied in order to look at the potential effect of age on the reconstruction process, from age class one to age class eight. For each studied site, a mean growth trajectory was calculated by averaging the individual growth trajectory from a single cohort. As the growth of *P. maximus* stops in winter (Chauvaud et al., 1998; Chauvaud et al., 2005; Lorrain et al., 2000), the procedure was performed for each season of growth. Calendar dates were assigned to each increment of the last year of growth (until catch) but not for previous years of life since winter slowdown duration cannot be estimated accurately. However, observations of the relationship between temperature and DSGR time series over several decades within

the EVECOS data set revealed that the growth trajectory can be reset in time, by aligning the highest DSGR value with the maximum value of temperature.

2.4. Food proxies

In an effort to identify relevant food proxies for *P. maximus*, the reconstructed food assimilation dynamics carried out over several years in the location of Brest (Site 5, **Fig. 1**, **Table 1**) were compared to various indicators of food availability measured in the field by the monitoring network SOMLIT (Service d'Observation en Milieu Littoral, INSU-CNRS, Brest): chlorophyll-*a* from the pelagic and benthic compartments ($\mu\text{g L}^{-1}$), phytoplankton cell counts (cells L^{-1}), and particulate organic matter ($\mu\text{g L}^{-1}$) in the water column. Other indicators were also available for the year 2011 only (Chatterjee et al., 2013): cell counts at the bottom (cells L^{-1}), phytoplankton biovolume ($\mu\text{m}^3 \text{L}^{-1}$), diatoms and dinoflagellates counts (cells L^{-1}) in both pelagic and benthic compartments, particulate organic matter and carbon ($\mu\text{g L}^{-1}$), as well as total suspended matter in the water column (mg L^{-1}). All these indicators were standardized between [0, 1] to allow for comparisons.

2.5. Statistical analysis

Reconstructed f time series obtained from different age classes were averaged site by site in order to look at specific patterns along the studied gradients. Statistical analyses were conducted with the R software (R Core Team, 2016) with a significance threshold of $\alpha = 0.05$. A Kruskal-Wallis analysis was conducted to test the separation of data sets (from site to site). To test for differences in average reconstructed f across locations, we used a one-way ANOVA followed by a Tukey HSD test for pairwise comparisons; this was done for each location with all reconstructed f included (i.e. for all age-classes and years). Linear regressions were used to establish relationships between the observed patterns in reconstructed f at the different locations and the two variables of interest (latitude and depth). For the food proxies study in 2011, data sets were first tested for normality with a Shapiro test. Covariance between variables (food availability indicators) was tested and a principal component analysis was applied after removing variables co-varying with another to find out which food indicators explained most of the variability observed in the reconstructed f that year.

3. Results

3.1. Latitudinal gradient

The reconstruction of food assimilation was applied on a total of 483 individual shells collected along a latitudinal gradient from Træna (66°30'N, Norway) south to Quiberon (47°48'N, France) and along a bathymetric gradient from 20 to 162 m off the coast of Brittany, France. Examples of reconstructed f time series along the gradient for one-year-old individuals (using averaged growth trajectories for that age class) are presented in **Fig. 2**. The procedure seemed to perform perfectly as the simulations of DSGR using the reconstructed f (strait dark lines) correctly reproduced the original growth trajectories (strait gray line). All data sets were significantly different from one station to the other (Kruskal-Wallis tests, all P value < 0.002). In northernmost locations (Træna and Austevoll, Norway), the average f among all age classes was 0.71 (**Table 2**, see details in Supporting Information, **Table A1**). Metrics of the mean

reconstructed f are presented in **Fig. 3**. In Holyhead and Plymouth, in the middle of *P. maximus* spatial distribution range (UK), mean reconstructed f amounted to 0.58 (average maximum of 0.82 and average minimum of 0.33 on 18 reconstructions) and 0.68 (average maximum of 0.91 and average minimum of 0.32 on 10 reconstructions) respectively. Finally, in the southernmost studied locations of Brest and Quiberon f reached a mean value of 0.57 (average maximum of 0.87 and average minimum of 0.29 on 13 reconstructions) and 0.53 (average maximum of 0.82 and average minimum of 0.22 on 3 reconstructions) respectively. Quiberon location seemed to stand out with the lowest mean f (**Fig. 3**).

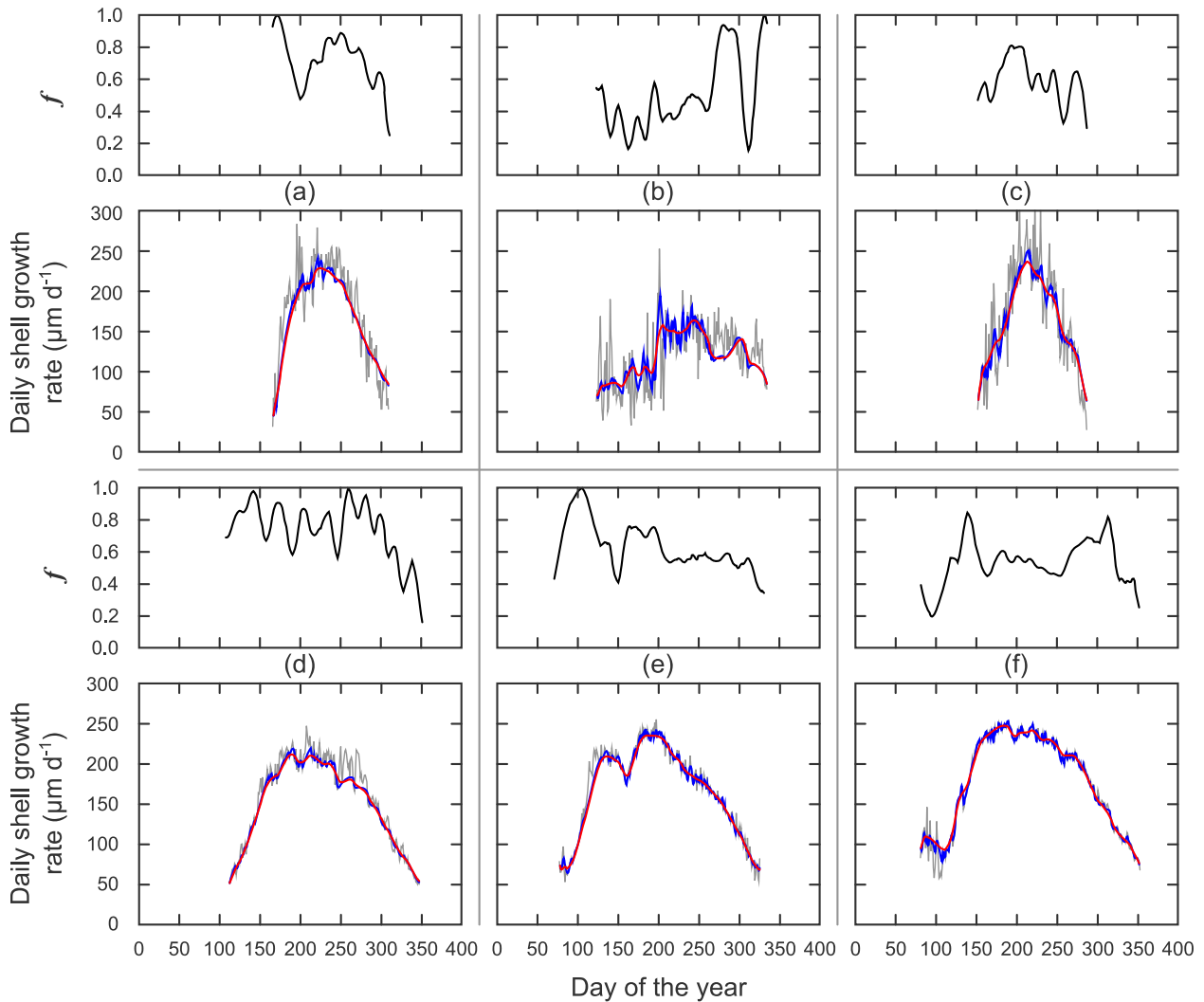


Fig. 2. Reconstruction of the functional response obtained from growth trajectories of *Pecten maximus*, during the first year of growth, in the 6 studied locations of the latitudinal gradient: (a) Træna, (b) Austevoll, (c) Holyhead, (d) Plymouth, (e) Brest and (f) Quiberon. Reconstructed functional response are presented in the upper graphs; the lower ones show the growth trajectory (gray line), the growth time series after being smoothed by the "DEB box" (blue line) and the back simulated growth trajectory using the reconstructed f (red line).

Table 2. Statistics of mean reconstructed functional response in the 10 studied locations.

