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UNIVERSITÉ DE LA ROCHELLE

ÉCOLE DOCTORALE GAY LUSSAC

Laboratoire Littoral, Environnement et Sociétés



THÈSE présentée par :

Anne PHILIPPE

17 Novembre 2016

pour obtenir le grade de : **Docteur de l'Université de La Rochelle**
Spécialité : **Biologie de l'environnement, des populations, écologie**

**Interactions between shorebirds and benthic
macrofauna: MAKING SMALL THINGS BIGGER**

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“It is a capital mistake to theorize before one has data. Insensibly one begins to twist facts to suit theories, instead of theories to suit facts.”

Sherlock Holmes Quote

-A Scandal in Bohemia

Sir Arthur Conan Doyle

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leurs cousins et cousines à venir!*



INTRODUCTION



ECOLOGY OF INTERTIDAL MUDFLATS

Ecology is at the same time a fundamental and recent research field (McIntosh, 1986). Its purpose is to study the dynamics and functioning of an ecosystem and the interactions between its various compartments: a habitat (physical, chemical and biological) and its inhabitants, including the intraspecific, interspecific - and trophic - interactions between them (Haeckel, 1866). Ecology is an integrative science (Barrett, 2001) and tends to be a transdisciplinary research field going across disciplines (*i.e.* biology, physiology, geology and ethology) to create new concepts and capture the complexity of nature (Piaget, 1972).

The notion of habitat is central in ecology and in conservation, ecology being literally the “study of the household” (from the Greek *oikos* and *logos*). Habitat can be defined as ‘*The environment of the individual, including all biotic and abiotic elements*’ (Fuller, 2012). Habitat conditions, continuity and stability drive species distribution and abundance (Guisan and Thuiller, 2005), and allow the maintenance of complex trophic interactions, nutrient recycling and the development of a stable community of organisms producing essential ecological services (Dobson et al., 2006).

In this thesis we dig into a very special habitat: intertidal mudflats (Fig. 1). Intertidal mudflats are shallow coastal areas (sometimes estuarine) that are inundated during high tides and uncovered during low tides. They are wetlands, rich in biodiversity and organic matter and play a central role in carbon recycling (MacLusky and Elliott, 2004). They are also an essential habitat for a large number of species, from eukaryots to protozoa, molluscs, annelids, *etc.* (Gray, 2009). Some species depend on these ecosystems during specific life stages (*e.g.* they are major nurseries for fishes: Beck et al., 2001) or during migration (*e.g.* intertidal mudflats host many shorebird species feeding on molluscs and/or annelids, van de Kam et al., 2004). Because of their ecological importance, some of them are protected by international conventions and organizations (“*The Ramsar Convention manual: a guide to the convention on Wetlands (Ramsar, Iran, 1971)*”), or more local and national organizations (van de Kam et al., 2004). Since they are important for human activities and development (*e.g.* harbours, fisheries, aquaculture, tourism, industries, leisure activities) but threatened by them (*e.g.* via land reclamation, sand replenishment, hunting, legal/illegal fishing, pollution), intertidal mudflats are progressively disappearing and the quality of these rare habitats is highly threatened (Costanza et al., 1997; Silliman, Grosholz, and

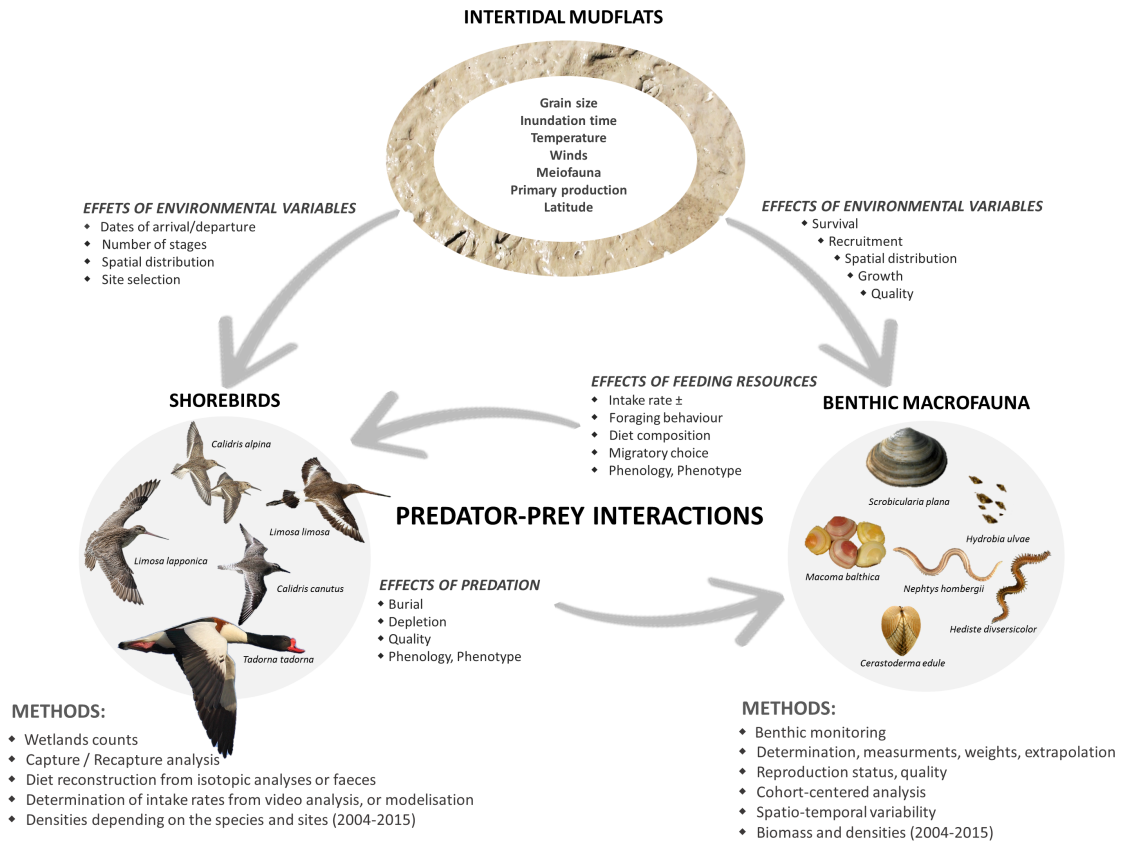


FIGURE 1: General scheme of the ecological interactions studied in intertidal mudflats, and common methods associated

Bertness, 2009; Fuller, 2012). More global threats are also affecting these coastal ecosystems, like climate change (incl. global warming), or sea-level rise affecting coastal erosion and saltmarsh habitats (Gill, 2012; Burton, 2012).

It is not a surprise to see an increasing number of shorebirds join the list of threatened species (Hilton-Taylor, 2000), like the critically endangered (CR) spoon-billed sandpiper *Eurynorhyncus pygmaeus*, or endangered (EN) species such as the great knot *Calidris tenuirostris*. Even when species are not listed as endangered, their numbers are seriously decreasing (van de Kam et al., 2004; Rodrigues et al., 2006): like for the red knot subpopulation *Calidris canutus canutus*.

PREDATOR-PREY INTERACTIONS (PPI)

Among ecological interactions, trophic relations between predator and prey are particularly relevant for the study and understanding of an ecosystem functioning (Barbosa and Castellanos, 2005), since in a broad sense they more or less encompass all interactions between a consumer and resources. Like many other science fields, ecology relies on observation, statistical description and modelling as well as experiments, and has developed its own paradigms and theories. Understanding the trophic links between compartments has always been one of the best ways to understand the broad functioning of an ecosystem. The interactions between predators and their prey may induce physiological adjustments (Piersma and van Gils, 2011), as well as changes in the population composition and densities (Sutherland, 1996), and involve decision making on the basis of Optimal Foraging Theory (Stephens and Krebs, 1986; Hughes, 2009). The study of predator-prey interactions is therefore at the cross-roads between behavioural ecology (*i.e.* feeding ecology), physiology and population ecology.

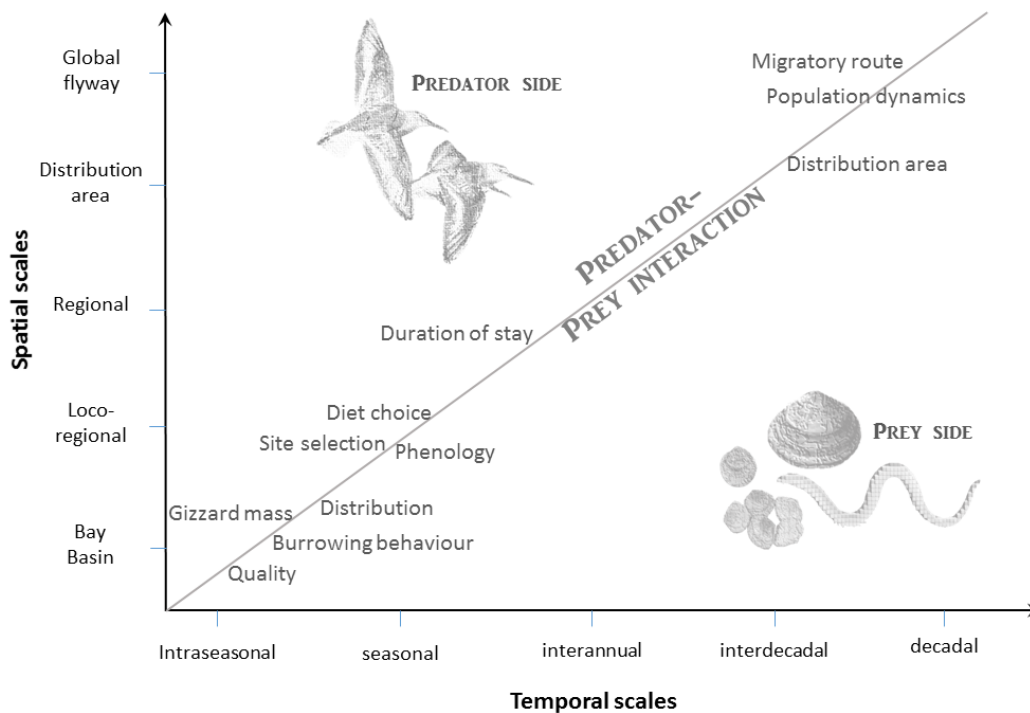


FIGURE 2: General scheme of the factors influencing predator-prey interactions depending on the spatio-temporal scales studied in the present thesis

In the present thesis we investigate the PPI between a group of predators: molluscivore migratory shorebirds, and their prey community: benthic macrofauna, in space and time (Fig. 7.6).

The prey: benthic community

The benthic community includes a wide range of organisms from bacteria to plants (phytobenthos) and animals (zoobenthos) that can be either epifaunal or infaunal. Benthic animals are generally classified according to size (*e.g.* microfauna $< \mu\text{m}$, meiofauna 63- 500 or 1,000 μm , macrofauna > 500 or 1,000 μm). Contrary to their density (ind. m^{-2}), their biomass importance (g.m^{-2}) decreases with decreasing size (macro $>$ meio $>$ microfauna), Gray, 2009 (p7 Fig. 1.6).

This thesis is based on the observation and description of benthic macrofauna (*i.e.* here defined as invertebrates larger than 1 mm found in the mudflat sediments, see Fig. 3), essentially gastropods, and infaunal polychaetes and bivalves. In ecology, these aquatic invertebrates are commonly used in laboratory essays (experiments), and in *in situ* or field surveys (Burton and Nordstrom, 2004a; Burton and Nordstrom, 2004b). These animals can reach important numbers and biomasses, and are often used as bioindicators (*e.g.* in ecotoxicology) since they are in constant contact with the sediments, and are in interaction both with primary producers (their major food source) and their consumers (top predators such as fishes or shorebirds, including humans for some).

Benthic macrofauna is a key element in this thesis, since it can be considered as the link between the benthic habitats and top predators of the ecosystem: shorebirds. It is mainly studied here through its spatio-temporal variations, spatial distribution, phenology and phenotype, all aspects that are central in its relations to predatory shorebirds.

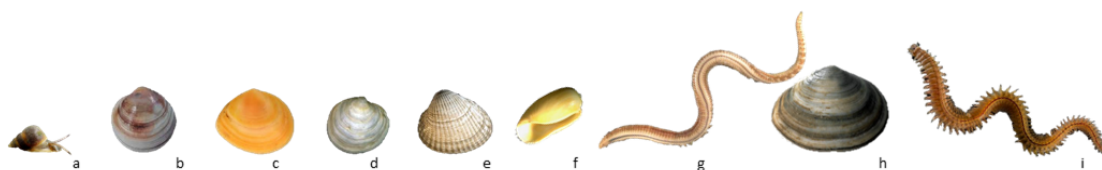


FIGURE 3: Principal benthic species studied in the present thesis. a) *Hydrobia ulvae*, b) *Dosinia isocardia*, c) *Macoma balthica*, d) *Loripes lucinalis*, e) *Cerastoderma edule*, f) *Retusa obtusa*, g) *Nephtys hombergii*, h) *Scrobicularia plana*, i) *Hediste diversicolor*.

N.B.: Although common species, some of them are still changing scientific names more often than common names: the bivalve *Macoma balthica* is now called *Limecola balthica* (Huber, Langleit, and Kreipl, 2015), and the gastropod *Hydrobia ulvae* became *Peringia ulvae* (de Jong, 2012). For more consistency between the chapters, as well as in the literature we will always refer to *Macoma balthica* and *Hydrobia ulvae* in the text, except in Chapter 6. The species *Dosinia isocardia* is a synonym of *Pelecypora isocardia* and the species *Loripes lucinalis*, as synonym of *Loripes orbiculatus*.

The predators: shorebirds

Shorebirds belong to the Charadriiforms order, which are long-distance migrants scattered over the globe from Arctic to tropical regions (van de Kam et al., 2004). In the AEWA region (African Eurasian Migratory Waterbird Agreement), 90 species of shorebirds are occurring in coastal areas, with no less than 162 subpopulations (Delaney et al., 2009). Most shorebirds reproduce in the arctic tundra, and fly very long distances to overwinter in the temperate or tropical areas (van de Kam et al., 2004). Shorebirds undergo an annual migratory cycle, which developed through their evolutionary history (inc. speciation), and evolved at the rate of geological changes (since the last glaciation, approx. 100,000 years ago, van de Kam et al., 2004; Alerstam and Lindström, 1990). Species that have survived until now may have survived thanks to their flexibility and adaptability (West-Eberhard, 1992; Bolnick et al., 2003), characteristics that again could be an advantage when faced with ongoing environmental changes (Gordon et al., 1982). Indeed, shorebirds fascinate scientists with their flexible phenotype (incl. gizzard, fat stores, thermoregulation and flying capacities, Piersma and van Gils, 2011). All these body traits tell something about the ecology of these migrants and play a role in their interactions with their prey, or their habitat selection and diet choice. In this thesis we will focus on two sandpiper species (the dunlin *Calidris alpina*, and the red knot *Calidris canutus*), because they are dominant species in the wintering sites studied, and because we have acquired a good knowledge about their behaviour, see Fig. 4.

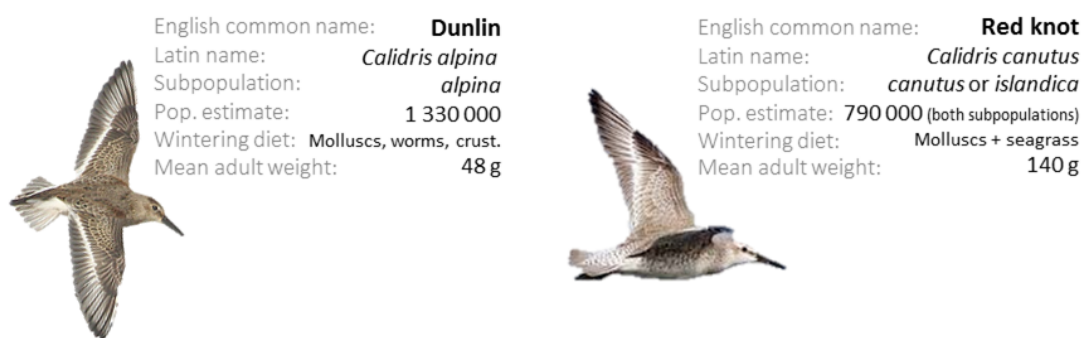


FIGURE 4: Principal shorebird species studied in the present thesis, on the left the Dunlin *Calidris alpina*, and on the right the Red knot *Calidris canutus*

Like mentioned before concerning shorebirds and benthic macrofauna, the phenotype embodies the ecological interactions between the different compartments of an ecosystem, and is a useful tool for studying predator-prey interactions (Kishida et al., 2014).

HABITAT SELECTION, DISTRIBUTION AND DIET CHOICE

Food is one of the major and ultimate factors in habitat selection (Fuller, 2012). Optimal Foraging Theory, using energy intake rate as a proxy for fitness (Emlen, 1966; MacArthur and Pianka, 1966), has strongly influenced ecology until now. At the landscape scale, intertidal mudflats and estuaries may appear uniform. However, they are very heterogeneous habitats and their inhabitants are usually patchily distributed (Gill, 2012). Because of interference (*i.e.* 'the decline in intake rate resulting from the behaviour of other individuals', Sutherland, 1996), shorebirds distribute 'ideally and freely' so that they would all achieve a similar intake rate (Fretwell and Lucas, 1970). As a consequence, shorebirds are more spread out on the mudflat than their invertebrate prey (van der Meer and Ens, 1997; Kraan et al., 2009b), the more so when over time 'depletion equalizes the resource density' (Sutherland, 1996). Birds spatial distribution is the result of decisions following rules in order for them to optimize fitness (MacArthur and Pianka, 1966; van Gils et al., 2005a; Bijleveld, 2015). In the case of invertebrates (including benthic macrofauna), for which one's decision making (or free will) is too seldom recognised (Brembs, 2011; Doyle, 2009), spatial distribution is mostly apprehended like a response to environmental pressures (*e.g.* inundation, predation pressure) and physiological limitations (*e.g.* desiccation, access to food, resistance to cold), see Ysebaert et al., 2002. However, benthic invertebrates do make decisions. For instance, even if they appear rather static, most benthic species do migrate on small spatio-temporal scales, both vertically and horizontally in the substrate (see examples in Zwarts, 1986; Roberts et al., 1989; Armonies and Hellwig-Armonies, 1992; Beukema, 1993a; Armonies, 1996 and review by Gibson, 2003).

At biogeographic scales however, it is hard to really talk about 'ideal free distribution'. Long distance migrants like shorebirds, allow us to study the drivers of site selection (Hanski, 1998; Levins, 1969; Hanski and Gilpin, 1991) on large scales thanks to various techniques (colour-ringing, tagging as well as isotopic analyses, Webster et al., 2002). In the case of shorebirds' migratory routes, at least for some species, historical constraints were shown to inhibit the adaptation of populations (Sutherland, 1996), and the changes of wintering site may be triggered by genetic control (Berthold et al., 1992). Hence, site fidelity is sometimes stronger than adaptation resulting in maladaptive or non-ideal habitat selection, or ecological trap (Fuller, 2012).

For benthic macrofauna, on such large scales, distribution is obviously the result of geological and past climatic changes rather than the expression of free will.

PROBLEM STATEMENT AND CHALLENGES OF THE THESIS

This thesis met the cross-scale challenge of ecology, where our understanding of interactions and processes is scale dependent (Fuller, 2012). Indeed, one can reach opposite conclusions on habitat selection or diet choice whether under a small *v.* large spatial or temporal scale study (Wiens, 1989). The other major challenge of the thesis was to investigate the three-way relationship between suitable foraging area, spatial predictability of food and survival; a challenge also met in previous theses of the domain (see Table 1). We investigated the determinants

TABLE 1: Previous theses in the research domain, linking foraging area, food predictability and survival

Year	Author	Title
1994	Theunis Piersma	Close to the edge: energetic bottlenecks and the evolution of migratory pathways in knots
1997	Leo Zwarts	Waders and their estuarine food supplies
2004	Jan A. van Gils	Foraging decisions in a digestively constrained long-distance migrant, the red knot (<i>Calidris canutus</i>)
2009	Carlos D. Santos	The use of intertidal areas by foraging waders: constraints on the exploitation of food resources
2010	Casper Kraan	Sélection de l'habitat et des ressources trophiques chez le Bécasseau maubèche <i>Calidris canutus</i> . Distribution à l'échelle européenne et particularités des sites d'hivernage français
2010	Gwenaël Quaintenne	Spatial ecology of intertidal macrobenthic fauna in a changing Wadden Sea
2011	Jutta Leyrer	Being at the right place at the right time: interpreting the annual life cycle of Afro-Siberian red knots
2012	Eelke Folmer	Self-organization on mudflats
2012	Frédéric Robin	Dynamique de la distribution, sélection de l'habitat et stratégie d'alimentation chez la barge à queue noire <i>Limosa limosa</i> à l'échelle des sites d'hivernage français
2013	Matthijs van der Geest	Multi-trophic interactions within the seagrass beds of Banc d'Arguin, Mauritania: a chemosynthesis-based intertidal ecosystem
2015	Allert Bijleveld	Untying the knot. Mechanistically understanding the interactions between social foragers and their prey
2016	Jimmy de Fouw	Bottom-up and top-down forces in a tropical intertidal ecosystem. The interplay between seagrasses, bivalves and birds

many more thesis are to come, table inspired by Bijleveld, 2015

of food resource availability in time and space (*e.g.* environmental gradients, recruitment, phenotypic flexibility, burial behaviour, toxicity). The challenges of the present research were to nest the spatio-temporal scales in each other, and acquire a global understanding from specific study cases, to address the following key ecological questions:

- What are the drivers of wintering bird densities along the East-Atlantic Flyway?
- What are the determinants of food choice along the migratory route?

To tackle these questions, different spatio-temporal scales were used (see Fig. 7.6), and most effort was made on the valorisation of 4 different benthic databases (Long-term monitoring in the French Pertuis-Charentais, the Dutch Wadden Sea and the Mauritanian Banc d'Arguin, as well as a monthly sampling in Aiguillon Bay in France), with additional data of bird counts and diet reconstruction (from faeces, prey selection, modelling, experiments and isotopic analyses).

THESIS OUTLINE

The present thesis is composed of 4 sections of one or two chapters. Each chapter adds a little piece to the complex puzzle presented in introduction, see Fig. 1. Section I begins with a study of the environmental bases of prey habitat preferences and its potential implications on the trophic spatial segregation of two sympatric shorebirds species: the dunlin *Calidris alpina* and the red knot *Calidris canutus* (Chapter 1). A box is introduced presenting the different techniques used for the reconstruction of shorebirds' diet (Box 1). A second study compares two Bays of the French Atlantic coast, and investigates diet as a response to habitat resources in dunlins (Chapter 2). Following is Section II, which presents the long-term benthic database in the Pertuis-Charentais (Chapter 3); this database bring a temporal dimension to our understanding of predator-prey interactions and underlays studies presented in following chapters. Section III focuses on the factors explaining temporal variability of benthic resources and begins with a study presenting the seasonal variations in macrobenthos in Aiguillon Bay, focusing on the quality of the bivalve *Scrobicularia plana* and its implications for the diet choice of sandpipers (Chapter 4). The data of this study is part of a monthly meio- and macrobenthic sampling in Aiguillon Bay (Annex 7.6). Stepping on this first study, a box is introduced which presents the various antipredation traits that marine molluscs can develop (Box 2). A second study aims at explaining interannual variability in *Macoma balthica* resources based on a cohort-based modelling of survival, recruitment and mortality (Chapter 5). At last, Section IV includes two studies illustrating how shorebirds' behavioural ecology can add knowledge on the determinants of food abundance and reveal ecological changes in intertidal areas. The first study evaluates how variability in food abundance in space and time can be reflected in predicted diets after multiple constraints on prey selection (Chapter 6). A box is added to investigate whether red knots distribute within the Pertuis Charentais depending on food abundance during 11 years (Box 2). A second study combines results from long-term datasets with experimental and laboratory analyses to link a decline in food resources with a diet shift and its consequences for the survival of the subspecies *Calidris canutus canutus* in Banc d'Arguin (Chapter 7). A general discussion is provided, echoing the reasons underlying the subtitle expression "making small things bigger"... Each chapter begins with a scheme highlighting which species are studied and the ecological interactions that are demonstrated (plain black arrows) or hypothesised (gray or light gray arrows), see p. 16, 44, 66, 84, 100, 126, 142 and 166.

**SECTION 1: SPATIAL VARIABILITY IN
FOOD ABUNDANCE AND POTENTIAL
EFFECTS ON SANDPIPERS**



Bécasseau variable



Barge rousse



Tadorne de belon



Courlis cendré



Tournepiere à collier



Bécasseau sanderling



Grand gravelot



Barge à queue noire

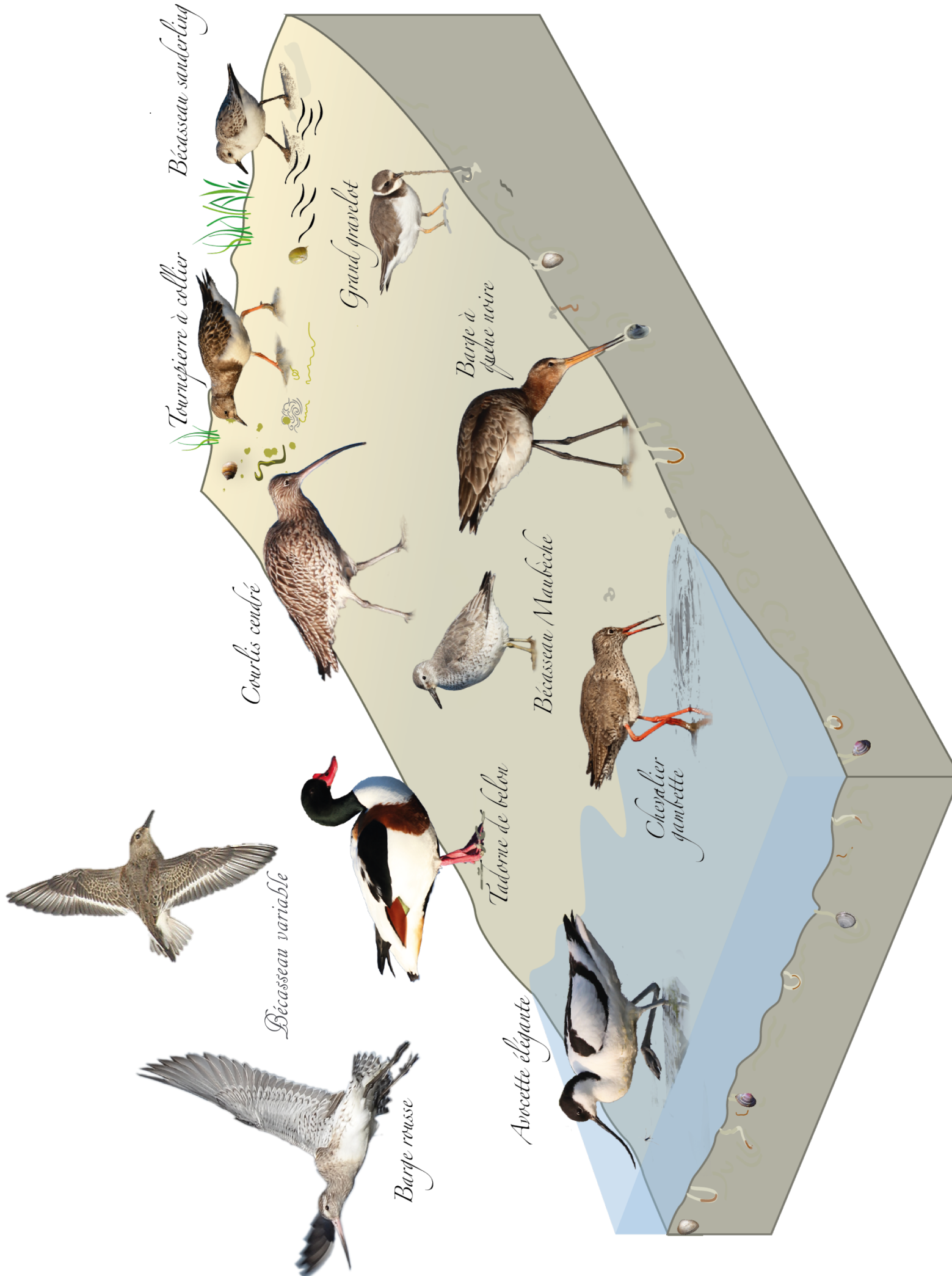


Bécasseau Mauviche



Chevalier gambette

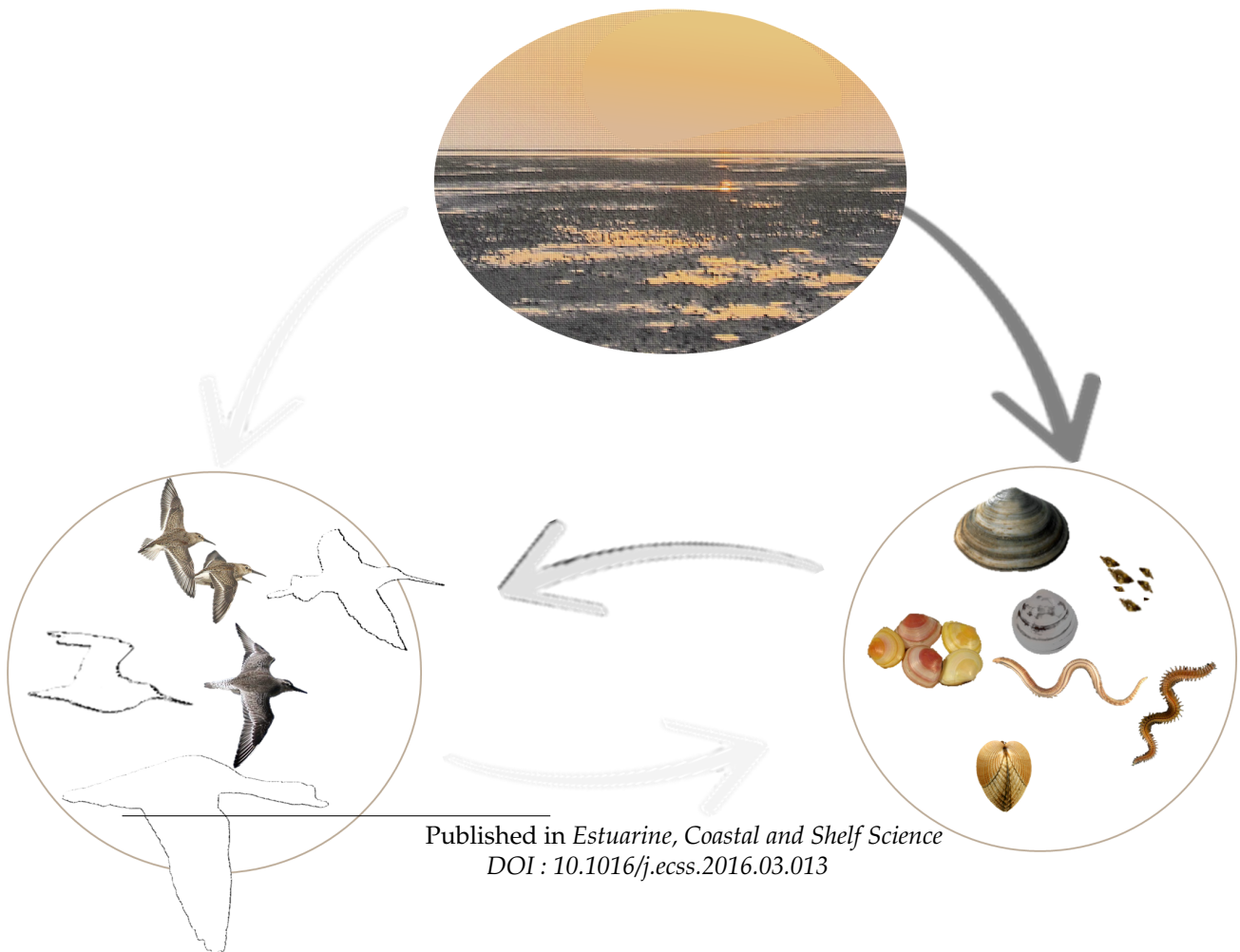
Avocette élégante



Chapter 1

Influence of environmental gradients on the distribution of benthic resources available for shorebirds on intertidal mudflats of Yves Bay, France

Anne S. PHILIPPE, David PINAUD, Marie-Laure CAYATTE, Cyril GOULEVANT, Nicolas LACHAUSSÉE, Philippe PINEAU, Mikhail KARPYTCHEV, Pierrick BOCHER



1.1 Abstract

The case study of Yves Bay (Pertuis Charentais, France) highlighted links between environmental gradients (*i.e.* sediment characteristics and emersion time) and prey distribution and availability for the two most numerous shorebird species overwintering in Yves Bay: the red knot *Calidris canutus* and the dunlin *Calidris alpina*. Two hundred and fifty-two stations were sampled on a predetermined 250 m regular grid covering the intertidal mudflats of this major wintering site in France for east-Atlantic migratory shorebirds. The distribution of principal benthic species abundance and biomass was modelled along two environmental gradients: sediment structure (particularly pronounced north–south sand–mud gradient) and emersion time. The effect of emersion time combined with sedimentary structure strongly explained abundances and biomasses of the main prey for *C. canutus* and *C. alpina* in the bay (*Cerastoderma edule*, *Hydrobia ulvae*, *Macoma balthica*, *Scrobicularia plana*, and *Nephtys hombergii*). This study highlighted prey species-specific spatial segregation/overlapping as well as spatial interferences in the trophic niche of the two shorebirds.

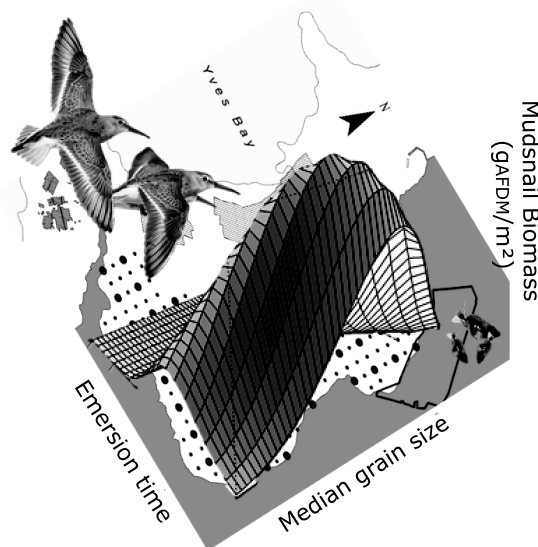


FIGURE 1.1: Graphical abstract

1.2 Introduction

The niche relationships between sympatric species have received early interest in ecology (Hutchinson, 1957; Hutchinson, 1959) and have been developed through the study of community structure (M'Closkey, 1976), inter-species interactions (Trainor et al., 2014), and behavioural ecology (MacArthur, 1958; Schoener, 1965). Feeding resource partitioning (*i.e.* trophic niche) in sympatric predators is the result of specialisation and co-evolutionary change in response to competition and complex interspecific interactions (Schoener, 1974). The prey spatial distribution together with prey size and taxa, plays a crucial role in the resource partitioning of predators, since it proceeds also from interspecific interactions among predators (Wells, 1978).

Most shorebird species are dependent on intertidal flats as feeding areas during the non-breeding period. Several species forage regularly together in the same habitat (intertidal mudflats) and share the same potential benthic invertebrates as a trophic resource. They often experience trophic niches overlap, and their segregation is partly the result of morphology, feeding methods, and a highly specialised diet (Baker and Baker, 1973; Nebel and Thompson, 2011). The trophic segregation between shorebird species can be described qualitatively (*e.g.* different prey species, prey quality, or preference), quantitatively (*e.g.* different prey sizes), as well as temporally (*e.g.* night/day foraging, different season) or spatially (*e.g.* in relation with the vertical or horizontal distribution of their prey). In the present study we investigate the spatial trophic segregation in two sympatric and common shorebird species: *Calidris canutus* and *Calidris alpina*, through the distribution of their feeding resource.

The red knots *Calidris canutus* and the dunlins *Calidris alpina* are long-distance migratory shorebirds that overwinter in intertidal mudflats. These two species are common and dominant shorebirds in the European mudflats, including the Pertuis Charentais and Yves Bay in France (Delaney et al., 2009). Locally, their trophic resource is composed exclusively of macrobenthic species with overlapping distribution on mudflats (Compton et al., 2008); however, both species exploit contrasted trophic niches (Bocher et al., 2014b). Their trophic niches differ chiefly because of distinct ecomorphological patterns (digestive capacity / flexibility), and dunlins are smaller individuals that are much more constrained by prey sizes and digestive quality. Dunlins can be described as generalists (*i.e.* eating molluscs and worms), and their regime shifts according to environmental conditions (Kuwae et al., 2010). Red knots are predominantly deposit-suspensivorous mollusc eaters, with *Hydrobia ulvae* as a principal prey in the

Pertuis Charentais (Quaintenne et al., 2010; Bocher et al., 2014b).

In the present study, prey habitat preference was modelled to better comprehend spatially the trophic niche of dunlins and red knots. Two environmental gradients were used to model prey distribution: median grain size (MGS) and emersion time (ET). The change in distribution between prey species depending on their availability for both predator species was analysed in the specific context of Yves Bay in October 2010, just before the peak of predation pressure.

In tidally structured ecosystems such as intertidal mudflats, benthic distribution is influenced by a large set of environmental variables with complex interactions (Ysebaert et al., 2002). However, benthic distribution is mainly driven by two of them: MGS and ET (Thrush et al., 2003; Kraan et al., 2010a; Compton et al., 2013). Indeed, among physical gradients, ET and MGS play a particularly important role in the functioning of intertidal areas, their biotic composition, and processes (Gray, 1974): these two gradients affect mobility, adsorption capacity, and desiccation resistance and are themselves correlated with other environmental variables such as particularities of local hydrodynamics or salinity (especially in estuaries). Links between sediment characteristics and animal distribution are complex two-way relationships (Rhoads and Boyer, 1982).

Previous studies used MGS or both gradients to predict/describe benthic species distributions (Sanders, 1958; Wells, 1978; Dankers and Beukema, 1981; Creutzberg et al., 1984; Beukema, 1993a; Yates et al., 1993). The recent development of ecological modelling allowed ecologists to describe these non-linear and asymmetric animal–sediment relationships in soft-bodied ecosystems with often zero-inflated data (Anderson, 2008; Compton et al., 2009) and taking account spatial autocorrelation (Kraan et al., 2010a). We propose to model the complex habitat preferences of main prey of shorebirds along two gradients, ET and MGS, in Yves Bay in order to study the trophic segregation of dunlins and red knots according to prey availability distribution.

Yves Bay is a wintering site of international importance in most years for dunlins and red knots and of national importance every year for no less than nine shorebird species (Delaney et al., 2009). Dunlins and red knots account for more than 2/3 of overwintering shorebirds in this bay. Shorebird densities of dunlins observed in winter during the peak of presence of shorebirds are among the highest recorded with approximately four birds per hectare (Santos, Granadeiro, and Palmeirim, 2005), with highest densities between October and January (Fig.S. 1.7, supplementary materials).

In the present work, we firstly describe the main macrobenthic prey distribution in the specific context of Yves Bay and analyse how this distribution changes

between the prey species, and also depending on the available fraction for red knots *vs.* dunlins. Then, we aim to predict their respective niches spatially by means of the two main abiotic environmental gradients of mudflats determinant for their prey distribution, MGS and ET. We will first model the prey distribution depending on these two environmental gradients. We hypothesise that (1) our results will confirm the conclusions of previous studies in comparable mudflats concerning prey site-specific and species-specific habitat preferences (Bocher et al., 2007; Compton et al., 2009).

Based on our knowledge of diets for red knots and dunlins in the Pertuis Charentais, we will compare this first distribution (*i.e.* the distribution of the total resource) with the distribution of available resources for red knots on the one hand and dunlins on the other hand. Due to quantitative and qualitative differences in their trophic niches (Bocher et al., 2014b), we hypothesise (2) spatial differences in the distribution of their respective available prey along the two explanatory gradients.

The final objective is to compare benthic distributions along these two environmental gradients and describe how environmental gradients can help predict the available biomass for shorebirds in a spatially structured environment.

1.3 Materials and methods

1.3.1 Study area

Yves Bay (46°02'N, 01°03'W) is located in the Pertuis Charentais, a series of straits around the islands of Oléron and Ré in the central part of the French Atlantic Coast (Fig. 1.2). This intertidal bay covers an area of 1,200 hectares of mudflat with a strong north–south substrate granulometric gradient. The sandier area in the north is partly covered with a seagrass bed, while the muddy-soft substrate towards the south is purely bare mudflat (Bocher et al., 2007). The lower tidal area of the bay is dedicated to oyster and mussel cultures. At the north of the bay, the coastal marshes are included in a nature reserve (RNN du Marais d'Yves, 192 ha) and used as a roost by shorebirds at high tide during the spring tide.

1.3.2 Sediment characteristics

Within each 500 m, a sediment sample was collected (Fig. 1.2) to a maximum depth of 8 cm. MGS (μm) and the percentage of silt (fraction $< 63 \mu\text{m}$) were determined using a Malvern Mastersizer 2000 diffraction laser (particle sizes analysed from 0.04 to 2,000 μm). MGS was preferred to the silt fraction — both are highly correlated with each other in our study case ($r = -0.90$, $n = 62$, Pearson) — to facilitate later comparison with the literature. For the stations where sediment samples were not taken, MGS was estimated by spatial interpolation using kriging with a "gstat" R package (Pebesma, 2004).

1.3.3 Emersion time (ET)

The time interval during which the mudflat stays emerged was estimated by using sea level predictions from a regional tidal model. This model resolves the shallow water equations on a high-resolution finite element grid by using the TELEMAC software (Hervouet, 2007). The spatial resolution of the grid varies from several km in deep water to about 30 to 50 m near the coast. More details about the method, open boundary forcing, and the calibration can be found in (Nicolle and Karpytchev, 2007; Nicolle, Karpytchev, and Benoit, 2009), where the model was applied for predicting tides and storm surges.

The current model version uses a recently updated finite element grid based on the latest bathymetric surveys and Lidar data as described in Guizien et al., (2014) and in Fossette et al., (2015), where the model was applied for tracking passive tracers and jellyfish in the Pertuis Charentais.

1.3.4 Benthic macrofauna sampling

From 18 October to 2 November 2010, benthic macrofauna were collected over a predetermined 250 m grid covering estuarine intertidal mudflats of Yves Bay (Fig. 1.2) following a proven sampling protocol (Bocher et al., 2007; Kraan et al., 2009a; Bijleveld et al., 2012). Each station was located using a handheld GPS device. Out of 252 stations sampled, 74 were sampled by foot (during low tide) using a sediment core covering an area of 0.018 m^2 down to a depth of 20 to 25 cm. The top fraction (first 4 cm in the sediment) was separated from the bottom fraction to be able to segregate the accessible benthos fraction for red knots and dunlins. We took an additional core (70 mm diameter) covering 0.0038 m^2 to a depth of 4 cm for sampling exclusively the very abundant mudsnail *Hydrobia ulvae* (Pennant) (Bocher et al., 2007). When the tide covered the mudflats with

water (0.4–2.0 m) and for the very soft and inaccessible southern part of the bay, sampling was done from boats using inflatable zodiacs or other small vessels. From the boats, two mud cores (100 mm diameter) covering a total of 0.018 m² to a depth of 20 to 25 cm were taken. Only one core was taken into account for *H. ulvae*, and both were taken into account for any other macrobenthic species. Sampling from boats or by foot yielded identical estimates (Kraan et al., 2007). The top fraction in the cores sampled by boat was interpolated from the proportions observed in cores sampled by foot, based on size-species-specific proportions in the top fraction as in Kraan et al., (2009a).

The cores were sieved over a 1 mm mesh, except for the *H. ulvae* cores, which were sieved over a 0.5 mm mesh. All living molluscs were collected in plastic bags and frozen until laboratory treatment. Polychaetes and crustaceans were preserved in 70% ethanol.

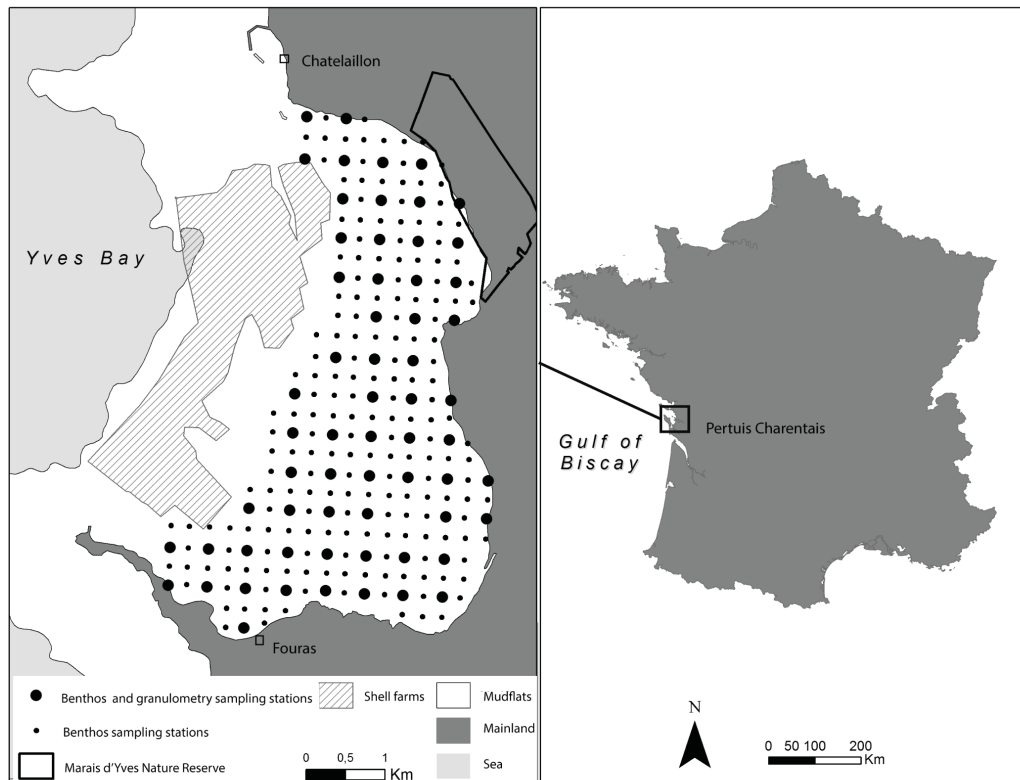


FIGURE 1.2: Map of Yves Bay and the sampling grid, with location in France

1.3.5 Determination of benthic densities and biomasses

Later in the laboratory, molluscs were determined and counted, and their maximum length was measured to the nearest 0.1 mm with Vernier calipers. *H. ulvae*

were size-categorised from 0 mm up to 6 mm (e.g. size class 2 consists of individuals with lengths ranging from 2 to 2.99 mm). The flesh of every mollusc specimen except *H. ulvae* was detached from the shell and placed individually in crucibles (pooled by size class, flesh and shell together). Crucibles containing molluscs were dried in a ventilated oven at 55 to 60 °C to a constant mass and then weighed (DM \pm 0.01 mg). Dried specimens were then incinerated at 550 °C for 4 h to determine their ash mass and then a proxy of their energy content: the ash free dry mass (AFDM). *H. ulvae* flesh biomass ($AFDM_{flesh}$) was estimated for each station from the total biomass ($AFDM_{flesh+shell}$) with the following linear regression: $AFDM_{flesh} = 0.6876AFDM_{flesh+shell} + 7E - 05$ ($R^2 = 0.99$; $N=60$ ind.).

Crustaceans and polychaetes were also identified, counted, and measured, but AFDM was not determined for these phyla. Crustaceans and polychaetes were not weighed due to insufficient numbers of entire individuals to build regression equations.

1.3.6 Available resources for shorebirds

Available prey biomasses for red knot *Calidris canutus* and dunlin *Calidris alpina* were determined from the original benthic dataset, first by isolating the accessible fraction (the top 4 cm of the core, corresponding to the maximal length of the bill for both species) and then considering suitable sizes of the prey (Piersma et al., 1993). Harvestable prey were discriminated by size based on previous studies of feeding ecology of both species in the French Pertuis Charentais (Quaintenne et al., 2010; Drouet et al., in prep.). Red knots are considered exclusive molluscivore shorebirds, and thus only mollusc species were kept according to profitable and ingestible size (i.e. all *Abra* spp., *Cerastoderma edule* [3–10 mm], *Macoma balthica* [3–15 mm], *Scrobicularia plana* [4–12 mm], and all *H. ulvae*). For the dunlins, molluscs and annelids were kept (i.e. all *Abra* sp., *C. edule* [2–8 mm], *M. balthica* [8–10 mm], *S. plana* [2–12 mm], all *H. ulvae*, all *Retusa obtusa*, all *Nephtys hombergii*, and all *Hediste diversicolor*). However, part of their diet may consist of bivalve siphons, especially of large and deeply buried *S. plana*, which are highly localised in the mudflats of the Pertuis Charentais (Bocher et al., 2007). Siphon cropping was never quantified in our ecosystem, but represented a significant fraction of the diet in both shorebird species in previous studies (Zwarts, 1986; Moreira, 1997; Martins et al., 2013).

