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1 Investigating down-shore migration effects on individual
2 growth and reproduction of the ecosystem engineer *Arenicola*
3 *marina*

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9 **Abstract**

10 *Arenicola marina* (Annelida Polychaeta) is a harvested ecosystem engineer in-
11 habiting galleries within soft-sediment foreshores from the Mediterranean to the
12 Arctic. It displays a typical distribution pattern on most foreshores, with the ju-
13 veniles inhabiting the mediolittoral shore and migrating to the infralittoral shore
14 while growing. In this study, we have characterized the shore migrations of a tem-
15 perate population of *A. marina* and estimated its potential individual growth and
16 reproduction under different migration scenarios using a Dynamic Energy Budget
17 model. A sand temperature model was developed in order to predict the temper-
18 ature experienced by lugworms according to the depth of their galleries and their
19 bathymetric level. The food availability and the associated scaled functional re-
20 sponse were estimated from *in situ* growth data and associated nitrogen content
21 and chlorophyll-a concentration (Chla) data. The metabolic response of lugworms
22 to temperature (temperature tolerance range, related Arrhenius temperatures) was
23 assessed from literature data. The sand temperature model outputs did not explain
24 alone spatial differences in individual growth and reproduction. However, an in-
25 crease of food availability with bathymetry, with Chla as a proxy, well explained
26 growth and reproduction. For now, the temperature hypothesis is discarded but
27 other factors (desiccation or hypoxia) should be considered in future studies.

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28 **Keywords**

29 Dynamic Energy Budget, Sand temperature model, Lugworm, Metabolic activity
30 and Intertidal ecosystem

31 **1. Introduction**

32 *Arenicola marina* (L.) is a marine benthic polychaete (Annelida) living in bur-
33 rows of 5 - 10 cm deep for juveniles and up to 30 cm deep for adults on intertidal
34 coastal sediments, and distributed from the Mediterranean to the Arctic (Long-
35 bottom, 1970; Volkenbron, 2005). This polychaete is considered to be an ecosystem
36 engineer, as it creates bioturbation through sediment reworking, enhancing sediment
37 oxygenation by flushing its burrow, selecting species (such as bacteria, microphyto-
38 benthos, some amphipods like *Urothoe poseidonis* and copepods) at the expenses of
39 others (such as tube worms or some marine plants like *Zostara noltii*) (Clarke et al.,
40 2017; Kristensen, 2001; Reise, 1985; Volkenborn, 2005). Lugworms are commonly
41 harvested for bait in several countries, where their commercial value can be substan-
42 tial (De Cubber et al., 2018; Watson et al., 2017), leading to some negative impacts
43 on the associated species or on the harvested *A. marina* population itself (Beukema,
44 1995; Clarke et al., 2017; Olive, 1993). Consequently, the need for implementing
45 management measures for some populations of *A. marina* has been evidenced in the
46 Eastern English Channel (De Cubber et al., 2018), and some management measures
47 have already been implemented in Europe, such as licensing in the UK (Watson,
48 2015) or quotas in Portugal (Xenarios et al., 2018).

49 However, those management measures rarely rely on the local ecology and life-
50 history traits of the species (Watson et al., 2017). *A. marina* displays a benthic
51 pelagic life cycle, with larvae dispersing in the water column and temporarily settling
52 for 6 to 7 months on subtidal bottoms (macroalgae and mussel beds), where they
53 live in mucus tubes attached to the substrate and feed on suspended and deposited
54 particles around their tube (De Cubber et al., 2019). Then, a second dispersal phase
55 precedes the lugworms' settlement on the foreshores (considered as the recruitment),
56 where the juveniles and later adults live in galleries and are psammivorous, swal-
57 lowing the sediment enriched with organic matter (De Cubber et al., 2019; Farke

58 and Berghuis, 1979a, b; Newell, 1948; 1949; Reise, 1985; Reise et al., 2001). Re-
59 cently, a Dynamic Energy Budget (DEB) model has been developed by De Cubber
60 et al. (2019) in order to explore the time scale of the appearance of the different
61 life-stages of *A. marina*. DEB models enable to predict individual growth and repro-
62 duction of a species as well as several of its life-history traits (age at metamorphosis,
63 puberty, etc.) according to the environmental conditions (temperature and food)
64 by quantifying the energy fluxes (Kooijman, 2010). Therefore, when local environ-
65 mental conditions (temperature and food resources) are known, the DEB models
66 can provide valuable data on the biology of a targeted species to help managers to
67 implement management measures.

68 Up to now, the DEB model implemented for *A. marina* only considered chang-
69 ing environmental conditions for the early life-stage phases (before recruitment) (De
70 Cubber et al., 2019). For juveniles and adults, mean (constant) environmental con-
71 ditions (seawater temperature and food proxy) have been used as forcing variables to
72 run the DEB model (De Cubber et al., 2019). However, since lugworms live within
73 the intertidal area, they experience daily temperature variations (De Cubber et al.,
74 2019) that may be highly variable according to their location on the shore (bathy-
75 metric level) and to the depth of their gallery. Specific physiological and behavioural
76 responses of intertidal species may be triggered by heat stress such as seen in the
77 mussel *Mytilus californianus*, where outside its optimal temperature tolerance range,
78 a decrease of its physiological performances has been revealed (Kish et al., 2016) or
79 in the gastropod *Echinolittorina malaccana*, where outside its optimal temperature
80 tolerance range, tower formation has been observed (Seuront and Ng, 2016). Theses
81 responses appear crucial to be taken into account when considering the metabolism
82 of intertidal species. As a matter of fact, the distribution of juvenile and adult lug-
83 worms on the foreshore is not random and has been widely documented, describing
84 juveniles recruiting on the high mediolittoral part of the shore and gradually migrat-
85 ing down to the high infralittoral part of the shore (Cadman, 1997; De Cubber et al.,
86 2019, 2018; Farke et al., 1979; Reise, 1985; Reise et al., 2001). Some exceptions of
87 this distribution in some sites may occur, where individuals are almost only present
88 on the lower mediolittoral to high infralittoral foreshore (De Cubber et al., 2018).

89 Understanding the dynamic of the distribution of the lugworm population might be
90 vital for further population dynamic models studies (Martin et al., 2012), used by
91 managers to conduct their management plans.

92 Several hypotheses have been raised to explain the down-shore migration of lug-
93 worms. First, environmental conditions (temperature and food resources) may be
94 more favourable to lugworms in the infralittoral compared to the high mediolittoral
95 (Flach and Beukema, 1994). Second, lugworms may migrate down the shore to
96 escape intra-specific competition for space and food (Farke et al., 1979; Flach and
97 Beukema, 1994; Longbottom, 1970; Reise et al., 2001). Finally, inter-specific com-
98 petition and predation might also happen (Farke et al., 1979). On the foreshore,
99 the temperature experienced by organisms is driven by the seawater temperature
100 during immersion and by the air temperature, solar radiation, wind, air humidity
101 and atmospheric pressure during emersion (Guarini et al., 1997). Models aiming at
102 simulating the temperature of sediment have already been implemented by several
103 authors in the case of mudflats (Guarini et al., 1997; Savelli et al., 2018). They rely
104 on the heat energy balance of the different fluxes applied to the sediment surface,
105 and on the parameters of the sediment (Guarini et al., 1997; Savelli et al., 2018).
106 Nevertheless, this has never been done yet for a sandy habitat on the foreshore to
107 our knowledge. In the present study, we tested the hypothesis that temperature and
108 food levels were the main forcing variables driving the lugworms to migrate down
109 the shore using a DEB model. Our specific objectives were:

- 110 1. to characterize the *in situ* shore migrations of a local population of *A. marina*,
- 111 2. to reconstruct the sand temperature of the shore according to the depth of the
112 galleries and the bathymetric level, as well as to measure local food levels,
- 113 3. to estimate the metabolic response of lugworms to temperature (via the Ar-
114 rhenius temperature) and to different proxies for food sources and quantities
115 (via the scaled functional response) using a DEB model,
- 116 4. to compare the potential for growth and reproduction of *A. marina* individuals
117 under different migration scenarios using a DEB model.

118 **2. Material and Methods**

119 *2.1. Study area*

120 Lugworms and the associated environmental parameters were collected at Wime-
121 reux (N 50°46'14", E 01°36'38"), located on the Eastern English Channel (Hauts-
122 de-France, France) (Fig. 1). The area is composed of a mixture of sandy and rocky
123 bottoms, and the tidal regime is semi-diurnal and macrotidal with amplitudes that
124 may exceed 8 m around 2 days before the full moon (Migné et al., 2004; Rolet et al.,
125 2015). In this area, the population of *Arenicola marina* is mainly found on the high
126 mediolittoral to low mediolittoral/infralittoral part of the foreshore and therefore
127 exposed to emersion periods of several hours (De Cubber et al., 2018).

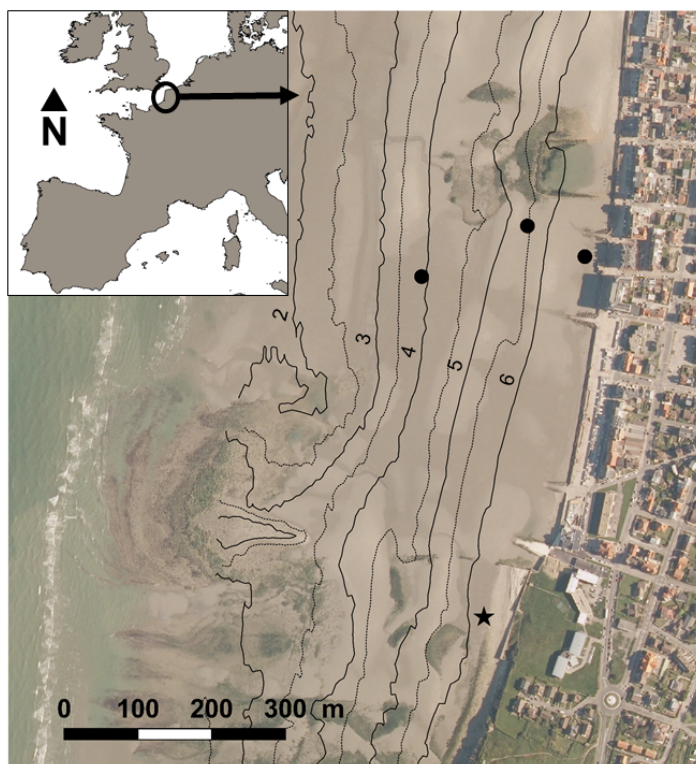


Figure 1: Study site of Wimereux (Eastern English Channel, France) and location of the sampling points for the sediment temperature measurements with two HOBO® Water Temp Pro v2 probes fixed on a metal rod embedded in the sediment (star), and for the size structure of the *Arenicola marina* population (dots) on different bathymetric levels (lines with numbers) of the foreshore.

128 Densities of *A. marina* have been reported to range from 0 to 61 individuals.m⁻²
129 with the greatest density on the high mediolittoral shore constituted by smaller

130 individuals. More details on the study site and the population of *A. marina* of the
131 area are given in De Cubber et al. (2018).