Site	N	Mean	Average maximum	Average minimum	Average amplitude	SD	Days of growth
Træna	6	0.71	0.98	0.18	0.80	0.18	130.0
Austevoll	12	0.71	0.95	0.34	0.61	0.18	131.7
Holyhead	18	0.58	0.82	0.33	0.49	0.14	108.1
Plymouth	10	0.66	0.91	0.32	0.59	0.13	181.7
Brest	13	0.57	0.87	0.29	0.56	0.13	203.5
Quiberon	3	0.53	0.82	0.22	0.60	0.16	246.3
Celtic Sea 98 m	12	0.64	0.97	0.20	0.77	0.23	146.5
Celtic Sea 109 m	7	0.64	0.94	0.15	0.79	0.22	139.0
Celtic Sea 150 m	17	0.66	0.99	0.06	0.93	0.29	123.0
Celtic Sea 162 m	9	0.67	0.97	0.08	0.89	0.29	129.3

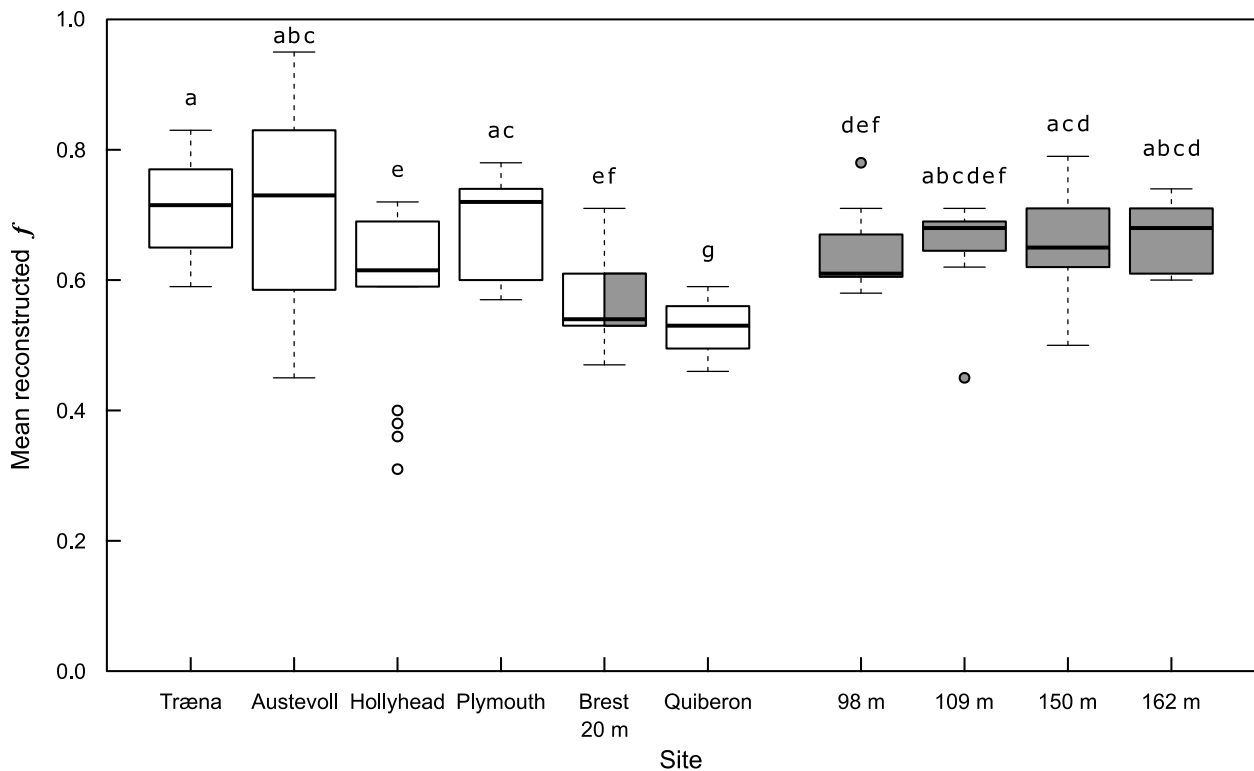


Fig. 3. Average reconstructed functional response f from the 10 studied locations. T: Træna; A: Austevoll; H: Holyhead; P: Plymouth; B: Brest; Q: Quiberon. The Brest location is also part of the bathymetric gradient as the 20 m depth station. Letters above boxplots indicate significant pairwise differences based on Tukey HSD post hoc test results.

When deep locations in the Celtic Sea were not considered, a positive linear relationship was found between the latitude and the average reconstructed f (Table 3, $r^2 = 0.6979$, P value = 0.0384). In the majority of the reconstructions carried out with shells from northern environments (11 out of 18), f reached a maximum value of 1 (Table A1). Actually, the DEB model used within the "DEB box" to

smooth growth rates variations at these locations was often very much constraining the observed time series. This led to periods longer than a month during which f remained at 1 and for some of these reconstructions the minimum f was 0, leading to an average amplitude of f of 0.8 in Træna and 0.61 in Austevoll. To the contrary, the amplitude of variation of the reconstructed time series in the southern locations (Plymouth, Brest, and Quiberon) remained under 0.6 and the average minimum never reached 0. The standard deviation of the reconstructed f in each location also presented a clear positive relationship with latitude (**Table 3**), showing more variability in Nordic locations (**Table 2**).

Table 3. Linear regressions between averaged reconstructed functional response among all age classes and latitude, depth and growth duration.

	Latitude			Depth		
	r ²	slope	P value	r ²	slope	P value
Mean	0.70	0.00860	0.04	0.98	0.00065	<0.001
Maximum	0.66	0.00730	0.05	0.84	0.00073	0.03
Minimum	0.09	-0.00260	0.56	0.94	-0.00150	0.01
Amplitude	0.56	0.01000	0.09	0.97	0.00240	<0.001
SD	0.61	0.00240	0.07	0.98	0.00110	<0.001
	Days of Growth along latitudinal gradient			Days of Growth along depth gradient		
	r ²	slope	P value	r ²	slope	P value
Mean	0.38	-0.00090	0.19	0.96	-0.00120	<0.001
Maximum	0.17	-0.00052	0.41	0.90	-0.00140	0.01
Minimum	0.09	-0.00037	0.56	0.88	0.00270	0.02
Amplitude	0.01	-0.00021	0.84	0.96	-0.00440	<0.001
SD	0.09	-0.00013	0.57	0.91	-0.00200	0.01

3.2. Bathymetric gradient

Five locations were studied along the bathymetric gradient. Because temperature was considered to be constant in these locations, growth curves could not be aligned in time and although the temporal variations are relevant, the starting time of the reconstructed f in these locations could not be set. **Fig. 4** presents the reconstruction of the functional response from growth trajectories of individuals of different age class living at 98 m and 162 m depth compared to a shallow coastal habitat. In some reconstructions in the deepest location (162 m), the growth trajectory often seemed to be very much constrained by the "DEB box" smoothing method, resulting in maximum values of f . The checking procedure consisting of simulating DSGR using the reconstructed functional response showed lower simulated growth rates compared to the observations in some parts of the time series for three-year-old individuals, indicating that the reconstructed functional response was probably under-estimated (**Fig. 4e, f**). However for younger individuals and shallower environments, the reconstruction process was correctly achieved. The amplitude of the reconstructed assimilation time series was greater in the two deeper sites compared to the coastal one: in average the maximum value of f was of 0.87 in Brest and 0.97 at both 98 m and 162 m depth in the Celtic Sea and the minimum reached in these location was 0.29, 0.20, and 0.08 respectively (**Table 2**).

