Ecole Doctorale Sciences de la Matière, du Rayonnement et de l'Environnement

Spécialité Géoscience, Ecologie, Paléontologie, Océanographie

Université de Lille

Laboratoire d'Océanologie et de Géosciences

UMR 8187 Univ. Lille, ULCO, CNRS

Etude des traits de vie de annélides polychète *Arenicola marina* et *A. defodiens* : développement d'un modèle de type "Dynamic Energy Budget" (DEB) et conservation de ces espèces

Thèse de doctorat présentée par **Lola DE CUBBER**

Soutenue publiquement le 7 Novembre 2019 devant le jury composé de :

Directeur de thèse	Sylvie Marylène GAUDRON	Maître de conférences HDR, Sorbonne Université
Co-directeur de thèse	Sébastien LEFEBVRE	Professeur, Université de Lille
Rapporteurs	Jaap VAN DER MEER	Professeur, Wageningen University
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Invité	Antoine MEIRLAND	CRPMEM Hauts-de-France

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Study of the life-history traits of two species of polychaetes, *Arenicola marina* and *A. defodiens*, implementation of a Dynamic Energy Budget model and conservation of the species

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L'homme est la nature prenant conscience d'elle-même Elisée Reclus

Ça ne recule pas ! Donc ça avance ! Sébastien

Foreword

I was funded by a Ph D studentship from the University of Lille.

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Several people participated in this study:

T. Lancelot designed and created the growth system with the help of D. Menu.

T. Lancelot and G. Duong helped with the carbon and nitrogen content analysis of the sediment.

T. Lancelot, V. Cornille and G. Duong provided technical support on the field.

T. Lancelot also provided technical support in the laboratory.

G. Watson provided precious advice on *in situ* temperature probes deployment.

A. Meirland introduced interesting discussion regarding the impact of recreational fisherman on lugworms' populations.

C. Rolet provided her expertise in Taxonomy to confirm the identification of the species allowing the description of the EUNIS habitats.

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Contents

Chapter 1

General framework of the thesis

1.1 General context of the study

1.1.1 A local need for managing lugworm populations ?

Coastal ecosystems are subject to many and intensifying anthropogenic pressures (Halpern et al., 2015) and therefore require better management by local stakeholders. In December 2012, a marine protected area (MPA) from the French coastal area of the Eastern English Channel, the 'Parc naturel marin des estuaires picards et de la mer d'Opale', was created to address these issues. Its territory includes three major estuaries (from South to North: the Somme, the Authie and the Canche estuaries), as well as a large area of intertidal soft and rocky bottoms, and subtidal habitats up to 50 m deep (Rolet at al., 2014; 2015 a,b) (Fig. 1.1). The objectives of the MPA are first to bring knowledge on the environment (fauna, flora, habitats and their interactions), second to protect the ecosystems and third to promote the sustainable development of the sea-related human activities (http://www.aires-marines.fr/Les-aires-marines-protegees/Categories-d-aires-marines-protegees/Parc-naturel-marin). Indeed, within its boundaries, a number of sea-related human activities such as professional and recreational fisheries, marine transport, harbour activities, pebble extraction, tourism, etc, might impact the environment. The French national framework program 'Life + Pêche à pied de loisirs' (EU funding) was one of the project early implemented within the MPA aiming at promoting sustainable recreational fisheries on several French foreshores frequented by recreational fishermen (Fig. 1.1). During the first phase of observation of the project, the managers of the MPA were amazed to notice a relatively high number of fishermen harvesting lugworms (*Arenicola* spp.) in comparison to the number of other recreational fishermen harvesting mussels or shrimps (Fisseau, 2016). Indeed, nowadays, lugworms are locally harvested

to be used as bait by cane fishermen. Collection by professional or recreational fishermen may impact the size and age structure of a population, such as its abundance and distribution (Blake, 1979; McLusky et al., 1983; Olive, 1993) with potential population crashes caused by overexploitation (Olive, 1993). The MPA managers thus contacted scientists to know if there was a need for management of lugworms, and if so, to bring more knowledge on the *Arenicola* spp. species and populations of the Eastern English Channel in order to consider potential management plans.

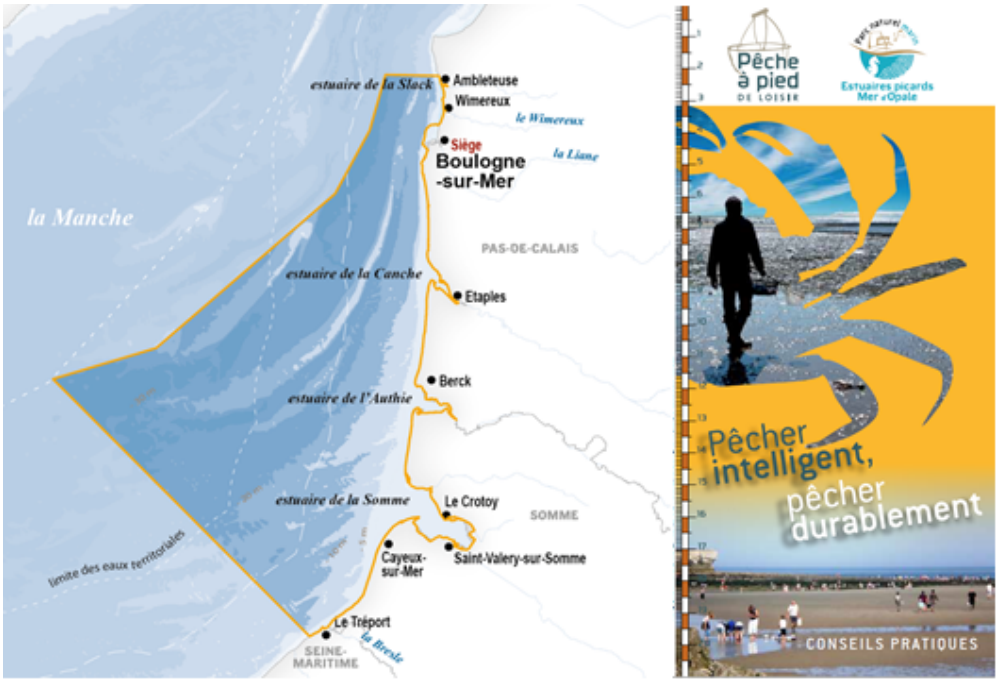

Figure 1.1 – Map of the limits of the 'Parc naturel marin des estuaires picards et de la mer d'Opale' marine protected area (left) and visual of the 'Life + Pêche à pieds de loisirs' project aiming at promoting sustainable recreationnal fisheries on the French foreshores (right).

1.1.2 Bait fishing for the lugworm *Arenicola marina* (Linnaeus, 1758) and the black lug *A. defodiens* (Cadman and Nelson-Smith, 1993)

Worldwide

Polychaetes are dug for bait worldwide, representing a global annual harvest estimated between 121 tons/year (Watson et al., 2017) and 327 tons/year in 2015 (FAO, 2018). Therefore, several authors insist on the need for managing these species (Watson et al., 2017; Xenarios, 2018). Fisheries management can be defined as "the integrated process of information gathering, analysis, planning, consultation, decision-making, allocation of resources and formulation and implementation, with enforcement as necessary, of reg-

ulations or rules which govern fisheries activities" in order to maintain a population at healthy status, which is, in terms of population's dynamics, a population with sustainable birth, growth and survival rates (Beverton and Holt, 1957; FAO, 2002). The harvested species of polychaetes differ according to the country, but the most common management measures consist in licensing for commercial harvesters and in maximum daily catches for recreational fishermen, with in rare cases (UK) local management strategies adapted to the stakes of the area (Fig. 1.2) (Cabral et al., 2019). These management measures aim at limiting the overall mortality, or the mortality of specific individuals in the population, based on its features (FAO, 2012).

Figure 1.2 – Compilation of the regulations and management measures for the polychaete fishery existing in different regions of the world (taken from Cabral et al., 2019).

Region/Country	Management Measures
Maine (USA)	• License required for commercial harvesters • Mechanical harvesting not allowed • Maximum daily catch: 25 worms/fisher (without license)
Nova Scotia (Canada)	• License required for commercial harvesters • Seasonal and area closures • Minimum legal size • Gear type • Required to report numbers of worms to fishing locations
United Kingdom	• Only small hand digging tools allowed • Recreational harvest not regulated (voluntary code of conduct in practice and local management strategies)
New South Wales (Australia)	• License required for commercial harvesters • Required logbooks with information on species, catch, effort, location and fishing method used • Limited harvested quantity for recreational fishers
Queensland (Australia)	• Annual permit required for commercial harvesters • Required logbooks with information • Limited harvested quantity for recreational fishers

Within the MPA

Historical perspective In the area of the MPA, *Arenicola* spp. have been used as baits for a long time (Bourgain, 1999; Louf et al., 1998). Historically, they were collected by women who sold them as bait to professional fishermen (Figs. 1.3, 1.4) (Bourgain, 1999; Louf et al., 1998). Longlines of up to 8000 hooks supplied with lugworms were used by local fishermen to fish mostly plaices (Louf et al., 1998). Thus, the number of fisherwomen might have been really high on some beaches to sustain the plaice fisheries, as represented on some paintings such as *Digging for bait* painted in 1877 at Ambleteuse by Charles William Wyllie (Fig. 1.4). However, although some fishing regulations already

existed for the harvest of mussels (also mostly collected by women back then), such as a closure of the harvest during the spawning season and the division in the mussel beds in fishing areas, no regulation was implemented for lugworms fishing (Bourgain, 1999; Louf et al., 1998).

Figure 1.3 – Diverse representations from the nineteenth century of fisherwomen while bait digging or selling their harvested worms on the French coast of the Eastern English Channel (illustrations and pictures were taken from Bourgain, 1999 and Louf et al., 1998).

Nowadays Fisseau (2016) reported the recreational activities the most commonly observed on the shore within the MPA. The recreational fisheries for mussels and lugworms were the most frequent, respectively accounting for 24 % and 14 % of the total recreational activities observed. In average, recreational fishermen collected approximately 30 worms per tide (Fisseau, 2016). In addition to the recreational harvest of lugworms, professional fishermen also collect *Arenicola* spp.. In total, 104 lugworm fishing licenses were delivered to professional fishermen within the MPA boundaries in 2015. Meirland et al. (2015) reported that those fishermen can collect up to 300 worms per tide. Up to know recreational shore fisheries for shellfish, crustaceans, marine plants and fish are regulated within the MPA with quotas, size limitations or closure periods, but no regulation were implemented yet for recreational fisheries for lugworms (Fig. 1.6) (Arrêté du 17 juillet 2014 encadrant la pêche à pied de loisir dans les départements du Pas-de-Calais et de la

Figure 1.4 – Reproduction of the painting 'Digging for bait' painted at Ambleteuse in 1877 by Charles William Wyllie.

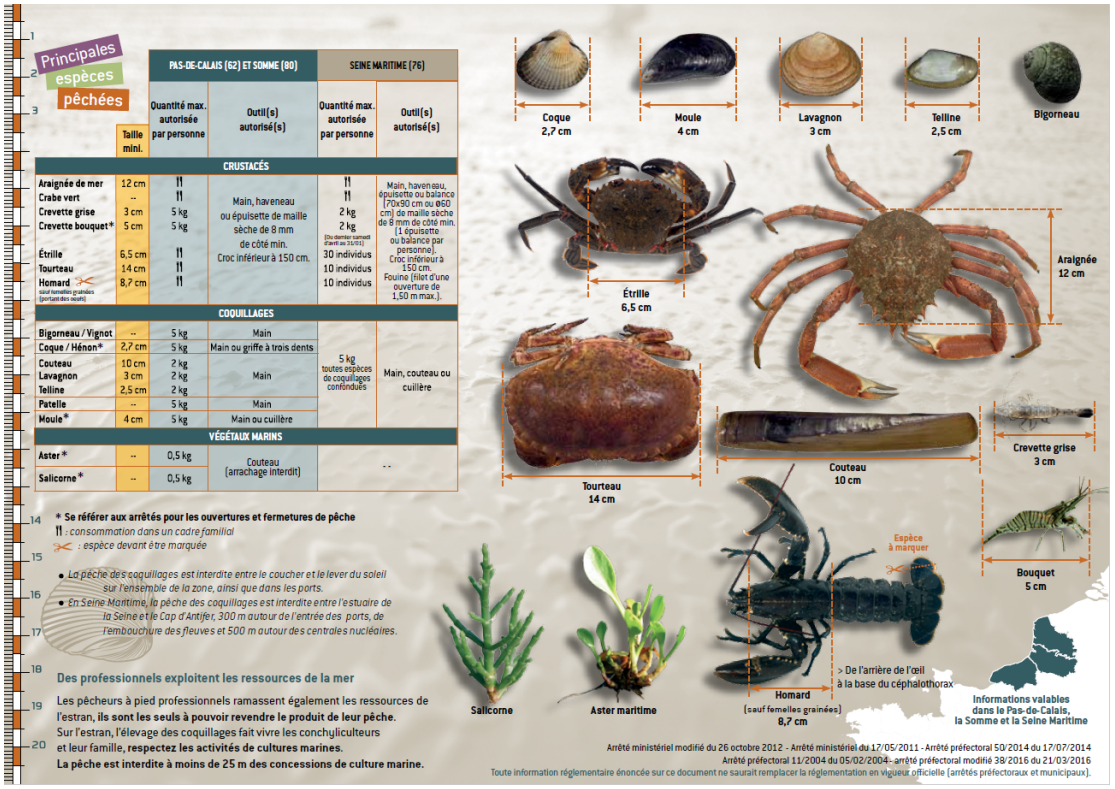

Figure 1.5 – Flyer from the Parc naturel marin des estuaires picards et de la mer d'Opale compiling the essential of the shore fisheries regulations existing within its boundaries (http://www.pecheapied-loisir.fr/je-suis-pecheur/reglementation/estuaires-picards-et-mer-dopale/)

Somme; Arrêté du 7 août 2018 encadrant la pêche à pied des moules sur les gisements naturels du Boulonnais; Arrêté du 30 mai 2018 modifié fixant les dates de récolte des

végétaux marins pour la saison 2018 dans les départements de la Somme et du Pas-de-Calais; Arrêté du 24 juillet 2014 encadrant la récolte des lavagnons et des couteaux sur les gisements du Pas-de-Calais et de la Somme). In the area, lugworms are dug up at low tide on the mediolittoral to infralittoral part of the shore, either with a fork or a shovel, or with an Alvey bait pump (extracting the worm by suction).

1.1.3 What do we wish to answer ?

In order to allow the best management strategies for the local lugworm species, we therefore need to tackle four main questions:

- Which species of lugworms are present within the MPA ?
- Is there a need for management of these species ?
- If so, based on the knowledge of the local biological and ecological features of the species, what kind of regulations could be implemented (Fig. 1.6) ?
- What would be the most efficient management strategy ?

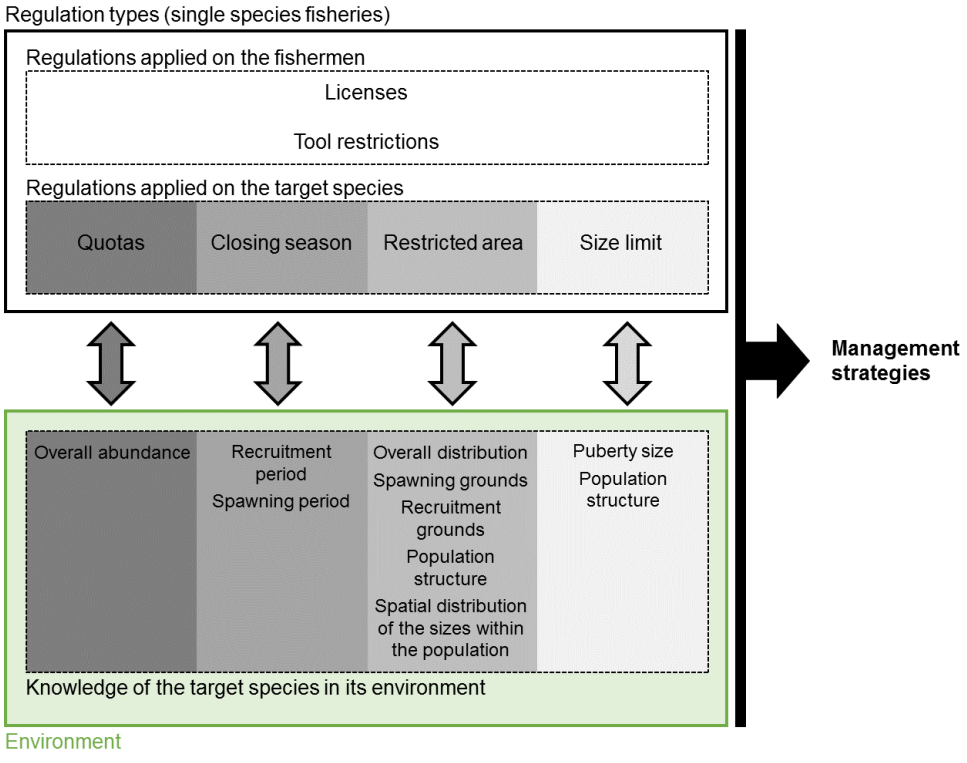

Figure 1.6 – Link between the possible regulations to implement in order to manage a target species and its local biological and ecological features that managers need to be aware of in order to implement these regulations and decide of a management strategy for this species.

1.2 Current knowledge on the biology and ecology of *Arenicola marina* and *A. defodiens*

1.2.1 The species

Arenicola marina (Linnaeus, 1758) and *A. defodiens* (Cadman and Nelson-Smith, 1993) (Annelida) are psammivarous benthic polychaetes mainly inhabiting sandy shores on the Western Atlantic coast from Portugal to the Arctic (Pires et al., 2015; Volkenborn, 2005). Both species live within galleries dug in the sediment up to 30 to 40 cm deep for *A. marina* and up to 70 cm deep for *A. defodiens*. Both species ingest the superficial sediment (for *A. marina*) or deeper sediment (for *A. defodiens*) to feed on the organic particles it contains, and create a water current to bring oxygen to their gills and tegument (Cadman and Nelson-Smith, 1993; Senga Green et al., 2016) (Fig.1.7). Lugworms are therefore considered to be ecosystem engineers. Indeed, this bioturbation modifies the abiotic conditions within the sediment (grain size, nitrogen and oxygen content) and impacts the associated communities' composition, enhancing selected species at the expense of the others (Clarke et al., 2017; Kristensen, 2001; Reise, 1985; Volkenborn, 2005). Apart from their ecological role, lugworms are still used as baits and commonly harvested in Europe (UK, France, the Netherlands, etc.) by professional and recreational fishermen (Watson et al., 2017). Besides, they are also reared for their particular haemoglobin that might represent a valuable blood substitute for humans in the future (Rousselot et al., 2006) and which is already used for organ conservation before transplantation (Hemarina ltd., see https://www.hemarina.com/).

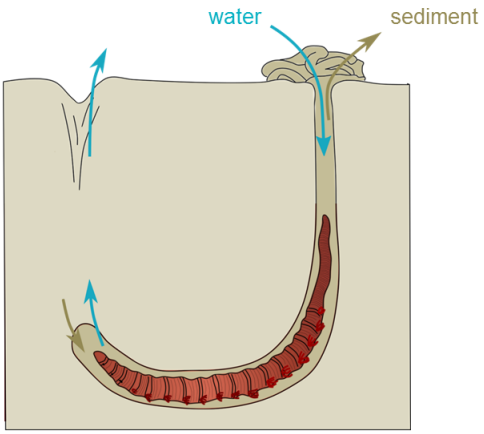

Figure 1.7 – Representation of one lugworm within its gallery and the associated water and sediment transports.

A. marina and *A. defodiens* are two cryptic species only showing small morphological dif-

ferences, the most notable being the annulations patterns of the first setigers and the shape of the gills (Cadman and Nelson-Smith, 1993). Both species have long been considered as two ecotypes of the same species. Indeed, *A. marina* is rather found on the high to low mediolittoral part of the shore and within estuaries, while *A. defodiens* occurs on the infralittoral to subtidal part of the shore, although both species may occur at the same shore level (Cadman and Nelson-Smith, 1993; Cadman, 1997; Luttikhuizen and Dekker, 2010; Pires et al., 2015). The species discrimination was proven by genetics in 1990 (Cadman and Nelson-Smith, 1990) and reconfirmed recently with modern methods using COI and 16S gene markers (Luttikhuizen and Dekker, 2010; Pires et al., 2015). Many studies on the biology of lugworms were performed before the discrimination of the two species, therefore providing data to use with caution.

1.2.2 Taxonomy and morphology

Arenicola spp. belong to the Bilateria, Lophotrochozoa, Annelida, Polychaeta (Brusca et al., 2016; Hickman et al, 2016). As such, they are bilaterally symetrical with three germ layers, displaying a trochophora larval stage during their development, and their body is divided into metameres arranged in linear series and externally marked by annuli (circular rings). Each metamere carrying parapods and chaetae (except prostomium, peristomium and pygidium that are not considered as metameres) contains similar components of all major organ systems and the segments are delimited internally by septa. The coelom of *Arenicola* spp. is filled with fluid and serves as a hydrostatic skeleton. Crawling motions are produced by alternating waves of contraction by longitudinal and circular muscles passing down the body (peristaltic contractions). Indeed, lugworms have lost most of the intersegmental septa, thus enabling segments not to be of constant volume, which helps them to burrow (Brusca et al., 2016; Hickman et al, 2016). The nervous system comprises a pair of cerebral ganglia within the prostomium (first segment) with connectives to a ventral longitudinal nerve cord. Two statocytes are present in the peristomium segment (second segment) (Tixier and Gaillard, 1957; Wells, 1950). The digestive system is not segmented: the gut runs through the length of the body perforating each septum, along with the longitudinal dorsal and ventral blood vessels and the ventral nerve cord (Hickman et al, 2016). It is constituted of the proboscis, the esophagus and its glands, a stomach and a long intestine ending on the anus carried by the pygidium (last segment) (Tixier and Gaillard, 1957; Wells, 1950). The excretory system consists in six pairs of thoracic nephridia (removing waste from blood and from coelom) producing urine through nephridiopores. The nephridiopores are also used for gametes expulsion. The gonads, really small, are attached to the last five nephridia and release rapidly the germinal cells in the coelomic fluid, where they develop (Tixier and Gaillard, 1957; Wells, 1950). The

respiratory gas exchanges happen through "skin" (= tegument) and gills. The circulatory system is closed with muscular blood vessels and two lateral aortic arches (“hearts”) for pumping blood. The respiratory pigment is the haemoglobin (Brusca et al., 2016; Hickman et al, 2016; Tixier and Gaillard, 1957; Wells, 1950).

The head of *Arenicola* spp. is constituted of the prostomium, a triangular bead with three lobes located behind the mouth, sometimes retracted in the nuchalin pocket, the peristomium, holding the mouth and eversible proboscis covered with papilla, and an

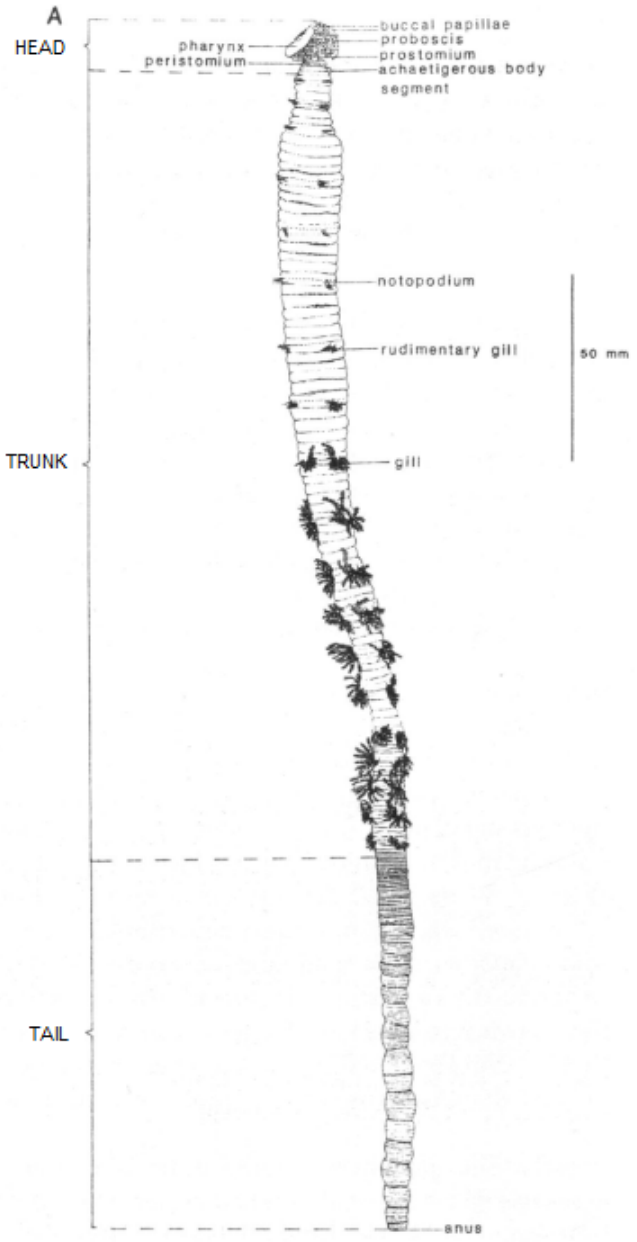

Figure 1.8 – Drawing of a specimen of *Arenicola defodiens* (dorsal view) from Jersey Marine, taken from Cadman and Nelson-Smith (1993).

achaetigerous segment (Fig. 1.8) (Cadman and Nelson-Smith, 1993). The trunk is constituted of 19 setigers (= metameres with chaetae). In *A. marina* the three first setigers have 2, 3 and 4 annulations, and in *A. defodiens*, the three first setigers have 2, 2 and 4 annulations (Cadman and Nelson-Smith, 1993). Parapods are present on the penultimate annulation of each metamere, comprising one dorsal notopodium with long chaetae and one ventral neuropodium with small hook-shaped chaetae (Fig. 1.8). The last 13 setigers also hold the red ramified contractile gills close to the notopodia (Fig. 1.8). Branchiae are pinnate with a palmar membrane connecting the branchial stems to the base in *A. defodiens* and present a dendritic arrangement in *A. marina* (Pires et al., 2015). The tail is narrower than the trunk and comprises an indefinite number of metameres of only one annulation not holding parapods nor gills. The anus carried by the pygidium (last segment not considered as a metamere) is at its extremity (Fig. 1.8) (Cadman and Nelson-Smith, 1993).

1.2.3 Reproductive aspects

Gametes production and development In *Arenicola* spp., sexes are separated and the gametes develop within the coelomic fluid (Cassier et al., 1997; Olive, 1984a,b). For *A. marina*, oogenesis has been reported to start between February and April (Betteley et al, 2008), and vitellogenesis generally ends up in August (Betteley et al. 2008; Mayes et Howie 1985). It leads to oocytes at stage prophase I of meiosis, with a diameter of approximately 175 µm for *A. marina* and 160 µm for *A. defodiens* (Watson et al., 1998) (Fig. 1.9). The reinitiation of meiosis from prophase I to metaphase I is controlled by

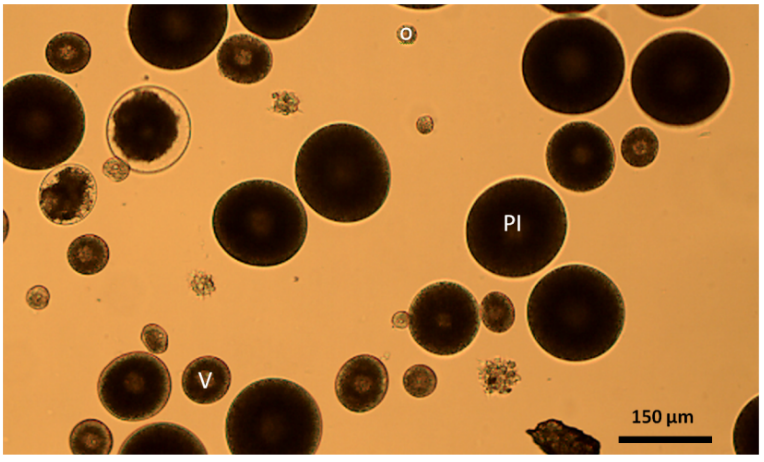

Figure 1.9 – Microscopic observation of oocytes from a *A. defodiens* female at different development stages: germ cells (o), vitellogenesis (V) and prophase I of meiosis (PI). Photograph taken by L.D.

two hormones in *A. marina*: the Prostomium Maturation Hormone (PMH), emitted by

secretion cells of the prostomium, that activates the Cœlomic Maturation Factor (CMF) in the coelomic fluid (Betteley et al., 2008; Howie, 1963; Watson et al., 1998; Watson and Bentley, 1998). For *A. defodiens*, the reinitiation of meiosis is only controlled by one neurohormone, the PMH.

For the males of both species, the gametes form a cluster of cells connected by their cytoplasm to a cytophore (extracellular cytoplasm) (Olive, 1984a; Pacey and Bentley, 1992). The cluster shape evolves during the gametes development from a spherical shape also called 'rosette' to a sun shape (spherical surrounded by the spermatids' flagella), also called 'morula' (prophase I stage) (Dillon and Howie, 1997; Meijer, 1979) (Fig. 1.10). The reinitiation of meiosis is controlled in both species by a single hormone, the Sperm Maturation Factor (SMF), that leads to the activation of flagella, the dissociation of the clusters and the expulsion of the gametes (Bentley, 1985; Howie, 1963; Pacey and Bentley, 1992).

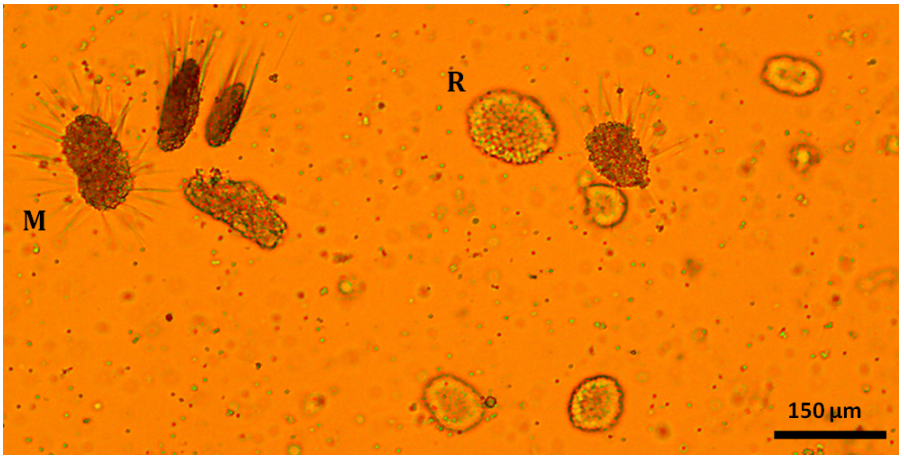

Figure 1.10 – Microscopic observation of male gametes of *A. defodiens* at the 'rosette' stage (R) and the 'morula' stage (M). Photograph taken by L.D.

Spawning Both lugworm species exhibit annual iteroparity (Watson et al., 2000). Populations of *A. marina* have been reported to spawn epidemically over a few days to two weeks during September to November (Luttikhuizen and Dekker, 2010; Howie, 1984; Watson et al., 2000) and populations of *A. defodiens* has been reported to spawn slightly later in late December to early January (Watson et al., 1998). During spawning events, sperm is released onto the surface of the beach as milky-white sperm puddles. Females retain their spawned oocytes within the burrows and fertilization happens there, spermatozoids being brought by the incoming tide, with an optimal concentration of 10^5 to 10^6 cell.ml^{-1} for fertilization success (Newell 1948; Howie 1959; Farke and Berghuis 1979a; Pacey and Bentley, 1992; Williams et al., 1997). Experimentally, the spawning periods

have been assessed through direct observation of the sperm puddles, or through the microscopic observation of the lugworms' gametes (oocytes diameter in females and shape of the gamete clusters in males) (Dillon and Howie, 1997; Mayes and Howie, 1985; Rashan and Howie, 1982; Watson et al., 2000). For *A. marina*, maturity is generally supposed to be reached in females when more than 50 % of the oocytes show a diameter greater than 150 µm and in males when more than 80 % of the gamete clusters show a 'morula' shape (Dillon and Howie, 1997; Mayes and Howie, 1985; Rashan and Howie, 1982).

Environmental effects on reproduction Geographically close lugworm populations can have quite different spawning times and spawn over a period of two days to two weeks (Watson et al., 2000). The synchronicity in spawning within a population as well as the heterogeneity of spawning dates in between close populations seem to indicate that spawning is both initiated and regulated by environmental conditions such as temperature, food availability and tides or lunar cycles, or a combination of those, since generally no single environmental parameter is wholly responsible of the reported spawning events. As a matter of fact, environmental conditions have been shown to trigger spawning in some polychaete species, enhancing the production of reproductive hormones above a certain concentration (Watson et al., 2000). Watson et al. (2000) found that some populations of *A. marina* always spawn on spring tides and that average air temperatures from May to July were moderately correlated with an earlier spawning date. They also proposed that temperature first stimulates PMH production to above a threshold level required for spawning, and that a second trigger is then required to bring about the release of the PMH into the coelomic cavity (Fig. 1.11).

1.2.4 Life cycle and distribution

As Lophotrochozoans, *A. marina* and *A. defodiens* both display a bentho-pelagic life cycle with a trochophore larval stage (Fig. 1.12) (Farke and Berghuis, 1979a, b; Newell, 1948).

Early life cycle The knowledge on *Arenicola* spp.'s early life cycle comes from direct field observations (Benham, 1893; Farke and Berghuis, 1979b; Newell, 1948; 1949) and from one fertilization and larval growth experiment (Farke and Berghuis, 1979a), all anterior to the discrimination of the two lugworm species (*A. marina* and *A. defodiens*). Assignment of data to one species or the other could therefore only be done considering the spawning dates given by the authors. The most comprehensive study was done by Farke and Berghuis (1979a,b) who studied larval growth, dispersal and habitat selection in the field and in the laboratory. To do so, they sampled ripe males and females, let them

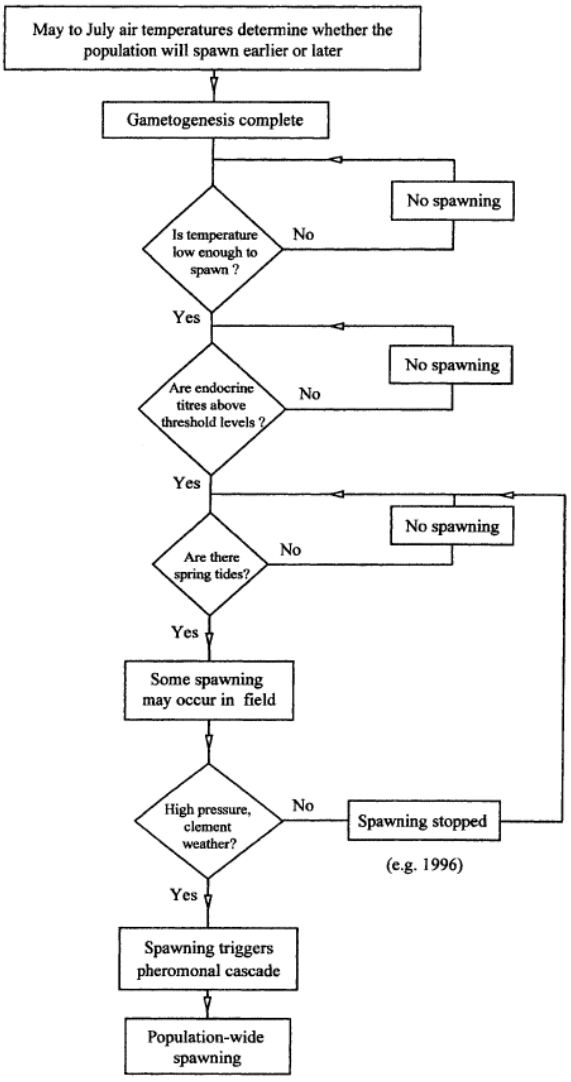

Figure 1.11 – Flow diagram showing environmental and endocrine control mechanisms during spawning of East Sands population of *Arenicola marina* taken from Watson et al. (2000).

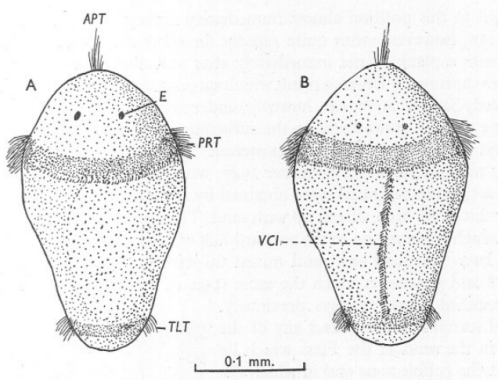

Figure 1.12 – Camera lucida drawings of *Arenicola marina* trochophore larvae taken from Newell (1948). A, dorsal view. B, ventral view. The apical tuft (APT), eyes (E), prototroch (PRT), teletroch (TLT) and the ventral ciliated band are represented (VCI).

spawn in the lab within a microsystem (Fig. 1.13) that enabled the larvae to disperse twice.

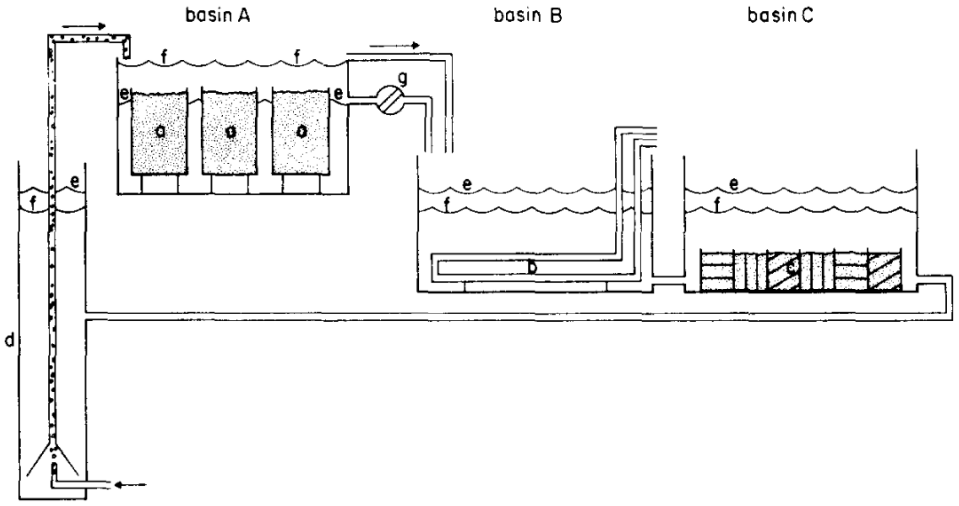

Figure 1.13 – Scheme of the microsystem used by Farke and Berghuis (1979a) showing the relative position of basin A with containers (a) filled with sediment in which adult *Arenicola marina* live, of basin B with cooling pipes (b), and basin C with three different types of sediment (c). The water is recirculated by an air lift (d); a tidal regime in water level (e or f) is maintained by a time-controlled magnetic valve (g).

First, the larvae dispersed from the adult grounds (around 3 setigers and 0.5 mm in length) to a sediment bare location (cooling pipes) where they settled from one to 3 weeks after spawning (around 6 setigers and 0.8 mm in length) and where they lived in mucus tubes attached to the cooling pipes eating the deposited particles outside their tube, being deposit-feeders (Figs. 1.13, 1.14) (Farke and Berghuis, 1979a). Second, from the cooling pipes to sediment, where they started reproducing the adults behaviour, living in galleries and ingesting sediment, being psammivorous feeders (around 6 mm in length, 19 setigers) (Figs. 1.13, 1.14) (Farke and Berghuis, 1979a). The morphological descriptions of the life cycle phases present within the microsystem were precise (Fig. 1.14), but the chronology remained unclear, especially because the authors might have mixed the two species in the microsystem. Indeed, they observed two distinct spawning events, one in early September and another one in late November for lugworms collected at the same location (Farke and Berghuis, 1979a). In parallel they performed field sampling during the same period that confirmed the observations made in the laboratory. Larvae up to 3 setigers were observed within the females gallery in late September and late November. Temporary settled larvae were observed in intertidal and subtidal sheltered sediment rich in diatoms, up to 4 cm deep (Farke and Berghuis, 1979b). Dispersing post-larvae enclosed in transparent gelatinous tubes were caught with plankton hauls (200 µm mesh) at night in periods with high tidal current velocities between the end of March and the end of April and the first recruits

were spotted in early April (Farke and Berghuis, 1979b).

Other authors made observations consistent with those of Farke and Berghuis (1979 a, b) and clarifying some obscure points. Newell (1949, 1948) reported the presence of *A. marina* metatrochophore larvae close to settle with 3 to 4 setigers and around 0.034 cm of length around 2 to 3 weeks after the occurrence of the spawning event at Whistable (UK) (limit between the English Channel and the North Sea). Moreover, observations of post-larvae in mucus tubes were commonly made on fucus and pebbles areas until the end of February at the same location (Benham, 1893; Newell, 1949, 1948) and up to April in some cases (Newell, 1949). First settlements of juveniles on adult grounds were reported by Newell (1949, 1948) at the end of April or beginning of May. The life cycle of *A. marina* deduced from these observations is presented on Fig. 1.15.

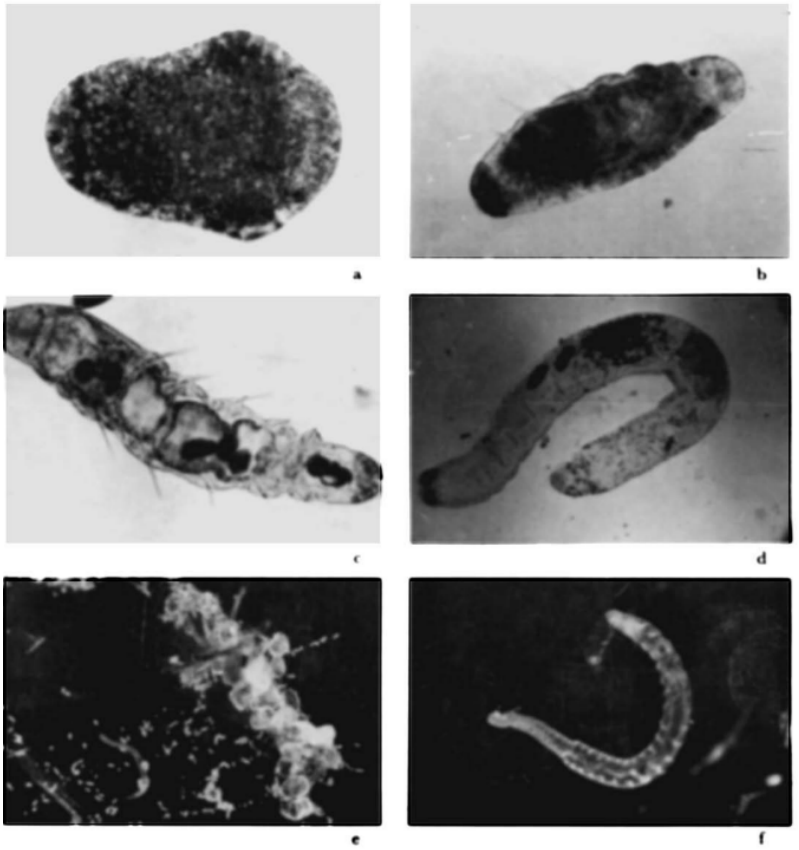

Figure 1.14 – Plates taken from Farke and Berghuis (1979a) describing (a) a newly hatched larva at trochophora stage (about 0.25 mm of length), (b) a larva with three setigers (about 0.5 mm, the head with two eyespots and the tail region are visible), (c) a larva with 6 setigers removed from its mucus tube (about 0.8 mm, the head with two eyespots, the pharynx, intestine, the gut containing food particles and the tail region are visible), (d) a larva in which the 19 setigers have been completed (about 2-3 mm, eyespots are still present), (e) similar stage as in (d) close to its mucus tube to which sand grains adhere, (f) post-larva just after migration (about 6 mm, part of the transparent gelatinous tube enclosing the whole body during swimming is adhering to the anterior part of the body).