1.3.7 Modelling of benthic spatial distribution

Generalised linear models (GLMs) were used to model the benthic distribution of the principal benthic species in our system according to ET and MGS gradients (*C. edule*, *M. balthica*, *N. hombergii*, *H. ulvae*, and *S. plana*), assuming the adequate family distribution depending on the prey species and dataset considered (e.g. Gaussian, Negative Binomial, Binomial). Variograms of model residuals were produced to confirm the absence of spatial autocorrelation, and models were validated by a visual inspection of the residuals. Explanatory variables included ET, MGS, their interaction, and their quadratic terms (Kraan et al. 2010). The response variables were the counts per core of the most occurring species (*C. edule*, *M. balthica*, *N. hombergii*, *S. plana*), presence/absence of macrobenthos, and biomass of *H. ulvae* and *M. balthica* for the total resource sampled, the available fraction for dunlins, as well as the available fraction for the red knots. Model selection was based on the Akaike information criterion considering best models with $\Delta\text{AIC} \geq 2$ (Akaike, 1974; Burnham, Anderson, and Huyvaert, 2011). In the case of models with equivalent AIC or when $\Delta\text{AIC} \geq 2$, the principle of parsimony was applied, keeping the model with the lower number of parameters. *H. ulvae* density and biomass showed some high residual values in the models, due to some local aggregations of individuals. Despite the difficulty to adjust the models with these values, we chose to keep them in the dataset because of their biological relevance for shorebirds, corresponding to a known fact and not to a sampling error [*i.e.* high densities of *H. ulvae* in ridges as a result of specific hydrodynamic conditions or floating ability of this mudsnail (Armonies and Hartke, 1995; Haubois et al., 2002)].

Statistical analyses of the data were performed using R version 3.2.1 (Team, 2015) using packages gstat (Pebesma, 2004) and MASS (Venables and Ripley, 2002). ArcGIS® software version 10.1 by ESRI was used for mapping results.

1.4 Results

Sediment characteristics

Results concerning sediment size distribution in Yves Bay (Bay of Biscay, France) revealed a strong gradient of sandy to muddy sediment (*i.e.* less than 8 km) with MGS ranging from 269 to 20 μm and silt fractions ranging from 0 to 51% (from north to south) and could be the result of coarse sand coming from beach replenishment in the north (M-L. Cayatte and C. Goulevant, *pers.com*). This gradient is

steeper than in previous studies analysing the effect of sediment size on benthic distribution (*e.g.* in Creutzberg et al., 1984 MGS ranged from 100 μm to 300 μm and silt fraction from 0 to 20%, in Kraan et al., 2010a MGS ranged from 100 μm to 250 μm) and provides us with a quasi-experimental setting for testing the combined effects of physical substrate characteristics and ET on species distribution and densities, as well as the biomass distribution of macrobenthic prey in this mudflat ecosystem. Original values revealed a strong north–south granulometric gradient with a significant increase of MGS values with increasing latitude (linear regression; *p-value* <0.0001). MGS values predicted by the model were much lower in the south (minimum 20 μm) compared to the north (maximum 269 μm) for a given distance to the coast (Fig. 1.3).

Emersion time (ET)

Across the stations, ET ranged from 0 to 9.2 hours for a mean tidal cycle of 12.5 h, with three stations located in the limit subtidal/intertidal (ET = 0 h) (Fig. 1.3). The sampling stations did not cover all of the intertidal area, but the number of stations with low ET values was sufficient to apply our models. In our study system, the two variables (ET and MGS) were weakly correlated (Pearson coefficient = 0.39).

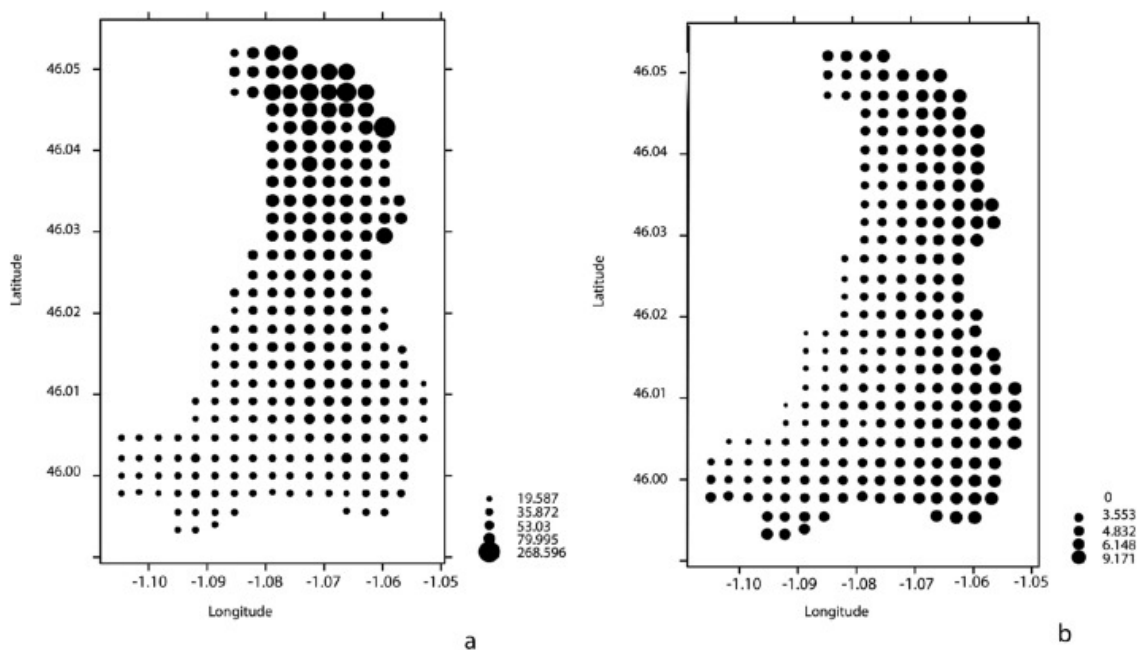


FIGURE 1.3: (a) Median sediment grain size distribution in Yves Bay, empirical values + interpolated values using kriging (on the left, in μm); (b) ET per sampled station using sea level predictions from a regional tidal model (on the right, in h)

Benthic macrofauna

A total of 32 OTUs (operational taxonomic units) were identified for all macrobenthic organisms collected, with 26 identified to the species level. Among these 32 OTUs, 13 belong to the phylum of molluscs (8 bivalves and 5 gastropods), 7 to the subphylum of crustaceans, and 12 to the phylum of annelids (Table 1.1). The mudsnail *Hydrobia ulvae* accounted for more than 91% of the total number of macrobenthos individuals, and four other taxa composed more than 70% of the remaining macrobenthos: the bivalves *Cerastoderma edule*, *Macoma balthica*, *Scrobicularia plana* and the polychaete *Nephtys hombergii*. The most common and widespread main occurring species (*i.e.* present in more than 9% of the stations) were *C. edule*, *M. balthica*, *S. plana*, *H. ulvae*, and *N. hombergii* (Table 1.1). The four common mollusc species represented more than 99% of the total molluscan biomass in the bay. The spatial distribution of these four dominant mollusc species and the polychaete *N. hombergii* in the bay were different (Fig. 1.4). *S. plana* formed a belt along the coast with the highest densities in the upper intertidal zone, and mostly in the south. *H. ulvae* was the most occurring species (present in more than 70% of the sampling stations), with lower densities in the lowest part of the intertidal. *C. edule* was patchily distributed and occurred in less than 10% of sampling stations, mostly concentrated in the north of the bay. *M. balthica* abundances were concentrated in the upper intertidal zone, but equally spread in latitude. The overall mollusc biomass was located mostly in the upper intertidal area, with no perceptible preference between the north and the south. *N. hombergii* was present in nearly 40% of the stations, with highest densities in the middle and lower intertidal area, mostly in the north of the bay.

Modelling of benthos densities and biomass along the two environmental gradients

GLMs were applied to total resource and available resources for dunlins and red knots, respectively (Table 1.2).

Predictions were represented in two dimensions when only one gradient was used in the model (Fig. 1.5). When the interaction between the two gradients better predicted benthos densities or biomass, we represented the predictions in three dimensions: X and Y axes horizontally projected representing MGS and ET, respectively, and Z axis vertically projected representing the prediction of

TABLE 1.1: Frequency of occurrence (Occ), mean densities with min. and max. values, total biomass, total number, and mean sizes with min. and max. values of benthic macrofauna, Yves Bay (2010)

Species	Abr.	Occ. %	Density <i>ind / m²</i>	AFDM <i>mg / m²</i>	Nb	Size mm
Bivalves						
<i>Nucula nitidosa</i>		3.2	2.8±17.3 (0-191.0)	—	11	4.5±2.8 (2.1-10.6)
<i>Mytilus edulis</i>		0.4	0.3±4.0 (0-63.7)	<0.1	1	—
<i>Cerastoderma edule</i>	CER	9.1	8.8±32.3 (0-282.9)	307.6	37	10.7±4.8 (2.1-23.9)
<i>Ruditapes sp.</i>		1.6	1.0±7.8 (0-63.7)	<0.1	4	—
<i>Macoma balthica</i>	MAC	24.6	27.5±64.7 (0-573.0)	1,159.0	114	10.3±4.0 (2.4-21.6)
<i>Scrobicularia plana</i>	SCR	9.1	13.6±55.2 (0-445.6)	2,152.4	55	18.4±10.1 (3.5-35.5)
<i>Abra tenuis</i>		0.8	0.5±5.7 (0-63.7)	<0.1	2	—
<i>Corbula gibba</i>		2.0	1.3±8.9 (0-63.7)	<0.1	5	6.9±2.3 (5.0-10.1)
Gastropods						
<i>Gastropoda sp.</i>		0.4	0.3±4.1 (0-63.7)	—	1	—
<i>Hydrobia ulvae</i>	HYD	73.4	6,148.4±11,687.3 (0-78,213.3)	830.6	8,267	2.4±1.4 (0-6)*
<i>Retusa obtusa</i>		2.0	2.5±20 (0-254.6)	—	10	2.7±0.7 (0-3.4)
<i>Bittium reticulatum</i>		0.4	1.8±28.5 (0-452.7)	—	8	—
<i>Cyclope neritea</i>		0.4	0.3±4.0 (0-63.7)	—	1	—
Crustaceans						
<i>Cyathura carinata</i>		0.4	0.2±3.6 (0-56.6)	<0.1	1	—
<i>Idotea chelipes</i>		0.4	0.2±3.6 (0-56.6)	—	1	—
<i>Gammarus locusta</i>		1.6	2.3±25.0 (0-382.0)	<0.1	9	6.7±2.0 (5.7-10.9)
<i>Urothoe marina</i>		0.4	0.7±10.7 (0-169.8)	—	3	—
<i>Corophium volutator</i>		2.0	68.1±1,015.1 (0-16,110.4)	—	66	—
<i>Pagurus sp.</i>		0.4	0.3±4.0 (0-63.7)	—	1	—
<i>Carcinus maenas</i>		0.8	0.5±5.4 (56.6-63.7)	—	2	—
Polychaetes						
<i>Arenicola marina</i>		1.2	0.7±6.1 (0-56.6)	—	3	—
<i>Notomastus latericeus</i>		1.6	1.0±8.0 (0-63.7)	—	4	—
<i>Diopatra spp.</i>		2.0	1.8±13.2 (0-127.3)	—	7	—
<i>Glycera convoluta</i>		0.4	0.2±3.6 (0-56.6)	<0.1	1	—
<i>Nephtys spp.</i>		2.4	1.5±9.7 (0-63.7)	—	6	—
<i>Nephtys hombergii</i>	NHO	36.9	40.5±66.0 (0-339.5)	230.4	169	22.2±5.7 (10.5-42.2)
<i>Nereis spp.</i>		0.8	0.4±5.0 (0-56.6)	—	2	—
<i>Hediste diversicolor</i>		4.0	3.1±17.6 (0-191.0)	—	13	60.8±12.6 (31.0-77.4)
<i>Allitta succinea</i>		2.8	2.4±16.6 (0-191.0)	—	10	53.1±21.6 (21.1-93.1)
<i>Neanthes irrorata</i>		0.4	0.2±3.6 (0-56.6)	—	1	—
<i>Pectinaria koreni</i>		0.4	0.3±4.0 (0-63.7)	—	1	—
<i>Owenia fusiformis</i>		2.0	1.2±8.1 (0-63.7)	—	5	—

**Hydrobia ulvae* individuals were categorized by 1 mm size classes

TABLE 1.2: Selection of the minimal adequate model (bold) based on AIC values ($\Delta AIC \geq 2$) for the most occurring prey in the system and in the diets of shorebirds, in counts (n), biomass (b), or presence/absence (P/A) depending on the species. Six models are compared; the 'Full' model represents the interaction of ET and MGS and their quadratic terms. Distribution family of the data is detailed, 'NB' for negative binomial, 'B' for binomial, 'G' for Gaussian. Abbreviations refer to Table 1.

TOTAL RESOURCE							
(1) HYD- (b)		(2) MAC - (b)		(3) CER - (n)		(4) NHO - (n)	
Family	NB	Family	G	Family	NB	Family	NB
Model	ΔAIC	Model	ΔAIC	Model	ΔAIC	Model	ΔAIC
Full	0	ET	0	MGS	0	ET×MGS	0
ET	30.88	ET+MGS	0.35	ET+MGS	1.46	Full	0
ET+MGS	30.15	ET×MGS	0.89	ET	4.12	MGS	14.38
ET×MGS	32.07	Full	1.23	ET×MGS	3.42	ET+MGS	15.25
MGS	141.32	Null	7.69	Full	3.42	Null	21.69
Null	144.69	MGS	9.66	Null	6.2	ET	23.68
(5) SCR - (n)		(6) MAC - (n)		(7) Benthos - P/A			
Family	NB	Family	G	Family	NB		
Model	ΔAIC	Model	ΔAIC	Model	ΔAIC		
ET+MGS	0	ET	0	ET	0		
ET×MGS	1.00	ET+MGS	1.95	ET+MGS	1.78		
Full	1.00	ET×MGS	3.87	ET×MGS	0.92		
ET	18.46	Full	3.87	Full	0.92		
MGS	30.30	Null	30.88	MGS	19.06		
Null	35.93	MGS	30.17	Null	23.18		
AVAILABLE RESOURCE FOR <i>C. alpina</i>							
(1) HYH - (b)		(2) MAC - (b)		(3) CER - (n)		(4) NHO - (n)	
Family	NB	Family	G	Family	NB	Family	NB
Model	ΔAIC	Model	ΔAIC	Model	ΔAIC	Model	ΔAIC
Full	0	ET+MGS	0	MGS	0	ET×MGS	0
ET	30.88	ET×MGS	1.62	ET	1.85	Full	0
ET+MGS	30.15	Full	0.57	ET+MGS	1.50	MGS	14.92
ET×MGS	32.07	MGS	4.51	Null	3.13	ET+MGS	16.19
MGS	141.32	ET	4.64	ET×MGS	3.48	Null	19.36
Null	144.69	Null	17.36	Full	3.48	ET	21.35
(5) SCR - (n)		(6) MAC - (n)		(7) Benthos - P/A			
Family	NB	Family	G	Family	NB		
Model	ΔAIC	Model	ΔAIC	Model	ΔAIC		
ET+MGS	0	ET	0	ET	0		
ET	2.2	ET+MGS	0.49	ET+MGS	1.83		
ET×MGS	1.85	ET×MGS	2.19	ET×MGS	3.83		
Full	1.85	Full	2.19	Full	3.83		
Null	7.73	MGS	16.26	MGS	50.02		
MGS	8.69	Null	19.63	Null	61.24		
AVAILABLE RESOURCE FOR <i>C. canutus</i>							
(1) HYD - (b)		(2) MAC - (b)		(3) CER - (n)		(4) NHO - (n) *	
Family	NB	Family	G	Family	NB	Family	NB
Model	ΔAIC	Model	ΔAIC	Model	ΔAIC	Model	ΔAIC
Full	0	ET	0	MGS	0	-	-
ET	30.88	ET+MGS	0.14	ET	1.13	-	-
ET+MGS	30.15	ET×MGS	2.04	ET+MGS	0.26	-	-
ET×MGS	32.07	Full	2.29	ET×MGS	2.25	-	-
MGS	141.32	Null	8.23	Full	2.25	-	-
Null	144.69	MGS	10.23	Null	4.95	-	-
(5) SCR - (n)		(6) MAC - (n)		(7) Benthos - P/A			
Family	NB	Family	G	Family	NB		
Model	ΔAIC	Model	ΔAIC	Model	ΔAIC		
ET	0	ET	0	ET	0		
ET+MGS	1.23	ET+MGS	2.00	ET+MGS	0.93		
ET×MGS	0.54	ET×MGS	4.00	ET×MGS	1.73		
Full	0.54	Full	4.00	Full	1.73		
Null	5.03	Null	27.93	MGS	66.85		
MGS	6.29	MGS	26.43	Null	71.94		

*Species not ingested by *C. canutus*

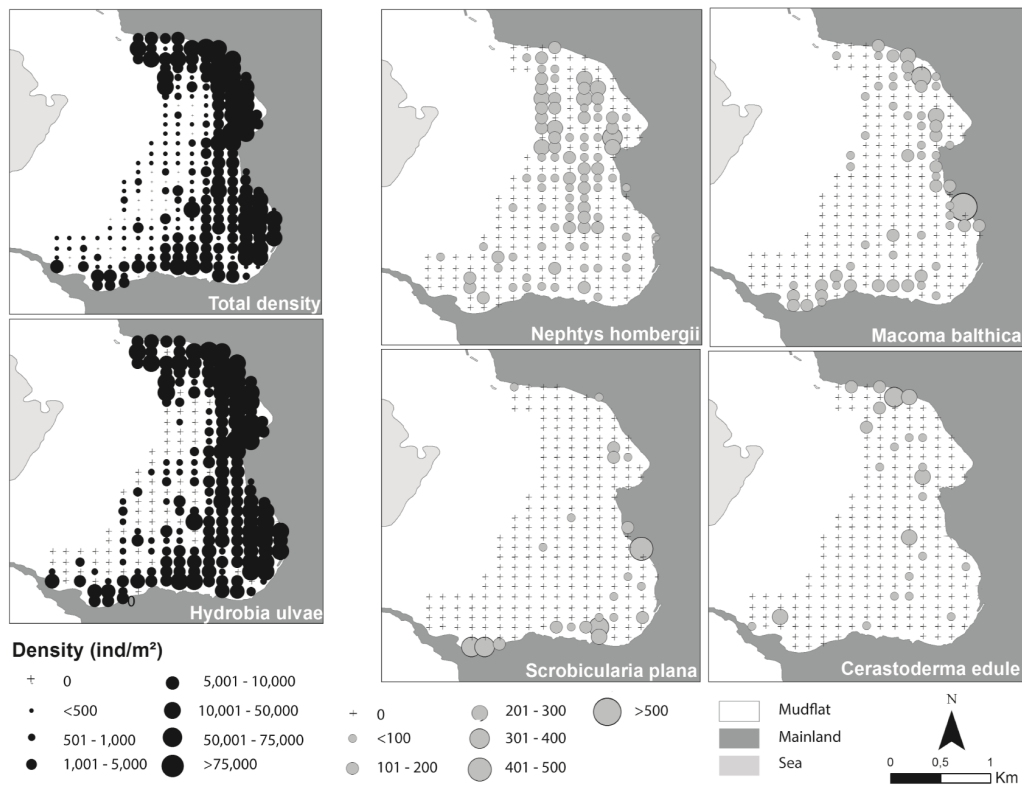


FIGURE 1.4: Spatial distribution of the four main mollusc species, the most abundant annelid species, and the total macrobenthos collected in Yves Bay: the cockle *Cerastoderma edule*, the mud snail *Hydrobia ulvae*, the tellinid bivalve *Macoma balthica*, the peppery furrow shell *Scrobicularia plana*, and the polychaete *Nephtys hombergii*. Due to much higher densities for *H. ulvae* and the total biomass, the two maps on the left are presented with a distinct legend (in black), whereas other species are represented with a gray legend.

response variable (Fig. 1.6). Depending on the species, the data constrained us to only model densities or biomass.

M. balthica numbers were predicted to reach 3 individuals per core in areas with the highest ET, and the available fraction predicted for the shorebirds followed the same perceived habitat preference, reaching 2–2.5 individuals per core for the dunlins and the red knots (Fig. 1.5). Macrobenthos was predicted to be absent from the samples (oligotrophic areas) with the lowest ET, with a maximal probability of 60% when the total macrobenthic resource is considered. The predicted distribution for the available fraction for dunlins and red knots was comparable, with highest probabilities (90% for both shorebird species when the ET was null) (Fig. 1.5). Cockles were predicted to be found in higher numbers in areas with a large MGS (150 μm –250 μm), with a maximum total resource predicted of ≈ 3 indcore, ≈ 2 indcore for dunlins and ≈ 2.5 indcore for red knots (Fig. 1.5).

S. plana was predicted in higher densities in areas with the longest ET and the lowest MGS for the total resource as for the available fraction for dunlins (Fig. 1.6

a,b). Available *S. plana* numbers for red knots were predicted to be found in areas with the highest ET (Fig. 1.6 c). The number of individuals per core was predicted to reach 40.00 $\text{g}\cdot\text{m}^{-2}$ for the total resource, and the predictions for dunlins and red knots dropped down to 3.00 $\text{g}\cdot\text{m}^{-2}$ and 0.60 $\text{g}\cdot\text{m}^{-2}$, respectively. The highest biomasses of *M. balthica* (0.70 $\text{g}_{(AFDM)}\cdot\text{m}^{-2}$) were predicted in areas with the longest ET for the total resource. Individuals available for dunlins were situated in areas combining large grain sizes and also long ET (up to 0.15 $\text{g}_{(AFDM)}\cdot\text{m}^{-2}$), and for red knot in areas with higher ET (up to 0.40 $\text{g}_{(AFDM)}\cdot\text{m}^{-2}$) (Fig. 1.6 d,e,f).

N. hombergii numbers were predicted to reach no less than 120 individuals per core in areas with the highest MGS and a minimal ET of 4 h. The available fraction for dunlins followed the same predicted distribution but with lower numbers (only the accessible fraction is available) (Fig. 1.6 h). *H. ulvae* biomass was predicted in higher density (up to 6.00 $\text{g}_{(AFDM)}\cdot\text{m}^{-2}$) in habitats combining long ET and an MGS of about 150 μm (Fig. 1.6).

1.5 Discussion

This study is the first description of macrobenthic fauna distribution on an intertidal mudflat, which presents such a strong granulometric gradient, according to our knowledge. This small-sized bay appears as a rare opportunity for testing independently the influence of ET gradient and sediment structure on the distribution of macrobenthic species as these two variables are uncorrelated in this study case. The independence of these usually highly correlated variables may be explained by anthropogenic causes. Such a steep granulometric gradient is probably caused by the conjunction of natural hydrodynamic conditions and anthropogenic input of sand from beaches on immediate northern coasts of the entrance of the Bay, (Prof. Eric Chaumillon, LIENSs laboratory, *pers. comm.*), resulting in extremely coarse sediment in the north of the Bay. This study highlighted species-specific distributions for benthic species along the two gradients considered, with sometimes overlapping perceived habitat preferences. The existence of animal–sediment relationships in mudflat ecosystems is undisputed (Anderson, 2008), but many other factors can influence prey spatial distribution. In this study, we only used two environmental gradients to model macrobenthic distribution. However, in the context of the present study, given the spatial scale covered by the sampling grid (< 12 km^2), environment variables like pollution or factors affecting colonisation could be considered constant across the study site. Among prey species, the principal occurring prey (species found in more than 20

stations out of 252, *i.e.* *Cerastoderma edule*, *Hydrobia ulvae*, *Nephtys hombergii*, *Macoma balthica*, and *Scrobicularia plana*) showed different distribution. Macrobenthos was concentrated in areas with the highest ET (*i.e.* near the coast) — a result that is consistent with all previous studies in intertidal mudflats, to the best of our knowledge — and explained mainly by the highest productivity of the upper intertidal areas, usually richer in nutrients thanks to a combination of reduced solute transport and increased microbial processes (Kuwae, Kibe, and Nakamura, 2003) and a higher exposition to light. When compared to previous studies, the distribution of the main species showed distributional trends consistent with those previously described for the Pertuis Charentais (Bocher et al., 2007; Compton et al., 2009).

Our predictions were applied on grids covering the entire range of ET values and MGS values interpolated. However, the combination of a high MGS (< 200 μm) and low ET (<5 h) was not realistic for Yves Bay, and did not represent any observable combination in the field. We therefore predicted prey distributions on their potential niche (including unrealistic combinations between ET values and MGS values) instead of their 'realised' niche (taking into account only the realistic combinations between the two variables) (Kraan et al., 2013). This bias forced us to constrain the grid representing *N. hombergii* numbers, for instance (Fig. 1.6), and yielded light over-predictions for *S. plana* in the grid cells corresponding with low MGS and high ET values as well as for *M. balthica* for high ET values.

The comparative analysis of the trophic niches of two dominant shorebird species in Yves Bay (*Calidris canutus* and *Calidris alpina*), based on the fraction of benthos that is potentially available to them (in terms of depth, size and taxa), highlighted trophic habitat overlap as well as segregation between the shorebird species via their prey habitat perceived preferences. Available resources for red knots and dunlins encompassed the main macrobenthic species in the system in terms of abundance and biomass. We showed contrasting distribution between prey species, but also depending on the harvestable sizes considered for a given species: habitat distribution was different between the available fraction for dunlins and red knots (*i.e.* for *M. balthica* and *S. plana* abundances).

All *H. ulvae* were available for dunlins and red knots; however, only a small portion of *S. plana* was available to them (1/3 for dunlins and 1/4 for red knots). As *Hydrobia* were dominant and widely spread over the bay, we could consider them as *ad libitum* for shorebirds. Segregation in space between the two shorebird species should therefore concern preferred species which differ in terms of quality and accessibility.

The available fraction for dunlins was always smaller than the available fraction for red knots when we considered only bivalve species abundances and biomass. Dunlins are more restricted by size and quality of their prey. Energy requirements of dunlins are smaller, since their body mass is less than half the body mass of red knots in the Pertuis Charentais (van de Kam et al., 2004).

Through the modelling of perceived habitat preferences of their main potential prey, we could highlight spatial trophic niches overlap, but models also showed potential segregation. We can hypothesise that trophic overlap carries over effects in terms of competition, particularly for very abundant and easily accessible species such as *H. ulvae*. However, the available fraction of *M. balthica* biomass and also *S. plana* numbers have highlighted distinct habitat preferences, and their distribution changed depending on the size of the fractions considered. Moreover, *N. hombergii* is a prey that is absent from the diet of red knots and could potentially constitute a sort of trophic way out for dunlins. Besides, *N. hombergii* could very well be a spatially segregative prey species for dunlins, as this prey was predicted in higher densities in lower ET and higher grain sizes in the north-western part of the bay, as opposed to nearly all other potential prey for the two shorebird species considered. Since dunlins have shown to experience trophic shifts depending on environmental conditions or seasons (Kuwae et al., 2010; Martins et al., 2013) and were described successively as worm eaters (Bocher et al., 2014b) or principally mollusc eaters in spatially close environments (Drouet et al., in prep.), it would be interesting to test whether this trophic shift demonstrated in the Pertuis Charentais is linked with the competition pressure between our two dominant shorebird species and translates into changing feeding areas in the Bay. Do dunlins feed more on worms and small *S. plana*, for instance, when red knots are found in very high numbers in the same area?

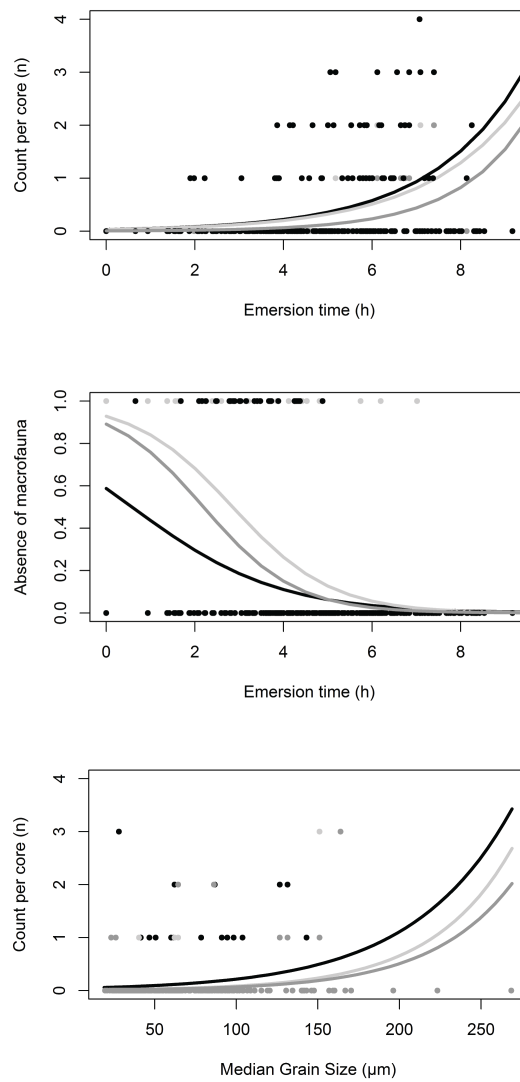


FIGURE 1.5: (a) *M. balthica* abundances distribution predicted along ET gradient, (b) benthic macrofauna absence probability modelled along ET gradient, and (c) *C. edule* abundances modelled distribution depending on MGS. Lines indicate the predictions and dots indicate the original data. In black the distribution for the total resource, in grey the resources available for dunlins, and in lighter grey the resources available for red knots.

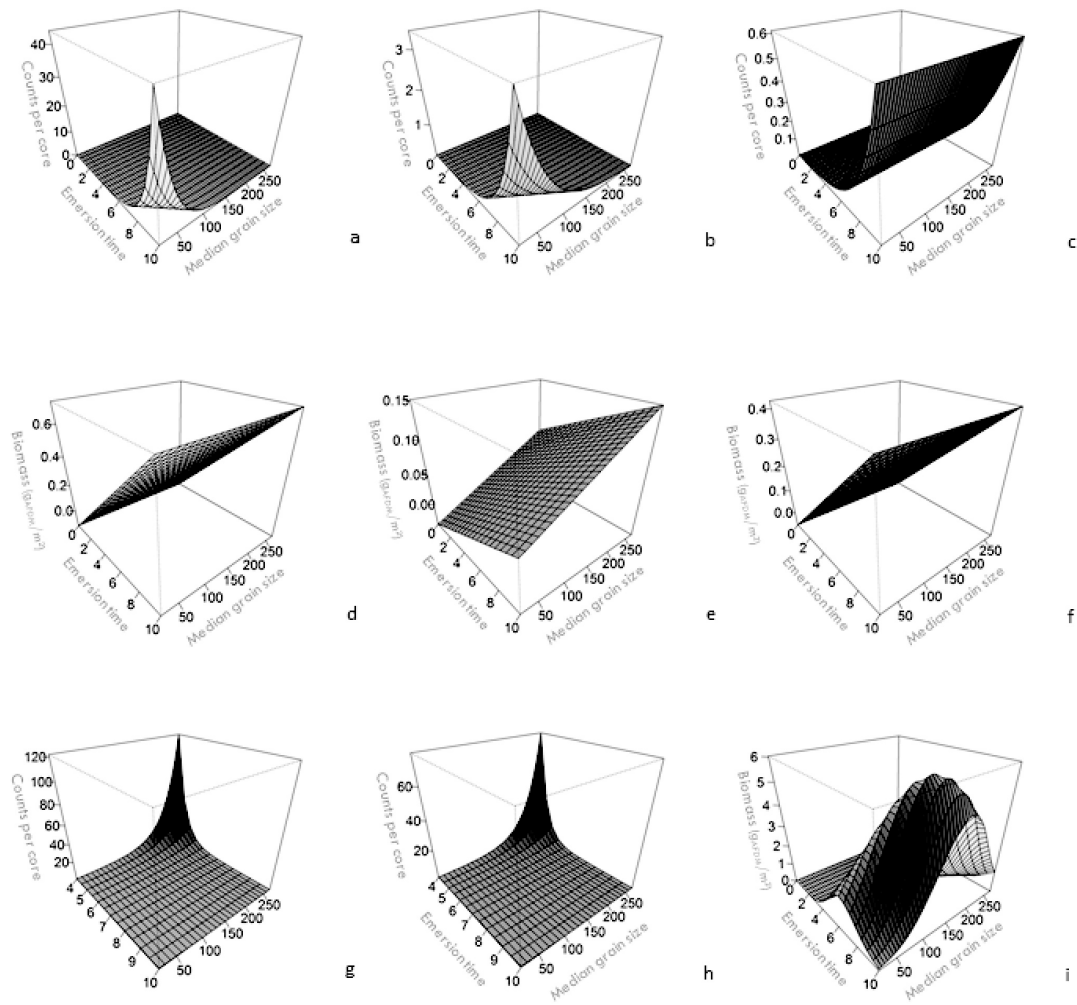


FIGURE 1.6: (a) *S. plana* abundances modelled distribution along two environmental gradients for total resource, (b)resources available for dunlins, and (c) depending on ET for red knots; (d) *M. balthica* biomass modelled distribution along ET gradient for the total resource, (e) along ET and MGS for dunlins, and (f) only ET for red knots; (g) *N. hombergii* abundances modelled distribution along two environmental gradients, MGS and ET, for the total resource and (h) for the resources available for dunlins; (i) *H. ulvae* modelled distribution along two environmental gradients, MGS and ET, for the total resource, the resources available for dunlins, and the resources available for red knots.

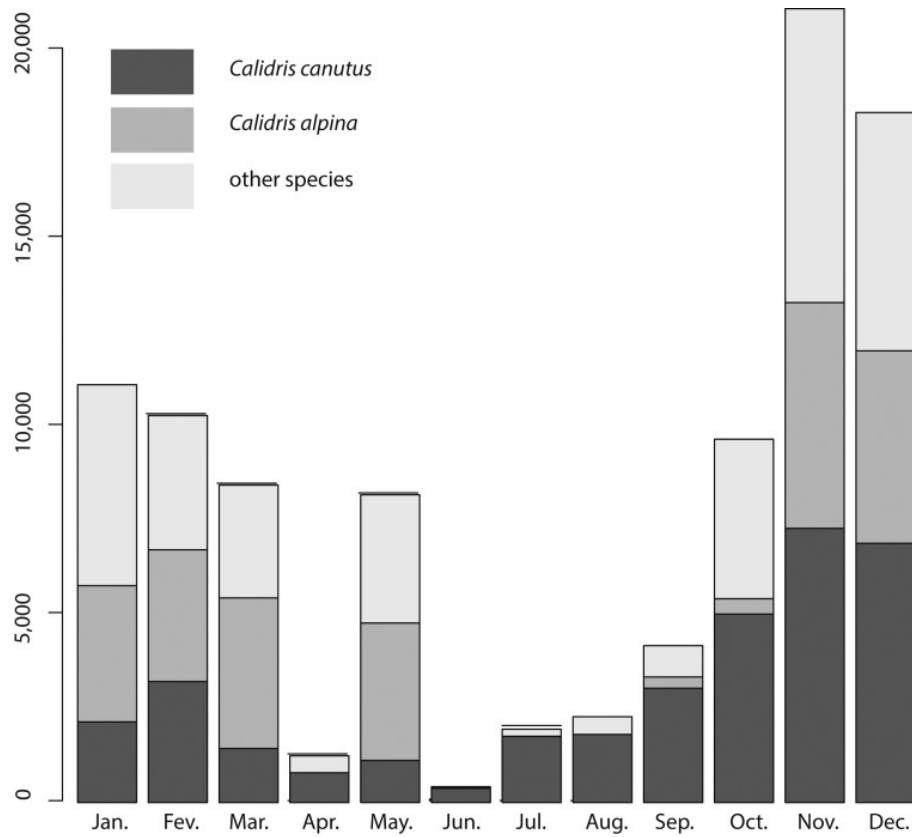


FIGURE 1.7: Monthly counts of shorebirds in 2010 in Yves Bay. From light grey to dark grey: red knots *Calidris canutus*, dunlin *Calidris alpina* and other species of shorebirds.

Box 1

TELL ME WHAT YOU EAT, AND I WILL TELL YOU WHO YOU ARE *

Anthelme Brillat-Savarin considered gastronomy as a science, and his famous sentence was based on the observation of nature, long before we knew an animal's body is actually composed of elements, atoms it ingests. Here we provide an overview of the techniques that can be used in shorebird ecology to infer diet.

Morphological cues

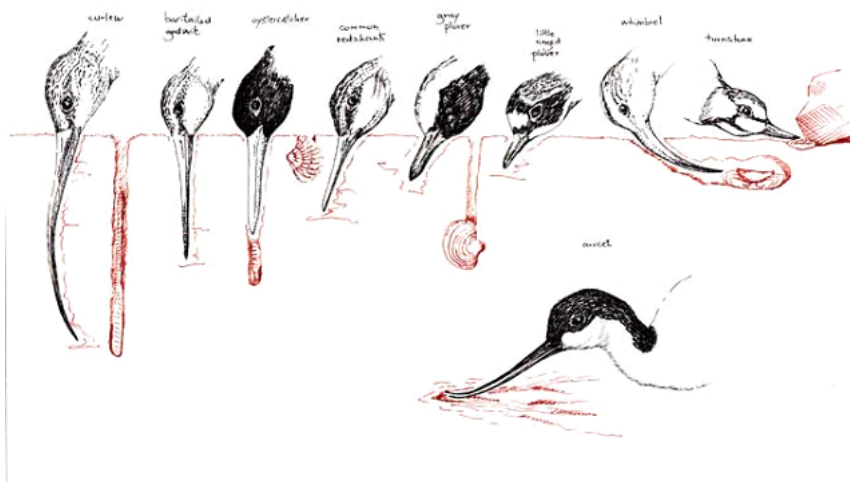


FIGURE 1.8: Bill sizes of shorebirds and their common prey species**

Morphology of the bill is the most obvious trait that drives trophic specialisation and partitioning within shorebirds (Chapter 1). Bill length determines the fraction that is accessible, and is often associated with sexual dimorphism in shorebirds. Females with longer bills will have access to different prey types, quantities as well as different foraging areas (Nebel and Thompson, 2011). Bill shape is a cue indicating which kind of prey can be searched for and handled. Less obvious morphological traits can be investigated, such as gizzard mass (van Gils, 2004) which is flexible

*Brillat-Savarin, (1853)

**<http://studentmag.acsedu.com/Articles/Seabirds-and-Waterbirds.aspx>, retrieved

in some species and was proved to be linked with the quality (flesh-to-shell ratio) of the molluscs ingested and the energy consumed, and to adapt to the migratory stage, and even personality (via its link to gizzard size, Bijleveld et al., 2014). Colour can even be an indicator of diet in *Phoenicopterus* species (*i.e.* Flamingos): the saturation of the colour of the plumage is a result of the carotenoids contained in the crustaceans they feed on.

Diet choice from direct observation

It is sometimes possible to assess prey types, sizes and quantities by simply observing the bird on the field. However one could easily miss small prey, especially since shorebirds can have extremely high pecking rates (Martins et al., 2013). In field conditions, observation is a matter of the material used, but also the weather conditions (light, warmth). It is easier when the bird is captive, and even more when the observations are made from videos that can be observed at lower speed (like in the experiment described in Chapter 7).

Diet reconstruction from faeces

Diet reconstruction from faeces is also possible, and was early detailed for a mollusc-eater in Dekinga and Piersma, (1993). This technique was used in Chapter 2, but is time consuming. Mollusc species and size can be derived from the fragments observed in the faeces of birds, after they crushed the shells in their gizzard and digested the soft materials. From these fragments (in particular bivalve hinges), one can infer the quantity and type of prey ingested (*e.g.* using calibration curves, shell length is inferred from hinge size, and then flesh biomass is inferred from shell length). This method can also be used to assess the diet of worm-eaters (*i.e.* setae and jaws are left undigested), however it is often labour-intensive and less accurate than for molluscs, since worms are not always ingested whole and some species remains are hard to identify (Scheiffarth, 2001). Crustaceans and plant materials (*e.g.* seagrass roots, biofilm) are also hard to identify and measure (Chapter 7).

Diet reconstruction from stomach content

Like faeces analysis, this method is precise, help assess the variety of prey, and depending on the diet the quantity ingested, and requires long working hours in the field and in the laboratory (Colwell, 2010). However, while faeces can be collected directly on the mudflat, stomach contents can only be obtained on captive (or dead) birds and is not well adapted for most of the shorebird species. Indeed most species are protected, and when they are captured by night they are roosting with an empty stomach (shorebirds have higher digestion rates compared with other sea birds). However, it can be used to infer the share of biofilm or plant material in the diet, when diet reconstruction from faeces fails (Mathot, Lund, and Elnor, 2010).

Diet reconstruction from isotopic analysis

Like in any other secondary producer, stable isotopes, and in particular carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) are useful tools for assessing diet composition (DeNiro and Epstein, 1978). It allows diet reconstruction provided knowledge about isotopic composition of the prey as well as trophic enrichment factors are known (Chapter 7). Given the turnover rate of isotopes in tissues, this technique can be applied to assess diet from a few days ago to several weeks ago (Hobson and Clark, 1992), and can be particularly relevant for long-distance migratory shorebirds. When different populations meet in a stopover site, isotopic signature of feathers for instance can be a precious help for assessing their place of departure, since habitats can yield very contrasted signals. Isotopic analyses can be performed on different tissues: blood cells or plasma, feather and even nails, depending on the objective of the study:

Blood : Either whole (provide information for at least 20 days, Bocher et al., 2014b), or plasma or cells (from a few days to weeks, Klaassen et al., 2010).

Feathers : Some feathers can be used to assess the migratory origin of the birds, via diet at the breeding site for juvenile and at the wintering site for adults considering the moult schedules in shorebirds (Bocher et al., 2014b).

Nails : Other keratin based tissues, like nails can be used. Because they grow progressively and slowly, nails have lower stable isotope turnover rates than blood tissues and can help assess diet up to 120 days back (Lourenço et al., 2015; Catry et al., 2016). Results are comparable with those of feathers, and more robust than those of blood components (Lourenço et al., 2015).

Diet reconstruction from molecular and DNA sequencing analyses :

Using freshly collected fecal material, researchers reached a higher diversity of diet reconstruction, including terrestrial, freshwater and pelagic food items in the semi-palmated sandpiper (*Calidris pusilla*) thanks to DNA sequencing (Gerwing et al., 2016). This technique confirmed that this species is a generalist forager in the Bay of Fundy (North America), with more precision but at higher costs.

Diet reconstruction from modeling

When enough is known about a species (prey preferences, encounter rate, handling time, digestive processing rates), after multiple studies combining different diet reconstruction methods and experiments, modelling can be considered. It is the case for a well studied shorebird species: the red knot *Calidris canutus* (van Gils, 2004). It is now possible to infer a red knot's diet in time and space (Chapter 6), provided detailed knowledge is known about the feeding ecology of the consumer, and the characteristics of the prey present in the system (e.g. quality, biomass, sizes, accessibility and toxicity, see Chapters 3, 4 and 7).

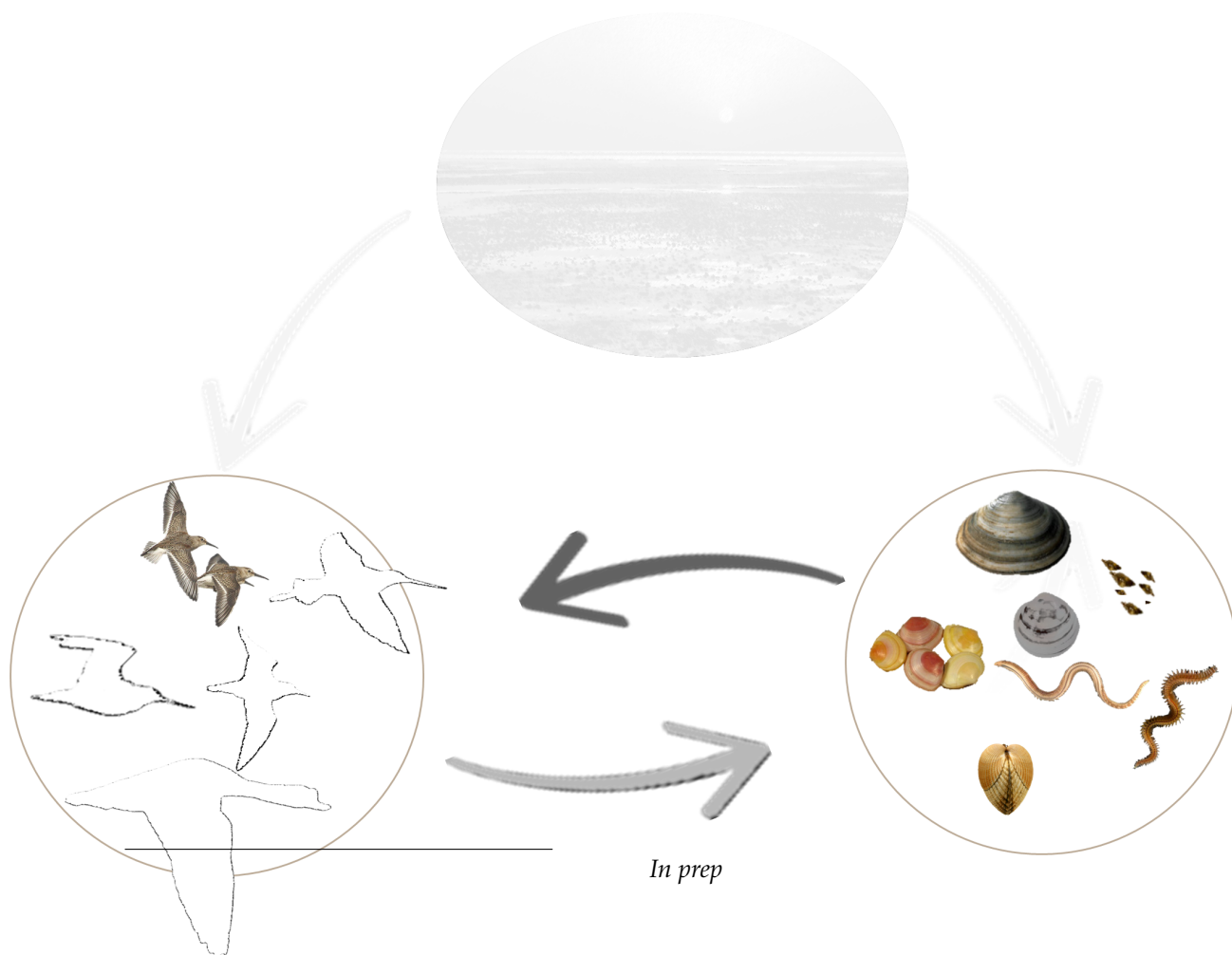
The techniques presented before can be better apprehended when combined with each other and are complementary (the advantage of one can compensate for the drawbacks of another). The good method depends on the research goals: assess prey types, quantities, over only several individuals or much larger numbers, on the catching site or back to breeding grounds, etc. Thanks to the variety of methods that can be used for a precise diet reconstruction, shorebirds - and especially mollusc-eating species such as the red knot - have become key species in feeding behaviour and ecology.



Chapter 2

Constrasting prey availability and selection by Dunlin *Calidris alpina* in two estuarine intertidal mudflats of the Bay of Biscay

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2.1 Abstract

In this study, we describe food availability and diet selection of Dunlin *Calidris alpina* wintering in two estuarine bays on the French Atlantic coast: Marennes-Oléron Basin (composed of the two sub-sites Moëze and Oléron), and Bourgneuf Bay. We examined whether the distribution of birds was related to the density and availability of high-quality prey. Results indicate a strong inter-annual variation in the abundance of birds, which was subject to considerable fluctuations since 1992 without any defined trend and considerable variation in prey-item abundance and diet selection depending upon site. At Bourgneuf Bay and Marennes-Oléron Bay, the prey community was dominated by *Hydrobia ulvae* and this gastropod remained the most important prey species, except at one subsite (Moëze). At Bourgneuf and Oléron, dunlins fed mostly on *H. ulvae*, *Srobicularia plana* and *Macoma balthica*. The polychaetes *Nephtys hombergii* and *Hediste diversicolor* contributed to a lesser extent to the diet of dunlins. However at Moëze, dunlins selected exclusively polychaetae species. Diet of dunlins was site specific with intra-site differences according to local foraging habitats. Prey were selected among the most abundant species in most of the sites with dominance of the very abundant and easy to collect *H. ulvae* except in Moëze where birds seemed to actively select the energetic prey, worms.