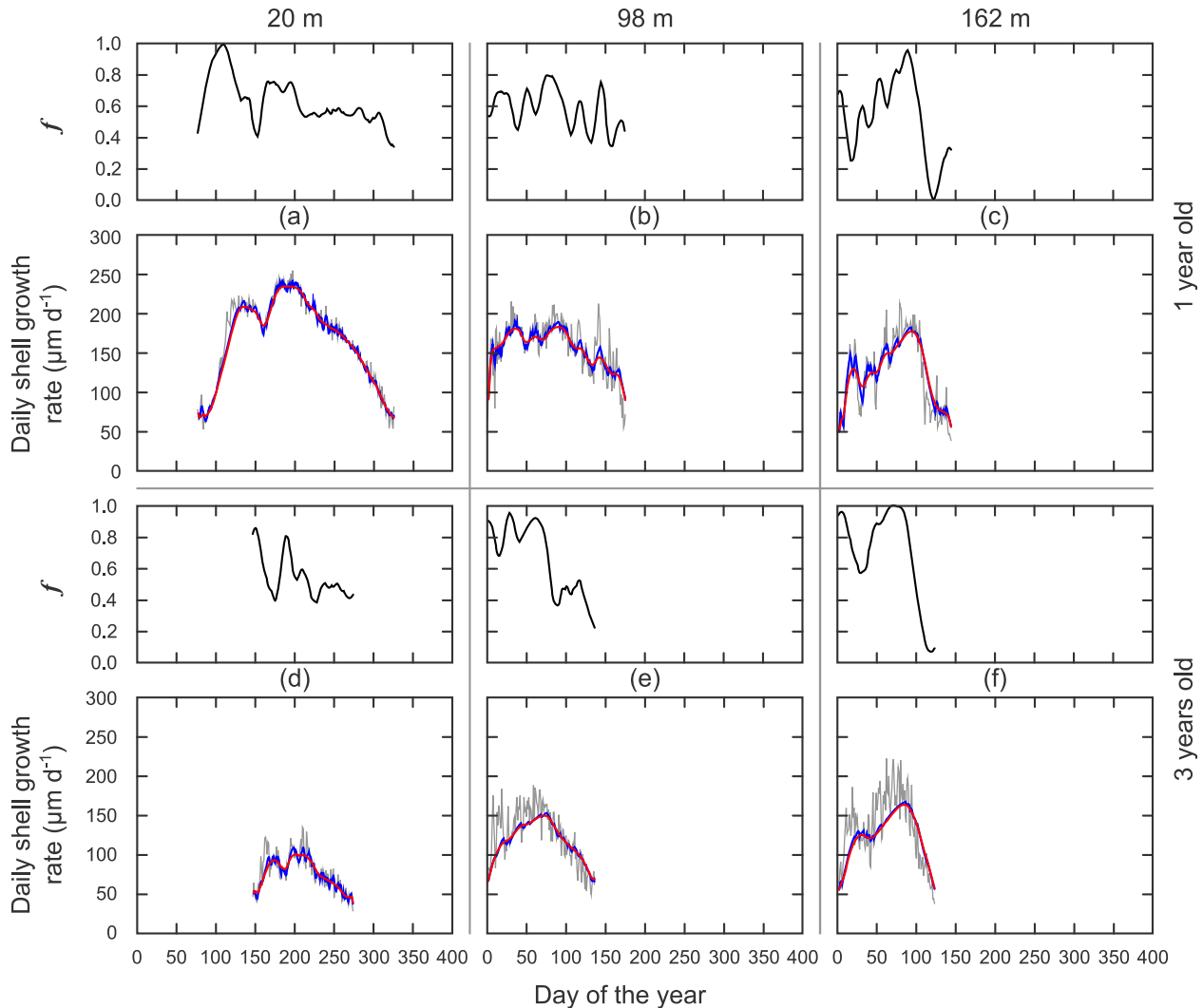


Fig. 4. Reconstruction of the functional response obtained from growth trajectories of *Pecten maximus*, (a, b, c) during the first and (d, e, f) third year of growth, in three locations of the bathymetric gradient: (a, b) at 20 m depth in a coastal site of Brest, (c, d) at 98 m and (e, f) 162 m depth in the Celtic Sea. In the upper graphs are the reconstructed functional response; in the lower ones are the growth trajectory (gray line), the growth time series after being smoothed by the "DEB box" (blue line) and the back simulated growth trajectory using the reconstructed f (red line).

When considering the five locations along the bathymetric gradient, a positive linear relationship was found between the depth and the average f (**Table 3**, $r^2 = 0.9685$, P value = 0.0024). The average value of f for all age classes in the location of Brest was 0.57 while it reached 0.64 at 98 m, 0.64 at 109 m, 0.66 at 150 m, and up to 0.67 at 162 m depth. While stronger relationships were found between the reconstructed f time series and depth (especially in terms of variability), functional response patterns in northern locations (Træna and Austevoll) and the deep stations in the Celtic Sea show similarities. The average f and its maximum value were very close in these two types of environment. On the other hand, deep locations seem to differ from the coastal stations in the minimum value of f and its standard deviation. Indeed, while no significant linear relation was found in the coastal environments, a close relationship was found between depth and these patterns (**Table 3**).

3.3. Ontogenetic patterns

The sensitivity of the reconstruction procedure was tested by analyzing different age classes during one calendar year (**Fig. 5**). Four sites provided enough data to compare three to four cohorts during a same year: Austevoll, Holyhead, Plymouth, and the 98 m deep location in the Celtic Sea (**Fig. 5a, b, c, d** respectively). In the first site, the reconstructed f from three age classes were very similar in both temporal dynamics and amplitude. After starting from high f values in the beginning of the season, a sharp decrease of feeding activity at Day of the year (DOY) 200 was reconstructed at every age. In Holyhead four age classes showed also a common decrease of the reconstructed functional response near day 240, followed by a peak on day 250. The rather elevated values at the beginning of the reconstruction showed higher temporal variability between age classes, with a peak on day 180 for the one-year-old time series, on JD 200 for the two-year-olds, and on day 210 for the two oldest age classes. In Plymouth, variability of the reconstructed f between the different age classes was more important and no clear tendency was deduced from this analysis. Finally, in the deep location of the Celtic Sea, at 98 m depth, the one- and three-year-old cohorts showed very similar variations of reconstructed f : on day 190, assimilation rapidly dropped from 0.9 to 0.3. In the meantime the reconstructed f from two-year-old scallops remained at 1 from day 175 to 225.

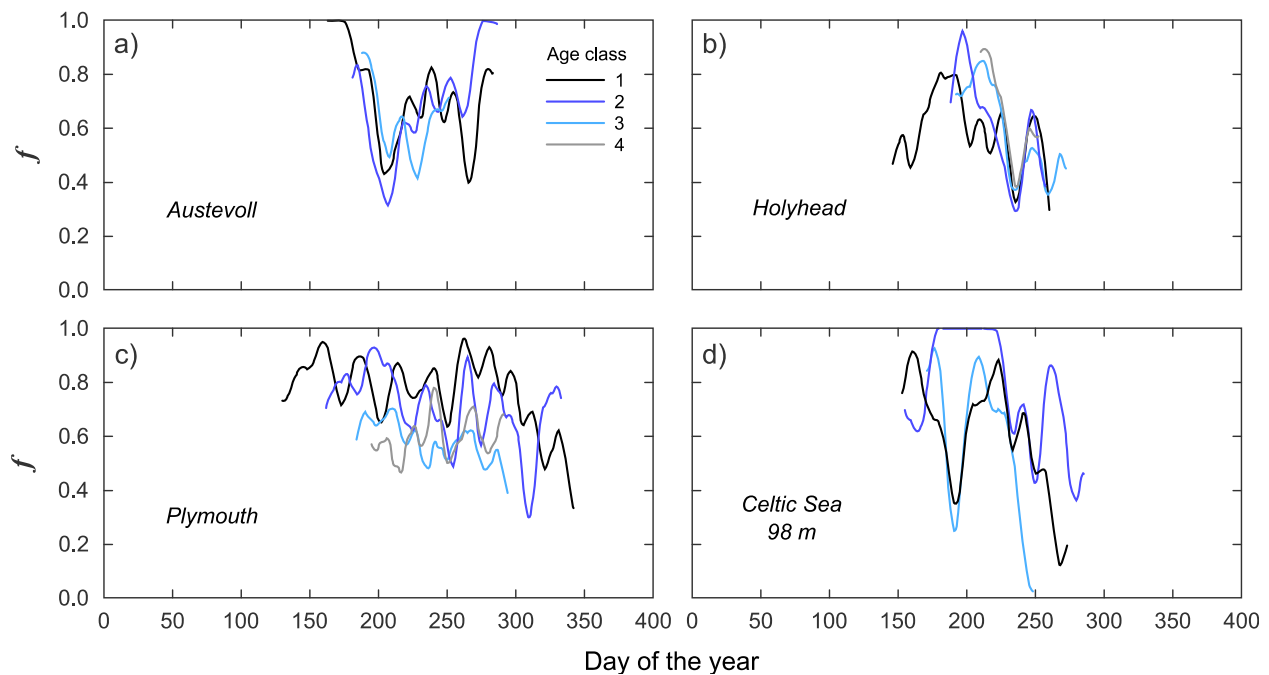


Fig. 5. Reconstructed functional response of different age classes during a same year in (a) Austevoll, (b) Holyhead, (c) Plymouth and (d) at 98 m depth in the Celtic Sea.