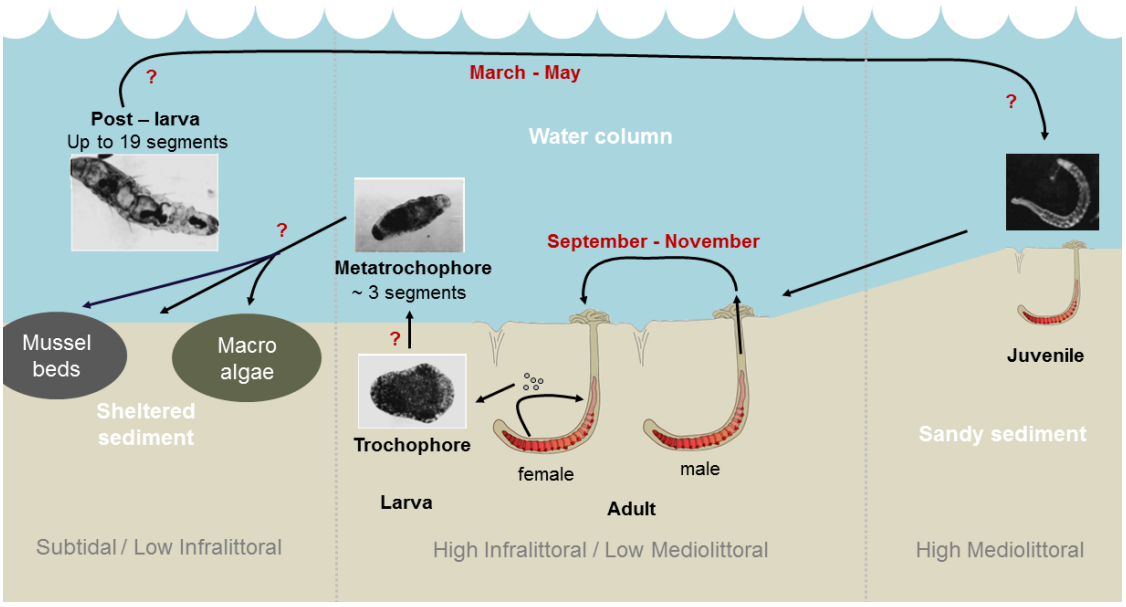

Figure 1.15 – Representation of the actual knowledge of the life cycle of *Arenicola marina*. The unknown duration of the life stages are specified with a red question mark.

Regarding *A. defodiens*, almost no data are available on its life cycle (Fig. 1.16).

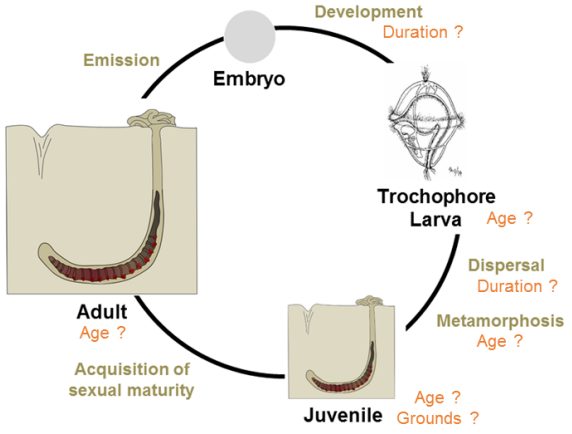

Figure 1.16 – Representation of the unknown life cycle of *Arenicola defodiens*. The juveniles and their recruitment grounds were never described, as well as the duration of the different life stages (as indicated by the orange question marks).

Recruitment and shore distribution Recruitment (period of the year, location) has only been described for *A. marina* up to now (Farke and Berghuis, 1979a, b; Newell, 1949; 1948; Reise, 1985; Reise et al., 2001). It is likely that *A. defodiens* juveniles recruit in subtidal areas since they were not described yet. Recruitment of *A. marina* has been reported to happen on the high mediolittoral shore in early spring, probably driven by high tide currents, and where adults are scarce, both in the UK and in the Netherlands

(Fig. 1.15) (Farke and Berghuis, 1979 a, b; Newell, 1949; 1948; Reise, 1985; Reise et al., 2001). Adults are generally in higher densities lower on the shore, which might indicate that more favourable environmental conditions (in terms of food and temperature mainly) are met there. Indeed, they have been reported to migrate down the shore in case of extreme climatic events (Wolff et de Wolf, 1977). The heterogeneity of the distribution of adults and of juveniles (Farke et al., 1979; Flach and Beukema, 1994; Reise et al., 2001) could thus be related to intraspecific competition for food or space (building up galleries) (as suggested by Flach and Beukema, 1994), heterogeneity of environmental conditions, or to a gradual and synchronous migration down the shore of both the adults and the juveniles.

Sexual maturity The first occurence of oocytes in *A. marina* females collected as juveniles and reared in the laboratory between 15 and 25 °C with food were observed by De Wilde and Berghuis (1979) in August, which is, less than one year after fertilization. However, at lower temperatures (5 and 10 °C) no gonad development had taken place at the end of the experiment. This seems in accordance with other field observations reporting that under *in situ* environmental conditions, with low winter temperatures, and probably suboptimal food level, *A. marina* matures at the end of its second year (Cazaux, 1967; Duncan, 1960; Newell, 1948; Smidt, 1951). Besides, De Wilde and Berghuis (1979) observed that the body weight of worms reaching maturity (or puberty) was negatively related to the experimental temperature. Indeed, the wet weight after depuration of the smallest worm becoming mature at 15 °C was much heavier (1.3 g) than at 20 °C (1.0 g) and at 25 °C (0.5 g).

1.2.5 Growth and food sources

Growth The main studies on *Arenicola* spp. growth were performed by Rikjen (1979), De Wilde and Berghuis (1979) and Olive et al. (2006). Rikjen (1979) compared the effect of different food types on the growth in wet weight of *A. marina* juveniles collected in the field (Wadden Sea, the Netherland) at one constant temperature (10 °C). The food types tested were bacteria (mainly *Desulfovibrio desulfuricans* and *Thiobacilllus denitrificans*), benthic diatoms obtained from a local mudflat and cultivated in the laboratory, dried powder of *Ulva lactuca*, and the natural superficial layer of the sediment (containing all the earlier possible types of food) (Rikjen, 1979). De Wilde and Berghuis (1979) followed the trunk length and dry weight of juveniles collected on the field (Wadden Sea, the Netherland) at five temperatures (5, 10, 15, 20 and 25 °C) under two different food conditions (fed and unfed). The upper 1 mm sediment layer scraped from places rich in benthic algae

or deposited organic matter was used to feed the lugworms in the fed condition. Olive et al. (2006) followed the wet weight of *A. marina* at one temperature varying between 16 and 20 °C under two different food conditions (fed with brewer yeast and unfed). Rijken (1979) observed the highest gains in wet weight while using the superficial layer of the sediment (with a 140 % increase in wet weight), then using bacteria (with a 91 % increase in wet weight), benthic diatoms (with a 63 % increase in wet weight) and *Ulva* (with a 55% increase in wet weight). In the two other studies comparing fed and unfed conditions, the lugworms grew more in the fed condition, gaining up to 7 times their initial trunk length within 150 days (De Wilde and Berghuis, 1979) and 10 times their initial wet weight within 120 days (Olive et al., 2006), suggesting that the food sources were adapted to growth.

Food sources Riisgard and Banta (1998) listed several potential food sources for *A. marina* including: nonliving deposited organic matter, bacteria at normal sediment density or enhanced in abundance externally by gardening or internally by microbial fermentation, microphytobenthos (MPB), dissolved organic material or suspended organic mater from the water column trapped in the sediment during irrigation.

Nonliving detrital organic matter from algae showed to lead to a really small growth of *A. marina* (Rijken, 1979), which is in accordance with the fact that lugworms do not secrete cellulase (Longbottom, 1970). The observed growth could thus be explained by the associated development of bacteria on the algae detritus during the experiment (in the headshaft of the burrow), or to the possible presence of bacteria able to digest cellulose within the gut of the lugworms (Riisgard and Banta, 1998). Retraubun et al. (1996) studied the presence of detritus of algae, bacteria, MPB and meiofauna in the surface sediment, the funnel, the headshaft, the lugworm foregut and the faeces of the lugworms. They noticed really high concentrations of diatoms and bacteria in the lugworms gut in comparison with their concentrations in the other compartments and concluded on the selectivity of *A. marina* for these two food sources. Riisgard and Banta (1998) calculated the maximum quantity of phytoplankton from the water column that could be ingested by *A. marina* according to the maximum irrigation rate of the burrow and concluded that lugworms could not feed exclusively on suspended phytoplankton. However, suspended and resuspended material from the sediment surface may be one of the several potential food sources. Indeed, phytoplankton was also reported in lugworms diet on the East Coast of the Cotentin Peninsula (English Channel, Normandy, France), where strong benthopelagic couplings were found (Gaudron et al., 2016).

The food sources might vary according to the period of the year, with a diet of the lugworms being constituted mainly of bacteria and microalgae (MPB mainly) between spring

and autum, and completed by other digestible detritus during winter (Andresen and Kristensen, 2002).

1.2.6 Interspecific interactions

Gardening The lugworms are considered to be 'gardeners' because they enhance the productivity of bacteria and MPB before to feed on them (Chennu et al., 2015; 2013; Grossmann and Reichardt, 1991; Retraubun et al., 1996). Indeed, the bioirrigation increases the oxygen supply and enhance the advective supply of nutrients, and the shape of the burrows provides a small-scale topography favouring the depositing of detritus in the headshaft, as the amount of bacteria was found correlated with the amount of detritus (Chennu et al., 2015; Retraubun et al., 1996). Both processes provide better conditions for bacteria and MPB growth in the headshaft of lugworms than in the surrounding sediment, and therefore locally increase the food available for the lugworm (Fig. 1.17) (Chennu et al., 2015; 2013; Retraubun et al., 1996; Riisgard and Banta, 1998).

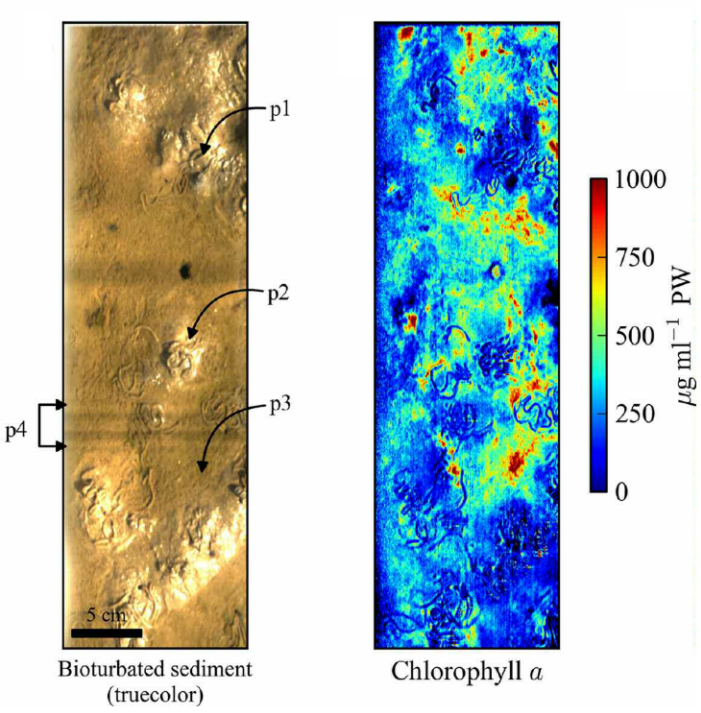

Figure 1.17 – *In situ* imaging of microphytobenthos biofilms on intertidal sediment affected by the bioturbation activity of the lugworm *Arenicola marina* taken from Chennu et al. (2013). Features of the lugworm habitat such as fecal mounds (p1, p2) and inter-burrow sediment (p3) are annotated.

Competition / Enhancement The effects of lugworm presence on the benthic community rely on three main mechanisms. First, it relies on the increase of oxygen supply via bioirrigation (as observed in the case of 'gardening'), that facilitates small zoobenthos and meiofauna along the burrows. Second, on the decrease in sediment stability via bioturbative disturbance, and third, on the change of overall sediment characteristics that may considerably affect other benthic species beyond the immediate vicinity of lugworm burrows, casts and funnels (Volkenborn, 2005). Through these mecanisms, lugworms have been reported to enhance an increasing diversity of species such as *Urothoe poseidonis* (Amphipoda), that inhabits preferentially *A. marina*'s funnels with densities up to 50-60 individuals per burrow (Lackschewitz and Reise, 1998); some copepods have been reported to aggregate in the headshaft of lugworms at low tide that become tiny pools (Reise, 1981), as well as MPB, bacteria and meiofauna present in the headshaft, and subsurface-feeding motile species (Volkenborn and Reise, 2007). On the other hand, the presence of lugworms may also inhibit other sedentary macrofauna species such as tubeworms (e.g. *Pygospio elegans*), subsurface deposit feeding worms (e.g. *Scoloplos armiger*), and even other ecosystem engineers such as marine plants (Kosche, 2007; Volkenborn and Reise, 2007). Indeed, *A. marina* has been shown to impact negatively populations of *Zostera noltii* (Govers et al., 2014; Kosche, 2007).

Predation on *Arenicola* spp. Birds (Clarke et al., 2017), flatfish (De Vlas, 1979a; Kuipers, 1977) and other polychaete species (De Wilde and Berghuis, 1979; Witte and De Wilde, 1979) have been reported to feed on *Arenicola* spp. When predated, the worm might remain alive when only part of the tail is eaten when the organism rises to the sediment surface for defecation (Bergman et al., 1988). However, neo-formation of tail segments does not occur in lugworms (De Vlas, 1979b) and the individual dies when only a few tail segments are left (De Vlas, 1979a). In the Balgzand tidal flat area (Dutch Wadden Sea), lugworms were reported to be tail-nipped by flatfish on average about once a week during the spring-summer season (De Vlas, 1979a), which might lead to high mortality rates (Bergman et al., 1988). De Vlas (1979b) also estimated that about 20 % of the annual production of *A. marina* was removed by plaice predation in this area. To our knowledge, no quantitative data for predation by birds or predator worms on *Arenicola* spp. have been reported up to now.

1.3 Bioenergetic modelling

Bioenergetic models are quantitative tools enabling to link animal individual physiology and behaviour to environmental conditions (Brandt and Hartman, 1993). Combined with

population dynamics, such models can lead to an understanding of ecological processes and phenomena from the individuals to the populations, communities and ecosystems, and therefore help managers to understand the possible consequences of their decisions (Brandt and Hartman, 1993; Kearney and White, 2012).

1.3.1 Bioenergetic models

The von Bertalanffy model Historically, the first bioenergetic model that has been developed is the von Bertalanffy model for fish growth (von Bertalanffy, 1938; 1957). This model describes the increase in weight of an individual as the difference between anabolism and catabolism following Equation (1.1), with W the weight, $a \cdot W^b$ the term for anabolism and $c \cdot W^d$ the term for catabolism. This relation leads to the growth equation of von Bertalanffy given in Equation (1.2), with L the length, L_∞ the asymptotic length, k the von Bertalanffy growth rate, a the age of the organism and a_0 the age of the organism for $L = 0$ (Pecquerie, 2007; von Bertalanffy, 1938; 1957). This model has been widely used in ecology, but does not account for variations of the environmental conditions (Kooijman, 2000; Pecquerie, 2007).

$$\frac{dW}{dt} = a \cdot W^b - c \cdot W^d \tag{1.1}$$

$$L(a) = L_\infty \cdot \left(1 - e^{-k(a-a_0)}\right) \tag{1.2}$$

Static energy budget models After that, static energy budget models based on energy balance equations similar to Equation (1.3) have been developed, the most recent and widespread being the Wisconsin model (Deslauriers et al., 2017; Kooijman, 2000; Pecquerie, 2007). Where C is the consumed food (energy input), R the standard metabolism, A the energy expenditure due to activity; SDA the specific dynamic action (energy required to digest food), F the waste losses in faeces, U the waste losses due to excretion and G the somatic and/or gonadal growth (Deslauriers et al., 2017). These models focus on empirically estimated rates and allometric responses, and allometric parameters are thus needed for each species (Deslauriers et al., 2017; Jorgensen et al, 2016; Pecquerie, 2007).

$$C = R + A + SDA + F + U + G \tag{1.3}$$

The Metabolic Theory of Ecology The Metabolic Theory of Ecology (MTE) (Brown et al., 2004) is an extension of Kleiber's law and states that the metabolic rate of organisms is the fundamental biological rate that governs most observed patterns in ecology. MTE describes how the standard (or basal) metabolic rate (SMR) of individual organisms vary

with body size and temperature (Brown et al., 2004; Van der Meer, 2006b). The theory is based on Equation (1.4) with Q the metabolic rate, M the adult mass, E_a the activation energy, B_0 an empirically determined constant and k Boltzmann's constant (Brown et al., 2004; Kearney and White, 2012). The mass scaling exponent (3/4) is mechanistically justified on the basis of the way that fractally branching distribution networks scale with body size (Kearney and White, 2012; West et al., 1997). However, researchers disagree about whether metabolic rate scales to the power of 3⁄4 or 2⁄3, or whether either of these can even be considered a universal constant, and about the mechanisms that predict an allometric scaling exponent of either 2⁄3 or 3⁄4 (Agutter and Wheatley, 2004).

$$Q = B_0 \cdot M^{3/4} \cdot e^{-E_a/kT} \tag{1.4}$$

1.3.2 The Dynamic Energy Budget theory

The Dynamic Energy Budget (DEB) theory is a formal metabolic theory which provides a single quantitative framework to dynamically describe the uptake and use of substrates (food) by an organism during its life cycle. The theory uses energy and mass budgets to quantify the energy allocation to growth and reproduction of a species at the individual level throughout the life cycle, according to environmental conditions such as temperature and food availability (Kooijman, 2010), even in species with complex and numerous life-stages (Llandres et al., 2015). Over the last 25 years, the theory has kept expanding (Fig. 1.18). Indeed, as developed from thermodynamic principle universally observed,

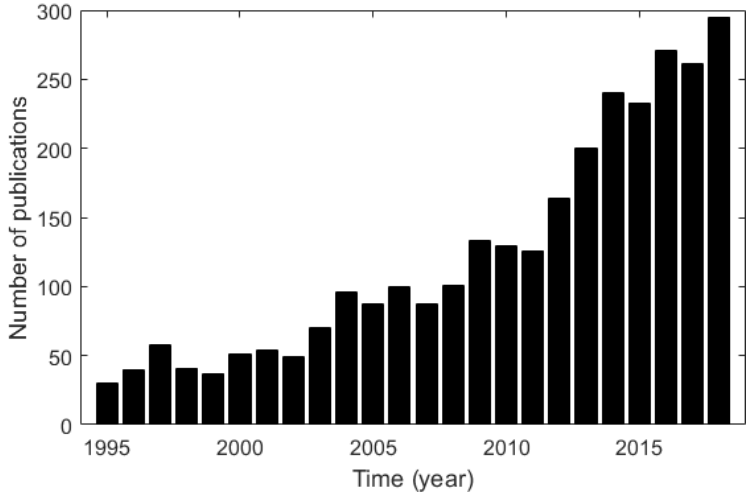

Figure 1.18 – Evolution of the number of publications related to the DEB theory between 1995 and 2018 available in the Web of Science collection.

it can be used for any species and provides a comprehensive framework enabling growth and reproduction output predictions at any life stage of an organism, but also the chronol-

ogy of these life stages throughout the life cycle of the organism at given environmental conditions. Up to now, models based on the DEB theory have been applied to over 2000 species with applications ranging from conservation, aquaculture, general ecology, and ecotoxicology (https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/).

1.3.3 The standard DEB model

According to the standard (std-) DEB theory, an organism is constituted by two main compartments: one reserve compartment and one structure compartment. The biochemical composition of reserve and structure is considered to be that of generalised compounds, and is constant (the assumption of strong homeostasis) but not necessarily identical. The assimilated energy (proportional to surface area of the structure) is fixed into the reserve compartment and then mobilized. A fixed fraction K of the flux from the reserve is spent on maintenance, heating (for endotherms) and growth (with a priority to maintenance), the rest (1 - K) is spent on maturity (i. e. development for embryos and juveniles) or reproduction (for adults) and maturity maintenance (Fig. 1.19) (Kooijman, 2010; van der Meer, 2006a).

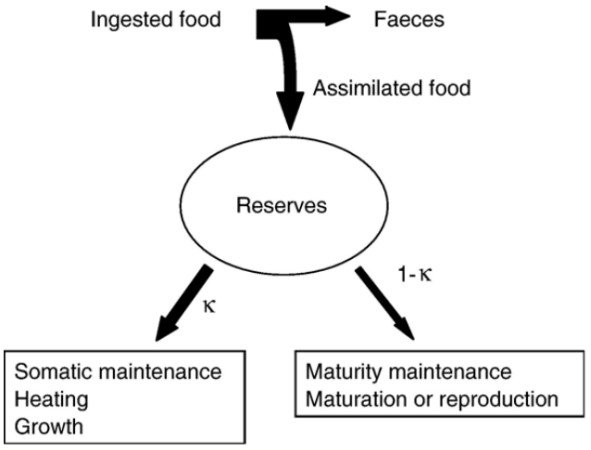

Figure 1.19 – Schematic representation of the DEB model taken from van der Meer (2006a). Part of the ingestion is assimilated, the rest is lost as faeces. The assimilated products enter the reserve compartment. A fixed fraction K of the flux from the reserves is spent on maintenance, heating (for endotherms) and growth (with a priority to maintenance), the rest goes to maturity (for embryos and juveniles) or reproduction (for adults) and maturity maintenance.

In the std-model, three life-stages follow one another throughout the life cycle of the organism: the embryo stage, which does not feed nor reproduce, the juvenile stage, which feeds but does not reproduce, and the adult stage, which both feeds and is allocating energy to reproduction. Transitions between these life stages occur at events specified as birth and puberty. These events are reached when energy invested into maturation (tracked

as 'level of maturity') reaches a certain threshold. Maturity does not increase in the adult stage, and maturity maintenance is proportional to maturity (Kooijman, 2010). In the std- model, growth is isomorphic throughout the life cycle of the organism, and follows a typical von Bertalanffy growth curve. Twelve primary parameters are sufficient for the implementation of a std-DEB model (Kooijman et al., 2008).

1.3.4 Extensions of the standard DEB model and applications

Extensions of the std-DEB model are sometimes needed to take into account the specific life cycle of a particular species or to address specific questions. In general, these extension consist in the addition of one life-stage or more (Llandres et al., 2015), in the use of several structure or reserve compartments (Kooijman, 2010), in the inclusion of more types of food or of one type of toxicant and its effects (Lavaud et al., 2014; Pousse et al., 2019), or in the deviation from the typical von Bertalanffy growth curve, when considering a change in shape during growth (Kooijman et al., 2011).

DEB models have also been combined to Individual-Based Models and larval dispersal models to understand the population dynamics of some species (Martin et al., 2012; Thomas and Bacher, 2018). Such population dynamics models could then be used by managers to predict the effect of different management plans.

1.4 Objectives

Much of the data relative to the lugworms' life cycle, growth and reproduction was present but incomplete (chronology of the life stages not given, experiments with some food or temperature conditions not specified) or not completely reliable (species identification), and none of it was related to lugworms population from the French Coast of the Eastern English Channel. Moreover, no data or model regarding the species's population dynamics was available.

The objectives of this study were thus:

1. to identify (or not) a potential need for management of the *Arenicola* spp. populations

2. to complement the knowledge on the species, and their life-history traits, growth and reproduction

3. to characterize *Arenicola* spp. populations and their responses to environmental variables to enable future population dynamics studies (Fig. 1.20).

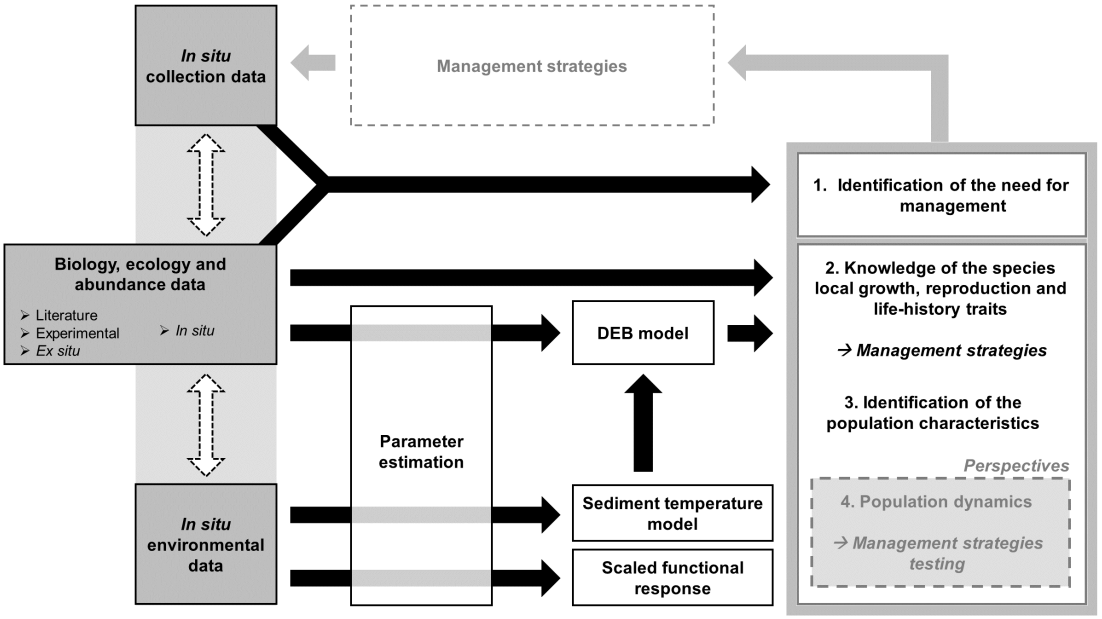

Figure 1.20 – General framework of the thesis

First, we tried to know if the *Arenicola* species and populations within the MPA needed management comparing the harvest data obtained directly from the MPA and the Life + project with our field observations of abundance and spatial distribution.

When the need for management was established in at least some of the studied areas, came the question of how to manage the *Arenicola* spp. local populations (Fig. 1.6). Up to now, no regulation on the lugworms harvest either on the size of the lugworms, on the number of collected individuals or on the period of collection are implemented within the MPA. Knowledge was then required first on the present species, their life cycle, growth and reproduction. To complete and detail the data available in the literature, we decided to combine field sampling, laboratory experiments and various modelling approaches to understand the species' biology and ecology. To do so, we followed the population size structure, reproduction and recruitment of one pilot site and some of these features on other sites within the MPA. Additionally, we performed preliminary growth experiments on *A. marina* and *in vitro* fertilization experiments on *A. marina* and *A. defodiens*, as well as oxygen consumption experiments on *A. marina* at several temperatures. The obtained data (when usable as such) and literature data were combined and used in the parameter estimation procedure of a Dynamic Energy Budget (DEB) model for *A. marina*, enabling us to quantify the energy allocation to growth and reproduction of individuals of the species during their life cycle according to environmental conditions such as temperature and food availability (Kooijman, 2010).

In order to be able to make relevant *A. marina* predictions on the species life cycle, growth

and reproduction, relevant data regarding the *in situ* environmental conditions, namely food and temperature met by the lugworms, were needed. Sediment temperature was shown to differ from water and air temperature and to be depth-dependent (Mayes and Howie, 1985; Guarini, 1997; Savelli et al., 2018). We therefore adapted a mud temperature model from Guarini (1997) to compute the sediment temperature met by the lugworms throughout the year according to the depth of their gallery and their location on the foreshore, assessed from field observations of the population of *A. marina*. Food sources of *A. marina* have been reported to be potentially a combination of bacteria, microphytobentos, macroalgae in decomposition, and phytoplankton from the water column (Riisgård and Banta, 1998; Retraubun et al, 1996; Rijken, 1979). The good proxy for food availability was thus tested from several sources such as the nitrogen content of the sediment and the chlorophyll-a content of the water column (Longbottom, 1970; Pecquerie et al., 2009). Once chosen, the DEB model for *A. marina* and the *in situ* environmental variables were combined to try to understand better the population migration, in view of bringing more knowledge and enabling future population dynamics model for the species (Martin et al., 2012).

We developed this study in three chapters (apart from this introduction), being scientific articles published, accepted or in preparation:

The second chapter focuses on showing the potential need for management of *Arenicola* spp. populations within the MPA, combining abundance data with harvest data, and brings knowledge on some of the species life-history traits usefull for management.

The third chapter presents the parameter estimation procedure of the DEB model for *A. marina*, using both literature, laboratory and field data. It presents preliminary inferences on the species early life cycle, as well as a global comparison of the species parameters with the parameters of other Lophotrochozoan species.

The fourth chapter consists in the implementation of a sediment temperature model, the choice of a proxy for food availability and the combination of those environmental variables to make predictions of the growth and reproduction of *A. marina* under various shore migration scenarios.

A conclusion on the contribution of this study and its perspectives will be finally made to close up this thesis.

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Chapter 2

Linking life-history traits, spatial distribution and abundance of two species of lugworms to bait collection: a case study for management plan

Linking life-history traits, spatial distribution and abundance of two species of lugworms to bait collection: a case study for management plan

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Abstract *Arenicola* spp. are marine benthic polychaetes dug for bait by anglers. Without regulation, this activity can lead to the decrease of lugworms' population meanwhile affecting the physical characteristics of the beach and the biodiversity. Here, we identified through morphology and genetics two species of lugworms, *Arenicola marina* and *A. defodiens*, within a Marine Protected Area of the Eastern English Channel (France). For each species, abundance and spatial distribution were assessed using a stratified random sampling and interpolation at four studied sites, as well as some life-history traits. These data were compared to lugworms' collection data to estimate its sustainability and to provide potential management measures. At one site, *A. marina* was present in large numbers on the higher and middle shore, whereas *A. defodiens* occupied the lower shore. At the other sites, both species co-occurred on the lower shore, and *A. marina* individuals were less numerous and lacking recruits. Spawning periods for *A. marina* occurred in early autumn and in late autumn for *A. defodiens*. The size at first maturity of *A. marina* was at 3.8 cm of trunk length (between 1.5 and 2.5 years old). One site (Au) appeared in need for management when linking abundance data with bait collection, where harvest of both species represented $\sim$ 14 % of the total amount of lugworms and was above the carrying capacity of the beach for *A. marina*. The retail value associated to lugworm harvesting within the MPA was estimated at the same level as the shrimp retail value. Our results highlight the need for some fishery regulations.

Key words *Arenicola marina*, *Arenicola defodiens*, Spawning, Population structure, Size at first maturity, Recreational fisheries, Conservation, English Channel

2.1 Introduction

Arenicola spp. (Annelida Polychaeta), are marine benthic coastal ecosystem engineers living in burrows on intertidal and subtidal soft- sediment beaches and estuaries from the Arctic to the Mediterranean (Volkenborn, 2005). Two cryptic species of the genus *Arenicola* were recorded in the North Sea and the English Channel: *A. marina* and *A. defodiens* (Cadman and Nelson-Smith, 1993). They were formerly described as two varieties of the same species, *A. marina* being the "littoral" variety, and *A. defodiens* the "laminarian" variety (Luttikhuizen and Dekker, 2010). Indeed, *A. marina* rather occupies the higher shore to mid-shore in a U-shape gallery, between 10 and 40 cm below the sediment surface, while *A. defodiens* is present on the lower shore to subtidal area in a deeper (up to 1-m deep) and J-shape gallery (Cadman and Nelson-Smith, 1993; Cadman, 1997). Only small morphological differences exist between the two species, the most notable being the annulations patterns of the first setigers and the shape of the gills (Cadman and Nelson-Smith, 1993). Thus, their species discrimination was proven by genetics (Cadman and Nelson-Smith, 1990) and reconfirmed recently using COI and 16S gene markers (Luttikhuizen and Dekker, 2010; Pires et al., 2015). Both species are dioecious and iteroparous (Watson et al., 1998) and their bentho-pelagic life cycle (Farke and Berghuis, 1979a; Reise, 1985), has only been described for *A. marina*. For this species, after the spawning event in early autumn, and before the recruitment in spring, young stages experience two successive dispersal phases, with a temporary settlement in between, where at a 'post-larval' stage the worm lives in a mucus tube attached to various substrates (sheltered soft-sediment, macroalgae or mussel beds) (Farke and Berghuis, 1979a; b; Reise, 1985; Reise et al., 2001).

Arenicola spp. play a key role in bioturbation of soft sediments (Kristensen, 2001) and in local trophic networks (Reise, 1985; Clarke et al., 2017). Moreover, despite lugworms are not considered yet as a fisheries species (as not directly consumed), they represent a high commercial marine value showing an important biomass extraction according to Watson et al. (2017a), who estimated a global landing for polychaete bait (including lugworms) up to 120 000 tonnes, representing £5.9 billion in 2016. Lugworm collection by professional or recreational fishermen may impact the size and age structure of a population, such as its abundance and distribution (Blake, 1979; McLusky et al., 1983; Olive, 1993) with possible population crashes caused by overexploitation (Olive, 1993). In addition, bait diggers can affect the physical characteristics of the beach perturbing the other associated fauna (invertebrates, wading birds, etc.) (Beukema, 1995; Clarke et al., 2017; Watson et al., 2017b). In consequence, several authors call for a management (Watson et al., 2017a), and particularly, a sustainable management of these species (Clarke et al., 2017).

Fisheries management can be defined as "the integrated process of information gathering, analysis, planning, consultation, decision-making, allocation of resources and formulation and implementation, with enforcement as necessary, of regulations or rules which govern fisheries activities in order to ensure the continued productivity of the resources and the accomplishment of other fisheries objectives" (FAO, 2002a). In other words, this consists in maintaining its population at healthy levels, which is, in terms of population's dynamics, a population with sustainable birth, growth and survival rates (Beverton and Holt, 1957). The management can be implemented through education, or through enforced harvest regulations (Watson et al., 2015). The latter are in general applied either on the fishermen themselves, implementing licenses or fees, gear or fishing methods restrictions, closing times, season or area restrictions, either on the resource, limiting the length or quantity (bags) of the collected species mainly (FAO, 2012). Both controls are used to limit the overall mortality, or the mortality of specific individuals in the population, based on its features (FAO, 2012).

Several kinds of regulations for bait collection have already been enforced around the world, either for recreational or professional fishermen: licensing has been implemented in the United States and the United Kingdom (Watson et al., 2015), quotas have been implemented in Portugal (Xenarios et al., 2018) and some areas have been closed in the UK (Olive, 1993; Rogers, 1997). For *Arenicola* spp. the last two options have already been implemented in some European places: a limitation to 100 individuals in a defined area in the North of France (Direction interrégionale de la mer Manche Est-mer du Nord, 2015) or the closure of areas where the lugworm population crashed in the UK (Olive, 1993; Rogers, 1997). Although protecting lugworms, the main purpose of these management methods is sometimes rather to protect the habitat features or the wading birds disturbed by fishermen (Watson et al., 2017b).

Besides, these management measures are merely restrictions, often taken without any considerations of the life-history traits of the local populations (Watson et al., 2017a). Studies linking bait collection data to abundance, spatial distribution and life-history traits of lugworm are scarce. Xenarios et al. (2018) assessed the sustainable levels of some polychaetes species (*Diopatra neapolitana*), only taking into account the harvest effort, and Blake (1979) combined the harvest effort to population data (e.g. density and size structure). Nevertheless, the only study of this kind dealing with lugworms (Blake, 1979) was performed before the knowledge of the co-occurrence of two potential species of the genus *Arenicola* inhabiting the intertidal area (Cadman, 1997).

In this study, we have assessed the abundance and the spatial distribution of several local populations of *Arenicola* spp. within a newly created MPA from temperate coastal areas located in the Eastern English Channel, as well as some life-history traits such as spawn-

ing period, size at first maturity, population structure and recruitment period. Additional data on lugworms' collection by recreational bait diggers within the MPA was included in order to estimate the potential sustainability of the different lugworms' population and to provide relevant potential management measures when needed.

2.2 Material and methods

2.2.1 Study area

The study area is located in the Eastern English Channel and is part of a marine protected area (MPA): the Parc naturel marin des estuaires picards et de la mer d'Opale created in 2012 (Fig. 2.1). The coastline is mainly composed of hydrodynamically exposed sandy beaches of fine to medium sands (0.05–0.5 mm grain size), as well as some rocky shores, and includes three major estuaries of muddy sands (2–3% silt): the Somme, the Authie and the Canche estuaries (Rolet et al., 2014, 2015). The tidal regime is semi-diurnal and macrotidal and, amplitude may exceed 8 m, with the largest amplitudes occurring around 2 days before the full moon (Migné et al., 2004; Rolet et al., 2015). Sampling sites (Fig. 2.1) were chosen at four locations along the shore of the MPA, where recreational fishermen had often been observed digging worms, in order to assess the need for management of this activity: 1) Wimereux (Wx) (50°46'14" N and 1°36'38" E), 2) Le Touquet (LT) (50°31'07" N and 1°35'42" E), 3) Fort Mahon (FM) (50°20'31" N and 1°34'11" E) and, 4) Ault (Au) (50°06'07" N and 1°26'58" E). LT and FM are composed of large exposed sandy beaches, when Wx and Au are a mixture of sandy beaches and rocky shores mainly colonized by algae and mussels on the intertidal and subtidal areas.

2.2.2 Spatial distribution and abundance of *Arenicola* spp.

Sampling strategy Spatial distributions of lugworms were investigated on the sandy shore in April-Mai 2016 at the four sites (Wx, LT, FM and Au) during spring tide periods. Formerly, lugworms distributions were assessed by samplings on uniformly distributed points along transects (Beukema and De Vlas, 1979; Beukema, 1995). However, on the studied sites, distributions of lugworms were highly aggregative (with spots of faecal casts and spaces without faecal casts next to them). Therefore, a stratified random sampling approach was chosen (Fagan and Nelson, 2017), in order to improve the performance of the spatial interpolation methods (Li and Heap, 2008). At each site, the area was subdivided into a grid of equally-sized rectangle boxes: a grid of 100 m × 50 m divided into 18 boxes at Wx and at Au, and, a grid of 100 m × 70 m divided into 24 boxes at LT and at FM

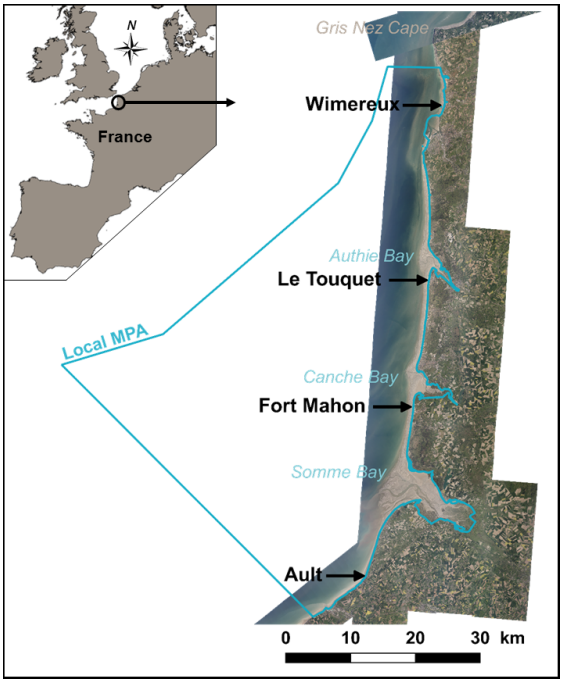

Figure 2.1 – Location of the four studied sites within the MPA where spatial distribution, abundance, life-history traits and survey of bait collection were carried out.

(Fig. 2.1). In each box, a random sampling point was computed (Fig. 2.1), where the abundance of lugworms (both species combined) was assessed by counting the number of faecal casts in three quadrates placed randomly, of 0.0625 m^2 (when densities were higher than 10 faecal casts), or of 1 m^2 (when densities were lower than 10 faecal casts). Every 3 to 5 sampling points, lugworms were dug using either an Alvey bait pump (Decathlon ltd, extracting the worm by suction), a fork or a shovel, and the proportion of each species was calculated at the different bathymetries to correct the number of individuals belonging to each species.

Species identification Species identification was determined morphologically by the observation of the annulations pattern on the second chaetigerous segment (two annulations for *Arenicola defodiens* and three for *A. marina*) (Cadman and Nelson-Smith, 1993). Subsamples of tissue of each worm were kept in a solution of absolute ethanol at - 20 °C. The DNA of 3 random individuals of *A. marina* and 3 random individuals of *A. defodiens* was then extracted using the NucleoSpin® Soil kit according to manufacturer's instruction (Macherey-Nagel), amplified and sequenced by Genoscreen ltd. (Institute Pasteur de Lille, France) in order to confirm the presence of the two different species within the MPA. Fragments of the mitochondrial cytochrome oxidase I-encoding gene (COImt DNA) (∼ 670 pb) were amplified using the universal primers: LCO 1490 (5'-GGTCAACAAATCATA AAG ATA TTG G-3') and HCO 2198 (5'- TAAACT TCA

GGG TGA CCA AAA AAT CA-3') (Folmer et al., 1999). Polymerase Chain Reaction (PCR) was performed according to Pires et al. (2015): an initial denaturing step of 3 min at 94 °C, followed by 34 cycles at 94 °C for 1 min, 45 °C for 30 s for hybridization, then 2 min at 72 °C, and a final extension for 5 min at 72 °C. COI sequences were manually checked using bioedit Ver. 7.0.0. (Hall, 1999). Each COI sequence was then deposited in GenBanK (Supplementary Material: Table 2.A) and aligned with other COI sequences of *A. marina* and *A. defodiens* (retrieved from GenBank), as described by Pires et al. (2015). This multiple alignment of COI sequences was exported to the software MEGA v7 (Kumar et al., 2016) using ClustalW, in order to construct a molecular phylogenetic tree analysis based on the maximum likelihood method (Supplementary Material: Fig. 2.B).

Data analyses To assess the spatial distribution and abundance of *Arenicola* spp., first, the total number of lugworms at each point was estimated by the number of faecal casts (Farke et al., 1979), assuming that one worm produced 0.84 cast.tide^{-1} in *A. marina* (Supplementary Material: Fig. 2.C). We assumed that both species produce approximately the same amount of casts per tide. The relative proportions of *A. marina* and *A. defodiens* were recorded for each collection point taking into account the bathymetry (height above chart datum). Since only few individuals could be collected in spring 2016, the data from autumn and winter 2015 was also used (Table 2.1). Bathymetries were obtained from the interregional project 'CLAREC, INSU – CNRS M2C-UNICAEN' (http://www.unicaen.fr/dat aclarec/home/elevations.html). When no bathymetry record was available (FM), we used the distance from the shoreline as a proxy. The shoreline HISTOLITT® was taken from the SHOM, the hydrographic and oceanographic service of the French navy (http://diffusi on.shom.fr/loisirs/trait-de-cote-histolittr.html). The existence of a correlation between the proportions of the two species and the bathymetry or the shoreline distance was investigated (Spearman correlation test) at each site separately. When a correlation between the proportion of *A. marina* and *A. defodiens* and bathymetry could be established (Wx), a fitting model was adjusted on Matlab R2015b using the Curve Fitting Toolbox and a sigmoid model inspired by Cadman (1997) (Supplementary Material: Fig. 2.D). The number of individuals of each species was then calculated following the fitted model at each collection point's bathymetry. When no particular correlation was noticed (LT, FM) (Supplementary Material: Fig. 2.E), the number of individuals of each species was calculated from the overall proportion of the individuals of both species from autumn 2015 to spring 2016. Eventually, when the number of individuals of *A. marina* and *A. defodiens* was assessed in every point of the grid, it was then interpolated on QGis 2.18.0 (QGIS development team, 2016) using the inverse distance faecal casts). Every 3 to 5 sampling points, lugworms were dug using the inverse

distance weight (IDW) method. Interpolations were superimposed to EUNIS habitat communities maps obtained from Rolet et al. (2014) and from additional samplings performed according to Rolet et al. (2014) at FM and Au in Spring 2016, which is based on species identification of the macrofauna and on the particle size analysis (Supplementary Material: Table 2.F). The number of individuals of each species was obtained on the whole grid from the interpolation and then reduced to $1m^2$ to get the mean density. The significance of the difference of densities between sites was then estimated with a chi-squared test for each species separately, performed on R (R Core Team, 2017).

2.2.3 Life-history traits of the lugworm populations

Sampling strategy

Spawning dates of both species were investigated for two successive breeding seasons, from September 2015 to January 2016 and from September 2016 to January 2017, at the four studied sites. Individuals were dug with a bait pump monthly on the lower shore or with a fork on the mid-shore, at low tide (Table 2.2). The population structure of *Arenicola marina* was investigated only at Wx (Fig. 2.1) within the intertidal area at three locations from the low/middle shore to the higher shore (0 m of bathymetry: 50°46'0.1" N and 1°36'20.3" E, 0.9 m of bathymetry (above 0 m): 50°46'1.7" N and 1°36'14.4" E and, 2.3 m of bathymetry (above 0 m): 50°46'2.5" N and 1°36'10.6" E) in July 2017. During low tide, 30 individuals from each location were collected by digging the sediment (between 5 and 30 cm beneath the surface), either with a pump, or a fork or by sieving (0.5 mm mesh) the sediment on the higher shore for the smaller individuals. This sampling strategy was repeated in September 2017 to assess the size at first maturity of *A. marina* at Wx.