132 *2.2. Compilation of in situ observations*

133 A dataset of physical measurements collected within the area of the study site
134 was compiled to force a sediment temperature model based on the one developed by
135 Guarini et al. (1997) for mudflats (Fig. 2). The wind speed U ($\text{m}\cdot\text{s}^{-1}$), the air temper-
136 ature T_{Air} (K), the relative humidity H_r (%), the atmospheric pressure P_{atm} (Pa) and
137 the irradiance R_s ($\text{J}\cdot\text{m}^{-2}$) were extracted from environmental data recorded hourly at
138 Boulogne-sur-Mer (N 50°43'35", E 01°36'53") (wind speed, air temperature, relative
139 humidity and atmospheric pressure) and Calais (N 50°56'53", E 01°51'23") (irradi-
140 ance) (France) by Meteo France ltd. (<https://donneespubliques.meteofrance.fr/>)
141 during the years 2017 and 2018. The water height H_w (m) (Fig. 2) was ob-
142 tained for the same years from the Marel Carnot station (<http://www.ifremer.fr/co->
143 [en/eulerianPlatform](http://www.ifremer.fr/co-en/eulerianPlatform)) at the tide gauge of Boulogne-sur-Mer. The water height was
144 compared to the elevation of the three shore points (Fig. 1), obtained from the inter-
145 regional project CLAREC, INSU-CNRS M2C-UNICAEN (<http://www.uni-caen.fr/>
146 [dataclarec/home/elevations.html](http://www.uni-caen.fr/dataclarec/home/elevations.html)) according to the local marine altimetric refer-
147 ences (SHOM, 2017). The water temperature T_w (K) consisted in hourly measure-
148 ments from the same Marel Carnot station coupled with monthly observations made
149 by the Service d'observation en milieu littoral (SOMLIT, <http://somlit-db.epoc.u->
150 [bordeaux1.fr/bdd.php](http://somlit-db.epoc.u-bordeaux1.fr/bdd.php)) at Wimereux (coastal bottom point), when data of the Marel
151 Carnot station were missing. The chlorophyll-a concentration of the seawater *Chla*
152 ($\mu\text{g}\cdot\text{L}^{-1}$) was also retrieved from the Service d'observation en milieu littoral (SOM-
153 LIT) at Wimereux (coastal point) in order to be tested as a proxy of the food levels.

154 *2.3. Field sampling and laboratory measurements*

155 *Follow-up of the Arenicola marina population structure at Wimereux.* From March
156 2017 to July 2018, around 30 individuals of *A. marina* were sampled 8 times at each
157 of the three locations on the foreshore from the mediolittoral/infralittoral to high
158 mediolittoral at the study site (Fig. 1).

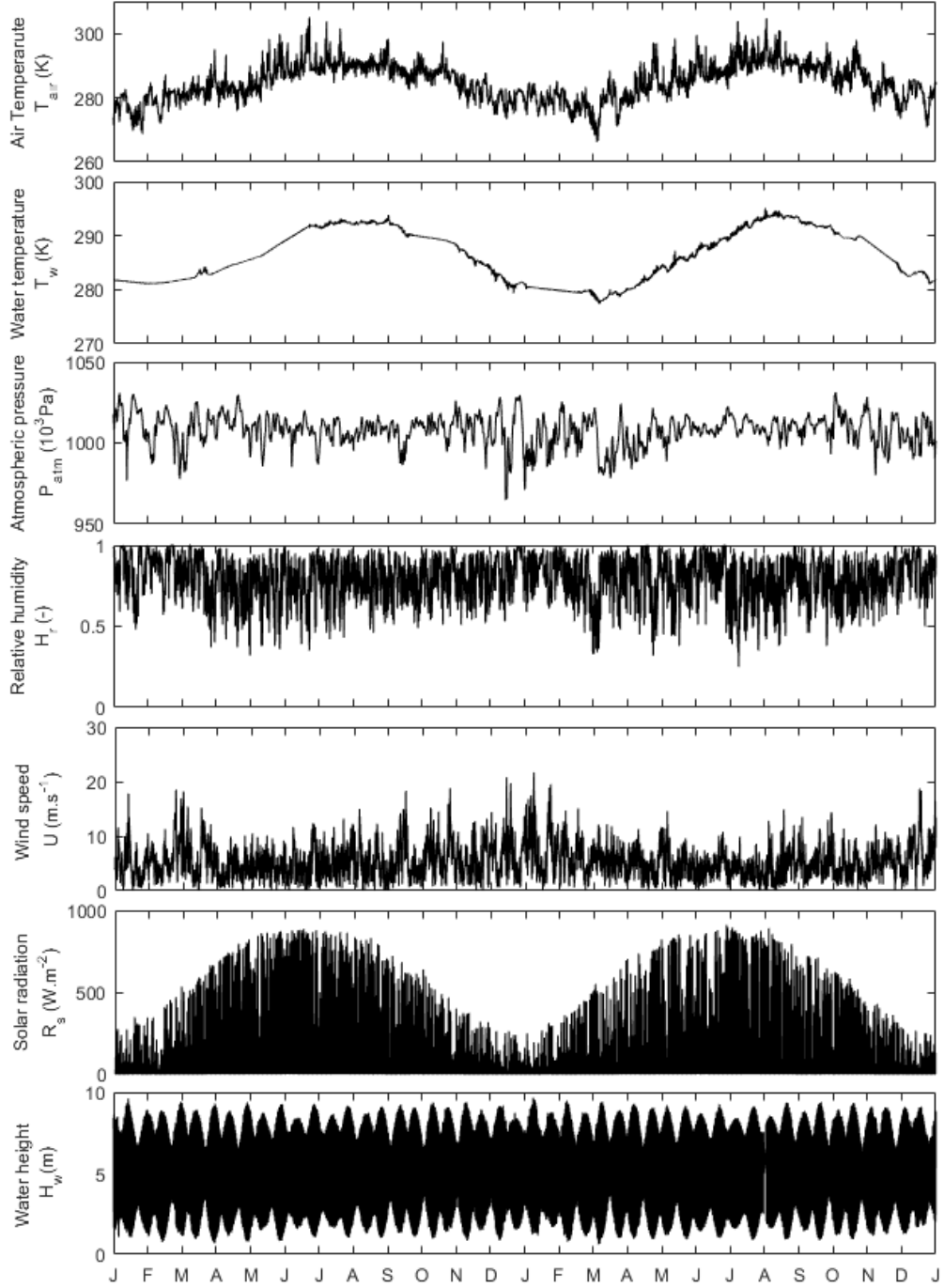


Figure 2: *In situ* air temperature (T_{air} , K), seawater temperature (T_w , K), atmospheric pressure (P_{atm} , 10^3 .Pa), relative humidity (H_r , -), windspeed (U , $m.s^{-1}$), solar radiation (R_s , $W.m^2$) and water height (H_w , m) used as forcing variables to constrain the sediment temperature model between January 2017 and December 2018. The data were recovered from the Marel Carnot station (H_w , T_w) (<http://www.ifremer.fr/co-en/eulerianPlatform>), Meteo France ltd. (T_{air} , P_{atm} , H_r , U , R_s) (<https://donneespubliques.meteofrance.fr/>), and the Service d'observation en milieu littoral (SOMLIT, <http://somlit-db.epoc.u-bordeaux1.fr/bdd.php>) at Wimereux (coastal bottom point) (T_w). The seawater temperature T_w was reconstructed from both the Marel Carnot station when data were available (high-frequency measurements) and SOMLIT otherwise (low frequency measurements).

159 There, the population of *A. marina* has already been shown to display the typ-
160 ical spatial distribution (De Cubber et al., 2018) described by other authors with
161 juveniles on the higher shore and adults elsewhere (Farke et al., 1979).

162 *Follow-up of the nitrogen content of sediment.* Triplicates of surface sediment cores
163 (1 cm deep x 10 cm of diameter) were collected at the same three locations of
164 the study site at every sampling period (n = 8) in order to assess the organic
165 matter content of the sediment. Once collected, samples were kept at -20°C until
166 analysis. Homogenised aliquots of around 30 g of each of the subsamples were
167 then put in separate tin containers and analyzed with an organic elemental analyzer
168 Thermofisher Flash 2000 after calibration, in order to measure the nitrogen content
169 of sediment. For each sample, one subsample was burnt during 5 h at 550°C in
170 order to remove the organic nitrogen, and another one was dried out at 40°C during
171 1 day. The calibration was performed by analyzing the nitrogen content of several
172 sediment samples for which the elemental contents were known. Given the low
173 nitrogen concentrations of the sediment and the detection levels of the device, only
174 the total nitrogen content (organic + inorganic) of the sediment could be measured.

175 *Follow-up of the temperature variations within the sediment.* Temperatures within
176 the sediment (*ca* 5 cm and 21 cm deep) were recorded with two HOBO® Water Temp
177 Pro v2 probes fixed on a metal rod embedded in the sediment on the higher shore
178 (high mediolittoral) of the study site between the 01/10/17 and the 24/10/17 and
179 between the 03/05/18 and the 01/07/18 (10 min interval between each measurement)
180 (Fig. 1).

181 2.4. Data analysis

182 2.4.1. Sediment temperature model

183 *The model.* The sediment temperature model helped to solve the sediment temper-
184 ature (T_s) equation adapted from Guarini et al. (1997), where t is the time (s),
185 z is the depth (m), η is the heat conductivity (W. m⁻¹. K⁻¹) and μ is the thermal
186 diffusivity (m². s⁻¹) of the sediment (Equation 1).

$$\frac{\eta}{\mu} \cdot \frac{\delta T_s(z, t)}{\delta t} = \frac{\delta}{\delta z} \cdot \eta \cdot \frac{\delta T_s(z, t)}{\delta z} \quad (1)$$

187 The partial differential equation was solved on Matlab 2015b using the pdepe func-
188 tion considering heat energy balance equations at the boundaries $z_0 = 0$ m (sediment
189 surface) and $z_1 = 1$ m deep (beyond this depth, the sediment temperature is sup-
190 posed equal to the one of the water) (Tables 1, 2).

Table 1: Equations of the heat energy balance at the boundary conditions (Guarini et al., 1997) and the associated heat fluxes (Brock et al., 1981; Guarini et al., 1997; Savelli et al., 2018) as implemented in the present study.

Heat Energy balance equations at the boundary conditions		
	immersion	emersion
$z_0 = 0$ m	$f_{HEB}(T_s(0, t)) = S_{s-w}$	$f_{HEB}(T_s(0, t)) = R_{sun} + R_{atm} - R_s - S_{s-a} - V_s$
$z_1 = 1$ m	$f_{HEB}(T_s(1, t)) = -S_{s-w}$	$f_{HEB}(T_s(1, t)) = -S_{s-w}$
Heat fluxes ($W \cdot m^{-2}$) equations		
Solar radiation	$R_{sun} = R_{obs}$	
Atmosphere radiation	$R_{atm} = \epsilon_a \cdot \sigma \cdot T_{air}^4 \cdot (\zeta - k)$ $\epsilon_a = 0.937 \cdot 10^{-5} \cdot T_{air}^2$ $k = R_{obs} / R_{std}$ $decl = 23.45 \cdot \sin\left(360 \cdot \frac{284 + day_{julian}}{365}\right)$ $R_1 = \left(\sqrt{1 + 0.33 \cdot \cos\left(\frac{360 \cdot day_{julian}}{365}\right)}\right)^{-1}$ $cos_z = \sin(decl) \cdot \sin(latitude) + \cos(decl) \cdot \cos(latitude) \cdot \cos((hour_{light} - 12) \cdot 15)$ $R_{std} = R_0 \cdot \frac{cos_z}{2 \cdot R_1^2} \cdot \left(1 + \cos\left(\frac{2 \cdot \pi \cdot (hour - 1)}{length_{daylight}}\right)\right)$	
Sand radiation	$R_s = \epsilon_M \cdot \sigma \cdot T_s(z_0, t)^4$	
Sand-air heat conduction	$S_{s-a} = \rho_a \cdot C_{Pa} \cdot C_b \cdot (1 + U) \cdot (T_s(z_0, t) - T_{air})$	
Evaporation	$V_s = \xi \cdot \rho_a \cdot L_V \cdot C_V \cdot (1 + U) \cdot (q_s \cdot (1 - q_a/q_s))$ $L_V = (250.84 - 2.35 \cdot (T_s(z, t) - 273.15)) \cdot 10^3$ $q_s = \frac{\lambda \cdot p_{sat}^V}{p_{atm} - (1 - \lambda) \cdot p_{sat}^V}$ $p_{sat}^V = \exp\left(2.3 \cdot \left(\frac{7.5 \cdot (T_{air} - 273.15)}{237.3 + (T_{air} - 273.15)} + 0.76\right)\right)$	
Sand-water heat conduction	$S_{s-w} = -\frac{\eta}{h_w} \cdot (T_s(z_0, t) - T_w(t))$	

191 At emersion time, the surface temperature was calculated from the heat energy
192 balance between the solar radiation, the atmosphere radiation, the sand radiation,
193 the sand-air heat conduction and the evaporation fluxes, and the 1 m depth tem-
194 perature from the sand-water heat conduction flux (Tables 1, 2) (Guarini et al.,
195 1997; Savelli et al., 2018). At immersion time, both the surface and the 1 m depth

196 temperatures were calculated from the sand-water heat conduction flux (Tables 1,
 197 2) (Guarini et al., 1997).