3.4. Physiological variables

The inversion of the DEB model not only allows the reconstruction of assimilation dynamics but also the past variations of several physiological variables. Reconstruction of reserve, reserve density, mobilization rate, and maintenance rate in three contrasted habitats (Træna, Brest, and at 98 m deep in the Celtic Sea) for young and older individuals (3 years old) showed that great scallops from the North and the deep environments contrasted most with the coastal south population (**Fig. 6**). The amount of reconstructed

reserve E was more important in great scallops from the location of Brest (**Fig. 6a, b**). Interestingly, the amount of reserve in three-year-old scallops living in the Celtic Sea tended to get closer to the quantity observed in individuals from the inshore location of Brest, as time went on. In terms of reserve density $[E]$, very similar dynamics were observed between the location of Træna and the Celtic Sea (98 m), while more stable time series occurred in Brest. The dynamics of reconstructed mobilization flux of reserve \dot{p}_C , for further allocation to reproduction and growth plus their maintenance, were again very similar in Træna and at 98 m. Values observed for individuals from Brest were 2 to 5 times higher. Finally, identical patterns were observed in the reconstruction of the somatic maintenance flux \dot{p}_M .

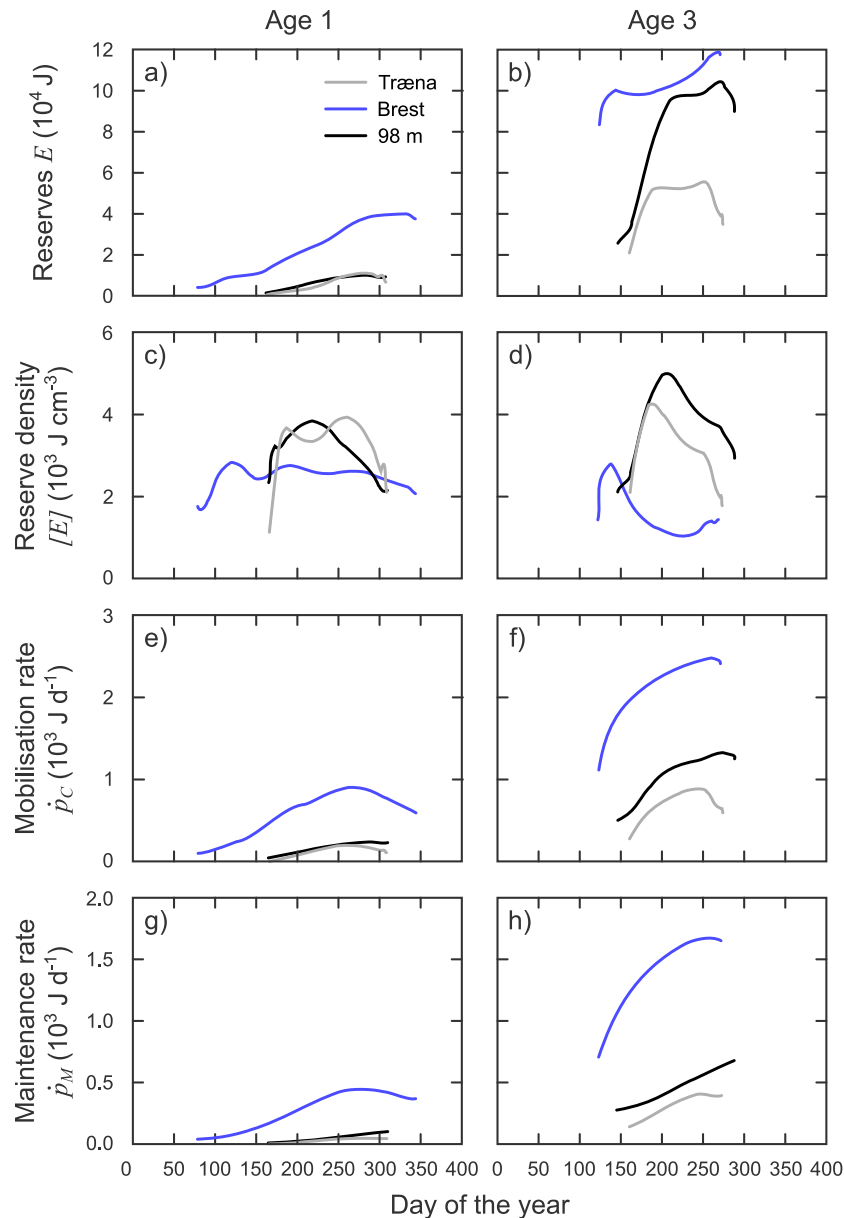


Fig. 6. Reconstruction of physiological variables from growth trajectories of individuals from age class (a, c, e, g) one and (b, d, f, h) three in Træna (dotted line), Brest (dashed line) and at 98 m deep in the Celtic Sea (solid line): (a, b) reserve amount E ; (c, d) reserve density $[E]$; (e, f) mobilization flux of energy from reserves \dot{p}_C ; and (g, h) maintenance rate coefficient \dot{p}_M .

3.5. Comparing reconstructed functional responses with observed food proxies

Growth trajectories obtained from age class one were selected to compare reconstructed functional responses to food availability measurements as they provide a more extended growing season and thus a wider reconstruction potential than older animals. Six years of reconstruction in the Bay of Brest were used based on the availability of environmental data (**Fig. 7**). The dynamics of f could not be related to a single food proxy: no significant correlation was found between any of the descriptors and the reconstructed functional response. The average value of f reconstructed from Brest shells was 0.57 (**Table 2**). Some sharp drops in the functional response of great scallops were observed in 1998 (**Fig. 7a**, DOY 150 to 155), 2001 (**Fig. 7d**, DOY 130), in 2002 (**Fig. 7e**, DOY 140 and 225), and in 2003 (**Fig. 7f**, DOY 145). No clear relationship with any food proxy could be identified, although food availability indicators were either at a very high or very low level during these drops of assimilation. For instance, in 1998 and 2002, all the trophic descriptors were close to their maximum when the drop in f was observed. Conversely, the sharp reduction of assimilation in 2001 happened between a peak of phytoplankton cell and a peak of chlorophyll- a .

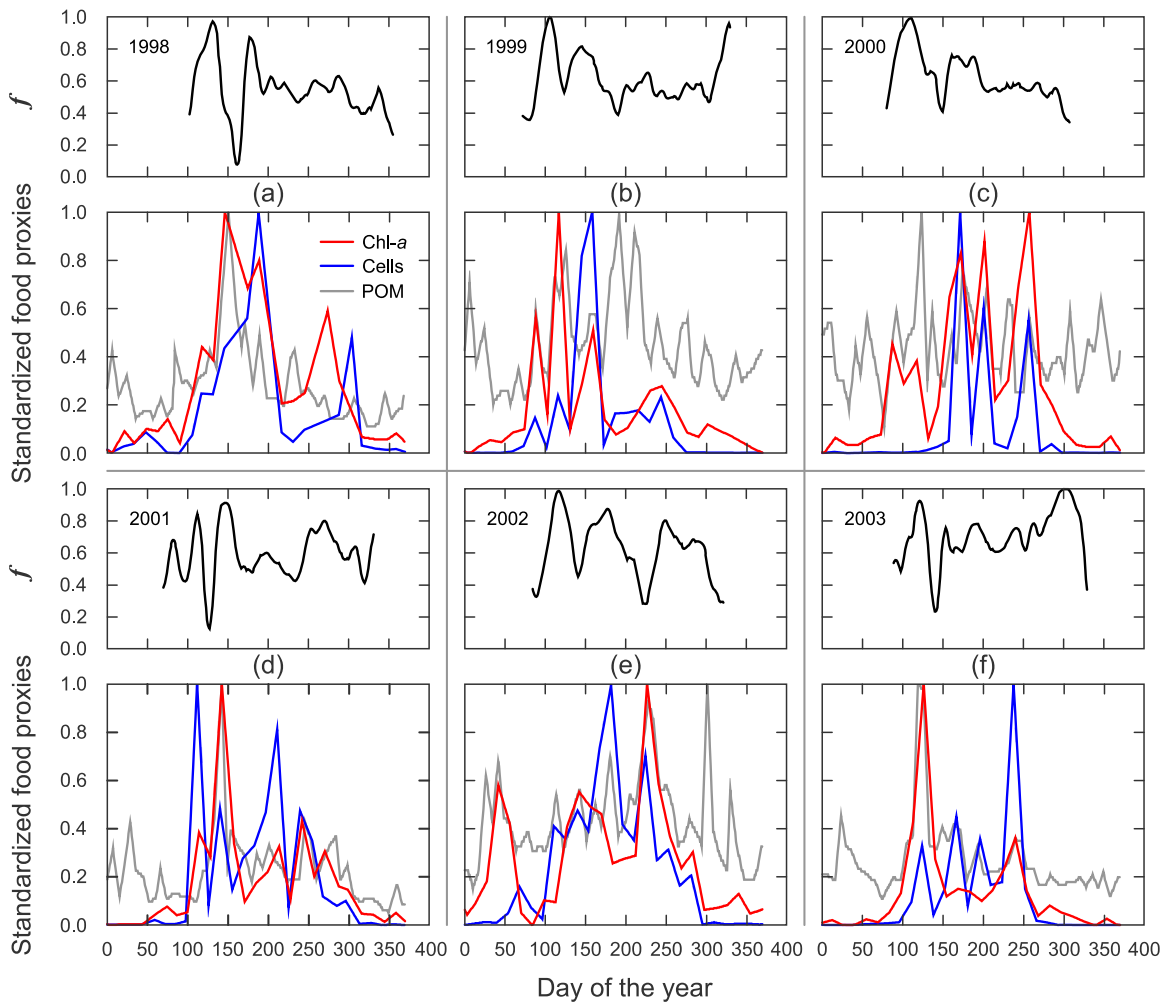


Fig. 7. Reconstructed functional response (upper graphs) from growth trajectories of 1-year-old scallops in the Bay of Brest during years 1998–2003 (a–f), compared to time series of chlorophyll- a (red line), phytoplankton counts (blue line) and POM concentration (gray line).