Laboratory measurements

After each sampling, all worms were put in separated containers filled with seawater. Worms were maintained in the laboratory during 24 h–48 h at 15 °C in a cold room to allow gut contents to devoid prior to observations (Watson et al., 2000). After identification, worms were anesthetized in three successive solutions of twice-filtered sea water (TFSW, 0.45 µm and 0.2 µm) at 1 %, 2.5 % and 5 % of ethanol (Gaudron and Bentley, 2002). Each individual was measured (total length and trunk length) and weighted (wet weight). To assess their reproductive status, biopsies of the coelomic fluid were performed on individuals of *Arenicola marina* and *A. defodiens* (Table 2.1) with a sterile hypodermic syringe. The gametes were then rinsed twice in TFSW and kept in ethanol (96%) at 4 °C. Fifty random oocytes of each female were measured under the microscope assisted by the

Table 2.1 – Summary of the number of samples and the associated name of the collected species, date, site and type of EUNIS habitat for the assessment of the biological traits of the two lugworm species at Wimereux (Wx), Le Touquet (LT), Fort Mahon (FM) and Ault (Au).*The species were identified with the second setiger annulation parrern (2 annulations for *Arenicola defodiens* and 3 for *A. marina*).** The EUNIS habitats were identified with the species composition and the grain size of the sediment (Rolet et al. (2014); this study).

Biological traits	Site	Species*	Number of individuals (n)	Type of EUNIS habitat **	Date
Population structure	Wx	*Arenicola marina*	186	A2.223	May and July 2017
Species distribution	Wx	*A. marina*	24	A2.223 + A2.23	March 2016
		A. defodiens	5	A2.223 + A2.23	
	LT	*A. marina*	4	A2.223 + A2.23	April 2016
		A. defodiens	1	A2.223 + A2.23	
	FM	*A. marina*	4	A2.223 + A2.23	April 2016
		A. defodiens	3	A2.223 + A2.23	
	Au	*A. marina*	1	A2.23	May and June 2016
		A. defodiens	11	A2.23	
Spawning period	Wx	*A. marina*	51	A2.223	Sept-Nov 2015
			86		Sept-Oct 2016
		A. defodiens	34	A2.23	Sept 2015-Janv 2016
			16		Oct-Dec 2016
	LT	*A. marina*	17	A2.223 + A2.23	Oct-Dec 2015
			8		Oct 2016
		A. defodiens	16	A2.23	Oct-Dec 2015
			12		Nov 2016
	FM	*A. marina*	5	A2.223 + A2.23	Sept-Nov 2015
			19		Oct 2016
		A. defodiens	17	A2.23	Sept-Nov 2015
			11		Nov 2016
	Au	*A. defodiens*	26	A2.23	$Oct_Nov2015$
Size at first maturity	Wx	*A. marina*	106	A2.223	Sept 2017

software Motic Image Plus 2.0. Reproductive structures of males (rosettes, morulae and spermatozoids) were analysed using the same method. To assess the size at first maturity, the occurrence of gametes was searched in coelomic fluids of 106 individuals of *A. marina*.

Data analysis

Spawning dates Spawning periods of both species were inferred by using both the oocyte diameter frequency distributions (Watson et al., 1998) and the presence of male gamete structures such as spermatozoids or morulae, only present in mature individuals (Dillon and Howie, 1997). Furthermore, observation of spontaneous spawning events in the laboratory was considered as additional evidence that lugworms were at a maturity stage and ready to release gametes. The estimated spawning periods were then compared

with environmental local data such as tidal coefficients and water temperature (data provided by "Service d'Observation en Milieu Littoral, INSU-CNRS, Wimereux", bottom coastal point: http://somlit.epoc.u-bordeaux1.fr/fr/).

Population and age structures of *Arenicola marina* In *Arenicola* spp., no permanent structures with year marks have been found (Beukema and De Vlas, 1979) and the population structure can only be approached through the analysis of the different size of cohorts, since spawning and recruitment only happen once a year and each cohort belongs therefore to a separate year. Only the population and age structures of *A. marina* at Wx were assessed through the analysis of size frequencies on the trunk length (TL) frequency distributions of 5-mm size class intervals, using a Bhattacharya analysis (N = 194) performed on the specific routine in FISAT II package (FAO, 2002b) according to Romano et al. (2013). To assess the goodness of the modal separation, separation indices (SI) were computed with values of SI > 2 being considered as successfully separated. Mean TLs, standard deviations and separation indices were calculated for each of the identified cohorts. Significant differences in TL of *A. marina* were assessed using a one-way analysis of variance (ANOVA) and a post-hoc Tukey test on R (R Core Team, 2017) (RStudio Team, 2016). Normality of residuals was assessed by the Shapiro test ($p > 0.05$), and homoscedasticity was tested by the Bartlett test ($p > 0.05$) on R (R Core Team, 2017).

First size and age at maturity of *Arenicola marina* The first size at maturity is the size at which more than 50% of the individuals are 'mature' (i.e. able to produce gametes, thus adult stage). Since reproductive organs are difficult to observe in *Arenicola* spp. (Cassier et al., 1997), the presence/absence of gametes in the coelomic fluid was checked at the end of the gametogenesis period (September). These observations allowed to estimate the number of individuals containing gametes (adults), and that without gametes (juveniles). The cumulated frequency of the proportion of 'mature' individuals per trunk length (TL) class was then calculated and the size at first maturity was considered the size at which the cumulated frequency equaled to 0.5 (or 50 %). The differences in TL between adult males and females of *A. marina* at Wx, and between adults and juveniles (at the same site) were assessed using a non-parametric Kruskal-Wallis (K-W) test as distributions were not normal (Shapiro test, $p < 0.05$, performed on R (R Core Team, 2017)).

2.2.4 Survey of bait collection within the MPA

On the whole MPA's foreshore, the number of recreational fishermen digging lugworms was assessed through on-site monitoring between one hour before and after the low tide at

least once a month. Given the high variability of the number of fishermen, four sites were chosen (Wx, LT, FM and Au) that represented the different intensities of digging effort met within the MPA. The number of worms collected per fisherman was assessed as in Xenarios et al. (2018), through field surveys, between 2014 and 2016. Given the high variability of the presence of diggers along the year (Xenarios et al., 2018), categories (in terms of numbers of fishermen) were established according to the weather conditions (temperature, pluviometry, photoperiod, maximum wind strength and atmospheric pressure), the tidal conditions (tidal coefficient, tidal range and low tide time), and the availability of fishermen (French and Belgium holidays, working days, week-ends, period of the year, morning or afternoon). The mean number of diggers per category and per site and the associated standard deviation were calculated, as well as the number of occurrences of each category in one year, which gave the number of diggers per site for this category in one year, as well as for the whole MPA. The total number of diggers for each site and for the whole MPA was then calculated summing the results of each category. The lugworms' extraction levels were calculated multiplying the total number of fishing sessions per site by the mean number of worms dug out by one fisherman in one fishing session. Finally, the retail value for the whole MPA and for each of the four studied sites was assessed from the numbers of dug lugworms and from the local retail prices taken from websites and from local retailers as in Watson et al. (2017a).

2.2.5 Linking abundance and spatial distribution to extraction levels of lugworms

At the four studied sites, the mean number of lugworms available for bait diggers was assessed from the mean densities of lugworms established in this study, the surface of the foreshore and the percentage of lugworms weighing more than 3 g (weight considered by Olive (1993) as the limit at which worms get valuable). Then, these data were compared to the estimated number of dug lugworms assessed by the survey.

2.3 Results

2.3.1 Species identification, spatial distribution and abundance

The 6 random individuals chosen for a molecular analysis based on the COI genes confirmed the morphological identification (barcoding) (Supplementary Material: Fig. 2.B, Table 2.A). A 14-15 % of nucleotide divergence was found between the COI genes of

Arenicola marina and *A. defodiens*. At Wx, a significant correlation was found between the proportion of each species and bathymetry (Spearman, $\rho = 0.9$, $p < 0.001$) and a relation could be established (Supplementary Material: Fig. 2.D). It appeared that *A. marina* was present above -1 m of bathymetry and *A. defodiens* below -2 m of bathymetry, with a small transition in between, where the two species could live in sympatry. On the other studied sites, no correlation was found between the proportion of each species and bathymetry or distance from the shoreline (LT: Spearman, $\rho = -0.09$, $p > 0.1$; FM: Spearman, $\rho = 0.25$, $p > 0.1$) (Supplementary Material: Fig. 2.E). At Wx, *A. defodiens* was found on the lower shore, on the A2.23 EUNIS habitat and *A. marina* was mainly present on the higher shore, on the A2.223 EUNIS habitat (Fig. 2.2; Supplementary Material: Table 2.F). At LT and FM, both species appeared to live in sympatry. Lugworms

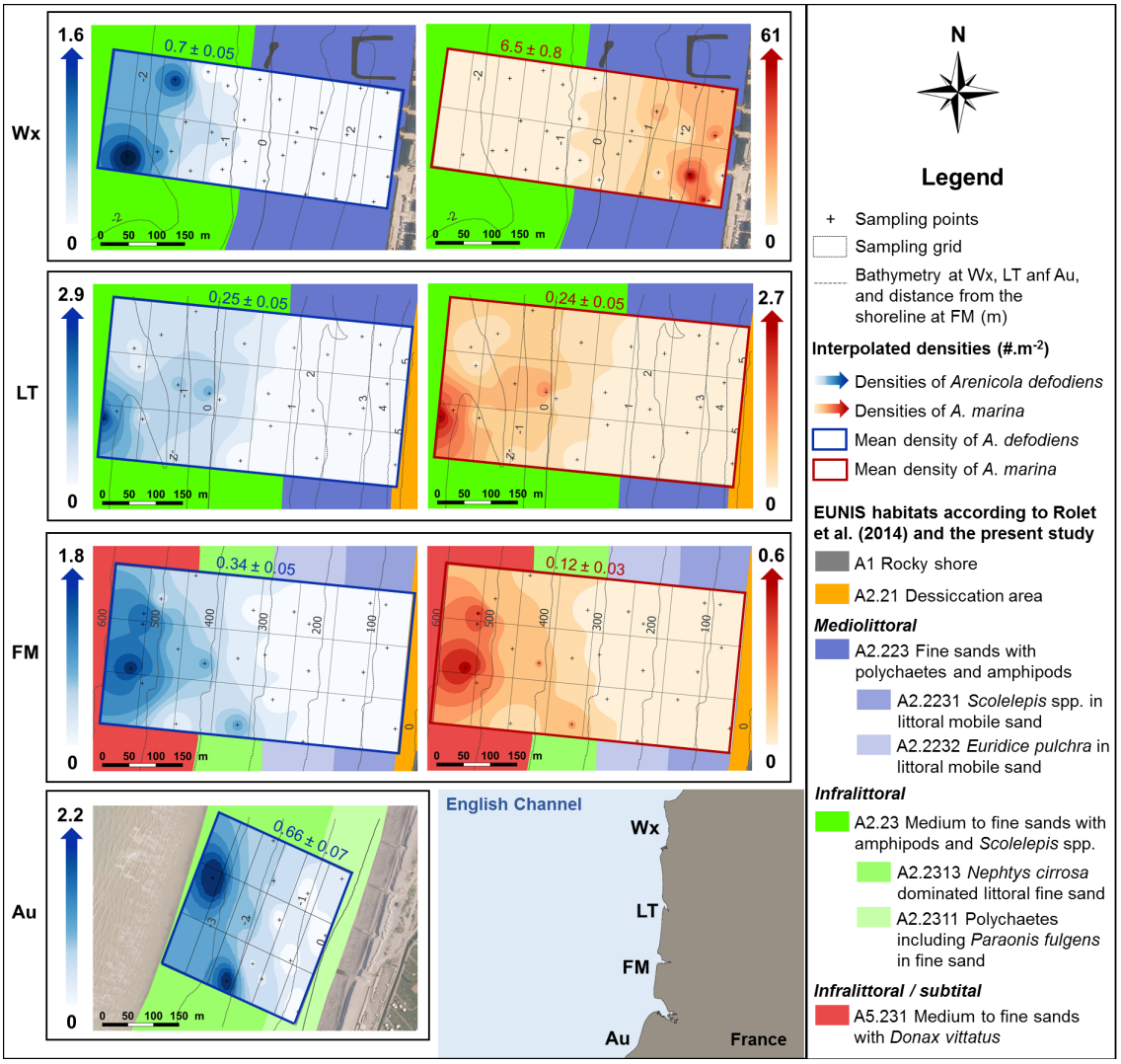

Figure 2.2 – Spatial distributions of the two species *Arenicola marina* and *A. defodiens* at the four studied sites: Wimereux (Wx), Le Touquet (LT), Fort Mahon (FM) and Ault (Au) (Eastern English Channel), and associated bathymetries (height above chart datum) or distance from the shoreline and EUNIS habitats.

at LT were present on the A2.23 EUNIS habitat and at FM, lugworms were found on the A5.231 EUNIS habitat (Fig. 2.2; Supplementary Material: Table F). At Au, *A. defodiens* was found on the lower shore, on the A2.23 EUNIS habitat (Fig. 2.2; Supplementary Material: Table 1.F), but no conclusions were made regarding the distribution of *A. marina* on this site since only a single individual was collected. The mean densities of *A. defodiens* did not appear to vary significantly between sites (between 0.25 ± 0.05 and 0.70 ± 0.05 individuals.m^{-2} at all sites) (CHI^2, $p = 0.96$) in comparison with *A. marina* (6.5 ± 0.8 individuals.m^{-2} at Wx, around 0.2 individuals. m^{-2} at LT and FM), where it varied significantly (CHI^2, $p < 0.01$) (Fig. 2.2).

2.3.2 Life history traits of lugworms

Spawning dates

For both species, the frequency distribution of the oocytes diameters evolved from a bimodal distribution for females carrying oocytes in oogenesis, with one peak of small oocytes (< 50 µm) and one peak of larger oocytes (> 100 µm), to a unimodal distribution with one single peak of large oocytes (∼ 150 µm for *Arenicola defodiens* and ∼ 180 µm for *A. marina*) for females where oocytes have completed vitellogenesis and are ready to be released (example at Wx for *A. defodiens* on Fig. 2.3, see further details in Supplementary Material: Figs. 2.G.1-4).

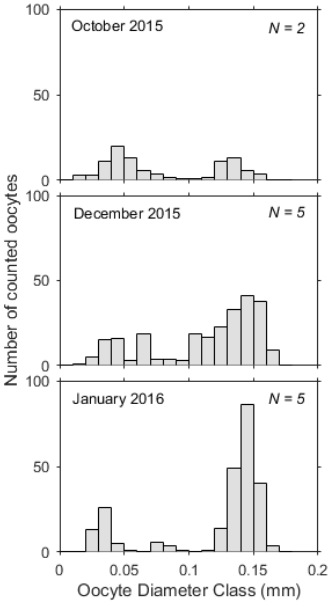

Figure 2.3 – Evolution of the oocyte diameter frequencies of *Arenicola defodiens* at Wimereux (Eastern English Channel) between October 2015 and January 2016, measured on 50 random oocytes of n individuals.

Spawning events of *A. marina* (Supplementary Material: Fig. 2.H) were assumed to take place at the beginning of autumn in 2015 and 2016 when water temperatures are ∼ 12 to 16 °C. We estimated that *A. marina* spawned between September (at Wx) and mid-November (at FM) in 2015, and, between September (at Wx) and October (at FM and LT) in 2016 (Supplementary Material: Figs. 2.G.1 and 2.G.2), possibly during spring tides. Spawning events of *A. defodiens* (Supplementary Material: Fig. 2.H) were assumed to take place at the end of autumn and at the beginning of winter in both 2015 and 2016 for water temperatures between ∼ 7 to 11 °C. We estimated that *A. defodiens* spawned between December (at Au, FM and LT) and January (at Wx) in 2015, and between November (at LT and FM) and December (at Wx) in 2016 (Supplementary Material: Figs. 2.G.3 and 2.G.4), possibly during spring tides. These periods of spawning were confirmed by the presence of spermatozoids within the coelomic fluid in males of both species (data not shown).

Population structure and age

At Wx, individuals of *Arenicola marina* ranged from 0.3 to 9 cm TL. The size-frequency distribution was multimodal (5 modes, SI > 2) (Table 2.2, Fig. 2.4A), suggesting the presence of 5 different age groups, the first one being the recruits' group (0.90 ± 0.37 cm TL). Since no recruits were spotted in April-May 2016 but some were observed in

Table 2.2 – Mean size and number of individuals and separation indices (SI) of every cohort found with the Bhattacharya analysis.

	Mean trunk length (cm)	Number of individuals	SI
Cohort 1	0.90 ± 0.37	27	-
Cohort 2	2.56 ± 0.60	36	3.42
Cohort 3	4.82 ± 0.55	76	3.93
Cohort 4	6.15 ± 0.56	41	2.40
Cohort 5	8.21 ± 0.46	14	4.04
Total sample	4.12 ± 1.93	194	-

July 2017, recruitment may happen at the end of spring and/or beginning of summer at Wx. TL means of the three groups of TL delimited by the high (2.3 m of bathymetry), medium (0.9 m of bathymetry) and low (0 m of bathymetry) levels on the shores were significantly different (ANOVA: $F(1,2) = 67.16$; $p < 0.001$; Post-hoc Tukey $p < 0.001$), which suggests that recruitment happens on the upper shore (Fig. 2.4B). Given the weight-size relationship found for *A. marina* at Wx (Fig. 2.4C), lugworms reached the weight of 3 g between 5 and 9 cm, which means not before reaching 3 years old. At Wx, 12.6 % of the sampled *A. marina* and 100 % of the sampled *A. defodiens* had a weight superior to 3 g. 100 % of the individuals of the two species were above 3 g at the other sites, except for

A. marina at Au, where the only individual collected weighted 2.5 g.

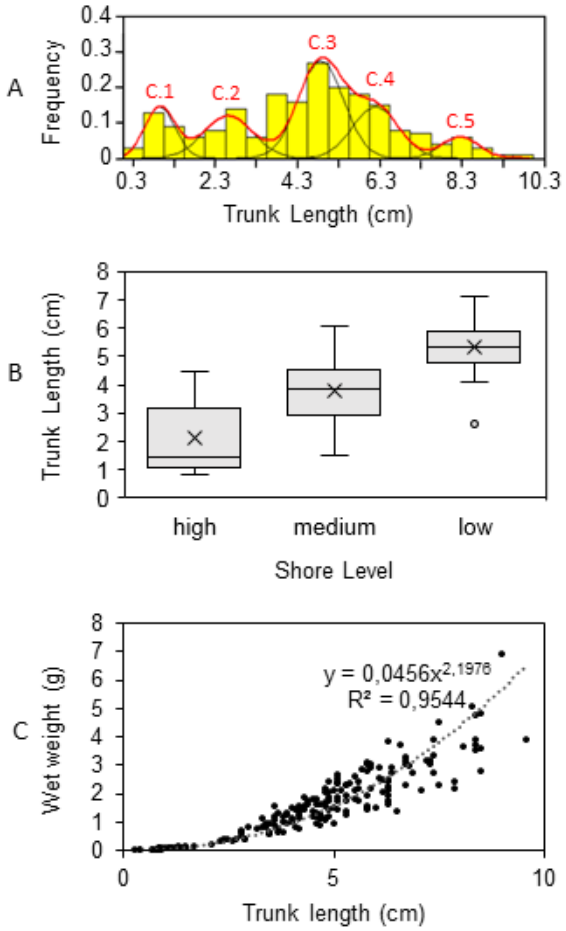

Figure 2.4 – Length-frequency distributions of the trunk lengths of all specimens of *Arenicola marina* obtained from Wimereux in summer 2017 analysed using FISAT II. Normal curves represent each detected cohort (C.1 to C.5) (A), spatial distribution of the different sizes along the shore level (low = 0.1 m of bathymetry, medium = 0.9 m of bathymetry and high = 2.3 m of bathymetry) (B) and associated length-weight relationship (C). Since recruitment happens once a year at the same period, each cohort represents an age group. Cohort C.1 comprises the newly recruits, born in autumn 2016, C.2 the 1.5 years old individuals, born in autumn 2015, etc.

First size at maturity of *A. marina*

Adult lugworms ranged from 2.5 to 6.3 cm (TL). The first size at maturity of *Arenicola marina* at Wx was assessed at 3.8 cm of TL (Fig. 2.5), which corresponds approximately to 1 g of wet weight (Fig. 2.4C). No significant difference was found between the lengths of males and females (K-W: 0.63, $p > 0.05$), then all the data were analysed together. A highly significant difference between the size of juveniles (2.29 ± 0.97 cm) and adults (3.92 ± 0.91 cm) was observed (K-W: 0.96, $p < 0.001$) (Fig. 2.5). According to the

population structure of *A. marina* from Wx, lugworms become adult between 1.5 and 2.5 years-old (Fig. 2.4A, Table 2.2).

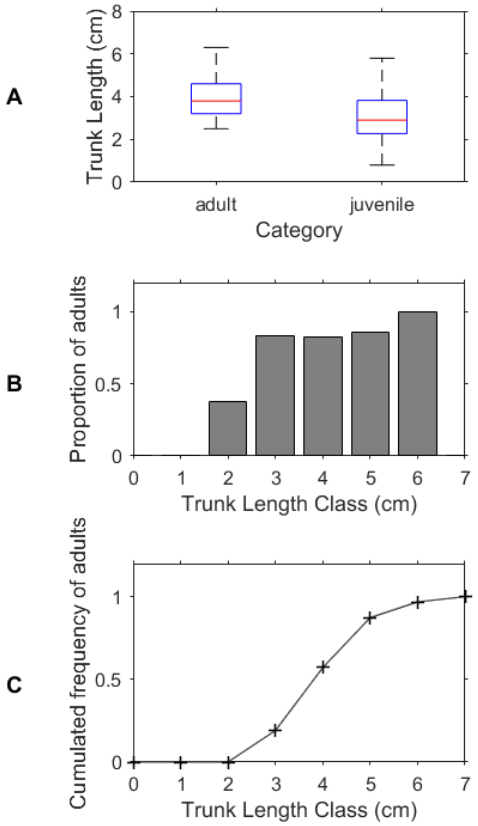

Figure 2.5 – Sizes in juveniles and adults of *Arenicola marina* at Wimereux (Eastern English Channel) (A), relative proportion of adults per size class (B) and its associated cumulated frequency (C).

2.3.3 Bait collection data and retail value

Most of the data presented here is available at https://estamp.afbiodiversite.fr/donnees. In total, 3 638 on-site observations were made within the MPA between 2014 and 2016. Among them, 88 were performed at Wx, 54 at LT, 60 at FM and 61 at Au. At these sites, 27 fishermen's baskets were randomly selected in order to estimate the number of dug lugworms (10 at Wx, 5 at LT and 12 at FM). The number of recreational diggers was highly variable along the MPA's foreshore. Au was the site where more lugworms' diggers were spotted on the whole MPA, with less than 4 000 diggers recorded in 2015. On the other studied sites, the number of recreational diggers ranged from $\sim$ 300 at FM, $\sim$ 700 at LT to $\sim$ 1 200 diggers at Wx (Table 2.3). The mean estimated catch per fishing session varied according to the studied site from $\sim$ 21 lugworms at FM to $\sim$ 40 lugworms

at Wx (Table 2.3). Since no value was available at Au, we used the mean value of the three other studies sites giving ∼ 31 lugworms per tide and per recreational fisherman (Table 2.3). The estimated number of dug lugworms at the studied sites ranged from ∼ 6 000 lugworms at FM to more than ∼ 110 000 *Arenicola* spp. at Au which led to a retail value varying between ∼ 3 000 € at FM to more than ∼ 49 000 € at Au in 2015 (Table 2.3). The total retail value of recreational arenicolid fisheries within the MPA (232 447 €) appeared to be about the equivalent to the retail value of the recreational shrimp *Crangon crangon* fisheries (215 714 to 414 727 €), and only 4 to 5 times less important than the one of the recreational mussel *Mytilus edulis* fisheries (1 203 449 €) (Table 2.3).

2.3.4 Linking lugworms' life-history traits to bait collection data

At the four studied sites, the number of lugworms above 3 g (e.g. considered as valuable by fishermen (Olive, 1993) ranged between ∼ 700 000 *Arenicola* spp. at FM to ∼ 1 300 000 *Arenicola* spp. at Wx (Table 2.3, Fig. 2.6). In 2015, the number of lugworms

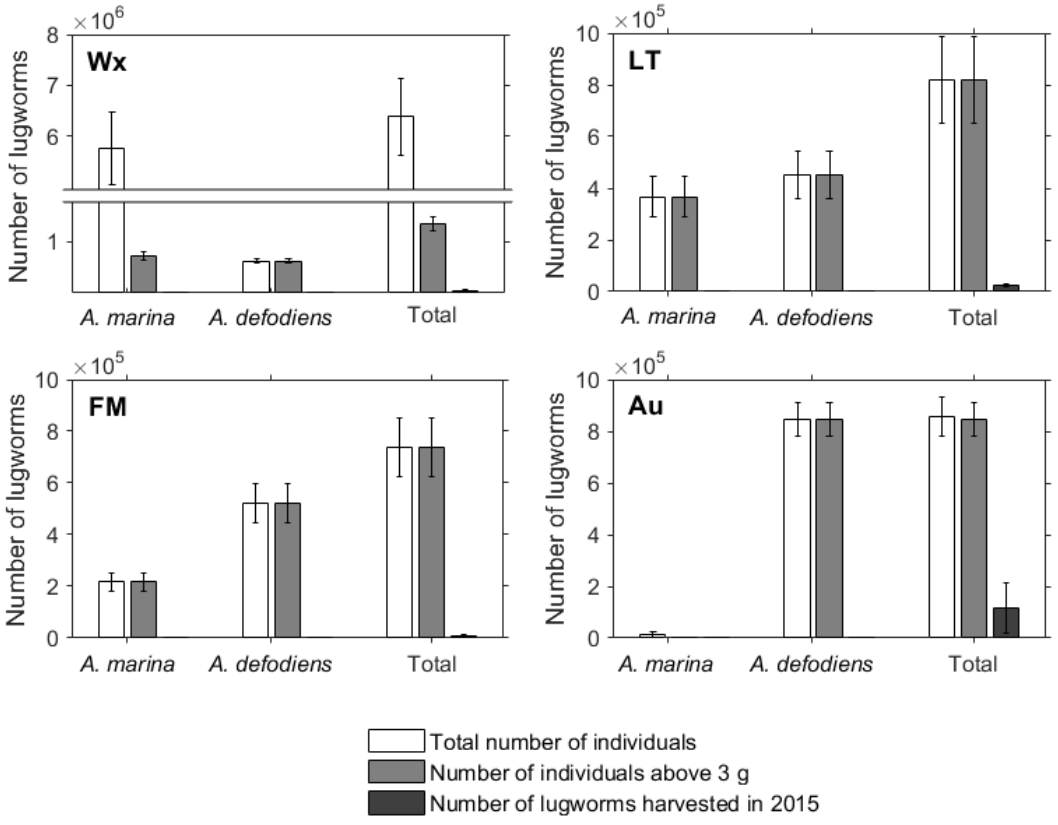

Figure 2.6 – Comparison of the total number of individuals, number of individuals above 3 g and number of lugworms harvested in 2015 by recreational fishermen respectively for *Arenicola marina* , *A. defodiens*, and both species combined at Wimereux (Wx), Le Touquet (LT), Fort Mahon (FM) and Ault (Au).

Table 2.3 – Extrapolated number of dug worms (per site and on the whole MPA) and its associated retail value, and comparison with the two other major recreational fisheries of the area (Eastern English Channel): *Mytilus edulis* and *Crangon crangon*, with Wx for Wimereux, LT for Le Touquet, FM for Fort Mahon, and Au for Ault.

	Sites / Species	Extraction area (km^2)	Estimated number of fishing session / year	Mean estimated catch / fishing session	Estimated removed number	Estimated removed wet weight (kg)	Retail price	Total retail value (euros)	References
Studied sites (*Arenicola* spp.)	Wx	0.9	1246 ± 40	39.8 ± 32.1	49590 ± 19755	198 to 744	4.19 euros / 10 worms	20778 ± 8277	https//www.decathlon.fr
	LT	1.5	692 ± 39	34.0 ± 15.2	23528 ± 5626	353 to 541		9858 ± 2357	https://estamp.afbiodiversite.fr
	FM	1.8	311 ± 32	21.3 ± 20.5	6624 ± 6702	86 to 179		2775 ± 2808	
	Au	1.8	3862 ± 173	30.5 ± 25.4	117791 ± 98203	1.885		49354 ± 41147	
Whole MPA	*Arenicola* spp.	-	18189 ± 2131	30.5 ± 25.4 worms	554765 ± 250323 worms	9875 ± 4456	4.19 euros /10 worms	232447 ± 105885	https//www.decathlon.fr
	Mytilus edulis	-	74287 ± 3054	3.6 ± 0.2 kg	-	267433 ± 12280	around 4.5 euros / kg	1203449 ± 55260	Local fishermen and http://www.manger-la-mer.org
	Crangon crangon	-	12652 ± 1440	1.1 kg	-	13917 ± 1584	15.5 to 29.8 euros / kg	215714 ± 24552 to 414727 ± 47203	Local fish retailers and FranceAgriMer (2017)

dug by recreational fishermen represented respectively 3.6 % of the number of lugworms (both species combined) greater than 3 g at Wx, 2.9 % at LT, 0.9 % at FM, and 13.9 % at Au, and respectively 0.8 % of the total number of lugworms (both species combined) at Wx, 2.9 % at LT, 0.9 % at FM, and 13.7 % at Au (Fig. 2.6). At Au only, the number of dug lugworms for the year 2015 (117 791 lugworms) was greater than the estimated abundance of *A. marina* (12 810 lugworms in total, all weights considered), only considering recreational fisheries (Fig. 2.6).

2.4 Discussion

2.4.1 Species identification, abundances and spatial distribution

Our results confirmed the occurrence of both *Arenicola marina* and *A. defodiens* on the French coast of the Eastern English Channel, only mentioned by Müller (2004) while other authors only reported *A. marina* in ecological studies (e.g. Rolet et al., 2014) and may have been confusing the two species, especially in sites where they live in sympatry on the same level of the shore (on the lower shore). However, since *A. defodiens* burrows deeper into the sand, it is therefore harder to collect and previous studies may have failed in collecting this latter species, for which only bait pumps proved to be efficient. Until now, *A. defodiens* has only been described in the UK, the Netherlands and Portugal (Atlantic Ocean). In this study, we have shown the evidence of the occurrence of *A. defodiens* on the French coast of the Eastern English Channel, suggesting that this species is widely distributed on the whole French coast of both the English Channel and the Atlantic Ocean.

The maximum abundance of *Arenicola marina* found in this study at Wx (61 individuals.m^{-2}) was comparable to those found in other studies in the Wadden Sea and Portugal ($\sim$ 40 to 70 individuals.m^{-2} max) (Beukema and De Vlas, 1979; Flach and Beukema, 1994; Pires et al., 2015) but did not reach the highest abundance recorded by Farke et al. (1979) (more than 150 individuals.m^{-2}). In comparison, the values found at LT and FM for this species (2.7 and 0.6 individuals.m^{-2} max respectively) appeared relatively low. This discrepancy may be linked to physical disturbances within the higher shore at these two sites caused by mechanical engines that remove debris deposited by the tide. Beukema (1995) showed that repeated mechanical harvest of lugworms using digging machines similar to what is present at LT and FM, could decrease the overall densities of worms. In these two sites no recruits were observed during the spring period and only few individuals were collected on the higher shore during the autumn. Some individuals of *A. marina* may have migrated on the lower shore, on the EUNIS habitat A2.23 (medium to fine sands with amphipods and *Scolelepis* sp.) or even on the EUNIS habitat A5.231 (medium to fine sands with

Donax vittatus), as lugworms may do during cold winters (Wolff and de Wolf, 1977). The trade-off made by sharing the same ecological niche with *A. defodiens* on the lower shore at FM and LT involves interspecific competition for food and habitat, higher predation rate by birds and flatfish. This would make the survival rate of *A. marina* lower, and consequently decrease its abundance in comparison with sites where *A. marina* could live not in sympatry with *A. defodiens* such as at Wx. For *A. defodiens*, the maximum abundance at all sites ranged from 1.6 to 2.9 individuals.m^{-2}. This is higher to what Pires et al. (2015) found in Portugal (between 0.25 and 1 individual.m^{-2}). The similar abundance of *A. defodiens* observed at all sites might be linked to the presence of a subtidal population of this species: when, for some reason, densities of population from the foreshore decrease, the subtidal individuals could colonize the empty spaces and reload the intertidal *A. defodiens* population. Indeed, the subtidal presence of *A. defodiens* was recorded in Portugal by Pires et al. (2015) and in France on the Eastern English Channel by the present authors (unpublished data). However, the density estimation for *A. defodiens* was made from data of cast production obtained for *A. marina*, and further investigation on the cast production of *A. defodiens* is needed to conclude more accurately on the abundance of this species.

2.4.2 Life-history traits of lugworms

The spawning period of *Arenicola marina* appeared to occur at the beginning of autumn and at the end of autumn to beginning of winter (at Wx) for *A. defodiens* . There was a time lag of two weeks to two months between the two species' spawning periods, as previously described by several authors (Dillon and Howie, 1997; Watson et al., 1998, 2000), probably to avoid species hybridization which was shown to be possible by *in vitro* fertilization (Watson et al., 2008). For both species, spawning periods vary according to the year. Environmental parameters such as tidal amplitude cycles, temperature (temperature at the beginning of the gametogenesis and temperature just prior to spawning) as well as weather conditions have shown to influence spawning periods in *A. marina* (Watson et al., 2008, 2000). The combination of these environmental parameters may explain the variation of spawning periods between years. In fact, spawning periods recorded in this study for both species are likely to have occurred during spring tides (Supplementary Material: Fig. 2.H), but not at the same water temperature. There was ~ 4°C difference between the minimum and the maximum of water temperature during the spawning period of the different sites for a respective species which might suggest that spring tides may play a role in the triggering of spawning events rather than water temperature. Watson et al. (2000) suggested for a Scottish population of *A. marina* that others spawning cues may be taken into account such as air temperature, air pressure, daily rainfall and/or wind speed, etc.

The size at first maturity found for *Arenicola marina* at Wx (3.8 cm) corresponds to an individual of approximately 1 g, which is close to the weight at which individuals of *A. marina* started developing gametes in the laboratory experiment performed by De Wilde and Berghuis (1979). Recruits of *A. marina* were only spotted at Wx and recruitment happened between the end of spring and the beginning of summer, which mirrored recruitment period recorded by Flach and Beukema (1994). No recruits of *A. marina* were detected on the other sites. Since sampling for spatial distribution pattern was performed at the beginning of spring at LT and FM, we might have come too early to detect recruitment of the first cohort of *A. marina* on these sites and further investigation will be needed since some small individuals were then detected on the upper shore in autumn 2016 at both sites. However, another possible explanation to the uneven distribution and abundance of *A. marina* recorded at the different sites might be explained by a particularly low survival rate of the recruits at LT, FM, and Au compared to Wx, due to physical disturbance as mentioned earlier. Another hypothesis is linked to the lifecycle of *A. marina* that involves a post-larval nursery grounds composed of sheltered soft sediments, macro-algae and/or mussel beds (Farke and Berghuis, 1979b; Reise, 1985). These transitory colonization habitats might have been degraded by anthropogenic disturbance at Au (Paute, 2015) or naturally absent close to LT and FM (as suggested by the subtidal macrobenthic community map for the area designed by Croguennec et al. (2011)), enhancing a post-larval mortality and subsequently a low recruitment of juveniles on the beach after the second larval dispersal phase. The low recruitment of *A. marina* at LT, FM and Au might also be linked again to the two phases of dispersal during its lifecycle, where, under certain weather conditions, a strong current may be directed up North (Bailly Du Bois et al., 2002; Ellien et al., 2000; Nicolle et al., 2017) during the second dispersal phase prior to the settlement of juveniles on the higher shore, favoring recruitment to North sites such as Wx (which could be considered as a sink of propagules) compared to the three others sites that are more south on the MPA (which could rather be considered as sources of propagules). Further studies on larval dispersal using a modeling approach based on biophysical model or population genetics should be applied to support this hypothesis.

2.4.3 Linking life-history traits, abundance and spatial distribution to bait collection data: management stakes and fishery

At Wx, LT and FM, according to the survey carried out in 2015 on recreational fishermen, extraction levels of lugworms appeared quite low compared to the lugworm abundances calculated in this study (less than 5 % of the population harvested). Moreover, the presence of numerous young individuals of *A. marina* at Wx seems to ensure a rapid renewal of the part of the population allocated to bait digging. However, 104 professional licenses

have been delivered to some fishermen specialized in lugworm digging within the MPA and some of them are able to extract more than 400 worms per tide (anonymous fisherman communication). The lugworm extraction may have been underestimated in this study as the survey was done only on recreational fishermen. Besides, the proportion of the lugworm population dug at Au was already quite high (13.7 % of the total number of individuals and 13.9 % of the individuals heavier than 3 g). If we consider that the maximum age of *Arenicola defodiens* is close to the one of *A. marina*, which is around 5 to 6 years old, it means that every year, around one sixth to one fifth (e.g. 17 % to 20 %) of the population is renewed (Beukema and De Vlas, 1979). In this case, maybe the managers of the MPA should consider following up the population's density of this species to make sure that its abundance does not decrease over time. If so, some preventive management measures should be implemented such as forbidding or restricting the bait collection during the spawning periods and giving a minimum size limit of worm collection. Again, the numbers of *A. marina* were really low at Au compared to the total number of dug individuals, and actions should be taken to follow up and manage this species in order to allow its recovery. The species was found to be able to produce gametes (adult) between the cohort 2 and 3 (1.5 to 2.5 years old and approximately 1 g) and managers should encourage local fishermen to harvest only lugworms from cohorts 4 or 5 (i.e. worms that spawned at least once, older than 3 years old), where worms are larger to 6.15 cm long (TL) and getting close to 3 g (Fig. 2.3C). Although, further study of the dynamics of population of this studied site is needed to determine the best "size limit" management strategy (Gwinn et al., 2015), especially since the weight/size/age relationships of *A. marina* were only studied at Wx, where the growth of the individuals of this species might be different from the one of the individuals of the same species at Au. However, as mentioned before, Au might not be a sink of larvae of *A. marina*. A second hypothesis is due to the natural mussels' beds of this site that is not in a good status and may lead to a mortality of the first settlers during their life cycle (Reise, 1985; Paute, 2015). These last considerations enlighten the need for an integrated management of the different activities, species and habitats in the area.

The total retail value of recreational fisheries for *Arenicola* spp. within the MPA appeared to be about equivalent to the one of the shrimp *Crangon crangon*, and only 4 to 5 times less important than the one of the mussel *Mytilus edulis* (in terms of recreational fisheries). These last two species benefit within the MPA from a number of catch restrictions (length and bags limits, closing fishing areas, restrictions on catch engines, etc.) (Direction interrégionale de la mer Manche Est-mer du Nord, 2015), when no restriction exists for *Arenicola* spp. recreational fisheries within the MPA. In order to give restrictions, distinguishing the two species of lugworms will be necessary, and especially, when sympatry of the two species occurs. Pires et al. (2015) suggested that there could be a difference

in the shape of the faecal casts, where the faecal casts of *A. defodiens* are more spiral-like than those of *A. marina*. These features could be taught to anglers when fishing for one of the two species must be limited. If size limit of the bait will be needed, size of the cast diameter of the lugworms may be used as an indicator, as this has been well correlated with the size of the worm itself such as in *A. marina* (Olive, 1993; unpublished data). Again, this information could be communicated to fishermen through education (Watson et al., 2015).

To conclude, the management of the lugworm populations within the MPA and some fishery regulation appear crucial given their ecological and economical importance with some populations (e.g. Au) that may be threatened by human activities.

Acknowledgements

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Supplementary Material

Table 2.A COI gene sequences used in the phylogenetic analyses in this study (in bold) and in the literature. For each haplotype, the species, acronym, GenBank accession number, and location (with GPS coordinates when available) are given.

Species	Acronym	Genbank access number	Location	Latitude	Longitude	Literature
Arenicola marina	AmAv1P	KM042097	Ria de Aveiro, Portugal	40° 36' 49" N	8° 44' 28" W	Pires et al., 2015
A. marina	AmAv2P	KM042098	Ria de Aveiro, Portugal	40° 36' 13" N	8° 44' 10" W	Pires et al., 2015
A. marina	AmR1F	JQ950326	Roscoff, France	48° 43' 40" N	3° 59' 16" W	Pires et al., 2015
A. marina	AmR2F	JQ950327	Roscoff, France	48° 43' 40" N	3° 59' 16" W	Pires et al., 2015
A. marina	AmAr1F	HQ023444	Arcachon, France	44° 39' 51" N	1° 09' 38" W	Carr et al., 2011
A. marina	AmAr2F	HQ023443	Arcachon, France	44° 39' 51" N	1° 09' 38" W	Carr et al., 2011
A. marina	AmAr3F	HQ023441	Arcachon, France	44° 39' 51" N	1° 09' 38" W	Carr et al., 2011
A. marina	AmK1R	GU672432	Kandalaksha Bay, Russia	66° 33' 07" N	33° 6' 43" E	Hardy et al., 2011
A. marina	AmK2R	GU670812	Kandalaksha Bay, Russia	66° 33' 07" N	33° 6' 43" E	Hardy et al., 2011
A. marina	Amh01NL	GQ487319	Netherlands	-	-	Luttikhuizen and Dekker, 2010
A. marina	Amh02NL	GQ487320	Netherlands	-	-	Luttikhuizen and Dekker, 2010
A. marina	Amh03NL	GQ487321	Netherlands	-	-	Luttikhuizen and Dekker, 2010
A. marina	**AmF2F**	**MF405759**	**Fort-Mahon, France**	**50° 20' 25" N**	**1° 32' 35" E**	**This study**
A. marina	**AmF4F**	**MF405760**	**Fort-Mahon, France**	**50° 20' 25" N**	**1° 32' 35" E**	**This study**
A. marina	**AmLT1F**	**MF405761**	**Le Touquet, France**	**50° 31' 13" N**	**1° 34' 17" E**	**This study**
A. defodiens	AdAv1P	KM042099	Ria de Aveiro, Portugal	40° 40' 37" N	8° 40' 35" W	Pires et al., 2015
A. defodiens	AdAv2P	KM042100	Ria de Aveiro, Portugal	40° 42' 43" N	8° 40' 39" W	Pires et al., 2015
A. defodiens	AdAv3P	JQ950325	Ria de Aveiro, Portugal	40° 41' 20" N	8° 42' 54" W	Pires et al., 2015
A. defodiens	Adh01NL	GQ487323	Netherlands	-	-	Luttikhuizen and Dekker, 2010
A. defodiens	Adh02NL	GQ487325	Netherlands	-	-	Luttikhuizen and Dekker, 2010
A. defodiens	Adh03NL	GQ487324	Netherlands	-	-	Luttikhuizen and Dekker, 2010
A. defodiens	Adh04NL	GQ487322	Netherlands	-	-	Luttikhuizen and Dekker, 2010
A. defodiens	**AdAO1F**	**MF405762**	**Ault-Onival, France**	**50° 06' 45" N**	**1° 27' 10" E**	**This study**
A. defodiens	**AdF1F**	**MF405763**	**Fort-Mahon, France**	**50° 20' 25" N**	**1° 32' 35" E**	**This study**
A. defodiens	**AdF2F**	**MF405764**	**Fort-Mahon, France**	**50° 20' 25" N**	**1° 32' 35" E**	**This study**

Fig. 2.B Maximum Likelihood tree of COI sequences of arenicolid species with bootstrapping values. The specimens sequenced in this study are highlighted and acronyms are described in Table 1.A

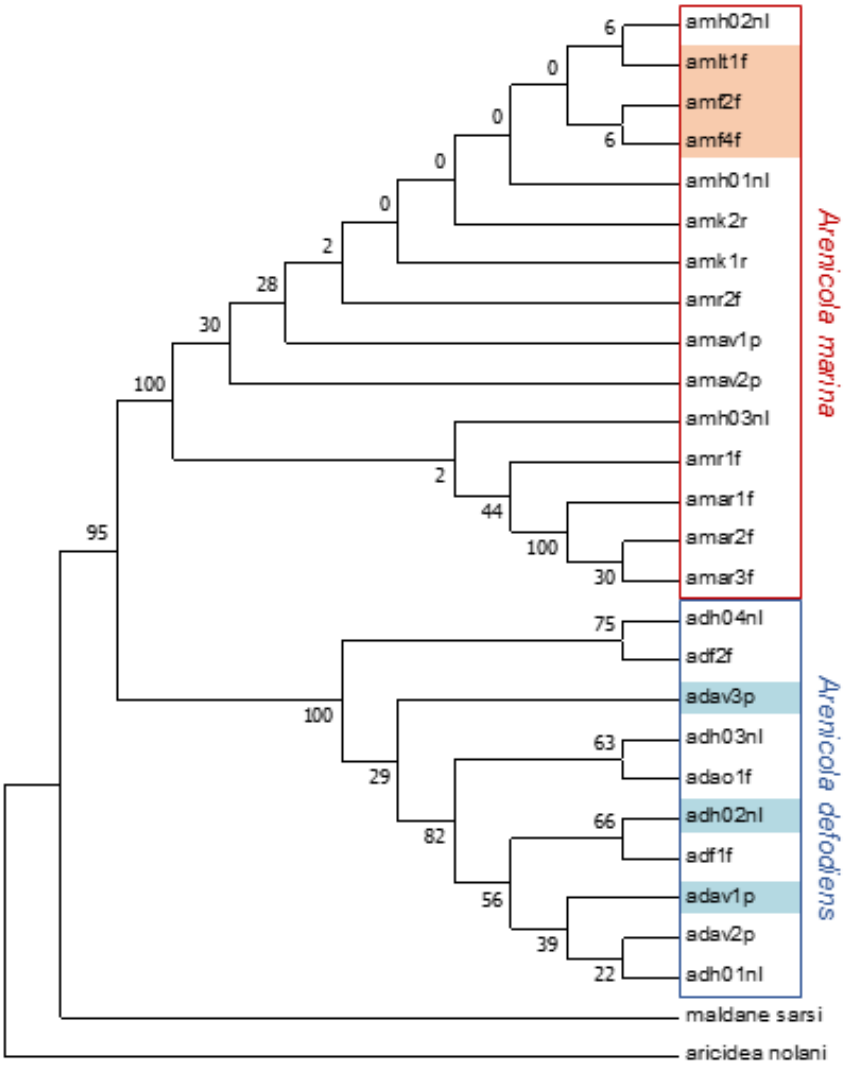


Fig. 2.C Linear relation between the number of faecal casts produced and the number of individuals of *Arenicola marina* .