Table 2: Parameters values and their references used in the sediment temperature model as implemented in the present study.

Parameters of the model		References
Thermal diffusivity of the sand*	$\mu = 5.2164 \cdot 10^{-7} \text{ m}^2 \cdot \text{s}^{-1}$	Calibrated in this study
Conductivity of the sand*	$\eta = 3.3182 \text{ W} \cdot \text{m}^{-1} \cdot \text{K}^{-1}$	Calibrated in this study
Constant*	$\zeta = 1.2118$ -	Calibrated in this study
Stephan-Boltzman constant	$\sigma = 5.67 \cdot 10^{-8}$ -	Guarini et al. (1997)
Sand emissivity	$\epsilon_M = 0.96$ -	van Bavel and Hillel (1976)
Bulk coefficient for conduction	$C_b = 0.0014$ -	Guarini et al. (1997)
Sand porosity	$\xi = 0.351$ -	Rauch and Denis (2008)
Solar constant	$R_0 = 1353 \text{ W} \cdot \text{m}^{-2}$	Brock et al. (1981)
Bulk coefficient for evaporation	$C_V = 0.0014$ -	Guarini et al. (1997)
Air volumetric mass	$\rho_a = 1.2929 \text{ kg} \cdot \text{m}^{-3}$	Guarini et al. (1997)
Specific air heat	$C_{Pa} = 1003 \text{ J} \cdot \text{kg}^{-1} \cdot \text{K}^{-1}$	Guarini et al. (1997)
Constant evaporation ratio	$\lambda = 0.621$ -	Guarini et al. (1997)

* Parameters estimated in this study to fit the model predictions to observations

198 *Validation of the model.* The parameters related to the sediment type for which no
 199 data for sandy sediments were available (η , μ , and ζ) were estimated comparing
 200 the model output with our *in situ* sediment temperature measurements (HOBO®
 201 probes) for two recording periods (Table 2). The estimation procedure was per-
 202 formed on Matlab 2015b using the `fminsearch` function. For each period, three tidal
 203 cycles of one emersion and one immersion period (approximately 36 hours) were
 204 chosen randomly among all, 23 times for the first and shortest *in situ* temperature
 205 recording period (October 2017, 36 cycles in total) and 63 times for the second *in*
 206 *situ* temperature recording period (May-June 2018, 107 cycles in total). The esti-
 207 mation procedure was applied to these periods minimizing the mean square error
 208 (MSE) between the data and the model predictions. For each *in situ* temperature
 209 recording period, the mean parameter value was computed as well as its standard
 210 deviation. These two means were compared with a non-parametric Kruskal-Wallis
 211 test performed on Matlab R2015b. The mean value of these means was used as pa-
 212 rameter value in the implementation of the model. The parameter values obtained
 213 were then used to compute the sediment temperature on the three sampled shore
 214 levels from the surface to 1 m deep as well as the daily mean and variance of the
 215 sediment temperature at these depths.

216 *2.4.2. Effect of temperature on the metabolic rates of Arenicola marina*

217 All metabolic rates depend on temperature (Kooijman, 2010). Within the species-
 218 specific temperature tolerance range, the effect of temperature on metabolic rates
 219 can be described with the Equation (2), with T the temperature (K), T_{ref} the ref-
 220 erence temperature (taken to be 293.15 K), T_A the Arrhenius temperature (K), \dot{k}_1
 221 the rate of interest at T_{ref} , and \dot{k} the computed rate at T . Outside the lower and
 222 higher boundaries of the species-specific temperature tolerance range (respectively
 223 T_L and T_H), the effect of temperature on metabolic rates changes and is calculated
 224 adding an extra term to the Equation (2) as presented in Equation (3), with T_{AL} the
 225 Arrhenius temperature below the lower boundary of the species-specific temperature
 226 tolerance range (K) and T_{AH} the Arrhenius temperature above the higher boundary
 227 of the species-specific temperature tolerance range (K) (Kooijman, 2010).

$$\dot{k}(T) = \dot{k}_1 \cdot \exp\left(\frac{T_A}{T_{ref}} - \frac{T_A}{T}\right) \quad (2)$$

228

$$\dot{k}(T) = \dot{k}_1 \cdot \exp\left(\frac{T_A}{T_{ref}} - \frac{T_A}{T}\right) \cdot \frac{1 + \exp\left(\frac{T_{AL}}{T_{ref}} - \frac{T_{AL}}{T_L}\right) + \exp\left(\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T_{ref}}\right)}{1 + \exp\left(\frac{T_{AL}}{T} - \frac{T_{AL}}{T_L}\right) + \exp\left(\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T}\right)} \quad (3)$$

229 The Arrhenius temperature of *A. marina* has been previously estimated, using
 230 equation 2, together with the other DEB parameters with the DEBTool package
 231 (De Cubber et al., 2019; Marques et al., 2018). However, the temperature tolerance
 232 range of the species, as well as the Arrhenius temperatures outside its temperature
 233 tolerance range, has not been estimated yet given that no data below 5 °C and
 234 above 20 °C were used in the previous DEB parameter estimation (De Cubber et
 235 al., 2019). Hence, new data outside this temperature range were added to the former
 236 dataset to allow to re-estimate the Arrhenius temperature of *A. marina* within its
 237 temperature tolerance range T_A and to estimate the boundaries of the temperature
 238 tolerance range, T_L and T_H , and the related Arrhenius temperatures, T_{AL} and T_{AH} ,
 239 as well as the whole parameters set for the species. The new data set consisted
 240 in one growth experiment (De Wilde and Berghuis, 1979), one fertilization success
 241 experiment (Lewis et al., 2002), one oxygen consumption experiment (Schröer et al.,
 242 2009) and one mitochondrial respiration experiment (Sommer and Pörtner, 2004),

243 all four at several temperatures. The whole DEB parameters (including T_A , T_L , T_H ,
244 T_{AL} and T_{AH}) were re-estimated using the DEBTool software on Matlab R2015b
245 (Marques et al., 2018).

246 2.4.3. Estimation of *in situ* growth and scaled functional response reconstruction

247 For each sampling date, the population structure was approached through the
248 analysis of size frequencies on the trunk length (TL) with a 5-mm size class interval,
249 using a Bhattacharya analysis (De Cubber et al., 2018). Each cohort belongs to a
250 separate year since spawning and recruitment only happen once a year (De Cubber
251 et al., 2018). In order to reconstruct the actual temperature experienced by the
252 collected lugworm, the mean depth of the lugworms between each sampling date
253 was assessed using the linear relation presented in Equation (4), with TL (cm) the
254 mean trunk length of the cohort and z (cm) the associated depth of the gallery
255 (considering that juveniles of 1 cm of trunk length dig a gallery of 5 cm of depth
256 while adults of 12 cm of trunk length dig a gallery of 30 cm of depth). The mean
257 sediment temperature at this depth was then calculated with the sand temperature
258 model assuming a bathymetric level obtained from Equation 6 (Fig. 10).

$$z = 30 - 25 \cdot \frac{12 - TL}{12 - 1} \quad (4)$$

259 The new DEB parameters for *A. marina* were used to model the growth and
260 reproduction of the lugworms according to the *in situ* sediment temperature previ-
261 ously estimated. The growth before recruitment (or up to metamorphosis) was re-
262 constructed using the environmental conditions detailed in De Cubber et al. (2019)
263 to recreate relevant initial conditions of the growth of recruits once settled. From
264 metamorphosis time, between each collection date, the trunk length growth was
265 reconstructed using the DEB equations detailed in De Cubber et al. (2019) for a
266 scaled functional response f varying from 0.01 to 1. The scaled functional response
267 enabling the best fit (with the lowest mean squared error MSE between growth ob-
268 servations and predictions) was then used as the mean scaled functional response
269 for this time step.

270 *2.4.4. Linking the scaled functional response to food resources*

271 The mean total nitrogen content of sediment available for the recruits was re-
272 constructed from values of the total nitrogen content obtained from each bathy-
273 metric level of the shore and the relative contribution of each bathymetric level to
274 the total recruits cohorts. The mean concentration of chlorophyll-a and the recon-
275 structed total nitrogen content of sediment each interval between sampling events
276 corresponding to one reconstructed f level were tested as proxy of food density. The
277 relation between the scaled functional response and the food density X (chlorophyll-
278 a concentration or nitrogen content) is presented in Equation (5), where X_K is the
279 half-saturation coefficient (Kooijman, 2010). For the mean chlorophyll-a concentra-
280 tion, the value of X_K was fitted using Equation (5) as the value for which the lowest
281 MSE value between simulations and observations was obtained.

$$f = \frac{X}{X + X_K} \quad (5)$$

282 *2.4.5. Effects of variations in environmental conditions on the small-scale migration*
283 *patterns of *Arenicola marina* after recruitment*

284 Several scenarios ($n = 18$ in total) were tested in order to assess the impact
285 of food and temperature conditions (according to the lugworm shore location and
286 the depth of its gallery) on the individual growth and reproduction of *A. marina*
287 (Fig. 3). Environmental conditions over 1.5 years were reconstructed from the 2-
288 years reconstructed sediment temperature, the 2-year Chla measurements and the
289 half-saturation coefficient (X_K) previously estimated. The associated temperature
290 corrections and functional response were applied to the abj-DEB model for *A. ma-*
291 *rina* developed by De Cubber et al. (2019), allowing predictions on the trunk length,
292 wet weight and egg number. The spawning event was triggered when the total wet
293 weight of the eggs reached 10 % of the total wet weight according to predictions on
294 growth under constant environmental conditions with annual spawning events made
295 by De Cubber et al. (2019). The initial conditions at metamorphosis (after which
296 juveniles recruit) were estimated at environmental conditions given by De Cubber
297 et al (2019). Three main scenarios were envisioned:

298 (1) lugworms were supposed to recruit on the high mediolitoral shore without

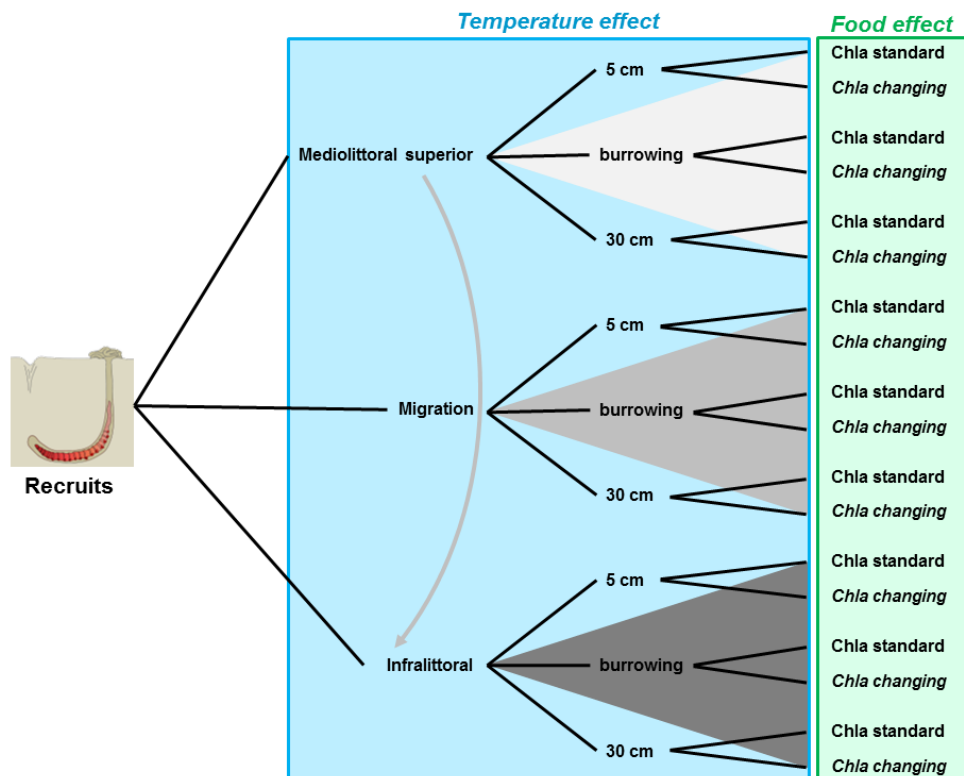


Figure 3: Representation of the different scenarios. In the light grey scenarios, lugworms recruit on the high mediolittoral shore without migrating. In the medium grey scenarios, lugworms migrate according to the Equation (4). In the dark grey scenarios, lugworms recruit directly on the infralittoral shore. For these three options, lugworms remain burrowed at 5 or 30 cm, or are able to burrow from 5 to 30 cm according to the Equation (4). For all these scenarios, we considered on the one hand that chlorophyll-a concentrations were the same everywhere on the shore, or on the other hand that chlorophyll-a concentrations were divided by 2 on the higher shore compared to the lower shore, increasing linearly between these two locations.

299 migrating

300 (2) lugworms were supposed to migrate according to the Equation (4) and the
 301 bathymetry-size relation shown in Fig. 10 (Equation 6)

302 (3) lugworms were supposed to recruit directly on the infralittoral shore (Fig. 3)

303 For these three options, lugworms remained burrowed at 5 or 30 cm, or were
 304 able to burrow from 5 to 30 cm according to the Equation (4). Finally, for all
 305 these scenarios, we considered on the one hand that chlorophyll-a concentrations
 306 were the same everywhere on the shore, or on the other hand that chlorophyll-a
 307 concentrations were divided by 2 on the higher shore compared to the lower shore,
 308 increasing linearly between these two locations. The effects of the change of food

309 and temperature were estimated by comparing the different DEB model outputs ran
 310 with those scenarios (Fig. 3).

311 3. Results

312 3.1. Spatial distribution of trunk length frequencies

313 The spatial distribution of trunk length frequencies present the common pattern
 314 usually observed on the shore with smaller individuals close to the coast line and
 315 larger ones down the shore (Fig. 4).

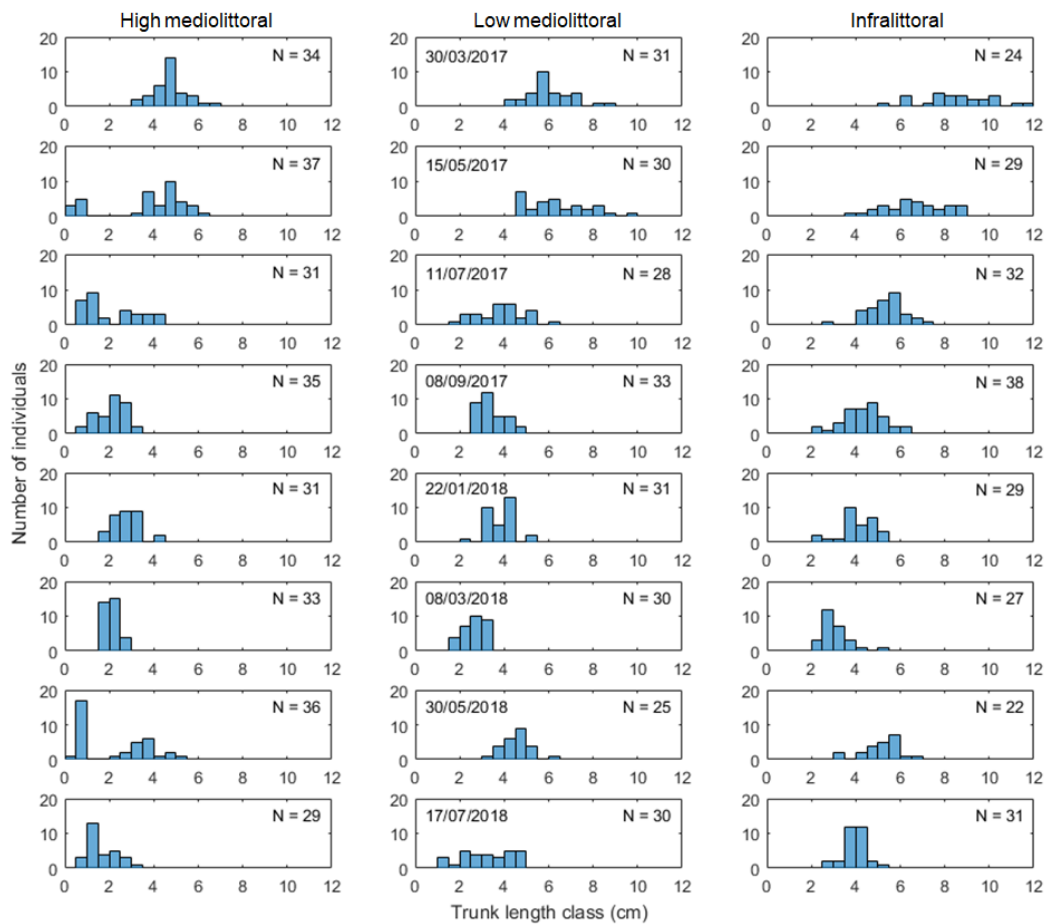


Figure 4: Distribution of the trunk length frequencies of *Arenicola marina* on the high mediolittoral (left), low mediolittoral (middle) and infralittoral (right) at the study site (Wimereux, Eastern English Channel) for each sampling date from the 30/03/2017 to the 17/07/2018. N stands for the number of individuals collected.

316 For both years, recruitment happened after March and before the end of May.
 317 The largest trunk classes (from 8 to 10 cm of trunk length) were mainly represented
 318 at the infralittoral sampling point but disappeared after mid May 2017. On the

319 high mediolittoral shore, some larger trunk length classes disappeared from one
 320 sampling event to the next (Fig. 4, for example between May 2018 and July 2018,
 321 the individuals larger than 3.5 cm disappeared from the high mediolittoral but were
 322 still found lower on the shore). This might be due to mortality, or more probably,
 323 small scale migrations down the shore.

324 3.2. Temperature within the sediment

325 *Validation of the sediment temperature model.* The mean fitted values of the constant
 326 ζ , the thermal diffusivity μ , and the conductivity η were respectively 1.21, 5.22 e^{-07}
 327 $\text{m}^2.\text{s}^{-1}$ and $3.32 \text{ W.m}^{-1}.\text{K}^{-1}$ (Table 3). The mean values of ζ and η did not show
 328 any significant differences if both parameters were estimated to fit the observations
 329 from October 2017 or the ones from May-June 2018 (Kruskal-Wallis test, $p > 0.05$).
 330 However, there was a significant difference between the value of μ estimated to fit
 331 the observations from October 2017 ($5.33 \text{ e}^{-07} \text{ m}^2.\text{s}^{-1}$) and the one estimated to fit the
 332 observations from May-June 2018 ($5.10 \text{ e}^{-07} \text{ m}^2.\text{s}^{-1}$) (Kruskal-Wallis test, $p < 0.05$)
 333 (Table 3, Fig. 5).

Table 3: Mean values of the fitted parameters ζ (constant, no unit), μ (thermal diffusivity, $\text{m}^2.\text{s}^{-1}$), and η (conductivity, $\text{W.m}^{-1}.\text{K}^{-1}$) and associated standard errors for each of the *in situ* measurement periods (October 2017 and May-June 2018) and both periods using their means. The p-values of the Kruskal-Wallis tests between the values of the two periods are also given.

Mean estimated value	October 2017	May-June 2018	p-value	All periods
η ($\text{W.m}^{-1}.\text{K}^{-1}$)	3.29 ± 0.22	3.35 ± 0.33	0.24	3.32 ± 0.29
μ ($\text{m}^2.\text{s}^{-1}$)	$5.33\text{e}^{-07} \pm 4.79\text{e}^{-08}$	$5.10\text{e}^{-07} \pm 4.72\text{e}^{-08}$	0.04	$5.22\text{e}^{-07} \pm 5.02\text{e}^{-08}$
ζ (-)	1.19 ± 0.19	1.23 ± 0.14	0.63	1.21 ± 0.17

334 The estimated mean parameter values of η , μ and ζ provided a good fit of the
 335 sediment temperature model for the May-June 2018 sediment temperature observa-
 336 tions at 5 cm deep and at 20 cm deep (Fig. 6 c, d). The fit was somewhat less good
 337 when considering the sediment temperature observations of October 2017 at both
 338 depths but still captured the main trends of temperature variations (Figs. 6 a, b).

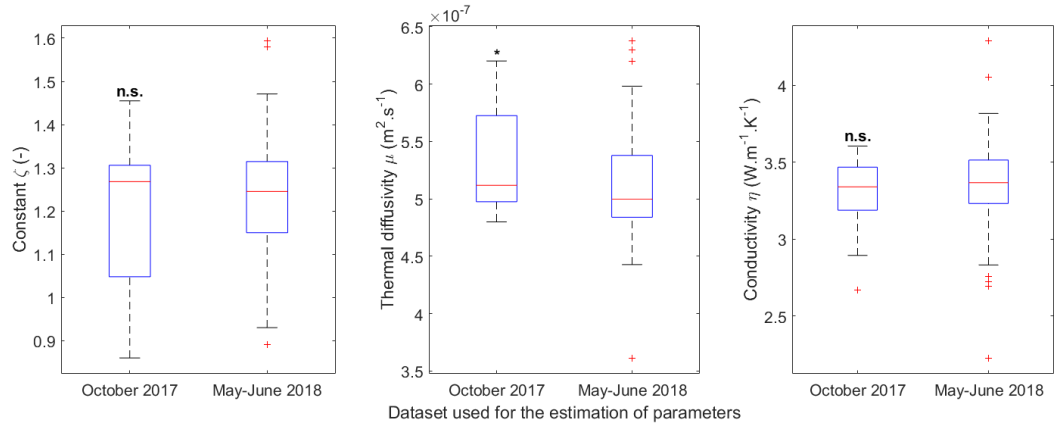


Figure 5: Boxplot representations of the distribution of the fitted values of the constant ζ (-, left), the thermal diffusivity μ ($\text{m}^2.\text{s}^{-1}$, middle), and the conductivity η ($\text{W}.\text{m}^{-1}.\text{K}^{-1}$, right). For each parameter, the red line is the median of the 23 values obtained for October 2017 and 63 values obtained for May-June 2018 when fitting the model predictions to the observations on a random period of approximately 36 hours. 50% of the values are comprised in the box, 95% in the range between the error bars. The red crosses are extreme values and the black star stands for the significant difference between the values of μ of each of the two recording periods. 'n.s.' is indicated when no significant difference was found between the value of a given parameter between the two temperature recording period.* indicates a significant difference ($p < 0.05$).