2.2 Introduction

Understanding how animals select their foraging habitat is a fundamental question when species and habitat conservation are of concern (Jonzén, 2008). Among birds, migrating shorebirds (Charadriiformes) are particularly dependent on a restricted number of key stopovers and wintering sites outside the breeding period. Consequently, they could be particularly vulnerable to habitat loss and many populations are nowadays in serious decline worldwide (Delaney et al., 2009; Watts, Reed, and Turrin, 2015). Food appears as a primary requirement for survival and therefore the most important determinant of habitat quality (Piersma, 2006) especially for shorebirds with relatively high daily energetic expenditure (Evans, 1976; Kersten and Piersma, 1987). Intertidal sand- or mudflats are the main foraging areas of coastal shorebirds feeding on macrofauna, and the relationship between shorebirds and marine invertebrates is a crucial point for understanding the survival issues of the species. Shorebird distributions through coastal sites have often been positively correlated to those of their benthic prey species (Colwell and Landrum, 1993; Yates et al., 1993; Quaintenne et al., 2011). Therefore, the prey and habitat selections of shorebirds vary according to their morphological, physiological and energetic constraints that result in a wide range of foraging strategies of coexisting bird species on same feeding areas (Jones, 2001; Piersma, 2002; Davis and Smith, 2001). Nevertheless, prey availability often does not equal prey density, and so shorebird foraging studies have to focus at first on the fraction of available food resources, which may sometimes represent a small fraction of potential total food stocks (*i.e.* the harvestability concept introduced to shorebird ecology by Zwarts and Wanink, (1993)).

Here, we focused on dunlin *Calidris alpina*, one of the most abundant shorebirds in the world, particularly along the coasts of Europe during wintering period (van de Kam et al., 2004; Delaney et al., 2009). The species is characterised by a circumpolar distribution during the breeding period and is present in Canada, Europe, central Siberia, Beringia, and Alaska (Engelmoer and Roselaar, 2012). They spread over the five continents during the non-breeding period and up to 11 subspecies have been described (Wenink, Baker, and Tilanus, 1993; Wenink et al., 1996; Wennerberg, 2001; Engelmoer and Roselaar, 2012). The three subspecies found along the East-Atlantic Flyway are *C. a. alpina*, *C. a. schinziii* and *C. a. arctica* (Greenwood, 1986). Along the European coasts, around 1 300,000 individuals mostly belonging to the *C. a. alpina*, winter each year mainly in estuarine bays (Delaney et al., 2009). Approximately a fourth (*c.* 300,000 ind.) of the dunlins overwintering in Europe is located along the Atlantic coast of France

(Bocher et al., 2014a), representing half of all the coastal shorebirds present on the territory (Delaney et al., 2009). Consequently, this shorebird appears as one of the main top predators on coastal habitats along the West-Atlantic French coast. During winter, most dunlins feed on benthic macrofauna (*i.e.* molluscs, crustaceans and worms) on intertidal mudflats but also on other habitats such as beaches, marshes or rocky shores (Cramp and Simmons, 1980). Its diet can be qualitatively and quantitatively reconstituted with various and complementary methods (Barrett et al., 2007): by direct observation (Santos, Palmeirim, and Granadeiro, 2010), by isotopic analyses of tissues as blood and feathers (Haramis et al., 2007; Kohler et al., 2009; Bocher et al., 2014b), or by residual fragment analyses of various prey kept in faeces or stomach contents (Dekinga and Piersma, 1993; Verkuil and Burg, 1996; Scheiffarth, 2001; Sánchez, Green, and Castellanos, 2005). Nevertheless, the method giving the most precise diet composition with respective contribution of each prey remains the analysis of faeces or stomach contents (Dekinga and Piersma, 1993), although is a highly time-consuming method.

We reconstructed the diet of the dunlins and sampled their trophic resource (benthic macrofauna) in two of the most important wintering areas in France for the species: Bourgneuf Bay and Marennes-Oléron Bay (Bocher et al., 2014a, Table 2.1). The diet selection of dunlins was then studied according to the accessibility, the availability and the digestive quality of their main prey at the two sites which were both divided into two subsites according to specific habitats. We examined how suitable the central French Atlantic coast is as an overwintering habitat for dunlins and we discussed the choice of the wintering sites in a broader context in relation to main traditional wintering sites of northwestern Europe. We examined whether the distribution of dunlins at favourable sites on the French Atlantic coast is related to the density and availability of highest quality prey or to most abundant and available prey.

2.3 Material and methods

2.3.1 Study sites

The two study sites are located along the French Atlantic coast between the Loire and Gironde estuaries (Fig. 2.1). The Bourgneuf and Marennes-Oléron bays are among dunlins' main wintering sites in France (Bocher et al., 2014a). Bourgneuf Bay ($47^{\circ}02'04''\text{N}$, $02^{\circ}08'35''\text{W}$), which covers 340 km² including 100 km² of intertidal mudflats, is located South of the Loire Estuary. Two distinct habitats were considered on the east side of the bay: a sandy-muddy sector (mean grain size of 74 μm , 41.9% of silt) at the immediate North of Le Collet Harbor (North Collet) and a muddy sector (mean grain size of 15 μm , 85.9% of silt) at the South (South Collet), (Drouet et al., 2015, Fig. 2.1). The Marennes-Oléron Bay ($45^{\circ}56'26''\text{N}$, $01^{\circ}09'66''\text{W}$) is located just north of the Gironde Estuary and 150 km south from Bourgneuf Bay. The bay is bordered by Oléron Island on its Western part and by the mainland on its Eastern part with a total area of 180 km², of which 110 km² are intertidal zones. In Marennes-Oléron, two distinct habitats were considered inside the national Natural Reserve of Moëze-Oléron: a bare muddy sector (mean grain size of 17 μm , 85.1% of silt) at Moëze on the mainland side and a *Zostera noltei* seagrass bed habitat with sandy-muddy mudflat structure (mean grain size of 132 μm , 39.3% of silt) on Oléron side (Bocher et al., 2007). Both bays present maximal tidal amplitude of about 6 m.

2.3.2 Bird counting

Annual counting of dunlins at high tide on roosting areas were achieved on January on the two sites from 1978 to 2013 and were obtained from the annual mid-winter counts of the Wetlands International program (Mahéo and Le Dréan-Quéneq'hdu, 2011).

Exhaustive monthly counts were coordinated and compiled from 2000 by the 'Observatoire du Patrimoine Naturel Littoral' under the auspices of the 'Reserves Naturelles de France' (network of National Nature Reserves) and the 'Agence des Aires Marines protégées'. Counts were made on around the 15th day of each month using a standardized method.

2.3.3 Benthos sampling

Both sites were sampled during the same winter. Bourgneuf was sampled by mid-December 2011 and Marennes-Oléron by January-February 2012 (Table 2.1).

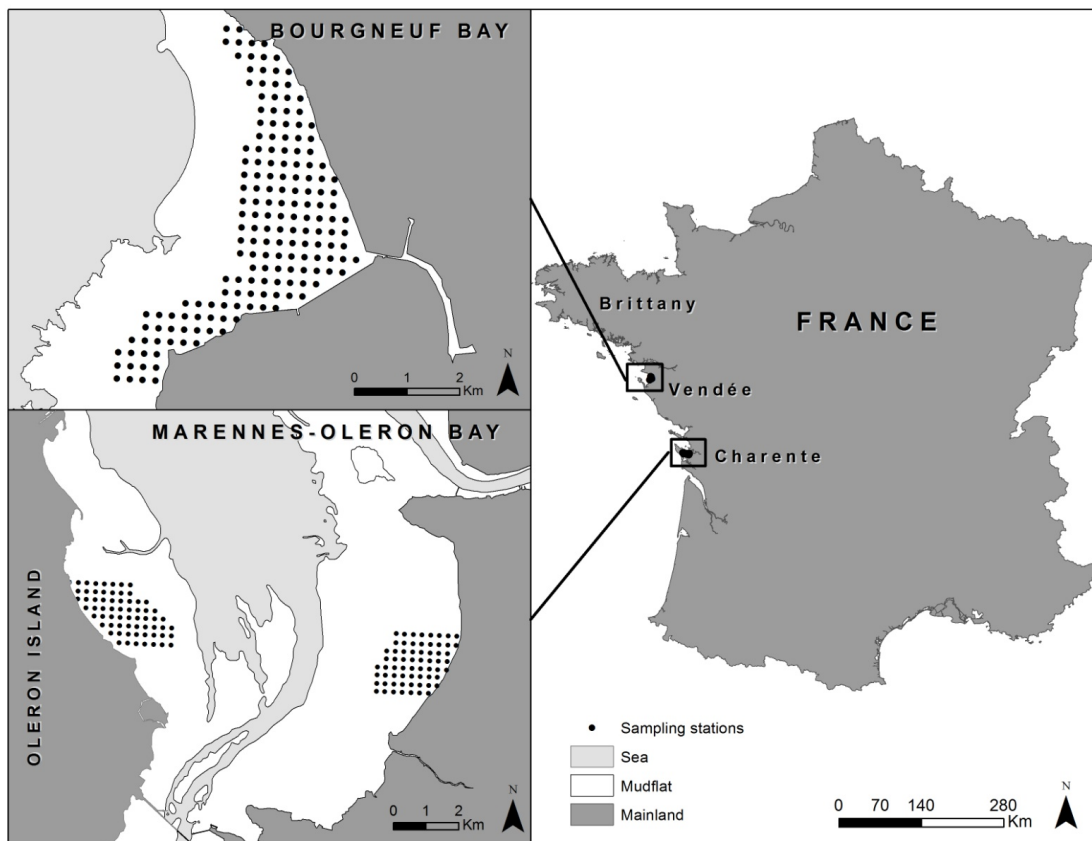


FIGURE 2.1: (a) Location of the two study areas on the French Channel coast, black spots mark sampling stations

Macrofauna was sampled systematically at stations arranged on a grid of 250 m intervals using a handheld GPS (WGS84 as a geographic coordinate system). Across both study sites, a total of 302 sampling stations were visited (Fig. 2.1), 174 stations at Bourgneuf and 128 stations at Marennes-Oléron according to methods described in Philippe et al., (under revision) (Chapter 3). Most of the stations were sampled by foot at low tide (56%) and the others by boat during high tide when access by foot on very soft substrate was difficult. Stations visited by foot were sampled taking sediment cores covering an area of $1/56 \text{ m}^2$ down to a depth of 20 to 25 cm. The upper 4 cm were separated from the rest of the core to determine accessible prey for dunlins according to the maximal size of their bill (Zwarts and Wanink, 1991). We took an additional core (70 mm diameter) to a depth of 4 cm for sampling exclusively the very abundant mudsnail *Hydrobia ulvae* (Pennant) (Bocher et al., 2007). When the tide covered the mudflats with water (0.4–2.0 m) and for the very soft and inaccessible lower intertidal areas, sampling was done from boats using inflatable zodiacs or other small vessels. From the boats, two mud cores (100 mm diameter) covering a total of $1/56 \text{ m}^2$ to a depth of 20 to 25 cm were taken. Only one core was taken into account for *H.*

TABLE 2.1: Study sites, periods of sampling, number of samples (benthos and sediment), tidal characteristics and sediment characteristics

Study sites	Study period	Nb. of samples		Tidal amplitude		Sediment characteristics	
		Nb. of samples $N_{sed.}$	Sampled by foot (%)	Neap tide (m)	Spring tide (m)	Median grainsize <63 μ m (μ m)	Sediment (%)
Bourgneuf Bay	10 Dec. to	174	56	2.5	7.1	-	-
North Collet	14 Dec.	100 (4)	53	-	-	74	41.9
South Collet		74 (4)	61	-	-	15	85.9
Marenne-Oléron Bay	23 Jan. to	57	56	2.4	5.1	-	-
Moëze	22 Feb. 2012	64 (2)	35-	-	17	85.1	-
Oléron		64 (12)	100	-	-	132	39.3

ulvae, and both were taken into account for any other macrobenthic species. The cores were sieved through a 1 mm mesh, except for the mudsnail *H. ulvae* cores, which were sieved over a 0.5 mm mesh to prevent the loss of individuals smaller than 1 mm (from the apex to the aperture). The top fraction in the cores sampled by boat was interpolated from the proportions observed in cores sampled by foot, based on size-species-specific proportions in the top fraction as in (Kraan et al., 2009b; Philippe et al., under revision). All living molluscs were collected in plastic bags and frozen (-18°C) until laboratory treatment. Polychaetes were preserved in 70% ethanol. Living specimens were determined using the identification key described in Hayward and Ryland, (1995).

2.3.4 Sample analysis

We limited the study of prey availabilities to polychaetes, gastropods and bivalves considering that crustaceans were rare in faeces samples and consequently did not appear to contribute to the diet of dunlins. At the laboratory, all molluscs and polychaetes were determined to the species level, counted and measured (for molluscs, maximum length) to the nearest millimetre. For each bivalve (with a shell length larger than 5 mm), the flesh was separated from the shell and both parts were dried for 3 days at 55°C to determine the dry mass of the flesh ($DM_{flesh+shell}$) and the shell (DM_{shell}). The ash-free flesh dry mass ($AFDM_{flesh}$) for each individual was determined after incineration at 550°C for 5 h. $AFDM_{flesh}$ and DM_{shell} were determined with a precision of 0.1 mg (Piersma, Goeij, and Tulp, 1993; Kraan et al., 2007; Quaintenne et al., 2010). To take into account damaged worms (due to manipulation and sieving), various individual measurements (width or anterior segment length) allowed to establish allometric relationships between the body length or width and biomass of corresponding individual. For *Hediste diversicolor*, the length (L3) from the end of the

prostomium to the posterior part of the first setiger was used according to Gillet, (1990), owing to its good correlation with worm ash-free dry mass. The tenth setiger width (WS10) was also taken for *H. diversicolor*, observed ventrally excluding parapodia (GarcíaArberas and Rallo, 2002), since it is not affected by the partial or total devagination of the proboscis, common phenomenon in individuals fixed in ethanol. For *Nephtys hombergii*, the tenth setiger (WS10) (Warwick and Price, 1975; Olive, 1977; Mathivat-Lallier and Cazaux, 1991), and the first setiger widths (WS1), excluding parapodia, and ventrally observed were measured. For other worm species, the maximum width was measured. Whole individual total length was also recorded systematically. By convention only body parts including a prostomium were identified and considered as one individual. The ash-free dry mass ($AFDM_{flesh}$) of complete worms was recorded.

2.3.5 Available resource for dunlins

The harvestable prey for dunlins was defined following Zwarts, Blomert, and Wanink, (1992) and Zwarts and Blomert, (1992) for Red Knots *Calidris canutus*, applying the concepts of accessibility (bivalves below the top 4 cm were excluded), ingestibility (large bivalves that could not be ingested were excluded) and profitability (bivalves that were too small and not profitable were excluded). The available prey was then defined as prey that was both accessible and ingestible. Available prey biomasses for dunlin *Calidris alpina* were determined from the original benthic dataset, first by isolating the accessible fraction (the top 4 cm of the core, corresponding to the maximal length of the bill of dunlins) and then considering suitable sizes of the prey (Piersma, Goeij, and Tulp, 1993). Harvestable prey were discriminated by size based on reconstructed size of prey found in faeces. Dunlins are considered generalist shorebirds, and thus mollusc species as well as principal worm species were kept according to profitable and ingestible size (*i.e.* all *Abra sp.*, *Cerastoderma edule* [2–8 mm], *Macoma balthica* [8–10 mm], *Scrobicularia plana* [2–12 mm], all *H. ulvae*, all *Retusa obtusa*, all *N. hombergii*, and all *H. diversicolor*).

2.3.6 Sediment characteristics

For each grid, within each 500 m, a sediment sample was collected to a maximum depth of 8 cm. MGS (μm) and the percentage of silt (fraction $< 63 \mu\text{m}$) were determined using a Median particle size and silt percentage (fraction $< 63 \mu\text{m}$) of

sediments were determined using a Malvern Instruments Hydro 2000 laser particle size analyser after treatment as described in Méléder et al., (2007), adapted from Baize, (2000).

2.3.7 Diet reconstruction

Diet was reconstructed from droppings collected during low tide on feeding area of dunlin flocks. Fifteen droppings were sampled per subsite during the macrofauna sampling period and geo-referenced using a GPS. At the laboratory, the droppings were frozen at -20°C . Dunlin diet was reconstructed from these samples following the protocols of Dekinga and Piersma, (1993) for molluscs and Scheiffarth, (2001) for polychaetes. All parts were identified to the species level whenever possible. For analyses, the droppings were pooled by five and sieved over a $64\ \mu\text{m}$ square mesh with distilled water to remove mud and organic material. The particles remaining in the sieve, mainly composed of shell fragments, were weighed (DM_{shell}). Every fragment including hinges of bivalves was selected, the species was identified and hinge height was measured. For all fragments, three representative sub-samples of 5% of DM_{shell} were weighed and used to reconstruct the composition of the entire droppings. The total or part of *H. ulvae* were also selected and weighed.

The filtrated part was placed in ultrasonic bath for 15 min, until the sediment remained at the bottom of the tube. After additional sedimentation for 5 min, the supernatant was poured in a $50\ \text{cm}^3$ cylindrical chamber with a diameter of 25 mm. Jaws, tooth, chaetae and aciculae of polychaetes sedimented and were identified to the species level whenever possible (Friedrich, 1938; Hartmann-Schröder, 1996) by using an inverted microscope ($\times 100$). All elements were photographed, then identified and measured. Lengths of molluscs and worms identified in droppings were reconstructed using predictive allometric equations between hinge height (or width of first whorl in the case of mudsnails) and shell lengths; and between jaw or teeth lengths and worm lengths.

Afterwards, the AFDM of each ingested bivalve and worm was reconstructed using regression equations. From the weighted shell fragments of each mollusc species, the relative DM_{shell} contribution of each prey species in the diet of dunlin was reconstructed. The relative $AFDM_{flesh}$ contribution of each mollusc species was calculated from the size-, species and site-specific $AFDM_{flesh}$ -to- DM_{shell} ratios.

2.4 Results

Annual occurrence of dunlins

Since the 1980s, an average of $12,370 \pm 1,651$ dunlins individuals are numbered in mid-winter in Bourgneuf corresponding to a mean density of *c.* 1.2 ind./ha of intertidal area; $23,025 \pm 3,825$ individuals in Marennes-Oléron (Fig. 2.2) corresponding to a mean density of *c.* 2.1 ind./ha. Dunlin abundance displayed a substantial inter-annual variability (coefficient of variations of 35% and 53% at Bourgneuf and Marennes-Oléron respectively). At Bourgneuf, dunlin number increased until 1992, and then fluctuated without any significant trend. A maximal number was recorded in 2002 with 22,078 individuals. At Marennes-Oléron, the number generally increased from 1977 until 2000, and then fluctuated between a minimum number of 12,700 individuals in 2011 and a maximal number of 47,437 individuals in 2008.

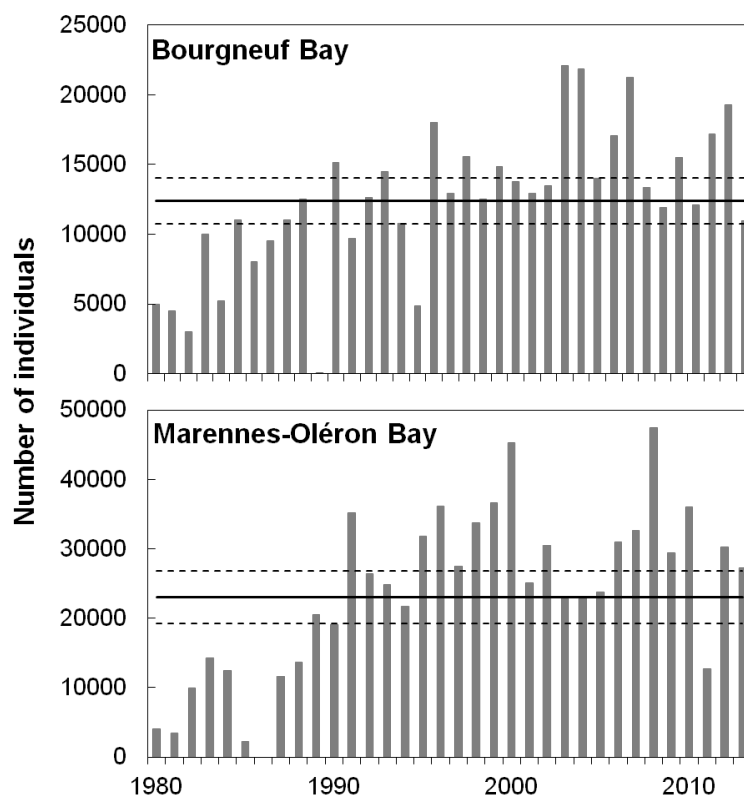


FIGURE 2.2: Annual abundance of dunlins at the two study sites (Bourgneuf Bay and Marennes-Oléron Bay) between 1976 and 2013 from IWC counts (mid-January). The solid lines stand for the mean and the dashed lines for the confidence interval at 95%

All dunlins breed from May to July, and indeed dunlin started arriving on the French coast in mid July (Fig. 2.3). Numbers of dunlins increased steeply between October and November on Marennes-Oléron Bay and on the site of Bourgneuf. At both sites, the highest numbers were recorded in January (Fig. 2.3). After the mid-winter peak, numbers declined steadily at both sites toward the end of the winter period. There were no dunlins recorded in June at either site.

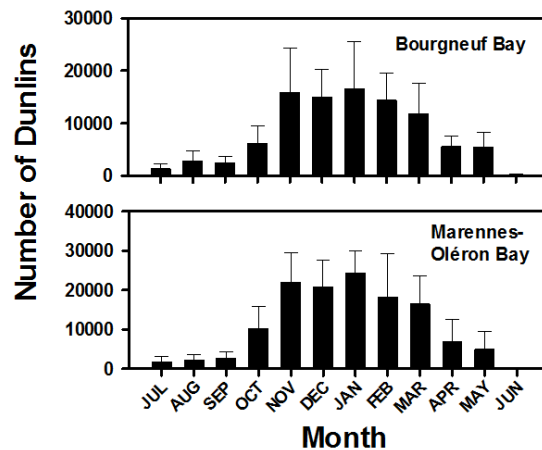


FIGURE 2.3: Mean number (\pm SD) of dunlin during each month for 2000-2012 at both study sites

Food resources

Seven species of bivalves, 2 species of gastropods and 8 species of polychaetes were identified in the cores for all stations (Table 2.2). Among the 17 species, 7 were common to the four subsites and appeared as the most abundant species: *Cerastoderma edule*, *Ruditapes* spp., *Macoma balthica*, *Scrobicularia plana*, *Hydrobia ulvae*, *Nephtys hombergii* and *Hediste diversicolor*. The gastropod *H. ulvae* was by far the most abundant species with the highest biomass and densities recorded in every subsite. The mudsnail was the most abundant in Oléron and South Collet and found with lower density in North Collet and Moëze, (Table 2.2). Nevertheless, considering smaller sizes of individuals in South Collet the mean biomass was much lower (c. 5,419 mg AFDM.m⁻²) than in Oléron (c. 29,698 ind. m⁻²). The second dominant species among molluscs was the bivalve *S. plana* especially at North Collet, South Collet and Moëze but poorly represented in Oléron. *M. balthica* was abundant in Bourgneuf particularly in South Collet with mean density of 409 ind.m⁻². *M. balthica* was much less abundant in Marennes-Oléron. In Marennes-Oléron, the assemblages were different between subsites with a dominance of *S. plana*, *M. balthica* and *A. tenuis* in Moëze and *Ruditapes* spp and *S. plana* in Oléron. The gastropod *Retusa obtusa* appeared only in Bourgneuf and

TABLE 2.2: Frequency of occurrence (Occ., %), mean density (Dens., ind/m²) and mean biomass (Biom., mg AFDM_{fresh}/m²) of mollusc and polychaete species at each subsites per site (sampled from December 2011 to February 2012). A 'NA' indicates that the parameter was not measured, and a dash indicates the absence of the species considered in the sampling site.

Species	Bourgneuf Bay						Marennes-Oléron Bay					
	North Collet			South Collet			Moëze			Oléron		
	Occ.	Dens.	Biom.	Occ.	Dens.	Biom.	Occ.	Dens.	Biom.	Occ.	Dens.	Biom.
Bivalves												
<i>Nucula nitidosa</i>	16	20	0.007	1	2	<0.001	-	-	-	-	-	-
<i>Cerastoderma edule</i>	4	3	0.009	8	7	0.029	2	1	<0.001	14	15	0.256
<i>Ruditapes</i> spp.	<1	<1	0.006	6	6	0.017	14	11	0.293	28	42	1.307
<i>Macoma balthica</i>	74	185	0.481	78	409	0.506	30	52	0.079	5	7	0.022
<i>Scrobicularia plana</i>	18	182	1.501	57	375	2.122	41	179	3.114	20	24	0.624
<i>Abra tenuis</i>	-	-	-	6	28	0.002	31	126	0.668	14	14	0.032
<i>Mya arenaria</i>	-	-	-	4	3	0.291	-	-	-	-	-	-
Gastropods												
<i>Hydrobia ulvae</i>	96	4,619	5.419	81	6,552	6.719	100	2,462	3.631	69	8,387	29.698
<i>Retusa obtusa</i>	53	155	0.449	31	52	0.130	-	-	-	-	-	-
Polychaetes												
<i>Ampharete acutifrons</i>	-	-	-	4	4	NA	-	-	-	-	-	-
<i>Arenicola marina</i>	-	-	-	1	<1	NA	-	-	-	2	1	NA
<i>Heteromastis filiformis</i>	-	-	-	1	<1	NA	-	-	-	2	1	NA
<i>Notomastus latericeus</i>	1	5	NA	7	8	NA	-	-	-	14	15	NA
<i>Cirriiformia tentaculata</i>	-	-	-	4	3	NA	-	-	-	-	-	-
<i>Nephtys hombergii</i>	5	100	0.145	54	75	0.222	58	50	0.317	17	16	0.049
<i>Hediste diversicolor</i>	74	13	0.074	15	39	0.082	8	5	0.045	17	13	0.036
<i>Alitta succinea</i>	-	-	-	3	2	<0.001	5	4	0.046	3	3	NA

was abundant particularly in North Collet (Table 2.2). Among the polychaetes, *H. diversicolor* and *N. hombergii* were the largely dominant among the 8 species recorded in both sites. *N. hombergii* was more abundant than *H. diversicolor* in South Collet and Moëze, appearing in more than half of the sampled stations, while *H. diversicolor* was more abundant in North Collet (Table 2.2).

Some relative inter- and intra-site differences in prey abundance and distribution were observed (Table 2.2 and Fig. 2.4 & 2.5). In Bourgneuf, the sampled stations contained up to 100 g_{AFDM}.m⁻² (total biomass) whereas in Marennes-Oléron, the maximum biomass measured was of c. 200 g_{AFDM}.m⁻². Considering and insulating the available biomass fraction for dunlin, mean total biomass decreased from 14.4 to 10.8 g_{AFDM}.m⁻² at North Collet and from 15.0 to 11.0 g_{AFDM}.m⁻² at South Collet. A heterogeneity in distributions of total and available biomasses of macrofauna was observed throughout the sampling area (Fig. 2.4). The total biomass seemed to decrease from the highest level of the intertidal area to the lowest. Most favorable feeding area for dunlins was located along a stripe parallel to the coast throughout the North part of the Bourgneuf Bay. A patch with higher available biomasses was also located in the south of the South Collet sector. For Marennes-Oléron, the mean biomass decreased from

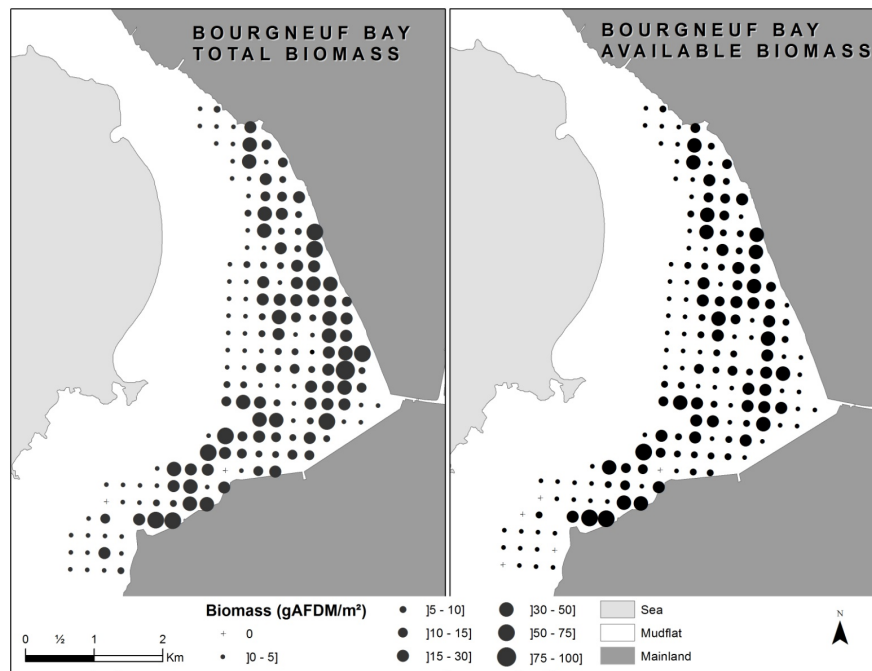


FIGURE 2.4: Distributions of total biomasses (all species, g_{AFDM}/m^2) of macrofauna and available biomasses (g_{AFDM}/m^2) for dunlins over the entire study area of Bourgneuf Bay. AFDM: ash-free dry mass

15.7 to $9.7 g_{AFDM} \cdot m^{-2}$ in terms of available fraction at Moëze and from 29.9 to $29.5 g_{AFDM} \cdot m^{-2}$ at Oléron. At Moëze and Oléron, the areas of total and available biomass were located closer to the shore. Very high concentrations in term of total and available biomasses were observed at Oléron with 42% of stations superior to $30 g_{AFDM} \cdot m^{-2}$ (Fig. 2.5).

From total to available biomass, the contribution of each prey species varied since these species were present differentially in the upper 4 cm fraction of sediment, (Fig. 2.6). In Bourgneuf and Marennes-Oléron, the dominant mollusc species was *H. ulvae* being the highest available biomass at each study subsite with a contribution increasing from accessible to available biomass, since all individuals were available. When focusing on the available prey fraction, *H. ulvae* predominated at North Collet (74%), at South Collet (92%), at Moëze (79%) and at Oléron (97%) (Fig. 2.6). In contrast, from accessible to available stocks of prey, the contribution of *S. plana* and *M. balthica* decreased because of larger individuals not available to be ingested by dunlins. The gastropod *R. obtusa* was solely found in Bourgneuf. The contributions of worms *H. diversicolor* and *N. hombergii* increased from the total to accessible biomass and decreased from the accessible to available biomass in Bourgneuf and at Oléron just for *H. diversicolor*. The opposite was observed at Moëze. The highest proportion of *N. hombergii* (2%) was observed in the available biomass at Oléron, (Fig. 2.6).

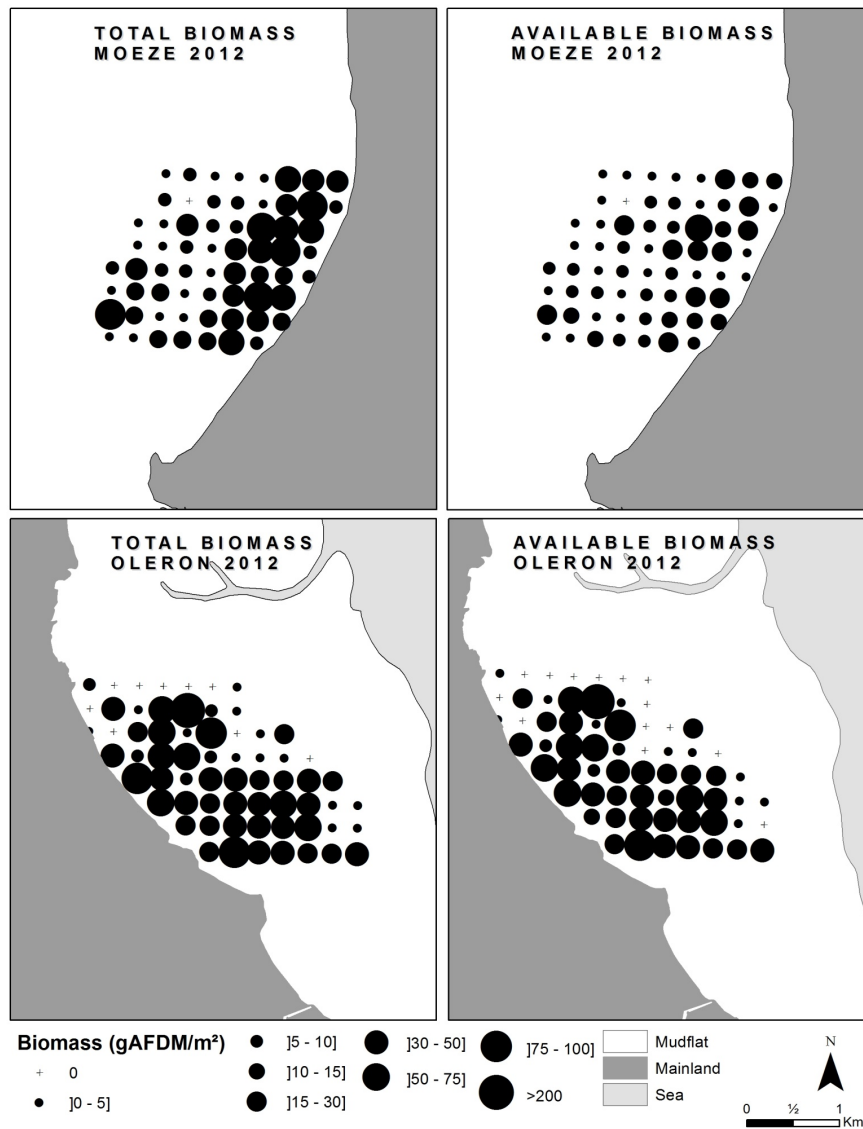


FIGURE 2.5: Distributions of total biomasses (all species, g_{AFDM}/m^2) of macrofauna and available biomasses (g_{AFDM}/m^2) for dunlins over the subsites of Moëze and Oléron. AFDM: ash-free dry mass

Dunlin Diet

No remains of crustaceans have been found in the analysed faeces. Two bivalves, *M. balthica* and *S. plana*; one gastropod *H. ulvae*; and two polychaetes, *H. diversicolor* and *N. hombergii* constituted the bulk of the diet of dunlin at both sampling sites. The contribution of each prey species to the reconstructed diet from faeces in each study subsite is depicted in the bottom panel of Fig. 2.6. The diet of dunlins in the four study subsites differed significantly (Chi-squared test: $df = 12$, $R^2 = 21.026$, $P < 0.0001$). At Bourgneuf and Oléron, the diet of dunlin was

dominated by the gastropod, *H. ulvae*, whereas they were specialised on worms at Moëze (50% *H. diversicolor* and 50% *N. hombergii*). At North Collet, dunlins fed on mostly *M. balthica* (26%), *S. plana* (5%), *H. diversicolor* (5%) and *N. hombergii* (2%). At South Collet and Oléron, the bivalves species, *S. plana* (respectively, 38% and 14%) and *M. balthica* (respectively, 17% and 40%), both predominated in the diet of dunlins and the worm contribution (4%) was much lower than the mollusc one.

2.5 Discussion

By examining food availability and diet selection of overwintering dunlins in the two bays of the French Atlantic coast, this study highlighted a high heterogeneity in prey abundance and distribution among sites and subsites. The biomass of food available for dunlins was of similar magnitude in north-, south-Collet and Moëze, but was much higher in Oléron due to densities and larger size of *Hydrobia ulvae*. Although it was not possible to distinguish densities of birds per subsites, the higher overall number of birds in Marennes-Oléron bay could be due to the highest density of *H. ulvae* on the Oléron side of the bay. The other explanation could be the high densities of available worms on Moëze side that could attract birds for feeding on very energetic prey. In Bourgneuf, the densities of *Hediste diversicolor* and *Nephtys hombergii* were higher than in Marennes-Oléron, but most of the worms were larger and located too deep in sediment to be predated by dunlins.

In this study, we show that dunlins feed on prey more opportunistically than other specialised shorebird species, they are generalist and seem to focus on the highest quality species. For example the long-distance migratory knot *Calidris canutus* feeds almost exclusively on marine molluscs and the diet is restricted to 1-3 species according to wintering sites (Piersma et al., 1993; Quaintenne et al., 2014). At Bourgneuf Bay and Marennes-Oléron Bay, dunlin were not so specialised and fed on diverse marine molluscs and polychaetes according to abundance, size and quality. Dunlin is a generalist species, able to feed on a high variety of prey as previously described in several studies on diet from the Baltic Sea to Cadiz Bay (Table 2.3). The maximum number of prey described in the diet of individuals in Humber Estuary in England (Evans et al., 1979) was 21 species, depicted from visual observations (Table 2.3). On other sites, the number of prey species ranged from 3 to 12 (Table 2.3). At both study sites, we showed

that dunlins fed on five prey species among the 17 species found in the sediments. Nevertheless, dunlins fed mainly on molluscs on three study subsites while they fed exclusively on worms at Moëze according to the faeces sorted (Table 2.3). This high specialisation on worms at Moëze is in accordance with diet preferences described by blood isotope analyses for the same site in previously study on trophic segregation inside a shorebird community (Bocher et al., 2014b). At Bourgneuf and Oléron, three major prey species predominated in the diet of dunlin, *H. ulvae*, *Scrobicularia plana* and *Macoma balthica*, even though *H. ulvae* remained the most important prey species. *N. hombergii* and *H. diversicolor* contributed to a lesser extent to the diet of dunlin. Previous studies showed that *H. diversicolor*, *M. balthica* and *H. ulvae* were presumed to be the preferred prey of dunlins in many wintering sites in Western Europe (Table 2.3). *Hydrobia ulvae* appeared in the diet of dunlin in 11 others studies over the 12 censused in Europe, *M. balthica* in eight and *H. diversicolor* in nine of them. Nevertheless, on most of the sites, the polychaetes constitute the dominant prey for dunlins, probably due to their high nutritional and energetic values (Zwarts and Wanink, 1993) and digestive quality (Zwarts et al., 1996).

The mudsnail *H. ulvae* is a very abundant prey easy to collect on mudflats (Bocher et al., 2007). *H. ulvae* might represent a safe, abundant and predictable stock of prey compared to stocks of buried bivalves, which can vary greatly in relation to recruitment success or burying depth from one winter to another (Reading and McGrorty, 1978; Beukema, 1982; Zwarts and Wanink, 1993). Therefore, the small size and the hard shell of *H. ulvae* lead to high handling and shell crushing costs for shorebirds compared to larger shelled prey that are easier to manipulate or even soft body prey like worms that have no crushing costs.

The gastropod *R. obtusa* was solely found in the study sites of Bourgneuf Bay. As far as we know, *R. obtusa* is solely mentioned as part of the diet of dunlins observed in the Humber and the Wash estuaries (Durell and Kelly, 1990; Stillman et al., 2005; Yates et al., 1993). We did not find any *R. obtusa* in dunlin droppings whereas *H. ulvae* was very abundant (Mouritsen, 1994; Worrall, 1984). *H. ulvae* is known to be a favourite prey for *R. obtusa* (Berry, 1988; Berry, Radhakrishnan, and Coward, 1992). Therefore, areas with high numbers of *H. ulvae* might be prized by *R. obtusa*, and these two species should be preyed upon by dunlins and associated in the faeces.

During the winter migration period, diet of dunlins was site specific with differences according to local foraging habitats (subsites). Prey were selected among the most abundant species in most of the sites with dominance of the very abundant and easy collectible *H. ulvae* except in Moëze where birds seemed to actively

select more energetic prey like worms.

The dunlin *C. alpina* wintering along the French coast, with a mean of 312,000 individuals over the last fourteen years (maximum 355,000 in 2002), represents 23% of the wintering dunlins wintering in Europe (Bocher et al., 2014a). Nevertheless, despite the 6,000 km length of French Atlantic coast, 50% of this total number is concentrated at only eight sites (Bocher et al., 2014a). About one third of the birds were located on sites bordering the North Sea and the Channel, while two thirds were distributed on the Atlantic coast. On the French Atlantic coast, the set of bays between Loire and Gironde estuary constitutes the first area for migrating and wintering dunlins in France (Bocher et al., 2014a). Consequently, Bourgneuf Bay and Marennes-Oléron Bay appear to be important migrating and wintering sites in France. The bay of Marennes-Oléron welcomes a higher number of dunlins, almost twice the number of individuals wintering in Bourgneuf, while the surfaces of intertidal habitats are quite similar. Consequently, the bay of Marennes-Oléron appeared much more attractive for the species in the core of the winter than Bourgneuf Bay.

Further investigation into the variability of mollusc and polychaete prey stocks needs to be carried out in regards of inter-annual variations in dunlins numbers in the studied areas. Further investigation needs to be conducted in order to link the population dynamics of both prey and predators, and try to explain this inter-annual variation in the abundance of dunlins observed along the French Atlantic coast.

Acknowledgements

We are very grateful for the help in the field to Philippe Pineau, Nicolas Lachaussée, Philippe Rosa, Pablo Gambin-Pozo, Camille Parrain and Ismaïl Benyoucef. We also thank the managers of the Nature Reserve of Moëze-Oléron for their collaboration, and two anonymous reviewers for helpful comments. Data-counts of the “Wetland International” Winter Census on waterbirds were provided by Roger Mahéo and Bernard Deceuninck.

TABLE 2.3: Prey species ingested by dunlins on soft-substrate in Western Europe (from north-east to south west) from feeding birds observations (Evans et al., 1979⁴), from droppings (Durell and Kelly, 1990⁶, Mouritsen, 1994², Cabral et al., 1999⁹, Santos, Granadeiro, and Palmeirim, 2005¹⁰, Stillman et al., 2005⁵, Martins et al., 2013¹¹), from stomach contents (Dierschke et al., 1999¹, Le Drean-Quenec'hdu, 1999⁸) or from both droppings and stomach contents (Worrall, 1984⁷, Yates et al., 1993⁶, Perez-Hurtado, Goss-Custard, and Garcia, 1997¹², Folmer, Olff, and Piersma, 2012³)

	Baltic Sea (D) ¹	Wadden Sea (DK) ²	Wadden Sea (NL,D) ³	River Tees Estuary (UK) ⁴	Humber estuary (UK) ⁵	The Wash (UK) ⁶	Severn Estuary (UK) ⁷	Mont St-Michel Bay (F) ⁸	Traicts-du-Croisic (F) ⁹	This study (F)	Mondego Estuary (P) ⁹	Tagus estuary (P) ^{10,11}	Cádiz Bay (SP) ¹²
Bivalvia													
<i>Cerastoderma edule</i>		+	+		+	+		+		+			+
<i>Macoma balthica</i>		+	+	+	+	+		+	+	+		+	
<i>Abra sp./ Scrobicularia plana</i>									+	+	+	+	?
<i>Mytilus edulis</i>												+	
<i>Mya arenaria</i>					+								
Gastropoda													
<i>Hydrobia ulvae</i>	+	+	+	+	+	+	+	+	+	+	+		
<i>Retusa obtusa</i>					+	+						+	
Amphipoda													
<i>Gammarus oceanicus/salinus</i>	+												
<i>Urothoe sp.</i>					+								
<i>Bathyporeia sp.</i>					+								
<i>Corophium arenarium/volutator</i>	+	+	+	+	+	+		+				+	
Isopoda													
<i>Cyathura carinata</i>												+	
<i>Idotea balthica/chelipes</i>	+												
Decapoda													
<i>Crangon crangon</i>	+		+										+
<i>Carcinus maenas</i>		+	+										+
Ostracoda													
<i>Ostracoda sp</i>								+					
Polychaete													
<i>Arenicola marina</i>		+			+								
Capitellids													
<i>Heteromastis filiformis</i>			+										
Cirratulids													
<i>Clymenella sp.</i>					+								
<i>Nephtys hombergii</i>		+	+		+				+	+	+		
<i>Other Nephtys sp.</i>		+			+	+							
<i>Hediste diversicolor</i>	+	+	+		+	+	+		+	+	+	+	
<i>Scoloplos armiger</i>			+		+								
Phyllodocids													
Spionidae													
<i>Streblospio shrubsolii</i>		+										+	
<i>Polydora ciliata</i>												+	
<i>Pygospio elegans</i>				+									
<i>Spio filicornis</i>					+								
<i>Lanice conchilega</i>			+		+								
<i>Marenzelleria virides</i>			+										
Clitellata													
Oligochaetes													
					+						+	+	

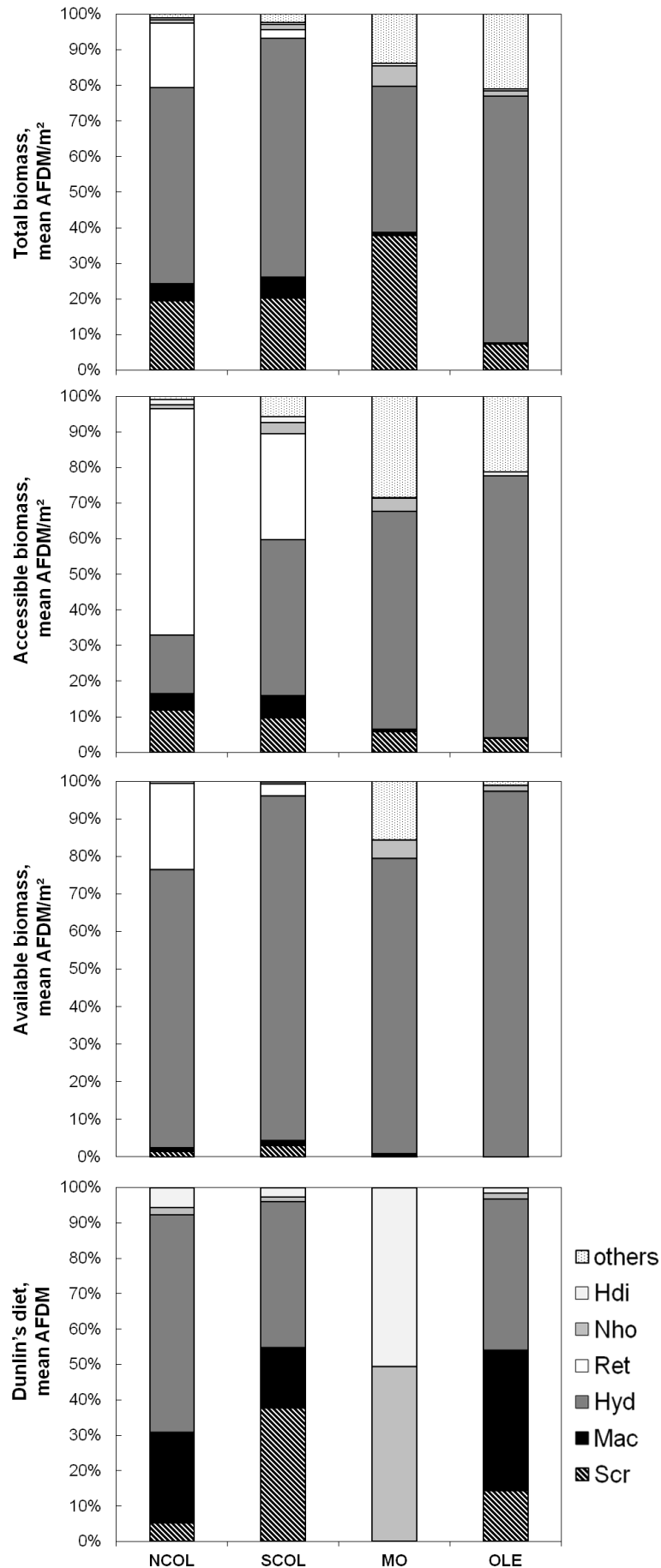


FIGURE 2.6: Comparison of the mean proportions of prey mollusc and polychaete species (g_{AFDM}/m^2) between total, accessible and available biomasses against the dunlin diet (mean percentage AFDM) at each study subsites: NCOL (North Collet), SCOL (South Collet), MO (Moëze) and OLE (Oléron) (AFDM: ash-free dry mass, Hdi: *Hediste diversicolor*, Nho: *Nephtys hombergii*, Ret: *Retusa obtusa*, Hyd: *Hydrobia ulvae*, Mac: *Macoma balthica*, Scr: *Scrobicularia plana*)

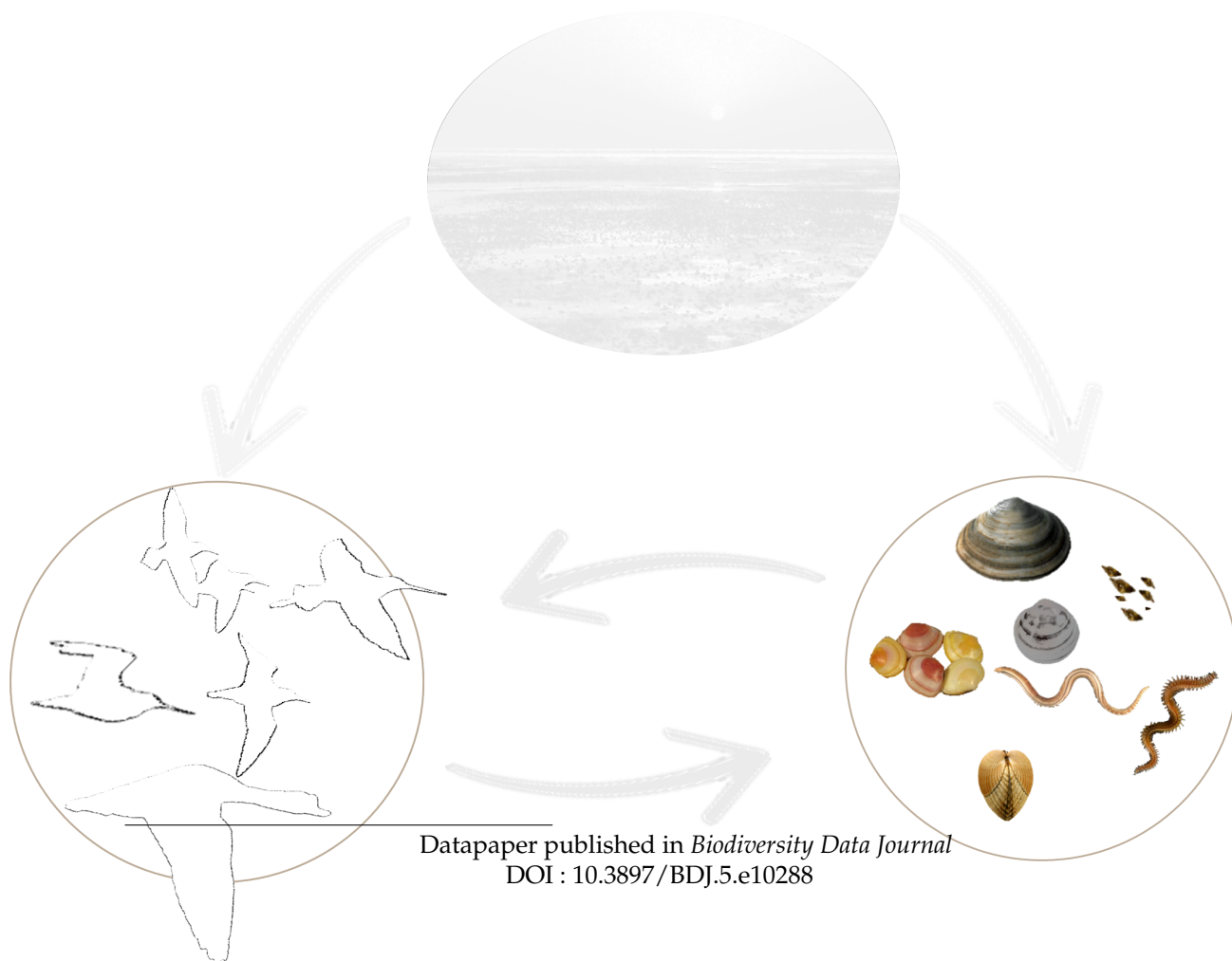
**SECTION 2: BENTHIC MONITORING,
INTO THE SHOES OF A WADER**



Chapter 3

Building a database for long-term monitoring of benthic macrofauna in the Pertuis-Charentais (2004-2014)

Anne S. PHILIPPE, Christine PLUMEJEAUD, Jérôme JOURDE, Philippe PINEAU, Nicolas LACHAUSSÉE, Pierrick BOCHER



3.1 Abstract

Background

Long-term benthic monitoring is rewarding in terms of science, but labour-intensive, whether in the field, the laboratory, or behind the computer. Building and managing databases require multiple skills, including consistency over time as well as organization via a systematic approach. Here, we introduce and share our spatially explicit benthic database, comprising 11 years of benthic data. It is the result of intensive benthic sampling that has been conducted on a regular grid (259 stations) covering the intertidal mudflats of the Pertuis Charentais (Marennes-Oléron Bay and Aiguillon Bay). Samples were taken by foot or by boats during winter depending on tidal height, from December 2003 to February 2014. The present dataset includes abundances and biomass densities of all mollusc species of the study regions and principal polychaetes as well as their length, accessibility to shorebirds, energy content and shell mass when appropriate and available. This database has supported many studies dealing with the spatial distribution of benthic invertebrates and temporal variations in food resources for shorebird species as well as latitudinal comparisons with other databases. In this paper, we introduce our benthic monitoring, share our data, and present a "guide of good practices" for building, cleaning and using it efficiently, providing examples of results with associated R code.