The results of the principal component analysis performed on data from 2011 indicated that biovolumes of phytoplankton cells in the water column and diatoms at the water sediment interface contributed the most to first principal component (explaining 28% of the variability of f ; **Table 4**). Biovolumes at the water-sediment interface and particulate organic carbon were removed from the analysis beforehand as they co-varied with other variables. Dinoflagellates in the water column and chlorophyll-*a* at the water-sediment interface were the major contributors to the second principal component (explaining 16% of the variability). It took 6 principal components to explain >80% of the variability observed in the reconstructed f . Another variable of importance for these two principal components was particulate organic matter (**Table 4**). The dynamics of the four major indicators are presented in **Fig. 8**, along with the reconstructed functional response for this year. The superposition of f dynamics with microalgae biovolumes measured in the pelagic compartment matched numerous peaks of the reconstructed f . The sharp decrease of f on day 120 was concomitant with a peak in diatom microalgae of two particular species: *Amphora sp.* and *Pseudo-nitzschia cf. delicatissima*. Although allegedly not toxic for the bivalve itself, these two species are known to release domoic acid, an amnesic shellfish poisoning toxin (Trainer et al., 2008).

Table 4. Results of the principal component analysis carried out on 11 food availability variables and the reconstructed functional response for 1-year-old scallops in the Bay of Brest in 2011. Variables retained for the analysis include: chlorophyll-*a* (Chl-*a*), phytoplankton cells counts (Cells), biovolumes (BioV), number of diatoms cells (Diat), number of Dinoflagellates cells (Dino), particulate organic matter (POM) and total suspended matter (TSM) in the pelagic (p as index) and benthic (b as index) compartments.

<i>Importance of components</i>											
	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11
SD	1.7706	1.3587	1.2042	1.1438	0.9712	0.8742	0.8638	0.6526	0.5701	0.3914	0.3052
% var.	0.2802	0.1650	0.1296	0.1169	0.08429	0.0683	0.0667	0.0381	0.0290	0.0137	0.0083
Cum. %	0.2802	0.4451	0.5747	0.6916	0.7759	0.8442	0.9109	0.9490	0.9780	0.9917	1.000
<i>PCA loadings</i>											
	Chl- <i>a</i> _p	Chl- <i>a</i> _b	Cells _p	Cells _b	BioV _p	Diat _p	Diat _b	Dino _p	Dino _b	POM _p	TSM _p
PC1	0.3878	0.2662	0.2632	0.4590	0.3322	0.1278	-0.0954	0.4071	0.2226	0.3547	0.1482
PC2	-0.2370	0.4342	0.3799	0.2004	-0.2142	0.4352	0.1157	-0.2303	0.3009	-0.3830	0.1785

4. Discussion

In this study inverted DEB models were used to reconstruct assimilation dynamics in order to describe and better understand energetic patterns behind the observed life history traits of *Pecten maximus*. The analysis of functional response patterns revealed significant variations with latitude and depth. The dynamics of energy input, which has long been recognized as a problem in bioenergetic modeling, especially for bivalves (Bayne, 1998; Bourlès et al., 2009; Alunno-Bruscia et al., 2011; Lavaud et al., 2014), was elucidated through comparisons of reconstructed functional responses with actual food availability proxies, indicating complex contributions of both pelagic and benthic compartments to the diet of great scallops.

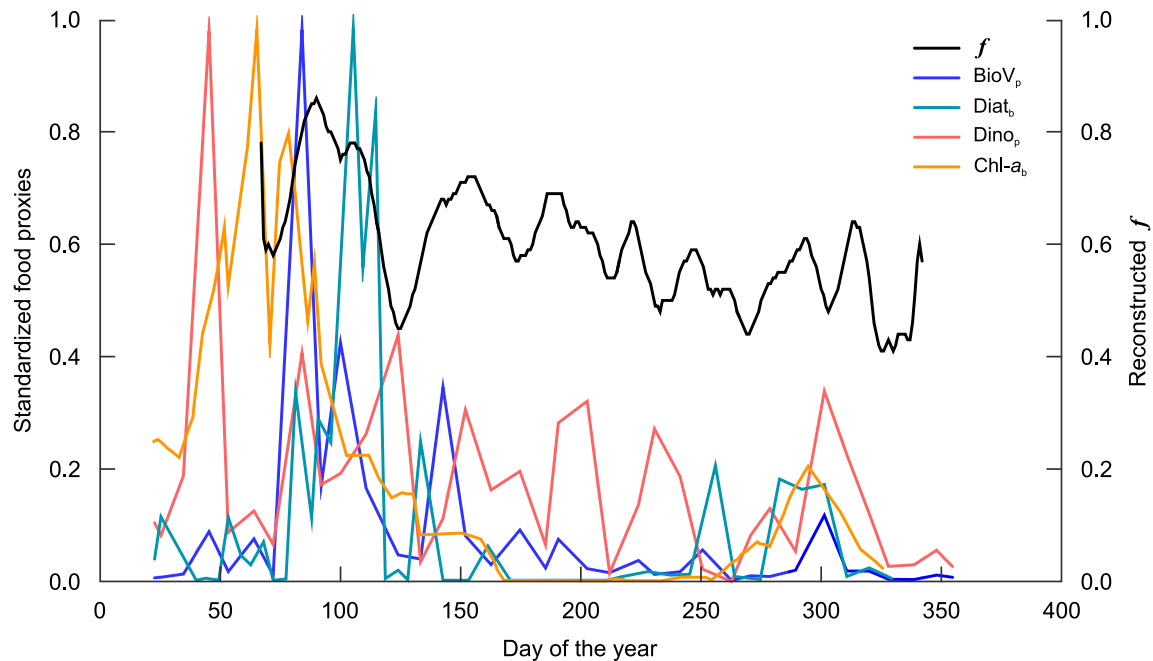


Fig. 8. Comparison of reconstructed functional response with standardized food availability indicators in the Bay of Brest in 2011. Major food availability indicators identified in the principal component analysis were: Biovolume of phytoplankton cells in the water column ($BioV_p$), Diatom cells at the bottom ($Diat_b$), Dinoflagellates cells in the water column ($Dino_p$), and Chlorophyll-*a* concentration from the bottom ($Chl-a_b$).

4.1. Shell growth

The growth pattern of the great scallop have been extensively studied through sclerochronological studies (Chauvaud et al., 1998; Lorrain et al., 2000; Owen et al., 2002a; Guarini et al., 2011; Chauvaud et al., 2012). Generally, during the first years of life, a positive correlation is found between DSGR and the duration of the growing season in a year: individuals growing over long periods also exhibit high growth rates. At the tested locations, the length of the growing period decreases when going northward or toward deep locations (**Table 2**; Chauvaud et al., 2012). However, when getting older, the growing period in deep habitats declines more slowly than in other environments (Chauvaud et al., 2012). This ontogenetic decrease in growth rate is generally explained by the increase of maintenance costs with volume, compared to assimilation rates (scaling with surface-area); available energy in later stages of life just meets somatic maintenance. The oldest shell used in this study had more than eight winter marks. The potential of environmental reconstruction for a such long period is interesting, however, younger individuals would provide more valuable information for the following reasons: (1) early years of growth allow for more extended reconstruction period as shell growth duration in juvenile and young adults spans longer than in older individuals (Chauvaud et al., 2012); (2) the range of DSGR values is higher in early years of growth, as the shell can then grow at rates of 0.3 mm d^{-1} or higher, which increases the resolution of growth rate variations – in comparison, the average maximum DSGR value of a four-year-old scallop in the middle of its spatial distribution range would only reach 0.1 mm d^{-1} ; (3) the measurement of the increment width is facilitated in a young scallop because its shell has not been much damaged by natural events (fixation of epibionths, attack of predators, friction of sediment, etc.). The amplitude of the reconstructed f seems to be less important for older individuals, which was also observed by Freitas et al. (2009) using a different reconstruction method. In the context of DEB theory, faster reserve dynamics in

young individuals linked to relatively more available energy (as a consequence of surface to volume ratio) can explain this ontogenetic pattern. This could also be attributed to the fact that shorter time series can be reconstructed from three-year-old or older individuals as their growing period is shorter in time. Ultimately, the use of growth trajectories limits our interpretations to periods when animals achieve a minimum growth rate (over 0.05 mm d^{-1}).