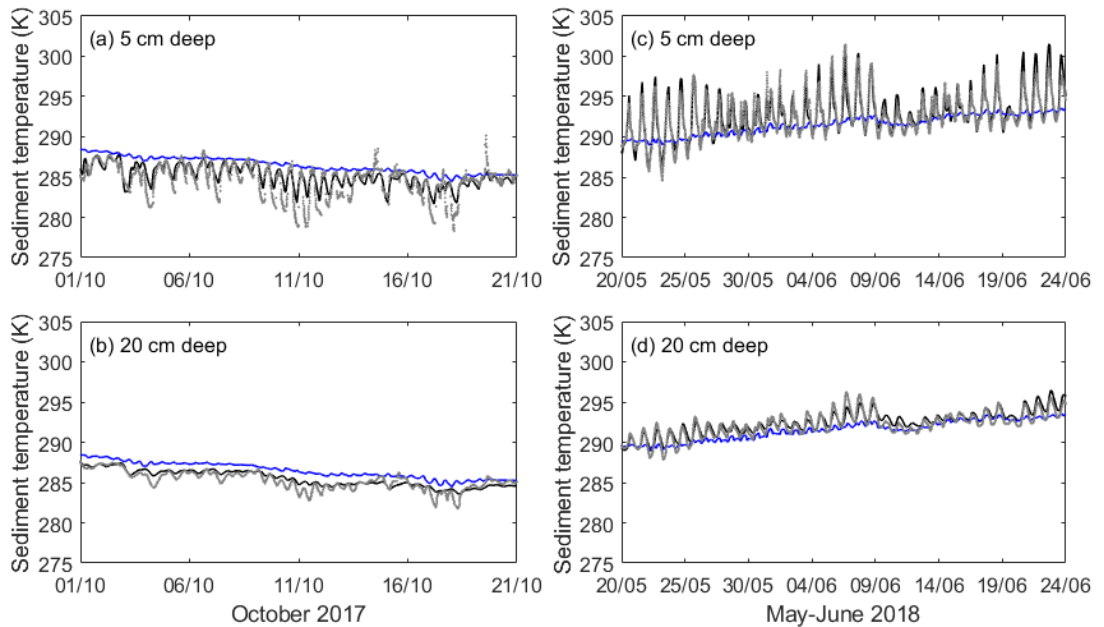


Figure 6: Comparison between the *in situ* sediment temperature measurements (grey dots) and the model output (black line) for October 2017 (a, b) and May-June 2018 (c, d) at 5 cm deep (a, c) and 20 cm deep (b, d) within the sediment using the mean fitted parameters ζ (constant, -), μ (thermal diffusivity, $\text{m}^2.\text{s}^{-1}$, and η (conductivity, $\text{W}.\text{m}^{-1}.\text{K}^{-1}$) all periods considered (Table 3). The blue line is the water temperature from the Marel Carnot station.

339 *Predicted trends of the sediment temperature variations according to time and space.*
 340 In general, the sediment temperature reconstructed by the model reproduced the
 341 trends of observed air, water temperatures and solar radiation, showing higher tem-
 342 perature in summer and lower temperature in winter at all bathymetric levels (Figs.
 343 7g, h, i). The amplitude of sediment temperature as well as its daily variation was
 344 smaller on the infralittoral (mostly driven by the water temperature) compared to
 345 the higher foreshore (mostly driven by the air temperature and the other forcing
 346 variables) at 5 and 30 cm deep (Fig. 7).

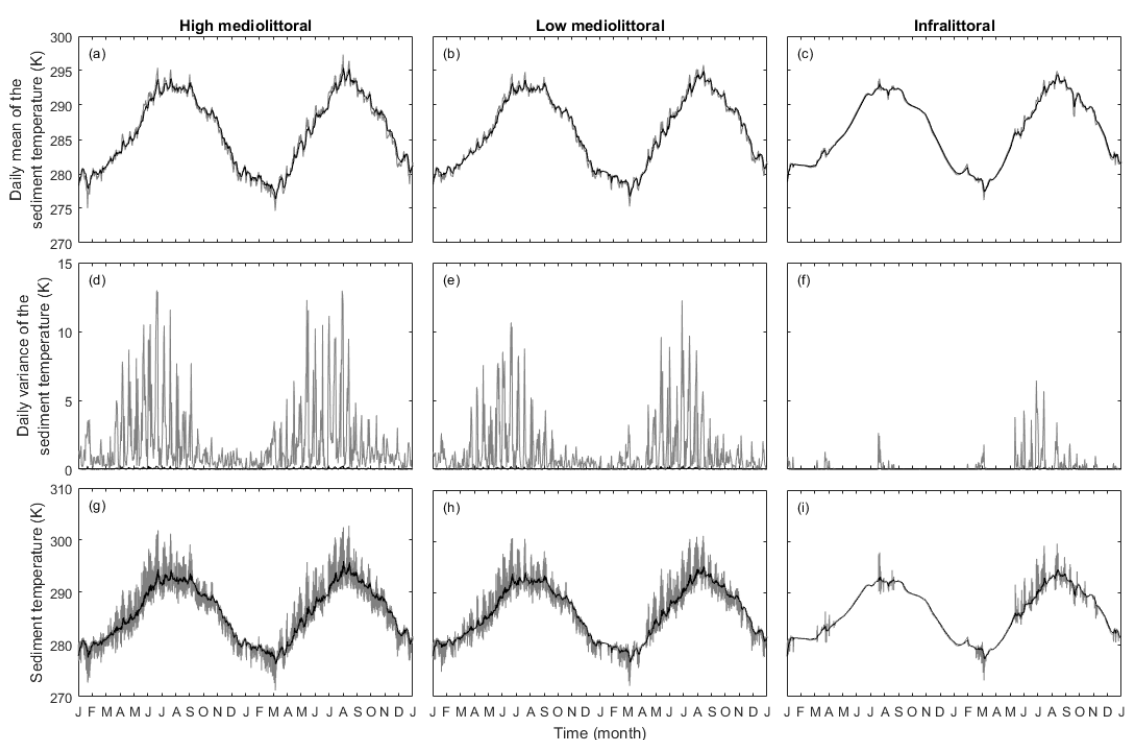


Figure 7: Daily means (a, b, c) and associated variations (d, e, f) of the sediment temperature (g, h, j) predicted by the sediment temperature model implemented in this study at 5 cm deep (grey lines) and 30 cm deep (black lines) on the high mediolittoral shore (a, d, g), the low mediolittoral shore (b, e, h) and the infralittoral shore (c, f, i) at Wimereux (Eastern English Channel, France).

347 The highest amplitude of sediment temperature variation occurred on the high
 348 mediolittoral foreshore at 5 cm deep, with associated daily variation of up to 14
 349 °C in summer time (Figs. 7d, g). At 30 cm deep at the same location, the daily
 350 variation of the sediment temperature was close to 0 °C (Fig. 7f).

351 3.3. Patterns in Arrhenius temperature of *Arenicola marina* outside its temperature
 352 tolerance range

353 The low and high boundaries of the temperature tolerance range of *A. marina*
 354 were estimated to be respectively $T_L = 272.8$ K and $T_H = 297.7$ K. The values of the
 355 Arrhenius temperature outside the species' temperature tolerance range were much
 356 higher than the Arrhenius temperature within the species' temperature tolerance
 357 range ($T_A = 4014$ K), with respectively $T_{AL} = 69080$ K and $T_{AH} = 82380$ K, high-
 358 lighting a rapid decrease in metabolic activity outside species' temperature tolerance
 359 range (Fig. 8).

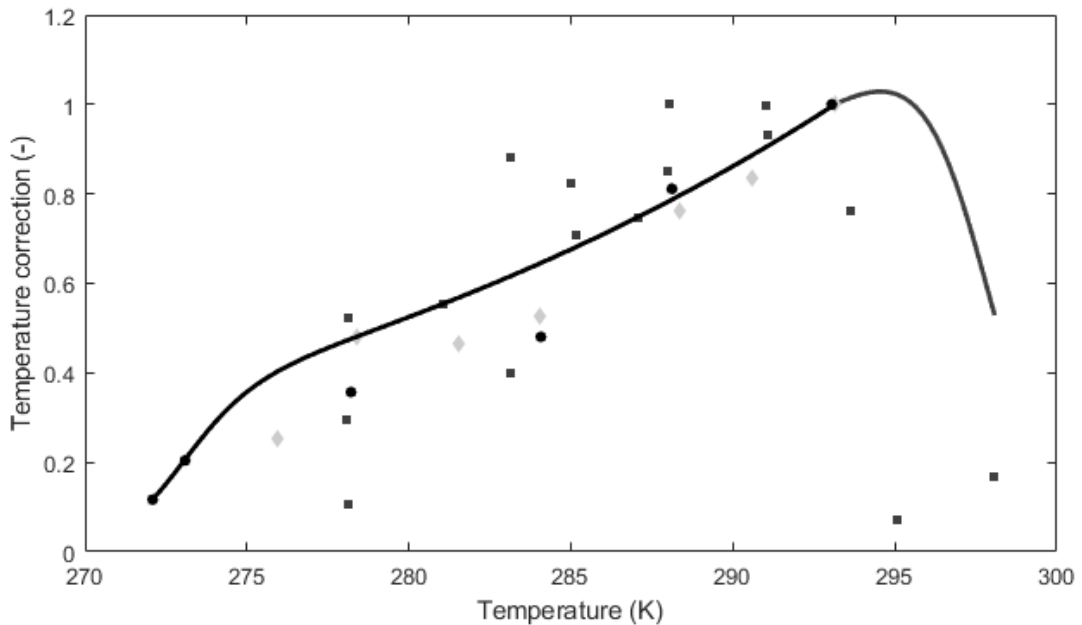


Figure 8: Arrhenius plot (line) obtained by fitting the parameters of an abj-DEB model for *Arenicola marina* as previously performed by De Cubber et al. (2019) with additional dataset consisting in: fertilization success rate data (dark grey squares, Lewis et al., 2002), oxygen consumption rate data (light grey diamonds, Schröder et al., 2009) and mitochondrial respiration rate data (black dots, Sommer and Pörtner, 2004) at several temperatures. The fitted values of the lower and the higher boundary (dashed lines) of the temperature tolerance range are respectively $T_L = 272.8$ K and $T_H = 297.7$ K. The value of the Arrhenius temperature within those boundaries is 4014 K. The fitted value of the Arrhenius temperature before the lower boundary is $T_{AL} = 69080$ K, and after the higher boundary is $T_{AH} = 82380$ K.

360 The complete parameter set of the updated abj-DEB model for *A. marina* is
 361 given in Sup. Mat. 1 to 8. No major changes in the parameters were observed
 362 compared to the previous parameter estimation (Sup.Mat.1, to compare with the

363 parameter set provided by De Cubber et al. (2019)) and slightly better fitness
364 values were obtained with the updated version concerning both the mean relative
365 error MRE (0.22 in the updated version vs. 0.23 in the former version) and the
366 symmetric mean squared error SMSE (0.27 vs. 0.28).