New information

The dataset has been formatted into a geo-referenced relational database, using PostgreSQL open-source DBMS. We provide density information, measurements, energy content and accessibility of thirteen bivalve, nine gastropod and two polychaete taxa (a total of 66,620 individuals) for 11 consecutive winters. Figures and maps are provided to describe how the dataset was built, cleaned, and how it can be used. This dataset can again support studies concerning spatial and temporal variations in species abundance, interspecific interactions as well as evaluations of the availability of food resources for small- and medium size shorebirds and, potentially, conservation and impact assessment studies.

3.2 Introduction

Genesis: This benthic monitoring was initiated in winter 2003-2004 with the aim of describing feeding resources for overwintering shorebird species (*e.g.* Curlews, Grey Plovers, Bar-tailed Godwits, Black-tailed Godwits, Red knots, Dunlins, Oystercatchers, Redshanks and one duck species: Shelducks). At first, spatial studies were initiated and led to reference papers in ecosystem comparisons in the domain of molluscan studies (Bocher et al., 2007; Compton et al., 2009) or shorebird ecology (*e.g.* Quaintenne et al., 2011; Quaintenne et al., 2010). Following the example of a long term monitoring at the NIOZ Institute (Netherlands Institute for Sea Research) through the SIBES program in the Dutch Wadden Sea and a sampling of the Banc d'Arguin (Mauritania) and Roebuck Bay (Australia) mudflats, sampling was continued on an annual basis at 259 stations.

Objectives: The initial purpose of the monitoring was to study the spatio-temporal variations of main macrobenthic species as available resources for shorebirds. Knowing individuals to the species level, their length, shell mass, accessibility (the top fraction was analysed separately) and flesh energy content, one can analyse for example:

- the spatial variability of densities of benthic prey, including comparisons with other countries (Bocher et al., 2007);
- the fraction available for *Calidris canutus* and *Calidris alpina* (sandpiper species), since the top 4 cm of the cores were analysed separately and shells were measured (Philippe et al., 2016);
- based on the quality of the molluscs (flesh to shell ratio) it is possible to predict the diets of red knots *Calidris canutus* using a digestive rate model derived from type II functional response curve, depending on the site and the year (van Gils, 2004; Quaintenne et al., 2011).

3.3 Project description

Title: Long-term mollusc and annelid monitoring in the Pertuis-Charentais, France

Personnel: The monitoring was conducted every year under the responsibility of Pierrick Bocher with constant participation of Philippe Pineau and Nicolas Lachaussée and managers of the National Nature Reserves of Aiguillon Bay and

Marennes-Oléron Bay. Additional help in the field was provided by multiple other colleagues and PhD candidates throughout the years.

Study area description: Sampling was performed on intertidal mudflats located in National Nature Reserves: RNN Aiguillon Bay and RNN Moëze-Oléron.

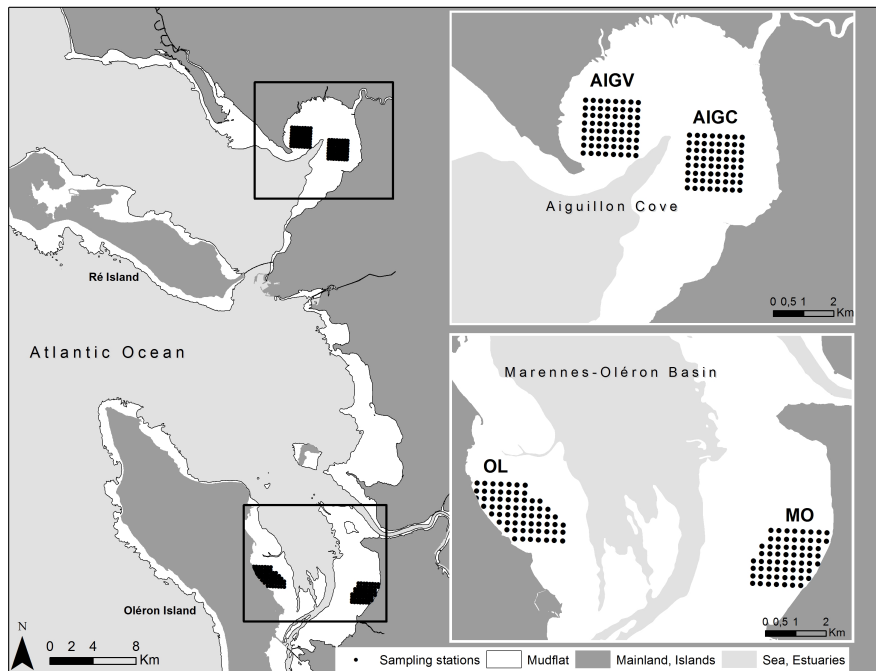


FIGURE 3.1: Sampling site with the 259 regular stations, across four study sites, in the Pertuis Charentais, on the French Atlantic coast.

Design description: Systematic sampling was performed on four regular 250 m grids, composed of 64 stations each (except for the subsite "Oléron" (OL) which contained 67 stations).

Funding: The monitoring was funded by the University of La Rochelle and the CNRS via laboratory dotations and staff time. Financial support was received from the Région Poitou-Charentes through a thesis grant to Anne Philippe (2013-2016). LIENSs laboratory and the DYFEA team also provided help with field work costs. The Office National de la Chasse et de la Faune Sauvage (ONCFS) and the Ligue pour la Protection des Oiseaux (LPO) supported this monitoring via staff time and nautical resources dedicated to sample collections.

3.4 Sampling methods

Sampling description: Benthic macrofauna was collected over a predetermined 250 m grid following a proven sampling protocol (Bocher et al., 2007; Kraan et al., 2010a; Bijleveld et al., 2012), see Fig. 3.1. Each station was located with a hand-held GPS device using WGS84 geodetic datum. Out of 259 stations sampled, only a minority (46%) was sampled by foot (during low tide), taking sediment cores covering an area of 1/56 m² down to a depth of 20 to 25 cm. The top fraction (first 4 cm of the sediment) was separated from the bottom fraction to be able to segregate the accessible benthos fraction for the two main shorebirds species: the red knot *Calidris canutus* and the dunlin *Calidris alpina* (Fig. 3.2). We took an additional core (70 mm diameter) covering 1/263 m² to a depth of 4 cm for sampling exclusively the very abundant mudsnail *Hydrobia ulvae* (Pennant) (Bocher et al., 2007). When the tide covered the mudflats with water (0.4–2.0 m) and for the very soft and inaccessible lower intertidal areas, sampling was done from boats using inflatable zodiacs or other small vessels. From the boats, two mud cores (100 mm diameter) covering a total of 1/56 m² to a depth of 20 to 25 cm were taken. Only one core was taken into account for *H. ulvae*, and both were taken into account for any other macrobenthic species.

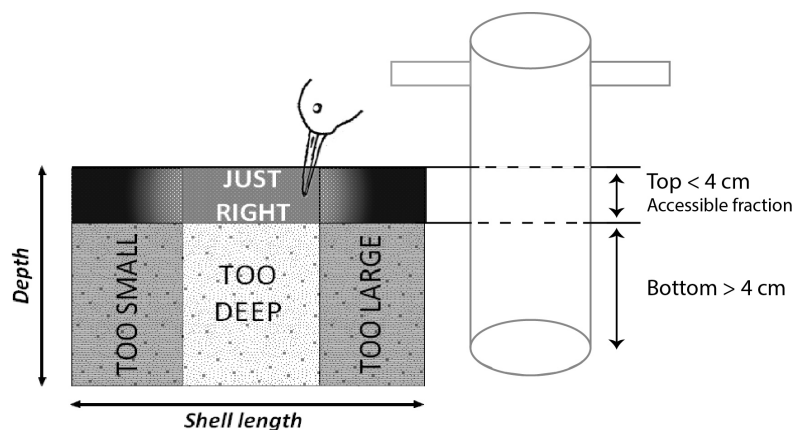


FIGURE 3.2: The harvestable fraction corresponding to the mean bill length of the sandpipers, the dunlin *Calidris alpina* and the red knot *Calidris canutus* and composed of the accessible fraction of benthos (found in the top 4 cm of the mud core) and of ingestible sizes (not too large and not too small). Ingestible sizes are species specific, and depend on the shape of the mollusc. Sizes available for *C. canutus* and *C. alpina* species are reported in Philippe et al., 2016.

The cores were sieved through a 1 mm mesh, except for the mudsnail *H. ulvae* cores, which were sieved over a 0.5 mm mesh to prevent the loss of individuals smaller than 1 mm (from the apex to the aperture). All living molluscs were collected in plastic bags and frozen (-18°C) until laboratory treatment (Fig. 3.3).

Polychaetes were preserved in 70% ethanol. Living specimens were determined using the identification key described in Hayward and Ryland, (1995).

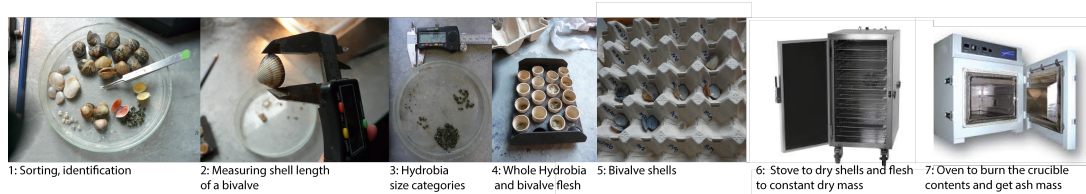


FIGURE 3.3: Processing of benthic samples in the laboratory

Sample processing: In the laboratory, molluscs were identified under the supervision of a benthic taxonomist. Individuals were counted, and their maximum length was measured to the nearest 0.1 mm using Vernier calipers, width was also measured for bivalves. Hydrobiid mudsnails were size-categorised from 0 mm up to 6 mm (e.g. size class 2 consisted of individuals with lengths ranging from 2 to 2.99 mm).

The flesh of every mollusc specimen except *H. ulvae* was detached from the shell and placed individually in crucibles (pooled by size class when sizes were smaller than 8.0 mm, flesh and shell together). Crucibles containing molluscs were placed in a ventilated oven at 55 to 60 °C for three days until constant mass and then weighed ($DM \pm 0.01$ mg). Dried specimens were then incinerated at 550 °C for 4 h to determine their ash mass and then a proxy of their energy content: the ash free dry mass (AFDM).

H. ulvae flesh biomass ($AFDM_{flesh}$) was estimated for each station from the total biomass ($AFDM_{flesh+shell}$) with the following linear regression: $AFDM_{flesh} = 0.6876 \times AFDM_{flesh+shell} + 7E - 05$ ($R^2 = 0.99$; N = 60 individuals sampled in July 2014 in Aiguillon Bay). Flesh biomass of bivalves (*Scrobicularidae*, as well as *Macoma balthica* individuals) smaller than 8.0 mm was determined from the total biomass ($AFDM_{flesh+shell}$) with the following linear regression: $AFDM_{flesh} = 0.7649 \times AFDM_{flesh+shell} - 7E - 05$ ($R^2 = 0.9656$, N = 122 *Scrobicularidae* individuals and 51 *M. balthica* ind. sampled in January 2014 in Aiguillon Bay).

For bivalves larger than 8.0 mm, shells were placed in adequate numbered stalls and dried in a ventilated oven at 55 to 60 °C ($DM \pm 0.01$ mg) for three days.

For *H. ulvae* individuals, the shell was not separated from the flesh, and shell dry mass was estimated from the total biomass using the following regression: $DM_{shell} = 5.5902 \times AFDM_{flesh+shell} - 0.0006$ ($R^2 = 0.98$; N=60 ind. sampled in July 2014 in Aiguillon Bay). For the same reason, dry mass of the shell (DM_{shell})

of small bivalves (< 8.0 mm) was extrapolated using the following regression: $DM_{shell} = 8E - 05 \times 2.6523Length$ ($R^2 = 0.8274$, $N=122$ *Scrobiculalidae* ind. and 51 *M. balthica* ind. sampled in January 2014 in Aiguillon Bay).

In the present dataset, we removed all epibenthic species (*e.g.* crustaceans) since they are nearly absent from the feeding regime of shorebirds in our study area (Bocher et al., 2014b). Polychaetes were also identified and counted but length and AFDM were not determined for these phyla due to insufficient numbers of entire individuals to build regression equations. Nearly all polychaete species were removed from the database because the precision of sample sorting and determination varied widely between the years depending on the laboratory operator. Only individuals from the Genus *Nephtys* (more than 90% of which were *Nephtys hombergii*) and individuals of the Family Nereididae (more than 90% of which were either *Alitta succinea* or *Hediste diversicolor*) were kept because they represent more than 80% of polychaetes in our study sites and comprise the biggest annelids and therefore biomass and prey for shorebirds (*pers. observation*). They are mentioned under the abbreviations "nepsp" (for *Nephtys* genus) and "neresp" (for Nereididae family) in the database. For these two polychaete taxa, the columns "length", "width", as well as "AFDM", "Biomass_dens" and "NewTBH" are not available (See Table 3.2 describing the columns), only densities are available.

3.5 Geographic coverage

Description: In winter 2003-2004, an extensive benthos sampling (864 stations) was conducted following a grid over the whole intertidal zone of Aiguillon Bay and Marennes-Oléron Bay (Bocher et al., 2007). In the following years, the grid was reduced for practical reasons to a 259 points grid spread in four subsites covering three different types of mudflats: Aiguillon Bay on the Charente-Maritime side (AIC, bare mudflat), Aiguillon Bay on the Vendée side (AIV, bare mudflat), Moëze intertidal area (MO, bare mudflat with runnels system) and Oléron Island intertidal area (OL, sandy mudflat covered with seagrass). The grids were defined as a square shape when possible to facilitate movements and navigation on the mud and at sea (Fig. 3.1). Because this sampling effort was designed primarily for the study of shorebird ecology, grids were placed in protected areas (National Nature Reserve of Moëze-Oléron, and National Nature Reserve of Aiguillon Bay) managed by the LPO (Ligue pour la Protection des Oiseaux)

and ONCFS (Office nationale de la Chasse et de la Faune Sauvage), matching wetlands international annual shorebird counting areas. Sampling stations are referenced by spatial coordinates using the WGS84 geodetic datum. The four sampled subsites present contrasted characteristics that are described in Degré et al., (2006) and Bocher et al., (2007).

Due to field complexities or bad weather, some stations were not sampled some years. Namely in 2004, stations 2131-2133 and 2136-2140; in 2006, stations 2103 and 1953; in 2005, stations 1860, 1391 and 1395; in 2008, station 1300; in 2010, station 1958; in 2012, station 2137; and in 2014, stations 2137 and 1311. To this list, all the stations from Marennes-Oléron (site 'OL' and 'MO') in years 2010 and 2011 should be added. The value NA (*i.e.* not available) is given in the data set to avoid misinterpreting these cases for 'true absence'.

3.6 Taxonomic coverage

Description: The dataset includes all occurrences of individuals for the taxa listed in Table 3.1. Annelids were grouped under the Genus *Nephtys* or the Family Nereididae. *Ruditapes sp.* was essentially individuals of the species *Ruditapes philippinarum*.

Scientific names and corresponding AphiaID were derived from the World Register of Marine Species (WoRMS). The combination of both scientific name and AphiaID prevents any confusion when names change over time. Indeed, in ten years of collecting data, various operators have used a list of species that was an extract of a taxonomy (with description of *phylum*, *subphylum*, *class*, *subclass*, *infraclass*, *superorder*, *order*, *suborder*, *infraorder*, *superfamily*, *family*, *genus*, *species*, and *authority*). However, classification evolves throughout time, and our dataset needed to be backed to an official registry of species linked to the semantic Web. The World Register of Marine Species (*World Register of Marine Species*) provides unique AphiaID for identifying marine species, and maintains a historic of changes of naming or classification. Furthermore, it provides semantic export of species description in RDF compatible with *Darwin Core* or *Dublin Core* metadata standards. We used this register in order to disambiguate the identification of species found in the dataset. For that, we have written a Python program querying the Web Service (*World Register of Marine Species Webservice*) provided by the World Register of Marine Species (WoRMS), for searching and resolving AphiaIDs of our species list, using the WSDL interface (*World Register of Marine Species WSDL interface*). For each record in our table, the program sends the

TABLE 3.1: Species collected, including total number of specimens in the database, and classification according to the World Register of Marine Species

Scientific name	Class	Family	Genus	Abr.	English name	Nr.	Authority	AfiaID
<i>Abra nitida</i>	Bivalvia	Semelidae	<i>Abra</i>	abn	-	23	(Müller, 1776)	141435
<i>Abra ovata</i>	Bivalvia	Semelidae	<i>Abra</i>	abo	-	3	(Philippi, 1836)	146467
<i>Abra sp.</i>	Bivalvia	Semelidae	<i>Abra</i>	abr	-	10	Lamarck, 1818	138474
<i>Abra tenuis</i>	Bivalvia	Semelidae	<i>Abra</i>	abt	-	3,726	(Montagu, 1803)	141439
<i>Cerastoderma edule</i>	Bivalvia	Cardiidae	<i>Cerastoderma</i>	cer	Edible cockle, common cockle	1,697	(Linnaeus, 1758)	138998
<i>Corbula gibba</i>	Bivalvia	Corbulidae	<i>Corbula</i>	corgib	European clam, Basket shell	1	(Olivieri, 1792)	139410
<i>Crepidula fornicata</i>	Gastropoda	Calyptraeidae	<i>Crepidula</i>	cre	Common Atlantic slip-persnail	56	(Linnaeus, 1758)	138963
<i>Tritia neritea</i>	Gastropoda	Nassariidae	<i>Tritia</i>	cyc	Cyclope	42	(Linnaeus, 1758)	876816
<i>Epitonium clathrus</i>	Gastropoda	Eulimidae	<i>Epitonium</i>	epi	European wentletrap	1	(Linnaeus, 1758)	146905
<i>Crassostrea gigas</i>	Bivalvia	Ostreidae	<i>Crassostrea</i>	gig	Pacific oyster	1	(Thunberg, 1793)	140656
<i>Haminoea hydatis</i>	Gastropoda	Haminoeidae	<i>Haminoea</i>	ham	-	55	(Linnaeus, 1758)	140074
<i>Hydrobia ulvae</i>	Gastropoda	Hydrobiidae	<i>Hydrobia</i>	hyd	Mudsnail, laver spire shell	45,796	(Pennant, 1777)	140126
<i>Littorina littorea</i>	Gastropoda	Littorinidae	<i>Littorina</i>	lit	Common periwinkle	38	(Linnaeus, 1758)	140262
<i>Littorina saxatilis</i>	Gastropoda	Littorinidae	<i>Littorina</i>	litsax	Black-lined periwinkle	8	(Olivieri, 1792)	140264
<i>Macoma balthica</i>	Bivalvia	Tellinidae	<i>Macoma</i>	mac	Baltic tellin	3,930	(Linnaeus, 1758)	141579
<i>Kurtiella bidentata</i>	Bivalvia	Montacutidae	<i>Kurtiella</i>	mys	-	20	(Montagu, 1803)	140380
<i>Mytilus edulis</i>	Bivalvia	Mytilidae	<i>Mytilus</i>	myt	Blue mussel	11	Linnaeus, 1758	140480
<i>Nassarius sp.</i>	Gastropoda	Nassariidae	<i>Nassarius</i>	nas	-	2	Duméril, 1805	138235
<i>Nereididae indet.</i>	Polychaeta	Nereididae	-	neresp	-	1,151	Blainville, 1918	22496
<i>Nephtys sp.</i>	Polychaeta	Nephtyidae	<i>Nephtys</i>	nepsp	-	1,648	Cuvier, 1817	129370
<i>Nucula nitidosa</i>	Bivalvia	Nuculidae	<i>Nucula</i>	nuc	-	1	Winckworth, 1930	140589
<i>Retusa obtusa</i>	Gastropoda	Retusidae	<i>Retusa</i>	ret	Arctic barrel-bubble	148	(Montagu, 1803)	141134
<i>Scrobicularia plana</i>	Bivalvia	Semelidae	<i>Scrobicularia</i>	scr	Peppery furrow shell	7,592	(da Costa, 1778)	141424
<i>Ruditapes sp.</i>	Bivalvia	Veneridae	<i>Ruditapes</i>	tapsp	-	660	Chiamenti, 1900	231748

name of the species in parameter of the `querymatchAphiaRecordsByNames` and the service finds for us matching taxa; the program asks then for the full `AphiaRecord` of the taxon (`getAphiaRecordByID`), parses it and checks it against our own classification. When a `AphiaRecord` matches our own table record, we retain it, else we log the uncertain case in order to search manually in the web interface. Only few cases (around 20), identified in the logs of our program, have been searched and solved manually using the web interface of WoRMS. The result is that we provide within our dataset the actual taxonomy of our species extracted from WoRMS, and most importantly their corresponding AphiaID in WoRMS.

3.7 Traits coverage

Description: The attributes of the database, including the traits measured in macrofauna individuals are presented in Table 3.2.

3.8 Temporal coverage

Sampling was undertaken during winter (between December and February) each year, starting in December 2003. The fieldwork team (about five to seven people) spent a yearly average of three weeks sampling during spring tides in winter season. For convenience in analyses, if sampling took place in December, the year associated with sampling corresponds with the following year in the dataset. For example samples taken in December 2006 will be attached to year 2007, together with samples from January 2007 or February 2007. First samples were taken in December 2003 (sampling year 2004) and last samples in February 2014 (year 2014). In the subsequent years (starting in winter 2015 until now) sampling was performed over a reduced spatial extent (only 'AIC' subsite, *i.e.* 64 stations). Sampling is planned to be continued in the future. The winter season was chosen because environmental conditions are stable for benthos (with a reduced growth rate and no recruitment for most species). Also, this is the period when the highest densities of overwintering migratory shorebirds can be observed and can be linked to the feeding resources thanks to the annual January counts of Wetlands international. No data are available for the subsites 'mo' and 'ol' in sampling years 2010 and 2011.

3.9 Usage rights

User licence: Open Data Commons Attribution License

IP rights notes: This work is licensed under a Creative Commons Attribution-NonCommercial-ShareAlike 4.0 International License. The associated dataset can be freely used for non-commercial purpose, provided it is cited. We draw your attention to the fact that you can contact the authors of the "benthos" dataset to prevent any misuse of the data. You can also consult us for reviewing articles based on our dataset.

TABLE 3.2: Table of attributes, with associated column names, description, units and constraints.

Attribute	Column name	Description	Units	Constraints
Unique identifier	'id'	Integer referring to one individual in the database	-	Integer, Unicity
Year	'year'	Sampling year	-	For convenience in the analyses, if sampling took place in December, the year associated with sampling corresponds to the following year (e.g. sampling in Dec.2008 = 2009). Integer [2004:2014].
Site	'site'	Sampling site	-	'MAROL' refers to Marennes-Oléron Basin and 'AIG' refers to Aiguillon Bay
Subsite	'st_sit_id'	Subsite	-	Each site is divided into two subsites (grids of approximately 64 stations). Oléron subsite ('ol') and Moëze subsite ('mo') are part of the site 'MAROL'. Aiguillon Charente subsite ('aic') and Aiguillon Vendée subsite ('aiv') are part of the site 'AIG'.
Station	'Poskey'	Station number	-	Each station refers to unique coordinates ('st_lat_dd' and 'st_long_dd') and are located in a single 'site' and 'subsite'. Subsite 'ol' has 67 stations, and subsites 'mo', 'aic', and 'aiv' have 64.
Latitude	'st_lat_dd'	Latitude	Decimal degrees, WGS84	Numeric, together with 'st_long_dd' refers to a single 'Poskey' value
Longitude	'st_long_dd'	Longitude	Decimal degrees, WGS84	Numeric, together with 'st_lat_dd' refers to a single 'Poskey' value
Abbreviation	'abr'	Refers to a unique species name, see Table 3.1	-	Character, value in (''abn', 'abr', 'abo', 'abt', 'cer', 'crogib', 'cre', 'cyc', 'epi', 'gig', 'ham', 'hyd', 'lit', 'litsax', 'mac', 'mys', 'myt', 'nas', 'neresp', 'nepsp', 'nuc', 'ret', 'scr', 'tapsp')
Phylum	'Phylum'	Phylum of the sampled individual	-	Character, value in ('Annelida', 'Mollusca')
Number	'number'	Number of individuals	-	Integer = 1
Shell length	'length'	Maximum length of the shell	mm	Numeric, decimal = 2. 'NA' when "Phylum" is 'Annelida'. Measured from the apex to the aperture when Gastropoda. Measured as the maximum length of the shell when Bivalve. For the species 'hyd', length is rounded to the closest lower integer.
Size class	'class_length'	Size class of the individual	mm	Integer, corresponds to the "length" value, rounded to the closest integer
Shell width	'width'	Width of the bivalve	mm	Numerical, decimal = 2, only measured for bivalves as the maximum width when both valve are taken together
Flesh AFDM	'AFDM'	Ash-Free Dry Mass of the soft part	g_{AFDM}	Numerical, decimal = 4. 'NA' when "Phylum" is 'Annelida
Shell DM	'ShellDM'	Dry mass of the shell	g_{DM}	Numerical, decimal = 4. 'NA' when "Phylum" is 'Annelida'
Sampling mode	'car_mod_id'	Sampling mode, either by boat or by foot	-	Integer, value in (1,2). If sampling was made by foot 'car_mod_id' = 1. If sampling was made from boats 'car_mod_id' = 2
Accessibility	'car_top_bottom'	Whether or not the top 4 cm were separated from the rest of the mud core	-	Logical, if 'car_mod_id' = 1 then "car_top_bottom" = TRUE
Sediment layer	'T.B.H'	Type of corer used	-	Integer, value in ('top', 'bott', 'hyd', 'all'). If "car_mod_id" = 1, then 'T.B.H' = 'hyd' if 'abr' is 'hyd' otherwise if the individual is a different species of mollusc 'T.B.H' = 'top' or 'bott' depending on the mud layer processed. If 'car_mod_id' = 2 OR 'Phylum' = 'Annelida' then 'T.B.H' = 'all'.
Extrapolated Accessibility	'newTBH'	Extrapolated value, from the column 'T.B.H'	-	Character, value in ('t', 'b'), for other constraints see section "Cleaning process" and the paragraph "Extrapolating top and bottom fractions" of the present article.
Sampled area	'area'	Sampled area, corresponding to the individual	m ²	Numerical, decimal = 8. If "T.B.H" is 'top' or 'bott', then diameter of the corer is 7.5 cm and area = $\pi \times 0.075^2$. If 'T.B.H' is 'hyd'. then a smaller corer was used with a 3.5 cm diameter and area = $\pi \times 0.035^2$. If 'T.B.H' is 'all' and 'car_mod_id' is 1, then area = $\pi \times 0.075^2$. If 'T.B.H' is 'all' and "car_mod_id" is 2, then two cores of 10 cm diameter were taken and area = $2 \times \pi \times 0.05^2$
Abundance density	'dens.ind'	Abundance density	$N_{ind} \cdot m^2$	Numerical, decimal = 4; 'number' / 'area'
Biomass density	'biomass.dens'	Density of flesh ash-free dry mass	$g_{AFDM} \cdot m^{-2}$	Numerical, decimal = 4; 'AFDM' / 'area'

3.10 Data resources

Data package title:

Resource link: <http://dx.doi.org/10.14284/247>

Number of dataset: 1

Data set name: Benthic monitoring in the intertidal mudflats of Pertuis-Charentais (Bay of Biscay) from 2004 on

Download URL: <http://dx.doi.org/10.14284/247>

Data format: .csv

Description: This dataset is hosted by EurOBIS and can be downloaded using the link above (see section 'Usage rights' for more information). The column names used in the present dataset don not always match the ones in the EurOBIS dataset. The Table below indicates this correspondance between the column names in the datapaper (including the names used in the script) and the column names in the EurOBIS dataset, see Table 3.3.

3.11 Additional information

3.11.1 Steps of database building

The database was built via the association of different original tables at different steps of the collection, sorting, measuring and weighing of samples. After each sampling session, we filled in a table "CORE" with columns: "year", "Poskey", "car_mod_id" and "car_top_bottom" as well as unique identifier "core_id". Subsequently, in the laboratory while determining and measuring the samples, we filled in a table "BENTHOS" with columns: "abr", "number", "length", "width", "class_length", "T.B.H", "AFDM", "Shell_DM" and "core_id". A unique identifier "id" was associated to each row in this table "BENTHOS".

Preliminary to the tables "CORE" and "BENTHOS", a table "SPECIES" with the scientific name associated to the abbreviation "abr" was built, together with a table "STATIONS" with coordinates, site and subsite associated to the sampling station identifier "Poskey".

All these tables were associated together, in strict respect of integrity criteria specified through 'foreign keys' and 'primary keys' constraints, to form a relational database (Fig. 3.4) and later the flattened database "benthos" presented in this datapaper. Foreign key "core_id" in table "BENTHOS" had to match primary key "core_id" in table "CORE". Primary key "Poskey" of table "STATIONS" had to match foreign key "Poskey" of table "CORE". Primary key "abr" in table "SPECIES" had to match foreign key "abr" in table "BENTHOS" (Fig. 3.4).

TABLE 3.3:

Column label	Column description
aphiaid	Unique number corresponding to a described species in WoRMS. [0.3ex] In the present datapaper the column refers to the column 'AphiaID'.
period	Winter period corresponding to the sampling. [0.3ex] In the present datapaper the column refers to the column 'Period'.
sampling_date	Date of sampling. [0.3ex] In the present datapaper the column refers to the column 'sampling_date'.
site	Sampling site. [0.3ex] In the present datapaper the column refers to the column 'site'.
st_sit_id	Subsite. [0.3ex] In the present datapaper the column refers to the column 'st_sit_id'.
station	Station number. [0.3ex] In the present datapaper the column refers to the column 'Poskey'.
st_lat_dd	Latitude. [0.3ex] In the present datapaper the column refers to the column 'st_lat_dd'.
st_long_dd	Longitude. [0.3ex] In the present datapaper the column refers to the column 'st_long_dd'.
number	Number of individual. [0.3ex] In the present datapaper the column refers to the column 'number'.
length	Maximum length of the shell. [0.3ex] In the present datapaper the column refers to the column 'length'.
class_length	Size class of the individual. [0.3ex] In the present datapaper the column refers to the column 'class_length'.
width	Width of the bivalve. [0.3ex] In the present datapaper the column refers to the column 'width'.
afdm	Ash-Free Dry Mass of the soft parts. [0.3ex] In the present datapaper the column refers to the column 'AFDM'.
shelldm	Dry mass of the shell. [0.3ex] In the present datapaper the column refers to the column 'ShellDM'.
car_mod_id	Sampling mode, either by boat or by foot. [0.3ex] In the present datapaper the column refers to the column 'car_mod_id'.
car_top_bottom	Whether or not the top 4 cm were separated from the rest of the mud core. [0.3ex] In the present datapaper the column refers to the column 'car_top_bottom'. [0.3ex]
tbh	Type of corer used. [0.3ex] In the present datapaper the column refers to the column 'T.B.H'.
newtbh	Extrapolated value, from the column "T.B.H". [0.3ex] In the present datapaper the column refers to the column 'newT.B.H'.
area	Sampled area, corresponding to the individual. [0.3ex] In the present datapaper the column refers to the column 'area'.
dens.ind	Abundance density. [0.3ex] In the present datapaper the column refers to the column 'dens.ind'.
biomass.dens	Density of flesh Ash-Free Dry Mass. [0.3ex] In the present datapaper the column refers to the column 'biomass_dens'.
scientific_name	Scientific name of the species. [0.3ex] In the present datapaper the column refers to the column 'Scientific name'.
phylum	Phylum of the sampled individual. [0.3ex] In the present datapaper the column refers to the column 'phylum'.
class	Class associated with the individual. [0.3ex] In the present datapaper the column refers to the column 'class'.
family	Family associated with the individual. [0.3ex] In the present datapaper the column refers to the column 'family'.
genus	Genus associated with the individual. [0.3ex] In the present datapaper the column refers to the column 'genus'.
English name	English common name associated with the individual. [0.3ex] In the present datapaper the column refers to the column 'English name'.
authority	The person credited to have formally named the species for the first time. [0.3ex] In the present datapaper the column refers to the column 'authority'.
nr	Total individuals of this species in the database. [0.3ex] In the present datapaper the column refers to the column 'nr'.

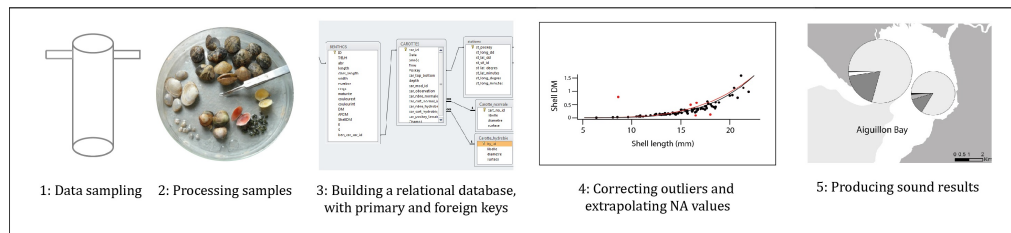


FIGURE 3.4: Benthic monitoring database building steps, from data collection to the production of results.

TABLE 3.4: Integrity checks, data cleaning and inferring of missing data

Check of integrity constraints, misspellings, uniqueness					
Attribute	Description	Modified	Total occurrence	% corrected	Criteria
"abr"	Species abbreviation	148	66.620	0.22%	misspelling
"car_top_bottom"	Whether the top fraction of the sediment was sampled separately	460	7.013	6.56%	logic
"AFDM"	Flesh ash-free dry mass	2.215	11.015	20.11%	"length" > 8
"ShellDM"	Shell dry mass	2.353	11.015	21.36%	"length" > 8
Cleaning process step, detecting outliers (replaced by NA values) and inferring missing data					
Attribute	Description	Modified	Total occurrence	% corrected	Criteria
"length"	Length of the shell	140	66.620	0.21%	"length" = 0
"AFDM"	Flesh ash-free dry mass	52.127	53.533	97.37%	"length" < 8
"ShellDM"	Shell dry mass	10.308	53.533	19.26%	"length" < 8
"newTBH"	Whether the individual belongs to the top or the bottom (inferring)	10.884	21.918	49.66%	probabilities

3.11.2 Cleaning process

Step 1. Check integrity constraints, misspellings, uniqueness: The preparation of the dataset (*e.g.* checking for data types, misspelling, uniqueness of identifiers and integrity constraints as described in Table 3.2) was performed through building the relational database under PostgreSQL, following the principles described in Chapman, (2005). The work was performed using SQL scripts, during and after the import of all raw CSV tables (BENTHOS, CORE, STATIONS, SPECIES), that were not linked together at the beginning, nor respecting all constraints for attributes type for instance. Some insights of the work led during this step are given in Table 3.4.

Step 2. Outliers and NA, using regression models on data: Once the relational database was built, and integrity criteria met, the database was cleaned in a systematic way, species by species, site by site and year by year. This step was done using R statistical software (Team, 2015). The first step aimed at unfolding the

dataframe (*i.e.* producing one row for each sampled individual). Then the column "length" was cleaned from its outliers or potential typing errors using common methods (Hawkins, 1980). Then, using extrapolation curves, outliers and missing values were derived from the column "length" for "width", "DM_{Shell}" and "AFDM" following the R code (see Suppl. material 1 in the online version, and Fig. 3.5). This process led to substantial improvement of the dataset, see Table 3.4.

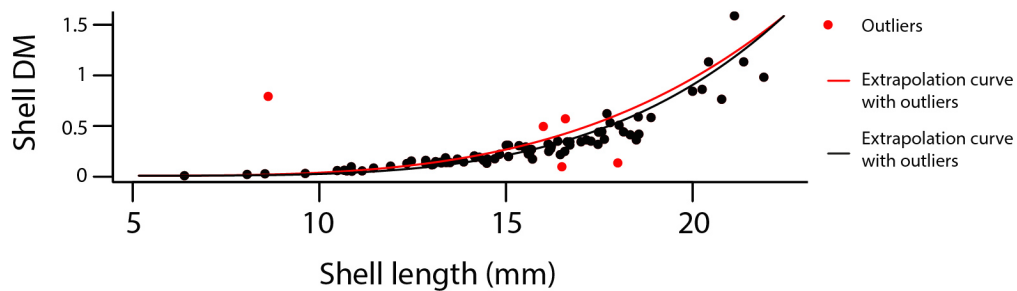


FIGURE 3.5: Data cleaning using extrapolation curves, an example of shell dry mass extrapolation based on shell length in the bivalve *Macoma balthica*

Assigning sampling area to each station in each year, depending on the sampling method: The columns "area" and "area_hyd" were filled in according to the sampling method (either by boat "car_mod_id" = 2 or by foot "car_mod_id" = 1). By boat, two cores are taken on a corer with radius 0.050 m (area = $2 \times \pi \times 0.050^2$), and by foot one core is taken with a radius of 0.075 m (area = $\pi \times 0.075^2$). *Hydrobia ulvae* were counted in one of the two cores taken by boat (area = $\pi \times 0.050^2$), and if sampling was made by foot an additional smaller core was taken, with a radius of 0.035 m (area = $\pi \times 0.035^2$), see Table 3.2.

Calculating abundance and biomass densities: The next step consisted of deriving abundance densities ("dens_ind") and biomass densities ("biomass_dens"), a script is added to the online version of the present datapaper as Suppl. materials 3.

Extrapolating top and bottom fractions: The last step of data cleaning aimed at assigning the sampled individuals to the top or the bottom fraction of the sediment (*i.e.* whether or not it was accessible to a sandpiper's bill). When samples were taken by foot ("car_mod_id" = 1), the top 4 cm were always separated from the bottom fraction ("car_top_bottom" = TRUE), and the sampled individuals

always received a "top" or "bott" or "hyd" value in the column "T.B.H", "hyd" corresponding to the top fraction of the sediment since *H. ulvae* are always accessible to sandpipers. However, when samples were taken from boats ("car_mod_id"=2), the top was not separated from the bottom fraction ("car_top_bottom"=FALSE), and the sampled individuals did not receive a "top" or "bott" value in the column "T.B.H". In that case, a script (see Suppl. materials 2 in the online version) was applied to infer for each individual whether it was more likely to belong to the top or the bottom fraction of the sediment based on species-site-year-length specific probabilities (except *Hydrobia* individuals that would always be accessible, and annelid species for which lengths were not available).

3.12 Discussion

Opportunities: There are multiple examples of the potential use of such data for further exploitation. The multidimensional dataset can be explored for various questions and following spatial or temporal dimension. For instance, in Fig. 3.6, the plots exemplify how spatial and temporal dimensions are associated, since we have time series for each station of each site. We can also examine how the harvestable biomass for *Calidris canutus* (which means accessible because found in the "top" and respecting certain criteria for length Fig. 3.2) is distributed amongst the various species, on a site for a given year (Fig. 3.7). The plot on the left shows that mean total biomass of *Scrobicularia plana* was of 0.24 g. m⁻² in 2014, varying between 0.10 and 0.25 g. m⁻² following site stations, with a mean value lower than biomass of *Macoma bathica*, but with also a smaller dispersion. The dataset allows us to analyse also how harvestable mean biomass varies according to time on this site for *S. plana* (Fig. 3.7, on the right) and allows mapping of densities or species composition (Figs 3.6, 3.8).

All the results presented in this datapaper can be obtained running the provided R code (online version, Suppl. materials 3).

Limits of data use: The database was designed to estimate temporal changes and spatial differences in biomass and densities, as well as possible changes in quality, depth or community composition in our study sites. However, for predictions at unsampled locations, additional analyses are required such as investigating spatial auto-correlation (Bijleveld et al., 2012; Kraan et al., 2010a). Regression lines derived from the present dataset shall be valid only for the particular species, site and year and should not be used to extrapolate missing data in any

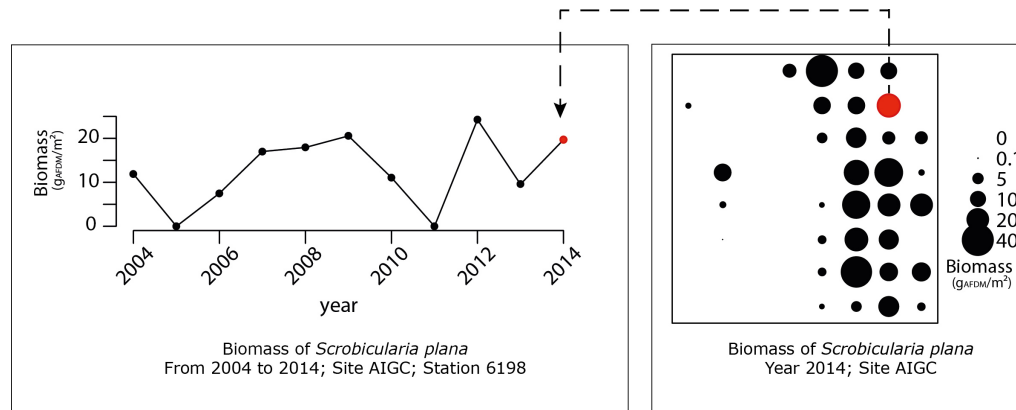


FIGURE 3.6: Right side: map of the biomass of *Scrobicularia plana* on Aiguillon Cove on the Charente-Maritime side (AIC) in 2014; Left side: temporal evolution of one station (n°1698) of this site for biomass in time since 2004.

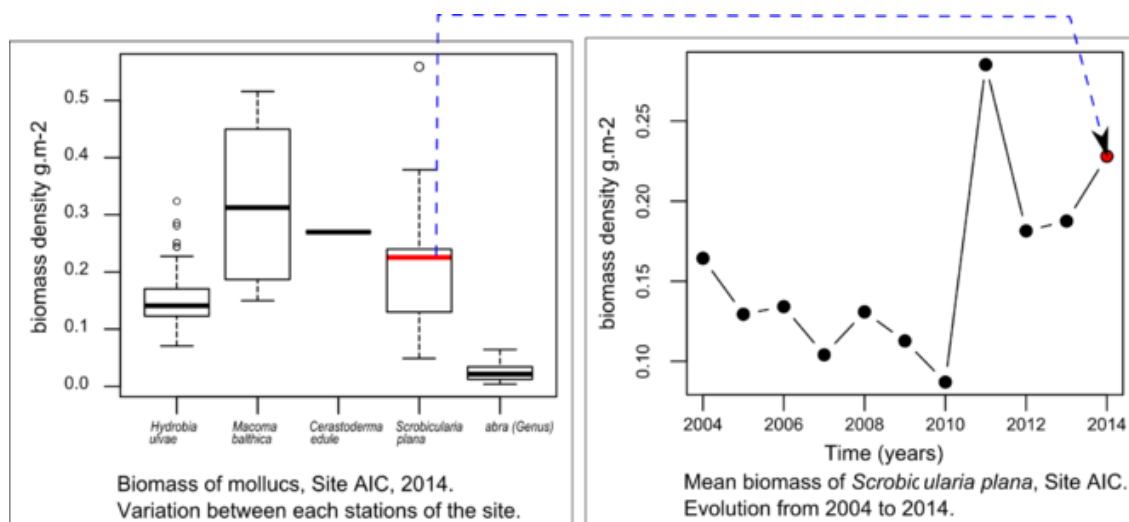


FIGURE 3.7: Left side: Variation of mollusc biomass harvestable to red knots between stations of Aiguillon bay on the Charente-Maritime side (AIC) in 2014. Right side: Evolution of mean harvestable biomass of *S. plana* in Aiguillon bay on the Charente-Maritime site (AIC) since 2004.

other context. However, the scripts provided in supplementary materials (online version) can be adapted to other database architectures, to clean the data and produce results.