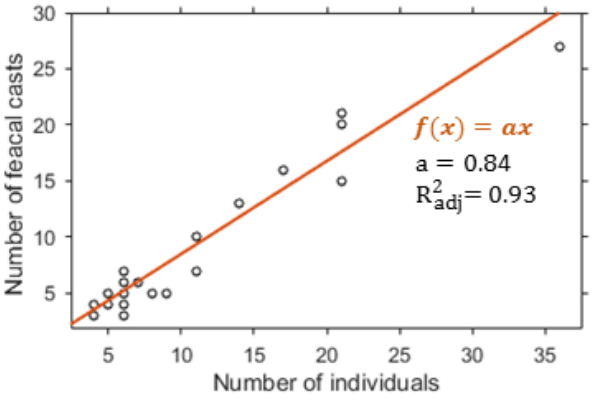


Fig. 2.D Proportion of *Arenicola marina* (red dots) and *A. defodiens* (blue dots) according to bathymetry at Wimereux (Eastern English Channel) and the associated fitting transition curves and functions, as well as the number of lugworms collected at each point to calculate the proportion (weight of the different proportion points).

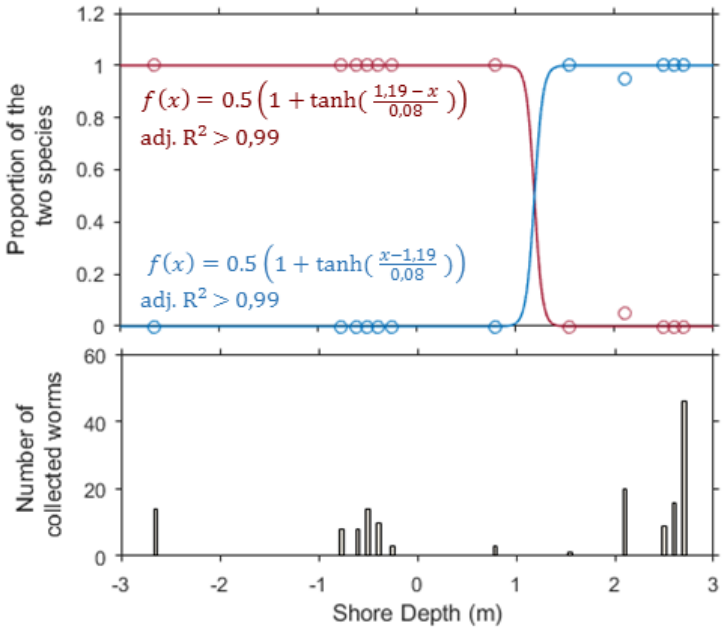


Fig. 2.E Proportion of *Arenicola marina* (red dots) and *A. defodiens* (blue dots) according to bathymetry or distance from the shoreline and the related number of individuals used to calculate the proportion at Le Touquet (LT) and Fort Mahon (FM).

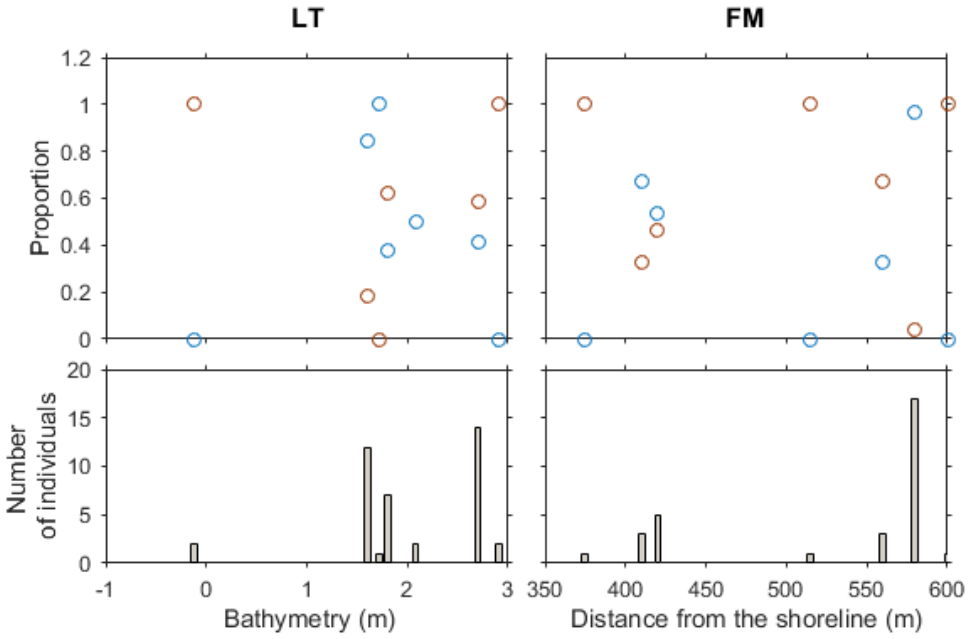


Table 2.F EUNIS habitats found at Fort Mahon and Ault based on particle size analysis and species identification at these sites.

Site	GPS location	Species abundancy (%)		Particle size analysis (%)		Corresponding EUNIS habitat
Fort Mahon (FM)	01°32'31.68" E 50°20'24.89" N	*Donax vittatus*	73	mudstones	0	A5.231 Medium to fine sands with *Donax vittatus*
		Urothoe poseidonis	10	fine sands	70.7	
		Nephtys cirrosa	8	medium sands	23.6	
		Spio martinensis	5	coarse sands	1.9	
		Urothoe brevicornis	5	fine gravels	1.8	
		Notrotopis falcatus	4	coarse gravels	2.1	
		Lanice conchilega	4			
		Eurydice pulchra	3			
		Vaunthompsonia cristata	2			
		Gastrosaccus spinifer	1			
		Spio sp.	1			
		Nephtys hombergii	1			
		Eteone picta	1			
Fort Mahon (FM)	01°32'39.03" E 50°20'24.36" N	*Nephtys cirrosa*	57	mudstones	0	A2.2313 *Nephtys cirrosa* dominated littoral fine sands
		Eurydice pulchra	21	fine sands	53.1	
		Portumnus latipes	14	medium sands	43.6	
		Nephtys hombergii	7	coarse sands	1.8	
				fine gravels	1	
				coarse gravels	0.5	
Fort Mahon (FM)	01°32'54.07" E 50°20'23.32" N	*Eurydice pulchra*	60	mudstones	0	A2.2232 *Eurydice pulchra* in littoral mobile sand
		Scolelepis squamata	39	fine sands	34.2	
		Haustorius arenarius	0.3	medium sands	63.5	
		Urothoe poseidonis	0.3	coarse sands	1.6	
		Bathyporeia pilosa	0.3	fine gravels	0.5	
		Nemertean	0.3	coarse gravels	0.2	
Fort Mahon (FM)	01°32'54.07" E 50°20'22.79" N	*Scolelepis squamata*	81	mudstones	0	A2.2231 *Scolelepis* spp. in littoral mobile sand
		Bathyporeia pilosa	13	fine sands	35.4	
		Carcinus maenas	2	medium sands	62.1	
		Ophelia rathkei	2	coarse sands	1.4	
		Haustorius arenarius	2	fine gravels	0.3	
				coarse gravels	0.7	
Ault (Au)	01°27'09.49" E 50°06'43.13" N and 01°27'04.04" E 50°06'44.05" N	*Nephtys cirrosa*	50	mudstones	0.1	A2.2313 *Nephtys cirrosa* ominated littoral fine sands
		Bathyporeia pelagica	19	fine sands	58.0	
		Portumnus latipes	6	medium sands	38.3	
		Haustorius arenarius	6	coarse sands	1.9	
		Nephtys hombergii	6	fine gravels	0.9	
		Lanice conchilega	6	coarse gravels	0.9	
		Oligochate	6			
Ault (Au)	01°27'15.07'' E 50°06'42.31" N	*Paraonis fulgens*	31	mudstones	0.1	A2.2311 Polychaetes including *Paraonis fulgens* in littoral fine sand
		Gastrosaccus spinifer	19	fine sands	30.8	
		Eurydice pulchra	19	medium sands	66.3	
		Nephtys hombergii	13	coarse sands	0.8	
		Bathyporeia pelagica	13	fine gravels	0.4	
		Bathyporeia pilosa	6	coarse gravels	1.6	

Fig. 2.G.1 Oocyte diameter distributions of the collected females of *Arenicola marina* (N is the number of females) at Fort Mahon and Le Touquet in autumn 2015. When boxes appear darker, the sites were not sampled at the corresponding date.

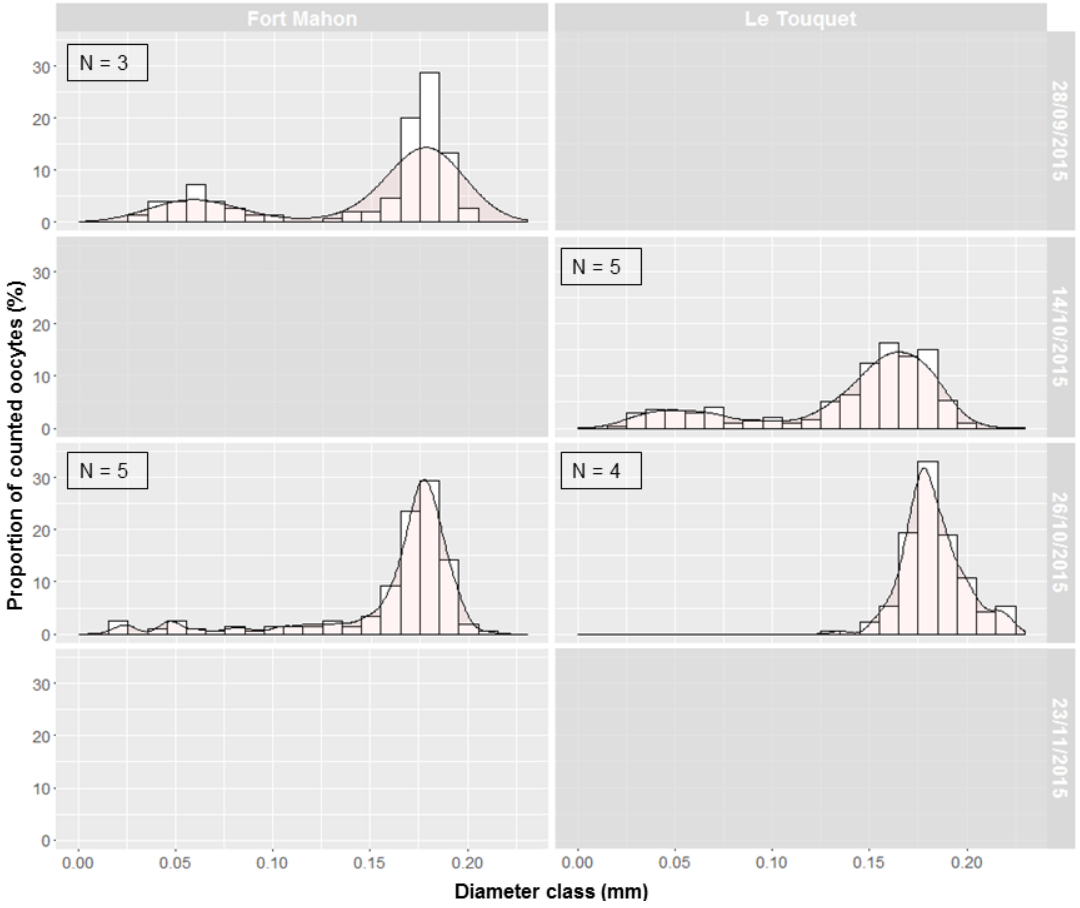


Fig. 1.G.2 Oocyte diameter distributions of the collected females (N is the number of females) of *Arenicola marina* at Fort Mahon, Le Touquet and Wimereux in autumn 2016. When boxes appear, darker the sites were not sampled at the corresponding date.

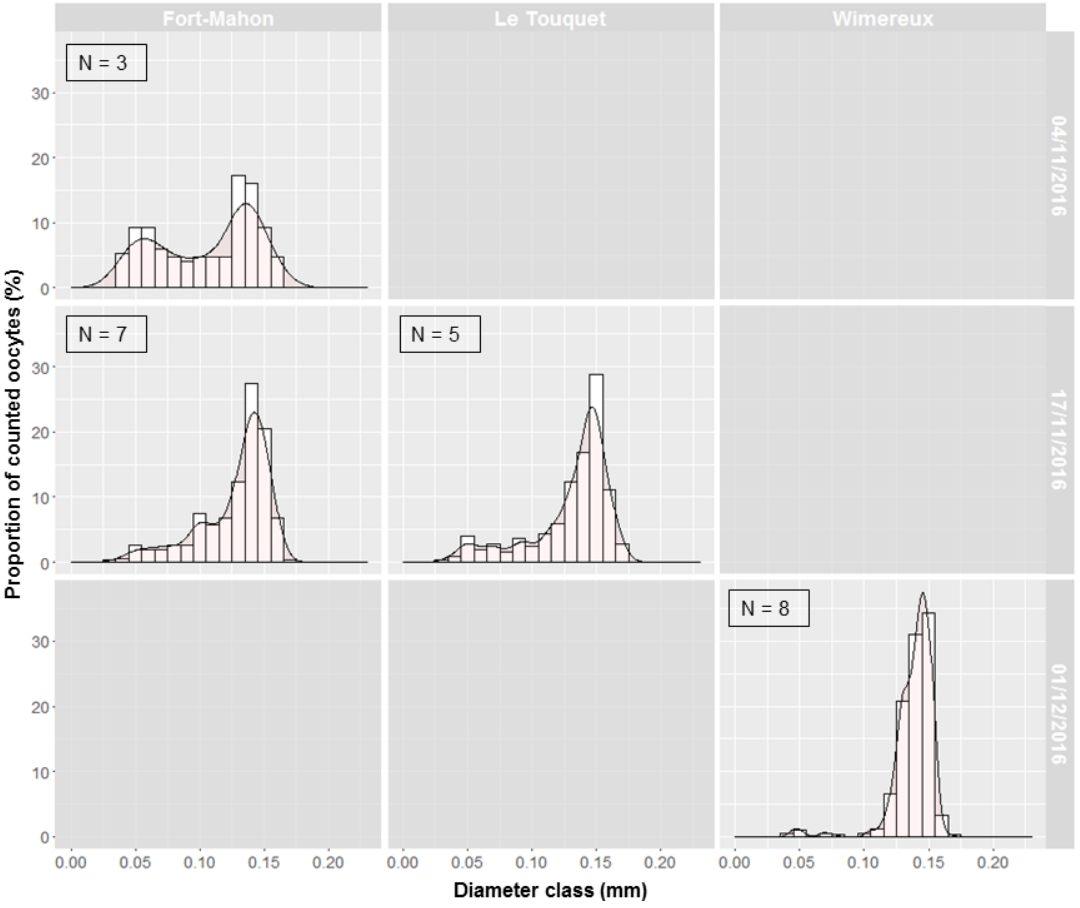


Fig. 2.G.3 Oocyte diameter distributions of the collected females (N is the number of females) of *Arenicola defodiens* at all sites in autumn and winter 2015/2016. When boxes appear darker, the sites were not sampled at the corresponding date.

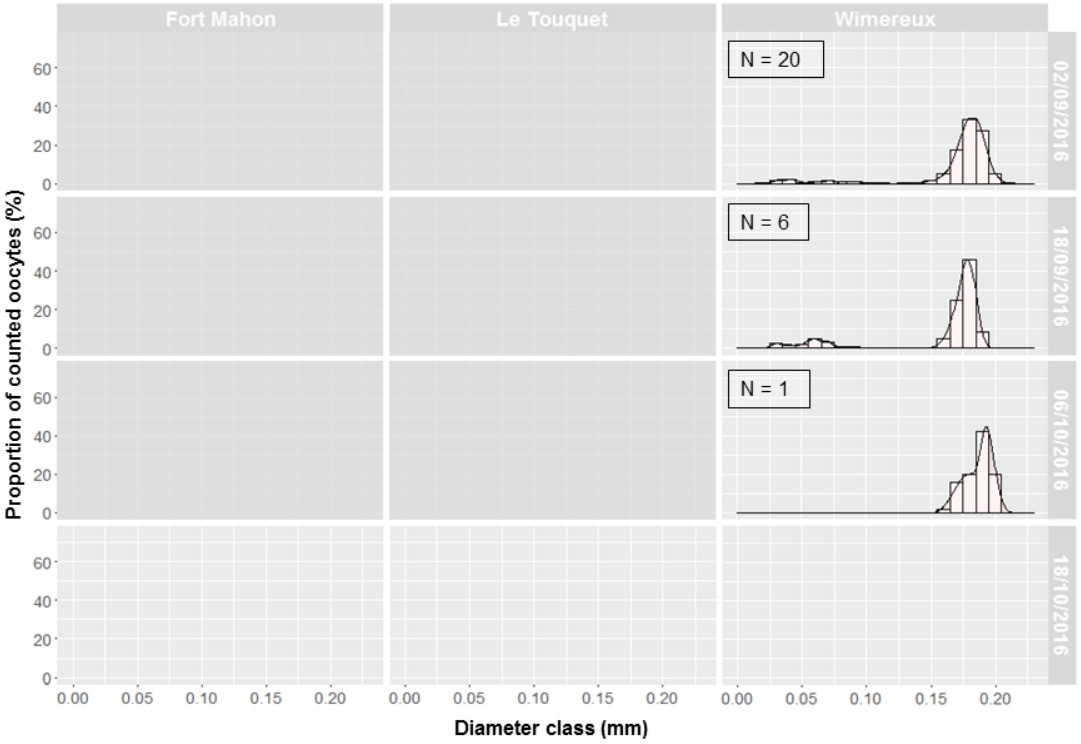


Fig. 2.G.4 Oocyte diameter distributions of the collected females (N is the number of females) of *Arenicola defodiens* at Wimereux, Le Touquet and Fort Mahon in autumn and winter 2016/2017. When boxes appear darker, the sites were not sampled at the corresponding date.

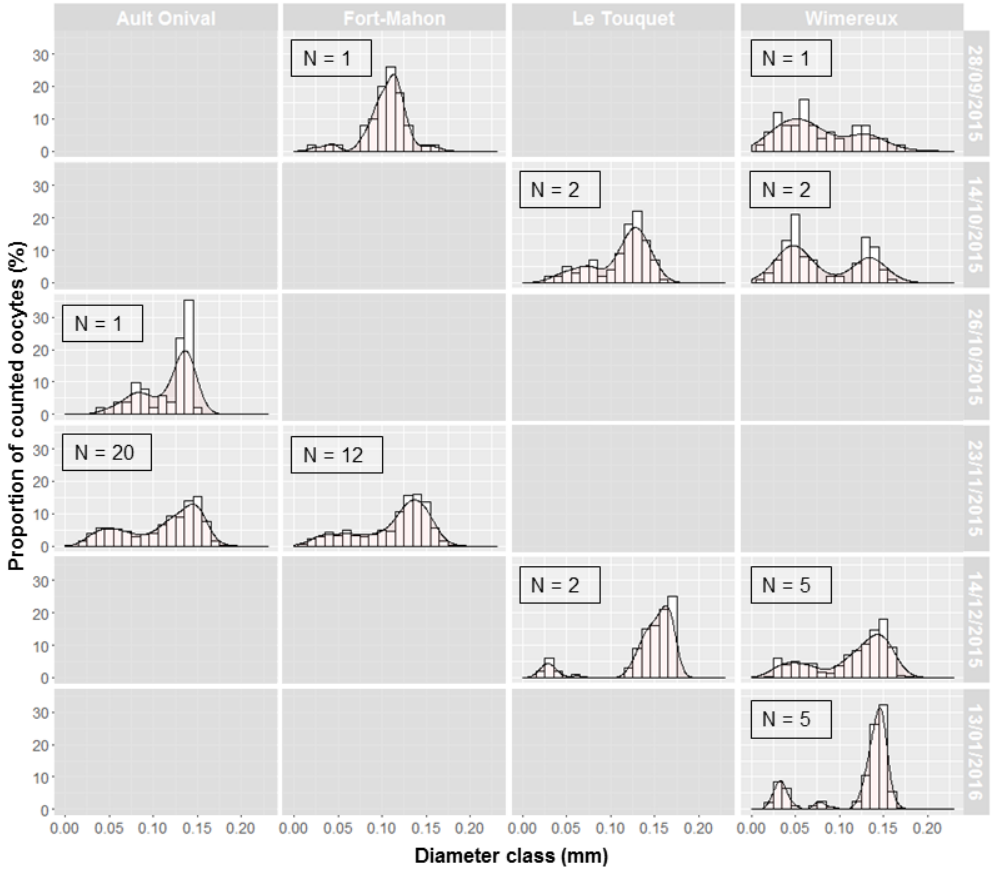
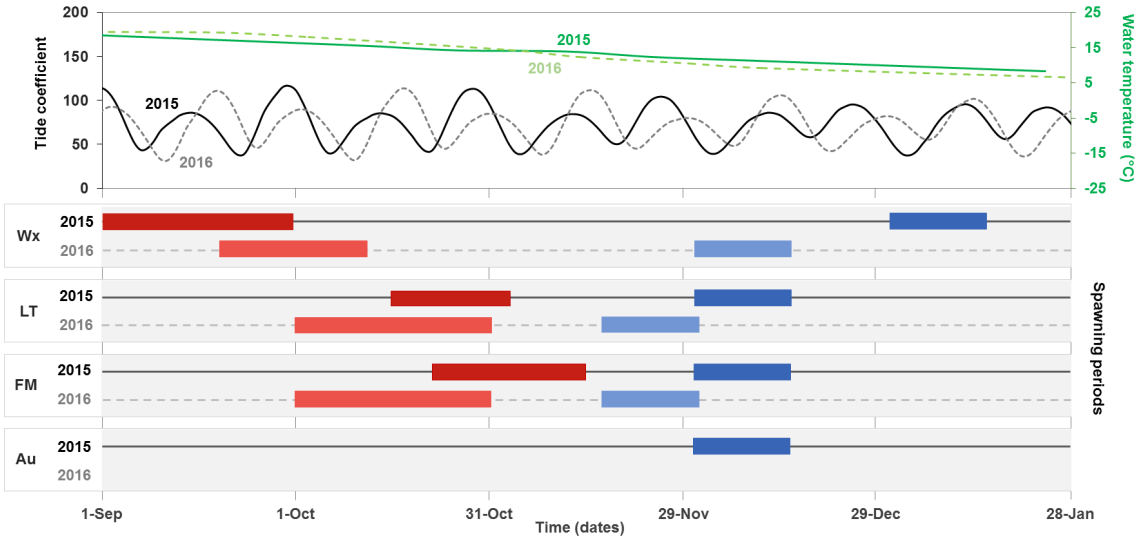


Fig. 2.H Inferred spawning dates of *Arenicola marina* (red) and *A. defodiens* (blue) at all sampled sites in 2015 (darker) and 2016 (lighter) and associated tide coefficients (in black) and water temperatures (in green).



Chapter 3

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

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

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***Ecological Modelling* (in press)**

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Abstract *Arenicola marina* is a polychaete (Lophotrochozoan) displaying a complex bentho-pelagic life cycle with two larval dispersal phases, only partially described up to now. A Dynamic Energy Budget (DEB) model was applied to the species in order to reconstruct its life cycle and growth under *in situ* environmental conditions. Two types of DEB models are usually applied to other Lophotrochozoans displaying similar life cycles: the standard (std-) model, applied to polychaetes (5 entries among the 1524 of the Add-my-Pet database on the 18/10/2018), and the abj-model, which includes an acceleration of metabolism between birth and metamorphosis, and which has been applied to most molluscs (77 abj- entries out of the 80 mollusc entries) enabling better fit predictions for the early life stages. The parameter estimation was performed with both models to assess the suitability of an abj-model for *A. marina*. The zero-variate dataset consisted of length and age data at different life cycle stages, the lifespan, the maximum observed length, and the wet weight of an egg. The uni-variate dataset consisted of two growth experiments from the literature at two food levels and several temperatures, laboratory data of oxygen consumption at several temperatures, and fecundity for different lengths. The predictions of the abj-model fitted better to the data (SMSE = 0.29). The acceleration coefficient was *ca* 11, which is similar to mollusc values. The field growth curves and the scaled functional responses (as a proxy of food levels) were suitably reconstructed with the new parameter set. The reconstruction of the early life-stages chronology according to *in situ* environmental conditions of a temperate marine ecosystem indicated a first dispersal phase of 5 days followed by a 7 months temporary settlement before a second dispersal phase in spring, at the end of metamorphosis. We emphasize the need for using abj-models for polychaetes in future studies.

Keywords Bioenergetics, lugworm, Growth, Oxygen consumption, Life-history traits, Dispersal

3.1 Introduction

Arenicola marina (Linnaeus, 1758) is a marine polychaete (Lophotrochozoan, Annelida) inhabiting most intertidal soft sediments from the Arctic to the Mediterranean. The species is intensively dug for bait by recreational fishermen (Blake, 1979; De Cubber et al., 2018; Watson et al., 2017) and the comparison between harvest efforts and observed populations abundance has evidenced the need for some regulation of this activity in some places (De Cubber et al., 2018). In aquaculture, *A. marina* is also reared for bait (Olive et al., 2006), and more recently, for its particular haemoglobin that might represent a valuable blood substitute for humans in the future (Rousselot et al., 2006) and which is already used for organs conservation before transplantation. However, its complex bentho-pelagic life cycle with two dispersal phases before recruitment has made the description of the early life stages and their chronology complicated, and still little is known about the development of *A. marina* between the trochophore larva stage and the benthic recruitment (Farke and Berghuis, 1979a, b; Newell, 1948; Reise, 1985). Moreover, the literature regarding *A. marina*'s life cycle and growth is quite ancient (mostly from 1979) and since 1990, it has been found that two cryptic species actually exist and might live in sympatry: *A. marina* and *A. defodiens*. Therefore ancient life-history description has to be used with caution (Cadman and Nelson-Smith, 1990).

The 'Dynamic Energy Budget' (DEB) theory quantifies the energy allocation to growth and reproduction of an individual during its life cycle according to environmental conditions such as temperature and food availability (Kooijman, 2010) even in species with complex and numerous life-stages (Llandres et al., 2015). Twelve primary parameters are sufficient for the implementation of a standard (std-) DEB model. However, among the assumptions implied in std-DEB models, some, like isomorphism during growth, the fact that growth always follows a typical Von Bertalanffy growth curve, or the presence of three life stages (embryo, juvenile and adult) are not found in every species. Therefore, extensions of the std-model (implying the use of more parameters) were created (Kooijman, 2014) accounting for deviations from typical development implied by the std-model, like foetal development, acceleration of metabolism, or extra life stages.

As of October 2018, Add-my-Pet (AmP) database estimated DEB parameters for 1524 animal species (Marques at al., 2018). Among these entries, only 11 were annelid species, 4 of them being polychaetes species for which std-models were applied. The closest phylum with a large amount of data is the molluscs' phylum (over 80 entries), also presenting a larval stage. Indeed, annelids and molluscs belong to the Lophotrochozoan clade and both, after the embryogenesis, lead to a trochophore larval stage. Mostly abj-DEB models have been applied only for the mollusc phylum, which are an extension of std-models con-

sidering an acceleration of metabolism between birth (first feeding) and metamorphosis (end of the change of shape) and are applied to most species with a larval phase (Kooijman, 2014). Although polychaete species often present a larval phase during their life cycle, until now, abj-models were not applied to this taxa.

A std- entry for *A. marina* is present in the AmP database and enables predictions of the growth and reproduction of the species. However, more than half of the dataset used for the parameter estimation consists of unpublished data (time since birth at puberty and maximum reproduction rate taken from Marlin: https://www.marlin.ac.uk/ and lifespan and ultimate total length taken from Wikipedia: https://www.wikipedia.org/), guessed data (wet weight at birth and puberty, ultimate wet weight), or data related to other species (age at birth from *A. cristata* and *A. brasiliensis*) (AmP entry: Bas Kooijman. 2015. AmP *Arenicola marina*, version 12/07/2015). We therefore completed the data set with literature, experimental and field data, and implemented a new parameter estimation for the species using both a std- and an abj-DEB models.

The objectives were:

(1) to calibrate a DEB model for *A. marina* based on a reliable and complete dataset and adapted to its life cycle features (and therefore to compare the relevance of the use a std- or an abj-DEB model for this species)

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

(3) to compare the parameters of the DEB models implemented for *A. marina* with the other Lophotrochozoan species' parameters and discuss the advantages of the use of an abj-model for this species.

3.2 Material and Methods

3.2.1 The DEB theory and its implementation for *Arenicola marina*

The model

The DEB theory describes the energy flows within an organism between three compartments (state variables) : the reserve (E), the structure (V), and the maturity (E_H) or the reproduction buffer (offsprings) (E_R) according to its life stage in order to describe its energy allocation to growth and reproduction for a given food level and at a reference

temperature T_{ref} (Fig. 3.1). The three differential equations linked to the state variables are obtained from the expression of the different fluxes (Table 3.1) (Kooijman, 2010; Van der Meer, 2006). Temperature corrections are made to the rates considered by the model

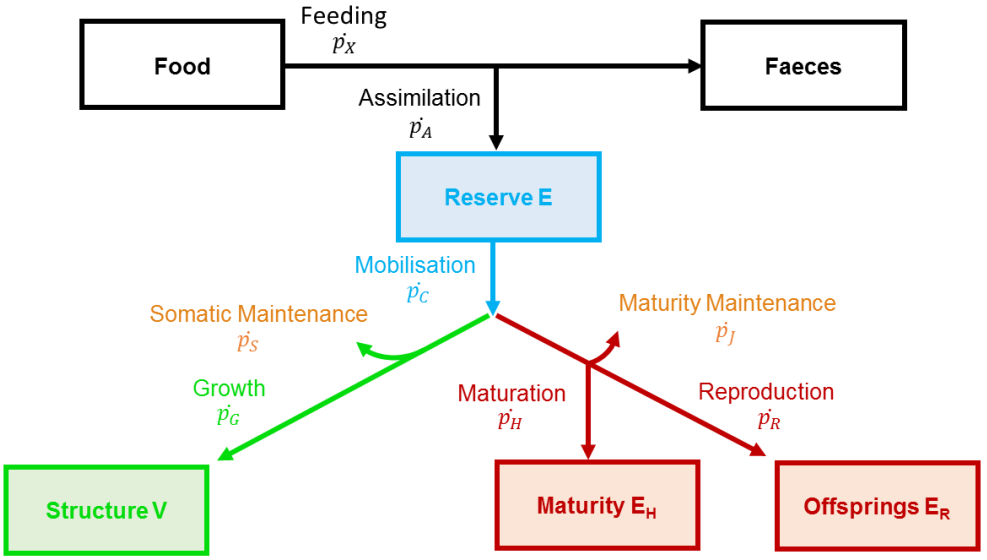


Figure 3.1 – Schematic representation of DEB model and associated state variables and fluxes, adapted from Kooijman (2010). Boxes are the state variables: 1) reserve E (J); 2) the structural volume, V (cm^3); 3) the cumulated energy invested in Maturity, E_H (J) or in reproduction E_R (J). Arrows are energy flows in $J.d^{-1}$. Details of $\dot{p}_X$, $\dot{p}_A$, $\dot{p}_C$, $\dot{p}_S$, $\dot{p}_G$, $\dot{p}_J$, $\dot{p}_H$ and $\dot{p}_R$ are given in Table 3.1.

in the equation of fluxes (e.g. the surface-area specific maximum assimilation rate, $\{\dot{p}_{Am}\}$ ($J.cm^{-2}.d^{-1}$), the energy conductance, $\dot{v}$ ($cm.d^{-1}$), the specific volume-linked somatic maintenance rate, $[\dot{p}_M]$ ($J.cm^{-3}.d^{-1}$), and the maturity maintenance rate coefficient, $\dot{k}_J$ (d^{-1}), see Tables 3.1 and 3.4). Indeed, when the temperature T (K) is different from the reference temperature T_{ref} (taken to be 293.15 K) these rates are multiplied by the correction given in Equation (3.1), where T_A is the Arrhenius temperature (K), $\dot{k}_1$ the rate of interest at T_{ref} and $\dot{k}$ the rate of interest at T.

$$\dot{k}(T) = \dot{k}_1 \cdot \exp\left(\frac{T_A}{T_{ref}} - \frac{T_A}{T}\right) \tag{3.1}$$

The links between observable metrics (physical length and wet weight) and the DEB model quantities are made with the shape coefficient δ (varying between $\delta = \delta_{Me}$ for embryos and $\delta = \delta_M$ after metamorphosis), the density of wet structure d_V ($g.cm^{-3}$), of wet reserve d_E ($g.cm^{-3}$) and of dry reserve d_{Ed} ($g.cm^{-3}$), the specific chemical potential of reserve μ_{Ed} ($J.Cmol^{-1}$ of reserve), and the molar weight of reserve w_{Ed} ($g.Cmol^{-1}$) (Table 3.1). Here, we assumed that $d_V = d_E = 1\ g.cm^{-3}$, $d_{Ed} = 0.16\ g.cm^{-3}$, $\mu_{Ed} = 550000\ J.Cmol^{-1}$ and that $w_{Ed} = 23.9\ g.Cmol^{-1}$.

Table 3.1 – State variables, fluxes, metric relationships, acceleration and shape coefficient of the abj-DEB model and associated mathematical expressions (Kooijman, 2014; Kooijman and Lika, 2014; Kooijman, 2010; Van der Meer, 2006). L is the structural length (cm) with $L = V^{1/3}$, and L_b and L_j are the structural lengths at birth and metamorphosis respectively. d_V is the density of wet structure, d_E the density of wet reserve, d_{Ed} the density of dry reserve, μ_{Ed} the specific chemical potential of reserve and w_{Ed} the molar weight of dry reserve. $L_w(t)$ is the physical total length at time t of the organism and $TL_w(t)$ its physical trunk length. $W_w(t)$ is the wet weight at time t of the organism. If $E_H^j = E_H^b$ the abj- model reduces to the std- model.

State variables	Reserve	$\frac{dE}{dt} = \dot{p}_A - \dot{p}_C$
	Structure	$\frac{dV}{dt} = \frac{\dot{p}_G}{[E_G]}$
	Maturity	if $E_H < E_H^p$ $\frac{dE_H}{dt} = \dot{p}_H$; else $\frac{dE_H}{dt} = 0$
	Allocation to reproduction	if $E_H \geqslant E_H^p$, $\frac{dE_R}{dt} = \kappa_R \cdot \dot{p}_R$; else $\frac{dE_R}{dt} = 0$
Fuxes	Ingestion	$\dot{p}_X = \frac{\dot{p}_A}{\kappa_X}$
	Assimilation	$\dot{p}_A = \{\dot{p}_{Am}\} \cdot s_M \cdot f \cdot V^{2/3}$
	Mobilisation	$\dot{p}_C = E \cdot \frac{\dot{v} \cdot s_M \cdot V^{2/3} \cdot [E_G] + \dot{p}_S}{\kappa \cdot E + V \cdot [E_G]}$
	Somatic maintenance costs	$\dot{p}_S = [\dot{p}_M] \cdot V$
	Maturity maintenance costs	$\dot{p}_J = \dot{k}_J \cdot E_H$
	Growth	$\dot{p}_G = \kappa \cdot \dot{p}_C - \dot{p}_S$
	Reproduction	$\dot{p}_R = (1-\kappa) \cdot \dot{p}_C - \dot{p}_J$
	Maturity	$\dot{p}_H = (1-\kappa) \cdot \dot{p}_C - \dot{p}_J$
Metric relationships	Physical length (cm)	$L_w(t) = \frac{V(t)^{1/3}}{\delta}$
	Wet weight (g)	$W_w(t) = d_V \cdot V(t) + (E(t) + E_R(t)) \cdot \frac{w_{Ed} \cdot d_E}{\mu_{Ed} \cdot d_{Ed}}$
Acceleration coefficient		if $E_H < E_H^b$ $s_M = 1$; if $E_H^b \leqslant E_H < E_H^j$ $s_M = L/L_b$; else $s_M = L_j/L_b$ if $E_H \geqslant E_H^j$
Shape coefficient		if $E_H < E_H^b$ $\delta = \delta_{Me}$; if $E_H^b \leqslant E_H < E_H^j$ $\delta = \delta_{Me} + (\delta_M - \delta_{Me}) \cdot (\frac{L - L_b}{L_j - L_b})$; else $\delta = \delta_M$ if $E_H \geqslant E_H^j$

Adaptation to *Arenicola marina*'s life cycle

The spawning event of *Arenicola marina* happens in late summer or early autumn (De Cubber et al., 2018; Watson et al., 2000). After the external fertilization, the embryo develops in the female gallery up to the post-embryonic stage, the trochophore larva, which is able to move vertically in the water column (Fig. 3.2, Farke and Berghuis, 1979a, b). At this time, the shape is changing from ovoidal (oocytes, with a shape coefficient

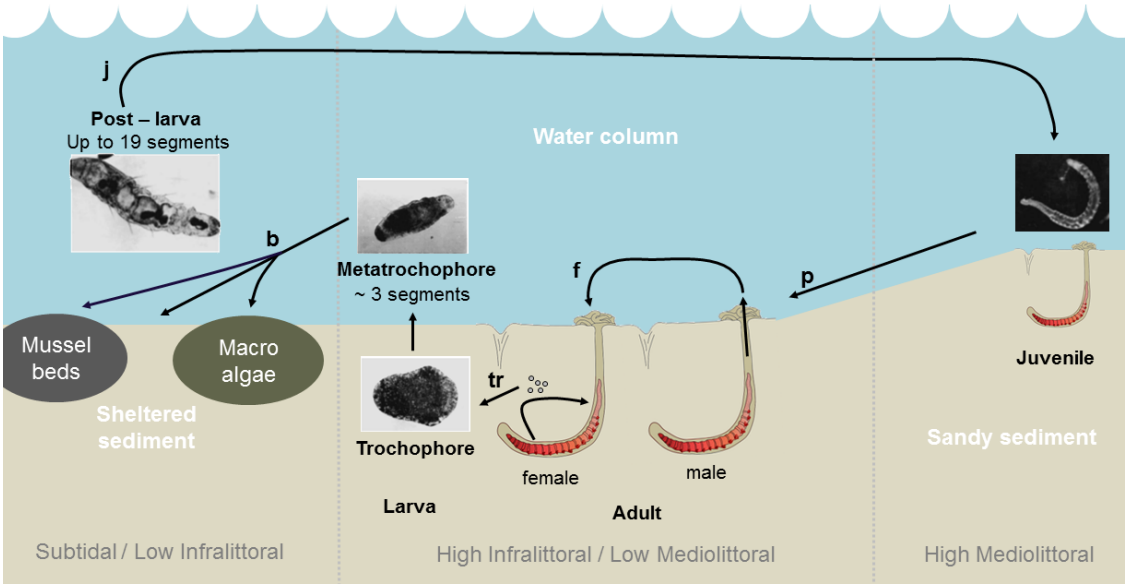


Figure 3.2 – Life cycle of *Arenicola marina* and associated habitats. f stands for fertilization; tr for when the trochophore larva appears; b for birth (e.g. first feeding, as described in the DEB theory); j for the end of metamorphosis; and p for puberty. Adapted from Farke and Berghuis (1979a, 1979b), Reise (1985) and Reise et al. (2001). Pictures of the different life stages of *A. marina* are taken from Farke and Berghuis (1979a).

$\delta = \delta_{Me}$) to cylindrical when the trochophore larva gradually acquires new setiger becoming a metatrochophore larva (of shape coefficient $\delta < \delta_{Me}$). The metatrochophore larva is released in the water column when it reaches 3 setigers and is transported by currents during several days. In lugworms, embryos and larvae are lecithotrophic, living on maternal reserve and therefore supposed not to be able to feed (the maturity threshold E_H did not yet reach its value for birth: $E_H < E_H^b$, where birth is the time when individuals start to feed). Therefore, there is no feeding or assimilation flux during the embryo and larval stage and $dE/dt = -\dot{p}_C$ (Table 3.1). Moreover, these young stages do not have enough complexity yet to be able to produce gametes and the reproduction flux goes to maturity (Table 3.1), which represents in this case the acquisition of complexity of the individual (Fig. 3.1).

The metatrochophore larva settles and begins eating as post-larva, when the gut appears

functional ($E_H = E_H^b$), either on mussel beds, macroalgae or sheltered soft sediment bottoms (Fig. 3.2). At this point, it lives inside a mucus tube stuck to the bottom and feeds on the particles deposited on the tube and around it, as well as on suspended particles (Farke and Berghuis, 1979a, b; Newell, 1949; Reise, 1985; Reise et al., 2001). During this temporary settlement period, the post-larva continues to gradually acquire new setigers up to the 19 final setigers found in adults (the shape coefficient δ keeps on decreasing until it reaches the shape coefficient value of the adults δ_M), developing a proboscis in the way of the adults (Farke and Berghuis, 1979a, b; Newell, 1949). These morphological changes are assimilated to metamorphosis (up to when the maturity threshold E_H reaches its value at metamorphosis: $E_H = E_H^j$). During this period, a metabolic acceleration (Kooijman, 2014) was considered, which is supposed to happen in most species that have a larval phase, frequently coinciding with morphological metamorphosis (Marques et al., 2018), and resulting in an exponential growth of the organism between the first feeding and the end of metamorphosis. From birth ($E_H = E_H^b$), feeding and assimilation are not null anymore, but individuals are not able yet to produce gametes ($\dot{p}_R = 0$).

When metamorphosis ends, a second dispersal phase of unknown period occurs in the water column and the newly juvenile lugworm settles on intertidal areas colonized by adults' lugworms, where it changes its mode of nutrition, becoming psammivorous like the adults (Beukema and De Vlas, 1979)(Fig. 3.2). The shape coefficient value stops changing, the growth starts to be isomorphic and follows the Von Bertalanffy growth curve for a constant scaled functional response (Kooijman, 2010), but it is not yet able to reproduce like the adults (since the maturity threshold E_H did not reach its value at puberty yet: $E_H < E_H^p$) .

Finally, the adults acquire the ability to reproduce (which is when $E_H > E_H^p$) and the energy flow formerly allocated to maturity is transferred to a reproduction buffer (offsprings) that empties, in the case of *Arenicola marina*, once a year in early autumn, during the spawning event.