367 3.4. *In situ estimated food resources*

368 3.4.1. *In situ growth of the recruits*

369 Because of the low number of individuals belonging to the larger trunk length
370 classes from 8 to 12 cm (older individuals) (Fig. 4), the decomposition of the popula-
371 tion in different age groups after 2 to 3 years was difficult and only the newest cohorts
372 were followed to reconstruct the *in situ* growth and associated scaled functional re-
373 sponse. The growth of the recruits from May 2017 was possible to be followed for
374 one year (from May 2017 to May 2018). The growth of the recruits from May 2018
375 was estimated only from the end of May to mid July 2018 (Fig. 9, Table 4). The
376 population growth appeared faster between July and September 2017 and between
377 the end of May and mid July 2018, and slower between January and March 2018
378 (Fig. 9, Table 4).

379 When considering the contribution of each foreshore level to the cohort followed,
380 it appeared that the recruits were gradually migrating from the high mediolittoral
381 bathymetric level (100 % of the recruits came from this level in May of both years)
382 to the low mediolittoral and infralittoral bathymetric levels (33 to 40 % of the
383 recruits came from the low mediolittoral and 7 to 20 % of the recruits came from the
384 infralittoral bathymetric levels after 10 to 12 months since recruitment) as previously
385 suggested in Fig. 4 (Table 4). The relation between the trunk length (TL , cm) of
386 *A. marina* and the bathymetric level ($bath$, m) could be established as:

$$bath = -0.29 \cdot TL + 6.60 \quad (6)$$

387 (Linear regression, $R^2 = 0.99$)(Fig. 10). It was used in the prediction scenarios part.
388 Here, it appeared clearly that lugworms were found lower on the foreshore when
389 they had grown larger.

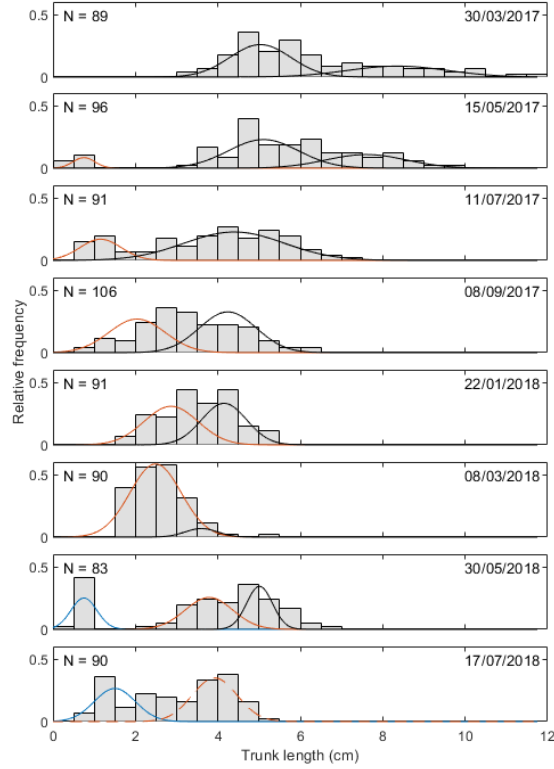


Figure 9: Cohorts decomposition of the population structure of *Arenicola marina* at Wimereux (Eastern English Channel) with a Bhattacharya analysis of the trunk length (TL) frequency distributions (5-mm size class intervals) at 8 sampling dates between March 2017 and July 2018. The histograms represent the relative number of individuals collected belonging to each trunk length class, the lines (orange, black and blue) are the cohorts given by the Bhattacharya analysis. The total number of individuals collected at each date are given on the left corner of each graph (as $N = \#$) and the corresponding dates are given in the right corner of each graph. The orange line represents the trunk length distribution of the recruits cohort of 2017 (the dashed line was not used in further analyses), the blue line represents the trunk length distribution of the recruits cohort of 2018. Their associated mean trunk length and standard error are given in Table 4. The black cohorts given by the Bhattacharya analysis were not used further in the study of the *in situ* growth of the population.

Table 4: Mean trunk lengths (TL) and standard deviation of the recruits cohorts of 2017 and 2018 and associated contributions of each foreshore level to the cohort followed (high = high mediolittoral, medium = low mediolittoral and low = infralittoral).

Date	Recruits 2017			Recruits 2018				
	Mean TL (cm)	High	Medium	Low	Mean TL (cm)	High	Medium	Low
15/05/2017	1.00 ± 0.26	100%	0%	0%	-	-	-	-
11/07/2017	1.40 ± 0.50	80%	20%	0%	-	-	-	-
08/09/2017	2.29 ± 0.68	87%	8%	5%	-	-	-	-
22/01/2018	3.11 ± 0.66	70%	23%	7%	-	-	-	-
08/03/2018	2.74 ± 0.62	41%	33%	27%	-	-	-	-
30/05/2018	4.04 ± 0.58	53%	40%	7%	1.00 ± 0.32	100%	0%	0%
17/07/2018	-	-	-	-	1.75 ± 0.50	85%	15%	0%

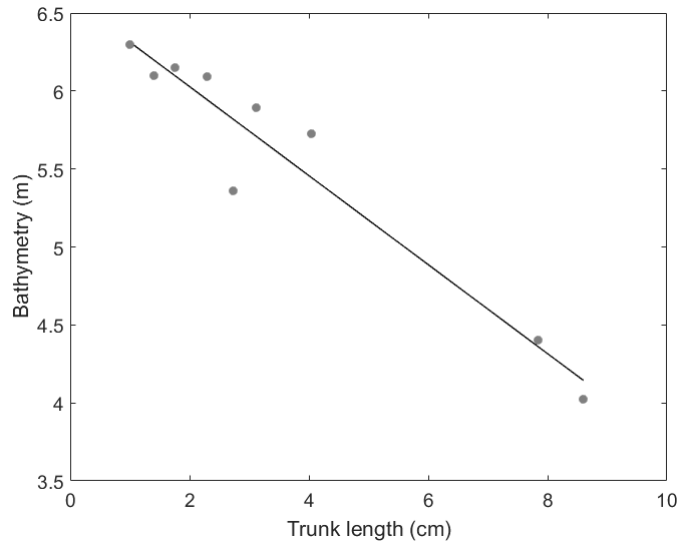


Figure 10: Observations (dots) and linear relation (line) between the trunk length (TL , cm) of *Arenicola marina* at Wimereux (Eastern English Channel) and the mean bathymetric level ($bath$, m) where they were collected (according to Table 4 and Figs. 4 and 9).

390 3.4.2. Reconstruction of the scaled functional response

391 The abj-DEB model for *Arenicola marina* associated to the sediment temperature
 392 model reconstruction at different depths and bathymetric levels, and the associated
 393 Arrhenius temperature correction, enabled a good fit between the predicted and the
 394 observed trunk lengths (Fig. 11 a). The reconstructed scaled functional response
 395 was lower in the autumn-winter period and higher during the spring-summer period,
 396 with values ranging from 0.01 in winter to 0.4 in summer 2017 and up to 0.5-0.6 in
 397 spring and summer 2018 (Figs. 11 a, b). In general, these trends were also observed
 398 when considering the chlorophyll-a concentration of the seawater ($Chla$, $\mu\text{g.L}^{-1}$), with
 399 the highest values in spring 2017 and 2018, and between the end of the summer and
 400 the beginning of the autumn 2017 (Fig. 11 c). The fitting of the scaled functional
 401 response to $Chla$ led to a half-saturation coefficient X_K value of $5.00 \mu\text{g.L}^{-1}$ of $Chla$
 402 (Fig. 12). The total nitrogen content of sediment (%) showed a spatial pattern
 403 with higher nitrogen concentrations on the lower shore level compared to a lower
 404 concentration on the higher shore. Besides, the nitrogen concentration on the high
 405 mediolittoral shore did not display significant seasonal variations compared to the
 406 nitrogen concentration of the infralittoral shore (Fig. 11 c).

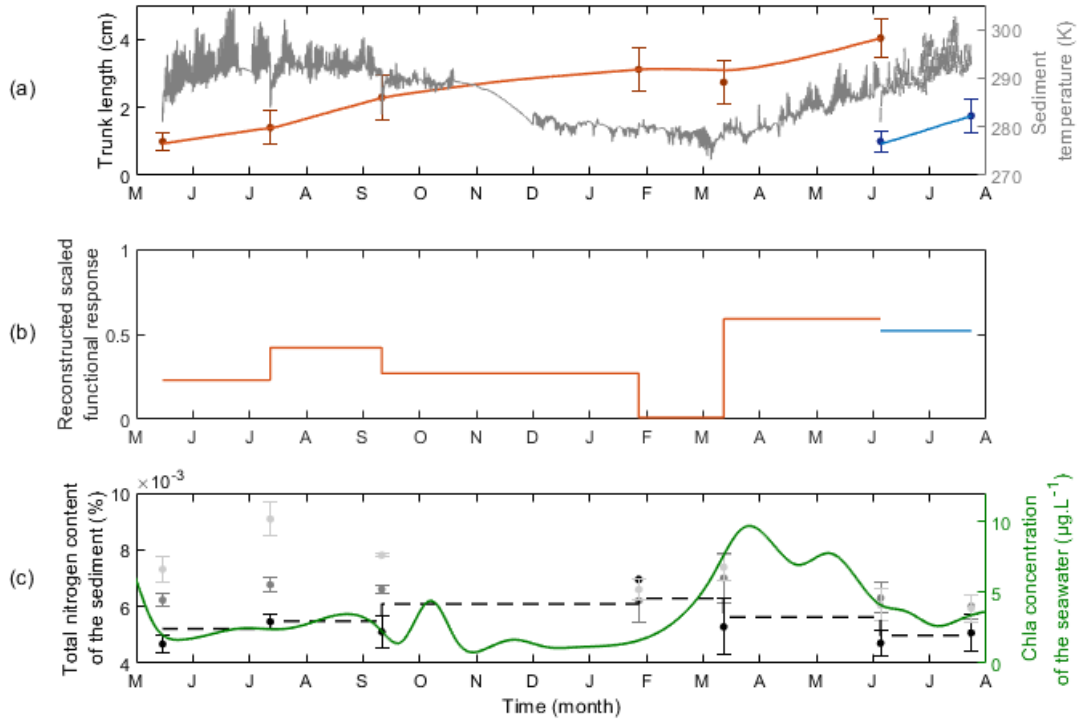


Figure 11: Reconstruction of the scaled functional response values (b) by fitting the predicted trunk length growth from a Dynamic Energy Budget model for *Arenicola marina* (red and blue lines) to the trunk length (cm) growth observations (red and blue dots) using the Arrhenius temperature (a) (Equation (3), Fig. 8) of the sediment temperature (K) reconstruction (grey line) according to the sediment temperature model as well as depth and the bathymetric level (a) and associated levels of the total nitrogen content of sediment (%) on the high, low mediolittoral and infralittoral bathymetric levels (dots, respectively in black, dark and light grey) and experienced by the recruits (dashed line) as well as the associated concentration in chlorophyll-a of the seawater ($\mu\text{g.L}^{-1}$) (green line, SOMLIT data) (c).