4.2. Latitudinal gradient

Several hypotheses can be made to explain the larger asymptotic size of great scallops living in northern locations. In nature as well as in DEB theory the ultimate length (i.e. the maximum length an organism can reach) is highly dependent on food conditions (Kooijman et al., 2008; Kooijman, 2010). Our results show that the average reconstructed f was significantly higher at these latitudes, which would lead to bigger organisms. Strohmeier et al. (2009) reported that *P. maximus* regulates its clearance rate in response to relatively small changes in phytoplankton quantity, especially in low seston systems. Great scallops inhabiting northern ecosystems, while facing extremely low seston conditions (Aure et al., 2007), do not seem to be limited by their ability to clear particles out of suspension (Strohmeier et al., 2009). The rather elevated values of f reconstructed in the two northernmost locations (Træna and Austevoll, Norway) confirm this biological pattern, with increased functional responses. Transplant experiments have shown that great scallops originating from various latitudinal locations did not display significant differences in growth when placed in the same conditions (MacKie and Ansell, 1993). Therefore, the high f observed in northern sites could be considered as a local response to environmental conditions.

This first explanation must be tempered as the reconstruction procedure cannot be applied when DSGR fall below $50 \mu\text{m d}^{-1}$, preventing us from estimating food availability during the winter period. Yet, the duration of this period extends when going north. Therefore, when considering the whole year and not the growing period only, the mean f might decrease substantially in northern locations. Norwegian waters are often described as oligotrophic (Aure et al., 2007) and experience large primary productivity during short bloom periods in spring (Erga and Heimdal, 1984; Dale et al., 1999; Erga et al., 2012). Nanoplankton communities dominate in winter and summer periods, while diatoms make up the main part of spring biomass (Erga and Heimdal, 1984). Therefore, another possible explanation to the larger ultimate sizes observed in the North could be the amplitude of variation of food availability. Muller and Nisbet (2000) studied the dynamic behavior of a simple DEB model in fluctuating environments and showed that scaled energy density (i.e. the ratio between the reserve density [E] and its maximum value [E_m]) not only increases with the highest food density, but also depends on the frequency of food density oscillations. Accordingly, organisms might grow bigger if food fluctuations are more intense, as compared to organisms growing in a stable environment with similar mean food availability. Furthermore, despite the lack of information on the nutritional composition of phytoplankton along latitudinal gradients, Chust et al. (2012) demonstrated the existence of a polewards increase in both diversity and immigration rates (i.e. drift of propagules from large regional pools) of phytoplankton species, probably caused by water mixing conditions and productivity. Stronger seasonal patterns and diversity in biochemical composition (i.e. energetic quality) of available phytoplankton would thus be expected in northern ecosystems, which might explain higher amplitudes in functional response of consumers. The larger amplitude of f observed in northern sites in this study might therefore explain the larger size of great scallops from these locations. Although we observed such a trend, we did not find a significant relationship between these variables.

The last descriptor of interest is the maximum value that f reached in the reconstructions carried out along the latitude gradient. In the center of its spatial distribution range (i.e. UK, France), results showed lower functional responses in average, as well as lower maximum values (**Table 2**). Waters of the English Channel and the Irish Sea are more eutrophic (Sathyendranath et al., 1995; Baan and van Buuren, 2003), which means that food availability is not likely to limit energy acquisition, with the exception of the winter period. Several authors also reported decreases of the functional response of bivalves when food availability increased (Widdows et al., 1979; MacDonald et al., 2006). Moreover, functional response of bivalves can decrease in overloaded environments (Bacon et al., 1998; Lorrain et al., 2000), mainly due to the production of pseudofeces. In Plymouth and Quiberon, situated near estuaries (of the river Tamar and the Loire River respectively) and in the Bay of Brest, a semi-enclosed area, food quantity and inorganic inputs likely cause sharp drops of the functional response during high riverine inputs periods. This is probably why we didn't observe higher values of maximum f in the South. Detailed expressions for feeding and filtering exist, where food and silt compete for access to the acquisition machinery of bivalves (Kooijman, 2006; Saraiva et al., 2011; Lavaud et al., 2014). The inversion of such models is, however, challenging as it would require solving a single equation with at least two unknown factors, therefore requiring additional assumptions regarding the feeding process.

To summarize, we showed that: despite a significant relationship with latitude, the mean f might not be representative of the yearly trends; the range of variation of f , although showing a positive trend was not significantly related to the geographical position; the maximum value of f appeared to be the best explanation of the larger asymptotic sizes observed in northern locations.

4.3. Bathymetric gradient

Reconstructed f patterns along the bathymetric gradient were highly correlated to depth: mean, maximum, minimum values of f , standard deviation, and amplitude (**Table 3**). The deeper the location, the higher the average f and its variability were. Little is known about the ecology of great scallops living on the continental shelf. Physical parameters such as cool and constant temperature of bottom water (12 °C in the Celtic Sea and the Bay of Biscay) and low quantity and poor quality of food may be responsible for major metabolic changes in deep water organisms, such as reduction of growth rate (Buick and Ivany, 2004), respiration (Smith and Teal, 1973) and reproduction (Rokop, 1974). As no light penetrates deep enough to sustain primary production at the bottom, organic matter inputs rely exclusively on the vertical export of phytodetritus from the upper photic layers (Pingree et al., 1982; Duineveld et al., 1997; Nérot et al., 2012). Therefore, the functional response of deep-sea populations follows a seasonal pattern based on open ocean pelagic primary production, reaching maxima when food becomes available. Although no evidence exists for deep-sea populations, plasticity of labial palps and gills dimensions has been suggested to explain relatively high clearance rate in low seston concentration (Strohmeier et al., 2009).

4.4. Local adaptations

DEB theory aims at providing a common mechanistic framework to model energy dynamics in variable environments, given a species specific set of parameters, for any individual of that species. This set of parameters is likely to evolve as more data are added to the estimation procedure of parameters. The use of the DEB parameters estimated by Lavaud et al. (2014) in this application study urged us to revise the value of some parameters linked to the metabolic acceleration experienced by scallops after their metamorphosis (for details on metabolic acceleration in DEB theory see Kooijman, 2014), which was

already suspected to cause the slight under-estimation of DSGR in previous study. Parameters were re-estimated considering these new constraints. Although it improved most of the simulations, results were not completely satisfying in some reconstructions carried out in the northern (Træna and Austevoll) and the deepest locations (162 m). The difficulties encountered in the reconstruction of functional response in these locations might result from potentially high physiologic and metabolic differences in animals living in such extreme environments when compared to inshore individuals. Indeed, a degree of local physiological adaptation may permit the survival of great scallops in deep-sea and polar environments (Buick and Ivany, 2004). Phenotypic differences (in growth and reproduction patterns) have long been reported between great scallops originating from different locations along Atlantic coasts (Antoine et al., 1979; Mackie and Ansell, 1993; Magnesen and Christophersen, 2008; Chauvaud et al., 2012). Two recent studies confirmed the presence of separated stocks within the distribution area of *P. maximus*: Morvezen et al. (2016) identified two clusters (Norwegian and Atlantic) on a latitudinal gradient, while Nicolle et al. (2016), using larval dispersal modeling, showed that the Celtic Sea and SW England populations constituted a separate group, showing a weak connectivity (<1.5%) with other coastal populations of the English Channel (compared to rates up to 20% within some English Channel local populations).

The very low values of the reconstructed \dot{p}_M in Træna and on the continental shelf are in line with lower growth rates observations of other species in these ecosystems (Parsons, 1997) and might result from environmental conditions as lower temperature reduce metabolic activity and thus maintenance. Lower reconstructed $[E]$ (reserve to structure ratio) observed in the Bay of Brest compared to the location of Træna and the Celtic Sea (at 98 m) might reflect the relative small size at age of northern and offshore individuals. Indeed, as these two populations present lower growth rates during the first years of growth, young great scallops remain smaller than their fast growing fellows from southern locations. DEB theory shows that the smaller the individual, the faster reserve density follows fluctuations in food density, leading to individuals capable of taking advantage of highly seasonal food availability. There might also be a dilution effect of growth in the larger young great scallops from Brest as more structure reduces reserve density.