3.2.2 Compilation of data for *Arenicola marina* and parameter estimation

Zero-variate and uni-variate data from the literature

Zero-variate data from the literature An important part of the zero-variate dataset found in the literature was composed of data taken from a larval culture performed by Farke and Berghuis (1979) before 1990, when the two species *Arenicola marina* and *A. defodiens* were not yet delimited (Cadman an Nelson-Smith, 1993): the lengths at tro-

chophore larva, at birth (first feeding) and at metamorphosis with their associated ages. Although the lengths data seem quite accurate (plates and pictures), the chronology description made by the authors remains vague. The precise time line had thus to be estimated from sometimes quite confused date references and we gave a weight of 0.5 to this data in the parameter estimation procedure. In the larval culture performed by Farke and Berghuis (1979), the temperature varied from 8 to 16 °C, so a mean temperature of 12 °C was used for the data taken from this experiment.

The second part of the zero-variate dataset from the literature was collected after 1990. First, the age for the occurence of the trochophore larva at 10 °C was communicated by S. Gaudron from unpublished *in vitro* fertilization experiments. The maximum observed trunk length (good biometric estimate, see De Cubber et al., 2018) was observed by S. Gaudron on a specimen kept in the Animal Biology Collection of the Sorbonne University (France). Finally, the age and length at puberty, the oocyte diameter and the lifespan were previously acquired by the authors at the same study site (De Cubber et al., 2018). The temperature used for this data was the mean temperature of the seawater over the year 2017 (13 °C, SOMLIT data: http://somlit-db.epoc.u-bordeaux1.fr/, bottom coastal sampling point at Wimereux). The age and the trunk length at puberty corresponded to a first mature adult of 2.5 cm and 1.5 years old. All the age data estimated from length analysis were given a weight of 0.5 in the parameter estimation procedure considering their potentially low accuracy. For all zero-variate data the f value was set to 1, considering that only the "best individuals" were used.

Uni-variate data from the literature The uni-variate dataset retrieved from the literature consisted in the datasets of two growth experiments:

- One growth experiment in which trunk length was measured at four different temperatures (5, 10, 15 and 20 °C) under two different food conditions (fed and unfed) taken from De Wilde and Berghuis (1979) (8 treatments). The corresponding f values were set at $f_{fed} = 0.8$ and $f_{unfed} = 0.1$ in view of growth comparisons made by the authors in the same study.
- One growth experiment in which wet weight was measured at one temperature varying between 16 and 20°C under two different conditions (fed and unfed) taken from Olive et al. (2006) (2 treatments). Temperature was set at 19.5°C and the f values were left free for both conditions.

For these two growth experiments, the temperature and feeding conditions met before the start of the experiment were not known so we had to assume the levels of reserve and

structure at the beginning of the experiment. Therefore, predictions of growth could only be made considering a physical trunk length $TL_w(0)$ at the beginning of the experiment and a physical wet weight $W_w(0)$ at the beginning of the experiment equalling to the one of the experiment.

Laboratory experiments and field data

Additional reproductive data (reproduction rate as a function of trunk length and wet weight of an egg), growth data (trunk length over time) and oxygen consumption data (oxygen consumption as a function of wet weight) were acquired by the authors in the laboratory and from field observations between 2016 and 2018 in order to complete the dataset collected from the literature.

Study area and sampling strategy Lugworms were collected at Wimereux (N 50°46'14" and E 01°36'38"), Le Touquet (N 50°31'07" and E 01°35'42") and Fort Mahon (N 50°20'31" and E 01°34'11"), located in the Eastern English Channel (Hauts-de-France, France) (Table 3.2). More details on the sites are given in De Cubber et al. (2018). For

Table 3.2 – Abiotic and biometric data related to the samples of *Arenicola marina* collected at Wimereux, Le Touquet and Fort Mahon and used later on for the parameter estimation of a DEB-model for *A. marina*

Type of data	Number of samples	Collection date	Temperature (°C)	Wet weight (g)		Trunk length (cm)	
				range	mean	range	mean
Oxygen consumption	39	16/05/2018	12	0.00 - 3.73	1.10 ± 1.00	0.36 - 5.60	2.85 ± 1.52
	63	13/06/2018	15	0.02 - 5.70	1.39 ± 1.69	0.80 - 7.30	2.95 ± 1.82
	55	25/07/2018	20.5	0.03 - 5.91	0.92 ± 1.33	0.90 - 6.80	2.64 ± 1.50
Growth	290	26/05/2018	13	0.00 - 0.11	0.05 ± 0.02	0.40 - 1.60	1.10 ± 0.20
Reproduction	9	Sept. to Nov. 2016 to 2018	13	2.30 - 17.60	6.10 ± 5.60	4.20 - 13.00	7.40 ± 3.70

the oxygen consumption experiment (Exp. A), the lugworms were collected at Wimereux from the high mediolittoral to the high infralittoral part of the foreshore (Fig. 3.2), in order to collect all the different age groups and sizes (De Cubber et al., 2018), on the sandy beach part, using a shovel. Collection happened three times between May and July 2018 in order to follow the summer increase of the seawater temperature of the English Channel (Table 3.2). For the reproductive data (Exp. B), ripe females of *A. marina* were collected at Wimereux, Le Touquet and Fort Mahon using a shovel or a bait pump (Decathlon ltd.) during the spawning period of each year (Table 3.2). For the growth experiment (Exp. C),

young individuals of *A. marina* were collected at Wimereux on the high mediolittoral part of the foreshore with a shovel (De Cubber et al., 2018) at the end of May 2018 (Table 3.2, see more details in De Cubber et al., 2018).

Laboratory measurements After each sampling, all lugworms were put in separate containers filled with seawater. Individuals of *Arenicola marina* were maintained in the laboratory during 24 h at the temperature of the English Channel at Wimereux at the time of their collection (12, 15 and 20.5 °C) for the oxygen consumption experiment (Exp. A), and at 15 °C otherwise (Exp. B and C), in a cold room, to allow gut to be devoided of their content prior to observations (Watson et al., 2000). Biometric measurements consisted in total length, trunk length (more reliable, see De Cubber et al., 2018 and De Wilde and Berghuis, 1979), and in wet weight measurements.

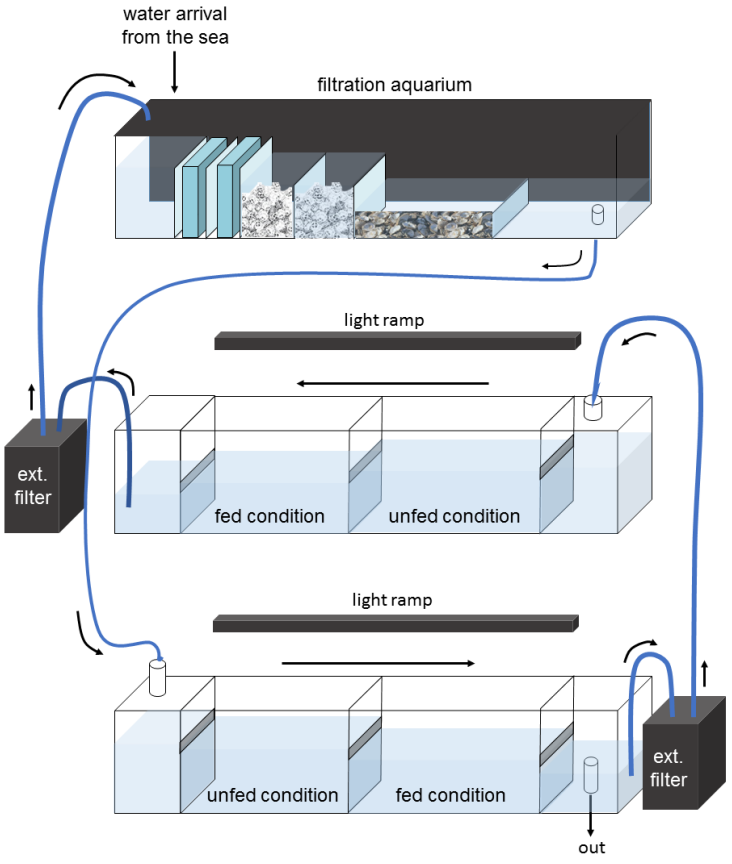
Experiment A: Oxygen consumption The oxygen consumption rates of lugworms were recorded as a proxy of metabolic activity (Galasso et al., 2018). Metabolic rates can vary between two fundamental physiological rates, one minimal maintenance metabolic rate (the standard metabolic rate) and one maximum aerobic metabolic rate (the active metabolic rate) (Galasso et al., 2018; Norin and Malte, 2011). In order to recreate these two situations of activity in the laboratory, and avoid any over- or underestimation of the metabolic rate, the oxygen consumption of lugworms was measured under two different conditions in which their metabolic activity was supposed close to the standard metabolic rate on one hand, and close to the active metabolic rate on the other hand. In the condition in which lugworms were supposed to experience a standard metabolic rate, around 30 of the collected individuals were transferred into Eppendorfs or Falcon centrifuge tubes (5 ml or 50 ml according to the size of the worms) half-filled with sand from Wimereux burnt at 550°C during 5 h, and with twice-filtered seawater (TFSW, 0.45 µm and 0.22 µm), enabling the lugworms to burry. The sediment was well mixed before the transfer in order to avoid air bubbles inclusions between sediment grains. In the condition in which lugworms were supposed to experience an active metabolic rate, around 30 of the collected individuals were transferred into centrifuge tubes filled with TFSW only, where they were constantly trying to burry (no sand). Blanks were also made for both conditions (centrifuge tubes without lugworms). Lugworms were acclimatized 24 hours at the experimental temperature in order to allow them to burrow when possible and relax. For each condition, centrifuge tubes were oxygenated using an air pump, and refilled with oxygenated TFSW when needed. At this point, lugworms in the "active" condition experienced regularly extra stress due to water movements. The oxygen content was then measured using a microelectrode Unisense® OX500 coupled to a picoammeter (Unisense PA 2000, Denmark). The data acquisition was performed using the software InstaCal®

and the tubes were then rapidly hermetically closed with Parafilm® M. For the 50 ml centrifuge tubes, measurement was renewed three times every 10 to 15 minutes after opening the Parafilm® M lid for a few seconds and homogenizing the water. For the 5 ml tubes, only two measurements were made at the beginning of the experiment and after 1 h given the low oxygen consumption observed. Before every measurement series, the whole system was calibrated (measurements of 100% and 0% oxygenated TFSW) and the salinity of the TFSW used for the experiment was measured using a refractometer. The temperature of the cold room was followed throughout the duration of the experiment. After the experiment, lugworms from the sand condition were sieved out of their tubes and maintained 24 h to allow gut contents to be devoided prior to biometric measurements. All lugworms were then measured (trunk length and total length) and weighed (wet weight).

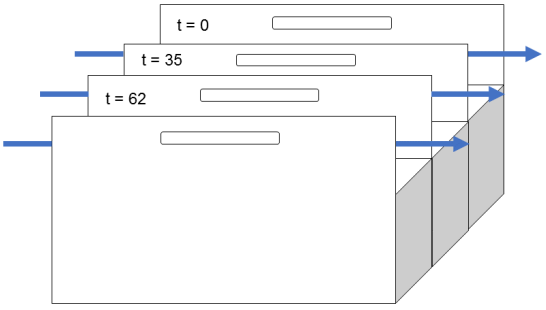
Experiment B: Reproductive data All oocytes were collected, from females that had been previously weighted and measured, in a 60 µm sieve, rinced with TFSW and placed in a 5 ml Eppendorf tube filled with TFSW (Table 3.2). A triplicate of 20 µL of the homogenized solution were then put on a microscope slide and the oocytes were counted under the microscope. When fecundity was estimated for each female, the supernatant was removed and the Eppendorf tubes were weighted with and without oocytes.

Experiment C: Growth experiment The growth experiment lasted for two months in a controlled room (temperature, photoperiod) at the Wimereux Marine Station (University of Lille, France) under a recirculating custom seawater system (Fig. 3.3). In the custom system, one aquarium tray was dedicated to water filtering and two aquaria held the lugworm growing experiment. The seawater, directly pumped from the sea, was kept several days in the filtering aquarium containing fine and coarse filter foam, crushed pozzolana and oyster shells and kept in the dark (Fig. 3.3). 10% of the seawater contained in the two growing aquaria was renewed every day or every second day with the water of the filtering aquarium. Two external filters (Eheim professional 4+ 250) and pumps allowed the circulation and additional filtration of the seawater system (Fig. 3.3a). A lightening system consisting in two light ramps (Alpheus Radiometrix 13C1001C) mimicking the external light intensity and photoperiod was added to the system (Fig. 3.3a), air pumps (Air pump 8000 and Eheim 400 from Europrix ltd., not represented on Fig. 3.3) linked to home-made finely punctured pipes allowed the oxygenation of the system. The temperature was kept around 15°C ($\pm$ 1°C). Each of the two growing aquarium trays were holding each twice 3 boxes filled with sediment burnt at 60°C during 24 h and lugworms (Fig. 3.3b). The first 3 boxes closer to the seawater arrival were dedicated to the unfed condition, the next 3 to the fed condition. A small waterfall between them prevented the seawater (and food) to circulate in the opposite direction of the main current, thus no food could reach the unfed

condition. The design of the boxes and of the separations prohibited the worms to leave their box and to circulate from one condition to another condition (Figs. 3.3a, b).



(a)



(b)

Figure 3.3 – Circulation, filtration of seawater and lightening (a) and boxes (b) of the custom *Arenicola marina* growing system with recirculating seawater (Experiment C). The filtration aquarium tray (a, top aquarium) contained (from left to right): fine and coarse filter foam, crushed pozzolana and oyster shells. The boxes (b) were placed in each of the fed and unfed condition in the remaining aquarium trays and removed at t = 0 (first feeding of the fed condition), t = 35 and t = 62 days. The light ramps consisted in Alpheus Radiometrix 13C1001C, and the external (ext.) filters in Eheim professional 4+ 250. The oxygenation ramps placed in the last two aquarium trays are not represented.

All lugworms were measured and only individuals ranging from 0.4 cm to 1.6 cm of trunk length were selected. Twelve batches of 30 individuals were made with the same size (trunk length) range. Each batch was placed in a separated box within the experimental set up (Fig. 3.3b). Feeding occurred twice at t = 0 and t = 35 days with yeast wastes (obtained from Brasserie du pays Flamand ltd., a local brewery) inserted within the sediment with 20 ml syringes (between 1.8 and $3.6.10^{10}$ cells added per box) (Olive et al., 2006). One batch of lugworms of each condition in both aquaria was withdrawn at the beginning of the experiment, after 35 days and after 62 days, kept 24 h in the cold room and weighted and measured.

Data analyses All data analyses were performed on Matlab R2015b. For the oxygen consumption experiment (Exp. A), for each measurement (blanks included), the associated percentage of oxygen within the tube was calculated according to the Equation (3.2).

$$O_{2\,\text{measured}}(\%) = \frac{O_{2\,\text{measured}}(V) - O_{2\,\text{min}}(V)}{O_{2\,\text{max}}(V) - O_{2\,\text{min}}(V)} \cdot 100 \tag{3.2}$$

With $O_{2\,\text{measured}}$(V) the oxygen measured, $O_{2\,\text{min}}$(V) the oxygen measured for 0% of oxygen, and $O_{2\,\text{max}}$(V) the oxygen measured for 100% of oxygen. The oxygen content (µmol.L^{-1}) was then calculated according to the temperature (T, in °C), salinity (S, in ‰) and the water content of each tube according to Aminot and Kérouel (2004, see on pages 110-118). The blank effect was deleted, and the individual oxygen consumption (µmol.h^{-1}) was then calculated as the inverse of the slope of the linear regression of the evolution of the oxygen content over time. Both conditions were analyzed together to consider an average level of activity.

For the reproduction data acquisition, the fecundity (F) was calculated for each female according to Equation (3.3) (with n the mean of the three counts).

$$F = \frac{n}{4 \cdot 10^{-3}} \tag{3.3}$$

Since spawning happens only once a year for *A. marina*, the reproduction rate for each female was calculated as the fecundity divided by the number of days in one year and plotted against the female trunk length (uni-variate data). The wet weight of an egg was calculated as the total weight of oocytes divided by fecundity (zero-variate data).

Parameters estimation

The parameters estimation of the DEB models was done using the covariation method described by Lika et al. (2011), using the dataset shown in Table 3.3. The estimation

was completed using the package DEBtool (as described in Marques et al., 2018) on the software Matlab R2015b using both a std-DEB model and an abj-DEB model, in order to select the best fit model and to compare the parameter obtained with both models. The parameter estimation procedures were evaluated by computing the Mean Relative Errors (MRE), varying from 0, when predictions match data exactly, to infinity when they do not, and the Symmetric Mean Square Errors (SMSE), varying from 0, when predictions match data exactly, to 1 when they do not (http://www.debtheory.org).

Table 3.3 – Data used in the abj- and std- model parameters estimations for *Arenicola marina* among the available dataset. The age and length at metamorphosis were only used for the abj-model parameter estimation.

Type of data	Data	References
Zero-variate	age at trochophore larva	Pers. comm. from S. Gaudron
	age at birth	Farke and Berghuis (1979)
	age at metamorphosis	Farke and Berghuis (1979)
	age at puberty	De Cubber et al. (2018)
	lifespan	Beukema and De Vlas (1979), De Cubber et al. (2018)
	egg diameter	Watson et al (1998), De Cubber et al. (2018)
	total length of the trochophore larva	Farke and Berghuis (1979)
	total length at birth	Farke and Berghuis (1979)
	total length at metamorphosis	Farke and Berghuis (1979)
	trunk length at puberty	De Cubber et al. (2018)
	total maximum length	Pers. comm. from S. Gaudron (Sorbonne Univ.)
	wet weight of an egg	This study
Uni-variate	TL-Ww	This study
	TL-Wd	De Wilde and Berghuis (1979)
	t-TL (4 temperatures, 2 feeding conditions)	De Wilde and Berghuis (1979)
	t-Ww (2 feeding conditions)	Olive et al.(2006)
	Ww-O2 (3 temperatures, experimental conditions)	This study
	TL-R	This study

3.2.3 Inferring environmental conditions from biological data and vice versa

Functional scaled response associated to growth data

The parameters of abj-model for *Arenicola marina* (best fit model), as well as two different growth datasets, were used to validate the model and infer the environmental conditions (in terms of food levels) of these datasets. The first growth dataset was taken from Beukema and De Vlas (1979). It represents seasonal changes in mean individual dry weight (9-year averages) in small lugworms from two populations of the Wadden Sea.

The second dataset consists of the observations of wet weight and trunk length of the experiment C. Since the results of the latest experiment seemed to indicate that food was lacking from t = 35 days to t = 62 days and since no significant difference between the two feeding conditions were observed, the abj-model applied in this study was used to reconstruct the scaled functional response (f) as a proxy of food levels during the whole experiment for the two conditions. Predictions on these different growth experiments were made at one temperature but for feeding conditions varying from f = 0.02 to f = 1. The best fit predictions were chosen as the ones presenting the smallest sum of squares of the differences between observations and predictions.

Life cycle chronology under *in situ* environmental conditions

The abj-DEB model for *Arenicola marina* was used to reconstruct the chronology of the early life stages of the species under the *in situ* environmental conditions of Wimereux (Eastern English Channel, Hauts-de-France), as well as its growth in wet weight and trunk length, and compared them with optimal food and temperature conditions (f = 1 and T = 20 °C).

Local environmental conditions The *in situ* temperature of the year 2017 were taken from SOMLIT. As a first approximation, the scaled functional response f was guessed from monitoring of the phytoplankton within the Eastern English Channel (Lefebvre et al., 2011) showing higher abundances in spring and autumn, as generally observed in the North Atlantic temperate ocean (Miller and Wheeler, 2012, Fig. 11.7).

Chronology of the early life-stages and associated lengths The parameters of the abj-model previously estimated were used to predict age and length at trochophore larva stage, birth, metamorphosis and puberty under the non-optimal environmental conditions of Wimereux previously defined.

Growth predictions The evolution of the compartments of reserve, structure and reproduction buffer from the fertilization to the lifespan a_m and further was calculated according to the equations of Table 3.1. For each environmental condition, the ages for all the life stages were predicted as previously and a temperature correction was applied when the temperature was different from 20 °C. The values of E, V and E_R over time were then converted into wet weight and/or physical trunk length with the equations found in Table 3.1.

3.2.4 Comparison of the DEB parameters of *Arenicola marina* with other Lophotrochozoan species

The parameters found with the abj-DEB model for *Arenicola marina* were compared with the ones found with the std-model, as well as with the parameters of other molluscs and annelid species. The parameters collected were taken from the Add-my-Pet collection (AmP) (Marques et al., 2018) using the function prtStat of the AmPtool package used on Matlab R2015b. All values were given for a reference temperature T_{ref} of 20 °C. The most complete data set for molluscs is for the gastropod *Lymnaea stagnalis* (completeness = 5). The maximum completeness value for annelids in AmP is 2.8, and is found in two species of polychaetes and four species of clitellates. The least complete data set for molluscs is for the symbiotic bivalve *Thyasira cf. gouldi* (completeness = 1.5) and the least complete data set for annelids is for the polychaete *Capitella teleta* (completeness = 1.5).

Some of the primary parameters of the two models for *A. marina* were not compared given the lack of data for these parameters (e.g. the searching rate $\{\dot{F}_m\}$, the digestion and the reproduction efficiencies κ_X and κ_R), as in Kooijman and Lika (2014). The acceleration factor s_M of *A. marina* was calculated as $s_M = L_j/L_b$, with L_b the structural length at birth and L_j the structural length at the end of the metamorphosis, and compared with the one of other species. For the species showing a metabolic acceleration ($s_M > 1$), the infinite length L_∞ was calculated as $L_\infty = L_m \cdot s_M$, with L_m the maximum structural length ($L_m = \kappa \cdot \frac{\{p_{Am}\}}{[p_M]}$). The energy conductance after metamorphosis v_j and the maximum assimilation rate after metamorphosis $\{p_{Am}\}_j$ were calculated as $v_j = v_b \cdot s_M$ and $\{p_{Am}\}_j = \{p_{Am}\}_b \cdot s_M$, with v_b the energy conductance at birth and $\{p_{Am}\}_b$ the maximum assimilation rate at birth (Kooijman, 2014; Kooijman and Lika, 2014). All ten parameters, as well as the expectations based on the general animal (Kooijman, 2010, Table 8.1), were represented as functions of L_∞ for all the considered species.

3.3 Results

3.3.1 Parameter estimation

Parameters of the model

The completeness of the models was set at 4.2 following Lika et al. (2011) according to the dataset used in the parameters estimation (Table 3.3). The implementation of the parameter estimation of the std-DEB model provided a Mean Relative Error (MRE) of

0.30 and Symmetric Mean Square Error (SMSE) of 0.38 (Marques et al, 2018). The implementation of the parameter estimation of the abj-DEB model provided a MRE of 0.23 and SMSE of 0.29. In addition to the fact that the abj-model provided a better fit to the data set, it appears that the std-model largely underestimates the age and length at birth, a_b and L_b (the relative errors, RE, are respectively 0.91 and 0.83), as well as the age when then trochophore larva appears, a_{tr}, (RE = 0.60). For both models, the values of the fraction of the metabolized energy allocated to soma, κ, appeared equal (Table 3.4). The specific somatic maintenance rate, $[\dot{p}_M]$, and the maximum assimilation rate at birth, $\{\dot{p}_{Am}\}_b$, and at metamorphosis, $\{\dot{p}_{Am}\}_j$, were respectively five, twenty and two times higher with the std-model than with the abj-model. However, the maturation thresholds for the occurring of the trochophore larva, E_H^{tr}, for birth, E_H^b, and for puberty, E_H^p, and the energy conductance at metamorphosis, $\dot{v}_j$, appeared higher with the abj-model, that considered a metabolic acceleration rate between birth and metamorphosis, s_M, around 11 (Table 3.4).

Table 3.4 – Summary of the primary and some auxiliary parameters provided by the parameter estimation of the std- and the abj-DEB models for *Arenicola marina*

Parameter	Symbol	Value		Unit
		std-model	abj-model	
Reference temperature[1]	T_{ref}	293.15	293.15	K
Fraction of food energy fixed in reserve[1]	κ_X	0.80	0.80	-
Arrhenius temperature	T_A	3800	3800	K
Energy conductance[2]	$\dot{v}$ ($\dot{v}_j$)	1.67 e^{-02} (-)	9.79 e^{-03} (0.12)	$cm.d^{-1}$
Allocation fraction to soma	κ	0.92	0.92	-
Reproduction fraction fixed in eggs[1]	κ_R	0.95	0.95	-
Volume specific costs of structure	$[E_G]$	4173	4127	$J.cm^{-3}$
Maturation threshold for the trochophore larva	E_H^{tr}	2.73 e^{-04}	8.44 e^{-04}	J
Maturation threshold for birth	E_H^b	2.73 e^{-04}	1.27 e^{-03}	J
Maturation threshold for metamorphosis	E_H^j	-	1.94	J
Maturation threshold for puberty	E_H^p	38.62	104.50	J
Weibull ageing acceleration	$\ddot{h}_a$	3.08 e^{-07}	6.69 e^{-08}	d^{-2}
Gompertz stress coefficient[1]	s_G	1.00 e^{-04}	1.00 e^{-04}	-
Acceleration rate[3]	s_M	-	11.46	-
Maximum assimilation rate[2]	$\{\dot{p}_{Am}\}$ ($\{\dot{p}_{Am}\}_j$)	280.08 (-)	10.62 (130.63)	$J.cm^{-2}.d^{-1}$
Specific somatic maintenance rate	$[\dot{p}_M]$	69.89	15.82	$J.cm^{-3}.d^{-1}$
Maturity maintenance rate[1]	$\dot{k}_J$	2.00 e^{-03}	2.00 e^{-03}	d^{-1}
Specific density of wet structure[1]	d_V	1	1	$g.cm^{-3}$
Specific density of wet reserve[1]	d_E	1	1	$g.cm^{-3}$
Specific density of dry reserve[1]	d_{Ed}	0.16	0.16	$g.cm^{-3}$
Specific chemical potential of dry reserve[1]	μ_{Ed}	550000	550000	$J.Cmol^{-1}$
Molar weight of dry reserve[1]	w_{Ed}	23.9	23.9	$g.Cmol^{-1}$

[1] Fixed parameters. The values were taken from the generalized animal (Kooijman, 2010).
[2] The values inside brackets are the ones after metamorphosis when using the abj-model: $\dot{v}_j = s_M \cdot \dot{v}$ and $\{\dot{p}_{Am}\}_j = s_M \cdot \{\dot{p}_{Am}\}$
[3] s_M is given for a scaled functional response of 1 after metamorphosis

Observations vs predictions

Zero-variate data For 9 of the 12 zero-variate observations of the estimation procedure with the abj-model, the predicted values were close to the observed ones (RE $\leqslant$ 0.27) (Table 3.5). The last three predictions for the age at birth a_b, the age at puberty a_p and the total length at birth L_b showed higher relative errors (RE $\sim$ 0.65). The predictions obtained with the std-model estimation procedure were overall less well adjusted to the zero-variate observations with 50% of the predictions associated RE higher than 0.45 (Table 3.5). For instance, the age at birth a_b, the age when the trochophore larva is first observed a_{tr} and the age at puberty a_p where highly underestimated with the std-model estimation procedure (RE respectively of 0.91, 0.6 and 0.74), as well as the total length at birth L_b and the length when the trochophore larva is first observed L_{tr} (RE respectively of 0.83 and 0.45).

Table 3.5 – Summary of the zero-variate observations values and associated predictions and relative errors (RE) obtained with both the abj- and the std-DEB models for *Arenicola marina*

Data	Symbol	Value	Predictions (RE)		Unit
			std-model	abj-model	
age at trochophore larva	a_{tr}	7	2.769 (0.60)	7.7 (0.1)	d
age at birth	a_b	30	2.774 (0.91)	10.52 (0.65)	d
age at metamorphosis	a_j	78	-	89.68 (0.15)	d
age at puberty	a_p	548	142.9 (0.74)	174.5 (0.68)	d
lifespan	a_m	2190	2194 (0.02)	2462 (0.12)	d
egg diameter	L_0	0.02	0.020 (0.02)	0.021 (0.07)	cm
total length of the trochophore larva	L_{tr}	0.025	0.014 (0.45)	0.019 (0.20)	cm
total length at birth	L_b	0.08	0.014 (0.83)	0.023 (0.71)	cm
total length at metamorphosis	L_j	0.89	-	0.85 (0.05)	cm
trunk length at puberty	TL_p	2.5	3.2 (0.28)	3.17 (0.27)	cm
maximum trunk length	TL_i	34	27.58 (0.19)	37.4 (0.10)	cm
wet weight of an egg	Ww_0	4.78 e^{-6}	4.45 e^{-6} (0.07)	5.15 e^{-6} (0.08)	g

Uni-variate data The RE of the uni-variate data set ranged from 0.06 to 0.41 with the abj-DEB model, and from 0.08 to 0.42 with the std-DEB model, with, in both cases, the highest values corresponding to the fit to the length-weight data collected on individuals of highly variable reserve and reproduction buffer levels, and to the oxygen consumption data set (most scattered values) (Figs. 3.4, 3.5, 3.6, 3.7). In both cases, the oxygen consumption increased with the increase of temperature (Fig. 3.4). The values of the shape coefficients δ_M varied for *a priori* the same measure of the trunk length between 0.14 and 0.20 with the abj-DEB model and between 0.09 and 0.13 with the std-DEB model according to the authors (Fig. 3.7), which is due to the lack of rigid measurable parts in *Arenicola marina* that could be used as a proxy for length.

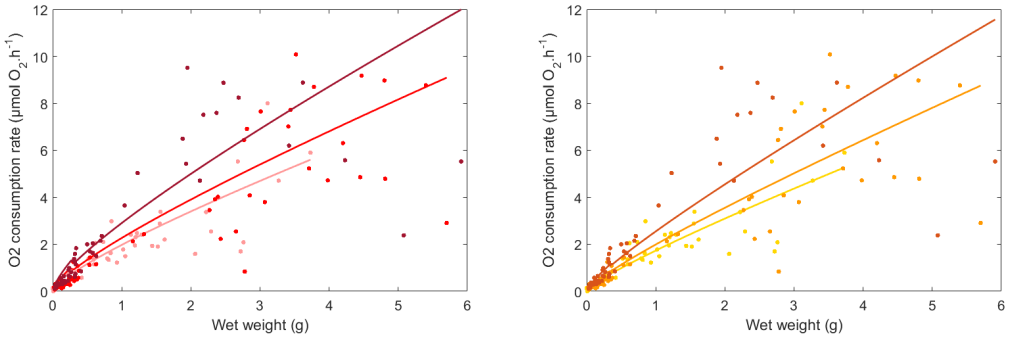


Figure 3.4 – Data (dots) and predictions (lines) of the oxygen consumption of the abj-DEB model (a) and the std-DEB model (b) of *Arenicola marina* measured by the authors as a function of wet weight at three different temperatures (from light to dark red: 12, 15 and 20.5°C). The respective relative errors from 12 to 20.5°C were 0.29, 0.38 and 0.40 with the abj-model and 0.28, 0.33, and 0.38 with the std-model.

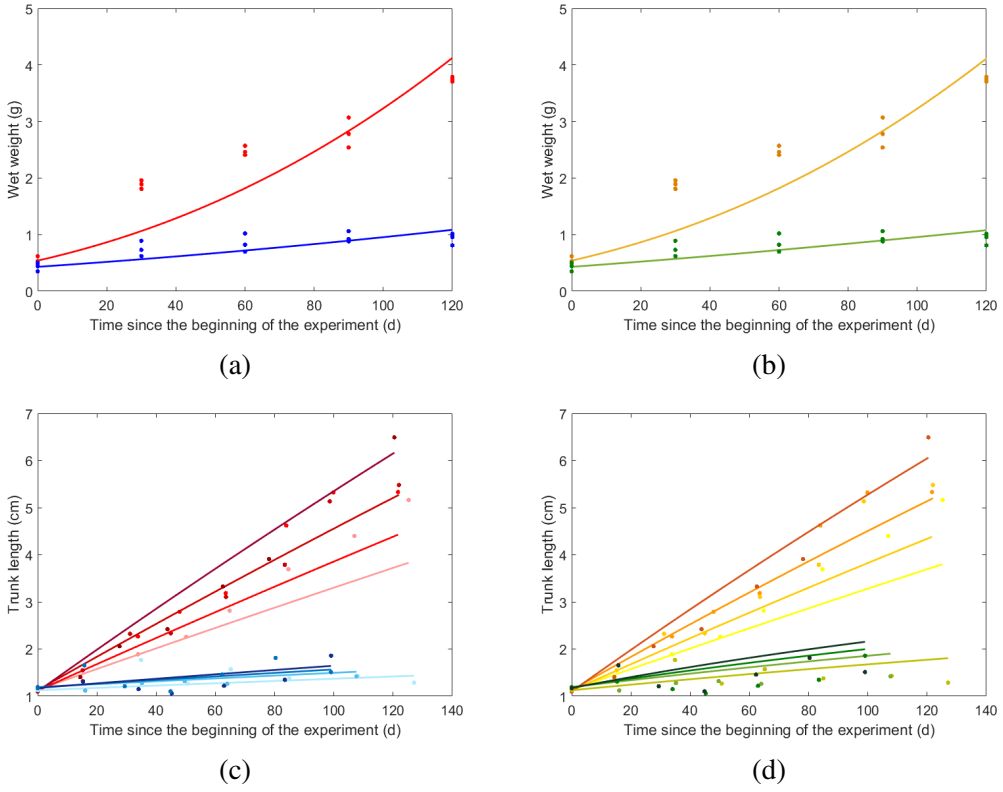
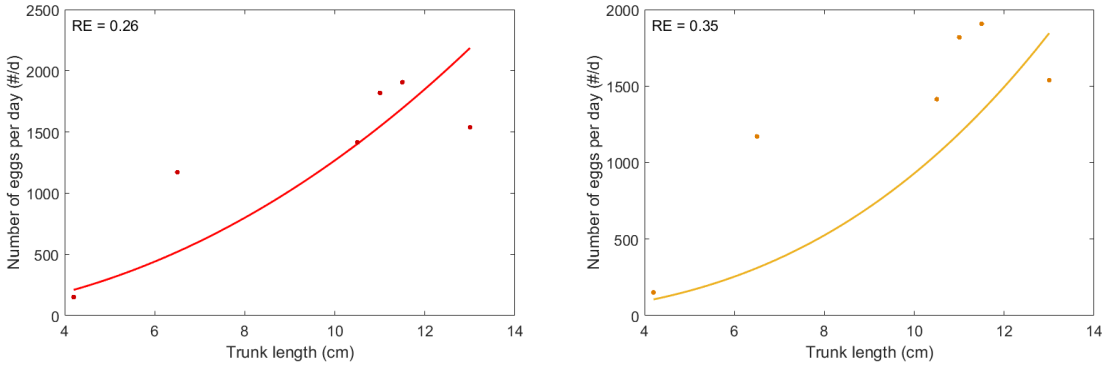
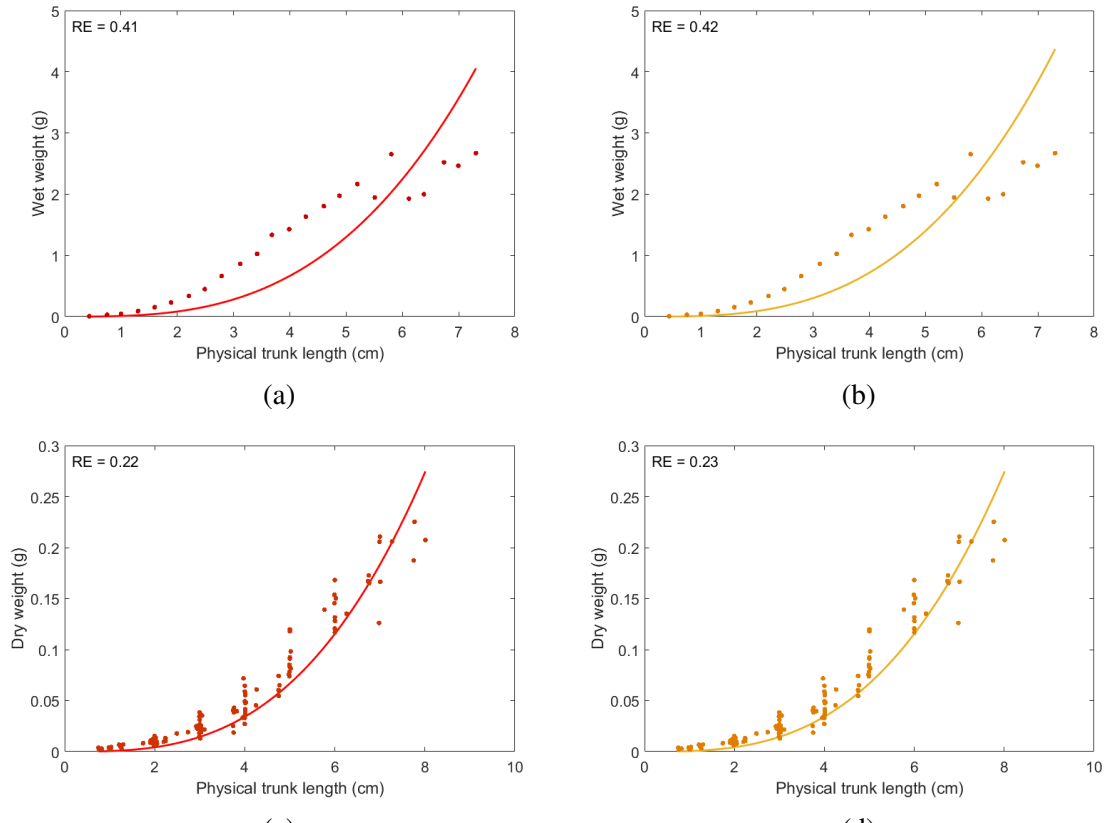


Figure 3.5 – Data (dots) and predictions (lines) of the growth of *Arenicola marina* juveniles in wet weight (a,b) and in trunk length (c,d) using both an abj-DEB model (a,c) and a std-DEB model (b,d). Data from (a,b) was taken from Olive et al. (2006). *A. marina* was reared in fed (red and orange) and unfed (blue and green) conditions between 12 and 20°C. The respective relative errors (RE) for the growth curves in fed and unfed conditions were 0.19 and 0.15 (a) 0.18 and 0.15 (b). Data from (c,d) were taken from De Wilde and Berghuis (1979). *A. marina* was reared in fed (red and orange) and unfed (blue and green) conditions at four different temperatures (from light to dark: 5, 10, 15 and 20°C). The respective (RE) for the growth curves in fed conditions at 5, 10, 15 and 20°C were 0.15, 0.17, 0.07 and 0.13 with the abj-model and 0.16, 0.18, 0.08 and 0.12 with the std-model. The respective RE for the growth curves in unfed conditions were 0.11, 0.06, 0.13 and 0.12 with the abj-model and 0.17, 0.19, 0.23 and 0.24 with the std-model.



(a) (b)

Figure 3.6 – Data (dot) and prediction (line) of the reproduction rate of *Arenicola marina* collected by the authors (Exp. B) (Eastern English Channel, France, see Table 3.2) as a function of trunk length using both an abj-DEB model (a) and a std-DEB model (b). RE stands for relative error.



(a) (b)

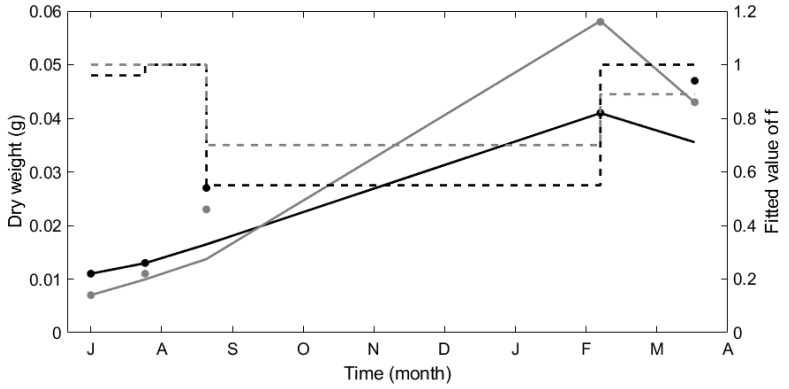
(c) (d)

Figure 3.7 – Data (dots) and predictions (lines) of the wet weight as a function of trunk (a,b) and total (b,c) length for *Arenicola marina* individuals collected at Wimereux (this study) and of the dry weight as a function of trunk length (e,f) for *A. marina* (data from De Wilde and Berghuis (1979)) using both an abj-DEB model (a,c,e) and a std-DEB model (b,d,f). The corresponding values of the shape coefficient are: (a) $\delta_M = 0.20$ (b) $\delta_M = 0.13$ (c) $\delta_M = 0.14$ (d) $\delta_M = 0.09$. RE stands for relative error.

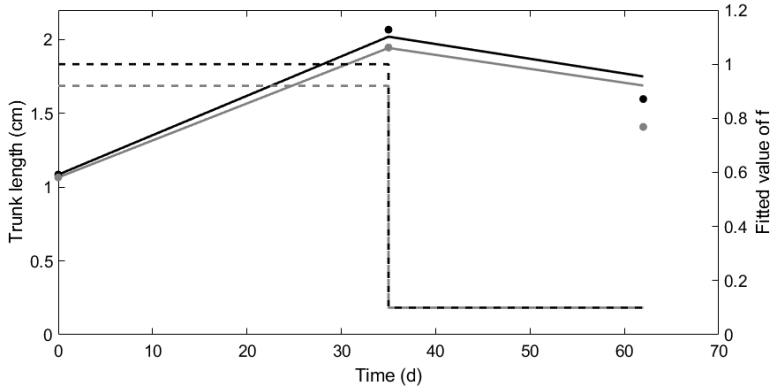
3.3.2 Reconstruction of environmental conditions with the abj-model for *Arenicola marina* from biological data and vice versa

Scaled functional response

From a field growth dataset The abj-model provided a good fit for the field growth data taken from Beukema and De Vlas (1979) for the two studied sites (Fig. 3.8a). The



(a)



(b)

Figure 3.8 – Reconstruction of the scaled functional response value (f, dashed lines) from field (a) and experimental (b) data (dots) with the abj-model for *Arenicola marina* from this study (lines are the model predictions). The observations of a field growth survey of *A. marina* (dots) are taken from Beukema and De Vlas (1979) in two beaches of the Wadden Sea (black and grey). The associated predictions of the DEB model (lines) for the best fitted values of f (dashed lines) are represented. Sea surface temperature were taken from Van Aken (2008). The laboratory observations (dots) on growth in trunk length of *A. marina* in different feeding conditions (fed in black and unfed in grey) are associated to the growth predictions of the DEB model (lines) with the fitted values of the scaled functional response f (dashed lines) for T = 16.5°C.

values of the scaled functional response f were shown to evolve on both sites during the year, with the highest values during spring and late summer periods compared to winter period (Fig. 3.8a).

From laboratory growth data Overall, the abj-model provided a good fit for the growth data obtained in the laboratory (Exp. C), although growth was slightly underestimated between t = 0 and t = 35 d, and slightly overestimated between t = 35 and t = 62 d (Fig. 3.8b). The reconstruction of the scaled functional response f provided indications on the fact that the food levels within the sediment between t = 35 d and t = 62 d might have been really low and did not allow an optimal growth.

Life cycle chronology and growth according to the environmental conditions

***In situ* environmental conditions** The seawater temperatures ranged from 5.5 to 20 °C at Wimereux, with the highest temperature between July and September and the lowest temperature between January and February (Fig.3.9a). The scaled functional response was supposed to range from 0.3 to 0.95 with higher values in spring and autumn and lower values in summer and winter (Fig.3.9b).