Author contributions

Data collection, sorting and processing of samples as well as database integrity was initiated and managed by Dr. Pierrick Bocher (Senior Scientist at the LIENSs laboratory, University of La Rochelle) in 2003. One Assistant engineer (Philippe

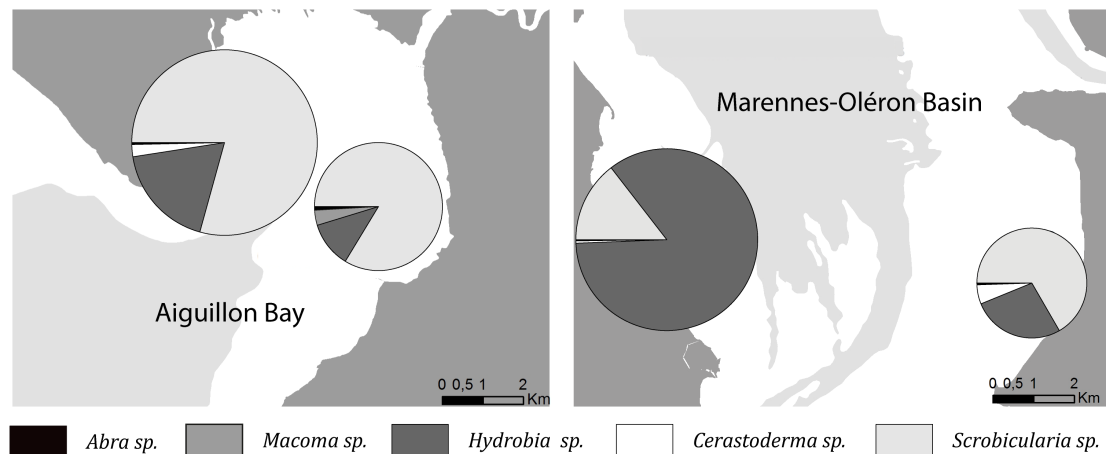


FIGURE 3.8: Share of common mollusc genera (*i.e.* *Hydrobia*, *Macoma*, *Cerastoderma*, *Scrobicularia* and *Abra*) in the four study sites in winter 2013-2014. Radius is proportional to the combined biomass density of the principal mollusc genera.

Pineau) and one technician (Nicolas Lachaussée) helped collecting the data every year. Anne Philippe helped in data collection, laboratory work, data uploading and was responsible for the design and integrity of the database. Transfer of the database into PostgreSQL format and preparation of the figures and scripts accompanying the present data paper was performed by Dr. Christine Plumejeaud-Perreau (Research engineer at the LIENSs laboratory) with help from Anne Philippe. Jérôme Jourde was in charge of taxonomy training and helped with identification and cleaning of the database when necessary.

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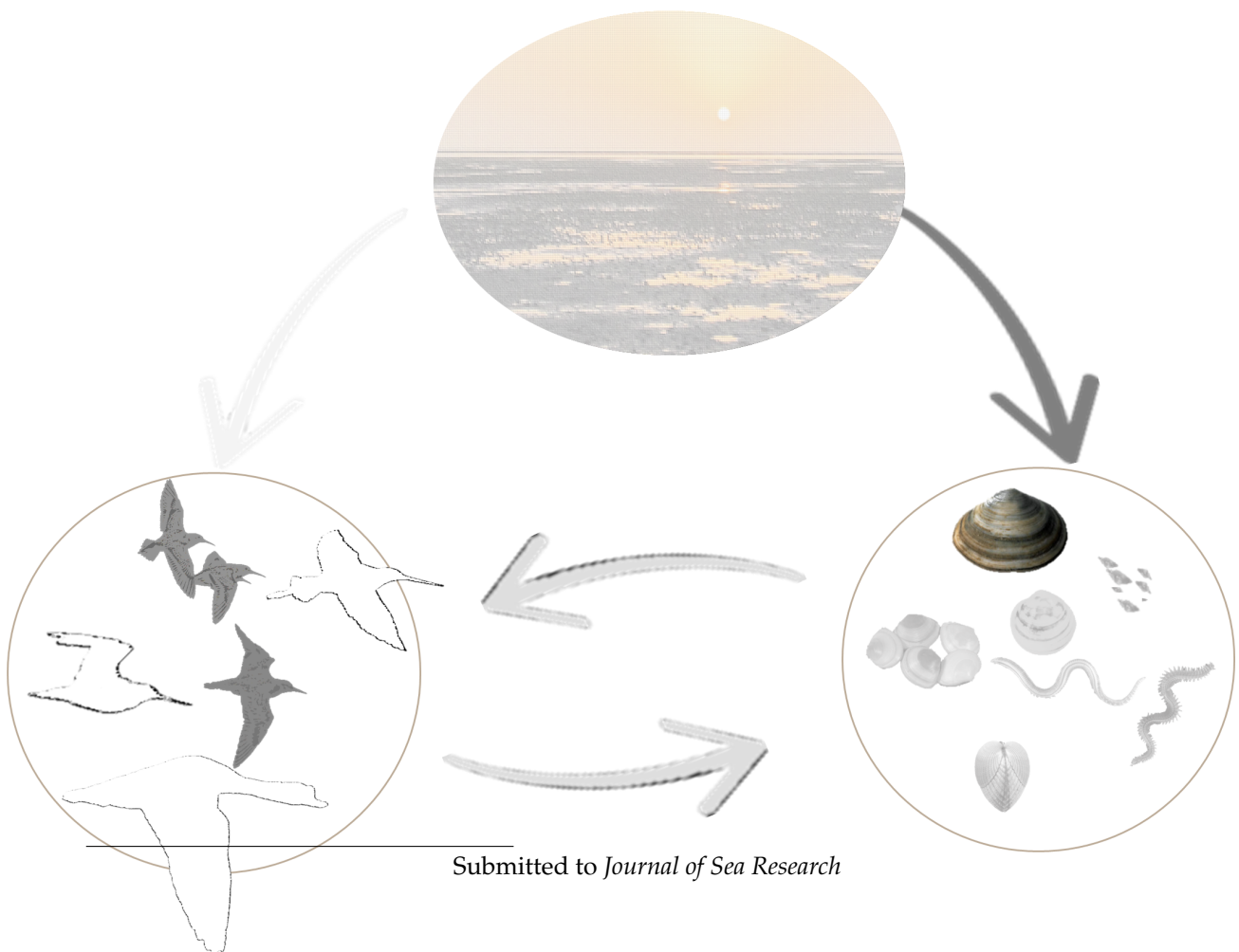
**SECTION 3: FACTORS EXPLAINING
TEMPORAL VARIABILITY OF BENTHIC
RESOURCES**



Chapter 4

Phenotypic variations in the thin-shelled bivalve *Scrobicularia plana* under seasonal predation

Anne S. PHILIPPE, Philippe PINEAU, Nicolas LACHAUSSÉE, Pierrick BOCHER



4.1 Abstract

In temperate mudflats along the East Atlantic Flyway, infaunal bivalves face seasonal predation by migratory shorebirds. Together with variations in temperature and primary production, predation is a major source of environmental stress for bivalves. Predation induces adaptive and evolutionary responses that often materialise in the thickness of the shell and burial depth, especially for prey species swallowed whole. This study presents seasonal variations in a flexible burrowing bivalve, *Scrobicularia plana*, depending on its life stages. Different condition indices (*i.e.* flesh-to-shell ratio, shell mass index, soft mass index and accessibility) are calculated for 15 consecutive months in Aiguillon Bay, France.

- Reproduction investment leads to the emergence of two cohorts during the study period: one in autumn and one in spring.

- Results show seasonal variations in condition indices and accessibility depending on the stage considered. During predation periods, the evolution of these indices differs between life stages.

- Contrasted effects of predation period on juveniles indicate varying responses to predation depending on the season, and cohort.

We highlight a contrast in the condition of available prey depending on seasonal predation. Individuals at risk of predation have a better quality in spring than in winter, and reveal different strategies in response to seasonal predation. *S. plana* is a flexible species, which reacts to its environment in various ways depending on its life stages and environmental conditions, including predation pressure.

4.2 Introduction

Molluscs of intertidal areas are faced with seasonal predation by migratory shorebirds (Delaney et al., 2009) that shape their behaviour (e.g. burial depth) and phenotype (e.g. thickness of the shell) (Piersma and Van Gils 2010). In temperate areas, these species also have to deal with seasonal changes in temperature and feeding conditions, which are determinant for the timing and success of life events (van der Meer, Beukema and Dekker 2001, Santos et al. 2011a, Beukema et al. 2014). In turn, this phenological variability carries effects on the interannual variability of food stocks for shorebirds (Beukema et al. 1993, van der Meer et al. 2001).

In the field of predator prey interactions, shorebirds and bivalves offer a particularly rich model thanks to their high flexibility in behaviour and phenotype (Piersma and Van Gils 2010). This article will address predator prey interactions through the study of temporal variations in the phenology, condition, behaviour and densities of *Scrobicularia plana*, to try and explain why such a dominant species in many European mudflats is so little consumed by shorebirds in the Pertuis Charentais (Quaintenne 2010, Robin13, Bocher et al. 2014).

When prey molluscs are swallowed whole with shell, their size (shell length), shape (globosity) and quality (flesh-to-shell ratio, shell weight, flesh weight and energy content) are determinant for gape-limited and digestively constrained predators such as migratory shorebirds (van de Kam et al., 2004; van Gils et al., 2005c; van Gils et al., 2005b; van Gils et al., 2006b). In temperate areas, quality highly depends on seasonal variations in environmental factors (e.g. cold temperatures in winter negatively affect body condition, Beukema, 1974; Zwarts, 1991; Beukema et al., 2014). Quality is also affected by predation, usually through enhanced shell thickness (Nagarajan, Lea, and Goss-Custard, 2006; Brookes and Rochette, 2007; Bijleveld et al., 2015). The quality of burrowing bivalves is, however, a much more complex ecological trait, resulting from intricate relationships between individual behaviour, population ecology and external forcing (e.g. weather, predation) (Reading and McGrorty, 1978; Zwarts, 1986; Zwarts and Wanink, 1989; Zwarts, 1991; Zwarts and Blomert, 1992; Wanink and Zwarts, 1993; Zwarts and Wanink, 1993; Zwarts et al., 1994; Wanink and Zwarts, 2001; Mouneyrac et al., 2008; van Gils et al., 2009; Santos et al., 2011a; Tankoua et al., 2011; Beukema et al., 2014).

This paper focuses on *S. plana*, a dominant species in terms of biomass and productivity in NE Atlantic area (Verdelhos et al., 2011), described as a facultative suspension-feeder and euryhaline bivalve (Orvain, 2005). In some areas, *S. plana* can be a very important species in terms of density, food web, and energy flow

(Hughes, 1970a). *S. plana* has been considered as a “key species” because of its ubiquity, local abundance (Santos et al., 2011b) and importance in the estuarine trophic chain (Keegan, 1986) (e.g. it is a prey for crabs, fishes and shorebirds, even humans). It sometimes plays a major role in the biogeochemical cycle of nutrients and contaminants as a consequence of its bioturbation activity (Orvain, 2005) and can be used as a sentinel species for assessing habitat quality (Tankoua et al., 2011). Its distribution shows preference for the upper intertidal zone where it dominates in terms of biomass in many mudflats (Freeman and Rigler, 1957; Orvain, 2005; Bocher et al., 2007; Orvain et al., 2007; Compton et al., 2009). This estuarine infaunal tellinid is a tolerant species which rapidly adapts its demography (Hughes, 1970b; Nott, 1980), which can explain:

- the species' large geographic distributional range from Norway to the Mediterranean and West Africa (14°N) allowing latitudinal comparisons (Essink et al., 1991; Santos et al., 2011b; Verdelhos et al., 2011).

- the high interannual variability in the production of this bivalve (Zwarts and Wanink, 1991; Essink et al., 1991)

- its flexibility depending on environmental factors (e.g. temperature, salinity, predation pressure, season) (Akberali, Brear, and Currey, 1983; Zwarts, 1986; Zwarts, 1991; Wanink and Zwarts, 1993; Zwarts and Wanink, 1993; Bouchet, Degré, and Sauriau, 1983; Mouneyrac et al., 2008; Santos et al., 2011a; Tankoua et al., 2011).

S. plana, although little studied compared to *Macoma balthica*, has been considered as prey for shorebirds in some studies (Zwarts, 1986; Boates and Goss-Custard, 1989; Wanink and Zwarts, 1993; Zwarts and Wanink, 1993; Wanink and Zwarts, 2001; Rosa et al., 2007), even though it is only a second-choice prey in shorebirds' diet (Zwarts and Blomert, 1992).

This study puts emphasis on seasonal variations in condition indices (body weight and quality), as key tools for studying the flexibility of the species faced with predation. Previous studies revealed that for a given place, size class and time period, differences in condition indices could be the result of age, parasitic infestation, gametogenesis (Hughes, 1970a), burying depth and siphon size (Zwarts and Wanink, 1989). Energy allocation, is often materialised by a stage and state-dependent trade-off between growth and reproduction (Kooijman, 2000). In bivalves, energy is transformed into tissues such as shell material

(length growth or in thickening of the shell), flesh tissues, and/or gonadal tissues, and is stage-dependent (van der Meer et al., 2005; Cardoso, 2007). Therefore, the patterns of growth and reproduction are the reflection of energy allocation, and depend on the state of individual, its life stage as well as its environment (van der Meer, 2006).

This paper presents original data from Aiguillon Bay (May 2014 - July 2015), on seasonal variations in (1) condition indices (2) burying depth, (3) total biomass as well as key elements for its population ecology: (4) reproduction investment and (5) recruitment. In Aiguillon Bay, predation pressure by red knots *Calidris canutus* and dunlins *Calidris alpina* concentrates on two contrasted periods: during winter months by birds overwintering during an extended period (from September to mid-March, with maximum abundances in December-January), and in spring (April -May) with an intense, but short predation pressure from shorebirds stopping over during their spring migration to their breeding grounds (Delaney et al., 2009; Leyrer et al., 2009; Shamoun-Baranes et al., 2010; Bocher et al., 2012). *S. plana* are swallowed whole by red knots, dunlins but also by black-tailed godwits *Limosa limosa*; while Eurasian curlews *Numenius arquata* and bar-tailed godwits *Limosa lapponica* are able to crop their inhalant siphon. The oystercatcher *Haematopus ostralegus* is the only shorebird spreading out valves to extract the flesh (Zwarts, 1986; Moreira, 1994; Wanink and Zwarts, 2001; Boileau and Delaporte, 2012; Martins et al., 2013; Robin et al., 2013). Although *S. plana* is the most abundant bivalve in Aiguillon Bay, it is a second-choice prey for migratory shorebirds such as the red knot, far behind the tellinid bivalve *Macoma bathica* and the very abundant gastropod *Hydrobia ulvae* (Quaintenne et al., 2010; Bocher et al., 2014b).

Building on previous studies investigating the reasons why some prey are less preferred than others (Zwarts and Blomert, 1992; Zwarts and Wanink, 1993), we investigated factors affecting quality in *S. plana*. Looking closer at differences in quality between the autumn cohort and the spring cohort, the present study revealed the importance of shell mass in seasonal changes in quality. We investigate the reasons underpinning shell mass variations in *S. plana* in relation to the presence of main potential predators, variation in food resource for the bivalve, and temperature. Only correlation with presence/absence and numbers of predators could be proposed, since enclosure experiments, in our study sites, as well as many other studies, proved unsuccessful in revealing the effects of predation on bivalves (“Eléments de dynamique de population de *Scrobicularia plana* (da Costa, 1778) de l’anse de l’Aiguillon (Charente-Maritime, Vendée) sous contrainte de la prédation par les limicoles hivernants”).

The aim of the present study is to understand why the largely dominant bivalve species in terms of biomass and density in our study site (Degré et al., 2006; Bocher et al., 2007) is so little consumed by shorebirds (Quaintenne et al., 2010; Bocher et al., 2014b). The study will apprehend what are the mechanisms/ strategies/ traits that may prevent them from being eaten throughout the seasons. The results of the present study are compared to a recent and extensive comparative study (Verdelhos et al., 2011), so that the life strategy and biomass of this bivalve in our study site can be discussed in contrast with other study sites and compared to other studies in the Bay of Biscay (Bachelet, 1981; Bachelet, 1982; Mouneyrac et al., 2008).

4.3 Materials and methods

4.3.1 Study area

Aiguillon Bay ($46^{\circ}16'29''\text{N}$, $01^{\circ}09'50''\text{W}$) is a large intertidal mudflat (28.7 km^2), located in the Pertuis Charentais in the middle of the French Atlantic Coast (Fig. 4.1). This semi-enclosed bay is of national and international importance for migratory shorebirds (Delaney et al., 2009). In this mudflat, *Scrobicularia plana* is the dominant bivalve in terms of density and the dominant species in terms of biomass (Degré et al., 2006). *S. plana* densities in this area are about the highest recorded in literature, with sometimes more than $3,000 \text{ ind.m}^{-2}$ (Bocher et al., 2007). *S. plana* form a belt on the upper mid-tide level of the mudflat all around the bay (Bocher et al., 2007), recognizable in the field by the star marks of siphons in the surface at low tide.

4.3.2 Shorebird counts

Every month during spring tides, shorebird counts were organized by the Nature Reserve of Aiguillon Bay. Birds were counted directly on the mudflat at incoming tide all around the Bay. All shorebird species were determined and counted.

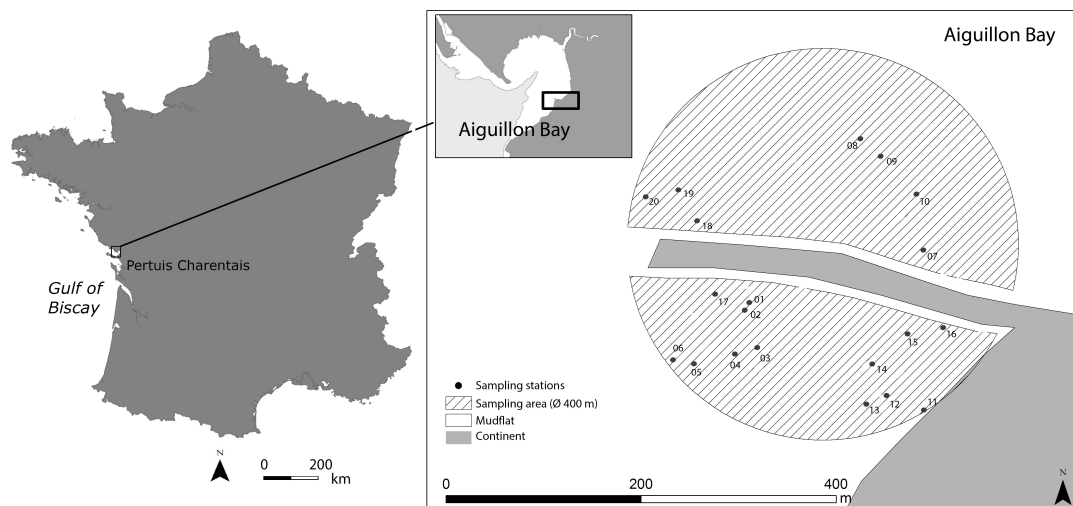


FIGURE 4.1: Sampling site with location in Aiguillon Bay and in France

4.3.3 Temperature

Temperature was measured every month at station N^o7. Three temperature probes (HOBO U23 prov2 data loggers) were inserted in the sediment at three different depths: 0 cm, 2 cm and 10 cm during sampling sessions (*ca.* 2 hours).

4.3.4 Primary production

Chlorophyll *a* (*Chl a*) concentrations were taken as a proxy for primary production, at the surface of the sediment, see Fig. 4.3. Samples were taken in the first 200-300 μm of the sediment in triplicates. Concentration of *Chl a* was determined fluorometrically in 90% acetone extracts using the equations of Holm-Hansen et al., (1965). After extraction and centrifugation (Jouan CR 412, 2000 rpm during 10 min. at 8°C), fluorescence was measured (Turner TD 700). *Chl a* Concentration was calculated using the Lorenzen's equation (Lorenzen, 1967), as described in Dupuy et al., (2015).

4.3.5 Sampling protocol

The data collection was undertaken during 15 months in 20 stations randomly distributed in a 400 m diameter circle area (Fig. 4.1). The sampling design was inspired by Ahmedou Salem et al., (2014) and coring was performed every month

at low tide during the spring tides, using corers of 1/56 m². The fraction accessible to sandpipers (*Calidris canutus* and *Calidris alpina*) was analysed separately (*i.e.* first 4 cm of the sediment core, hereafter referred to as “top” based on Dekinga and Piersma, (1993)).

4.3.6 Determination of macrobenthic densities and biomasses

Macrobenthos was identified to the species level and all molluscs were measured to the nearest 0.1 mm. For *Scrobicularia plana*, the length of the shell was measured, and $AFDM_{flesh}$ (*i.e.* ash-free dry mass of the flesh) was obtained from subtracting ash mass (after burning the samples in crucibles at 550°C in an oven for 4 hours) from DM_{flesh} (after 2.5 days in a 55°C stove) (Bocher et al., 2007). DM_{shell} was obtained after drying shells in numbered egg cartons for 3 days in a 55°C stove. Individuals smaller than 7 mm were only measured, counted and their $AFDM_{total}$ (flesh + shell together) was weighed.

Only individuals larger than 2 mm were kept because in smaller individuals it was impossible even using a binocular dissecting scope to distinguish visually between *S. plana* and *Abra tenuis*.

4.3.7 Quality indices

In shorebird ecology, quality index of prey is commonly expressed as a ratio between a proxy for energy content (*i.e.* the flesh mass, $AFDM_{flesh}$) and the ballast content (*i.e.* shell mass DM_{shell}), see section 2.4, van Gils et al., (2005c). In order to achieve a better estimation of the energy available in a mollusc for shorebirds, energy density and assimilation rate are included in the calculation. Energy density and assimilation rate are assumed to be constant whatever the species and equals respectively 22 kJ.g⁻¹ (Zwarts and Wanink, 1993) and 0.8 (Piersma, Verkuil, and Tulp, 1994). $Q = (AFDM_{flesh}(g)/DM_{shell}(g)) \times 22 \text{ KJ.g}^{-1} \times 0.8$

However, this ratio does not capture the relative contribution of the soft mass and shell mass, which are important for the assessment of body condition in bivalves. Therefore, a flesh mass index (FMI), and a shell mass index (SMI) was calculated for each individual larger than 7 mm:

$$FMI = AFDM_{flesh}(mg)/length^3(cm)$$

$$SMI = DM_{shell}(mg)/length^3(cm)$$

Because shell mass and flesh mass were extrapolated for recruits (see section 2.4), quality indices were calculated only for juvenile larger than 7 mm and adults (>

17 mm).

4.3.8 Reproduction investment

Reproduction investment describes the energy allocated to reproduction (mainly through building gonadal tissues) and was measured using maturation stages (Caddy, 1967; Zwarts, 1991; Mouneyrac et al., 2008; Santos et al., 2011a). Maturation stages were determined by visual inspection using a binocular dissecting scope. Scores were given to each individual depending on the relative importance of the gonads (as a fraction of the digestive gland covered by gonad tissues): (0) gonads absent, (1) undifferentiated ($\frac{1}{4}$ or less), (2) developing ($\frac{1}{2}$), (3) ripe ($>\frac{3}{4}$), or (4) absent after spawning. Individuals larger than 17 mm were referred to as adults considering that the smallest individual with a reproductive stage > 1 measured 17 mm. An individual with a reproductive stage > 2 was considered reproductively active since its gonads were developing.

In reproductively active individuals, gonadal tissues were separated from somatic tissues, and their respective ash-free-dry mass ($AFDM_{gonad}$ and $AFDM_{somatic}$) were determined (see protocol in section 2.4). A gonado-somatic ratio was calculated (GSR) using the following equation: $GSR = AFDM_{Gonad} / (AFDM_{Somatic} + AFDM_{Gonad})$. The assessment of the percentage of individuals that are reproductively active in the population, as well as the gonadic status and gonado-somatic ratios are common tools for assessing reproduction investment in this bivalve species (Sola, 1997; Rodriguez-Rúa et al., 2003; Mouneyrac et al., 2008; Verdelhos et al., 2011; Santos et al., 2011a).

4.3.9 Determination of life stages

Results are presented depending on life stages: recruits, juveniles and adults. Recruits were defined as individuals smaller than 7 mm, for which flesh and shell were not separated and quality not assessed. Juveniles were defined as individuals with sizes ranging from 7 to 17 mm, sizes that were ingestible by red knots *Calidris canutus*. Adults were defined as individuals potentially able to reproduce, and comprised all individuals larger than 17 mm (see Section 4.3.8).

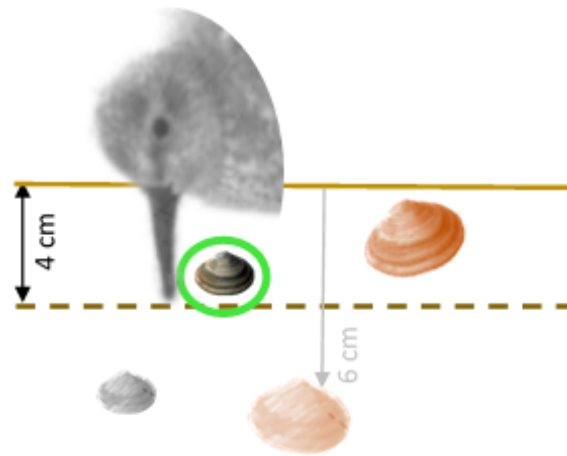


FIGURE 4.2: An available *Scrobicularia plana* individual for red knots (*Calidris canutus*): accessible (not blurred) and ingestible (over-sized individuals in red)

4.4 Results

Temperatures at the mud surface followed seasonal trends and increased in spring to reach a maximum in July (about 30°C in July 2014, Fig. 4.3). Temperatures at depth appeared more stable, with lower values in summer and higher values in winter relative to the surface, suggesting sediment to act as a buffer from temperature variations. Chlorophyll a concentrations reached a peak during winter months, with more than 120 $\mu\text{g/g}$ in February 2015. Numbers of red knots

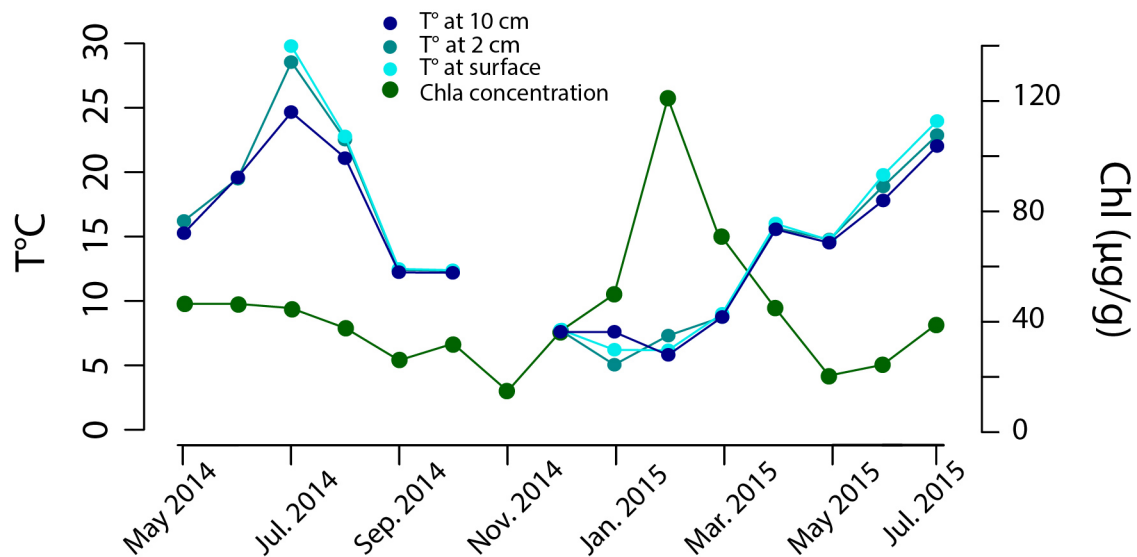


FIGURE 4.3: Monthly variations in temperature (in °C, at three different depths in the sediment: 0, 2 and 10 cm, station 7) and monthly variations in Chlorophyll a density ($\mu\text{g/g}$) in Aiguillon Bay (mean value between the two stations sampled, stations 3 and 14).

Calidris canutus and Dunlins *Calidris alpina* depicted seasonal trends linked with their migration cycle and their population (Fig. 4.4). They are found in high numbers in April/May and in winter (from November to January included, from

January 2004 to December 2015). They were rare in June and July, during the breeding period.

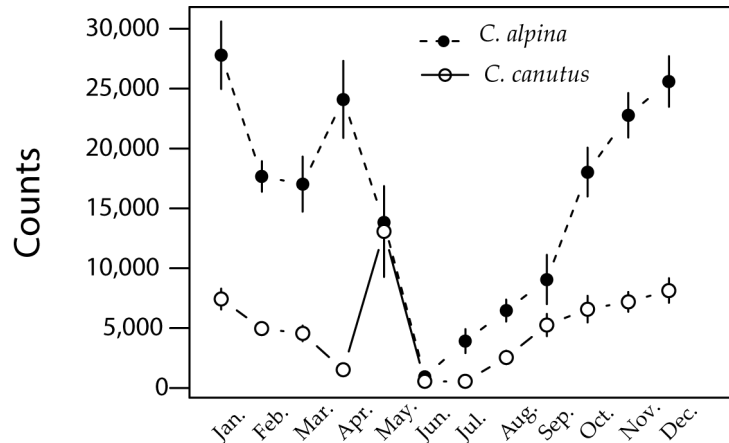


FIGURE 4.4: Seasonal variation of *C. alpina* and *C. canutus* mean counts between 2004 and 2015 in Aiguillon Bay, with associated *s.e.*

Together with biomass density and quality, flesh mass index of adults *S. plana* increased at the beginning of spring and decreased during summer and winter months (Fig. 4.5). Adults were found in majority in the top 4 cm of the sediment only in July 2014 and July 2015. Reproductive investment (measured through the density of reproductively active adults, see section 2.6) seemed to extend from April to August with a slowing phase in July 2014 and a stop in July 2015 (Fig. 4.6), unfortunately April 2014 and August 2015 were not sampled to confirm this reproductive pattern. This two-phase reproduction investment protracted along 5 months led to the emergence of two cohorts during the study period as represented by the presence of recruits in October 2014, and May 2015 (Fig. 4.7). In spring 2015, recruitment was two times higher than in autumn 2014 and clearly much higher than in spring 2014. Recruits were found always in majority in the top 4 cm of the sediment, accessible to the shorebirds (Fig. 4.7).

The accessible fraction of juvenile *S. plana* (7-17 mm) varied between *c.* 40% and *c.* 100% depending on months, with lowest values between December 2014 and March 2015 and highest values between April and September 2014 or 2015 (Fig. 4.8). Flesh mass index increased in the beginning of spring, while quality decreased in the same period, together with shell mass index.

Quality in juvenile *S. plana* varied seasonally between *c.* 1.83 and 5.19 KJ.g^{-1} (Fig. 4.8). Quality values were not significantly different between the accessible fraction and individuals found in the bottom, except between October 2014 and December 2015 when individuals from the bottom were in better condition than individuals from the top (Kruskal-Wallis test, $p\text{-value} < 0.05$).

ADULT SCROBICULARIA PLANA ≥ 17 mm

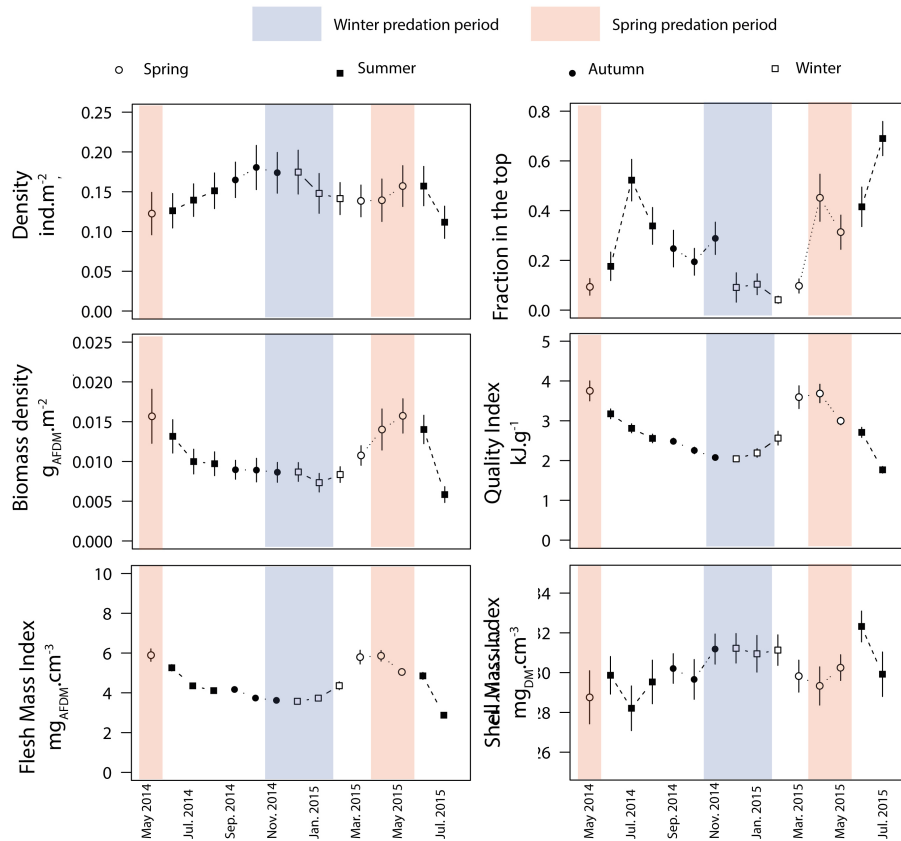


FIGURE 4.5: Seasonal dynamics of abundances, biomass densities, condition indices (*i.e.* Flesh mass index, Shell mass index and Quality), and accessibility of adult *S. plana* in Aiguillon Bay (May 2014 - July 2015)

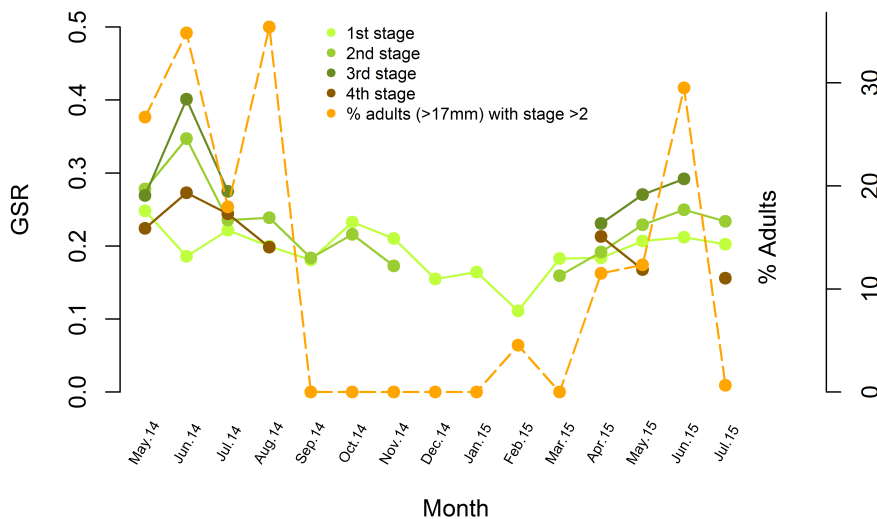


FIGURE 4.6: Percentage of the adult population with developing gonads, and associated Gonado-somatic ratio depending on reproductive stages for *S. plana* individuals in Aiguillon Bay (May 2014 - July 2015)

Quality of juvenile individuals in April-May 2015 was higher than quality of

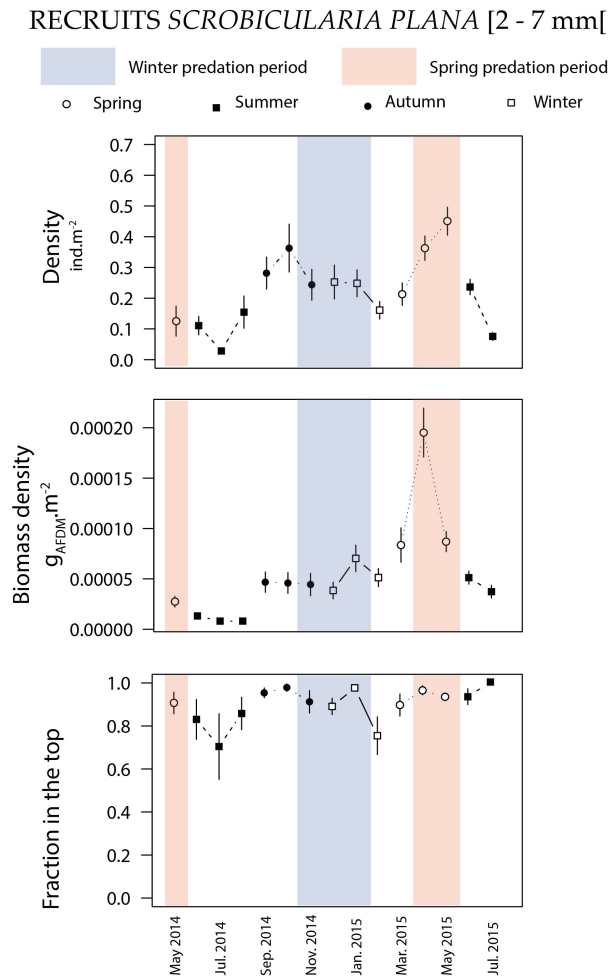


FIGURE 4.7: Seasonal dynamics of abundances, biomass densities and accessibility of recruits *S. plana* in Aiguillon Bay (May 2014 - July 2015)

available individuals in winter months (December 2014-March 2015) and summer months (July, August, September 2015) (Kruskal-Wallis test, p -value < 0.05), except for individuals with shell length of 7 and 8 mm (Kruskal-Wallis test, p -value > 0.05) (Fig. 4.9). When decomposing quality (flesh-to-shell ratio) into two of its major components (*i.e.* $AFDM_{flesh}$ and DM_{shell}), results showed higher shell masses for the summer and the winter individuals compared with the spring individuals (Kruskal-Wallis test, p -value < 0.05) (Fig. 4.9), except for individuals with shell lengths of 7, 8 and 14 mm. Concerning flesh masses, no significant differences appeared depending on the season (Kruskal-Wallis test, p -value > 0.05), Fig. 4.9.

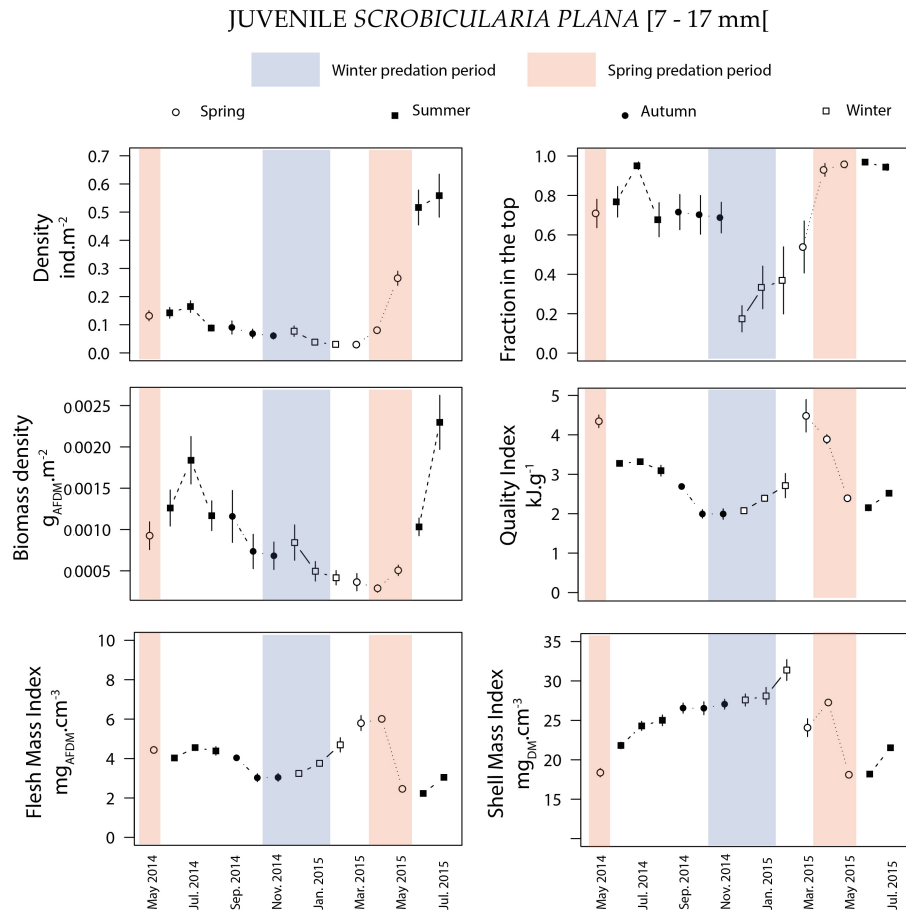


FIGURE 4.8: Seasonal dynamics of abundances, biomass densities, condition indices (*i.e.* Flesh mass index, Shell mass index and Quality), and accessibility of juvenile *Scrobicularia plana* in Aiguillon Bay (May 2014 - July 2015)

4.5 Discussion

Scrobicularia plana is the dominant species in terms of density and biomass in Aiguillon Bay (Bocher et al., 2007). However, it is one of the less preferred prey in the diet of shorebirds in this area (Quaintenne, 2010; Robin et al., 2013; Bocher et al., 2014b). Seasonal variations in quality for the burrowing bivalve *S. plana* were investigated, in relation to life stages, season, burial behaviour and environmental variables (primary production, temperature and presence of shorebirds). Results revealed different seasonal dynamics in adults, juveniles and recruits that could be linked with environmental variables, including the presence/absence of predation pressure. Results concerning reproduction and density of juveniles reveal the recruitment of two cohorts per year during the study period. The present study revealed contrasted availability, accessibility and quality of size categories under risk of predation in spring or winter by shorebirds in Aiguillon Bay, especially for juveniles from different cohorts.

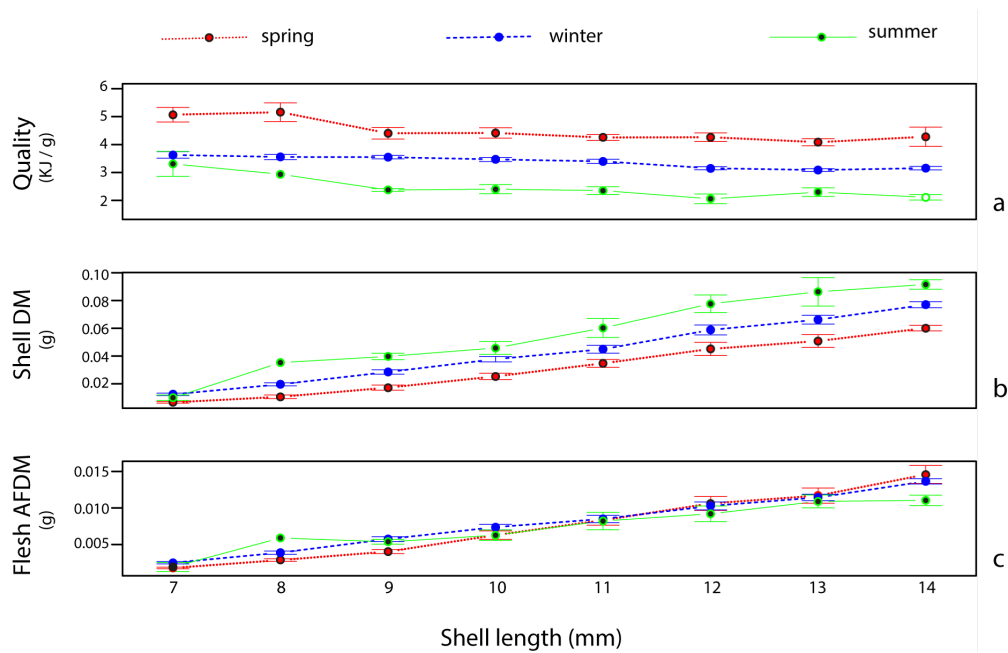


FIGURE 4.9: Contrasted results between a) mean quality ($\text{KJ}\cdot\text{g}^{-1}$) of available *S. plana* per size class and its two components: b) shell dry mass (g) and c) flesh ash free dry mass (g) for spring (April and May 2015) summer (July, August and September 2014) and winter (December 2014 and January 2015)

To our knowledge, reproduction and recruitment had never been described before for *S. plana* in our study area. Reproduction investment revealed a protracted reproductive investment and spawning in *S. plana* in Aiguillon Bay in 2014. Spawning took place in spring and in early autumn, as it was observed in Tunisia in a previous study (Casagranda and Boudouresque, 2005). Only individuals with a shell greater than 17 mm underwent sexual development, a result that is consistent with all other studies (Sola, 1997; Guerreiro, 1998; Raleigh and Keegan, 2006). Reproduction investment was responsible for body mass differences in adults during spring and summer, as shown in Zwarts, (1991). These variations had no direct effect on the resources available for sandpipers (because adults are too large to be swallowed whole) but were responsible for two recruitment events in the study period: in autumn 2014 and in spring 2015. When larvae settle after one or two months depending on temperature (Santos et al., 2011b), two recruitment periods can occur, one in spring (in April-May) and the other one in autumn (in October for 2014), Fig. 4.10.

Therefore in Aiguillon Bay, as in other estuaries or intertidal mudflats of the southern part of its distributional area, *S. plana* experiences a protracted reproduction investment (Sola, 1997) with two major spawning events at the beginning of spring and in summer (Casagranda and Boudouresque, 2005; Rodriguez-Rúa et al., 2003; Bachelet, 1982), Fig. 4.6. Adults invest in a long reproduction

investment with a slowing phase in July (adults may suffer due to high temperatures and potential hypoxia, they reach the surface of the sediment and then their quality indices decrease, possibly causing a decrease in biomass densities). Depending on the study and place (*i.e.* latitude), one uninterrupted settlement period of 6 months was observed, or two separate settlement periods (Santos et al., 2011a). *S. plana*'s ecological patterns and life strategies are latitude-related (Essink et al., 1991; Verdelhos et al., 2011): high densities are characteristic of southern populations such as in Aiguillon Bay, as well as rapid growth and longer reproduction and spawning periods, long life and higher productivity. The results of the present study confirm Aiguillon Bay is located in optimal ecological conditions for this species (between 40 and 45 ° N, Verdelhos et al., 2011). In Aiguillon Bay, an extended spawning period yielded two cohorts in the same year just as it was described in the Gironde Estuary before (Bachelet, 1982) and other regions as well (Hughes, 1970b; Worrall and Widdows, 1983; Essink et al., 1991).

This study also revealed important seasonal variations in the accessibility of *S. plana* to shorebirds in correlation with temperatures. This can be partly explained by the buffering properties of sediment against extreme temperatures, since *S. plana* is sensitive to winter conditions (Zwarts and Wanink, 1989). A study showed *S. plana* was sensitive to high summer temperatures as well, above a temperature of 30.75 °C respiration was abnormal (Hughes, 1970a). Such high temperatures were attained in July at the surface in our study sites but never measured at depth 2 cm and 10 cm in the mud, illustrating the insulating properties of the mud.

After settlement, siphoned juveniles grow at a rate that is dependent on temperature and feeding resources (Santos et al., 2011b), therefore the two cohorts may evolve differently (Fig. 4.10). When they are recruits (*i.e.* in the present study, 2-7 mm), due to their relatively short siphon, they have no choice but to live in the first centimetres of the sediments in order to have access to food resources, as revealed by the present study and earlier studies: Zwarts and Wanink, (1989) and Zwarts et al., (1994). When these recruits grow and reach what is called juvenile stage (in the present study, sizes ranging from 7 to 17 mm), with preference for individuals smaller < 14 mm (Quaintenne et al., 2010), they are potential prey for *C. canutus* and *C. alpina*, especially during winter and spring predation months. Our study revealed that these potential prey for shorebirds presented variable traits depending on the season, and on the cohort. These traits may result from different strategies and could help us explain why *S. plana* is so little consumed by shorebirds. First, they are not present in similar numbers during spring and

winter predation, despite comparable initial densities of recruits. Indeed, the autumn cohort only yielded a couple of individuals between 7 and 14 mm during winter (which could be the consequence of high mortality of recruits or slow growth). In contrast, the spring cohort yielded important densities of available individuals, especially in late spring 2015.