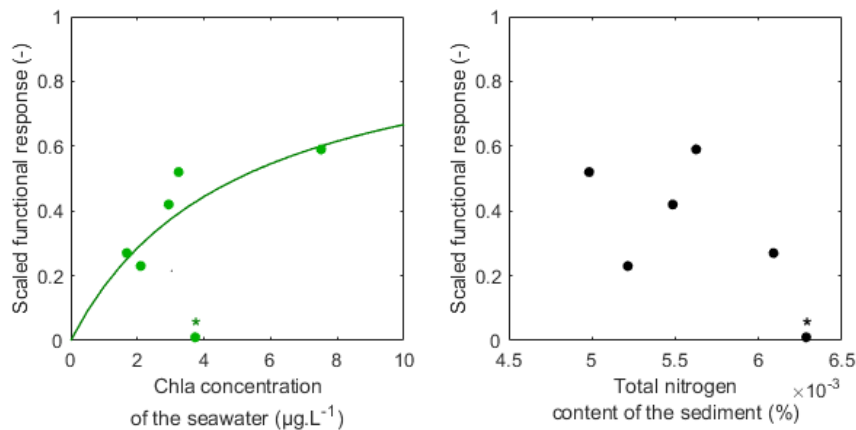


Figure 12: Reconstructed scaled functional response according to (left) chlorophyll-a concentration ($\mu\text{g.L}^{-1}$) (green dots) and associated fitted response $f = Chla / (Chla + X_K)$ (green line, $X_K = 5.00 \mu\text{g.L}^{-1}$) and (right) total nitrogen content of sediment reconstructed from the observations of nitrogen content of sediment on the different levels of the beach and the contribution of each bathymetric level to the recruits cohorts (Fig. 11, Table 4). The dots with asterisk were not used for the fitting (other mechanisms such as migration might be implied).

407 However, although the nitrogen content trend of the infralittoral seem to be
 408 correlated with the reconstructed scaled functional value, there was no clear relation
 409 between the reconstructed scaled functional response and the nitrogen content of the
 410 sediment in which lugworms live (Fig. 12).

411 3.5. Bathymetric level and depth effects on growth and reproduction

412 The different migration scenarios induced different temperature patterns experi-
 413 enced by lugworms (Fig. 13). As expected, the lugworms remaining on the high
 414 mediolittoral shore in superficial galleries (light grey scenario) experienced the most
 415 extreme daily temperatures, especially in summer and winter time, with temper-
 416 ature variations between the sediment and the seawater reaching up to 14 °C in
 417 summer time and 8 °C in winter time (Fig. 13).

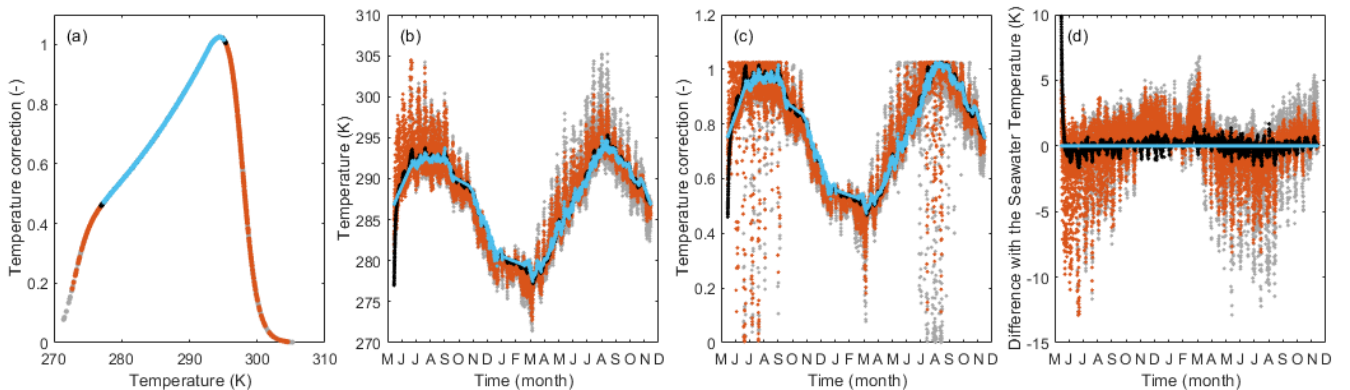


Figure 13: Comparison of temperatures and temperature corrections associated to differ-
 ent migrations scenarios to water temperature. Distribution of temperature corrections
 associated to different migration scenarios according to temperature (a) and the period of
 the year (c), sediment temperature corresponding to the different scenarios and seawater
 temperature according to the period of the year (b) and difference between seawater tem-
 perature and sediment temperature of the different scenarios according to the period of
 the year (d). Blue dots correspond to the seawater temperature. Black dots correspond
 to the sediment temperature experienced by the lugworms remaining on the infralittoral
 shore level and buried at 30 cm deep, light grey dots to sediment temperature experi-
 enced by the lugworms remaining on the high mediolittoral shore level and buried at 5 cm deep.
 Red dots correspond to the sediment temperature experienced by the lugworms migrating
 down the shore and gradually burying deeper in the sediment.

418 The lugworms remaining on the infralittoral shore in deep galleries experience
 419 the least extreme daily temperatures (black scenario), with temperature variations
 420 between the sediment and the seawater rarely reaching more than 2 °C (Fig. 13).

421 The lugworms migrating and digging deeper galleries experienced intermediate tem-
 422 peratures in between these two extremes, gradually getting closer to the deep and
 423 infralittoral sediment temperature. However, differences with the seawater temper-
 424 ature are still high after one year in both horizontal and vertical migrations, still
 425 reaching up to 8 °C in summer and 3 °C in winter (Fig. 13). Nonetheless, the tem-
 426 perature effect on growth and egg production, was minimal compared to the effect
 427 of food limitation on the higher shore (Fig. 14).

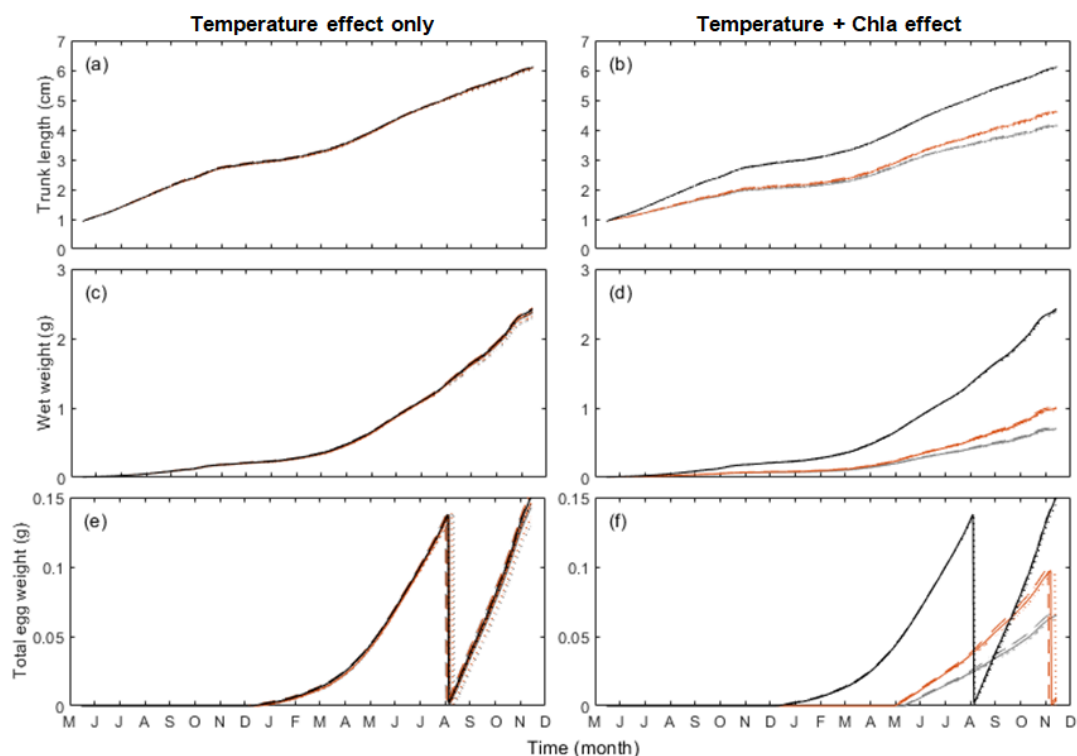


Figure 14: Evolution of the predicted (lines) trunk length (cm) (a,b), wet weight (g) (c,d) and egg weight (g) (e,f) of *Arenicola marina* at Wimereux (Eastern English Channel) according to the period of the year when considering that the food level was the same everywhere (temperature effect only) (a,c,e) or that the food level on the higher shore was half of the food level on the lower shore (b,d,f). The light grey lines correspond to the scenarios where lugworms remain on the high mediolittoral shore, the black lines to the scenarios where lugworms remain on the infralittoral shore, and the orange lines the scenarios where lugworms migrate down the shore. Dashed lines correspond to lugworms staying in 30 cm deep galleries, dotted lines to lugworms staying in 5 cm deep galleries and plain lines to lugworms digging deeper galleries when growing according to Equation (4).

428 Indeed, when considering that the food level was the same everywhere on the
 429 foreshore, growth and egg production differences between scenarios were barely no-

430 ticeable (Figs. 14 a,c,e). When considering that the food level on the higher shore
431 was half of the food level on the lower shore, the growth was much higher on the
432 lower shore than on the higher shore, even allowing an earlier spawning event in
433 August (Figs. 14 b,d,f).

434 4. Discussion

435 4.1. Sediment temperature and metabolic response to temperature

436 The model output of the sediment temperature model fits to the observations
437 of May-June 2018. However, the adjustment is not as good when considering the
438 data of October 2017. This could be linked to a higher hydrodynamism at this
439 period of the year and the subsequent sediment reworking leading to a displacement
440 of the temperature probes in its vertical position towards the surface within the
441 sediment (higher wind speed, see Fig. 2). The estimated parameter values of η and
442 μ ($\eta = 3.32 \text{ W.m}^{-1}.\text{K}^{-1}$ and $\mu = 5.02e^{-7} \text{ m}^2.\text{s}^{-1}$) for the sand habitat in this study are
443 4 times higher and almost equal respectively to the ones presented by Guarini et al.
444 (1997) and Savelli et al. (2018) ($\eta = 0.8 \text{ W.m}^{-1}.\text{K}^{-1}$ and $\mu = 4.8e^{-7} \text{ m}^2.\text{s}^{-1}$) for a mud
445 habitat. However, the value of η given in this study ($\eta = 3.32 \text{ W.m}^{-1}.\text{K}^{-1}$) is close
446 to the value of the thermal conductivity of the saturated medium sand according
447 to Hamdhan and Clarke (2010), who measured $\eta = 3.34 \text{ W.m}^{-1}.\text{K}^{-1}$. The estimated
448 value of ζ ($\zeta = 1.21$) lies in the range of what was estimated by Guarini et al.
449 (1997) and Savelli et al. (2018), with respectively $\zeta = 1$ in Savelli et al. (2018) and
450 $\zeta = 1.68$ in Garini et al. (1997). Improvements of the temperature recording set up
451 such as the fixation of a metal rod to large rocks embedded within the sediment and
452 the daily depth follow-up of the probes could be considered to refine the estimated
453 parameters.

454 The body temperature of lugworms might also be different from the temper-
455 ature of the surrounding environment, even in ectotherms (Kearney et al., 2008;
456 Porter et al., 1973; Smith et al., 2016). Indeed, Kearney et al. (2008) predicted
457 discrepancies of up to 5 - 6 °C between body and air temperature for cane toad indi-
458 viduals in Australia using the equation of the standard steady state energy balance:
459 $Q_{solar} + Q_{IRin} + Q_{metab} + Q_{conv} + Q_{cond} = Q_{resp} + Q_{evap} + Q_{IRout}$. In the case of

460 marine benthic organisms, dug in a sediment saturated in water and not exposed
461 to solar radiations, the main energy flux driving the body temperature must be the
462 conduction flux from the sediment, depending on the surface/volume ratio of the
463 individual, leading to higher thermal inertia in larger individuals. The fluxes linked
464 to solar radiation, respiration, convection and evaporation, which are the more likely
465 to induce discrepancies between the body temperature and the environment tem-
466 perature in terrestrial environments (Kearney et al., 2008), can be neglected in the
467 present study. However, on the high mediolittoral part of the shore mainly, the dry-
468 ing of the surface sediment during the long emersion periods, in addition of causing
469 anaerobic stress, could lead to unsaturated sediments and increase the evaporation
470 flux. It might also accentuate the extreme sand temperatures causing higher stress
471 to the recruits present on this level and should be taken into account in further
472 studies.