4.5. Linking functional response to food proxies

The identification and quantification of energy input proxies in bioenergetic modeling of bivalves is a recurrent issue, which often constitutes the major control of the goodness of fit and the accuracy of simulations. The approach developed by Lavaud et al. (under review, this issue) allows inverting the problem in order to better understanding the feeding dynamics of great scallops. The comparison between the different food proxies and the reconstructed functional response highlighted the complexity of the linkage between food availability, ingestion, and assimilation, as shown by many authors using other methods (Ward et al., 1998; Lorrain et al., 2002; Nérot et al., 2012). There is also a time scales discrepancy between the high frequency modelled time series of f and the daily to weekly time scale of environmental conditions monitoring. Nevertheless, during the six years study (1998–2003) in the Bay of Brest, the dynamics of the reconstructed functional response seemed to be more related to chlorophyll-*a* variations than to any other food proxy. More precisely, chlorophyll-*a* concentrations measured in the water column (and not at the bottom) showed the best match to f time series. However, when compared to additional potential food availability descriptors, as done in 2011, variables such as biovolumes and dinoflagellates concentrations in the water column and diatoms and chlorophyll-*a* at the bottom actually explained most of the variability of the reconstructed assimilation. The interpretation of the dynamics of f

can be further detailed when considering data of phytoplankton species description. The concomitant bloom of *Amphora sp.* and *Pseudo-nitzschia cf. delicatissima* and the decrease of f on day 120 in 2011 might indicate a reduction of feeding due to the predominance of these species in the water. Although these species are likely not harmful to the scallop itself (Trainer et al., 2008), some studies showed reduction of filtering activity in oysters exposed to *Pseudo-nitzschia* cells (Mafra et al., 2009). Particulate organic matter was also found to be of significant importance. This last food source could sustain energy requirements during late autumn, winter, and early spring, i.e. outside blooming periods of phytoplankton (Lavaud et al., 2014). Nevertheless, the reconstruction of the functional response can only be applied to periods of growth, as it is based on growth increments width. Therefore, the conclusions on the relevance of these food proxies must be taken with care and at least limited to the periods of growth. Chlorophyll-*a* has long been used as the food proxy for filter feeding organisms (e.g. Bacher et al., 1997; Pouvreau et al., 2006; Sarà et al., 2012) for this pigment is present in every phytoplankton species. In coastal locations from the middle of *P. maximus*' spatial distribution range (e.g. France and the UK), phytoplankton is abundant during more than half of the year (from March to October). Results from this work suggest that during the period of growth of the great scallop, chlorophyll-*a* seems to remain a good enough indicator of food availability in these ecosystems. Studies comparing the use of other markers of food availability (Bourlès et al., 2009; Handå et al., 2011; Hawkins et al., 2014; Lavaud et al., 2014), such as POM, SPM or phytoplankton cell counts, came to similar conclusions: the relevance of other seston variables than chlorophyll-*a* is likely to increase along with decreasing phytoplankton densities. However, as phytoplankton composition and abundance is extremely variable from one year to another (Figs. 7 and 8; Lorrain et al., 2000), the need for an easily measured variable such as chlorophyll-*a* in numerical modeling seems to outweigh the gain from more specific descriptors, especially in larger scale studies (both geographically and temporally).

4.6. Limitations

The approach used in this study has some limits that need to be acknowledged. Firstly, it is not possible to directly assign calendar dates to growth increments deposited before the last winter stop experienced by the animal (although indirectly achievable through isotopic analysis). The method used to resettle older growth trajectory in time thanks to the temperature is based on the statistical correlations between temperature and DSGR variation. However, uncertainties persist as other factors such as the timing and intensity of primary production could influence the seasonal growth rate maximum (L. Chauvaud, pers. comm.), maybe through hormonal activity. Secondly, the reconstruction procedure relies on growth data provided by the incremental width of growth striae. In turn, it can only be applied to periods of significant growth. As the measurement of DSGR cannot be conducted below a threshold of 0.05 mm d^{-1} , no information can be extracted from the winter period when growth is extremely slowed which, instead of producing clearly visible striae, results in a dense accumulation of tiny increment appearing as a large “winter” mark in macroscopic observation.

4.7. Perspectives and prospects

4.7.1. Reconstruction of reproduction

The current knowledge on the reproductive physiology of *P. maximus* is detailed regarding the process itself, however, the overall physiology of organisms during reproduction is still understudied. For instance, questioning persist about the potentially negative effect of spawning on assimilation.

Understanding these processes might allow us to decipher such activity from assimilation time series in the past. The current approach could bring valuable information on the evolution of reproduction activity (e.g. number of eggs release during spawning, gonado-somatic index) dynamics in the past. Validation of the estimation of the physiological variables (E , $[E]$, \dot{p}_C , and \dot{p}_M) is still a prerequisite, which could be achieved through the seasonal biochemical analysis of great scallops (Pazos et al., 1997; Strohmeier et al., 2000) from various locations of its spatial distribution range.

4.7.2. Coupling DEB reconstruction and geochemical analysis of shells

The use of bivalve shells as biogenic archives of past environmental conditions constitutes a remarkable source of information for the understanding of paleoclimate and paleoenvironments (Jones, 1983; Goodwin et al., 2001; Schöne et al. 2011). Indeed, the analysis of various geochemical proxies from sequential sampling along the shell growth axis provided high-resolution records of spatial and temporal patterns in temperature, food, primary production or large scale climatic events (Jones et al., 1983; Chauvaud et al., 2005; Thébault et al., 2009; Lavaud et al., 2013; Thébault and Chauvaud, 2013). Only few potential proxies of the trophic availability measured from carbonated skeleton of marine bivalve have been reported and are still being debated (Barats et al., 2010; Thébault et al., 2009; Thébault and Chauvaud, 2013; Jolivet et al., 2015). The present work provides a new perspective in the reconstruction of past environmental conditions. The possibility of studying the variability of assimilation patterns and its seasonality over the long term could help understanding present and past ecological mechanisms impacting the great scallop. Since the study of oxygen isotopes ratios allows the reconstruction of temperatures at the moment of growth (Chauvaud et al., 2005), an attractive perspective would be to use these reconstructed temperature time series, extracted from the shell, to reconstruct the dynamics of food assimilation and physiological variables. Therefore, one could determine past environmental (thermal and trophic) conditions from a shell even when field data are not available, which open perspectives in paleoecological studies.

4.8. Conclusions

The inversion of the DEB model for the great scallop carried out in this study indicated that the growth patterns of *P. maximus* along its spatial distribution range are essentially influenced by the dynamics of environmental conditions (food assimilation and temperature), rather than by differential physiological responses that might arise in contrasted habitats. The reconstruction of functional response is a novel approach to study food proxies for suspension-feeding organisms, indicating the relevance of several descriptors at different time of the year or in certain systems. However, modeling experiments carried out on such a large scale (both geographically and temporally) urge us to select easily measured variables such as chlorophyll-*a*, which seems to outweigh the gain from more specific descriptors in this case. Finally, this work emphasized the (sometimes neglected) fact that the physiological performance of organisms depends not only on average environmental conditions (temperature and food availability) but also on their variability, their seasonality, and on the diversity of trophic sources.

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Appendix

Table A1. Statistics of the reconstructed functional responses for each year of the different age classes in the 10 studied locations. AC: age class; AYL: age and year of life measured; L_i : initial length at the beginning of the year; DG: number of days of growth.