Our results also highlighted important differences in burial behaviour between the spring cohort (nearly all the ingestible individuals are found in the top) and the autumn cohort (half of the good-sized individuals are buried more than 4 cm deep in the sediment). Burial behaviour in winter was consistent with literature reports (Zwarts and Wanink, 1991; Zwarts and Wanink, 1993). Winter mortality in young spat is commonly observed as spat usually live within the first 5 cm of the mud surface due to their reduced siphon size, which makes them more vulnerable to extreme temperatures, wave action and predation (Hughes, 1970a; Ruiz, Bryan, and Gibbs, 1994; Casagrande and Boudouresque, 2005). We could illustrate the fact that burrowing in winter positively influences the quality of juveniles at a moment of the year when predation pressure is high and temperatures are low. These differences in density and accessibility can explain why *S. plana* is so little consumed in winter in our study site: the good-sized prey are rare, and half the few prey ingestible for red knots are not accessible. The quality of juveniles in winter is also lower than in spring, due to thicker shells (Fig. 4.9). In the light of these results, it appears obvious why overwintering sandpipers do not select the rare, inaccessible and relatively lower-quality prey *S. plana* when other prey in the system (e.g. *Hydrobia ulvae*, *Macoma balthica*) are present (Zwarts and Blomert, 1992).

However, when we analysed the spring cohort, *S. plana* appeared much more attractive for sandpipers stopping over during their spring migration. First of all, densities were higher (especially when we consider the spring 2015 recruitment event), with important numbers of *S. plana* reaching ingestible sizes as early as April and May 2015. Secondly, these ingestible individuals are accessible, and nearly a 100% were found in the top 4 cm of the sediment, in the scope of a sandpiper's bill length. Therefore, ingestible individuals were nearly always accessible even under intense predation in that season in our study site (Shamoun-Baranes et al., 2010). Burial is considered as a trade-off between feeding and being fed upon, the so-called "asset-protection principle" (Clark, 1994). This trade-off could explain why these spring juvenile individuals faced the risk of predation to stay in the top of the sediment: in order to have better access to food with their siphons. Earlier studies revealed growth is accentuated during

the first two years in *S. plana*, with individuals reaching 18 mm the first year, outgrowing gape size for shorebirds (Bachelet, 1982). Indeed, net growth efficiency (production 100/assimilation) was proven to be much larger in smaller individuals and decreasing as the animal gets larger (Hughes, 1970a). We hypothesize that spring juvenile *S. plana* invest in growth (length) at the detriment of shell mass to outgrow predation as soon as possible.

When considering the factors influencing quality (*i.e.* shell mass and flesh mass), results revealed that quality differences observed between the autumn 2014 and spring 2015 cohorts were mainly explained by shell mass variations (Fig. 4.9). The scarcity, inaccessibility and bad quality of the prey could explain why *S. plana* are absent from red knots winter diet in this area. However, in spring, good-sized individuals are numerous, accessible and of relatively high quality (with a thinner shell). We question whether thin shells of available *S. plana* individuals can constitute a defensive strategy during spring predation, even though they can be described as “high quality” prey. We hypothesize that such a thin shell would be potentially harmful to the birds since broken the shells present sharp edges which may cause injuries to the bird’s digestive track. Diet choice experiments are needed to test for this hypothesis, as well as experiments assessing the impact of predation on shell mass. Based on our results it is possible that *S. plana* would respond to predation by enhanced growth rates and thinner shells, as opposed to another prey in the system: *Macoma balthica* (Zwarts and Blomert, 1992).

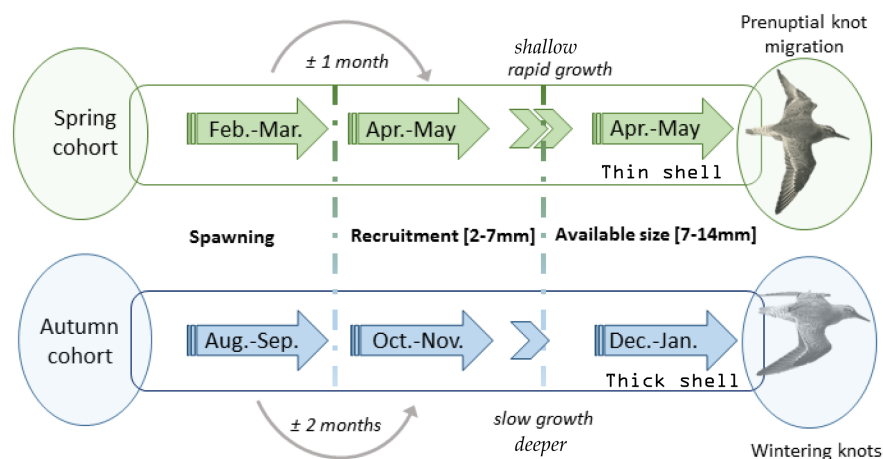


FIGURE 4.10: Scheme illustrating development trajectories of *Scrobicularia plana* cohorts until they reach available sizes for migrating red knots *Calidris canutus* in spring or winter in Aiguillon Bay, based on the results and literature (Santos et al., 2011b)

4.6 Acknowledgements

The benthos sampling in Aiguillon Bay and sorting of samples was only possible with the precious help of volunteer interns and staff of our laboratory. Sampling authorisation was provided by the French Ministry of Environment. Financial support was received from the Région Poitou-Charentes through a PhD grant. We thank anonymous reviewers for their insightful comments and suggestions.

Box 2

ANTI-PREDATION TRAITS IN MARINE MOLLUSCS

Marine molluscs are among the most ancient living animals on earth, and appeared more than 500 million years ago. This phylum has survived multiple dramatic events certainly thanks to their diversity (*The conservation biology of molluscs. Including a status report on molluscan diversity*, Fig. 4.11), and can resist a lot of threats including predation.



FIGURE 4.11: Shells and molluscs, illustration (Illustré, 1897)

The effects of predation are commonly exemplified by the direct lethal effects of predators on their prey. However there is a wide range of more subtle effects of predation pressure on their prey, and they can be apprehended through the study of anti-predation traits. Anti-predation traits can be defined as inducible defenses or particular features (either physical or behavioural) that an animal develops in response to predation pressure and which constitute an adaptive advantage (Harvell, 1990). Molluscs are ideal candidates for the study of anti-predation traits since they

show an extraordinary wide range of defensive traits. They have been favourite models for anti-predation and natural selection studies since predator attempts (from fish, birds, or human beings) can leave marks that are observable on their shell directly, sometimes in the long-term (fossil records give tools to put these traits into an evolutionary perspective, Vendrasco et al., 2011). For conciseness and because they represent the vast majority of examples of mollusc antipredation-traits in the literature, this small review concentrates on marine molluscs exclusively. There are two principal challenges to such a study: identify only those traits that are adaptive responses to predation and categorise them as to best illustrate their diversity. In the present insert, these anti-predation traits are presented as a list under different phenotypic constituents: morphology, development, behaviour, biochemistry (and physiology) and phenology (Dugatkin 2004). Examples from literature are given.

- MORPHOLOGY

Shape : Predator prey interactions shape the diversity of animal form (Vermeij, 1982, 1987; 1995) through selection pressure or adaptation. Shape can influence handling time for instance, a round and small shell being harder to manipulate (Emerson, Greene, and Charnov, 1994).

Size : The notion of size-refuge has been introduced by Vermeij, (1982) and applies to many organisms, including molluscs. A mollusc can be too big vs. too small. When it is too small, it is detrimental to predators that manipulate prey (and increase searching and handling times); when it is too large, it is detrimental mostly for shell-breaking predators such as birds and fishes (Palmer 1978), since predator can not swallow them. Together with size, globosity also plays a role since it is the circumference rather than the size that determines if a prey can be swallowed (Zwarts and Blomert, 1992).

Shell strength / shell thickness : In the literature shell thickness is often mixed up with shell strength. Both traits are linked together as shell thickness increase shell crushing resistance (like in *Anadara trapezia*, Wright et al., (2012) or the blue mussel *Mytilus edulis*, Leonard, Bertness, and Yund, (1999)). Enhanced thickness has been proven to be a response to predation for example in *Nucella lapillus* (adapting to increasing number of shell-breaking predator *Carcinus maenas*, Vermeij, 1982) and also in the fluted giant clam (*Tridacna squamosa*, Neo and Todd, 2011) where the presence of crabs enhanced thickness. However a thin shell can be deterrent to predators as well, as sharp edges could damage predators (maybe *Scrobicularia plana* see Chapter 5, and even bivalves like oysters *Crassostrea gigas*, or fan mussels *Atrina fragilis*, that are easily breakable).

However this constitutes more a defensive advantage than an adaptive response to predation since no experiment showed reduced shell thickness as a response to predation, to our knowledge. Most probably it is linked with a rapid growth, maybe itself a way to prevent being eaten (see hypothesis in Chapter 5). Shell thickness and apertural width were also key anti predation traits in *Littorina rudis* and *L. Nigrolineata* (Elner and Raffaelli, 1980) and *Nucella lamellosa* (Hughes and Elner, 1979). Predators can induce amplification of tooth development (Appleton et al 88), which thickens the apertural lip and reduces vulnerability to predators (Appleton and Palmer, 1988).

Pigmentation : Camouflage can be an excellent way to avoid being seen by a predator. Sometimes induced by epibionths via settlement among lamellae or spines (Feifarek, 1987), pigmentation can also be characterized directly by patterns on the shell, and appears more genetically driven (Appleton and Palmer, 1988).

External sculpture : Ornamentation (like stout spines or nodes) is among the most striking anti-predation trait that was studied. Spine growth and length is highly variable including between individuals of the same species, suggesting its flexibility and early interpretation as a physical defense against predation (Stanley, 1970). These external sculptures are detrimental to animals that handle and break shells, such as fishes, rays, and birds.. They act in different ways to injure the predator and protect the prey (Palmer, 1979).

- (co)DEVELOPMENT & PHENOLOGY

Phenology : Phenology (e.g. generation rate, growth, seasonality of recruitment) allows prey to mismatch their predator's presence (for instance migration waves of shorebirds), but has not been proven to be an adaptive trait in molluscs yet. Like for other invertebrates, phenology can be essential for the survival of populations (see the example of growth below). Because it reduces individual vulnerability, marine invertebrates often have large population sizes during their early life stages. The phenological trait of aggregation allows them to survive in sufficient numbers and develop (De Vito, 2003).

Growth : For invertebrates, the energy uptake is mainly invested in reproduction or allocated to growth (Nakaoka, 2000). There is always this choice to make between stressing defensive traits against growth or reproductive success. Usually, predator induces a slower growth because molluscs invest more energy in escaping from predation. The rate of

growth induces large consequences on the morphology of the shell (Appleton and Palmer, 1988). Some molluscs survive by outgrowing their predators (*i.e.* they reach a size refuge that protects them from predation, Ray-Culp, Davis, and Stoner, 1999; Paine, 1976; Whetstone and Eversole, 1981; Jensen and Jensen, 1985). It is hard to test whether growth (or phenology) is an adaptive response to predation (it would require growing molluscs in control conditions and making them reproduce, which is a hard piece of work), but it is obviously a defensive advantage.

Facultative mutualism: Mutualism is a win-win scenario where two individuals benefit from each other. In the spiny bivalvia *Spondylus americanus*, spines favour the settlement of epibionts, which were shown to reduce mortality from predators via concealment (Feifarek, 1987). Here again, this strategy protects the prey from the predator, but has not been characterised as adaptive.

- BEHAVIOUR

Migration : Molluscs can escape predation by migrating horizontally and vertically in the sediment. Horizontal migration (*e.g.* migrating lower in the tidal zone), can prevent individuals of certain developmental stages from being eaten by shorebirds at low tide on intertidal areas, like in *Macoma balthica* (Beukema, 1993b), this strategy is coupled with phenology. Most commonly, migration is vertical and individuals burrow in the sediment to escape predation (*e.g.* *Mercenaria mercenaria* under predation by sea stars, Doering, 1982).

Inking : Alarm signals, see section “Biochemistry, Physiology”.

Valve closure and aperture occlusion: Soft tissues are the weak point of molluscs, and what predators are seeking. Under predation pressure by shore crabs *Carcinus maenas*, *Littorina saxatilis* and *Littorina obtusata* showed smaller aperture opening (linked to thickening of the shell (Johannesson, 1986; Edgell et al., 2008). This defense mechanism is common in gastropods in order to defend themselves from crabs inserting their claws in the aperture (Appleton and Palmer, 1988).

Soft-tissue withdrawal : Withdrawal of soft tissues is common in molluscs. When passed over by a shadow, the giant clam protects its mantle (Neo and Todd, 2011); under predation by *Carcinus maenas*, *Littorina obtusata* hides into its shell (Edgell et al., 2008).

Crypsis : Some molluscs, like Cephalopods can mimic fishes (mixing behaviour with morphological traits such as pigmentation and shape) in order to fool potential predators, such as *Octopus insularis* (Krajewski et al., 2009),

and many other cephalopods adopt camouflage and mimicry (Hanlon and Messenger, 1998; Hanlon, 2007). Nocturnality has also been described, for example in giant cuttlefish *Sepia apama* (Hanlon et al., 2007), in association with a sessile behaviour.

- BIOCHEMISTRY, PHYSIOLOGY

Adductor muscle: To enhance resistance to shell opening a larger adductor muscle is an advantage (e.g. *Anadara trapezia* in Wright et al., (2012), Blue mussel in Reimer and Tedengren, (1996)). The development of a larger muscle is the result of a behavioural response of valve closure, through development, and a physiologic advantage.

Mucins : Mucins covers a wide range of secretions, particularly varied in the “slimy” Mollusca phylum. Prezant has summarized the subject nicely in a study entitled ‘Molluscan mucins: a unifying thread’ and presents the multiple advantages of mucins (e.g. locomotory lubrication, nacre formation, paralytic secretion, byssal attachment etc.), (Prezant, 1985). Of course these mucins are often the first responses to waterborne predator cues, even before the muscles or shell is adapted to the thread.

Alarm signals : Inking is the most famous alarm signal among marine molluscs (although it is principally a defensive tool to hide from the predator). Not only cephalopods secrete ink as a response to stress, also sea hares do (e.g. *Aphysia californica* Derby, 2007). Inking can act in a variety of ways: an alarm signal, which could act chemically or through a visual modality, however in sea hares there are evidence that their action is essentially chemical. Other *Aphysia* secretions were proven to diminish their predator’s appetite (reviewed in Carefoot, 1987, and Johnson and Willows, 1999). Communication is, in most cases, induced by waterborne cues such as for the giant clam, or by chemicals in sea hares (Fiorito and Gherardi, 1999; Nolen et al., 1995), they induce escape responses in conspecifics, and sometimes even other species. The reception of waterborne predation cue or cues of damaged conspecifics have a phylogenetic basis (Fässler and Kaiser, 2008), therefore cues given by a group of animal can be decrypted by other closely related taxa (Derby, 2007).

Repulsion : ‘skin and mucus of snails can deter predatory attacks because they contain distasteful and deterrent compounds, some of which have been identified’, quoted from (Derby, 2007). Numerous studies have revealed the existence of chemical deterrents in the mucus, or the skin composition. Some of these deterrents have toxic effects, all are a response to disturbance or

stress, but only few studies have explained how they might constitute a defensive trait from predation.

These defensive traits correspond with a list of torturing techniques of predators: shell-peeling, shell-drilling, shell-breaking, shell-crushing, shell-cutting, flesh-pulling. Another vibrant example is the technique used by starfishes which directly insert their stomach in the shell of bivalves after opening them (Norberg and Tedengren, 1995). Faced with a diversity of dangers, marine molluscs have developed extremely diverse defenses. Most of these traits are flexible, and can be indicators of environmental change and ecological state (Compton et al. 2016) and have consequences for predators. In response, predators can adapt to the morphology, behaviour or phenology of their prey and can suffer from increased handling, digesting, metabolic and searching costs at the expense of their energy intake rate.

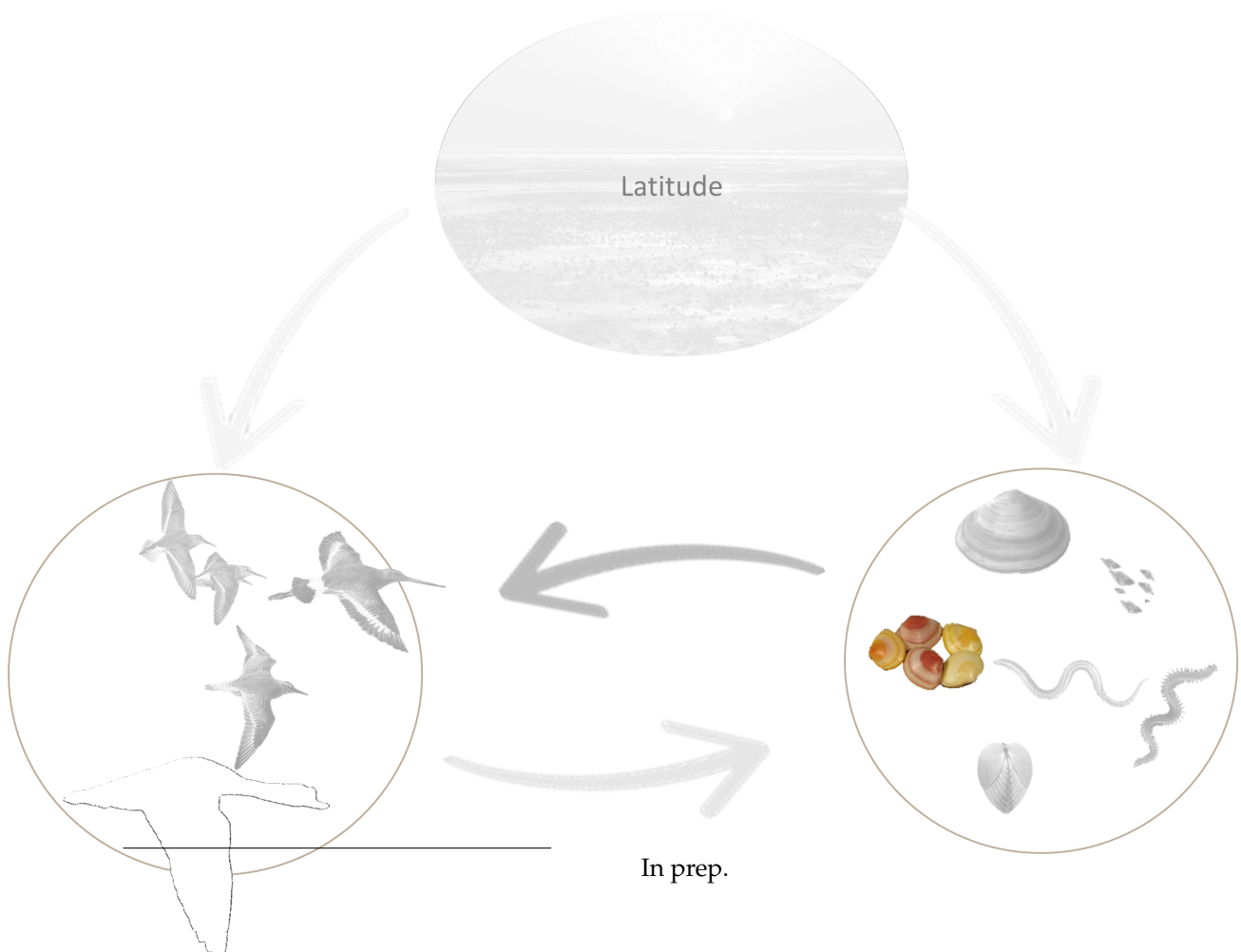
Very few traits are known to offer a selective advantage when faced with predation (Liew and Schilthuizen, 2014), among them some are adaptive. For instance, shell thickness could be the simple result of slower growth due to poor feeding conditions, or a trait inherited through evolution and not necessarily an adaptive response to shorebird predation. This short review highlighted the interplay between various phenotypic constituents, as defensive traits can cascade up from behaviour to physiology, and shape. Anti-predation traits must be comprised in an ecological context where many factors (*e.g.* food resources, temperature, light) influence the response of a prey to its predator. These predator-prey interactions can be modified or weakened by ecological changes such as invasions or climatic changes, and are involved in so-called 'trait-mediated interactions': "*Trophic interactions in ecological communities not only affect consumer-resource densities, but also induce phenotypic responses that can ripple through a food web to influence prey resources, competitors and other predators*", quoted from Kamiya and Poulin, (2012). In ecology, it is sometimes hard to categorise, isolate facts, and distinguish between adaptation and evolution; the study of defensive traits in marine molluscs is therefore a real scientific challenge.



Chapter 5

Death toll at the edge of a distribution area: *Macoma balthica* secondary production in a southern estuarine mudflat

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5.1 Abstract

The Baltic tellin is a common infaunal bivalve in soft-bottom intertidal mudflats in the northern hemisphere. The eastern Atlantic population spreads over a large latitudinal range from Norway to the South-Western coasts of France, and is found both in marine and estuarine mudflats. Production of the infaunal bivalve *Macoma balthica* was assessed based on 11 years of data, at the southern edge of its distribution: Aiguillon Bay (AB). Using the approach of van der Meer et al. (2001) the relative influence of the components of production (*i.e.* recruitment, survival and mass at death) was estimated for 8 consecutive cohorts (2004-2011). Results revealed high interannual variability in recruitment, as well as density-dependent negative effects on mortality and mass at death. Across all cohorts, 64% of the individuals died within their first year and did not grow larger than 10 mm. Recruitment was positively correlated with secondary production and accounted for most of its variability. Results were compared with similar ecosystems in the Dutch Wadden Sea (WS) at the centre of their distribution area. Comparable secondary production values between AB and WS were the results of different underlying processes and population dynamics. Over all sites, recruitment was higher in AB but individuals showed much lower survival after 1 year, resulting in comparable values of secondary production for a given cohort after growth had taken place. Results and literature suggest this lower longevity to be more the consequence of less suitable habitats (AB is a very muddy area comparable to the Dollard Estuary, located in the Wadden Sea) than the consequence of low recruitment or lower latitude. Together with higher mortality in early life stages, higher recruitment in macrofauna species could be the signature of populations on the edge of their distribution (particularly the edge closer to lower latitudes),

as revealed by several studies.

5.2 Introduction

Intertidal mudflats are variable ecosystems under the influence of many parameters operating at various spatio-temporal scales: inundation time, primary production, seasons (*e.g.* via temperature changes, or densities of migratory shorebirds), sediment dynamics, anthropogenic pressure *etc.* (Ysebaert et al., 2002; Elliott, 1980; Wilson and Elkaim, 1991). Therefore, their inhabitants, including infaunal macrobenthic invertebrates, do suffer from important spatiotemporal variations in their distribution and abundance, even if sometimes tempered by relatively flexible phenotypes (Scapini, 2014) and density-dependent effects (Wilson, 1983).

Together with the assessment of biomass variability or P\B ratio, the study of secondary production was proposed in many benthic studies, providing a better understanding of the population dynamics of invertebrates (Bachelet, 1982). Secondary production is a measure of the biomass production in heterotrophs and corresponds with the energy or material flow within one community or population (Thienemann, 1931). For benthic invertebrates, secondary production variability is the result of the combination of varying demographic parameters such as mortality (*inc.* depletion), growth (Zwarts and Wanink, 1993) but seems to be primarily driven by recruitment variability (van der Meer, Beukema, and Dekker, 2001).

Recruitment refers to the abundance of the zero-year class at the first sampling occasion, *i.e.* at the end of their first winter for *Macoma balthica* (from van der Meer, Beukema, and Dekker, 2001). Recruitment is highly variable in time and space, and probably responsible for the patchiness of benthic macrofauna in intertidal ecosystems (Eleftheriou, 2013; Underwood and Denley, 1984).

For many marine invertebrates, survival in the first life stages is lower than during the adult phase, as recruitment success (*i.e.* survival of the recruits into the adult population) suffers from a wide range of parameters including predation, climate, larviphagy and sediment dynamics (Malham, Hutchinson, and Longshaw, 2012). Survival is expressed as the amount of individuals of a given cohort that survived at a given time, divided by the size of the cohort at age 0.

For survivors, growth can be expressed as the increment of soft-tissue biomass of an individual during a given period of time. During its lifetime, an individual flesh mass equals the initial body mass (mass at recruitment) plus its growth increments, year after year. When decomposed, recruitment, survival and growth of a cohort shed light on the various processes responsible for the variability of secondary production.

Some studies revealed density-dependent mechanisms to play a negative role in secondary production via reduced growth (Olafsson, Peterson, and Ambrose, 2014) and survival rates (*e.g.* via predation, Seitz et al., 2001), in particular during juvenile stages when the population is dense. However, understanding these density-dependent mechanisms and their effects on long-term secondary production can only be achieved via the study of its three major components together (*i.e.* recruitment, growth and survival, van Straalen, 1985; Aldenberg, 1986). Usually, studies concentrate on only one or two aspects, and are over a limited number of sampling years. There are only rare studies that propose to decompose secondary production through its various components, and analyse their variability and covariance on long-term datasets with consistent measures of density, biomass and length -or age- (van der Meer, Beukema, and Dekker, 2001, van der Meer et al., *in prep*).

The present study focuses on the Baltic tellin *Macoma balthica*, a common suspension and deposit-feeder and can be found in a variety of substrates from sandy to muddy marine sediments (Kraan et al., 2010a; Compton et al., 2009), from the intertidal to the subtidal area (Dekker, 1989). It is one of the most studied wild bivalve species, because of its biogeographical history (Becquet et al., 2012), and its importance in the trophic web (Zwarts and Blomert, 1992; Hiddink, Hofstede, and Wolff, 2002), but also for its flexibility (Reading and McGrorty, 1978; Zwarts, 1991; Beukema, 1993a; Compton et al., 2016). In the present study, we decompose the variability of secondary production of *M. balthica* into its various components, following a pre-existing methodology (van der Meer, Beukema, and Dekker, 2001, van der Meer et al., *in prep*), using the removal-summation method (Crisp, 1984). Based on an 11-year dataset (Philippe et al., *under revision*, Chapter 3), 8 consecutive cohorts were followed from recruitment until their fourth year. Recruits correspond with individuals with no rings and were measured after the settlement process, in a reproducible way in time and space. In *M. balthica*, since age classes can be determined using annual rings, cohorts are easily identifiable. A cohort-based study provides more strength than individual-based studies and enables us to derive survival estimates, together with growth functions (Eleftheriou, 2013). In the present article, we study the factors responsible for changes in secondary production of the Baltic tellin *M. balthica*. We studied a population at one of its more southern habitats: Aiguillon Bay (46°16'29"N, 01°09'50"W). In this very muddy mudflat, *M. balthica* is found in relatively high numbers with mean densities of 70 ind.m⁻² and occurs in approximately half of the stations (Bocher et al., 2007). Aiguillon Bay is located

close to the southern edge of the distribution of the eastern-Atlantic *M. balthica* population: the Gironde Estuary (c. 45°30'N, Bachelet, 1980). Like for some other bivalve species (Helmuth et al., 2006), the distribution area of *M. balthica* is experiencing a poleward shift due to warming temperatures as early acknowledged by a study 9 years ago (Jansen et al., 2007). Possibly now, it is in Arcachon where the most southern population of *Macoma* is to be found in France (X. de Montaudouin, pers. comm.). A linear relationship was revealed between growth constant k (derived from von Bertalanffy curves, von Bertalanffy, 1938) and latitude (Bachelet, 1980). The same results were obtained in an earlier study, which also suggests that maximum size and longevity increase with increasing latitude as an effect of cooler temperatures and shorter growing seasons (Gilbert, 1973). These studies suggest that *M. balthica* reach lower recruitment, survival and growth rates under warmer temperatures (cited in Beukema, Dekker, and Jansen, 2009).

If recruitment is not proportional to the adult reproductive stock in this species (Andresen, Strasser, and Meer, 2014), recruitment plays a major role in among cohort variance of production (van der Meer, Beukema, and Dekker, 2001; Magalhães, Freitas, and Montaudouin, 2016). In our study system, we hypothesise that recruitment is a major driver of secondary production and its variability in time. However, because Aiguillon Bay is located at the edge of the distribution area and may suffer from warming conditions, *M. balthica* are expected to have reduced longevity and increased growth rates (Bachelet, 1980; Gilbert, 1973). How will this position in the distribution area affect secondary production in this species?

Because Aiguillon Bay is located at the southern edge of the distribution of the eastern-Atlantic *M. balthica* population, we hypothesise survival rates and mass at death to be lower in Aiguillon Bay compared with values in higher latitudes like the Wadden Sea intertidal areas (van der Meer et al., in prep), resulting in lower secondary production in this species.

This study proposes original estimates of secondary production for 8 consecutive *M. balthica* cohorts in Aiguillon Bay based on the evaluation of recruitment, survival and growth. In the discussion, a comparison with three sampling areas in the Dutch Wadden Sea is provided, in order to investigate the potential consequences of living at the edge of the distribution area on population dynamics.

5.3 Materials and Methods

5.3.1 Study area

Aiguillon Bay is a large estuarine intertidal area (28.7 km²) divided into two by the Sèvres River and located in the Pertuis-Charentais in the middle of the French Atlantic Coast (Fig. 5.1). The area is homogeneous in sediment characteristics with mean median grain size of 8 μm and almost 90% silt (Degré et al., 2006; Bocher et al., 2007).

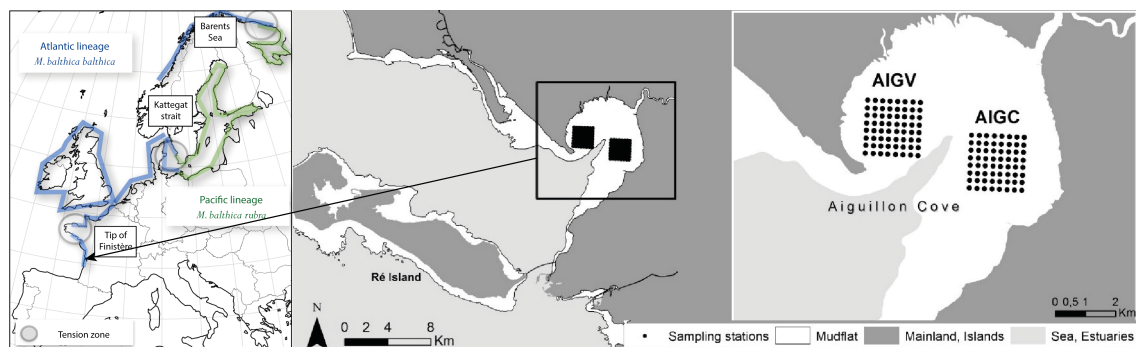


FIGURE 5.1: Aiguillon Bay sampling site with the 128 regular stations, with location at the southern edge of the *M. balthica balthica* subpopulation

5.3.2 Sampling protocol

The data supporting the present study have been collected via a long-term winter monitoring programme and involved coring during spring tides, using corers of 1/56 m² (Bocher et al., 2007; Philippe et al., under revision). Sampling was performed on two 250 m grids of approximately 64 stations (Chapter 3).

5.3.3 Determining of length and flesh mass

Samples were sieved over a 1 mm mesh and living *Macoma balthica* specimens were identified and measured. The length of their shell was measured to the nearest 0.01 mm, and $AFDM_{flesh}$ (i.e. ash-free dry mass of the flesh) was obtained from subtracting ash mass (after burning the samples in crucibles at 550°C in an oven) from DM_{flesh} (after 3 days in a 55°C stove) (Bocher et al., 2007). In specimens smaller than 7 mm, flesh and shell were not separated, and values for $AFDM_{flesh}$ were extrapolated from $AFDM_{total}$ values (i.e. ash-free dry mass of the total individual, flesh and shell together). For this extrapolation we used small *Macoma* individuals sampled in January 2014 in Aiguillon Bay. Their

flesh was carefully detached from the shells and individual fleshes and shells pooled by size class in a cremation oven. This operation yielded the following extrapolation curves for small individuals (size independent): $AFDM_{flesh} = 0.765 \times AFDM_{total} - 4e-05$ ($R^2 = 0.97$, $N = 50$).

5.3.4 Determining age from length to identify cohorts

For shelled individuals like *M. balthica*, age can be determined by counting annual growth rings formed during winter, a period of growth cessation due to colder temperatures (Eleftheriou, 2013; Cardoso et al., 2013). We used individuals from Aiguillon Bay for which ring scores were assessed in sampling year 2004 ($n = 1139$) and derived an age-length key based on this data (Fig. 5.2). Based on this age-length key, age was assigned to each individual in the database from 0 (recruits, individuals < 9.4 mm) to 1 (< 12.8 mm), 2 (< 15.3 mm) and 3+ (individuals of three years old or more, with length ≥ 15.3 mm). Because ring scores were less precise for individuals older than 3 years old, individuals with more than 3 rings were included in the age class '3+'. Since we applied the same age-length key to every sampling year, secondary production for each cohort was modelled under the assumption of a constant growth rate throughout the study period.

A cohort can be simply defined as “a group of individuals who are born at more or less the same time” (Eleftheriou, 2013). In this study, 8 cohorts were followed from recruitment to 3 years old (or more). Using individuals instead of cohorts would have led to various complications, starting with the fact that our sampling method is destructive (since we use ash free dry mass to weight the animals) so that we cannot expect to follow the same individuals over time, but most importantly, inter-individual variations are often considerable when we consider growth and mortality for instance (Eleftheriou, 2013).

5.3.5 Estimating recruitment, mortality, initial mass, growth and production

Recruitment:

Recruitment (μ_i) of cohort i refers to the mean number (Y_j) of zero year class individuals ($j = 0$) averaged over all sampling stations k (from 1 to K), and empirically determined using sampling results.

$$\hat{\mu}_i = \frac{\sum_{k=1}^K Y_{i,0,k}}{K}$$

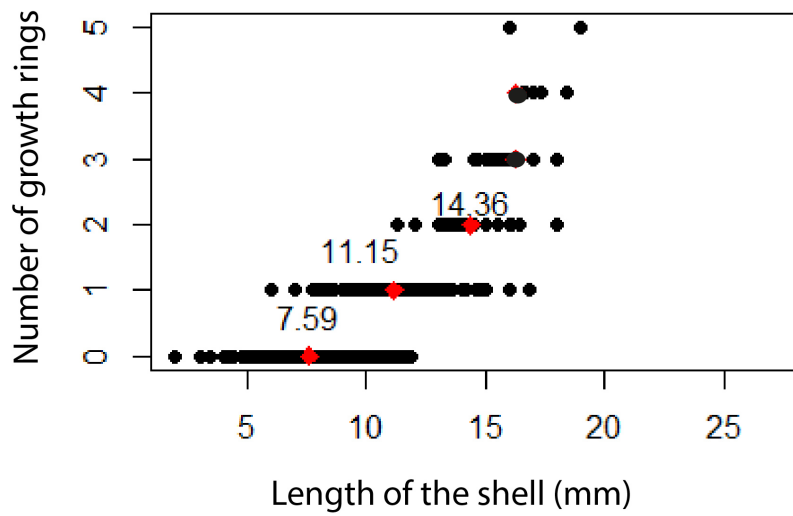


FIGURE 5.2: Ageing of *Macoma* individuals (n = 1339) sampled in winter 2003-2004, with average shell length depending on the number of rings.

Mortality:

For each cohort (i) and year class (j), mortality ($\lambda_{i,j}$) corresponds to the fraction of individuals that dies in the period between $j - 1$ and j

$$\hat{\lambda}_{i,j} = \frac{\sum_{k=1}^K Y_{i,j-1,k} - \sum_{k=1}^K Y_{i,j,k}}{\sum_{k=1}^K Y_{i,0,k}}$$

where $Y_{i,j,k}$ is the density of cohort i , at year class j and sampling station k .

Growth increments:

Growth increments were defined as the variation of biomass per individual (B/Y) of cohort i at station k during the period between $j - 1$ and j .

$$\hat{\gamma}_{i,j} = \frac{\sum_{k=1}^K B_{i,j,k}}{\sum_{k=1}^K Y_{i,j,k}} - \frac{\sum_{k=1}^K B_{i,j-1,k}}{\sum_{k=1}^K Y_{i,j-1,k}}$$

Individual mass at recruitment:

Individual mass at recruitment ($\hat{\Gamma}_i$) refers to the sum of the biomasses of the cohort i at every station k for age class $j = 0$, divided by the total size of the cohort at age class $j = 0$ for all stations k .

$$\hat{\Gamma}_i = \frac{\sum_{k=1}^K B_{i,0,k}}{\sum_{k=1}^K Y_{i,0,k}}$$

Mass at death:

Mass at death $\hat{\omega}$ for cohort i , at age j is given by its mortality at age j (λ_j) times the sum of initial mass at recruitment (Γ_i) and its growth increments at age j ($\gamma_{i,j}$).

$$\hat{\omega}_{i,j} = \hat{\mu}_i \left(\hat{\lambda}_{ij} \left(\hat{\Gamma}_i + \frac{\hat{\gamma}_{ij}}{2} \right) \right)$$

Half of the growth increment is taken, as it is not known when exactly animals die within an age class.

Production:

$$\hat{p}_i = \hat{\mu}_i \left(\hat{\lambda}_{i,1} \left(\hat{\Gamma}_i + \frac{\hat{\gamma}_{i,1}}{2} \right) + \dots + \hat{\lambda}_{i,J} \left(\hat{\Gamma}_i + \hat{\gamma}_{i,1} + \dots + \hat{\gamma}_{i,J-1} + \frac{\hat{\gamma}_{i,J}}{2} \right) \right)$$

Production \hat{p}_i of cohort i was expressed as the product of recruitment of cohort i ($\hat{\mu}_i$) and the sum of its mass at death for each age class j (from 0 to J).

5.4 Results

In Aiguillon Bay, *Macoma balthica* individuals did not grow large, with most sampled individuals smaller than 10 mm (Fig. 5.3). Among years, important variations in numbers and size distribution were observed (Fig. 5.3). Over all years, the age-length key applied to our dataset matched normal distribution between age classes (Fig. 5.4), suggesting that our determination of age from length was adequate for our dataset.

On average, recruitment numbers were a bit less than 130 individuals.m⁻² (Table 5.1). On average over 8 cohorts, more than 60% of a cohort dies within the first year, with an expected mass at death of about 6 mg. Overall sampling stations and cohorts, production equals *c.* 0.70 g.m⁻².

Recruitment was highly variable among cohorts (Fig. 5.5, A), with values ranging from close to 0 in 2006 and 2008 to *c.* 300 ind. m⁻² in 2011. Mean mass at death was also highly variable among cohorts, and negatively correlated

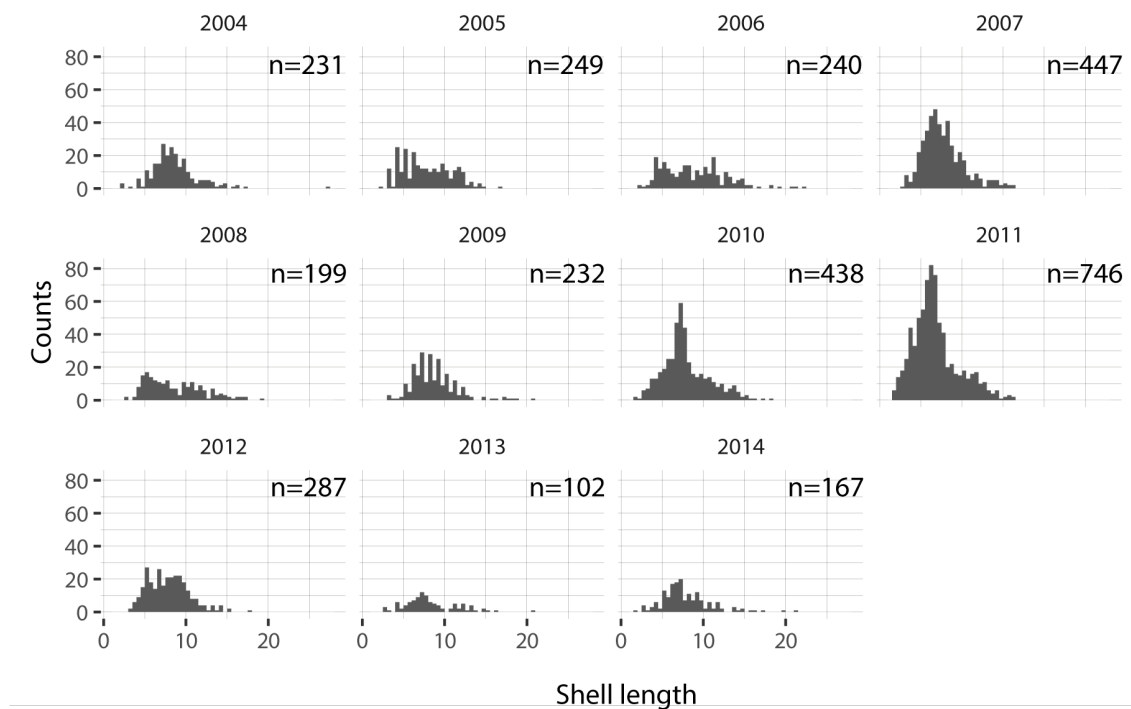


FIGURE 5.3: Size distribution depending on sampling year of *Macoma balthica* in Aiguillon Bay (2004-2014).

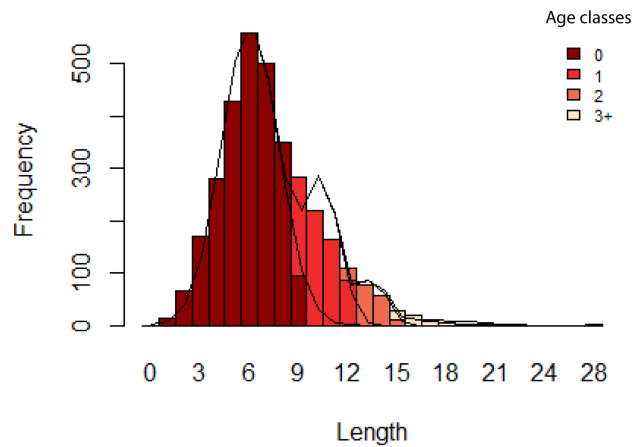


FIGURE 5.4: Year class distribution based on shell length in *Macoma* individuals sampled in winter 2003-2004 in Aiguillon Bay ($n = 1339$); based on a normal distribution of length within each age class considered. The lines correspond to a normal distribution.

with recruitment numbers (Fig. 5.5, B and D). Values of secondary production between cohorts from 2004 to 2011 varied widely as well, and were positively correlated with the number of recruits (Fig. 5.5, C).

TABLE 5.1: Mean recruitment, fraction mortality during the first year, mass at recruitment, mass after the first year, expected mass at death, and production for *M. balthica* in Aiguillon Bay for the period 2004 - 2011. Values are expressed as mean and associated standard deviation.

Variable	Aiguillon Bay
Recruitment per year (m^{-2})	126.83 ± 84.95
Mortality in first year (-)	0.64 ± 0.16
Mass at recruitment (mg)	1.32 ± 0.25
Growth in first year (mg)	5.38 ± 0.62
Expected mass at death (mg)	6.18 ± 1.45
Production per year ($g.m^{-2}$)	0.69 ± 0.28

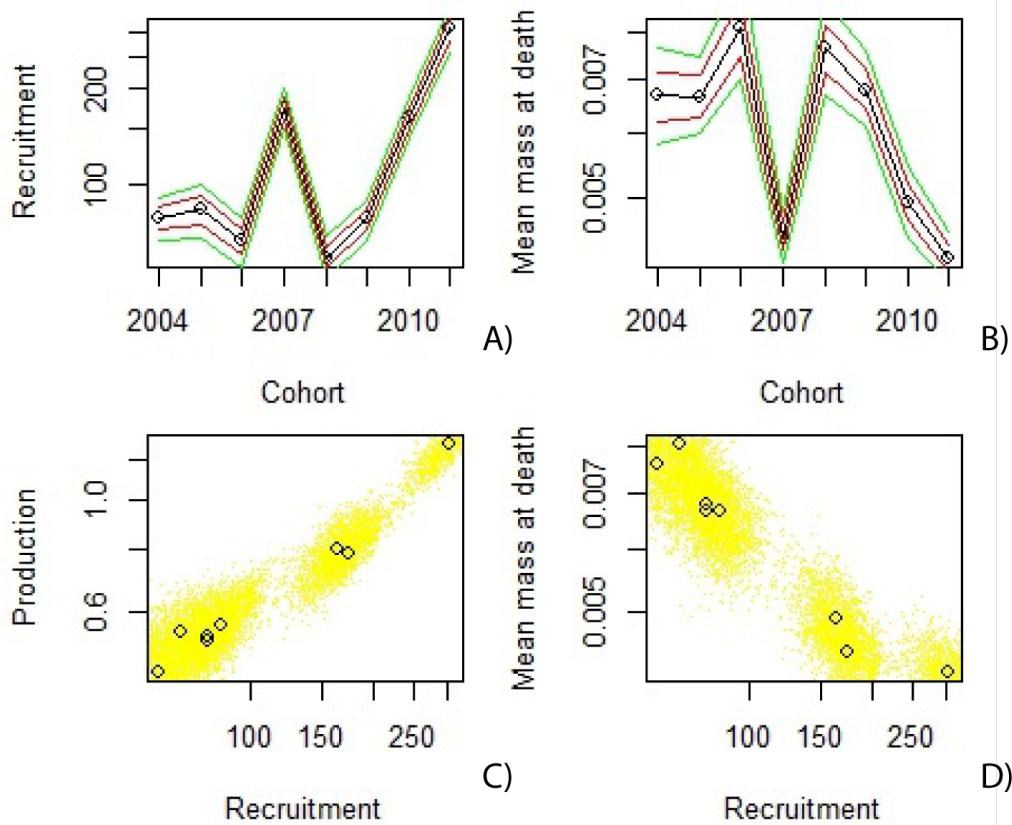


FIGURE 5.5: A) Number of recruits depending on the cohort (from 2004 until 2011); B) Mean individual mass at death depending on the cohort; C) Secondary production depending on the number of recruits and D) Mean individual mass at death depending on the number of recruits.

When decomposing variability of secondary production into its various components (recruitment, mortality, initial size and growth: Table 5.2), recruitment represented the largest contribution to the among-cohort variance of production of *M. balthica* in Aiguillon Bay (0.276). Negative covariances were also captured in the covariance matrix, indicating density dependence effects between recruitment (μ) and mortality (λ), as well as between recruitment and initial size (Γ).

TABLE 5.2: Summary of the covariance matrix of the parameters of the function determining secondary production multiplied by the outer product of the vector of partial derivatives of the function to each parameter. The sum of all elements of this matrix approximates the among-cohort variance of production. See van der Meer et al., [in prep](#) for further explanation. For convenience, the elements representing the variances and covariances among all survival parameters are lumped in a single cell. The same is done for all growth parameters.

<i>M. balthica</i> Aiguillon	μ	λ	Γ	γ
Recruitment μ	0.276	-0.092	-0.009	0.017
Mortality λ	-0.092	0.037	0.002	-0.005
Initial size Γ	-0.009	0.002	0.001	-0.002
Growth γ	0.017	-0.005	-0.002	0.004

TABLE 5.3: Recruitment, fraction mortality during the first year, mass at recruitment, mass after the first year, expected mass at death, and production for *M. balthica* in Aiguillon Bay and three other sampling locations in the Dutch Wadden Sea (Balgzand, Piet Scheveplaat and the Dollard Estuary). Mean and standard deviation.

Variable	Aiguillon Bay	Balgzand	Piet Scheveplaat	Dollard
Recruitment (m^{-2})	126.83±84.95	44.4±34.4	28.9±27.0	17.6±9.6
Mortality in first year (–)	0.64±0.16	0.33±0.19	0.32±0.49	0.07±0.37
Mass at recruitment (mg)	1.32±0.25	3.12±1.11	2.57±0.99	3.74±1.46
Growth in first year (mg)	5.38±0.62	16.1±3.6	15.1±4.6	10.9±2.8
Expected mass at death (mg)	6.18±1.45	29.7±8.1	27.8±14.6	18.3±2.3
Production ($g.m^{-2}$)	0.69±0.28	1.24±0.88	0.63±0.46	0.31±0.17

5.5 Discussion

Compared to the three sampling sites of the Dutch Wadden Sea where the same methodology was applied (*i.e.* Balgzand, Piet Scheveplaat and the Dollard Estuary, van der Meer et al., [in prep](#)), recruitment values were much higher in Aiguillon Bay, at the southern edge of the species distribution (Table 5.3). Together with higher recruitment, individuals grew much less than in the Wadden Sea during their first year. Mortality within the first year was at minimum twice as much as in the Wadden Sea, with 60% of juveniles dying in Aiguillon Bay. As a consequence, mass at death in Aiguillon Bay was much lower than in the Dutch sampling sites since a majority of individuals died in their first year, with an initial mass 2 to 3 times lower and a limited growth during the first year. However, certainly due to a compensating effect of having higher number of recruits, production in Aiguillon Bay was comparable to that of the Dutch sites (Table 5.3). It is interesting to note that the Dollard estuary, a very muddy area, recruitment was the lowest of all stations examined, and growth and mass at death was lowest among Dutch sites.

The covariance matrix of Aiguillon Bay was also compared to the three Dutch sampling sites (Table 5.4). In this covariance table, the highest numbers (recruitment), represent the largest contribution to the among-cohort variance of production, for all four sites. Recruitment drives secondary production variability, whether at the edge or in the heart of *Macoma balthica* distribution area. Negative

TABLE 5.4: Summary of the covariance matrix of the parameters of the function determining secondary production multiplied by the outer product of the vector of partial derivatives of the function to each parameter. The sum of all elements of this matrix approximates the among-cohort variance of production. See van der Meer et al., [in prep](#) for further explanation. A means Aiguillon Bay, B Balgzand, PS Piet Scheveplaat and D Dollard.