473 The re-estimation of the Arrhenius temperature within the species temperature
474 tolerance range boundaries T_A ($T_A = 4014$ K) lead to a value close to the previous
475 estimation ($T_A = 3800$ K) (De Cubber et al. (2019). The Arrhenius temperatures at
476 lower ($T_{AL} = 69080$ K) and upper ($T_{AH} = 82380$ K) limits of the species tolerance
477 range are overall close to what was observed by Monaco and McQuaid (2018) for
478 *Mytilus galloprovincialis* and *Perna perna*, two species of bivalves living on the
479 intertidal rocky shore, with T_{AL} respectively ranging from 22670 K to 55400 K and
480 T_{AH} respectively ranging from 34540 K to 250600 K. The higher boundaries of the
481 two species tolerance range were higher than the one estimated for *A. marina* (297.7
482 K) with values of 309 K for *Perna perna*, and 306.1 K for *Mytilus galloprovincialis*,
483 which was to be expected given their distribution in warmer waters (Mediterranean,
484 subtropical and tropical areas). The lower boundaries of the two species tolerance
485 range were close to the one estimated for *A. marina* (272.8 K) with respective values
486 of 273 K for *Perna perna*, and 279.6 K for *Mytilus galloprovincialis*. These values are
487 important to understand the possible climate migration enhancing new geographical
488 distribution of marine species due to global warming, as done by Thomas and Bacher
489 (2018) with three European marine bivalve species.

490 *4.2. Food level reconstruction and scaled functional response*

491 The reconstructed scaled functional response range of this study appears in ac-
492 cordance with the annual mean value previously estimated around 0.4 at the same
493 site during approximately the same period (De Cubber et al., 2019). The increase
494 of the total nitrogen content of sediment when going down the shore seems consis-
495 tent with the shorter emersion periods met there. The organic nitrogen content of
496 sediment from the shore could come from various sources of primary producers (mi-
497 crophytobenthos (MPB), deposited phytoplankton, macroalgae in decomposition,
498 bacteria...) (Gaudron et al., 2016). The absence of correlation between the evolu-
499 tion of nitrogen content of sediment and the scaled functional response found in this
500 study might be due to the evolution of the contribution of non- or less-assimilated
501 nitrogen sources to the total nitrogen content such as macroalgae debris to the to-
502 tal nitrogen of the sediment. Indeed, lugworms are supposed to feed mainly on
503 MPB and bacteria but are almost unable to digest macro debris (Andresen and
504 Kristensen, 2002; Retraubun et al., 1996; Rikjen, 1979). The high hydrodynamism
505 during winter periods could bring more debris leading to higher nitrogen contents of
506 the sediment than what the scaled functional response seems to point out because
507 of their potential low digestibility.

508 However, the scaled functional response was quite well correlated to the chlorophyll-
509 a concentration of the seawater. This could be part of the food source contribution
510 to the lugworms diet at their early life-stages as it is known that there is a strong
511 benthic-pelagic trophic coupling between benthic species and pelagic sources in some
512 coastal habitats. Indeed, phytoplankton was also reported in lugworms diet on the
513 East Coast of the Cotentin Peninsula (English Channel, Normandy, France) (Gau-
514 dron et al., 2016). The correlation with the chlorophyll-a concentration of the sea-
515 water could also be explained by the fact that the food sources (MPB and bacteria)
516 show in average similar growth and production patterns than phytoplankton (Lefeb-
517 vre et al., 2009). Therefore, chlorophyll-a concentration is a good proxy to estimate the
518 level of food in the lugworms' diet.

519 Besides, the estimation of the scaled functional response from the observation
520 of cohort growth instead of individual growth might show some limitations. In-

521 deed, other population processes such as migration (between February and March
522 2018) or on-going recruitment (between May and July 2017) might have lead to
523 some under- or over-estimation of the growth and the associated scaled functional
524 response. Moreover, the assessment of the scaled functional response and its asso-
525 ciated food proxy might be site-dependent to some extent, and our results should
526 therefore be taken with caution when considering different locations. Indeed, food
527 sources might vary among sites, potentially leading to different scaled functional
528 responses for the same food proxy (Chla in our study) since the latter is not the
529 only component of lugworms' diet. Nonetheless, we believe that our study site is
530 similar to many other sandy beaches described as inhabited by lugworms and only
531 small variations of the half-saturation coefficient (linked to the assimilation of food)
532 might occur. Further studies on *in situ* sources of food and the link between food
533 sources and scaled functional response are needed. Besides, other proxies for food
534 such as benthic chlorophyll-a might be interesting to explore.

535 4.3. Growth scenarios

536 The trunk length and wet weight growth as well as the total egg weight were
537 not really influenced by the temperature changes along the shore. However, the
538 increase of food levels down the shore induced higher wet weight and trunk length
539 growth as well as a higher total egg weight, and lead to an earlier first spawning
540 event, suggesting that lugworms migrate down the shore to get access to more food
541 rather than avoiding extreme temperatures. Since individuals recruiting down the
542 shore experience higher growth, the recruitment location on the higher shore might
543 be linked to other constraints such as the fact that juveniles can not swim against
544 the tide current, or to intraspecific competition for food and space with juveniles
545 avoiding the adults grounds as already suggested by several authors, or to avoid
546 predation (De Vlas, 1979; Farke et al., 1979; Flach and Beukema, 1994).

547 A number of active movement behaviours to avoid whether cold or warm extreme
548 temperatures have already been documented both in terrestrial and marine species,
549 among which digging (Fitzpatrick et al., 2019; Kearney et al., 2009; Kolbe et al.,
550 2010) or moving to sheltered places (Chapperon and Seuront, 2011; Kearney et al.,
551 2009; Malishev et al., 2017; Monaco et al., 2016). In *A. marina*, shore migrations

552 due to extreme cold temperatures (below 0 °C) have already been reported by Reise
553 et al. (2001) but the depth at which the galleries of lugworms was dug into was not
554 considered. In the present study, the down-shore migration of *A. marina* recruits
555 started quite early (in July) but with a slight acceleration of the process between
556 January and March. Although this is when the coldest sediment temperature of
557 the year was recorded, given the low response of growth and egg production to
558 temperature variations, other clues might explain a migration at this period of the
559 year. Extreme temperatures (whether warm in July or cold in January) might indeed
560 not be the actual trigger of the down-shore migrations of lugworms. However, the
561 increase of primary production at this period of the year might induce lugworms to
562 migrate down the shore.

563 Although the effect of temperature alone seems limited, other parameters, such
564 as the desiccation of the superficial sediment at low tide, could, if taken into account,
565 change this observation increasing the variability of temperature and the subsequent
566 occurrence of extreme temperatures. Moreover, the potential hypoxia experienced
567 by lugworms at low tide was not considered, although hypoxic metabolic activity
568 has been reported by several authors for this species (Schöttler et al., 1984), and
569 hypoxia was shown to impact growth and reproduction in marine bivalves (Aguirre-
570 Velarde et al., 2019). As lower levels of the shore are emerged on shorter periods and
571 deeper galleries give access to interstitial water within the sediment (Shumway and
572 Davenport, 1977), this parameter should also be explored to explain the down-shore
573 migrations of *A. marina*. Indeed, the oxygen consumption of lugworms decreases
574 with oxygen saturation (Shumway, 1979), leading to a possible change in metabolic
575 activity. As an example, if we compare the oxygen consumption of 1 g and 6 g
576 lugworms respectively at 12 °C and 20 °C to the oxygen quantity contained in
577 oxygen-saturated seawater, it appears that smaller lugworms consume 20 % of the
578 oxygen in 15 to 30 hours while larger lugworms consume the same quantity in only
579 3.8 to 8.5 hours (considering lugworm densities are not too high). At low tide, large
580 lugworms on the higher mediolittoral shore (where emersion periods are longer and
581 water renewal is lower) might have a decrease in their metabolic activity linked to a
582 depletion in dissolved oxygen concentration within the sediment. This effect might

583 be amplified when temperatures above 25 °C are reached, potentially explaining
584 why lugworms migrate downwards on the shore. For larger individuals (rarely found
585 on the higher shore), food concentration might therefore not be the only trigger
586 for down-shore migration and might be the result of several interplaying variables.
587 To account for this reduction of metabolic activity of adults at low tide, an extra
588 parameter combined to the temperature correction could be computed according to
589 the shore level and the depth of the gallery as previously explored by Monaco and
590 McQuaid (2018) in two intertidal bivalve species.

591 4.4. Management perspectives

592 The present study constitutes a valuable first step to better understand the effects
593 of temperature on juvenile and adult populations of *Arenicola marina* such as their
594 small-scale migration behaviour once recruited in a temperate ecosystem.

595 Between March 2017 and July 2018, most lugworms larger than 7 cm disap-
596 peared, traducing the disappearance of older individuals. The disappearance of the
597 largest age classes coincided with the presence of higher number of fishermen in
598 summer 2017 on the study site (pers. observation). De Cubber et al. (2018) has
599 shown the need for some regulation on *Arenicola* spp. fisheries for some areas of the
600 Eastern English Channel based on the density of individuals. The study of the pop-
601 ulation structure might also be another criteria to decide on the need to implement
602 relevant management measures.

603 Besides, this study opens new insights on the migration of the lugworms within
604 a population showing the typical distribution pattern, as well as tools to model pop-
605 ulations *in situ* growth and reproduction. This could prove useful for management
606 purposes to test scenarios for the prediction of spawning events (Pecquerie et al.,
607 2009; Watson et al., 2000) or predict *in situ* lengths at puberty or harvest sizes and
608 where these lengths are found on the shore. These models could then be associated
609 to individual-based model and larval dispersal models in order to better understand
610 the population dynamics and connectivity of the species (Bacher and Gangnery,
611 2006; Martin et al., 2012; Nicolle et al., 2017) which would also prove useful for
612 conservation managers.

613 The knowledge of environmental conditions, behavioural and metabolic responses

614 of the organism to those and DEB models has also been used to model ecological
615 niches (Kearney et al., 2010; Thomas and Bacher, 2018). Modelling the ecological
616 niche of *A. marina* could help to estimate the impact of fisheries on the species by
617 comparing the species potential distribution with the current species distribution.
618 An ecological niche model could also enable to make predictions on the effect of global
619 change on the species distribution (Thomas and Bacher, 2018) and the possible
620 related impact on other key species. As an example, *A. marina* has been shown to
621 impact negatively populations of *Zostera noltii* (Kosche, 2007) and to influence the
622 local community compositions (Donadi et al., 2015). Its expansion in southern areas
623 (suggested by Pires et al., 2015) might lead to shift in species communities in these
624 areas.

625 **5. Conclusions**

626 In the present study, we have successfully identified and simulated relevant en-
627 vironmental variables needed for the implementation of a DEB model for *Arenicola*
628 *marina*, as well as their spatial variations along the foreshore. Combining the char-
629 acterization of the down-shore migration of a local population of *A. marina* with
630 these environmental variables as inputs for the DEB model, we were able to discard
631 the hypothesis that temperature constituted the main trigger for lugworm migration.
632 The increase of food level when migrating down the shore seems to account for an
633 important trigger, but other potential temperature-related factors such as desicca-
634 tion and hypoxia should also be explored in future studies. The present study could
635 prove useful for conservation managers *per se* when defining relevant management
636 measures linked to lugworm individual life-traits. Besides, the association of the
637 present DEB model to further population dynamics models will permit a complete
638 management plan for *A. marina* populations.

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