N	AC	AYL	L_i	Mean f	Maximum f	Minimum f	Amplitude	SD	DG
<i>Træna</i>									
9	3	1 (1999)	1.8	0.77	0.99	0.02	0.97	0.24	178
4	6	1 (1994)	1.8	0.72	1.00	0.25	0.75	0.23	144
		2 (1995)	3.7	0.83	1.00	0.18	0.82	0.09	152
		3 (1996)	6.0	0.71	1.00	0.00	1.00	0.21	114
		4 (1997)	8.3	0.59	0.98	0.21	0.77	0.11	98
		5 (1998)	9.8	0.65	0.93	0.42	0.51	0.18	94
<i>Austevoll</i>									
5	3	1 (1986)	1.9	0.55	0.89	0.04	0.85	0.33	132
		2 (1987)	4.5	0.83	1.00	0.46	0.54	0.16	141
		3 (1988)	6.5	0.71	1.00	0.40	0.60	0.17	142
11	4	1 (1985)	1.9	0.49	1.00	0.16	0.84	0.23	212
		2 (1986)	4.5	0.76	0.96	0.33	0.63	0.14	134
		3 (1987)	6.5	0.85	1.00	0.60	0.40	0.13	127
		4 (1988)	8.2	0.68	1.00	0.31	0.69	0.19	127
23	5	1 (1984)	1.9	0.45	0.70	0.18	0.52	0.16	85
		2 (1985)	4.5	0.75	1.00	0.00	1.00	0.25	165
		3 (1986)	6.5	0.83	1.00	0.35	0.65	0.22	140
		4 (1987)	8.2	0.95	1.00	0.83	0.17	0.05	90
		5 (1988)	9.6	0.62	0.88	0.41	0.47	0.13	85
<i>Holyhead</i>									
2	3	1 (2000)	2.3	0.31	0.39	0.25	0.14	0.05	85
		2 (2001)	4.4	0.59	0.81	0.29	0.52	0.15	136
		3 (2002)	7.1	0.72	1.00	0.50	0.50	0.16	97
5	4	1 (1999)	2.2	0.36	0.60	0.21	0.39	0.10	140
		2 (2000)	4.4	0.60	0.86	0.30	0.56	0.14	146
		3 (2001)	7.0	0.59	0.85	0.35	0.50	0.17	102
		4 (2002)	8.7	0.69	0.92	0.34	0.58	0.14	76
3	5	1 (1998)	2.0	0.40	0.67	0.25	0.42	0.13	130
		2 (1999)	4.3	0.62	0.77	0.16	0.61	0.14	154

Table A1 (continued)

		3 (2000)	7.0	0.67	0.98	0.36	0.62	0.16	134
		4 (2001)	8.6	0.61	0.96	0.29	0.67	0.18	91
		5 (2002)	9.7	0.70	0.88	0.57	0.31	0.10	73
3	6	1 (1997)	2.3	0.38	0.57	0.25	0.32	0.08	101
		2 (1998)	4.6	0.59	0.90	0.12	0.78	0.18	144
		3 (1999)	7.5	0.69	0.94	0.30	0.64	0.17	118
		4 (2000)	9.4	0.69	1.00	0.46	0.54	0.20	102
		5 (2001)	10.1	0.63	0.89	0.37	0.52	0.16	64
		6 (2002)	10.7	0.64	0.74	0.51	0.23	0.07	52
<i>Plymouth</i>									
8	2	2 (2005)	6.5	0.74	1.00	0.16	0.84	0.15	234
7	3	2 (2004)	6.5	0.78	0.98	0.05	0.93	0.19	236
		3 (2005)	8.6	0.71	0.93	0.30	0.63	0.12	193
8	4	2 (2003)	6.5	0.73	1.00	0.19	0.81	0.18	263
		3 (2004)	8.6	0.75	1.00	0.46	0.54	0.15	176
		4 (2005)	9.6	0.59	0.71	0.40	0.31	0.06	132
2	5	2 (2002)	6.5	0.73	1.00	0.40	0.60	0.18	198
		3 (2003)	8.6	0.64	0.94	0.37	0.57	0.13	170
		4 (2004)	9.6	0.57	0.76	0.38	0.38	0.08	97
		5 (2005)	10.1	0.60	0.78	0.46	0.32	0.07	118
<i>Brest</i>									
55	1	1 (1998)	3.6	0.54	0.97	0.07	0.90	0.18	275
39	1	1 (1999)	3.4	0.61	1.00	0.35	0.65	0.15	279
39	1	1 (2000)	3.3	0.63	0.99	0.34	0.65	0.15	249
27	1	1 (2001)	3.0	0.59	0.91	0.13	0.78	0.15	283
19	1	1 (2002)	3.0	0.63	0.99	0.28	0.71	0.18	259
31	1	1 (2003)	2.6	0.71	1.00	0.23	0.77	0.17	262
32	1	1 (2011)	2.8	0.60	0.86	0.41	0.45	0.10	282
10	3	3 (1998)	9.1	0.52	0.83	0.24	0.59	0.12	149
10	3	3 (1999)	9.1	0.53	0.80	0.29	0.51	0.12	144
10	3	3 (2000)	9.4	0.54	0.86	0.38	0.48	0.13	128
10	3	3 (2001)	9.2	0.47	0.67	0.32	0.35	0.10	129
11	3	3 (2002)	8.7	0.54	0.71	0.41	0.30	0.09	83
10	3	3 (2003)	8.8	0.50	0.70	0.38	0.32	0.08	123
<i>Quiberon</i>									
20	1	1 (2001)	2.4	0.59	0.98	0.18	0.80	0.26	258
35	2	1 (2000)	2.2	0.53	0.84	0.20	0.64	0.15	272
		2 (2001)	6.1	0.46	0.65	0.27	0.38	0.07	209
<i>Celtic Sea 98 m</i>									
3	4	1 (1995)	2.0	0.60	1.00	0.13	0.87	0.26	187
		2 (1996)	4.5	0.61	0.92	0.12	0.80	0.21	142
		3 (1997)	6.4	0.66	0.95	0.23	0.72	0.23	136
2	5	1 (1994)	2.0	0.61	0.85	0.26	0.59	0.19	155

Table A1 (continued)

		2 (1995)	4.5	0.71	0.97	0.23	0.74	0.25	155
		3 (1996)	6.4	0.78	1.00	0.36	0.64	0.21	152
		4 (1997)	7.8	0.65	1.00	0.32	0.68	0.20	157
6	6	1 (1993)	2.0	0.58	1.00	0.13	0.87	0.13	175
		2 (1994)	4.5	0.68	1.00	0.19	0.81	0.27	160
		3 (1995)	6.4	0.61	1.00	0.18	0.82	0.27	133
		4 (1996)	7.8	0.60	0.93	0.02	0.91	0.29	99
		5 (1997)	8.9	0.61	1.00	0.18	0.82	0.29	107
<i>Celtic Sea 109 m</i>									
2	4	2 (1996)	4.0	0.68	1.00	0.26	0.74	0.18	181
		3 (1997)	6.3	0.67	1.00	0.07	0.93	0.30	132
2	5	1 (1994)	2.1	0.45	0.67	0.08	0.59	0.13	113
		2 (1995)	4.0	0.70	1.00	0.05	0.95	0.26	175
		3 (1996)	6.3	0.71	1.00	0.15	0.85	0.26	167
		4 (1997)	8.2	0.68	0.98	0.13	0.85	0.27	92
		5 (1998)	9.2	0.62	0.91	0.33	0.58	0.16	113
<i>Celtic Sea 150 m</i>									
3	4	1 (1995)	2.5	0.56	1.00	0.04	0.96	0.31	129
		2 (1996)	4.3	0.74	1.00	0.18	0.82	0.26	126
		3 (1997)	6.2	0.73	1.00	0.00	1.00	0.36	128
3	6	1 (1993)	2.5	0.62	1.00	0.00	1.00	0.32	116
		2 (1994)	4.3	0.69	1.00	0.10	0.90	0.32	137
		3 (1995)	6.2	0.71	1.00	0.00	1.00	0.29	132
		4 (1996)	7.9	0.63	1.00	0.02	0.98	0.35	123
		5 (1997)	8.8	0.65	0.99	0.00	0.99	0.22	89
4	7	1 (1992)	2.5	0.56	1.00	0.15	0.85	0.21	163
		2 (1993)	4.3	0.71	1.00	0.10	0.90	0.28	145
		3 (1994)	6.2	0.70	1.00	0.00	1.00	0.34	118
		4 (1995)	7.9	0.65	1.00	0.08	0.92	0.26	132
		5 (1996)	8.8	0.62	1.00	0.01	0.99	0.32	87
2	8	1 (1991)	2.5	0.50	0.87	0.05	0.82	0.24	119
		2 (1992)	4.3	0.65	1.00	0.30	0.70	0.24	154
		3 (1993)	6.2	0.79	1.00	0.01	0.99	0.25	112
		4 (1994)	7.9	0.64	1.00	0.05	0.95	0.32	81
<i>Celtic Sea 162 m</i>									
3	4	2 (1996)	4.2	0.60	0.98	0.07	0.91	0.24	192
		3 (1997)	5.8	0.64	1.00	0.00	1.00	0.31	137
3	5	1 (1994)	2.0	0.61	0.85	0.26	0.59	0.25	144
		2 (1995)	4.2	0.68	1.00	0.16	0.84	0.32	124
		3 (1996)	5.8	0.74	1.00	0.00	1.00	0.32	134
		4 (1997)	7.1	0.72	0.95	0.07	0.88	0.31	96
2	6	2 (1994)	4.2	0.69	1.00	0.05	0.95	0.27	115
		3 (1995)	5.8	0.71	1.00	0.08	0.92	0.31	123
		4 (1996)	7.1	0.60	0.93	0.02	0.91	0.29	99

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