<i>M. balthica</i> A	μ	λ	Γ	γ
Recruitment μ	0.276	-0.092	-0.009	0.017
Mortality λ	-0.092	0.037	0.002	-0.005
Initial size Γ	-0.009	0.002	0.001	-0.002
Growth γ	0.017	-0.005	-0.002	0.004
<i>M. balthica</i> B	μ	λ	Γ	γ
Recruitment μ	1.030	-0.098	-0.006	-0.002
Mortality λ	-0.098	0.089	-0.002	0.007
Initial size Γ	-0.006	-0.002	0.002	-0.002
Growth γ	-0.002	0.007	-0.002	0.023
<i>M. balthica</i> PS	μ	λ	Γ	γ
Recruitment μ	0.549	-0.134	0.005	-0.026
Mortality λ	-0.134	0.158	-0.002	0.002
Initial size Γ	0.005	-0.002	0.001	-0.002
Growth γ	-0.026	0.002	-0.002	0.016
<i>M. balthica</i> D	μ	λ	Γ	γ
Recruitment μ	0.0309	-0.0074	-0.0004	0.0028
Mortality λ	-0.0074	0.0053	-0.0003	-0.0003
Initial size Γ	-0.0004	-0.0003	0.0007	-0.0013
Growth γ	0.0028	-0.0003	-0.0013	0.0066

covariances, indicative of negative density-dependent effects, are also revealed for all sites between recruitment and mortality λ , and recruitment and initial size Γ (except for Piet Scheveplaat), see Table 5.4.

Higher recruitment values could be a distinctive trait of populations at the edge of their distribution area (especially the edge closer to lower latitudes), as revealed for other species of marine invertebrates: Lester, Gaines, and Kinlan, 2007; Dekker and Beukema, 1999; Fiori and Defeo, 2006; Lewis, 1986. Previous studies also showed higher mortalities in population at the edge of their distribution: Bowman and Lewis, 1987. Our results showed most of *M. Balthica* individuals in Aiguillon Bay died before they reached their first year, at a size which is not profitable for sandpiper species (Zwarts and Blomert, 1992). The feeding resource for predatory shorebirds in our study system is highly variable and rather scarce, with most individuals being too small for sandpipers. The present study however does not distinguish between mortality and depletion by shorebirds, and further studies should be conducted to determine the impact of shorebird predation on the population dynamics of *M. balthica*.

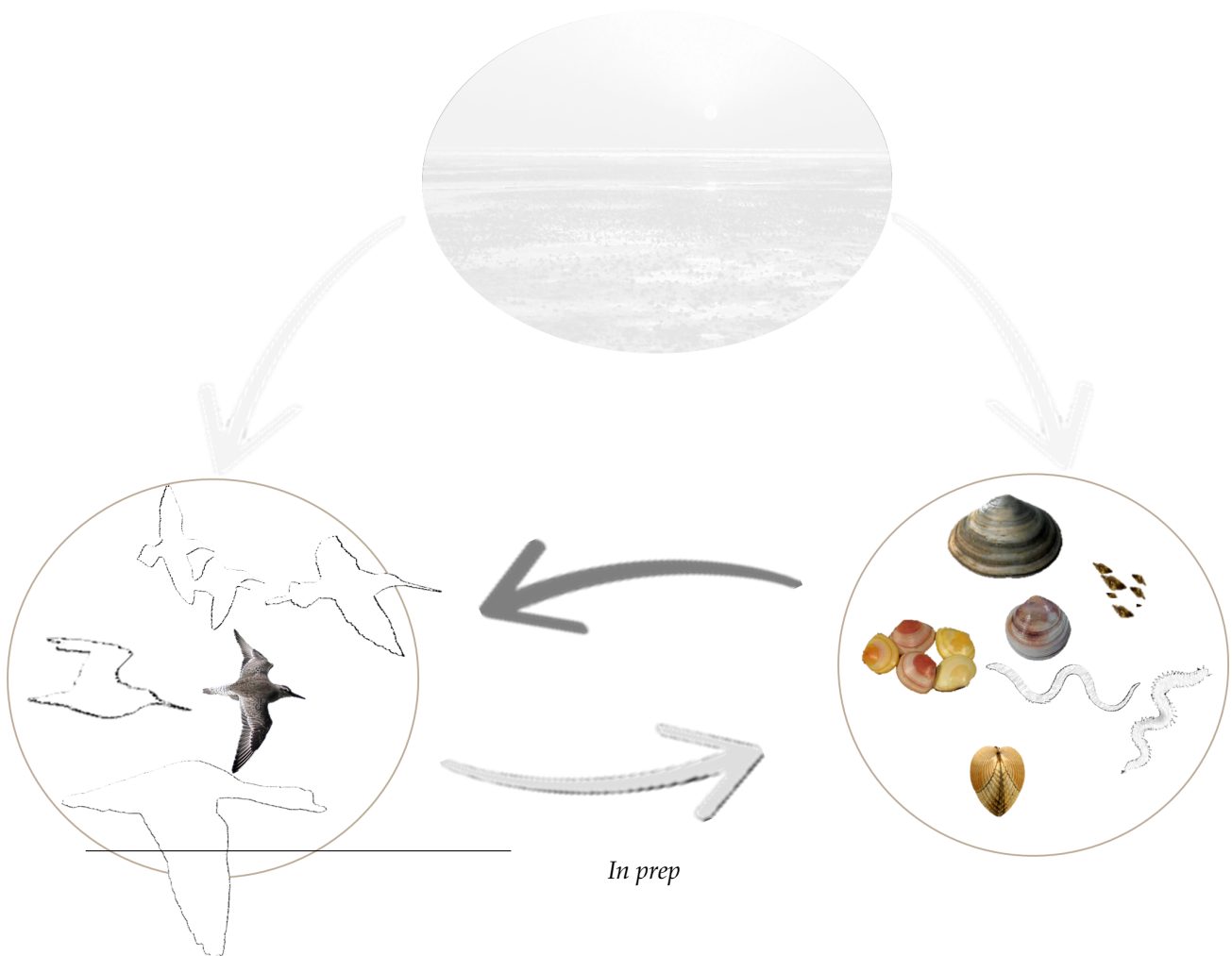
**SECTION 4: WHEN DIET CHOICE
AND BIRD NUMBERS REFLECT
RESOURCES IN TIME AND SPACE**



Chapter 6

Latitudinal contrasts in the determinants of food intake rates for a migrating bird

Anne S. PHILIPPE, Tanya J. COMPTON, Jaap van der MEER, Pierrick BOCHER, Theunis PIERSMA, Jan A. van GILS



6.1 Abstract

Spurred by seasonal changes in feeding resources, millions of shorebirds leave their arctic breeding grounds to overwinter in mudflats ranging from temperate to tropical latitudes. Their feeding conditions along the migration route are important for their survival. The ecology and feeding behaviour of a molluscivore shorebird, the red knot *Calidris canutus*, has received continued attention. It is now possible to study and compare these different but connected ecosystems from the point of view of this consumer. Thanks to intensive benthic surveys, temporal variations of the available prey biomass for the red knots were determined along the East-Atlantic flyway. An optimal diet model taking digestive constraints into account predicted site- and year-specific diet composition and intake rates. Benthic composition of total biomass, harvestable biomass and predicted diets highlighted the different foraging constraints operating in each ecosystem. Total biomass or harvestable biomass were poor predictors of food abundance for the red knot, implying digestive constraints to be decisive for this consumer. Temporal trends in total biomass were captured in predicted diets suggesting diet variability to be an indicator of ecological changes. Based on our results, we question why red knot densities remain much higher in the far away tropics when a temperate area provides much better feeding conditions.

6.2 Introduction

Animals do select for a limited number of prey types and, to a certain extent, can adapt their diet to their environmental conditions. Diet is the result of a complex interplay between energetic needs, physiology, metabolism, prey diversity and abundance, as well as competition; it is the result of active selection following decision rules (Hughes, 2009). Fifty years ago, the theory of optimal foraging (OFT) was first introduced, describing how animals could optimize their foraging behaviour for survival (Emlen, 1966; MacArthur and Pianka, 1966). Energetics, physiology and ecology have to be combined in order to understand how vertebrates reach maximum rates of energy intake in the long-term (Karasov, 1986; Karasov and McWilliams, 2005). Prey selection is defined as the strategy of prey choice which maximizes long-term energy intake rate (Stephens and Krebs, 1986). Prey uptake is rarely described as a linear function of prey density, and diet composition often differs from total resource composition. There are numerous determinants to food abundance for a consumer. Together with the type and quantity of prey items, their quality, toxicity, searching, handling and digestive times and efficiencies also determine the optimality of a diet over the long term (Hughes, 2009).

Predator-prey interactions are often complicated by the multiplicity of environmental factors they involve and, for most ecosystems, a lack of knowledge concerning their ecological functioning. When it comes to migratory species, understanding feeding ecology requires long-term datasets and large-spatial-scale studies. Therefore there are only rare opportunities to study the determinants of food abundance along the migration route. Continued research was conducted on shorebirds, and especially the red knot *Calidris canutus* along the East-Atlantic Flyway (Piersma, 2012). East-Atlantic red knots are long-distance migrants that breed in northern latitudes (arctic tundra) and overwinter over a large latitudinal range, from the Wadden Sea (53°N) to the French Atlantic coast (45-46°N) and mostly in the Banc d'Arguin in Mauritania (20°N), hosting 3/4th of the *Calidris canutus canutus* subpopulation (Piersma, Prokosch, and Bredin, 1992, van de Kam et al., 2004; Delaney et al., 2009, Table 6.1).

The model formed by this shorebird and its mollusc prey has been the subject of many studies that unraveled their flexibility and complex interactions along the flyway (van Gils et al., 2005c; Quaintenne et al., 2010, van Gils et al., 2013; Bocher et al., 2014b). Outside their breeding grounds, red knots feed essentially on molluscs they swallow whole, allowing a precise diet reconstruction (Dekinga and Piersma, 1993). Because they are gape-limited, only a certain range of sizes are

TABLE 6.1: Information concerning the study sites: abbreviations, total surface of intertidal flats, mean number of red knots and densities (Wetlands International mid-winter counts with associated *s.d.*), and length of datasets.

Site	Abbr.	Surface intertidal flats (ha)	<i>n</i> red knots mean \pm s.d.	mean density (ind.ha ⁻¹ \pm s.d.)	<i>n</i> years in the datasets benthos and birds
Dutch Wadden Sea	DWS	32,711	25,743 \pm 12,180	0.79 \pm 0.37	6 (2008-2013)
French Pertuis Charentais	FPC	6,570	17,259 \pm 4,578	2.63 \pm 0.70	11 (2004-2014)
Mauritanian Banc d'Arguin	BDA	2,300	15,811 \pm 3,034	6.87 \pm 1.32	8 (2008-2015)

available to them, depending on the shape and crushability of the prey species. Only available individuals buried in the first four centimetres of the mud are accessible to a knot's bill and can be harvestable (Fig. 6.1). Red knots possess the sensory equipment that allows them to detect the best prey among different profitabilities (energy intake / handling time, Piersma et al., 1998). Their ingestion rate is best describe by the type II functional response, also known as the Holling's disc equation (Holling, 1959; Stephens and Krebs, 1986; Piersma et al., 1995). Their prey choice is also determined by their muscular gizzard which allows them to crush their shelled prey and determines their digestion rates (van Gils et al., 2005b). This organ is flexible and can adapt to prey availability and quality (Hirakawa, 1995, van Gils et al., 2003, van Gils et al., 2005b). Thanks to the large literature about the feeding ecology of this consumer along its migratory route, we can now address ecological questions of large spatio-temporal relevance.

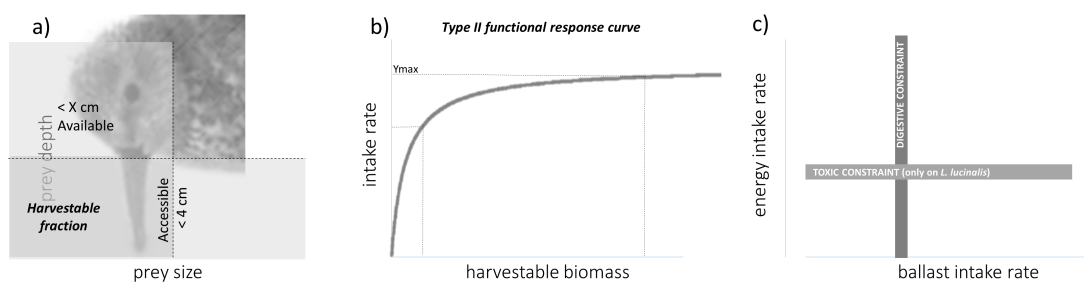


FIGURE 6.1: The fraction of benthos harvestable is composed of individuals of appropriate size and within reach of the bill (a), following Piersma, Goeij, and Tulp, 1993. The quality of the feeding habitat is evaluated through the intake rate the bird can attain and is function of the harvestable biomass, following Holling, 1959; Piersma et al., 1995 (b). Digestive as well as toxic constraints (the latter only described under the consumption of *Loripes lucinalis* in Banc d'Arguin), are also determinant for intake rates and prey selection, after van Gils et al., (2013) and Oudman et al., (2014) (c).

The present study describes the changes in mollusc abundance in three major overwintering areas along the East-Atlantic Flyway: the Dutch Wadden Sea

(DWS), the French Pertuis Charentais (FPC) and the Mauritanian Banc d'Arguin (BDA) from 2004 until 2015 (Table 6.1). The study focuses on 9 prey species (8 bivalve species: *Anadara senilis*, *Abra tenuis*, *Cerastoderma edule*, *Diplodonta sp.*, *Dosinia isocardia*, *Loripes lucinalis*, *Macoma balthica*, *Scrobicularia plana*, and the gastropod *Peringia ulvae*). Their relative importance in the ecosystem and in the harvestable resources for red knots is assessed using empirical data. Their share in the diet is predicted based on the DRM (Digestive Rate Model), a modelling tool adapted to the red knot (Hirakawa, 1995, van Gils et al., 2005b). Because the dominant constraints limiting prey selection may vary depending on the prey species, we analysed the changes in total biomass, harvestable biomass and predicted intake rates on each prey species individually. For example, the temperate cockle *Cerastoderma edule* would always be accessible whereas the tellinid *Macoma balthica* would present varying accessibility depending on the temperature and body condition, therefore depending on the year and site (Griffiths and Richardson, 2006, van Gils et al., 2009). In Mauritania, depending on the years and the relative abundance of *Dosinia isocardia* or *Loripes lucinalis*, the red knot's intake rates would either be limited by the digestive constraint (*Dosinia isocardia* shells are relatively thick), or the toxic constraint (*Loripes lucinalis* is a sulfur rich bivalve) (van Gils et al., 2013; Onrust et al., 2013; Oudman et al., 2014). The present study sheds light on what are the determinants of a consumer's prey choice and their variations in space and time, and doing so, compares ecosystems that are distant in terms of species composition and ecological functioning from the point of view of a migratory consumer: the red knot.

6.3 Materials and Methods

6.3.1 Study areas

Over the past decade, intense benthos monitoring have taken place in the Dutch Wadden Sea, the French Pertuis Charentais and the Mauritanian Banc d'Arguin in order to study the ecology of these connected mudflats, wintering grounds for numerous shorebird species (Fig. 6.2). In France, a total of 259 stations were visited every winter [December-February] between 2004 and 2014. In the Dutch Wadden Sea, 389 stations were visited each summer [June – October] between 2008 and 2013. In Mauritania, 256 stations located around 8 different towers were visited each winter between 2008 and 2015. Due to high seasonal variability of prey resources in the Banc d'Arguin (Ahmedou Salem et al., 2014) we kept

only the years when stations had been sampled between December and February, therefore the results presented here include 5 years (*i.e.* 2008, 2012, 2013, 2014, 2015) (Table 6.1). In the three sites, sampling was performed by foot or by boats using a method that supported lots of studies already (van Gils et al., 2006a, van Gils et al., 2006b; Bocher et al., 2007; Compton et al., 2008; Kraan et al., 2009b; Kraan et al., 2009a; Quaintenne et al., 2011; Bijleveld et al., 2012; Philippe et al., *under revision*; Philippe et al., 2016).

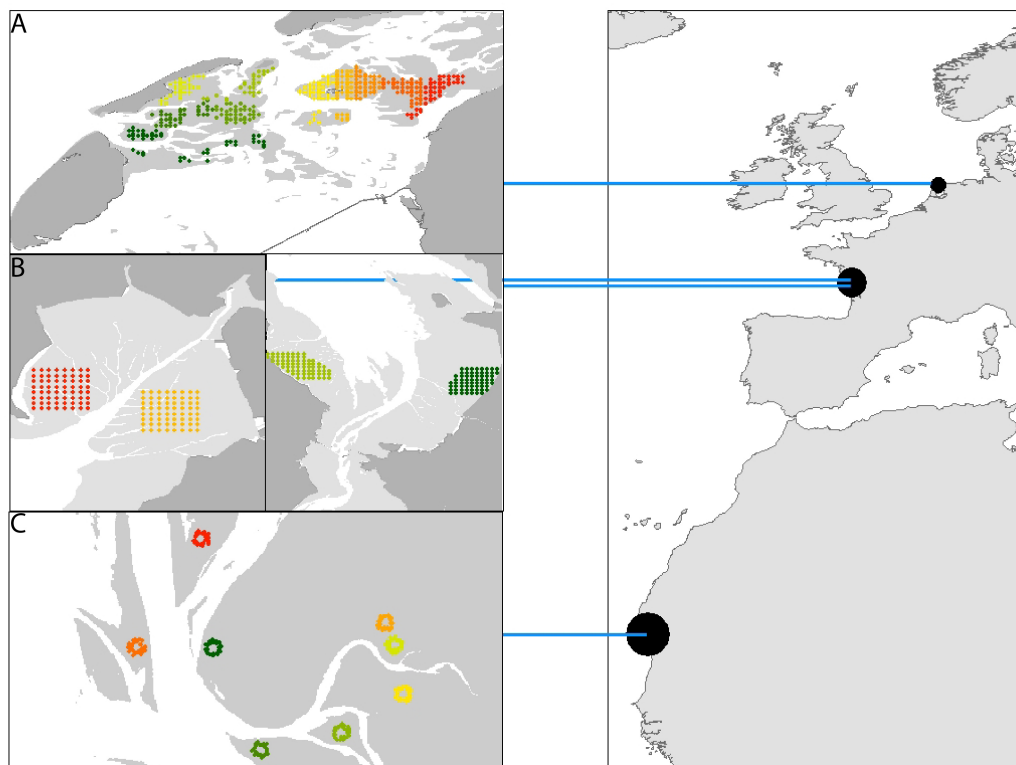


FIGURE 6.2: Sampling stations in the French Pertuis Charentais (A), the Dutch Wadden Sea (B) and the Mauritanian Banc d'Arguin (C). On the right, map of the Est-Atlantic flyway of red knots *Calidris canutus*, size of the circles indicates mean densities in the three study sites over the study period (see Table 6.1).

6.3.2 Determination of benthic biomass available

After collection, every mollusc prey was determined to the species level and measured to the nearest 0.1 mm in the laboratory using Vernier calipers. For bivalves, the shell was separated from the flesh and weighed at constant dry mass (DM) after 3 days in a ventilated oven (60°C). Ash-free dry mass (AFDM) of the flesh was obtained after incineration at 550°C for 4 hours and by subtracting the remaining ash mass from the DM. For small gastropods like *Peringia ulvae*,

AFDM was determined from whole individuals and flesh biomass ($AFDM_{flesh}$) was estimated for each station from the total biomass, with the following linear regression: $AFDM_{flesh} = 0.6876 \times AFDM_{flesh+shell} + 7E-05$ ($R^2 = 0.99$; $N=60$ ind.) (Philippe et al., 2016). DM_{shell} was estimated from the total biomass using the following regression: $DM_{shell} = 5.5902 \times AFDM_{flesh+shell} - 0.0006$ ($R^2 = 0.98$; $N=60$ ind.). Regressions were obtained from samples taken in July 2014 in Aiguillon Cove. They were applied to all study sites and years in order to avoid potential biases caused by the varying methods used to extrapolate $AFDM_{flesh}$ and DM_{shell} for this small gastropod.

We analysed the total biomass, the harvestable biomass and the predicted intake rates of red knots for the principal mollusc prey species in the environment (Table 6.2). Harvestable fraction was derived following a well-proven method (Dekinga and Piersma, 1993). The sizes and species available for red knots were derived from previous studies, either from the analysis of droppings, stable isotope analyses in blood samples, direct observations or in-door experiments (Table 6.2). These available prey and sizes, when accessible to the knot (found in the top 4 cm of the sediment), compose what is called the harvestable fraction (Fig. 6.1, a).

6.3.3 Intake rates estimation

Gross energy intake rate at each station each year ($mgAFDM_{flesh} \cdot s^{-1}$) was predicted using the so-called ‘digestive rate model’ (DRM) (van Gils et al., 2005c). This mathematical model was derived from Holling’s disc equations (Holling, 1959) and first introduced by Hirakawa (Hirakawa, 1995). The functional response was adapted to the red knots by first adding a digestive constraint (van Gils et al., 2005c), and then a toxic constraint induced by the ingestion of the sulphur-rich *Loripes lucinalis* in Mauritanian Banc d’Arguin (van Gils et al., 2011, van Gils et al., 2013; Onrust et al., 2013, Fig. 6.1, b and c). For further details on the model, refer to Piersma et al., (1995), van Gils et al., (2005c) and Quaintenne et al., (2011) and Table 6.3). In the DRM model, prey types were represented by 1 mm size classes for each of the nine selected prey species (see Table 6.3 for parameter details). For each prey type, we calculated year and station-specific intake rates. Values for available density, energy content ($AFDM_{flesh}$) and ballast mass (DM_{shell}) were based on our benthic datasets; site or prey specificity concerning handling times, research efficiency, gizzard masses are given in Table 6.3. In order to achieve a sound comparison between the three sites, we fixed gizzard mass of red knots to 9 g (having a digestive processing capacity c of $c. 4.1$

TABLE 6.2: Dominant species in the sample areas and in the diet of the red knot, with sizes and fraction available for knots derived from literature.

Region	Species	Max-min sizes available (mm)	% in the diet of knots	% of total flesh biomass of molluscs	% of harvestable flesh biomass for knots
Dutch Wadden Sea *	<i>Abra sp.</i>	all	optional	-	1%
	<i>C. edule</i>	[5-12]	40%	-	82%
	<i>M. balthica</i>	[9-16]	5%	-	10.5%
	<i>P. ulvae</i>	all	55%	-	4%
	<i>S. plana</i>	< 14	optional	-	2.5%
				$\sum > 90\%$	$\sum = 100\%$
French Pertuis Charentais **	<i>Abra sp.</i>	all	NA	<1 %	5%
	<i>C. edule</i>	[3-10]	2%	6%	2%
	<i>M. balthica</i>	[9-15]	10%	3%	5%
	<i>P. ulvae</i>	all	80%	41%	78%
	<i>S. plana</i>	[7-13]	8%	43%	10%
				$\sum > 90\%$	$\sum = 100\%$
Mauritanian Banc d'Arguin ***	<i>Abra sp.</i>	all	optional	-	< 1%
	<i>A. senilis</i>	< 13.2	optional	-	90%
	<i>Diplodonta sp.</i>	< 13.2	optional	-	< 1%
	<i>D. isocardia</i>	< 13.2	nearly 100%	-	1%
	<i>L. lucinalis</i>	< 13.2	alternative	-	8%
	<i>P. ulvae</i>	all	optional	-	< 1%
				$\sum > 80\%$	$\sum = 100\%$

* from Goss-Custard, Jones, and Newbery, (1977), Zwarts, Blomert, and Wanink, (1992), and Zwarts and Blomert, (1992) Dekinga and Piersma, (1993), Piersma et al., (1993), Quaintenne et al., (2010), and Folmer, Olf, and Piersma, (2012)

** from Quaintenne et al., (2010) and Bocher et al., (2014b)

***from Zwarts, Blomert, and Wanink, (1992), Honkoop et al., (2008), van Gils et al., (2011), Onrust et al., (2013), and van Gils et al., (2013)

$mgDM_{shell} \cdot s^{-1}$), in accordance with gizzard measurements of red knots overwintering in the Wadden Sea (van Gils et al., 2003; Quaintenne et al., 2011).

6.3.4 Variability of the resource and intake rates

Variability measures of the benthic resource were obtained from a 2-way ANOVA with “year” as a random factor. To compare our three regional datasets (which differ in their number of stations, years, species and densities), we used coefficients of variation which are good tools for comparing datasets of different spatio-temporal extents. A coefficient of variation (CV) is defined as the ratio of the standard deviation (σ) to the mean (μ). Therefore, irrespective of the mean value, a higher CV will indicate a more variable region. For each ecosystem considered and each dominant species, a temporal coefficient of variation (between years, α_j) was calculated, a higher α_j indicating a higher inter-annual variability within a region. The same analysis of variance was performed on the total mollusc resource, the harvestable fraction and on the predicted intake rates. We also calculated spatial variability (with “subregions” as a random factor) and spatio-temporal variability (with “year” and “subregions” as random factors) following

TABLE 6.3: Symbols, definitions, units, derivation and value of parameters used in the “digestive-rate model” to predict gross energy intake rates of red knots on each sampled stations, each year.

Symbol	Definition	Units	Derivation	Value	References
A	Assimilation efficiency	-		0.8	Kersten and Piersma, (1987) and Piersma, (1994)
a_i	Searching efficiency	$m^2 \cdot s^{-1}$		0.0010	van Gils et al., (2005c)
c	Digestive processing capacity	$gDM_{shell} \cdot s^{-1}$	$c = 10^{-4.293} \cdot G^2$		van Gils et al., (2005c)
D	Energetic density of the flesh	$J/mgAFDM_{flesh}^{-1}$		22	Zwarts and Wanink, (1993)
e_i	Energy contents	$mgAFDM_{flesh}$		Based on sampling data	
G	Gizzard mass	g		9	Zwarts and Wanink, (1993), van Gils et al., (2003) Quaintenne et al., (2011) and van Gils et al., (2013)
h_i	Handling time	s		*3.44(L/10) ² (Cer) 0.33 (Hyd); 2.9213(L10) ² (Mac, Scr, Abr, Dip, Dos, Lor); 3.44(L/10) ² (Ana)	Piersma et al., (1998) and van Gils et al., (2005c)
k_i	Ballast mass	$mgDM_{shell}$		Based on sampling data	
n_i	Available density	ind. m^2		Based on sampling data	
p_i	Probability prey is accepted upon encounter			See graphical procedure	Hirakawa, (1995)
q	Toxic constraint	$g \cdot s^{-1}$		$q = 0.11000$ (Lor)	
λ_i	Encounter rate	s^{-1}		$\lambda_i = a_i \cdot n_i$	

*Abr: *Abra tenuis*; Cer: *Cerastoderma edule*; Hyd: *Peringia ulvae*; Mac: *Macoma balthica*; Scr: *Scrobicularia plana*; Lor: *Loripes lucinalis*; Dos: *Dosinia isocardia*, Ana: *Anadara senilis*; Dip: *Diplodonta sp.*.

the same method (Table 6.4). Statistical analyses of variance were performed using lme4 R package (Bates et al., 2015).

6.4 Results

Banc d'Arguin presents the highest total biomass (c. 7 times more than the temperate areas considered), see Fig. 6.3 and Table 6.4; this biomass reduces dramatically when we consider the harvestable fraction for the knots (-94% in the Banc d'Arguin compared with -91% in the Wadden Sea and -55% only in the Pertuis Charentais). In the end, mean predicted intake rate is 3 to 4 times higher in France than in the Netherlands or in Mauritania, with mean values over the stations and years of $0.85 \text{ mgAFDM} \cdot \text{s}^{-1}$ in the French Pertuis Charentais, $0.26 \text{ mgAFDM} \cdot \text{s}^{-1}$ in the Dutch Wadden Sea and $0.17 \text{ mgAFDM} \cdot \text{s}^{-1}$ in the Mauritanian Banc d'Arguin.

When we consider total biomass, France appears more diverse, compared to the other two study sites where one species dominates largely (Fig. 6.3). However, when we focus on harvestable biomass, it is less diverse (Fig. 6.3). This is due to the fact that all sizes of the very dense *Peringia ulvae* are ingestible and accessible to the red knots, contrary to *Scrobicularia plana* for instance (less than 1% of the total biomass of *S. plana* is harvestable). Variation in the *P. ulvae* biomass is directly responsible for more than 97% of the variations in the harvestable biomass as well as in the predicted intake rates (Table 6.4, Fig. 6.3).

In the Dutch Wadden Sea, the total biomass was increasing during the study period, from less than $5 \text{ mgAFDM} \cdot \text{m}^{-2}$ in 2008 to more than $14 \text{ mgAFDM} \cdot \text{m}^{-2}$ in 2013 (Fig. 6.3). The total biomass of mollusc was less varied with *Cerastoderma edule* accounting for 82% and *Macoma balthica* accounting for another 10% of the total biomass; both species were responsible for the increase in the total biomass over the study period (Fig. 6.3). However, the harvestable fraction was more varied and composed (all years together) of 45% *P. ulvae*, 24% *M. balthica*, 22% *C. edule* and 8% *Abra sp* (Table 6.4, Fig. 6.3). 2011 seemed to be a remarkably rich year with a higher harvestable biomass compared with other years, due to increased numbers of good sized *C. edule*. From the composition of the harvestable fraction to the composition of predicted intake rates, a decrease in the share of *C. edule* was observable in favour of an increase in the share of *P. ulvae* in this site, certainly due to the better digestive quality of the latter (Fig. 6.3). However predicted diet composition changed gradually between 2008 and 2013 with, progressively, a lower share of *M. balthica*, *C. edule* and *Abra sp* and increasing

dominance of *P. ulvae* in the predicted feeding regime (Fig. 6.3).

In the Mauritanian Banc d'Arguin, the total biomass was also less varied, and dominated by *Anadara senilis* (90% of the total biomass), the most important species in terms of biomass before *Loripes lucinalis* (approximately 8% of the total biomass) (Fig. 6.3). The harvestable fraction was also not varied, but then the dominant species was not *A. senilis* anymore but *L. lucinalis* (accounting for 92% of the harvestable fraction) (Fig. 6.3). The reason why *A. senilis* was nearly absent from the harvestable fraction was due to its large sizes: less than 12% of the individuals had ingestible sizes for the knots. When we consider diet composition, over all 5 years, the diet was a relatively varied one with 4 prey composing 93% of the feeding regime of knots: (*Diplodonta sp.* 5%, *Dosinia isocardia* 33%, *L. lucinalis* 44% and *P. ulvae* 11%) (Fig. 6.3). However this diet composition evolved towards a less diverse feeding regime over the most recent years, with an increasing share of *L. lucinalis* and a decreasing share of *Diplodonta sp.* and *Dosinia isocardia* (Fig. 6.3).

When we consider the total biomass of the principal species together, Banc d'Arguin showed the lowest temporal coefficients of variations ($c\alpha_j = 0.16$). The very stable species *A. Senilis* representing 90% of the total biomass there was largely influencing this figure ($c\alpha_j = 0.13$) (Table 6.4). Two taxa allowed a direct comparison of temporal variability since they were found in the three regions studied: *P. ulvae* and *Abra sp.*. Their temporal coefficients (either of total, harvestable or from predicted intake rates), showed higher values in the tropics. In a temporal point of view, the Pertuis Charentais showed lower coefficients of variation for the predicted intake rates ($c\alpha_j = 0.03$) than the Banc d'Arguin ($c\alpha_j = 0.21$) and the Dutch Wadden Sea ($c\alpha_j = 0.22$).

6.5 Discussion

The effects of constraints on intake rates and their variations

The present study revealed contrasting trends between the temperate areas and the tropical mudflat studied, and highlighted different constraints operating over diet composition, intake rate levels and variability depending on the study site (Fig. 6.3, Table 6.5). In the temperate areas, temporal variability decreased when the total biomass, the harvestable biomass and the predicted intake rates were

TABLE 6.4: Variability of total biomass, harvestable biomass and predicted Intake Rates for main species in the Dutch Wadden Sea area, the Pertuis-Charentais and the Mauritanian Banc d'Arguin. Variability is expressed through the temporal CV among years ($c\alpha i$); the spatial CV among sub-regions ($c\beta j$); and the CV of the interaction between the two ($c\alpha\beta ij$); μ represents the mean density ($gAFDM_{flesh} \cdot m^{-2}$) or predicted Intake Rates ($mgAFDM_{flesh} \cdot s^{-1}$).

Region	CV	All	ANA	ABR	CER	DIP	DOS	HYD	LOR	MAC	SCR
TOTAL BIOMASS											
Dutch	$c\beta j$	0.58	-	1.62	0.66	-	-	1.07	-	0.56	1.31
Wadden	$c\alpha i$	0.45	-	0	0.51	-	-	0.37	-	0.28	0.36
Sea	$c\alpha\beta ij$	0.57	-	1.04	0.69	-	-	0.73	-	0.25	0
	μ	8.45	-	0.09	6.93	-	-	0.34	-	0.89	0.20
Pertuis	$c\beta j$	0.10	-	0.49	1.31	-	-	0.87	-	0.63	0.48
Charentais	$c\alpha i$	0.22	-	0.33	0.38	-	-	0.14	-	0.31	0.14
	$c\alpha\beta ij$	0.20	-	0.50	0.78	-	-	0.32	-	0.26	0.18
	μ	8.91	-	0.05	0.59	-	-	3.89	-	0.30	1.08
Banc	$c\beta j$	0.57	0.64	0	-	0.30	0.18	0.90	0.28	-	-
d'Arguin	$c\alpha i$	0.16	0.18	0.93	-	0.50	2.08	1.74	0.16	-	-
	$c\alpha\beta ij$	0.33	0.38	0.68	-	0.21	0.28	0	0.16	-	-
	μ	55.74	50.22	<0.01	-	0.34	0.59	0.05	4.55	-	-
HARVESTABLE BIOMASS											
Dutch	$c\beta j$	0.79	-	1.63	0.33	-	-	1.07	-	0.82	0.77
Wadden	$c\alpha i$	0.36	-	0.27	1.46	-	-	0.37	-	0	0.24
Sea	$c\alpha\beta ij$	0.97	-	1.06	3.28	-	-	0.73	-	0.68	49.45
	μ	0.76	-	0.06	0.17	-	-	0.34	-	0.18	<0.01
Pertuis	$c\beta j$	0.83	-	0.49	0.75	-	-	0.87	-	0.50	0.40
Charentais	$c\alpha i$	0.14	-	0.31	0.19	-	-	0.14	-	0.05	0.50
	$c\alpha\beta ij$	0.31	-	0.49	0.42	-	-	0.32	-	0.47	0.84
	μ	4.03	-	0.05	0.01	-	-	3.89	-	0.05	0.03
Banc	$c\beta j$	0.23	<0.01	<0.01	-	0.52	0.26	0.90	0.26	-	-
d'Arguin	$c\alpha i$	0.13	0.92	0.92	-	0	0.47	1.52	0.23	-	-
	$c\alpha\beta ij$	0.25	0.18	0.79	-	0.68	0	0	0.24	-	-
	μ	3.24	0.05	<0.01	-	0.05	0.13	0.04	2.97	-	-
PREDICTED INTAKE RATE											
Dutch	$c\beta j$	0.84	-	1.56	0.46	-	-	1.11	-	0.46	0.74
Wadden	$c\alpha i$	0.22	-	0.40	0.83	-	-	0.51	-	0.17	1.87
Sea	$c\alpha\beta ij$	0.44	-	0.96	1.39	-	-	0.78	-	0.71	0.58
	μ	0.26	-	0.02	0.01	-	-	0.16	-	0.06	<0.01
Pertuis	$c\beta j$	0.07	-	0.66	0.50	-	-	0.08	-	0.62	0.69
Charentais	$c\alpha i$	0.03	-	0.27	0	-	-	0.04	-	0.45	0.39
	$c\alpha\beta ij$	0.11	-	0.39	0	-	-	0.12	-	0	0.66
	μ	0.85	-	<0.01	<0.01	-	-	0.83	-	<0.01	<0.01
Banc	$c\beta j$	0.13	<0.01	0	-	0.64	0.36	0.90	0.14	-	-
d'Arguin	$c\alpha i$	0.21	0.86	0.91	-	0	0.34	1.22	0.04	-	-
	$c\alpha\beta ij$	0.14	<0.01	0.80	-	1.09	0.31	<0.01	0.04	-	-
	μ	0.17	<0.01	0.01	-	0.01	0.05	0.02	0.08	-	-

ANA: *Anadara senilis*; ABR: *Abra tenuis*; CER: *Cerastoderma edule*; DIP: *Diplodonta sp.*; DOS: *Dosinia isocardia*; HYD: *Peringia ulvae*; LOR: *Loripes lucinalis*; MAC: *Macoma blathica*; SCR: *Scrobicularia plana*.

considered successively, suggesting variability in intake rates to originate 'upstream', in the availability of the prey species in the environment (densities, accessibility or sizes). However, for the Banc d'Arguin, the predicted intake rates were more variable than the total and harvestable biomasses suggesting that variability in intake rates is primarily the consequence of other constraints such as digestive quality or toxicity of the prey (Table 6.5).

In the Dutch Wadden Sea, harvestable biomass was relatively low. Intake rates were primarily limited by the relatively poor harvestable biomasses (four to five times lower than in the Mauritanian and the French sites respectively). Harvestable biomass also showed higher temporal variability compared with the other two sites. This could be explained by the important variability of accessibility and recruitment depending on the year in this area, linked to wider variations in temperatures (Zwarts and Blomert, 1992; Zwarts and Wanink, 1993) and possibly acting as a major determinant of prey availability there (Fig. 6.1, Fig. 6.3). For instance, the relatively larger share of *C. edule* in the harvestable biomass and predicted diet in 2011 could be explained by a successful recruitment event, after which a large number of good sized individuals were present. However, the share of *C. edule* in the harvestable fraction in 2011 compared with the predicted diet in the same year revealed that birds positively selected the more qualitative *P. ulvae* over the hard-shelled *C. edule* (Bijleveld et al., 2015). Apart from the limited harvestable food abundance which *de facto* limits intake rates, recruitment variability as well as quality also played a role in prey selection and diet composition.

In the French Pertuis Charentais, harvestable food was high compared to the Dutch Wadden Sea and the Mauritanian Banc d'Arguin. However, temporal variability of intake rates was very low ($\text{co}_j = 0.04$). Both high intake rates and low intake rate variability can be explained by the fact that birds face a digestive constraint on their very abundant and nearly unique prey: *P. ulvae*. Indeed, for a digestive processing capacity c of $4.1 \text{ mgDM}_{shell} \cdot \text{s}^{-1}$ (Table S2), theoretical maximum intake rates on *P. ulvae* (under a *quasi* mono-specific diet in France), are expected to be around $4.1 \times (e/k) \approx 0.86 \text{ mgAFDM} \cdot \text{s}^{-1}$ (see Table 6.6 for details concerning values of e and k of French *P. ulvae*). Because this prey is potentially present *ad libitum* every year in the Pertuis Charentais (with no account of intra or interspecific competition), intake rates were stable over time since they were always capped to this maximum plateau set by digestive capacity. In addition, results show that about half the *P. ulvae* individuals in the Pertuis Charentais would not be used in the diet, compared to only 15% and 35% in the Dutch Wadden Sea and Mauritanian Banc d'Arguin respectively, supporting the fact that

TABLE 6.5: Characteristics of harvestable food in terms of mean biomass and temporal variability; major constraints operating on intake rates in the three study sites: The Dutch Wadden Sea, the French Pertuis Charentais and the Mauritanian Banc d'Arguin; temporal variability of the predicted intake rates

Site	Harv. food	Intake rate (IR)	IR variability
Dutch Wadden Sea	Low ($\mu = 0.76 \text{ g}_{AFDM} \cdot \text{m}^{-2}$), medium variability ($c\alpha i = 0.36$)	Not digestively constrained, intake rates are limited by low harvestable resources	Medium ($c\alpha i = 0.22$)
French Pertuis Charentais	High ($\mu = 4.03 \text{ g}_{AFDM} \cdot \text{m}^{-2}$), low variability ($c\alpha i = 0.14$)	Digestively constrained on the only prey: <i>P. ulvae</i>	Very Low ($c\alpha i = 0.03$)
Mauritanian Banc d'Arguin	High ($\mu = 3.24 \text{ g}_{AFDM} \cdot \text{m}^{-2}$), low variability ($c\alpha i = 0.13$)	Digestively constrained on a major prey that is toxic: <i>L. lucinalis</i>	Medium ($c\alpha i = 0.21$)

knots feed *ad libitum* on this plentiful prey in the French site (Bocher et al., 2007; Quaintenne et al., 2010; Bocher et al., 2014b), see Table 6.6.

On the other hand, in Mauritania, temporal variability was comparable between the total biomass and the harvestable biomass. However, the additional toxic constraint induced by the ingestion of *L. lucinalis* may have amplified the effects of the relative variations between the two principal prey in the diet (*i.e.* *Dosinia isocardia* and *L. lucinalis*), resulting in more variable intake rates over time (van Gils et al., 2011, van Gils et al., 2013; Ahmedou Salem et al., 2014). In Mauritania, the major constraint operating on intake rates and diet choice seems to be the toxic constraint induced by a second-choice prey: the sulphur-rich *L. lucinalis* (Table 6.5). This result matches the conclusions of an earlier study (van Gils et al., 2013). An essential hypothesis in biogeography is that prey defenses are better developed in tropical areas where predator-prey interactions are more intense (MacArthur, 1972). Earlier studies revealed higher toxicity, or lower palatability in tropical marine and salt-marshes and freshwater plants compared with higher latitudes (Pennings, Siska, and Bertness, 2001; Bolser and Hay, 1996; Morrison and Hay, 2012). The present study is adding strength to this hypothesis, in our case, concerning molluscs however our conclusions concerning the major constraints operating on prey selection should be mitigated since the selection of one prey species depends on the availability/quality/toxicity of others, and prey selection is context dependent (van Gils et al., 2011; Onrust et al., 2013).

In a rich environment, a specialised diet yields higher intake rates, more stability over time

Results concerning predicted intake rates and diet composition in the three study sites revealed that the French Pertuis Charentais provides more constant and

higher intake rates than the Dutch Wadden Sea or the Mauritanian Banc d'Arguin. Mean predicted intake rates in France are high, and yield more than three times more energy per unit time than the maintenance metabolism required in January there ($0.24 \text{ mgAFDM} \cdot \text{s}^{-1}$) (Wiersma and Piersma, 1994; Quaintenne et al., 2011). However, in the Banc d'Arguin, the mean predicted intake rate is lower than the maintenance costs red knots incur during winter. Red knots adjust their feeding ecology to the availability of mollusc prey. Because the Banc d'Arguin is located in the tropics, biodiversity of molluscs is higher there than in temperate mudflats (Stevens, 1989; Rex et al., 2005), and red knots' diet is likely to be composed of more species. A varied diet may spread the risk of resource variability and yield more predictable intake rates over time. However, as revealed by the present study and a review of 161 earlier studies, it is not always the best option (Lefcheck et al., 2013). When the preferred prey is abundant, alternative prey are left alone, resulting in a more specialised diet. Surprisingly, this highly specialised diet yielded more stable intake rates over time in the French Peruis Charentais than varied diets in the Mauritanian Banc d'Arguin or the Dutch Wadden Sea.

It is believed that inter-annual variability in a tropical mudflat is lower than in temperate areas where harsh winters can cause dramatic decrease in food resources for shorebirds (Beukema et al., 1993; van der Meer, Beukema, and Dekker, 2001; Strasser et al., 2003). The present study revealed that total biomass is indeed more stable over time in the tropics compared with temperate mudflats. However, when additional constraints affecting prey selection are included (e.g. quality, toxicity), intake rates are more variable in the tropics compared with the temperate overwintering areas. This result is consistent with a previous study showing important seasonal variations in intake rates in the Banc d'Arguin (Ahmedou Salem et al., 2014). However, conclusions concerning temporal variability in the Dutch Wadden Sea and in the Banc d'Arguin might be alleviated given the medium term changes these two environments are facing (pers. observations).

When diet composition reflects environmental change

The variations in species composition of both total and harvestable biomass reflected trends already described in the literature especially for *C. edule* and *Macoma balthica* biomasses in the Dutch Wadden Sea (Kraan et al., 2007; Compton et al., 2016), but also for *D. isocardia*, in the Mauritanian Banc d'Arguin (van Gils et al., 2013, van Gils et al., in prep or Chapter 7). The example of the Banc d'Arguin also revealed a decrease in the total predicted intake rates and in particular a

progressive reduction of the share of *D. isocardia* in the diet, already detectable in the harvestable fraction and total fraction in the ecosystem. With less *D. isocardia* and more *L. lucinalis* in the diet, these results might illustrate a dietary change in Mauritania. Indeed, recent studies detected a decrease in the number of *D. isocardia* in the environment and in the diet of the shorebirds, together with the increase of second choice prey, including *L. lucinalis* and seagrass *Zostera noltei* (van Gils et al., [in prep](#)). These examples show that the temporal variability of intake rates may be biased by potential regime shifts in the Dutch Wadden Sea (Compton et al., [2016](#)) as well as in Mauritania (pers. observations). This study empirically illustrated that variations in biomass might affect diet composition more than biomass itself. However, changes in the environment may not always be detectable in the diet of predators, as the harvestable fraction and intake rates, through multiple successive constraints, could potentially act as many buffers from change. For example, variations in densities may not always be reflected in the diet as intake rate can decline with increasing prey density, as illustrated by recent studies (Bijleveld et al., [2016](#)). However, the present study seems to support the idea that diet changes in the red knots reveal ecological changes in their migratory sites.

Why are there so many birds in Mauritania?

Relative to the harvestable resources and maintenance costs (Piersma, Goeij, and Tulp, [1993](#)), predation pressure is higher in Mauritania than in the European wintering sites (Zwarts et al., [1990](#)), with a density of feeding shorebirds between 15 and 20 birds/ha recorded in past studies (Engelmoer, Piersma, and Altenburg, [1984](#); Piersma, [1989](#); Zwarts et al., [1990](#)), and *c.* 7 red knots/ha *f* in the present study (Table [6.1](#), [6.2](#)). This discrepancy between relatively low amounts of harvestable food compared to the large numbers of predators in Mauritanian Banc d'Arguin is still puzzling the community. In the '80s and early '90s, an hypothesis was developed in order to explain such high numbers of shorebirds in the area: the stability of the environment there (*i.e.* mainly the absence of harsh winters and the seasonal stability of physical conditions, Wolff and C.J., [1984](#); Wolff, [1991](#)). Since the results of the present study revealed higher temporal variability in predicted intake rates in Mauritania than in two other temperate mudflats, this hypothesis could not be supported. Of course many other elements play a role in shorebirds' distribution and migratory route, among which include predation pressure, energy budget and breeding location (Piersma, Goeij, and Tulp, [1993](#); Bauer, Ens, and Klaassen, [2010](#)), and even more cryptic elements such as vertical distribution of food resources for instance (Mathot, Smith, and Elner,

TABLE 6.6: Characteristics of *P. ulvae* in each study site: mean energy contained in the flesh (e), mean ballast mass contained in the shell (k) in the environment, handling time as set in the 'digestive rate model', mean biomass densities, with associated average length in the diet and in the environment

Parameter	Wadden Sea	Pertuis-Charentais	Banc d'Arguin
Metabolizable energy $e(gAFDM_{flesh})$	0.0010	0.0011	0.0012
Ballast mass $k(gDM_{shell})$	0.0035	0.0046	0.0056
Handling time h (s)	0.33	0.33	0.33
Mean available density $n(gAFDM.m^{-2})$	0.76	4.03	3.24
Average length (in diet) l (mm)	2.9600	3.1747	3.8021
Average length (available) l (mm)	3.2024	3.6494	3.9567
% individuals included in the diet	85%	49%	65%

2007). Temperature for instance is a major driver of wintering migrations, and although Banc d'Arguin does not seem to be attractive in terms of available food resources, it is attractive in terms of temperatures. However, we think that the results presented in this study might not reflect long-term conditions but a potential regime shift operating in the Mauritanian Banc d'Arguin. Therefore the high densities of red knots observed in Mauritania might be the reflection of more stable long-term conditions in the past, since developmental constraints, as well as phylogenetic constraints may slow down the responses of top predators to environmental changes (Stephens and Krebs, 1986). As advocated by the theory of the trophic mismatch (Edwards and Richardson, 2004), and because predators usually are of larger size and have lower generation times than their invertebrate prey (Pianka, 1970; Pianka, 2011), predator densities may not always match the densities of their resources. Recent studies concerning the ecology of the red knots revealed the impact of changing resources, in the breeding grounds as well as in overwintering grounds, on the survival of red knots (van Gils et al., in prep, van Gils et al., 2016). Other studies highlighted the importance of food conditions in non-breeding grounds for the fitness of migratory bird species (Alves et al., 2013; Cooper, Sherry, and Marra, 2015; Clark, 2015). In the long-term, the increasing mortality of *C. c. canutus*, might unfortunately make bird numbers match more closely decaying feeding conditions (Intake rates) in their major overwintering area. However, two recent studies also revealed that red knots could adapt, to a certain extent, their feeding behaviour and phenotype in response to environmental changes (van Gils et al., in prep, van Gils et al., 2016), providing fuel to the idea that animals accept adaptability at the expense of predictability (Provenza and Cincotta, 1993).