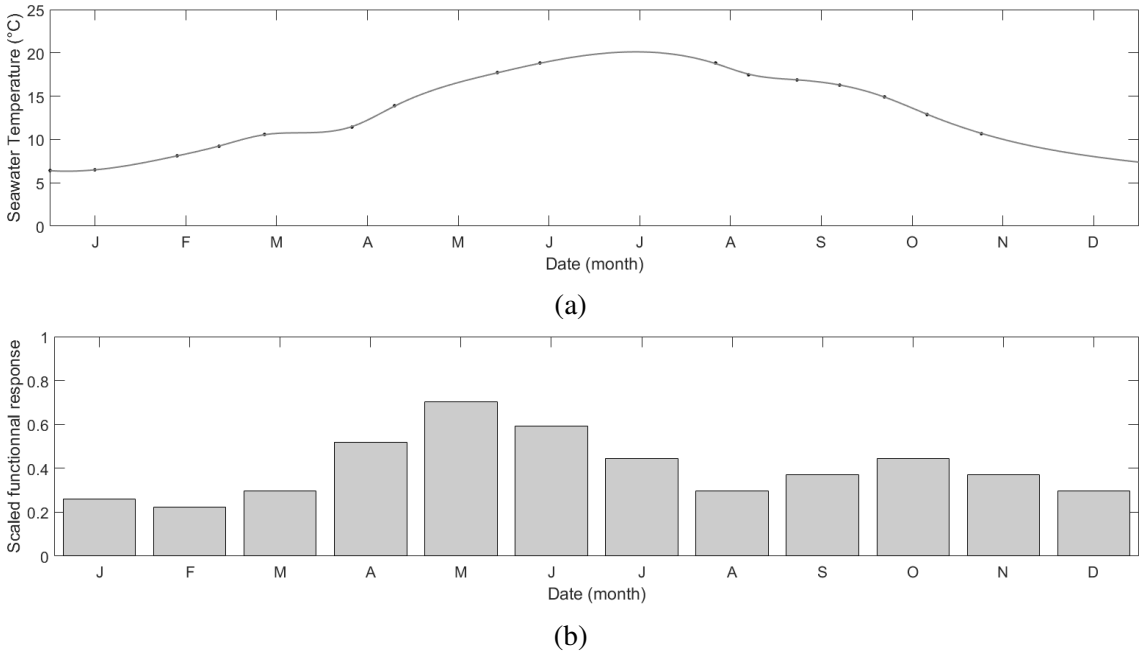


Figure 3.9 – *In situ* temperature of the seawater at Wimereux (Hauts-de-France, Eastern English Channel) during the year 2017 (a), and estimated scaled functional response f at this site (b), used for the predictions of the chronology of the first life stages of the life cycle of *Arenicola marina* and of the wet weight and trunk length growth of the species at this site.

Chronology of the first life stages The abj-model predicted an age at trochophore larva stage a_{tr} of 10.3 days and an age at birth a_b (used as an approximation of the age at the first settlement) of 15.5 days at Wimereux, considering the environmental conditions presented in Fig. 3.9 (Table 3.6), suggesting a first dispersal phase in between these two events of

around 5 days. The age at the end of metamorphosis a_j was predicted to be 208 days (a little less than 7 month) in local environmental conditions, which means around mid April for a spawning period in mid September. The age and trunk length at puberty of the lugworms of Wimereux, a_p and TL_p, were predicted to be respectively 373.2 days and 3.5 cm.

Table 3.6 – Predictions on the chronology and lengths of different life cycle stages of *Arenicola marina* according to the *in situ* environmental conditions at Wimereux (Hauts-de-France, Eastern English Channel) made by the abj-DEB model.

Event	Length (cm)	Age (d)
Trochophore larva	0.021	10.29
Birth (first feeding)	0.034	15.51
End of the metamorphosis	1.12	208.26
Puberty	3.50	373.19

Growth predictions according to the environmental conditions The total wet weight of *Arenicola marina* (considering the structure, reserve and reproduction buffer compartments) predicted by the model at the maximum age a_m was around 20 times superior in optimal conditions (f = 1 and T = 20°C, around 400 g) compared to *in situ* conditions recorded at Wimereux (f = 0.4 and T = 13°C, around 20 g) (Fig. 3.10).

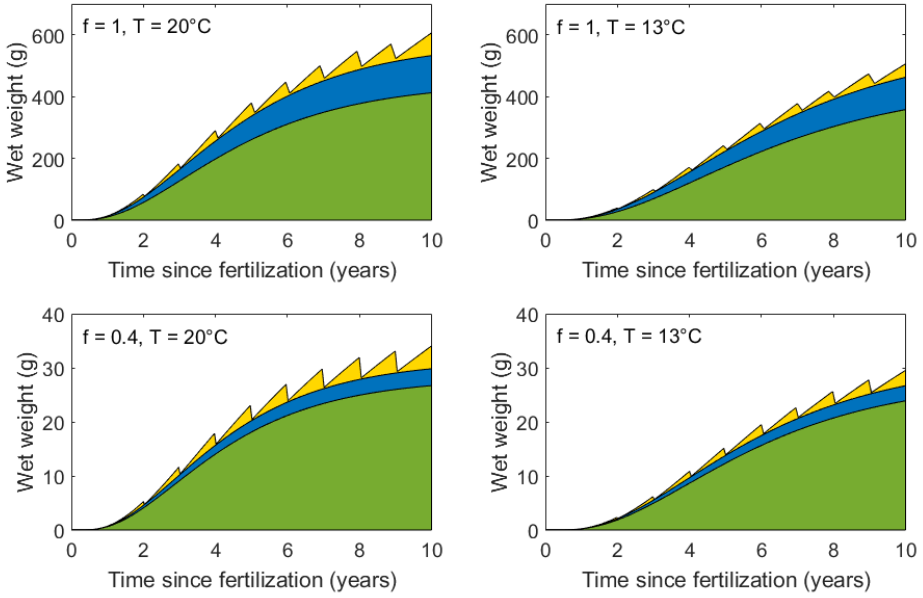


Figure 3.10 – Predictions of the abj-DEB model of the evolution of the wet weight of the structure S (green), the reserve E (blue) and the reproduction buffer E_R (yellow) compartments of *Arenicola marina* under different environmental conditions from fertilization time: f = 1 (food available *ad libitum*) & T = 20 °C; f = 1 & T = 13 °C; f = 0.4 & T = 20 °C; f = 0.4 & T = 13 °C (mean environmental conditions found at Wimereux).

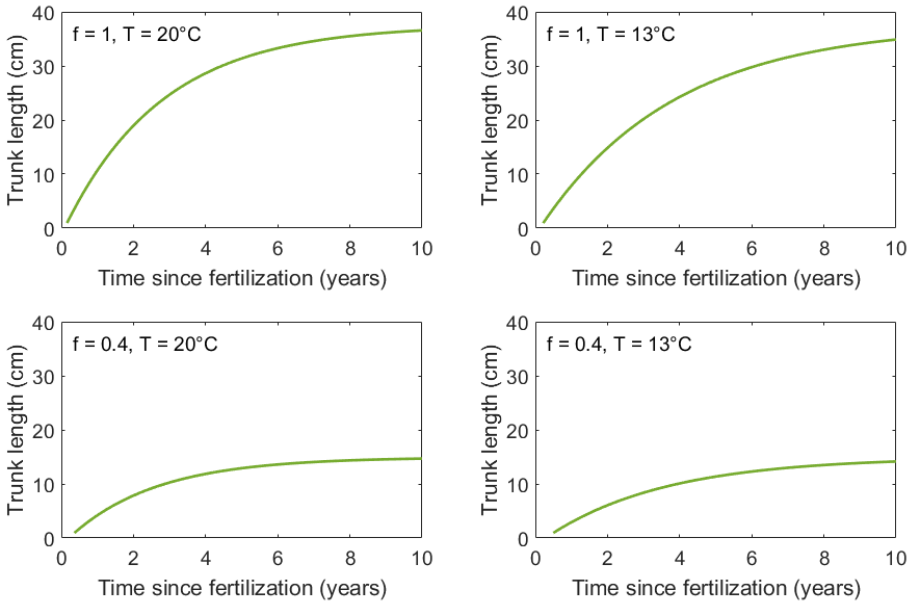


Figure 3.11 – Predictions of the abj-DEB model of the evolution of the trunk length of *Arenicola marina* under different environmental conditions (f = 1 & T = 20 °C; f = 1 & T = 13 °C; f = 0.4 & T = 20 °C; f = 0.4 & T = 13 °C) from the age at puberty a_p.

The total trunk length of *A. marina* predicted by the model was more than twice superior in optimal conditions (f = 1 and T = 20°C, around 33 cm) than in the environmental conditions recorded at Wimereux (f = 0.4 and T = 13°C, around 14 cm) (Fig.3.11).

3.3.3 Comparison of the abj-DEB parameters of *Arenicola marina* with other Lophotrochozoan species

In annelids and molluscs, the maximum assimilation rate, $\{\dot{p}_{Am}\}$, increased with the maximum structural length as expected, and more markedly after metamorphosis and the associated metabolic acceleration phase (Fig. 3.12). The values for *Arenicola marina* with the abj-model appeared lower than those of most of the other polychaetes and clitellates species before and after metamorphosis, except for the values of *Urechis caupo* (echiurian species), the only other annelid species for which an abj-model was applied. The value of the maximum assimilation rate after metamorphosis, $\{\dot{p}_{Am}\}_j$, of *A. marina* with both models was close to the one expected for the generalized animal, and followed the tendency found in most of the others mollusc species, which was not the case for the other polychaetes species, mostly showing higher values. The allocation fraction to soma, κ, was higher for *A. marina* ($\sim$ 0.92) than the one expected for the generalized animal (0.8), and did not appear inconsistent with the values of κ calculated in molluscs species (Fig.

3.12).

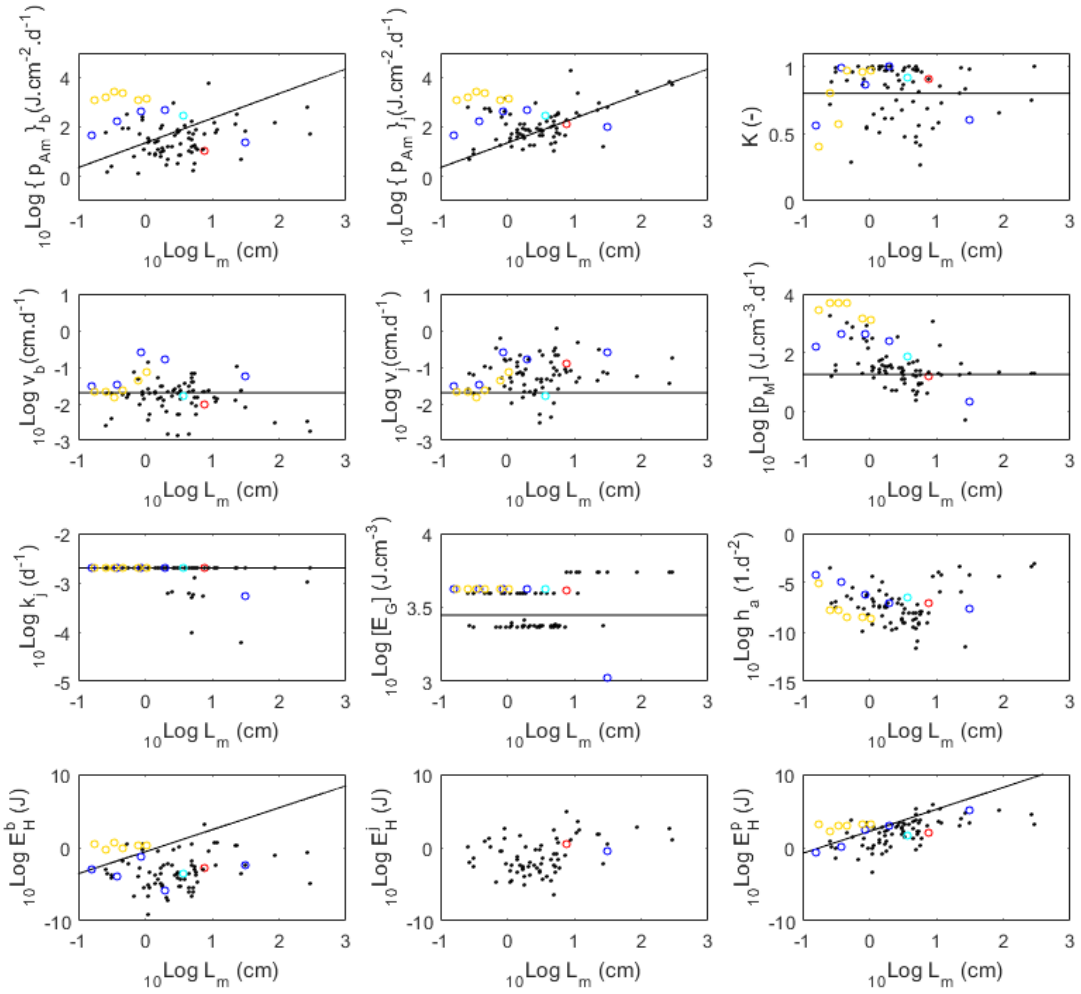


Figure 3.12 – Comparison of log-log plots of $\{\dot{p}_{Am}\}_b$ at birth and $\{\dot{p}_{Am}\}_j$ after the metamorphosis, κ, $\dot{v}_b$ at birth and $\dot{v}_j$ after the metamorphosis, $[\dot{p}_M]$, k_j, $[E_G]$, $\ddot{h}_a$, E_H^b, E_H^j, and E_H^p in Mollusca (black), Annelida Clitellata (yellow), Annelida Polychaeta (blue), standard model values for *Arenicola marina* (cyan) and abj model values from this study (red). $\{\dot{p}_{Am}\}$ is the maximum assimilation rate, κ the fraction of mobilised reserve allocated to soma, $\dot{v}$ the energy conductance, $[\dot{p}_M]$ the specific somatic maintenance costs, $\dot{k}_j$ the maturity maintenance rate coefficient, $[E_G]$ the costs of structure, $\ddot{h}_a$ the Weibull ageing acceleration, and E_H^b, E_H^j, and E_H^p the maturity thresholds for birth, metamorphosis and puberty. The lines correspond to expectations on the basis of the generalized animal (Kooijman, 2010, Table 8.1).

The energy conductance value, $\dot{v}$, for *A. marina* appeared lower in the abj- than in the std-model before metamorphosis, but the opposite happened after metamorphosis, where the abj-model's value was higher than the generalized animal but closer to molluscs' values. The specific somatic maintenance costs values, $[\dot{p}_M]$, of *A. marina* were much lower than those predicted for most of the other species of annelids (except for *Urechis caupo*) but were close to the one of the generalized animal and are consistent with the values for the molluscs species (Fig. 3.12). The value of the costs of structure, $[E_G]$, of *A. marina*

appeared equal to those of the other annelids' and most of the molluscs' species (Fig. 3.12). The value of the maturity maintenance rate coefficient, $\dot{k}_j$, of *A. marina* was equal to those of the other annelids' and of most of the molluscs' species (Fig. 3.12). The values of the maturity thresholds for birth, metamorphosis and puberty, E_H^b, E_H^j, and E_H^p, of the abj-model for *A. marina* were lower than those of the generalized animal but similar to most of the mollusc species' values (Fig. 3.12).

3.4 Discussion

In the present study, we successfully estimated the parameters of both a std- and an abj-DEB model for the lugworm *Arenicola marina*, combining the use of literature, experimental and field data. We found that the abj-model was more appropriate for modelling *A. marina*'s energy budget and life cycle and implemented it under field conditions to reconstruct feeding levels as well as *A. marina*'s growth and life cycle chronology.

3.4.1 Physiological implications of the std- and the abj- parameter estimation results

Major differences in the organisms physiology were implied by the parameter results obtained with a faster metabolism for *Arenicola marina* with a std-DEB model compared to an abj-DEB model. Indeed, $\{\dot{p}_{Am}\}_b$, $\{\dot{p}_{Am}\}_j$, $[\dot{p}_M]$ and $\dot{v}_b$ appeared higher with the std-parameter estimation, and $\dot{v}_j$ higher with the abj- parameter estimation. First, a higher value of the maximum assimilation rate $\{\dot{p}_{Am}\}$ implies a higher value of the assimilation flux from the same amount of food, and a higher value of the energy conductance $\dot{v}$ implies a larger mobilization flux (Agüera et al., 2015). The reserve capacity $[E_m]$, defined by the ratio $[E_m] = \{\dot{p}_{Am}\}/\dot{v}$ (Montalto et al., 2014) was found to be 16766 J.cm^{-3} with the std- parameter estimation compared to 1177 J.cm^{-3} with the abj- parameter estimation (considering a temperature of 20°C). In comparison, $[E_m]$ values for accelerating molluscs species were estimated around 4500 J.cm^{-3} and $[E_m]$ values for non-accelerating molluscs species were estimated around 11600 J.cm^{-3} (Add-my-Pet collection consulted in November 2018). Second, a higher value of the volume-specific maintenance costs, $[\dot{p}_M]$, implies a higher level of energy needed for the same amount of structure acquired. The comparison of the parameter estimation of the abj- and std- models therefore resulted on the one hand, with the parameter estimation of the std-model, in one organism able to store more energy in the reserve compartment, but also using more energy for the maintenance of its structure, and on the other hand, with the parameter estimation of the abj-model, in

one organism able to store less energy in the reserve compartment, but using less energy for the maintenance of its structure. Indeed, although the predictions of the std- and abj-versions of the model were quite similar (except for the early life-stages predictions), they implied really different bioenergetics in two kinds of organisms storing and using energy differently.

3.4.2 Implications of using an abj-model for *Arenicola marina* in relation with its biology and ecology

For *Arenicola marina*, the abj-model gave better fit results than the std-model (smaller MRE and SMSE), even when only few observations within the data set accounted for the acceleration period (only the zero-variate observations a_j and L_j were added, but no uni-variate observations made between birth and metamorphosis). The presence of a metabolic acceleration between birth and metamorphosis in *A. marina* might be related to its bentho-pelagic life cycle. Indeed, accelerating species have longer incubation time (before birth) than non-accelerating species (Kooijman, 2014; Kooijman et al., 2011), which might be linked to the presence of a larval dispersal phase, since a lower metabolism (in comparison with a non-accelerating species, or with juvenile or adult from the same species) allows for more dispersal time, especially when dispersal rate mainly depends on passive water transport (Kooijman, 2014). This seems in accordance with the presence of a dispersal phase happening before birth for *A. marina* and with the fact that predictions of a_{tr} and a_b of the std- model presented in this study appeared much smaller than observations, compared to predictions made by the abj-model. In lugworms, the gradual change of feeding behaviour between the first feeding at birth, the temporary settlement between birth and metamorphosis, and the semi-permanent settlement after metamorphosis on the foreshores inhabited by adults (Farke and Berghuis, 1979a, b) might be a mechanism of the increase of the metabolic acceleration s_M, also increasing the resulting specific assimilation rate (since $\{\dot{p}_{Am}\}_j = s_M \cdot \{\dot{p}_{Am}\}_b$) of the individual. The increase of the organic matter concentration within the water column during spring (spring blooms), before the second dispersal phase when metamorphosis is almost completed, might also play a role in the increase of the specific assimilation rate, increasing the amount of food available for the same feeding effort.

3.4.3 Phylogenetic implications of using abj-models for polychaetes

The metabolic acceleration rate value for *A. marina* (~ 11) falls in the range of what can be found in mollusc species (for more than 95% of the mollusc species, $1 \leqslant s_M \leqslant 27$ in the

AmP database), which seems consistent with the fact that polychaetes and molluscs both belong to the Lophotrochozoan clade, having both a common trochophore larval stage after the embryogenesis. However, although all annelids are part of the Lophotrochozoan clade, they do not all share the presence of at least one larval dispersal phase during their life cycle, and therefore, might not all experience a metabolic acceleration during their life cycle. As an example, clitellates have a direct development with no larval phase (related to their terrestrial habitat) and std-models might show better fit for these species that may not experience a metabolic acceleration during their life cycle. From an evolutionary point of view, metabolic acceleration might first have been common to all Lophotrochozoans and secondarily lost in clitellate species (as suggested by Marques et al., 2018, for other taxa). Nevertheless, since some species with no larval phase might also experience a metabolic acceleration (Kooijman, 2014), and since metabolic acceleration seem common to a large part of the species belonging to the Lophotrochozoan clade (Kooijman, 2014; Marques et al., 2018), a comparison of the use of both abj- and std- models for clitellate species should be considered.

3.4.4 Energy budget and *in situ* life cycle predictions

The predictions on the chronology of *Arenicola marina*'s life cycle stages under the *in situ* environmental conditions met at Wimereux (metamorphosis completed at around 7 months, in mid April) seemed in accordance with observations made by De Cubber et al. (2018), who spotted the first recruits of the species (e.g. juveniles after metamorphosis) in May at the same site. This would suggest a second dispersal period of less than one month if lugworms migrate after metamorphosis. Moreover, the age and length at puberty of the lugworms at the Wimereux site were predicted with the abj-model to be respectively 373.2 days and 3.5 cm, which is close to the observations made by De Cubber et al. (2018) with a length at first spawning (after the acquisition of maturity) of 3.8 cm and an age of 1.5 to 2.5 years. Newell (1949, 1948) reported the presence of *A. marina* metatrochophore larvae close to birth (and thus close to the first settlement stage) with 3 to 4 setigers and around 0.034 cm of length around 2 to 3 weeks after the occurrence of the spawning event at Whistable (UK) (limit between the English Channel and the North Sea). His observations also seem in accordance with the abj-model predictions. Indeed, the age and length at birth predictions at Wimereux in October were of 15.5 days and 0.034 cm. Since temperatures are lower in November in the English Channel and even lower in the North Sea, birth might have been slightly delayed in their study and their observations seem to be in accordance with the abj-model implemented in our study. Observations of post-larvae in mucus tubes were commonly made on fucus and pebbles areas until the end of February (Benham, 1893; Newell, 1949, 1948) and up to April in some cases (Newell, 1949). First

settlements of juveniles on adult grounds were reported by Newell (1949, 1948) at the end of April or beginning of May, which is in accordance with our model predictions (after the age at metamorphosis, which is around 5 months-old) and correspond to a dispersal period after metamorphosis of a maximum of one month.

The biggest individuals of *A. marina* collected at the studied sites might give indications on the *in situ* environmental conditions met by the lugworms on these sites. Indeed, at Wimereux, the heaviest individual collected by the authors between 2015 and 2018 weighted 10 g and the longest one measured 15.2 cm of trunk length (data not shown), which is in accordance with the length and weight predicted by the abj-model for *A. marina* at an age of 5 to 6 years old (age of the last cohort calulated by De Cubber et al. (2018)) for f = 0.4 and T = 13°C. At Le Touquet (Eastern English Channel, De Cubber et al., 2018), the heaviest individual collected weighted 53.1 g and the longest one measured 20.2 cm of trunk length (data no shown), and at Fort Mahon (Eastern English Channel, De Cubber et al., 2018), the heaviest individual collected weighted 26 g and the longest one measured 18.4 cm of trunk length (data not shown). Since no major difference between the seawater temperature at the three different sites exist, the main difference was possibly the food availability. The comparison of these biometric values with the ones predicted by the abj-model (around 600 g of maximum wet weight and 35 cm of maximum trunk length for f = 1 and T = 13°C) seems to indicate that f was higher at Le Touquet and Fort Mahon compared to Wimereux.

In the different sites of the Eastern English Channel cited previously, De Cubber et al. (2018) showed that the lugworms' recreational harvest in 2017 removed more than 500 000 lugworms and represented a total retail value of around 232 447 euros. The need for implementing management measures was also evidenced for at least one beach by these authors. Knowing the food levels of the different sites might then enable predictions with the abj-model on the *in situ* ages and lengths at puberty, which could help managers to implement relevant regulations if needed such as a relevant harvest minimum size limit on the different sites showing highly variable food levels and maximum lengths and weights.

3.4.5 Possible future extensions of the model

In order to provide the best model possible for *Arenicola marina* further adjustments could be implemented linked to the species life cycle and habitats. First, defining the temperature tolerance range of the species could improve the abj-model by applying better temperature corrections. Growth experiments from Farke and Berghuis (1979) seem to point out a higher boundary of the temperature tolerance range T_H around 25 °C. Other studies suggest a lower boundary of the temperature tolerance range T_L under 5°C (Sommer et

al., 1997; Wittmann et al., 2008), but no Arrhenius temperatures beyond the temperature tolerance (T_{AH} and T_{AL}) range could be calculated yet. Further experiments on growth or respiration under temperatures beyond the temperature tolerance range could be performed to define T_{AH} and T_{AL} and thus improve the temperature correction.

During their life cycle, the different stages of *A. marina* inhabit different marine habitats with different ranges of temperature variation. From the metatrochophore to the post-larval stage the lugworms inhabit the subtidal area were seawater temperature does not fluctuate that much daily, compared to the intertidal areas inhabited by the juveniles and adults, where temperature can change dramatically during one day. As an example, a variation of 15°C was recorded within the sediment at the Wimereux site in November 2017 (Fig. 3.13). In this study, the Arrhenius temperature was calculated from the oxygen consumption rate of juveniles living on the upper shore. We hypothetize that a different Arrhenius temperature may exist for the larval and post-larval stages living in habitats with a more stable temperature, as suggested by Kooijman (2010). Further experiments could be implemented on larvae in order to record physiological rates and estimate their Arrhenius temperature.

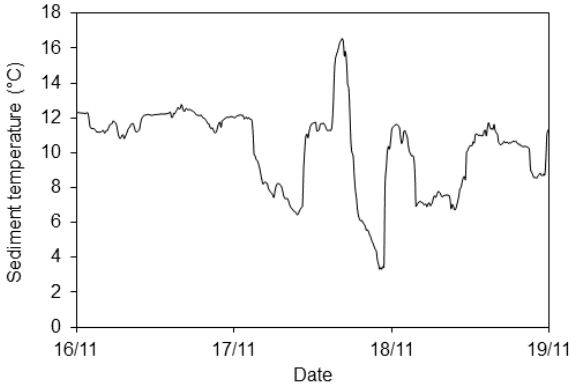


Figure 3.13 – Sediment temperature (upper shore, 10 cm deep) recorded every 10 min at Wimereux (Hauts-de-France, Eastern English Channel) between the 16 of November and the 19 of November 2017 with a HOBO probe.

Monaco and McQuaid (2018) highlighted the interest of adding to the temperature correction an aerial exposure term M_d (linked to tidal height and the position of organisms on the shore) in foreshore habitats showing wide fluctuations in temperature and desiccation. Given the intense variations experienced by juvenile and adult lugworms (Fig. 3.13), it might be interesting to add an aerial exposure term for the species. Indeed, the underestimation of growth by the model compared to our observation of growth of juveniles in the laboratory (Exp. C) might be linked to the fact that no tide was simulated and lugworms stayed immersed during all the experiment time, without the stress brought by high temperature variations and aerial exposure. However, it was found that lugworms

gradually migrate down the shore while growing (De Cubber et al., 2018), so the aerial exposure correction, if implemented, should gradually decrease during the life cycle of the organism as well.

DEB models as implemented here enable to reconstruct the growth and the reproduction of a species at the individual level. However, in order to be used in a population context, DEB theory can be associated to individual-based models (IBM) in order to explore properties of both individual life-history traits and population dynamics (Bacher and Gangnery, 2006; Martin et al., 2012). The association of the abj-model developed here, and providing predictions on the duration of the larval dispersal phase, with biophysical larval dispersal models (Nicolle et al., 2017) could also allow the understanding of the populations' connectivity in the area and thus give valuable information for the conservation of the species.

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Chapter 4

Life is better down the shore: investigating migration effects on individual growth and reproduction of the ecosystem engineer *Arenicola marina*

Life is better down the shore: Investigating migration effects on individual growth and reproduction of the ecosystem engineer *Arenicola marina*

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Abstract *Arenicola marina* (Annelida Polychaeta) is an ecosystem engineer inhabiting galleries within soft-sediment foreshores from the Mediterranean to the Arctic. The species is commonly harvested for bait, and some regulation may be necessary in some areas. *A. marina* displays a typical distribution pattern on most foreshores, with the juveniles inhabiting the higher mediolittoral shore and adults inhabiting the lower shore (low mediolittoral to infralittoral). Individuals are supposed to migrate gradually down the shore when growing. In this study we characterized the *in situ* shore migrations of a local population of *A. marina* by repeated field samplings on different levels of the shore at Wimereux (Eastern English Channel). A sand temperature model was developed in order to predict the temperature experienced by lugworms according to the depth of their galleries and their bathymetric level. The availabilityof food and the associated scaled functional response were estimated from *in situ* measurements of the nitrogen content of the sand and chlorophyll-a concentration of the seawater data, and from *in situ* growth data. The metabolic response of lugworms to temperature (temperature tolerance range, related Arrhenius temperatures and subsequent temperature correction to the metabolic rates) was assessed from literature data (growth, oxygen consumption, fertilization success and mitochondrial respiration experiments). The potential for individual growth and reproduction of *A. marina* under different migration scenarios was estimated with a Dynamic Energy Budget model. Sediment temperature alone when migrating did not allow greater growth and egg production. However, an increase of food concentrations down the shore increased growth and egg production. Other factors could be taken into consideration in further studies such as desiccation or hypoxia during emersion periods at low tide.

Keywords Dynamic Energy Budget, Sediment temperature model, Lugworm, Metabolic activity, Intertidal environment

4.1 Introduction

Arenicola marina (L.) is a marine benthic polychaete (Annelida) living burrows of 5 - 10 cm deep for juveniles and 30 cm deep for adults on intertidal coastal sediments, and distributed from the Mediterranean to the Arctic (Longbottom, 1970; Volkenbron, 2005). This polychaete is considered to be an ecosystem engineer, as it creates bioturbation through sediment reworking, enhancing the oxygenation of the sediment by flushing its burrow, selecting species at the expense of others (Clarke et al., 2017; Kristensen, 2001; Reise, 1985; Volkenborn, 2005). Lugworms are commonly harvested for bait in several countries, where their commercial value can be considerable (De Cubber et al., 2018: Watson et al, 2017), leading to some negative impacts on the associated species or on the harvested *A. marina* population itself (Beukema, 1995; Clarke et al., 2017; Olive, 1993). Consequently, the need for implementing management measures for some populations of *A. marina* has been evidenced in the Eastern English Channel (De Cubber et al., 2018), and some management measures have already been implemented in Europe, such as licensing in the UK (Watson, 2015) or quotas in Portugal (Xenarios et al., 2018).

However, those management measures rarely rely on the local ecology and life-history traits of the species (Watson et al., 2017). *A. marina* displays a bentho-pelagic life cycle, with larvae dispersing in the water column and temporarily settling for 6 to 7 months on subtidal bottoms (macroalgae and mussel beds), where they live in mucus tubes attached to the substrate and feed on suspended and deposited particles around their tube. Then, a second dispersal phase precedes the lugworms' settlement on the foreshores (considered as the recruitment), where the juveniles and later adults live in galleries and are psammivorous, swallowing the sediment enriched with organic matter (De Cubber at al., 2019; Farke and Berghuis, 1979a, b; Newell, 1948; 1949; Reise, 1985; Reise et al., 2001). Recently, a Dynamic Energy Budget (DEB) model has been developed by De Cubber et al. (2019) in order to explore the time scale of the appearance of the different life-stages of *A. marina*. DEB models enable to predict individual growth and reproduction of a species as well as several of its life-history traits (age at metamorphosis, puberty, etc.) according to the environmental conditions (temperature and food) by quantifying the energy fluxes (Kooijman, 2010). Therefore, when local environmental conditions (temperature and food resources) are known, the DEB models can provide valuable data on the biology of a targeted species to help managers to implement management measures.

Up to now, the DEB model implemented for *A. marina* only considered changing environmental conditions for the early life-stage phases (before recruitment) (De Cubber et al., 2019). For juveniles and adults, mean (constant) environmental conditions (mean seawater temperature and mean food proxy) were used to be compared with field data

(De Cubber et al., 2019). However, since lugworms live within the intertidal area, they experience high daily temperature variations (De Cubber et al., 2019) that may change according to their location on the shore (bathymetric level) and according to the depth of their gallery. Specific physiological and behavioural responses of intertidal species may be triggered by heat stress such as a decrease in physiological performances in the mussel *Mytilus californianus* outside its optimal temperature tolerance range, or tower formation in the gastropod *Echinolittorina malaccana* (Kish et al., 2016; Seuront and Ng, 2016). Theses responses appear then crucial to be taken into account when considering the metabolism of intertidal species. As a matter of fact, the distribution of juvenile and adult lugworms on the foreshore is not random and has been widely documented, describing juveniles recruiting on the high mediolittoral part of the shore and gradually migrating down to the high infralittoral part of the shore (Cadman, 1997; De Cubber et al., 2019, 2018; Farke et al., 1979; Reise, 1985; Reise et al., 2001). Some variations of this distribution in some sites, where individuals are almost only present on the lower mediolittoral to high infralittoral foreshore, may occur (De Cubber et al., 2018). Understanding this typical distribution pattern might be vital in further population dynamic models (Martin et al., 2012), used by managers to predict the effect of their management plans.

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

1. to reconstruct the sand temperature of the foreshore according to the depth of the galleries and the bathymetric level, as well as to measure local food levels
2. to estimate the metabolic response of lugworms to temperature (via the Arrhenius temperature) and to different proxy for food sources and quantities (via the scaled

functional response)

3. to characterize the *in situ* shore migrations of a local population of *A. marina*
4. to compare the potential for growth and reproduction of individuals of *A. marina* under different migration scenarios.

4.2 Material and Methods

4.2.1 Study area

Lugworms and the associated environmental parameters were collected at Wimereux (N 50°46'14", E 01°36'38"), located on the Eastern English Channel (Hauts-de-France, France) (Fig. 4.1). The area is composed of a mixture of sandy and rocky bottoms, and the tidal regime is semi-diurnal and macrotidal with amplitudes that may exceed 8 m around 2 days before the full moon (Migné et al., 2004; Rolet et al., 2015). In this area, the population of *Arenicola marina* is mainly found on the high mediolittoral to low mediolittoral/infralittoral part of the foreshore and therefore exposed to emersion periods of several hours (De Cubber et al., 2018). Densities of *A. marina* have been reported to range from 0 to 61 individuals.m^2 with the greatest abundancy on the high mediolittoral shore constituted by smaller individuals. More details on the study site and the population of *A. marina* of the area are given in De Cubber et al. (2018).

4.2.2 Compilation of *in situ* observations

A dataset of physical measurements collected in the area of the study site was compiled to force a sediment temperature model based on the model developed by Guarini et al. (1997) for mudflats (Fig. 4.2). The wind speed U (m.s^{-1}), the air temperature T_{Air} (K), the relative humidity H_r (%), the atmospheric pressure P_{atm} (Pa) and the irradiance R_s (J.m^{-2}) were extracted from environmental data recorded hourly at Boulogne-sur-Mer (N 50°43'35", E 01°36'53") (wind speed, air temperature, relative humidity and atmospheric pressure) and Calais (N 50°56'53", E 01°51'23") (irradiance) (France) by Meteo France ltd. (https://donneespubliques. meteofrance.fr/) during the years 2017 and 2018. The water height H_w (m) (Fig. 4.2) was obtained for the same years from the Marel Carnot station (http://www.ifremer.fr/co-en/eulerianPlatform) at the tide gauge of Boulogne-sur-Mer and compared to the elevation of the three shore points (Fig. 4.1), obtained from the inter-regional project CLAREC, INSU-CNRS M2C-UNICAEN (http://www.unicaen.fr/ data-clarec/home/elevations.html) according to the local marine altimetric references (SHOM,

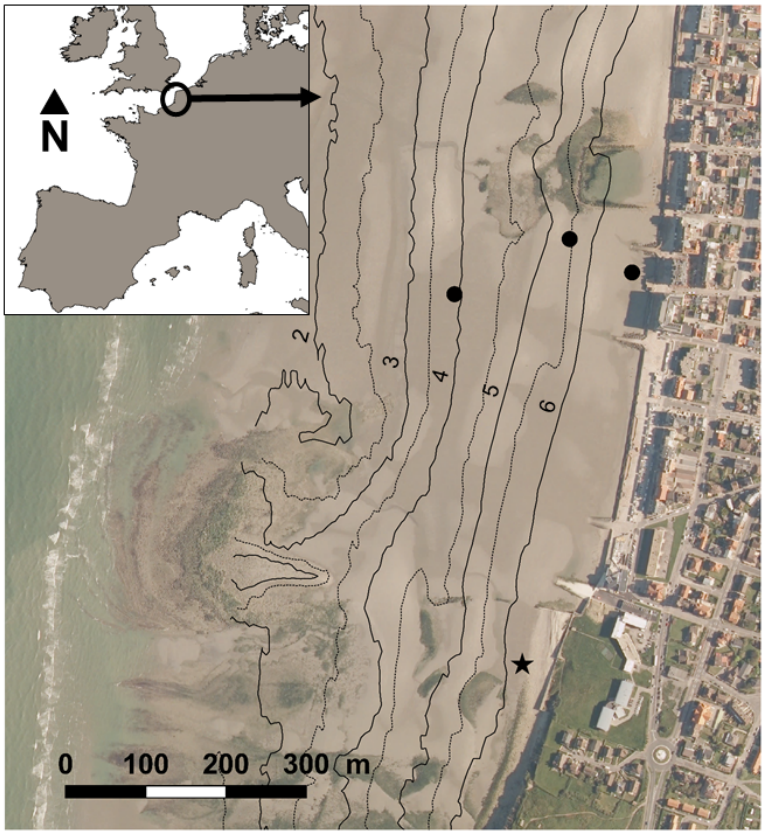

Figure 4.1 – Study site of Wimereux (Eastern English Channel, France) and location of the sampling points for the sediment temperature measurements with two HOBO® Water Temp Pro v2 probes fixed on a metal rod embedded in the sediment (star), and for the size structure of the *Arenicola marina* population (dots) on different bathymetric levels (lines with numbers) of the foreshore.

2017). The water temperature T_w (K) consisted in hourly measurements from the same Marel Carnot station coupled with monthly observations made by the Service d'observation en milieu littoral (SOMLIT, http://somlit-db.epoc.u-bordeaux1.fr/bdd.php) at Wimereux (coastal bottom point), when data of the Marel Carnot station were missing. The chlorophyll a concentration of the seawater *Chla* ($\mu g.L^{-1}$) was also retrieved from the Service d'observation en milieu littoral (SOMLIT, http://somlit-db.epoc.u-bordeaux1.fr/bdd.php) at Wimereux (coastal point) in order to be tested as a proxy of the food levels.

4.2.3 Field sampling and laboratory measurements

Follow-up of the *Arenicola marina* population structure at Wimereux From March 2017 to July 2018, around 30 individuals of *A. marina* were sampled 8 times at three locations of the foreshore from the mediolittoral/infralittoral to high mediolittoral at the study site (Fig. 4.1). There, the population of *A. marina* has already been shown to display

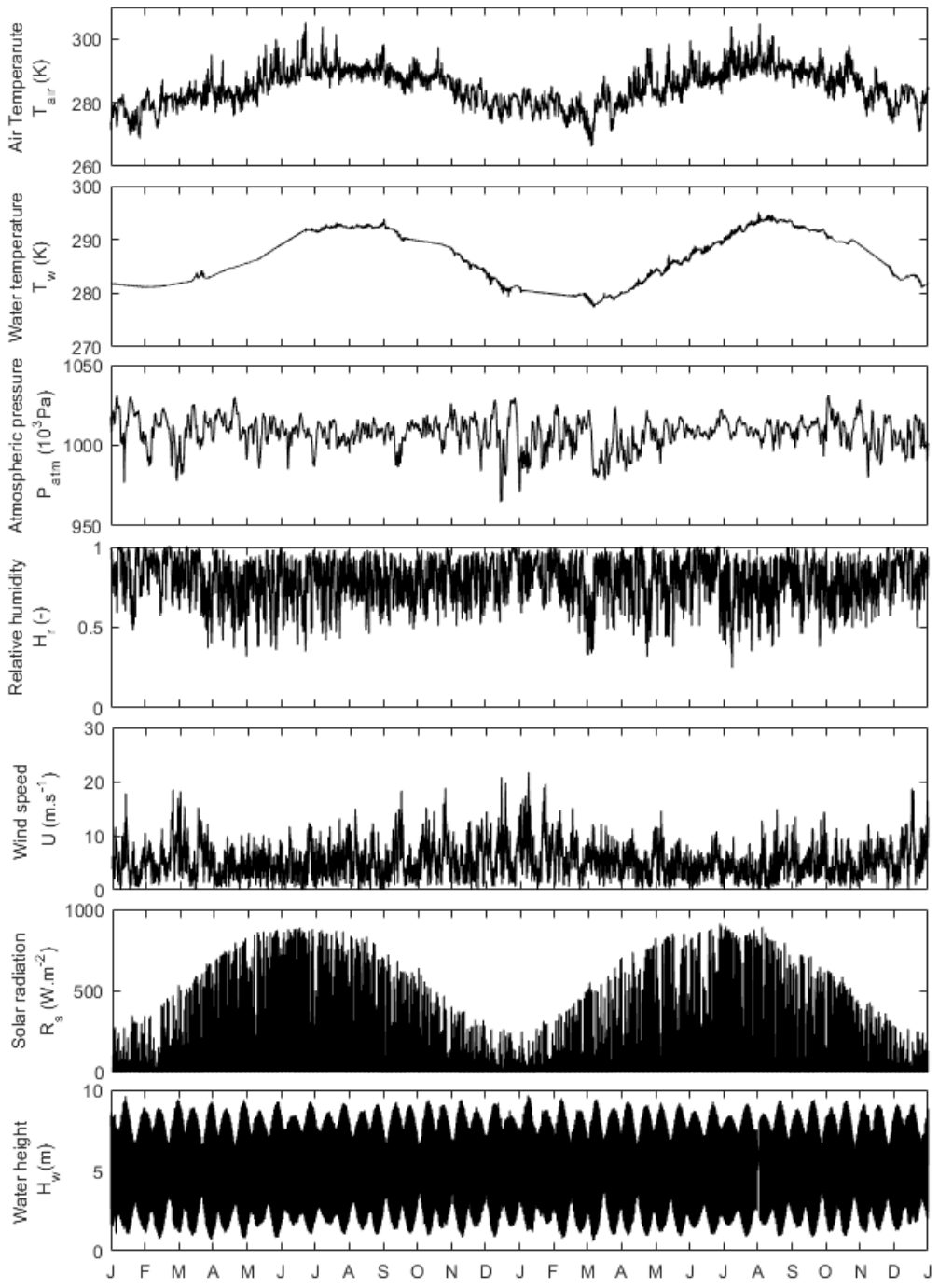

Figure 4.2 – *In situ* air temperature (T_{air}, K), seawater temperature (T_w, K), atmospheric pressure (P_{atm}, 10^3.Pa), relative humidity (H_r, -), windspeed (U, m.s^{-1}), solar radiation (R_s, W.m^2) and water height (H_w, m) used as forcing variables to constrain the sediment temperature model 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 was available (high-frequency measurements) and SOMLIT otherwise (low frequency measurements).

the typical spatial distribution (De Cubber et al., 2018) described by other authors with juveniles on the higher shore and adults elsewhere (Farke et al., 1979).

Follow-up of the nitrogen content of the sediment Triplicates of surface sediment cores (1 cm deep x 10 cm of diameter) were collected at the same three locations of the study site at every sampling period in order to assess the organic matter content of the sediment. Once collected, samples were kept at -20°C until analysis. Homogenised aliquots of around 30 g of each of the subsamples were then put in a separate tin containers and analyzed with an organic elemental analyser Thermofisher Flash 2000 after calibration, in order to measure the carbon and nitrogen contents of the sediment. For each sample, one subsample was burnt during 5 h at 550°C in order to remove the organic carbon and nitrogen, and another one was dried out at 40°C during 1 day. The calibration was performed by analyzing the carbon and nitrogen contents of several sediment samples for which the elemental contents were known. The organic carbon content of the sediment was obtained substracting the amount of inorganic carbon (estimated from the sediment burnt at 550 °C) to the total amount of carbon (estimated from the sediment dried out at 60°C during 1 day). Given the low nitrogen concentrations of the sediment and the detection levels of the device, only the total nitrogen content (organic + inorganic) of the sediment could be measured.

Follow-up of the temperature variations within the sediment Temperatures within the sediment (*ca* 5 cm and 21 cm deep) were recorded with two HOBO® Water Temp Pro v2 probes fixed on a metal rod embedded in the sediment on the higher shore (high mediolittoral) of the study site between the 01/10/17 and the 24/10/17 and between the 03/05/18 and the 01/07/18 (10 min interval between each measurement) (Fig. 4.1).

4.2.4 Data analysis

Sediment temperature model

The model The sediment temperature model helped to solve the sediment temperature (T_s) equation adapted from Guarini et al. (1997), where t is the time (s), z is the depth (m), η is the heat conductivity (W. m^{-1}. K^{-1}) and μ is the thermal diffusivity (m^2. s^{-1}) of the sediment (Equation 4.1).

$$\frac{\eta}{\mu} \cdot \frac{\delta T_s(z,t)}{\delta t} = \frac{\delta}{\delta z} \cdot \eta \cdot \frac{\delta T_s(z,t)}{\delta z} \tag{4.1}$$

The partial differential equation was solved on Matlab 2015b using the pdepe function considering heat energy balance equations at the boundaries z_0 = 0 m (sediment surface) and z_1 = 1 m deep (beyond this depth, the sediment temperature is supposed equal to the one of the water) (Tables 4.1, 4.2). At emersion time, the surface temperature was calculated from the heat energy balance between the solar radiation, the atmosphere radiation, the sand radiation, the sand-air heat conduction and the evaporation fluxes, and the 1 m depth temperature from the sand-water heat conduction flux (Tables 4.1, 4.2) (Guarini et al., 1997; Savelli et al., 2018). At immersion time, both surface and 1 m depth temperatures were calculated from the sand-water heat conduction flux (Tables 4.1, 4.2) (Guarini et al., 1997).

Table 4.1 – 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.m^{-2}) equations		
Solar radiation	$R_{sun} = R_{obs}$	
Atmosphere radiation	$R_{atm} = \varepsilon_a \cdot \sigma \cdot T_{air}^4 \cdot (\zeta - k)$	
	$\varepsilon_a = 0.937 \cdot 10^{-5} \cdot T_{air}^2$	
	$k = R_{obs}/R_{std}$	
	$decl = 23.45 \cdot sin\left(360 \cdot \frac{284 + day_{julian}}{365}\right)$	
	$R_1 = \left(\sqrt{1 + 0.33 \cdot cos\left(\frac{360 \cdot day_{julian}}{365}\right)}\right)^{-1}$	
	$cos_z = sin(decl) \cdot sin(latitude) + cos(decl) \cdot cos(latitude) \cdot cos((hour_{light} - 12) \cdot 15)$	
	$R_{std} = R_0 \cdot \frac{cos_z}{2 \cdot R_1^2} \cdot \left(1 + cos(\frac{2 \cdot \pi \cdot (hour - 1)}{length_{daylight}}\right)$	
Sand radiation	$R_s = \varepsilon_M \cdot \sigma \cdot T_s(z_0,t)^4$	
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	$S_{s-w} = -\frac{\eta}{h_w} \cdot (T_s(z_0,t) - T_w(t))$	

Validation of the model The parameters related to the sediment type for which no data for sandy sediments were available (η, μ, and ζ) were estimated comparing the model output with our *in situ* sediment temperature measurements (HOBO® probes) for the two recording periods partly according to Guarini et al. (1997) (Table 4.2). The estimation procedure was performed on Matlab 2015b using the fminsearch function. For each period, three tidal cycles of one emersion and one immersion period (approximately 36 hours) were chosen randomly among all, 23 times for the first and shortest *in situ* temperature recording period (October 2017, 36 cycles in total) and 63 times for the second *in situ* temperature recording period (May-June 2018, 107 cycles in total). The estimation procedure was applied to these periods minimizing the mean square error (MSE) between the data and the model predictions. For each *in situ* temperature recording period, the mean parameter value was computed as well as its standard deviation. These two means were compared with a non-parametric Krukal-Wallis test performed on Matlab R2015b. The mean value of these means was used as parameter value in the implementation of the model. The parameter values obtained were then used to compute the sediment temperature on the three sampled shore levels from the surface to 1 m deep as well as the daily mean and variance of the sediment temperature at these depths.

Table 4.2 – 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*	$\mu = 5.2164 \cdot 10^{-7}$ m^2.s^{-1}	Calibrated in this study
Conductivity of the sand*	$\eta = 3.3182$ W.m^{-1}.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	$\varepsilon_M = 0.96$ -	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	$R_0 = 1353$ W.m^{-2}	Brock et al. (1981)
Bulk coefficient for evaporation	$C_V = 0.0014$ -	Guarini et al. (1997)
Air volumetric mass	$\rho_a = 1.2929$ kg.m^{-3}	Guarini et al. (1997)
Specific air heat	$C_{Pa} = 1003$ J.kg^{-1}.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

Effect of temperature on metabolic rates for *Arenicola marina*

All metabolic rates depend on temperature (Kooijman, 2010). Within the species-specific temperature tolerance range, the effect of temperature on metabolic rates can be described with the Equation (4.2), with T the temperature (K), T_{ref} the reference temperature (taken to be 293.15 K), T_A the Arrhenius temperature (K), $\dot{k}_1$ the rate of interest at T_{ref}, and $\dot{k}$ the computed rate at T. Outside the lower and higher boundaries of the species-specific temperature tolerance range (respectively T_L and T_H), the effect of temperature on metabolic rates changes and is calculated adding an extra term to the Equation (4.2) as presented in Equation (4.3), with T_{AL} the Arrhenius temperature below the lower boundary of the species-specific temperature tolerance range (K) and T_{AH} the Arrhenius temperature above the higher boundary of the species-specific temperature tolerance range (K) (Kooijman, 2010).

$$\dot{k}(T) = \dot{k}_1 \cdot \exp\left(\frac{T_A}{T_{ref}} - \frac{T_A}{T}\right) \tag{4.2}$$

$$\dot{k}(T) = \dot{k}_1 \cdot \exp\left(\frac{T_A}{T_{ref}} - \frac{T_A}{T}\right) \cdot \frac{1 + \exp\left(\frac{T_{AL}}{T_{ref}} - \frac{T_{AL}}{T_L}\right) + \exp\left(\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T_{ref}}\right)}{1 + \exp\left(\frac{T_{AL}}{T} - \frac{T_{AL}}{T_L}\right) + \exp\left(\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T}\right)} \tag{4.3}$$

The Arrhenius temperature of *A. marina* within its temperature tolerance range T_A was taken from De Cubber et al. (2019). The boundaries of the temperature tolerance range T_L and T_H and the related Arrhenius temperatures T_{AL} and T_{AH} were then fitted using a dataset constituted of one growth experiment (De Wilde and Berghuis, 1979), one fertilization success experiment (Lewis et al., 2002), one oxygen consumption experiment (Schröer et al., 2009) and one mitochondrial respiration experiment (Sommer and Pörtner, 2004), all four at several temperatures. All rates of each experiment were divided by the maximum rate recorded for this experiment in order to be scaled between 0 and 1. T_L and T_{AL} on the one hand, and T_H and T_{AH} on the other hand, were estimated by fitting a temperature correction equation (Equation 4.3) to the observed scaled rates minimizing the MSE using the fminsearch function on Matlab 2015b. For the estimation of T_L and T_{AL}, only the rates corresponding to a temperature $T < Tref$ were used. For the estimation of T_H and T_{AH}, only the rates corresponding to a temperature $T > 275.65$ K were used.

Estimation of *in situ* growth and scaled functional response reconstruction

For each sampling date, the population structure was approached through the analysis of size frequencies on the trunk length (TL) with a 5-mm size class interval, using a Bhattacharya analysis (De Cubber et al., 2018). Each cohort belongs to a separate year

since spawning and recruitment only happen once a year (De Cubber et al., 2018). In order to reconstruct the actual temperature experienced by the collected lugworm, the mean depth of the lugworms between each sampling date was assessed using the linear relation presented in Equation (4.4), with TL (cm) the mean trunk length of the cohort and z (cm) the associated depth of the gallery (considering that juveniles of 1 cm of trunk length dig a gallery of 5 cm of depth while adults of 12 cm of trunk length dig a gallery of 30 cm of depth). The mean sediment temperature at this depth was then calculated by considering the proportion of individuals belonging to this cohort collected on the different bathymetric levels of the beach.

$$z = 30 - 25 \cdot \frac{12 - TL}{12 - 1} \tag{4.4}$$

The DEB parameters of an abj-DEB model for *A. marina* estimated by De Cubber et al. (2019) were used to model the growth and reproduction of the lugworms according to the *in situ* sediment temperature previously estimated. The growth before recruitment (or up to metamorphosis) was reconstructed using the environmental conditions detailed in De Cubber et al. (2019) to recreate relevant initial conditions of the growth of recruits once settled. From metamorphosis time, between each collection date, the trunk length growth was reconstructed using the DEB equations detailed in De Cubber et al. (2019) for a scaled functional response f varying from 0.01 to 1. The scaled functional response enabling the best fit (with the lowest MSE between growth observations and predictions) was then used as the mean scaled functional response for this time step.

Linking the scaled functional response to food resources

The mean total nitrogen content of the sediment available for the recruits was reconstructed from the values of total nitrogen content obtained on each bathymetric level of the shore and the proportions of the contribution of each bathymetric level to the total recruits cohorts. The mean concentration of chlorophyll a in the water column for each time step corresponding to one reconstructed f level and the reconstructed total nitrogen content of the sediment were then tested as a proxy of the food density. The relation between the scaled functional response and the food density X (chlorophyll a concentration or nitrogen content) is presented in Equation (4.5), where X_K is the half-saturation coefficient (Kooijman, 2010). For the mean chlorophyll a concentration, the value of X_K was fitted using Equation (4.5) as the value for which the lowest MSE value between simulations and observations was obtained.

$$f = \frac{X}{X + X_K} \tag{4.5}$$

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

Several scenarios were tested in order to assess the impact of the food and temperature conditions (according to the shore location of the lugworms and the depth of the gallery) on the individual growth and reproduction of *A. marina* (Fig. 4.3). The environmen-

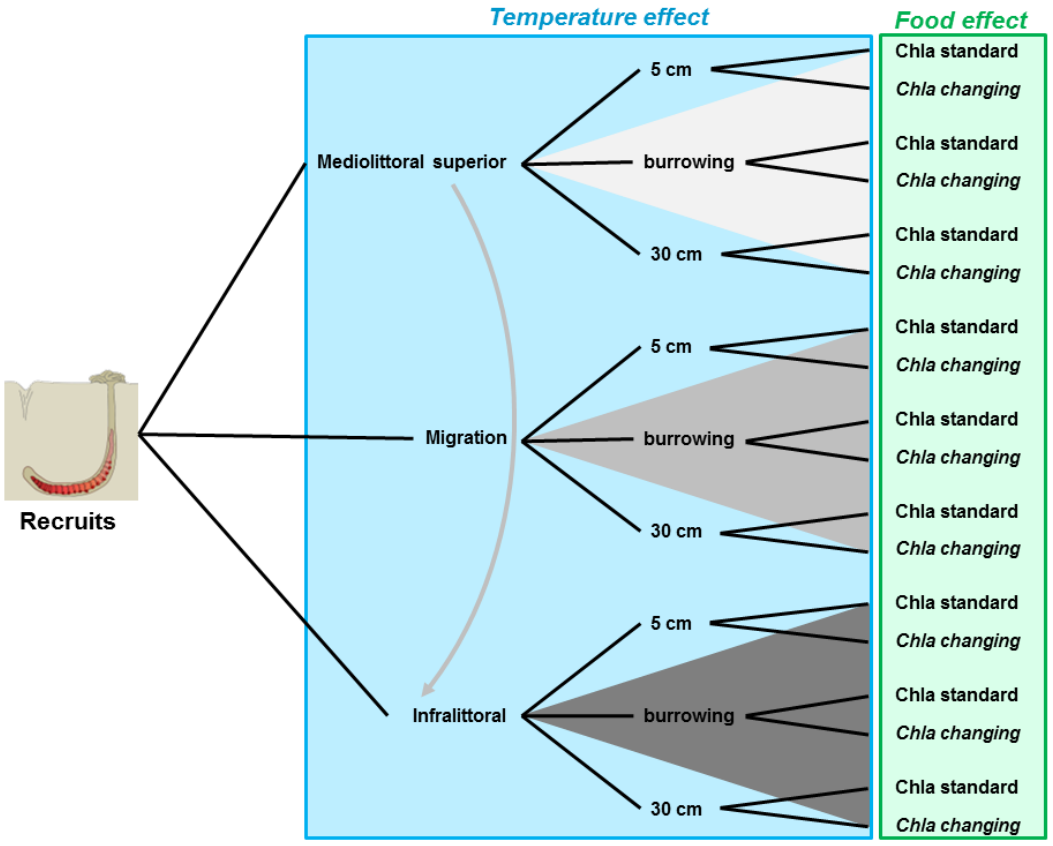

Figure 4.3 – Representation of the different scenarios. In the light grey scenarios, lugworms recruit on the high mediolitoral shore without migrating. In the medium grey scenarios, lugwormd migrate according to the Equation for bathymetry estimated previously. In the dark grey scenarios, lugworms recruit 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 (4.4). for all these scenarios, we considered on the one hand that chloropyll-a concentrations were the same everywhere on the shore, or on the other hand that chloropyll-a concentrations were divided by 2 on the higher shore compared to the lower shore, increasing linearly between these two locations.

tal conditions over 1.5 year were reconstructed from the repeated 2-years reconstructed sediment temperature, the 2-year measurements of the Chla concentration of the seawa-

ter and the half-saturation coefficient previously estimated. The associated temperature corrections and functional response were applied to the abj-DEB model for *A. marina* developed by De Cubber et al. (2019), allowing predictions on the trunk length, wet weight and egg number. The spawning event was triggered when wet weight of the eggs reached 10 % of the total wet weight according to predictions on growth under constant environmental conditions with annual spawning events made by De Cubber et al. (2019). The initial conditions at metamorphosis (after which juveniles recruit) were estimated at environmental conditions given by De Cubber et al (2019). Three main scenarios were emisionned:

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

(2) lugworms were supposed to migrate according to the Equation for bathymetry estimated previously

(3) lugworms were supposed to recruit directly on the infralittoral shore (Fig. 4.3)

For these three options, lugworms remained burrowed at 5 or 30 cm, or were able to burrow from 5 to 30 cm according to the Equation (4.4). Finally, 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. The effects of the change of food and temperature were estimated comparing the different DEB model outputs ran with those scenarios (Fig. 4.3).

4.3 Results

4.3.1 Spatial distributions of trunk length frequencies

The spatial distribution of trunk length frequencies showed the common pattern with the smaller individuals closer to the coast line than the longer ones (Fig. 4.4). For both years, recruitment happened after March and before the end of May. The largest trunk classes (from 8 to 10 cm of trunk length) were mainly represented at the infralittoral sampling point but disappeared after mid May 2017. At the higher sampling points, some larger trunk length classes disappeared at the next sampling period lower on the shore (Fig. 4.4, for example between May 2018 and July 2018, the individuals larger than 3.5 cm disappeared from the high mediolittoral but were still found lower on the shore). This might be due to mortality, or more probably, small scale migrations down the shore.

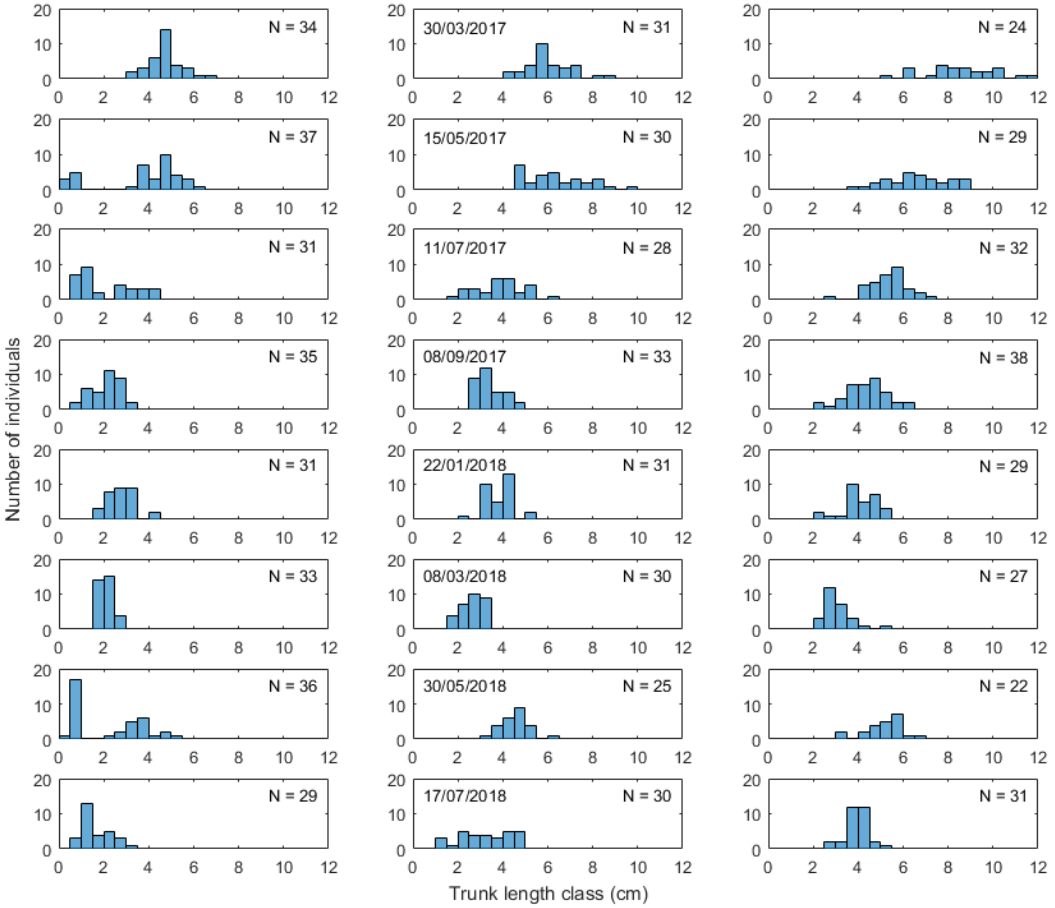

Figure 4.4 – Distribution of the trunk length frequencies of *Arenicola marina* on the high mediolittoral (left), low mediolittoral (middle) and infralittoral (right) at the study site (Wimereux, Eastern English Channel) for each sampling date from the 30/03/2017 to the 17/07/2018. N stands for the number of individuals collected.

4.3.2 Temperature within the sediment

Validation of the sediment temperature model The mean fitted values of the constant ζ, the thermal diffusivity μ, and the conductivity η were respectively 1.21, 5.22 e^{-07} $m^2.s^{-1}$ and 3.32 $W.m^{-1}.K^{-1}$ (Table 4.3). The mean values of ζ and η did not show any significant difference if both parameters were estimated to fit the observations from October 2017 or the ones from May-June 2018 (Kruskal-Wallis test, $p > 0.05$). However, there was a significant difference between the value of μ estimated to fit the observations from October 2017 (5.3307 e^{-07} $m^2.s^{-1}$) and the one estimated to fit the observations from May-June 2018 (5.1021 e^{-07} $m^2.s^{-1}$) (Kruskal-Wallis test, $p < 0.05$) (Table 4.3, Fig. 4.5).

The estimated mean parameter values of η, μ and ζ provided a good fit of the sediment temperature model for the May-June 2018 sediment temperature observations at 5 cm

deep and at 20 cm deep (Fig. 4.6 c, d). The fit was not as good when considering the sediment temperature observations of October 2017 at both depths (Figs. 4.6 a, b).

Table 4.3 – Mean values of the fitted parameters ζ (constant, no unit), μ (thermal diffusivity, $m^2.s^{-1}$), and η (conductivity, $W.m^{-1}.K^{-1}$) 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 ($W.m^{-1}.K^{-1}$)	3.2887 ± 0.2237	3.3477 ± 0.3301	0.24	3.3182 ± 0.2850
μ ($m^2.s^{-1}$)	$5.3307e^{-07} \pm 4.7936e^{-08}$	$5.1021e^{-07} \pm 4.7197e^{-08}$	0.04	$5.2164e^{-07} \pm 5.0239e^{-08}$
ζ (-)	1.1903 ± 0.1854	1.2332 ± 0.1412	0.63	1.2118 ± 0.1675

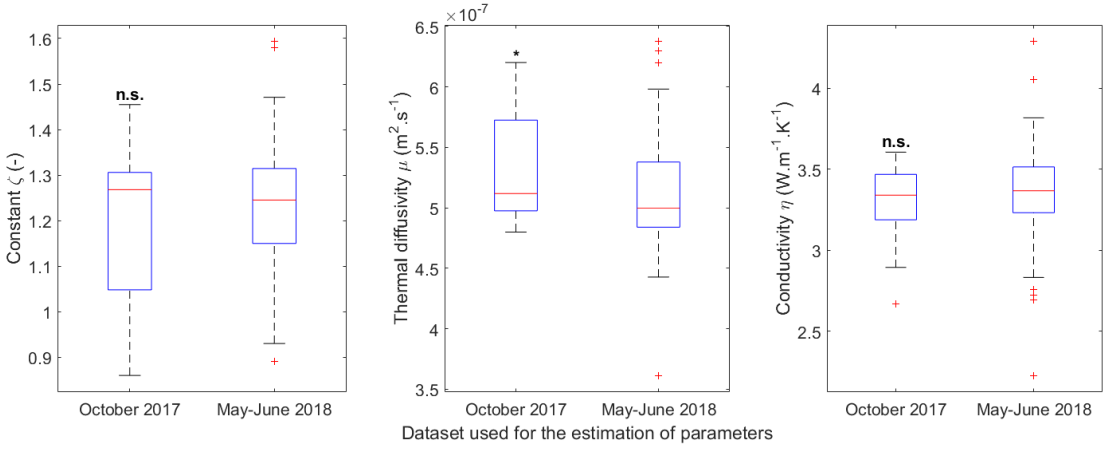

Figure 4.5 – Boxplot representations of the distribution of the fitted values of the constant ζ (-, left), the thermal diffusivity μ ($m^2.s^{-1}$, middle), and the conductivity η ($W.m^{-1}.K^{-1}$, right). For each parameter, the red line is the median of the 23 values obtained for October 2017 and 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 ($p < 0.05$).

Predicted trends of the sediment temperature variations according to time and space

In general, the sediment temperature reconstructed by the model reproduced the trends of the observed air, water temperatures, and solar radiation, showing higher temperature in summer and lower temperature in winter at all bathymetric levels (Fig. 4.7a, b, c). The amplitude of the sediment temperature as well as its daily variance was smaller on the infralittoral (rather driven by the water temperature) compared to the higher foreshore

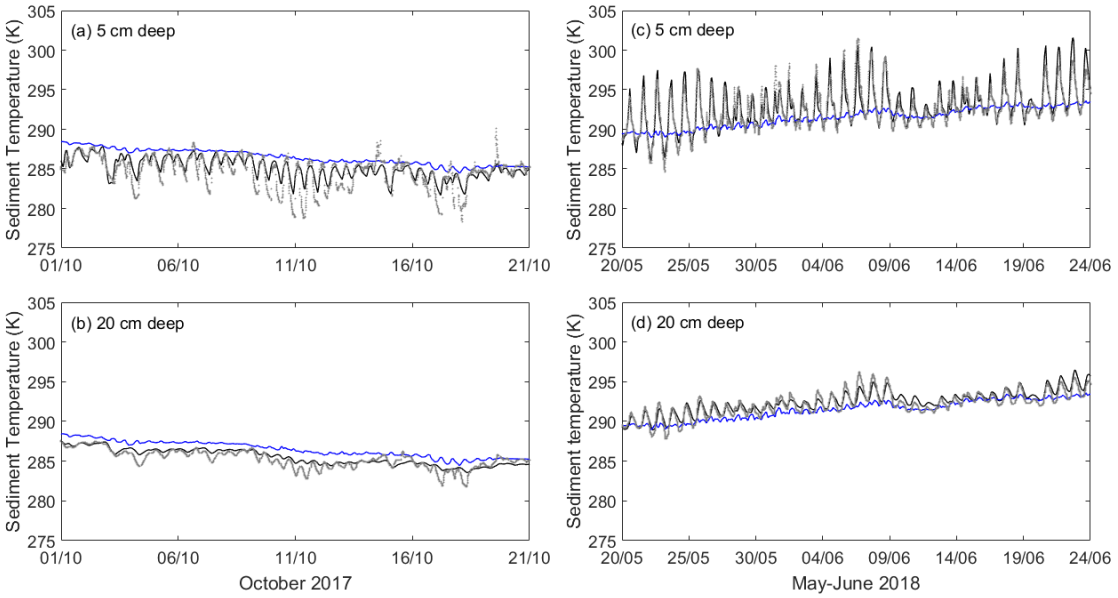

Figure 4.6 – Comparison between the *in situ* sediment temperature measurements (grey dots) and the model output (black line) for October 2017 (a, b) and May-June 2018 (c, d) at 5 cm deep (a, c) and 20 cm deep (b, d) within the sediment using the mean fitted parameters ζ (constant, -), μ (thermal diffusivity, $m^2.s^{-1}$, and η (conductivity, $W.m^{-1}.K^{-1}$) all periods considered (Table 4.3). The blue line is the water temperature from the Marel Carnot station.

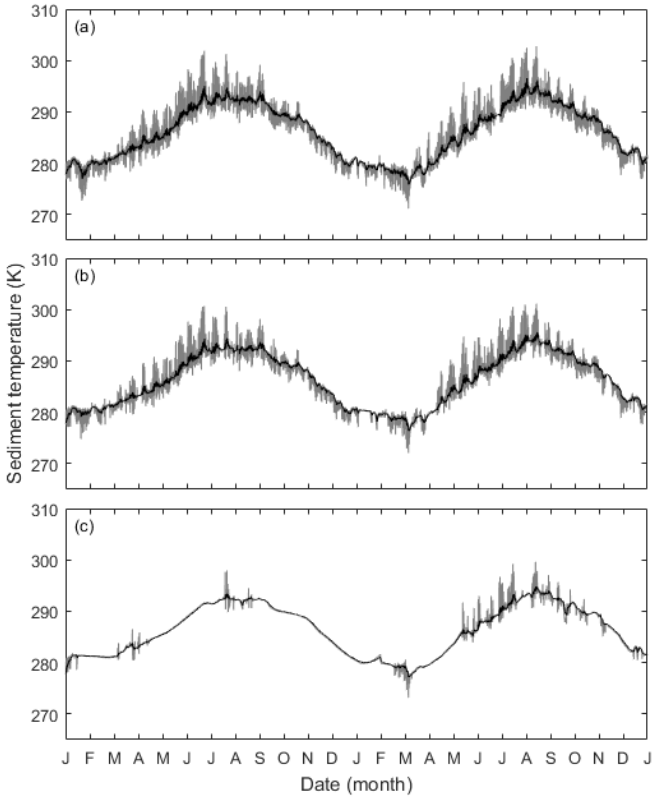

Figure 4.7 – Reconstructed evolution of the sediment temperature (a, b, c) at 5 cm-deep (grey line) and 30 cm-deep (black line) on the high mediolittoral (a), low mediolittoral (b) and high infralittoral (c) foreshore at the study site (Eastern English Channel) between January 2017 and December 2018.

(also driven by the air temperature and the other forcing variables) at 5 and 30 cm deep (Fig. 4.7, Sup. Mat. 1). The highest amplitude of sediment temperature variation occurred on the high mediolittoral foreshore at 5 cm deep, with daily variances of up to 14 °C in in summer time (Fig. 4.7, Sup. Mat. 1). At 30 cm deep at the same location, the daily variance of the sediment temperature was close to 0 °C (Fig. 4.7, Sup. Mat. 1).

4.3.3 Patterns in Arrhenius temperatures of *Arenicola marina* outside its temperature tolerance range

The low and high boundaries of the temperature tolerance range of *A. marina* were estimated to be respectively $T_L = 274.06$ K and $T_H = 293.15$ K. The values of the Arrhenius temperatures outside the species' temperature tolerance range were much higher than the Arrhenius temperature within the species' temperature tolerance range ($T_A = 3800$ K), with respectively $T_{AL} = 32042$ K and $T_{AH} = 36957$ K, traducing a rapid decrease in metabolic activity outside species' temperature tolerance range (Fig. 4.8).

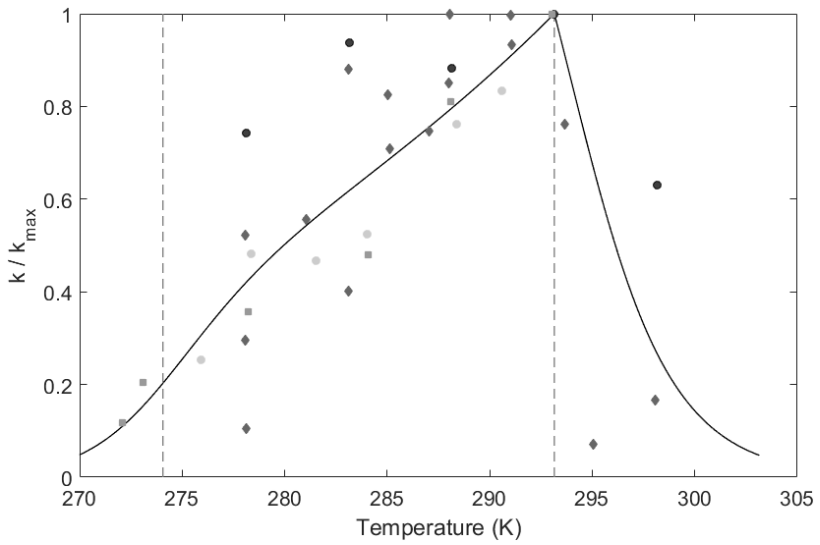

Figure 4.8 – Arrhenius plot (line) of both the fertilization success rate (dark grey diamonds, Lewis et al., 2002), the oxygen consumption rate (light grey dots, Schröer et al., 2009), the von Bertalanffy growth rate (black dots, De Wilde and Berghuis, 1979) and the mitochondrial respiration rate (squares, Sommer and Pörtner, 2004) at several temperatures. For each dataset, all rates were divided by the associated fitted maximum rate at the higher boundary of the temperature tolerance range T_H (293.15 K, dashed line). The fitted values of the lower and the higher boundary (dashed lines) of the temperature tolerance range are respectively $T_L = 274.06$ K and $T_H = 293.15$ K. The value of the Arrhenius temperature within those boundaries is 3800 K (De Cubber et al., 2019). The fitted value of the Arrhenius temperature before the lower boundary is $T_{AL} = 32042$ K, and after the higher boundary is $T_{AH} = 36957$ K.

4.3.4 *In situ* estimated food resources

In situ growth of the recruits

Because of the low number of individuals belonging to the larger trunk length classes from 8 to 12 cm (older individuals) (Fig. 4.4), the decomposition of the population in different age groups after 2 to 3 years old was difficult and only the newest cohorts were followed to reconstruct the *in situ* growth and associated scaled functional response. The growth of the recruits of May 2017 was possible to be followed for one year (from May 2017 to May 2018) and the growth of the recruits of May 2018 was estimated only from the end of may to mid July 2018 (Fig. 4.9, Table 4.4).

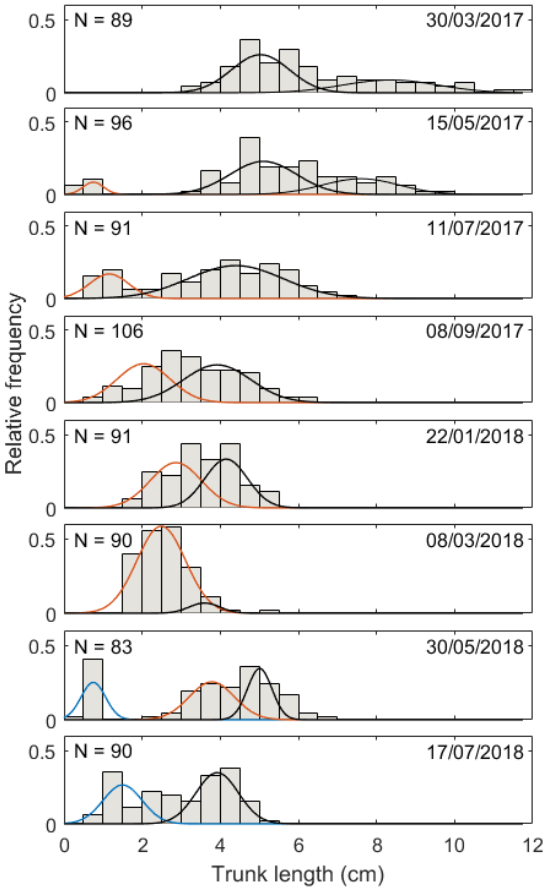

Figure 4.9 – Cohorts decomposition of the population structure of *Arenicola marina* at Wimereux (Eastern English Channel) with a Bhattacharya analysis of the trunk length (TL) frequency distributions (5-mm size class intervals) at 8 sampling dates between March 2018 and July 2018. The histograms represent 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 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 4.4. The black cohorts given by the Bhattacharya analysis were not used further in the study of the *in situ* growth of the population.

The population growth appeared faster between July and September 2017 and between the end of May and mid July 2018, and slower between January and March 2018 (Fig. 4.9, Table 4.4). When considering the contribution of each foreshore level to the followed cohort, it appeared that the recruits were gradually migrating from the high mediolittoral bathymetric level (100 % of the recruits come from this level in May of both years) to the low mediolittoral and infralittoral bathymetric levels (33 to 40 % of the recruits come from the low mediolittoral and 7 to 20 % of the recruits come from the infralittoral bathymetric levels after 10 to 12 months after recruitment) as previously suggested in Fig. 4.4 (Table 4.4).

Table 4.4 – Mean trunk lengths (TL) and standard deviation of the recruits cohorts of 2017 and 2018 and associated contributions of each foreshore level to the followed cohort (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 ± 0.264	100%	0%	0%	-	-	-	-
11/07/2017	1.404 ± 0.501	80%	20%	0%	-	-	-	-
08/09/2017	2.289 ± 0.679	87%	8%	5%	-	-	-	-
22/01/2018	3.114 ± 0.655	70%	23%	7%	-	-	-	-
08/03/2018	2.739 ± 0.623	41%	33%	27%	-	-	-	-
30/05/2018	4.035 ± 0.578	53%	40%	7%	1 ± 0.315	100%	0%	0%
17/07/2018	-	-	-	-	1.75 ± 0.499	85%	15%	0%

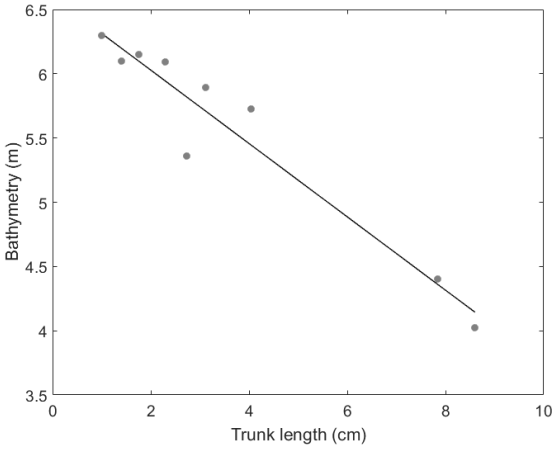

Figure 4.10 – Observations (dots) and linear relation (line) between the trunk length (TL, cm) of *Arenicola marina* at Wimereux (Eastern English Channel) and the mean bathymetric level ($bath$, m) they were collected (according to Table 4.4 and Figs. 4.4 and 4.9). The equation of the linear regression is $bath = -0.2854 \cdot TL + 6.5989$ ($R^2 = 0.99$).

The relation between the trunk length (TL, cm) of *A. marina* and the bathymetric level ($bath$, m) could be established as $bath = -0.2854 \cdot TL + 6.5989$ ($R^2 = 0.99$) and was used in the prediction scenarios part (Fig. 4.10). Here, it appeared clearly that lugworms were found lower on the foreshore when they grew larger.

Reconstruction of the scaled functional response

The abj-DEB model for *Arenicola marina* associated to the sediment temperature model reconstruction at different depths and bathymetric levels and the associated Arrhenius temperature correction enabled a good fit between the predicted and the observed trunk length. The reconstructed scaled functional response was lower in the autumn-winter and higher during the spring-summer periods, with values ranging from 0.01 in winter to 0.5 in summer 2017 and up to 0.7 in spring and summer 2018 (Figs. 4.11 a, b). In general,

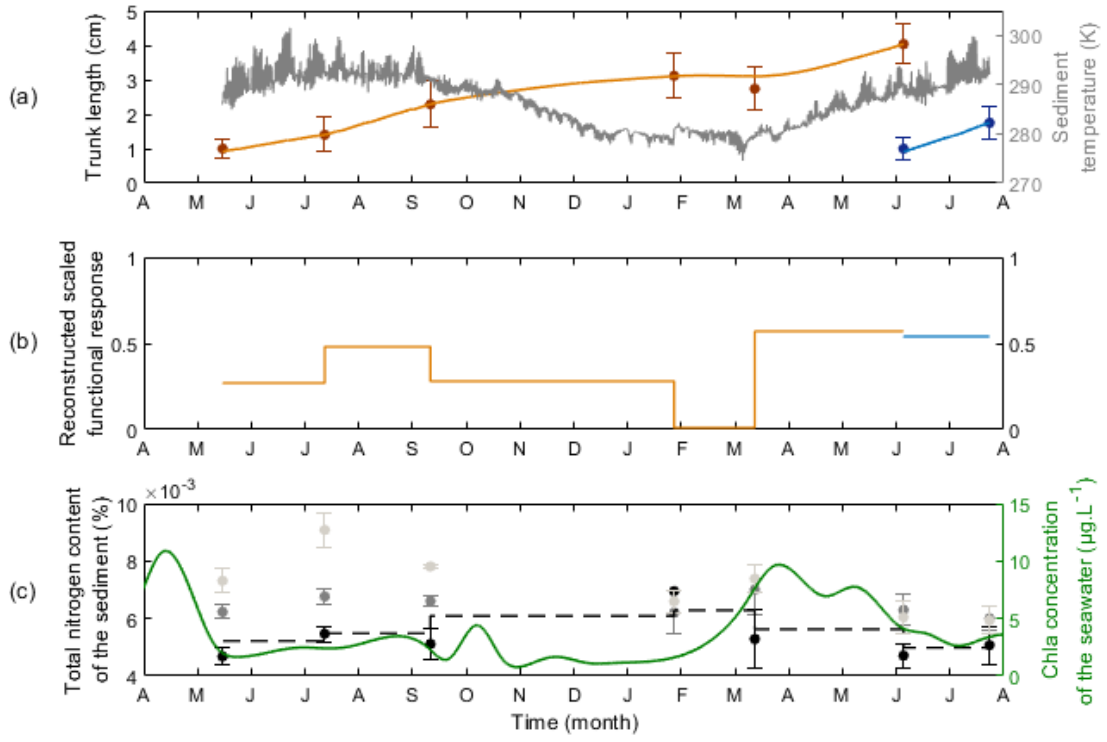

Figure 4.11 – Reconstruction of the scaled functional response values (b) by fitting the predicted trunk length growth from a Dynamic Energy Budget model for *Arenicola marina* (red and blue lines) to the trunk length (cm) growth observations (red and blue dots) using the Arrhenius temperature (Equation (4.3), Fig. 4.8) 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 the 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 ($\mu g.L^{-1}$) (green line, SOMLIT data) (c).

these trends were also observed when considering the chlorophyll-a concentration of the seawater (µg.L^{-1}), with the highest values in spring 2017 and 2018 and between the end of the summer and the beginning of the autumn 2017 (Fig. 4.11 c). This is supposed by fitting the scaled functional response to the chlorophyll-a concentration of the seawater, that lead to a value of the half-saturation coefficient X_K of 4.48 µg.L^{-1} of chlorophyll-a (Fig. 4.12). The total nitrogen content of the sediment (%) showed a spatial pattern with higher nitrogen concentrations on the lower levels of the shore compared to the higher level of the shore. Moreover, the nitrogen concentration on the high mediolittoral foreshore did not display significant seasonal variations compared to the nitrogen concentration of the infralittoral foreshore (Fig. 4.11 c). However, although the nitrogen content trends of the infralittoral seem to be correlated with the reconstructed scaled functional value, there was no clear relation between the reconstructed scaled functional response and the nitrogen contents of the sediment experienced by the lugworms (Fig. 4.12).

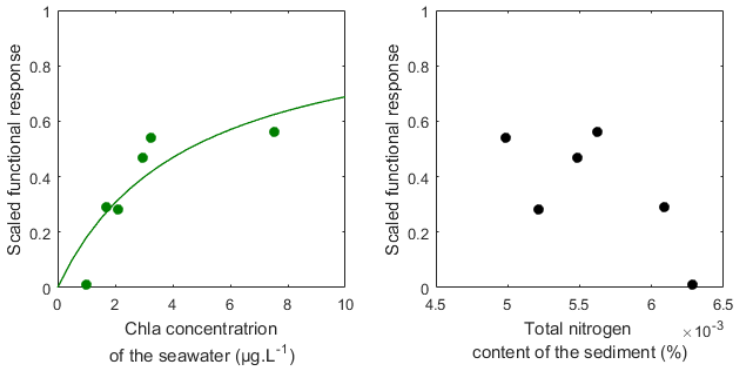

Figure 4.12 – Reconstructed scaled functional response according to (left) the chlorophyll-a concentration on the seawater (µg.L^{-1}) (green dots) and associated fitted response $f = Chla/(Chla + X_K)$ (green line, $X_K = 4.48$ µg.L^{-1}) and (right) the total nitrogen content of the sediment reconstructed from the observations of nitrogen content of the sediment on the different levels of the beach and the contribution of each bathymetric level to the recruits cohorts (Fig. 4.11, Table 4.4).

4.3.5 Bathymetric level and depth effects on growth and reproduction

The different migration scenarios induced different temperature patterns experienced by lugworms (Fig. 4.13). As expected, the lugworms remaining on the high mediolittoral shore in superficial galleries (light grey scenario) experienced the most extreme temperatures, especially in summer and winter time, with temperature differences between the sediment and the seawater reaching up to 14 °C in summer time and 5 °C in winter time (Fig. 4.13). The lugworms remaining on the infralittoral shore in deep galleries experience the least extreme temperatures (black scenario), with temperature differences be-

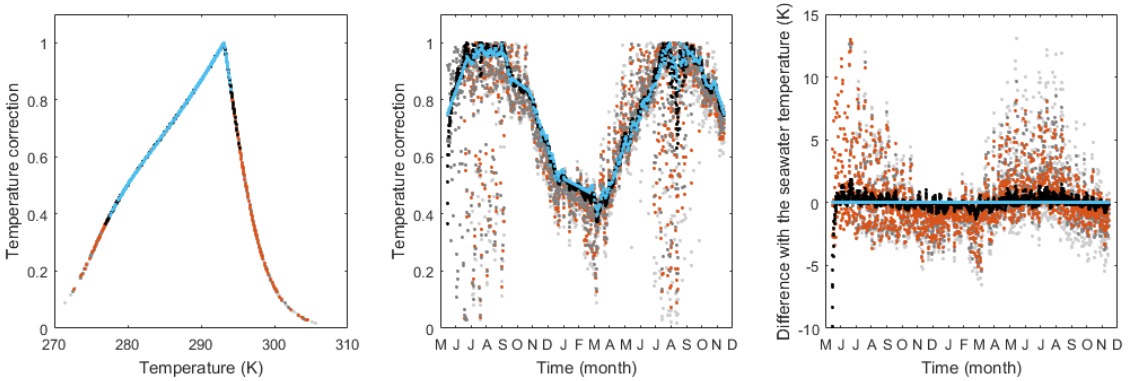

Figure 4.13 – Distribution of the temperature corrections associated to different migration scenarios according to the temperature (left) and the period of the year (middle), and difference between the seawater temperature and the sediment temperature of the different scenarios according to the period of the year (right). 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 the sediment temperature experienced by the lugworms remaining on the high mediolittoral shore level and buried at 5 cm deep. Dark grey dots correspond to the sediment temperature experienced by the lugworms remaining on the high mediolittoral shore level and gradually burying deeper in the sediment according to Equation (4.4). Red dots correspond to the sediment temperature experienced by the lugworms migrating down the shore and gradually burying deeper in the sediment.

tween the sediment and the seawater rarely reaching more than 2 °C (Fig. 4.13). The lugworms migrating and digging deeper galleries experience intermediate temperatures in between these two extremes, gradually getting closer to the deep and infralittoral sediment temperature. However, differences with the seawater temperature are still high after one year of both horizontal and vertical migration, still reaching up to 8 °C in summer and 3 °C in winter (Fig. 4.13). However, the temperature effect on growth and egg production, was minimal compared to the effect of food restriction on the higher shore (Fig. 4.14). Indeed, when considering that the food level was the same everywhere on the foreshore, growth and egg production differences between scenarios were barely noticeable (Figs. 4.14 a,c,e). When considering that the food level on the higher shore was half of the food level on the lower shore, the growth was much higher on the lower shore than on the higher shore, even enabling a spawning event at the end of the first year (Figs. 4.14 b,d,f).

4.4 Discussion

4.4.1 Sediment temperature and metabolic response to temperature

The model output of the the sediment temperature model was well fitted to the observations of May-June 2018. However, the fit was not as good when considering the data of October 2017. This could be linked to a higher hydrodynamism at this period of the

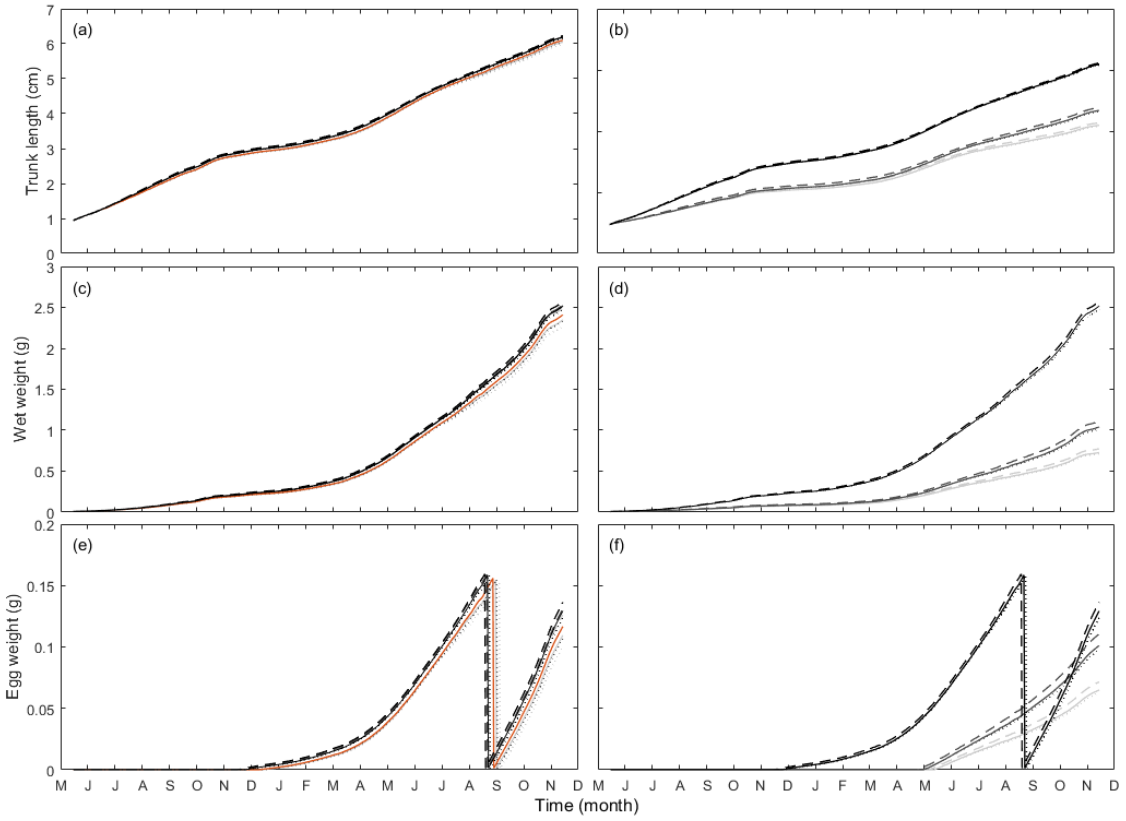

Figure 4.14 – Evolution of the predicted (lines) trunk length (cm) (a,b), wet weight (g) (c,d) and egg weight (g) (e,f) of *Arenicola marina* at Wimereux (Eastern English Channel) according to the period of the year when considering that the food level was the same everywhere (temperature effect only) (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 dark grey and 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 (4.4).

year and the subsequent sediment reworking leading to changing probe depths within the sediment (higher wind speed, see Fig. 4.2). The estimated parameter values of η and μ ($\eta = 3.32$ W.m^{-1}.K^{-1} and $\mu = 5.02e^{-7}$ m^2.s^{-1}) for the sand of this study were respectively 4 times higher and almost equal to the ones presented by Guarini et al. (1997) and Savelli et al. (2018) ($\eta = 0.8$ W.m^{-1}.K^{-1} and $\mu = 4.8e^{-7}$ m^2.s^{-1}) for mud. However, the value of η given in this study ($\eta = 3.32$ W.m^{-1}.K^{-1}) is close to the value of the thermal conductivity of the saturated medium sand according to Hamdhan and Clarke (2010), who measured $\eta = 3.34$ W.m^{-1}.K^{-1}). The estimated value of ζ ($\zeta = 1.21$) lies in the range of what was estimated by Guarini et al. (1997) and Savelli et al. (2018), with respectively $\zeta = 1$ in Savelli et al. (2018) and $\zeta = 1.68$ in Garini et al. (1997). Improvements of the temperature recording set up such as the fixation of the metal rod to large rocks embedded in

the sediment and the daily depth follow-up of the probes could be considered to refine the estimated parameters.

The body temperature of the lugworms might also be different from the temperature of their environment, even in ectotherms (Kearney et al., 2008; Porter et al., 1973; Smith et al., 2016). Indeed, Kearney et al. (2008) predicted discrepancies of up to 5 - 6 °C between body and air temperature for cane toad individuals in Australia using the equation of the standard steady state energy balance: $Q_{solar} + Q_{IRin} + Q_{metab} + Q_{conv} + Q_{cond} = Q_{resp} + Q_{evap} + Q_{IRout}$. In the case of marine benthic organisms, dug in a sediment saturated in water and not exposed to solar radiations, the main energy flux driving the body temperature must be the conduction flux from the sediment, depending on the surface/volume ratio of the individual, leading to higher differences between sand and body temperature in larger individuals. The fluxes linked to solar radiation, respiration, convection and evaporation, which are the more likely to induce discrepancies between the body temperature and the environment temperature in terrestrial environments (Kearney et al., 2008), can be neglected in the present study. However, on the high mediolittoral part of the shore mainly, the drying of the surface sediment during the long emersion periods, in addition of causing anaerobic stress, could lead to unsaturated sediments and increase the evaporation flux. It might also accentuate the extreme sand temperatures causing higher stress to the recruits present on this level and should be taken into account in further studies.

In this study, the Arrhenius temperature within the species temperature tolerance range boundaries T_A was taken from De Cubber et al. (2019), who estimated it using growth and oxygen consumption measurements at several temperatures within the species temperature tolerance range interval. However, it was estimated for only a small window of the temperature actually experienced by lugworms in this study. Thus, further study might be needed to adjust it and possibly the reference temperature T_{ref} together. This might indeed change the subsequent effect of temperature on reproduction and growth during the migration. The Arrhenius temperatures at lower ($T_{AL} = 32042$ K) and upper ($T_{AH} = 36957$ K) limits of the species tolerance range fell in the range of what was observed by Monaco and McQuaid (2018) for *Mytilus galloprovincialis* and *Perna perna*, two species of bivalves living on the intertidal rocky shore, with T_{AL} respectively ranging from 22670 K to 55400 K and T_{AH} respectively ranging from 34540 K to 250600 K. The higher boundaries of the two species tolerance range were higher than the one estimated for *A. marina* (293.15 K) with values of 309 K for *Perna perna*, and 306.1 K for *Mytilus galloprovincialis*, which was to be expected given their distribution in warmer waters (Mediterranean, subtropical and tropical areas). The lower boundaries of the two species tolerance range were close to the one estimated for *A. marina* (274 K) with respective values of 273 K for *Perna perna*, and 279.6 K for *Mytilus galloprovincialis*. These values are important

to understand the possible climate migration enhancing new geographical distribution of marine species due to global warming, as done by Thomas and Bacher (2018) with three European marine bivalve species.

4.4.2 Food level reconstruction and scaled functional response

The reconstructed scaled functional response range of this study appears in accordance with the annual mean value previously estimated around 0.4 at the same site during approximately the same period (De Cubber et al., 2019).

The increase of the total nitrogen content of the sediment when going down the shore seems consistent with the shorter emersion periods met there. The organic nitrogen content of the sediment from the shore could come from various sources of primary producers (microphytobenthos (MPB), deposited phytoplankton, macroalgae in decomposition, bacteria...) (Gaudron et al., 2016). If at one period of the year the contributions of the different sources are similar at each shore level, then lugworms should experience higher food levels down the shore. The absence of correlation between the evolution of nitrogen content of the sediment and the scaled functional response found in this study might be due to the evolution of the contribution of non- or less-assimilated nitrogen sources to the total nitrogen content such as macroalgae debris to the total nitrogen of the sediment. Indeed, lugworms are supposed to feed mainly on MPB and bacteria but are almost unable to digest macroalgae debris (Andresen and Kristensen, 2002; Retraubun et al., 1996; Rikjen, 1979). The high hydrodynamism during winter periods could bring more debris leading to higher than expected nitrogen contents of the sediment.

However, the scaled functional response was quite well correlated to the chlorophyll-a concentration of the seawater. This could be part of the food source contribution to the lugworms diet at their early life stages as it is known that there is a a strong benthopelagic trophic coupling between benthic species and pelagic sources in some coastal habitats. Indeed, phytoplankton was also reported in lugworms diet on the East Coast of the Cotentin Peninsula (English Channel, Normandy, France) (Gaudron et al., 2016). The correlation with the chlorophyll-a concentration of the seawater could also be explained by the fact that the food sources (MPB and bacteria) show in average similar growth and production patterns than phytoplankton (Lefebvre et al., 2009).

Besides, both our *in situ* growth estimation from trunk length cohorts and our growth reconstruction by the DEB model might be slightly inaccurate leading to a slightly different scaled functional response. Indeed, the arrival of new recruits between mid May 2017 and July 2017 might have lead to the underestimation of the growth of the recruits from

before mid May 2017. Moreover, since growth was slightly overestimated by the model compared to the observations between February 2018 and mid March 2018 and slightly underestimated between mid March 2018 and June 2018, the scaled functional response might be slightly different from the one estimated. Moreover, there might be a dilution effect leading to a lower assimilation when food concentrations of the sediment are below a certain threshold, similarly to what was found in bivalves that produce pseudofaeces (although in the case of *A. marina* the sand is ingested) (Kooijman, 2006; Lavaud et al., 2014). Further studies on *in situ* sources of food and the link between food sources and scaled functional response are needed.

4.4.3 Growth scenarios

The trunk length and wet weight growth as well as the egg number were not really influenced by the temperature changes along the shore.

However, the increase of food levels down the shore induced higher wet weight and trunk length growth as well as a higher egg weight, and lead to an earlier first spawning event, suggesting that lugworms migrate down the shore to get access to more food rather than because they avoid extreme temperatures. Since individuals recruiting down the shore experience higher growth, the recruitment location on the higher shore might be linked to other constraints such as the fact that juveniles can not swim against the tide current, or to the fact that there is indeed intraspecific competition for food and space and the juveniles avoid the adults grounds as already suggested by several authors, or to avoid predation (De Vlas, 1979; Farke et al., 1979; Flach and Beukema, 1994).

A number of active movement behaviours to avoid whether cold or warm extreme temperatures have already been documented both in terrestrial and marine species, among which digging (Fitzpatrick et al., 2019; Kearney et al., 2009; Kolbe et al., 2010) or moving to sheltered places (Chapperon and Seuront, 2011; Kearney et al., 2009; Malishev et al., 2017; Monaco et al., 2016). In *A. marina*, shore migrations due to extreme cold temperatures (below 0 °C) have already been reported by Reise et al. (2001) but the depth at which the galleries of the lugworms was dug in was not considered. In the present study, the down-shore migration of *A. marina* recruits started quite early (July, see Table 4.4) but with a slight acceleration of the process between January and March. Although this is when the coldest sediment temperature of the year was recorded (Fig. 4.7, Table 4.4), given the low response of growth and egg production to temperature differences, other clues might explain a migration at this period of the year. Extreme temperatures (whether warm in July or cold in January) might indeed not be the actual trigger of the down-shore migrations of lugworms. However, the increase of primary production at this period of

the year might induce lugworms to migrate down the shore (Fig. 4.11c).

Although the effect of temperature alone seems limited, other parameters, such as the desiccation of the superficial sediment at low tide, could, if taken into account, change this observation increasing the variability of temperature and the subsequent occurrence of extreme temperatures. Moreover, the potential hypoxia experienced by lugworms at low tide was not considered, although anoxic metabolic activity has been reported by several authors for this species (Schöttler et al., 1984), and hypoxia was shown to impact growth and reproduction in marine bivalves (Aguirre-Velarde et al., 2019). As lower levels of the shore are emerged on shorter periods and deeper galleries give access to interstitial water within the sediment (Shumway and Davenport, 1977), this parameter should also be explored to explain the down-shore migrations of *A. marina*. For this purpose, an extra parameter combined to the temperature correction could be computed according to the shore level and the depth of the gallery as previously explored by Monaco and McQuaid (2018).

4.4.4 Perspectives

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

The disappearance of the largest age classes (Fig. 4.9) coincided with the presence of higher number of fishermen in summer 2017 on the study site (pers. observation). De Cubber et al. (2018) has shown the need for some regulation on *Arenicola* spp. fisheries for some sites in the area of the study site on the Eastern English Channel. This study opens new insights on the migration of the lugworms within a population showing the typical distribution pattern, as well as tools to model populations *in situ* growth and reproduction. This could prove useful for management purposes to test scenarios for the prediction of spawning events (Pecquerie et al., 2009; Waston et al., 2000) or predict *in situ* lengths at puberty or harvest sizes and where these lengths are found on the shore. These models could then be associated to individual-based model and larval dispersal models in order to better understand the population dynamics and connectivity of the species (Bacher and Gangnery, 2006; Martin et al., 2012; Nicolle et al., 2017) which would also prove useful for conservation managers.

The knowledge of environmental conditions, behavioural and metabolic responses of the organism to those and DEB models has also been used to model ecological niches (Kearney et al., 2010; Thomas and Bacher, 2018). Modelling the ecological niche of *A. marina*

could help to estimate the impact of fisheries on the species by comparing the species potential distribution with the current species distribution. An ecological niche model could also enable to make predictions on the effect of global change on the species distribution (Thomas and Bacher, 2018) and the possible related impact on other key species. As an example, *A. marina* has been shown to impact negatively populations of *Zostera noltii* (Kosche, 2007) and to influence the local community compositions (Donadi et al., 2015). Its expansion in southern areas (suggested by Pires et al., 2015) might lead to shifts in the communities and species in these areas.

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Supplementary Material

Supplementary Material 1

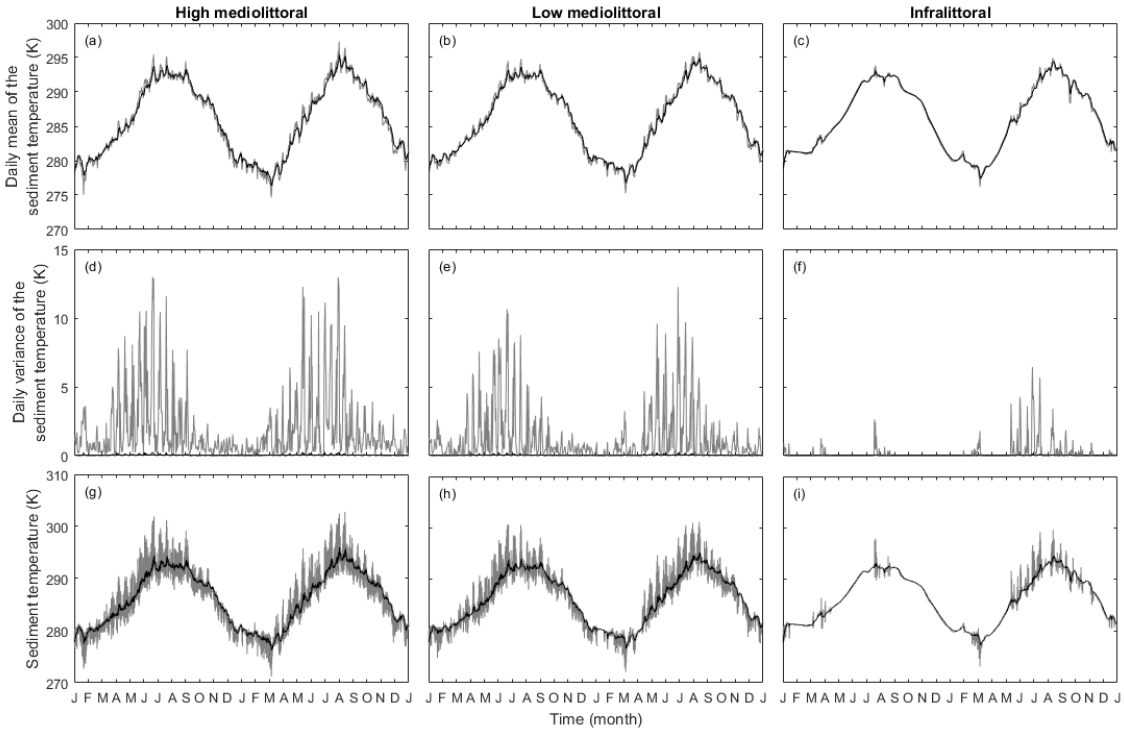

Figure 4.15 – Daily means (a, b, c) and associated variances (d, e, f) of the sediment temperature (g, h, j) predicted by the sediment temperature model implemented in this study at 5 cm deep (grey lines) and 30 cm deep (black lines) on the high mediolittoral shore (a, d, g), the low mediolittoral shore (b, e, h) and the infralittoral shore (c, f, i) at Wimereux (Eastern English Channel, France).

General discussion

Main results

Which species of lugworms are present within the MPA ?

We identified two species of lugworms on the French coast of the Eastern English Channel, *Arenicola marina* and *A. defodiens*. The latter species had only been mentioned so far by Müller (2004) while other authors only reported *A. marina* in ecological studies on the French Coast of the Eastern English Channel (e.g. Rolet et al., 2014). Nevertheless, *A. defodiens* has been described in the UK, the Netherlands and Portugal (Atlantic Ocean), suggesting that this species is widely distributed on the whole French coast of both the English Channel and the Atlantic Ocean (Cadman and Nelson-Smith, 1993; Luttikhuizen and Dekker, 2010; Pires et al., 2015).

The distribution pattern of *A. defodiens* was similar on all the studied sites, with adult specimens occupying the lower shore, while the distribution pattern of *A. marina* was highly variable following the studied site. At Wimereux (Wx), *A. marina* population was typically distributed with large numbers of recruits and other individuals on the higher and middle shore. At Fort-Mahon (FM) and Le Touquet (LT), the population of *A. marina* lived in sympatry with the population of *A. defodiens* on the lower shore, with *A. marina* individuals less numerous and lacking recruits. At Ault (Au), almost no individuals of *A. marina* were observed. No recruits of *A. defodiens* were observed at any of the four studied sites (De Cubber et al., 2018). Thus, further study should be carried out to locate them.

Is there a need for management of these species ?

On the whole Marina Protected Area (MPA) territory, over 18 000 fishing sessions were estimated, corresponding to more than 500 000 lugworms harvested, only by recreational

fishermen. One site (Au) appeared in need for management when linking abundance data with bait collection, where harvest of both species represented $\sim$ 14 % of the total amount of lugworms and was above the carrying capacity of the beach for *A. marina*. The retail value associated to lugworm harvesting within the MPA (232 447 euros) was estimated at the same level as the shrimp retail value (215 714 to 414 727 euros) and only 4 to 5 times less important than the one of the recreational mussel fisheries (1 203 449 euros). Our results highlight the need for some fishery regulations for the *Arenicola* spp. species within the MPA (De Cubber et al., 2018).

What are the biological and ecological features of the local species ?

Spawning periods of *A. marina* occurred in early autumn, between September and early November, and in late autumn, between December and January, of *A. defodiens*, with variations of up to one month according to the site and the year. The size structure of the Wx population of *A. marina* showed 5 that the largest individuals were present lower on the foreshore and the recruits were mainly present on the higher shore. The size at first maturity of *A. marina* at Wx was at 3.8 cm of trunk length, corresponding to an age between 1.5 to 2.5 years old, although gamete production starts earlier. Indeed, measurement were made in September when gametes were already almost fully grown, therefore age and size at first maturity have been overestimated (De Cubber et al., 2018).

Spatial distributions, abundances and population size structures seemed highly variable between sites, leading to a need to adapt management measures to the considered site (De Cubber et al., 2018). Changes in environmental conditions or human disturbances could explain these differences. Their effects on lugworms should then be explored to implement relevant management strategies.

The parameter estimation of a Dynamic Energy Budget (DEB) model (Kooijman 2000; 2010) for *A. marina* has enabled the prediction of some of its life-history traits, as well as individual growth and reproduction under constant or changing environmental conditions (De Cubber et al, 2019). The combination of literature, field and experimental data enabled to choose the best fit DEB model to the lugworms's life cycle, the abj-model. The abj-model, an extension of the std-model considering an acceleration of metabolism between birth (first feeding) and metamorphosis (end of the change of shape) and used for most species with a larval stage, provided a better fit between observations and predictions (SMSE = 0.29), with an acceleration coefficient around 11, which was similar to mollusc values from the Add-my-Pet collection.

The parameters enabled to reconstruct relevant scaled functional responses (as a proxy of

food levels) of field populations of lugworms and laboratory growth experiments. The reconstruction of the early life-stages chronology with our set of parameters, according to *in situ* environmental conditions of a temperate marine ecosystem, indicated a first dispersal phase of the trochophore larva lasting for 5 days, followed by a 7 months temporary settlement during which metabolic acceleration change of shape was happening. This temporary settlement was followed by a second dispersal phase in spring, at the end of metamorphosis (De Cubber et al, 2019). These predictions were consistent with the observations of other authors in quite similar environments (Benham, 1893; Farke and Berghuis, 1979 a,b; Newell, 1948; 1949).

Predictions on growth and reproduction for different constant food and temperature conditions were consistent with our own observations made at Wx suggesting that food levels may be different on the different foreshore studied, with a lowest food level at Wx compared to that at FM and LT. Although variability of food levels may occur between sites, it may also occur at the different levels of a specific foreshore (De Cubber et al., in prep.). These changes in environmental conditions may lead to different life-history traits between populations, which highlight the need for adapting the management measures to the targeted lugworm populations.

What regulations could be implemented ?

In view of the local and ecological features of the species, several kinds of regulations could be implemented. First, at some sites such as at Au, quotas to limit the number of lugworms (and *A. marina*) harvested could be implemented. At this site, a closing season could also be considered during the spawning season of *A. marina* (probably between September and December). When the spatial distributions of the two species are following the typical pattern observed at Wx, limiting the lugworm collection to spring tides so that the fishermen rather target *A. defodiens* could also be an option. Besides, this management measure could also be implemented to encourage the collection of bigger individuals of *A. marina* that already reproduced, since lugworms are bigger down the shore. The use of pumps rather than shovel might also make fishermen target *A. defodiens* rather than *A. marina*. Finally, fishermen could be taught to make the difference between the casts of the two species (Pires et al., 2015) in order to avoid fishing *A. marina* individuals when possible.

What would be the most efficient management strategy ?

To develop in further studies DEB - Individual Based Models (IBM) enabling to predict the population dynamics of the species according to different management strategies, the down-shore migration characteristics of one population of *A. marina* was investigated (De Cubber et al., in prep.). The follow-up of the population size structure enabled to estimate the *in situ* growth of the recruits at Wx and the subsequent scaled functional response they experienced, as well as the linear relations between the length and the bathymetric level and the length and the depth of the gallery. The growth and scaled functional response appeared higher in spring and summer than in autumn and winter. The individuals of *A. marina* were shown to be found lower on the shore where the grew larger. Their position on the foreshore was then computed according to the equation $bath = 0.2854 \cdot TL + 6.5989$. The depth of the gallery was computed according to the equation $z = 30 - 25 \cdot (12 - TL)/(12 - 1)$, considering empirical knowledge on the fact that lugworms burrow deeper when they grow larger (De Cubber et al., in prep.).

The total nitrogen content of the sediment was measured from field samples. It was lower on the high mediolittoral shore than on the infralittoral shore. However, the total nitrogen content of the sediment did not prove to be a good proxy for food when comparing it with the reconstructed *in situ* scaled functional response, while the chlorophyll-a concentration of the seawater (SOMLIT data) did (De Cubber et al., in prep.).

The temperature conditions met by the lugworms within the sediment were successfully reconstructed with a sediment temperature model adapted from a mud temperature model (Guarini et al., 1997). The boundaries of the temperature tolerance range as well as the Arrhenius temperature outside these boundaries were successfully estimated combining the literature data of four experiments. The optimal temperature tolerance range was from T_L = 1 °C to T_H = 20 °C. The Arrhenius temperature for T < T_L was T_{AL} = 32042 K and the Arrhenius temperature for T > T_H was T_{AH} = 36957 K. The sediment temperatures reproduced the trends of the observed air, water temperatures, and solar radiation, with higher temperature in summer and lower temperature in winter at all bathymetric levels. Daily variances of the sediment temperature on the high mediolittoral foreshore at 5 cm deep of up to 14 °C were predicted in summer time, with sediment temperature reaching quite often temperatures superior to the higher boundary of the temperature tolerance range of the species (De Cubber et al., in prep.).

Predictions of individual growth and reproduction output were successfully made under several migration scenarios combining the DEB model for *A. marina*, the reconstructed sediment temperature and the associated temperature correction to the metabolic rates, the reconstructed scaled functional response, and the observed migration features of the

A. marina population of Wx. It appeared that the effect of sediment temperature alone during lugworm migration did not allow significantly higher growth and egg production, but that the decrease of food levels on the higher shore (deduced from the decreasing observed nitrogen contents) declined significantly both the growth and the egg production, and lead to a delay of the spawning event (De Cubber et al., in prep.). We conclude that temperature might not be the main parameter leading to a migration of juveniles down the shore. The migration could be linked to the need to access higher food concentrations or to flee from other constraints not taken into account in this study such as dessication or hypoxia (De Cubber et al., in prep.). Further studies on the food sources, the metabolic response to temperature and the spawning rules of *A. marina* will be needed to enable the implementation of population dynamics models to help conservation managers.

Perspectives

Improvement of the DEB model predictions for *A. marina*

Metabolic response to temperature In this study, the metabolic response to temperature estimated increases sharply before the reference temperature (T_{ref} = 293.15 K) and decreases similarly after T_{ref}, with a pike at T_{ref} (Fig. 4.8). This transition might however be much smoother, as it has been reported in other species (Kish et al., 2016). We therefore believe that the Arrhenius temperatures within and outside the species temperature tolerance range, and associated boundary temperatures and reference temperature, should be refined by estimating them with the DEBtool, associated to all the other data relative to the biology of *A. marina* present in the already existing Add-my-Pet entry (Bas Kooijman, Lola De Cubber, Sébastien Lefebvre, Sylvie Marylène Gaudron. 2019. AmP Arenicola marina, version 2019/05/20). Moreover, there may be a change in the Arrhenius temperature of the species during its life cycle. Indeed larvae and post-larvae are supposed to inhabit a subtidal environment, thus experiencing a more stable temperature compared to adults and juveniles inhabiting the foreshore, possibly leading to a higher Arrhenius temperature (Kooijman, 2010). Two different Arrhenius temperatures before and after metamorphosis (T_{A0} until metamorphosis and T_{Aj} after metamorphosis) should be considered in further developments of the DEB model for *A. marina* (Fig. 3.2). In this prospect, preliminary trials on *in vitro* fertilization experiments and larval culture at several temperature have been started. These experiments, combined with oxygen consumption measurements at several temperatures (similar to the ones performed by De Cubber et al., 2019), should lead to a better knowledge of the early life cycle of *A. marina* and of the associated Arrhenius temperature.

Metabolic response to food Further studies on *in situ* sources of food and the link between food sources and scaled functional response are needed. Since the diet of *A. marina* seems to be constituted of multiple food sources (e.g. MPB, bacteria, phytoplankton, decomposed macroalgae, see Rikjen, 1979; Retraubun et al., 1996; Riisgård and Banta, 1998) more attention should be given to the production of these different food sources throughout the year and their respective contribution to the lugworm's diet according to the period of the year. For this purpose, stomach contents of individuals collected all over one year period could be observed and combined with stable isotopes analysis (Gaudron et al., 2016; Retraubun et al., 1996). Preliminary trials for juvenile growth experiments with one food source have been performed (Fig. 3.3, De Cubber et al., 2019). These experiments should be continued to explore the relation between the food sources and levels and the associated scaled functional response through the half saturation coefficient (see Equation 4.5).

In this regards, the implementation of a multiple reserve DEB model (Kooijman, 2010) with at least one carbon and one nitrogen reserve compartment might be needed as the different food sources might contain different ratios of carbon and nitrogen. Moreover, post-larvae and juveniles do not display the same feeding regime, post larvae being deposit-feeders and juveniles being psammivorous. Thus, the food sources of post-larvae as well as their age at first feeding (as trochophore and metatrochophore larvae are supposed to be lecithotrophic) might also be explored within the framework of the *in vitro* fertilization experiments and larval culture.

An additional dilution effect of the food sources within the sand could also lead to a lower assimilation when food concentrations of the sediment are below a certain threshold. This would lead to a scaled functional response equation similar to the one used for bivalves when dealing with particulate inorganic matter (PIM), that also create a dilution effect (Kooijman, 2006; Lavaud et al., 2014; Thomas and Bacher, 2018):

$$f = \frac{X}{X + K \cdot \left(1 + \frac{Y}{K_Y}\right)} \tag{4.6}$$

where X is the food density, Y the PIM concentration, K the half saturation coefficient related to food density and K_Y the half saturation related to inorganic matter concentration.

Spawning rules Up to know, really basic spawning rules have been implemented in the DEB models for *A. marina* based on the period of the year (De Cubber et al., 2018) or simple biological characteristics such as the ratio of the wet weight of the gametes over the total wet weight of the individual (De Cubber et al., 2019). None of those rules enabled

to make precise predictions concerning the spawning period of the lugworm. However, such predictions could prove usefull for managers, since one possible management measure consists in forbidding the fisheries in a defined area before and during the spawning period. More elaborate rules for predicting spawning events (which is, in terms of DEB, when the reproduction buffer empties) according to knowledge on the biology of a certain species have been applied. As an example, the DEB model implemented for the European anchovy (Pecquerie et al., 2009; Pethybridge et al., 2013) combined a temperature threshold, a minimum energy content of the gametes and a minimum gametes development duration depending on the experienced temperature. Such rules could be chosen according to Watson et al.(2000) (Fig. 1.11) and included in the DEB model for *A. marina*. The predictions could then be compared to our own field observations of spawning dates, recruitment and first observations of gametes in the coelomic fluids to identify the relevant spawning rules for the DEB model for *A. marina*.

Bringing further knowledge on *A. defodiens* biology and ecology

Really few data are available in the literature about the growth, reproduction, habitat and life cycle of *A. defodiens*. Combining field and experimental data and a DEB model approach, using if needed DEB parameters of *A. marina* with corrections, could help bringing further knowledge on *A. defodiens* biology and ecology. Several experiments have been and are still currently being undertaken under the CPER MARCO project (2016-2020) (Axe 2.4) (resp. S.M. Gaudron) or will be implemented on *A. defodiens* based on the trials and successful experiments carried already with *A. marina* such as oxygen consumption, laboratory growth, *in vitro* fertilization and larval culture. *A. defodiens* individuals that we have been collected are generally larger individuals, probably because they live deeper in the sand compared to *A. marina* and because they are living further down the shore where food level might be higher (De Cubber et al., 2019). However, the species is more difficult to handle, showing unfortunately high mortality in our growth experiment trials carried in 2017. Exploratory boat samplings with a Van Veen grab in summer 2017 and 2018, following a personal communication from M. Crouvoisier (UMR 8187 LOG), enabled us to identify one recruitment area of *A. defodiens* with small individuals. Those individuals could be used in future growth experiments. Besides, similar location along the coast could be explored for the presence of *A. defodiens* juveniles.

We have been starting the parameter estimation for *A. defodiens* with some zero-variate and univariate data (diameter of an egg, wet weight of an egg, length of the trochophore larva, length - wet weight relationships) that already gave consistent results. Thanks to a batch of experiments and analyses carried under the CPER MARCO (axe 2.4) (resp.

S.M. Gaudron), data regarding the length at puberty (histology), growth measurements on larvae at one and several temperature (*in vitro* fertilization and larval culture being performed in autumn-winter 2019), and oxygen consumption data according to trunk length or wet weight at several temperatures will be used to further improve the latter parameter estimation of a DEB model for *A. defodiens*. In the future, the DEB models for *A. marina* and *A. defodiens* or their outputs could be combined to better understand the interactions between the two species.

From individuals to populations

Larval dispersal and connectivity between populations In organisms with a benthopelagic life cycle, the dispersal happens mainly during the larval phase (Ayata, 2010), although in the case of *A. marina*, post-larval dispersal and adult migration also happen. The recruitment (the input of new juvenile individuals in the settled population) therefore strongly depends on the larval dispersal phase and on the survival of the settled juveniles (Lewin, 1986). A juvenile can settle on its parents' grounds (in the case of retention) or on other grounds, already colonized or not, on favorable or unfavorable habitats, which can lead to the expansion of the population or the death of the recruits.

Larval dispersal can be studied through biophysical modelling, which combines a model of physical circulation (MARS model developed in the English Channel (Ayata et al., 2009)) and a larval transport model based on biological parameters such as the date of spawning, the number of emitted larvae, and the pelagic larval dispersal duration (PLD) (e.g. time spent in the water column) (Ayata, 2010, Failletaz, 2015). The DEB model for *A. marina* could thus provide the biological parameters needed to implement the larval dispersal model. Such a model could then allow to understand the populations' connectivity in the area (identifying the possible sources and sinks of propagules for example) and thus give valuable information for the conservation of the species. Populations genetics through the study of the gene fluxes could be combined with this approach (Hedgecock et al., 2007; Wright 1931).

Population dynamic models : DEB-IBM Lately, DEB models have been associated to Individual Based Models (IBM) in order to predict population dynamics (Bacher and Gangnery, 2006; Martin et al., 2012; Thomas and Bacher, 2018). IBMs, also called agent-based models, focus on individual growth, reproduction, foraging and dispersal in order to understand higher levels of biological complexity such as population dynamics (De Angelis and Grim, 2014; Martin et al., 2012). Although other approaches to model population dynamics exist, such as differential equation population models (Gangnery et

al, 2001), DEB-IBM are easier to implement and have proven more flexible (Bacher and Gangnery, 2006).

In practice, the population is divided into a large number of cohorts followed as discrete entities. The cohorts are treated individually as super-individuals with the same DEB state variables and a given number of individuals. New cohorts can be generated depending on the reproductive status of the followed cohort (Pethybridge et al., 2013; Thomas and Bacher, 2018). IBM-DEB models could therefore be used for both *A. marina* and *A. defodiens*, independently or not, to make predictions on the impact of a given management measure on local populations of the two species. The interactions between the two species could also be explored via the use of DEB-IBM models.

Niche modelling and the implications of climate change

Climate change can affect the distribution and population dynamics of marine organisms (Kearney et al., 2009; Thomas and Bacher, 2018). The Intergovernmental Panel on Climate Change predicted a warming of sea surface temperature of 1 to more than 3 °C by 2100 (IPCC, 2014). Understanding the impact of this increase of temperature on the species distribution patterns is thus currently a main challenge, especially for intertidal species subject to increasing multiple anthropogenic pressures (Halpern et al., 2015).

Species distribution models (SDM) or ecological niche models aim at understanding how the changing environment affects species distribution patterns (Karasiewicz, 2017). The first SDMs implemented were correlative models based on statistical response curves between species observation data and prediction variables (Bacher and Thomas, 2018; Hutchinson, 1957; Kearney et al., 2010). These models are still used nowadays (Briscoe et al., 2019), but may implicitly represent many different processes without explaining the reasons behind the changing distribution patterns and therefore have poor predictive power when transferred to novel environments (Davis et al., 1998; Kearney et al., 2010). To address this issue, mechanistic SDMs based on the knowledge of the physiological, phenological, behavioural or other responses of organisms to environmental variables have been developed (Malishev et al., 2017; Thomas and Bacher, 2018). They constitute promising tools for predicting species distribution pattern responses to climate change and understanding the mechanisms behind those responses.

In practice, these models can combine environmental data or environmental prediction models, DEB models, physiological response to environmental condition models and IBM models (Kearney et al., 2010; Kearney and Porter, 2009; Malishev et al., 2017; Thomas and Bacher, 2018). One heat budget model calculating changes in individual thermal

state in response to varying habitat microclimates has been developped for terrestrian ectotherms (NichMapR, see Kearney and Porter, 2017). This model could be adapted to lugworms from the sedimant temperature model developped in this study and combined to a DEB-IBM model for *A. marina* and *A. defodiens* to predict the species distribution patterns in response to climate change. Given the ecosystem engineering of these species, such SDM could probably give insights on the possible evolution of the whole associated benthic community. As an example, *A. marina* has been shown to impact negatively populations of *Zostera noltii* (Kosche, 2007) and to influence the local community compositions (Donadi et al., 2015). Its expansion in southern areas (suggested by Pires et al., 2015) might lead to shifts in the communities and species in these areas. Besides, such a modelling approach could help to better understand the interactions of *A. marina* with *A. defodiens* (De Cubber et al., 2018).

DEB-based toxicokinetics models for *A. marina*

Short-term sediment tests using the polychaete *A. marina* have been routinely used in Europe to assess the acute toxicity of marine sediments (Allen et al., 2006; Pires at al., 2016; Senga Green et al., 2015; Casado-Martinez et al., 2008). For example, microplastics have been reported to be ingested by *A. marina* and to affect the health and behaviour of lugworms (Senga Green et al., 2015; Van Cauwenberghe et al., 2015). Trace metal bio accumulation has also been studied and modelled for *A. marina*, showing that Zn, Cd and Ag are accumulated by lugworms from sediment ingestion at realistic environmental concentrations (Casado-Martinez et al., 2008; 2009). However, some inaccuracies aroused when comparing the model prediction to the observed accumulation (Casado-Martinez et al., 2009).

Toxicokinetics (TK) models describe the kinetics of toxicants accumulation and detoxification in marine organisms by modelling either ingestion processes or toxin biotransformation (Pousse et al., 2019). The accumulation of toxicants is linked to the physiological status of the organism (Pousse et al., 2017). Thus, the use of a DEB model accounting for the physiological status of the organism combined with a bio-accumulation model seems relevant. This kind of DEB-based TK model have already been developped for a number of organisms and toxicants, and proved accurate in most cases, even when using simplified DEB models (Jager et al., 2013; Jager and Zimmer, 2012). Since DEB parameters of a complete DEB model were estimated in this study for *A. marina*, DEB-based TK models accounting for the effects of toxicants, trace metals or microplastics on lugworms could easily be implemented in further studies using the data already available in the literature, or new experimental data.

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Abstract

Arenicola spp. are marine benthic polychaetes displaying a complex bentho-pelagic life cycle with two larval dispersal phases, only partially described up to now, and intensively dug for bait by anglers on many foreshores of the Eastern English Channel. Without regulation, this activity can lead to the decrease of lugworms' population while affecting the physical characteristics of the beach and the associated biodiversity.

First, we identified through morphology and genetics two species of lugworms, *Arenicola marina* and *A. defodiens*, and assessed their abundance and spatial distribution at four studied sites, as well as some life-history traits such as the spawning periods and the size at first maturity. These data were compared to lugworms' collection data to estimate its sustainability and to provide potential management measures (De Cubber et al., 2018). At one studied site, *A. marina* was present in large numbers on the higher and middle shore, whereas *A. defodiens* occupied the lower shore. At the other sites, both species co-occurred on the lower shore, and *A. marina* individuals were less numerous and lacking recruits. Spawning periods for *A. marina* occurred in early autumn and in late autumn for *A. defodiens*. One site appeared in need for management when linking abundance data with bait collection, where harvest was above the carrying capacity of the beach for *A. marina*.

Second, a Dynamic Energy Budget (DEB) model was applied to the species combining the former as well as new field data, experimental data (growth and oxygen consumption data), and literature data in order to reconstruct the life cycle and growth of *A. marina* under *in situ* environmental conditions (De Cubber et al., in press). The reconstruction of the early life-stages chronology by the DEB model for *A. marina* according to *in situ* environmental conditions indicated a first dispersal phase of 5 days followed by a 7 months' temporary settlement before a second dispersal phase in spring, at the end of metamorphosis, which appeared consistent with field observations.

Finally, we followed-up the population size structure of *A. marina* at one studied site during 1.5 year to explore the down shore migration of lugworms recorded by several authors. To do so, we adapted a sediment temperature model from a mud temperature model (Guarini et al., 1997), measured the nitrogen content and tested several proxys for the food sources. The metabolic responses of lugworms to food (scaled functional response) and temperature (temperature tolerance range and Arrhenius temperature) were then assessed. We combined those data with the former DEB model to explore the effects of the fine changes in temperature and food conditions met by the individuals along the foreshore gradient and according to the depth of their galleries. The follow-up of the population size structure of *A. marina* showed clearly a migration pattern. The effect

of sediment temperature alone when migrating did not allow significantly higher growth and egg production, while an increase of food concentrations down the shore did. Other factors might be taken in consideration in further studies such as desiccation and anaerobic metabolism during emersion periods at low tide.

All these data constitute valuable information for conservation managers to better understand and regulate the lugworm populations. Further combination of the DEB model developed in this study with an individual-based model and a larval dispersal model could enable to understand the dynamics of the local lugworm populations.

Keywords

Conservation, Bioenergetic modelling, Lugworm, Life cycle, Growth, Reproduction

Résumé

Les arénicoles sont des polychètes benthiques présentant un cycle de vie bentho-pélagique complexe avec deux phases de dispersion larvaire seulement partiellement décrit jusqu'à présent. Ces espèces sont intensément pêchées comme appât sur les plages de la Manche orientale, notamment au sein d'une aire marine protégée, le Parc naturel marin des estuaires picards et de la mer d'Opale. Sans mesures de gestion, cette activité pourrait entraîner une diminution des populations d'arénicoles tout en affectant les caractéristiques physiques des plages et la biodiversité associée.

Tout d'abord, deux espèces d'arénicoles ont été identifiées, *Arenicola marina* et *A. defodiens*, et leurs abondances, leurs distributions spatiales, ainsi que certains de leurs traits de vie (période de ponte, taille de première maturité sexuelle) ont été mesurées sur 4 sites d'étude. Ces données ont été comparées à des données de pêche pour estimer si les populations d'arénicoles étaient exploitées durablement, et pour fournir de potentielles mesures de gestion (De Cubber et al., 2018). Sur l'un des sites étudiés, *A. marina* était présente en grands nombres en médiolittoral supérieur et moyen tandis que *A. defodiens* occupait les niveaux médiolittoral inférieur et infralittoral de l'estran. Sur les autres sites, les deux espèces occupaient les niveaux médiolittoral inférieur et infralittoral, et les individus de *A. marina* étaient moins nombreux, et sans recrus. Les pontes de *A. marina* ont eu lieu en début d'automne et celles de *A. defodiens* en fin d'automne. Le besoin de mise en place de mesures de gestion de *A. marina* a été mise en évidence sur un site en comparant les abondances et les données de pêche.

Ensuite, un modèle de type Dynamic Energy Budget (DEB) a été appliqué à *A. marina* en combinant des données de terrain, des données expérimentales (de croissance et de consommation d'oxygène) et des données de la littérature pour reconstruire le cycle de vie et la croissance de l'espèce dans des conditions environnementales *in situ* (De Cubber et al., in press). La reconstruction de la chronologie des premiers stades de vie avec le modèle DEB pour *A. marina* en fonction des conditions environnementales *in situ* a permis de prédire une première phase de dispersion de 5 jours suivie d'une période d'installation temporaire de 7 mois avant une deuxième phase de dispersion au printemps, à la fin de la métamorphose, qui semble concorder avec les observations de terrain.

Enfin, la structure en taille de la population de *A. marina* sur un des sites d'étude a été suivie pendant 1.5 an pour explorer les migrations des adultes vers le bas d'estran reportées par plusieurs auteurs. Pour cela, un modèle permettant la reconstruction de la température au sein du sédiment a été adapté d'un modèle de température pour la vase; le contenu en azote du sédiment a été mesuré et différents proxys pour la nourriture ont été testés. Les réponses métaboliques des arénicoles à la nourriture (réponse fonctionnelle)

et à la température (intervalle de tolérance et température d'Arrhénius) ont été estimées. Ces données, combinées au modèle DEB pour *A. marina* ont permis d'étudier les effets de variations de la température et la de nourriture rencontrés par les arénicoles suivant leur position sur l'estran et la profondeur de leur galerie. Le suivi de la structure en taille de la population de *A. marina* a clairement indiqué la présence de migration au cours du temps vers le bas d'estran. L'effet de la température seul pendant cette migration n'a pas permis de prédire une croissance plus rapide ni une augmentation de la quantité d'œufs produits mais une augmentation de la nourriture en bas de l'estran l'a permis. D'autres facteurs pourraient être pris en compte comme la dessication et un métabolisme anaérobie pendant les périodes d'émersion à marée basse.

Toutes ces données constituent des informations qui pourraient être utilisées par les gestionnaires pour comprendre et réguler les populations locales d'arénicoles. L'utilisation couplée du modèle DEB développé dans cette étude avec des modèles de type individu centré (IBM) et de dispersion larvaire pourrait à l'avenir permettre de comprendre la connectivité entre les populations locales d'arénicoles ainsi que leurs dynamiques de population.

Mots Clés

Conservation, Modèle bioénergétique, Arénicole, Cycle de vie, Croissance, Reproduction

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