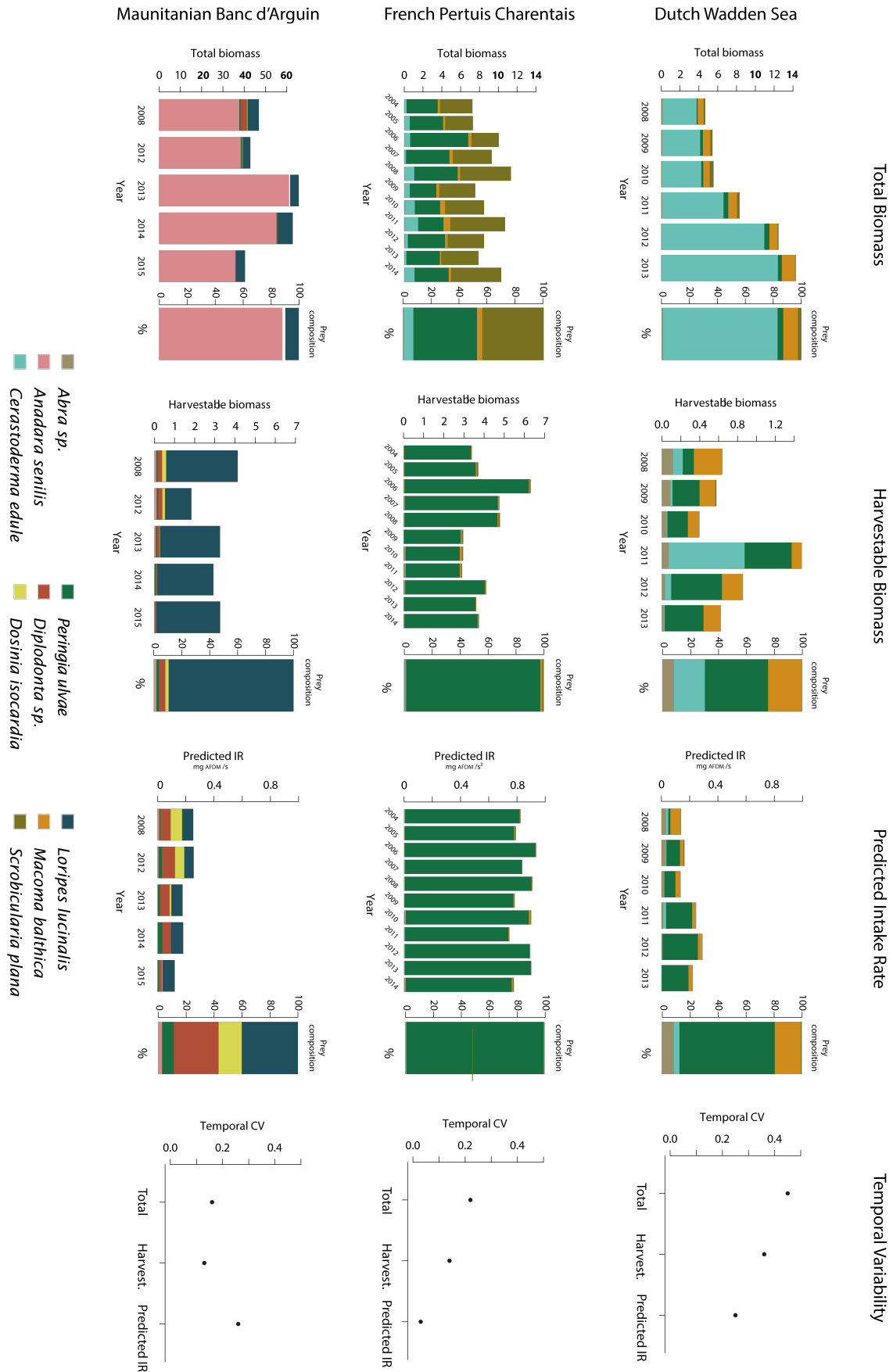


FIGURE 6.3: Total mollusc biomass composition ($gAFDM.m^{-2}$), harvestable biomass composition ($gAFDM.m^{-2}$) and share of each prey species in the predicted intake rates ($mgAFDM.s^{-1}$) in the French Pertuis Charentais, the Mauritanian Banc d'Arguin and the Dutch Wadden Sea; On the right, temporal variability (expressed through coefficients of variation) for the total biomass, harvestable biomass and predicted intake rates on the three sites.

Box 3

DOES SITE PREFERENCE BY SHOREBIRDS REFLECT FEEDING CONDITIONS?



FIGURE 6.4: LPO staff counting shorebirds in Moëze-Oléron Nature Reserve

Introduction

Do the birds respond, in terms of site preference, to changes in food resources? This question seems reasonable on a small spatial scale like the region Pertuis-Charentais. Since birds are likely to be able to collect information and assess food conditions in both bays, we hypothesize that they might respond to relative changes in feeding conditions between Marennes-Oléron Bay and Aiguillon Bay (see study region map in Chapter 3, Fig. 1). Here we propose to step on previous results (see Chapter 6) and investigate whether shorebirds change their site preference, on a regional scale, depending on feeding conditions between 2004 and 2014.

- BIRD COUNTS AND SITE PREFERENCE

Methods : In January each year, annual mid-winter counts of the Wetlands International Programme are performed and synchronized between the Nature Reserves of Aiguillon Bay and Moëze-Oléron Bay. In Marennes-Oléron Bay, birds are counted on their roosts around high tide during spring tides every January. In Aiguillon Bay, high tide roost sites are more scattered, therefore birds are directly counted on the mudflat at incoming tide, on the same day as in Marenne-Oléron Basin. Here we

analyse the variations in red knot (*Calidris canutus*) counts between January 2004 and January 2014. We also calculate site preference between our two subregions (*i.e.* Marennes-Oléron Basin, 'MAROL' and, Aiguillon bay, 'AIG'). Bird density is assessed for each year and each site, taking account of the mudflat area ($a_{Aig} = 2,870ha$ for Aiguillon Bay and $a_{Marol} = 3,700ha$ for Marennes-Oléron Bay). Then, for each year (i), mean density over the study region of bird counts is assessed as follows :

$d_{i,Marol+Aig} = \frac{n_{i,Marol}+n_{i,Aig}}{a_{i,Marol+Aig}}$. On year i , the preferred site would be the site with a bird density $d_{i,site} = \frac{n_{i,site}}{a_{i,site}}$ larger than the mean density of the study region ($d_{Marol+Aig}$, if all the counted birds would be homogeneously distributed on the studied area). Site preference for year (i) at a given site a ($Pref_{i,sitea}$) is expressed as the percentage of difference between density of birds at site a and year i and the mean density of birds in the study region ($d_{i,sitea}$). Site preference can vary between -100% (absolute rejection of the site) and +100% (absolute preference for the site): $Pref_{i,sitea} = \frac{100 \times (d_{i,sitea} - d_{Marol+Aig})}{d_{Marol+Aig}}$. This way, site preference is expressed irrespective of global trends in the species population.

Results : Over the study period, red knot counts in Marennes-Oléron were often superior to the counts in Aiguillon Bay, the sum of the counts varied between 14,000 and 28,000 individuals, Fig. 6.5. Site preference varied between 61 % rejection in Aiguillon Bay in January 2010 and 47 % preference in Marennes-Oléron Bay in January 2010, Fig. 6.5.

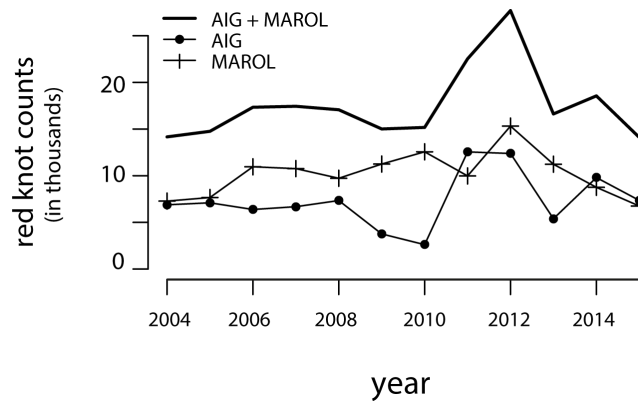


FIGURE 6.5: Annual counts of *Calidris canutus*, in Marennes-Oléron Bay, Aiguillon Bay

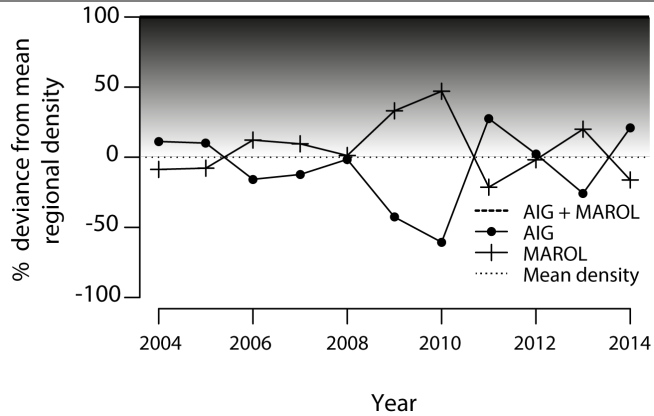


FIGURE 6.6: Site preference of *Calidris canutus* between Marennes-Oléron Bay and Aiguillon Bay

- FEEDING CONDITIONS

Methods : Feeding conditions are measured through predicted intake rates, calculated thanks to a Digestive Rate Model adapted to the red knot and our study sites (Hirakawa, 1995, van Gils et al., 2005b, the same values as in Chapter 6 are used). All details concerning the benthos sampling supporting this study and the determination of the harvestable fraction for the red knot can be found in Chapters 3 and 6. The difference between the sites' mean predicted intake rates (for a given year) will be used as a measure of the difference of feeding conditions between the two bays. As mentioned in Chapters 3 and 6, no data is available for this analysis in Marennes-Oléron Bay in 2010 and 2011.

Results : Mean predicted intake rates varied between $0.69 \text{ mgAFDM} \cdot \text{s}^{-1}$ (Marennes-Oléron, 2014) and $1.07 \text{ mgAFDM} \cdot \text{s}^{-1}$ (Aiguillon, 2006), Fig. 6.5. Marennes-Oléron nearly always showed higher intake rates.

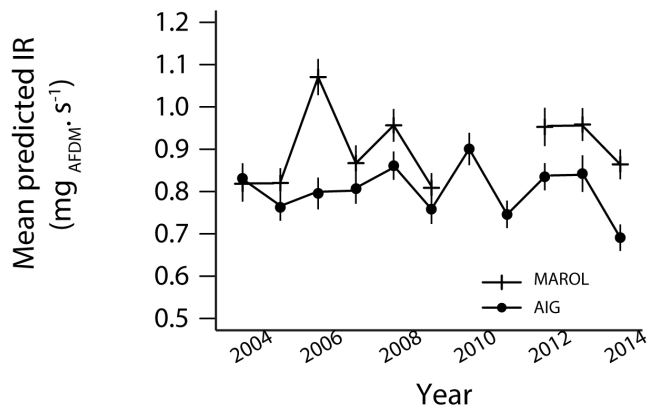


FIGURE 6.7: Variations of mean predicted intake rates in the study sites, with associated *s.e.*

Discussion:**Impact of changing feeding conditions on site preference**

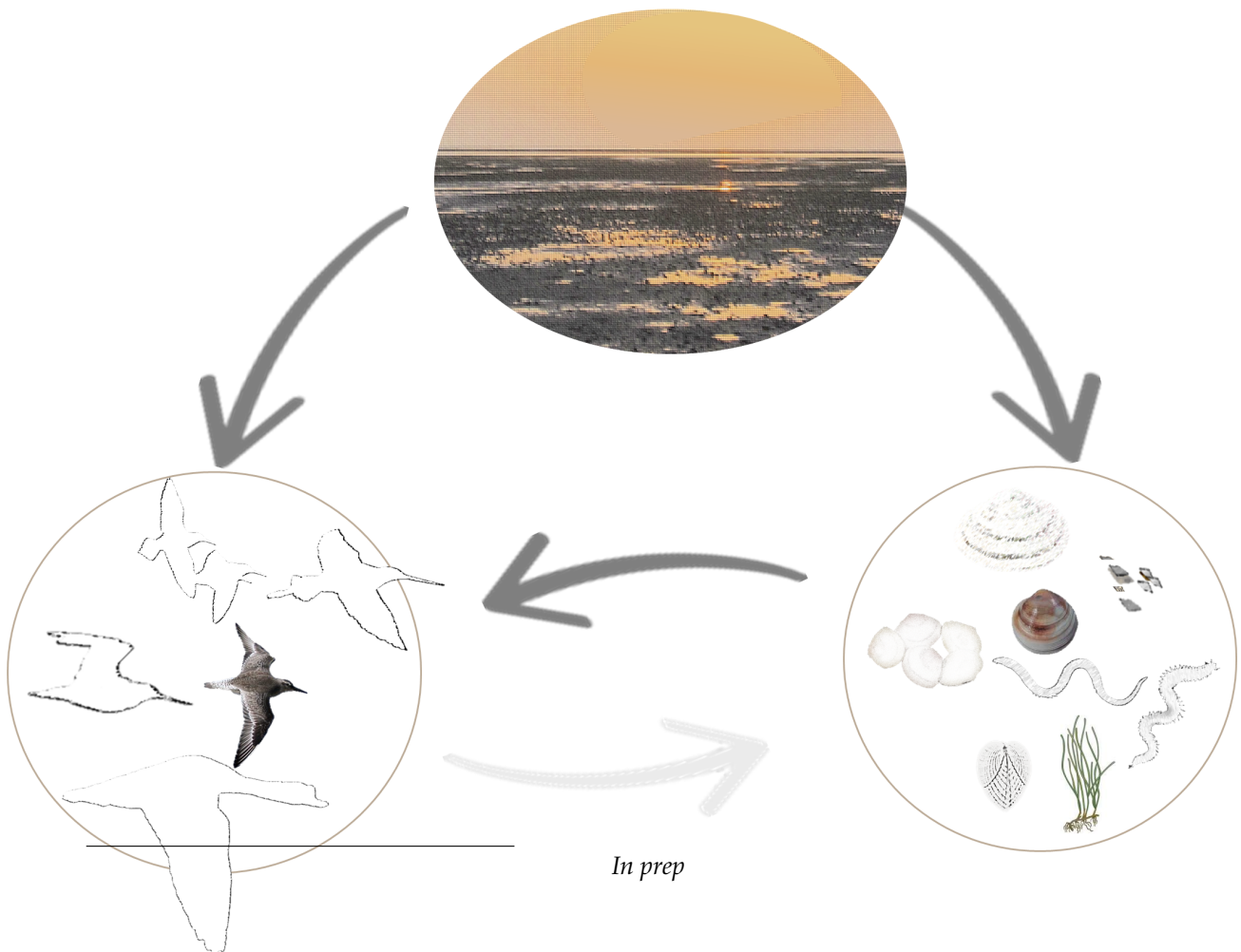
In January each year, red knot counts reached 14,000 to 28,000 individuals in our two study sites; densities observed on the feeding and roosting areas by the Nature Reserve (LPO) each month are among the highest recorded (Santos, Granadeiro, and Palmeirim, 2005), making the Pertuis Charentais an essential migrating site for this species. Depending on the year, birds can be equally distributed between Marennes-Oléron Bay and Aiguillon Bay, with sometimes high preference/rejection for one site over the other. We investigated whether these changes in site preference reflect changes in feeding conditions in our study sites. By means of simple statistical tools (correlation coefficients, regression curves) we analysed the correlation between red knots numbers and their predicted intake rates. Namely, we tested whether bird densities are higher at site *a* (via the measured site preference presented in Fig. 6.5) when predicted intake rates at site *a* are superior to predicted intake rates at site *b* (using the difference between sites from the results presented in Fig. 6.5). No correlation was shown between site preference and relative predicted intake rates in our study sites (Person coeff. = -0.26) and there was no significant linear relationship between both variables (Anova, p .value > 0.3). Results suggest that food abundance does not determine the preference of red knots, or not only. This result is not surprising as site preference in one site depends on a variety of factors not taken into account in the present insert: *e.g.* intra and inter-specific competition, interference, disturbance - by hunters, of other leisure activities-, predation by birds of prey (Sutherland, 1996). Distribution of birds between estuaries or intertidal mudflats may be determined by larger-scale processes (Gill, 2012). Answering this research question would require more complex models, including measures of competition, disturbance and predation; lines of research that have never been taken in our study sites yet.



Chapter 7

Using herbivory by 'predators' as a behavioral indicator of survival prospects

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7.1 Abstract

Optimality models have been useful in understanding diet choice for species being either herbivore or carnivore. Here we report on a diet study in the red knot (*Calidris canutus*), a shorebird that was long known as a molluscivore specialist but surprisingly turned out to include plant material in its diet. We show that red knots consume plant material (seagrass rhizomes) on a regular basis, and increase significantly their consumption when more profitable molluscs are getting scarce. This was true in an indoor experiment and in 11 years of stable-isotope data on > 1,000 free-living birds. The critical mollusc density below which red knots consumed seagrass matched with theoretical optimal diet predictions using mollusc and seagrass profitabilities as inputs. We discuss how the vegetable contribution to the diet of supposedly true carnivores might be used as a behavioral indicator of habitat quality and even a warning signal for increased mortality .

7.2 Introduction

Each year, about 300,000 Afro-Siberian red knots (*Calidris canutus canutus*, Delaney et al., 2009; Spaans et al., 2011) fly a distance of more than 10,000 km to overwinter on the protected mudflats and seagrass meadows of Parc National du Banc d'Arguin (PNBA, Mauritania). During eight months, they rely on the food resources and habitat quality of PNBA, where they form one of the most abundant bird populations.

Except during the breeding season when they feed on small insects, their diet is mainly composed of small bivalves (< 15mm length) and gastropods living in the soft sediments of intertidal areas (Piersma et al., 1993). Through the advanced study of its feeding behaviour, it has become a scientific model to investigate changes in migration routes and timing (Leyrer et al., 2009; Shamoun-Baranes et al., 2010), phenotypic flexibility (Piersma and van Gils, 2011), population dynamics and survival (Spaans et al., 2011), diet selection (Quaintenne et al., 2010; Onrust et al., 2013), habitat choice (Kraan, 2010; Quaintenne et al., 2011), and by extension, the ecology of its migratory sites (e.g. the Wadden sea, the Pertuis-Charentais and the PNBA).

Every year at the end of the summer, red knots (*canutus* subspecies) fly to PNBA (Stroud et al., 2004), where they spend 8 months in seagrass-covered mudflats. The red knots are known to feed preferably on the two most abundant bivalve species: the hard-shelled *Dosinia isocardia*, and the sulfur-rich *Loripes lucinalis* (Honkoop et al., 2008; van Gils et al., 2011), a toxic prey causing diarrhea (van Gils et al., 2013; van der Heide et al., 2012; Johnson and Fernandez, 2001). In this study we described and tried to explain a newly observed feeding behavior of red knots in PNBA: seagrass consumption (*Zostera noltei*).

Since 2012, we have gathered a body of evidence for this herbivory behavior (direct observations in the field and during indoor experiments, reconstruction of diet from faeces, stomach contents, videos, and isotopic calibration from blood samples (Jan van Gils, Piet van den Hout, Thomas Oudman, Eva Kok, Marwa Kavelaars, Theunis Piersma, unpublished data). This consumption of seagrass *Zostera noltei* is intriguing. A basic diet choice experiment prior to this study clearly showed the preference of red knots on seagrass roots and rhizomes (below-ground parts) rather than on leaves when offered the two at the same time, supporting the fact that "Herbivorous birds capable of flight must always be highly selective and consume plant parts that are relatively high in protein and low in fibers, such as rhizomes" (quoted from Klasing, 1998). We therefore supposed that an important part of the diet of red knots in PNBA is composed of roots and rhizomes

of seagrass *Zostera noltei*, in addition to bivalves (their exclusive diet in all other wintering areas).

Strict herbivory is highly challenging since it brings much more digestible carbohydrates, indigestible fibers, and much less proteins and lipids than insectivory which explains why few avian have adapted to it (Klasing, 1998). The energy intake rate of knots is limited by its digestive processing rate (van Gils, 2004; van Gils et al., 2005b). Here, we question how feeding on such low-nutrition food can be optimal for the digestively constrained red knots in PNBA and what may be the consequences of this behaviour on survival.

In order to explain this unusual behaviour for shorebirds, six red knots were individually offered natural patches with a constant seagrass density. Into these patches, varying numbers of the *L. lucinalis* were introduced as treatments. We determined the energy contents of *Loripes* and seagrass for each experimental patch. We could derive main values describing the functional response of the red knot on seagrass (intake rates, handling times, profitability), and analyse their diet changes under different experimental conditions.

Additionally, diet composition was derived from Carbon and Nitrogen isotopic analyses and the contribution of seagrass to the diet was assessed for > 1,000 birds, captured from 2003 to 2013. In parallel, bivalve densities in the system were evaluated from a long-term monitoring, and intake rates on bivalves (both *D. isocardia* and *L. lucinalis*) were estimated using a Digestive Rate Model adapted to this subspecies (Hirakawa, 1995, van Gils et al., 2005b). Then, survival rates from other studies on this subspecies (in the same study area, and time period) were provided to highlight our results.

Two hypotheses can be tested. Under the first hypothesis (the detoxication hypothesis), red knots feed on seagrass to detoxicate their organisms after the ingestion of the sulphur-rich *Loripes*, the more so when densities of the bivalve is increasing). Under the second hypothesis, seagrass is expected to be a poorly nutritious and harder to digest food item, compared with the bivalve *Loripes lucinalis*. Hence, birds are expected to feed on seagrass only in the absence of other prey in the system, in order to optimize their long-term intake rate. Red knots fed on seagrass at every density proposed, and increased their intake rate when densities of *L. lucinalis* decreased. Combined results from diet reconstruction from modelling and from isotopic analysis revealed that red knots consume more seagrass when densities of bivalve in the system are not sufficient. Hence, seagrass consumption is a second-choice feeding behaviour. Between 2003 and 2013, bivalve densities decreased in the PNBA in favour of an increase share of *Zostera noltei* in the diet (isotopic analyses + modelled diet composition). Our

TABLE 7.1: AFDM of the prey inserted in the patches: *Loripes lucinalis* and seagrass item

Type of item	AFDM (mg)
Roots and rhizomes	3.575
<i>Loripes</i> (8 mm \pm 5 mm)	8.773

preliminary results reveal seagrass consumption to be negatively correlated with survival estimates. We discuss whether this newly described feeding behaviour can be a warning signal for habitat degradation and population decline in shorebirds.

7.3 Methods

7.3.1 Experiment

On 12 January 2013, 58 red knots were caught by cannon-netting on Zira, a small island in the midst of the study area (19°52'N; 16°18'W), in PNBA, Mauritania. From these birds, six adult individuals were randomly chosen (see Table 7.1 & Table 7.2) and kept as experimental birds (5 males and 1 female, as determined later by molecular sexing). The birds were kept indoors at the Iwik research station in a holding pen measuring 1.5 \times 1.0 \times 0.5 m. They were given freshwater and a mixture of daily collected bivalve species as staple food, mainly being *Senilia senilis* (flesh only) and *Loripes lucinalis* which were much easier to collect on a daily basis than *D. isocardia*, see more housing methodology in Onrust et al., (2013) and Oudman et al., (2014). Body mass of the birds was monitored daily (see Table 7.3), and the amount of staple food offered was adjusted accordingly (the birds were kept at a mass of 80-112 g). About six hours prior to the daily start of the trials, staple food was removed in order to motivate them to feed at a maximum rate during the trials. The experiment ran from 23 January till 2 February 2013, during 11 consecutive days. After the experiment was finished, the birds were given *ad libitum* *Senilia* flesh for a few days before being released. AFDM contents were determined for the prey, and converted to intake rates expressed in items/sec to intake rates expressed in mg AFDM/sec, see Table 7.1. In each experimental trial, a single bird fed in a seagrass-covered patch (diameter 20 cm, height 10 cm), which contained a manipulated initial bivalve density (0, 10, 30, 50 or 150 per patch), see Fig. 7.1. The bivalve species offered was *Loripes lucinalis*, of which items of a single size class (shell length 8 \pm 0.5 mm) were randomly distributed over the patch, which were then pushed into the sediment to a fixed burial depth of 3 cm using a small rod (following methodology in Piersma et al., 1995). These *Loripes* were collected daily at Abelgh Eiznaya (located 2 km

TABLE 7.2: Identity and biometry of the experimental birds

Identification		Biometry						
Metal ring	Color ring	Wing length (mm)	Bill length (mm)	Total head (mm)	Tarsus (mm)	Tarsus plus toe (mm)	Body mass (g)	Gizzard mass (g)
Z072541	N2RGRR	171	36.9	65.5	33.0	60	116	9.36
Z072543	N2RGRY	162	34.5	62.5	32.4	59	119	8.41
Z072544	N2RGRN	163	33.3	61.6	31.1	59	104	6.53
Z072545	N2RGGG	170	35.0	63.5	32.0	58	109	7.66
Z072546	N2RGGY	177	35.3	63.4	33.2	59	121	8.21
Z072548	N2RGGR	165	34.3	62.4	31.5	59	110	7.95

TABLE 7.3: Body mass variations (in g) during the experiment

Bird ID	mean	SD	min	max
N2RGRR	104.30	±1.25	98	112
N2RGRY	85.83	±1.02	80	93
N2RGRN	89.92	±1.88	82	105
N2RGGG	91.67	±1.11	84	99
N2RGGY	99.92	±0.917	96	106
N2RGGR	89.58	±1.25	84	98

NW from the research station at 19°54'N 16°19'W; Leyrer et al., 2012), and were kept fresh and alive in the refrigerator during the few hours remaining between collection and experimental usage. Each treatment was repeated once for each bird, resulting in a total of 60 trials, results were analysed statistically using a linear mixed effect model (LME, package nlme) with bird-identity as a random factor.

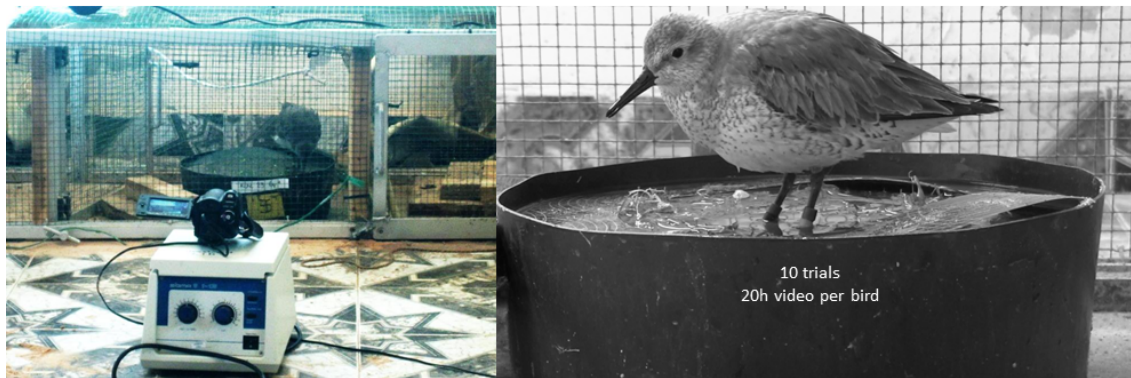


FIGURE 7.1: Feeding experiment on seagrass covered patches. Birds are placed individually into cages with a seagrass patch containing bivalves, each of the six experimental birds is filmed under 5 experimental conditions (different bivalve densities)

Seagrass patches were minutely reconstructed for experimental conditions, see Fig. 7.1. First, a PVC core (diameter 20 cm, height 10 cm) was inserted in the sediment at a random spot in a dense *Zostera noltei* seagrass bed (at Abelgh Eiznaya). Then, before taking out the core, a wooden plate with long nails sticking

through was added on top of the core. Then, the core would slowly be taken out of the sediment, with the nails keeping the horizontal structure of the seagrass rhizomes intact, Fig. 7.2. Then, after turning the patch up-side-down (using the wooden plate as the bottom), a dozen thin wooden sticks were inserted horizontally through premade small holes in the core (ca. 2 cm below the surface), such that a 2 by 2 cm grid would keep the vertical rhizome structure intact during the next step, which was washing out the sediment and bivalve prey in a nearby gully. Next, the core including the washed seagrass was inserted in a larger patch (diameter 30 cm, height 10 cm), which was prefilled with sieved sediment and seawater. Then, the wooden plate and the wooden sticks were removed and the predetermined number of bivalves could be inserted. Before each trial we covered the 5-cm wide edge of bare sand with plastic such that the focal bird would only feed in the seagrass part of the patch.



FIGURE 7.2: Detailed method to make a seagrass patch for the feeding experiments. This technique preserve the horizontal and vertical structure of the rhizomes.

In order to estimate seagrass density in each patch, we followed the procedures outlined by Folmer et al., (2012). A small core (diameter 7 cm) was inserted to a depth of 10 cm just next (20 cm) to the spot where the seagrass patch was collected. The sample was sieved over 500 μm mesh to remove sediment. In the laboratory, detritus was removed and above-ground leaves were separated from below-ground roots and rhizomes. Subsequently, samples were dried at 60° C

for 3 days, weighed (to nearest 0.1 mg, yielding dry mass DM), incinerated at 550° C for 4 h, and weighed again (to nearest 0.1 mg, yielding ash-free dry mass AFDM). In 28 out of the 60 samples we also counted the number of rhizomes, which could later be used to convert rhizome intake to AFDM intake. Similarly, we also determined *Loripes* AFDM on 31 specimens of 8 mm long. The full length of each trial (2 h at most) was recorded on video (Canon VIXIA HG21). In order to prevent interpretation problems due to prey depletion and digestive constraints, we only analysed the first 3 minutes of active feeding (we know that red knots face digestive and toxin constraints after rapidly ingesting about 10-15 prey (Oudman et al., 2014; van Gils et al., 2003); based on earlier experiments and the size of the experimental patch we know that they cannot find this critical amount of prey in just 3 minutes (Piersma et al., 1995). Videos were played back using the Observer XT software (v. 10.0, Noldus Information Technology), which enabled us to assign behavior in slow motion (used when a bird would encounter and handle food) at a temporal precision of 0.04 s. The following behavioral categories were recognized: searching (*i.e.* probing), handling *Loripes*, handling seagrass, resting and disturbance (the latter two behaviors were not considered as active feeding and were thus excluded from the analyses).

7.3.2 Field

Bivalve intake rate

The intake rate on bivalves in the field was predicted by a functional response model using available densities of the two most abundant bivalves as inputs, *i.e.* those of *Loripes lucinalis* and *Dosinia isocardia* (which together make up 80-90% of the diet of red knots on molluscs at PNBA; Onrust et al., 2013). The functional response model used is the so-called Toxin-Digestive Rate Model (TDRM; van Gils et al., 2013), which is a multispecies Holling's type II functional response model taking account of toxin and digestive constraints that red knots face when feeding for multiple hours. Due to a symbiosis between *Loripes* and sulfur-oxidizing bacteria, red knots become mildly intoxicated after consuming considerable amounts of *Loripes*, with diarrhea as the main symptom (Oudman et al., 2014). If not bottlenecked by this toxin's constraints, red knots are often digestively constrained by the rate at which ingested shell mass can be processed (van Gils et al., 2003), *e.g.* when feeding on the non-toxic but thick-shelled *Dosinia* (Oudman et al., 2014; van Gils et al., 2013). Observed diet choices between *Loripes* and *Dosinia* were correctly predicted by this model in the laboratory (Oudman

et al., 2014) and in a 5-yr time series on field diets (van Gils et al., 2013). Furthermore, year-round depletion trajectories matched with this model's predictions (Ahmedou Salem et al., 2014) and red knot annual survival rate in a 7-yr time series correlated significantly with energy intake rate predicted by this model (van Gils et al., 2013).

Predicted energy intake rates for 2003-2010 are published in van Gils et al., (2013); Table S4. For 2011-2013 we collected new data on the available densities of *Loripes* and *Dosinia*. Both in 2011 (Mar-Dec) and 2012 (Jan-Feb) this was done monthly at 16 stations at Abelgh Eiznaya (near one of the two high-tide roosts in our study area), see Ahmedou Salem et al. (2014) for more details.

Additionally, in January 2012 we sampled an extra 16 stations in Baie d'Aouatif, study sector I in van Gils et al. (2015), which is located near the other high-tide roost in our study area (Leyrer et al., 2012).

Diet composition

From 2003 to 2013 we caught red knots, mostly during early winter (Nov/Dec), while some birds were caught in January and April. Catches were mostly done by using mist-nets, except for one catch for which we used canon-nets. Upon capture, birds were tagged using a combination of four color-bands and a flag, allowing individual recognition in the field, yielding estimates of survival rate, see below and Leyrer et al., (2012), Leyrer et al., (2013), and van Gils et al., (2013). Furthermore, body mass and structural size measurements were recorded and from the brachial vein a small blood sample (10-100 μ L) was taken, which was stored in 70% ethanol. At NIOZ, samples were stored at -80°C until analysis. After extracting DNA to molecularly identify each individual's sex (Baker, Piersma, and Greenslade, 1999), the remainder of the sample was used to determine the stable isotope ratios of carbon ($^{13}\text{C}/^{12}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$), expressed as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively, in units of per-mille (‰) difference from the VPDB reference. In order to do so, samples were freeze-dried before analysed in a Thermo Scientific (Flash 2000) element analyzer coupled to a Delta V isotope mass spectrometer. Also the three main food sources of red knots in PNBA were isotopically analysed, being rhizomes of seagrass *Zostera noltei* and two bivalve species *Loripes lucinalis* and *Dosinia isocardia* (earlier work showed that these two bivalve species make up > 80% of the molluscs in a knot's diet; Onrust et al., 2013). Fractionation of isotopes when consumed by red knots was determined in an unpublished experiment in which six captive red knots were fed either *Dosinia* or *Loripes* for a period of three weeks (Ahmedou Salem and van Gils, unpub. data). This showed fractionation values of +6‰ for $\delta^{15}\text{N}$ and

0‰ for $\delta^{13}\text{C}$ for both bivalve species. Although the values for nitrogen fractionation are somewhat higher than reported in the literature (van der Zanden and Rasmussen, 2001), we assumed similar fractionation values in red knots consuming seagrass rhizomes. This value could not be derived experimentally since red knots cannot survive on a 100% seagrass diet.

Survival rate

Survival rates were estimated on the basis of resighting data on red knots, marked and resighted between 2002 and 2013. These individuals were largely the birds described above, plus birds caught during NIOZ's first expedition in Nov/Dec 2002 (as this was the first expedition, we cannot estimate a survival rate over the year 2002 and hence left out the isotope analyses for these birds – the more so because no benthos samples were collected in this first year). Using this dataset, we could estimate survival rate over ten consecutive years (2003-2012; when modelling time dependence, survival rate over the final year, 2013, cannot be separated from resighting rate). For more details concerning the method, refer to van Gils et al., (2016) and Lok et al., (2013).

7.4 Results

In the feeding experiments, bivalve intake rate followed a typical Holling's type II functional response with increasing intake rate under increasing density of bivalves (Fig. 7.3, A), and levelling off to an asymptote. Under the same experiment, seagrass consumption described the opposing trend, with reduced seagrass intake rate under increasing bivalve densities (Fig. 7.3, B). Subsequently, the share of seagrass in the diet decreased under increasing densities of bivalves offered in the patch (Fig. 7.3, C).

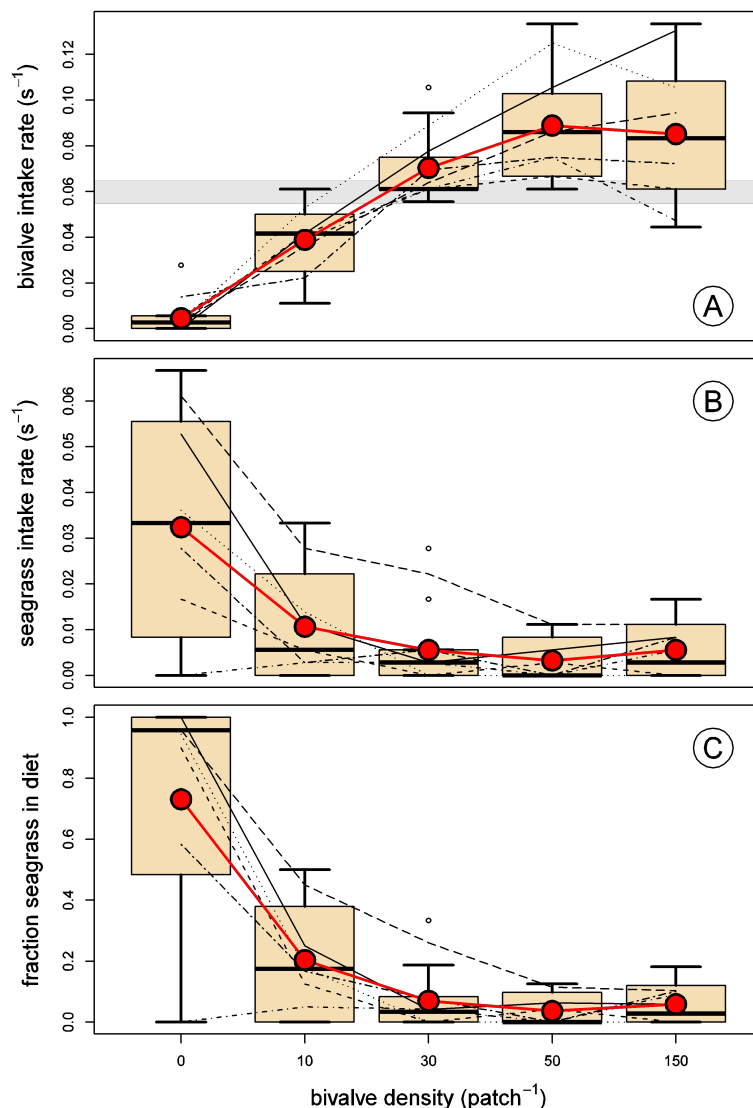


FIGURE 7.3: As a function of experimentally controlled bivalve density the intake rate (items/s) on bivalves increased (A), while the intake rate (items/s) on seagrass declined (B), causing the proportion of seagrass in the diet (from isotopic analyses) to decline (C), with proportion given by (seagrass items)/(bivalve items + seagrass items). In all graphs, thin lines connect individual averages, while red dots connected by red line give overall averages. Gray bar (A) gives critical bivalve intake rate below which red knots should, according to optimal diet theory, include seagrass in their diet (see main text for calculation).

Concerning *in situ* multinannual survey, using benthic monitoring, TDRM and diet composition from isotopic analyses between 2003 and 2013, a negative correlation was found between the share of seagrass in the diet and intake rate on bivalves (Fig. 7.4).

Preliminary results on years 2004 to 2013 revealed a strong negative correlation between the fraction of seagrass in the diet and survival estimates, and a positive correlation between the fraction of bivalves in the diet and survival estimated, Fig. 7.5.

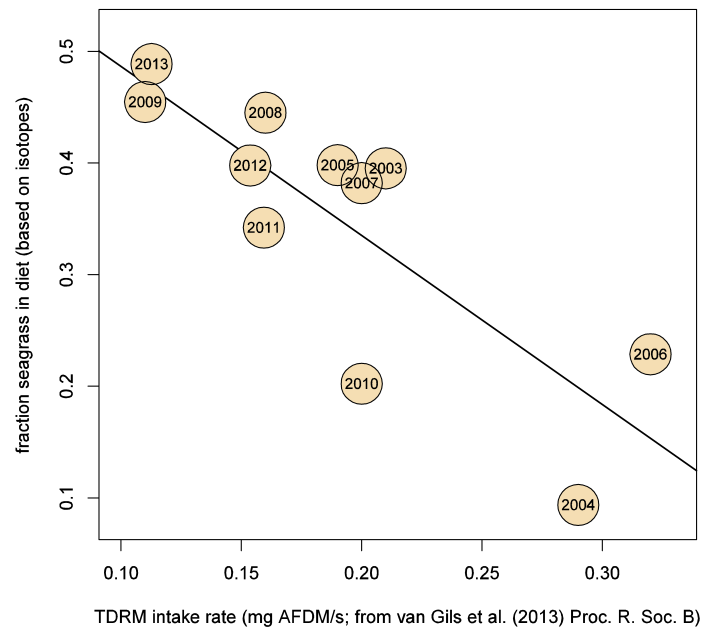


FIGURE 7.4: In a time series of 11 years (2003-2013), the proportion of seagrass in the diet of red knots (inferred from isotope samples) tends to couple negatively with the intake rate predicted when feeding on bivalves only (calculated by the so-called TDRM, see main text).

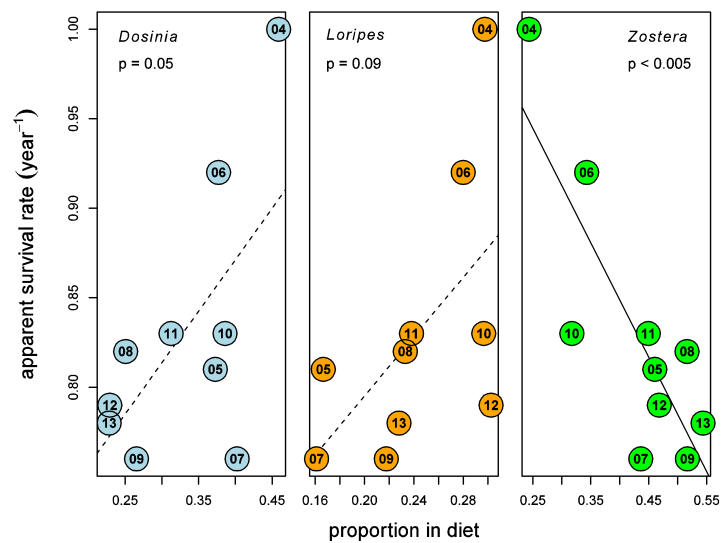


FIGURE 7.5: In a time series of 10 years (2004-2013), the proportion of seagrass in the diet of red knots (inferred from isotope samples) couples negatively with the annual survival rates estimated, when the proportion of bivalves in the diet (*i.e.* *D. isocardia* and *L. lucinalis*) couples positively with the annual survival rates estimates.

7.5 Discussion

Results of the present study confirm that red knots feed on seagrass quite intensively. We described better this feeding behavior and the profitability of this “new” feeding item in different feeding conditions. We tested our two hypotheses and concluded that red knots feed on *Zostera noltei* to maximize their energy intake when bivalve densities are low, and not as a means to detoxify themselves after the ingestion of the sulphur-rich *Loripes lucinalis*.

A new feeding regime

Although seagrass is often described as a poor energy source compared to molluscs, the results showed that red knots use seagrass as an alternative food source in PNBA to reach a minimum energy intake and survival. Either in absence of bivalves or when fed *ad libitum* on bivalves, red knots ingest at least some seagrass. Red knots do not eat more seagrass when faced with higher loripes densities and consequent increasing toxic constraint. Results of the present study confirm that red knots can feed on seagrass quite intensively depending on the feeding conditions. The experiment demonstrated that red knots consume seagrass when they cannot achieve a sufficient energy intake rate on bivalves. Moreover, we could identify some individual traits that could be related to this behaviour: Gizzard mass, bill length and body mass (unpublished data). The present study gives support to the idea that herbivory in shorebirds is an new adaptive feeding behavior. We have indications that this feeding behaviour is not related to the seagrass coverage (which varies amongst years in BdA, unpublished data), but to the density of bivalve prey in the mudflats of BdA (present study).

This new feeding behaviour has been observed and studied lately for other shorebirds (*i.e.* Kuwae et al., 2008; Robin et al., 2013). In the Wadden Sea seagrass beds have nearly disappeared so we cannot say whether this feeding behaviour is exclusive to PNBA. However, it would be interesting to see whether red knots *Canutus canutus canutus* feed on *Zostera noltei* in the Pertuis-Charentais as it has lately been showed for *Limosa limosa* based on field observations, isotopic analyses and dropping contents, Robin et al., 2013.

Diet as a Behavioural Indicator

The present study demonstrates that diet composition (seagrass signature) can be used as a behavioural indicator of habitat quality (like it was shown earlier for *Limosa limosa* in the Bay of Biscay, Robin et al., 2013). But most importantly, diet composition could be used as a warning signal for endangered populations. Recent studies demonstrated a link between climate change, phenotype (body

shrinkage, including bill length) and survival (van Gils et al., 2016). If bivalve densities decrease, access to the buried bivalve (already made harder by seagrass roots and rhizomes, de Fouw, 2016) will be strengthened and the competition should help primarily long-billed individuals. Consequently, short-billed individuals (mainly males since bill length is a sexually dimorphic trait in this species) may suffer even more from the decrease in bivalve densities in their wintering grounds. Therefore, we question whether this feeding behaviour may affect primarily short-billed individuals, starting with males.

7.6 **Aknowledgements**

José Alves and Anne Dekinga were indispensable in catching the experimental birds. Jim de Fouw, Rob Oldenburg, Thomas Oudman, Mohamed Vall Ahmedou Salem, and Amadou Abderahmane Sall are thanked for their help in various ways with the experiment. Additionally, Rob is acknowledged for measuring *Loripes* AFDM. Anne S. Philippe together with JAvG ran the feeding experiments (seagrass patches, design and maintenance of the birds), Anne S. Philippe measured intake rates of birds on the different experimental conditions and produced statistical results related with the feeding experiment. Field work in Mauritania would not have been possible without the numerous interns and assistants, as well as the PNBA staff and direction. This work is funded by an NWO-VIDI grant (864.09.002) awarded to JAvG.



GENERAL DISCUSSION



ENVIRONMENTAL CHANGE AND ITS EFFECTS ON PREDATOR-PREY INTERACTIONS

The general research goals of this thesis were to identify the drivers of wintering bird densities and the determinants of food choice in the French Pertuis Charentais. However, in three years time the research goals evolved. Because we had the chance to deal with multiple spatio-temporal scales, we could identify some changes in the environment and highlight their consequences on predator-prey interactions.

For instance, we gave support to the idea that granulometric gradient and inundation time (at risk when faced with beach replenishment, coastal erosion, and sea level rise) may affect the densities, biomass and distribution of benthic species at the scale of a whole bay like Yves Bay. As a consequence, competition between prey species can be modified, and this could have carry over effects on their shorebird predators (the red knots *Calidris canutus* and the dunlin *Calidris alpina*), their distribution (and densities on the site) as well as their competition for food and diet (Chapter 1). A second chapter compared two sites along the French Atlantic Coast in terms of food resources for dunlins (Chapter 2). Diet reconstruction from faeces revealed that diet choice was highly flexible in this species (from a diet dominated by molluscs to a diet dominated by polychaetes). This dietary flexibility was hypothesised to be linked with differing food availabilities, but also potentially with the inter-specific competition with the numerous red knots (resulting in strengthened trophic segregation, like mentioned in Chapter 1). These two studies, forming the first section, were fixed in time, but illustrated how changes in the environment may carry over effects on benthic population and distribution, and ultimately on predator local distribution and diet choice at a loco-regional scale.

The third section, building on monitoring effort in the French Pertuis Charentais (Chapter 3 and Suppl. materials), analysed two aspects of benthic variability: phenotype and secondary production. Seasonal trends in phenotype were studied for the species *Scrobicularia plana*, in response to environmental factors including the presence or absence of shorebirds (Chapter 4). Results revealed seasonal trends in quality indices of the bivalve, and particularly in shell mass. These results were discussed in the light of Optimal Theory and explained as a strategy and the result of a trade-off between feeding and being fed in this potential prey for shorebirds (Chapter 4). Following was a study of *Macoma balthica*, and the factors influencing the secondary production of 8 consecutive cohorts in Aiguillon Bay (Pertuis Charentais). When comparing our results with results from the Dutch Wadden Sea we could highlight phenological traits (*i.e.* a high

recruitment mortality, and a short life expectancy), characteristic of populations at the edge of their distribution area (area that is shifting poleward due to warming climatic conditions), and/or in very muddy areas (Chapter 5). These two examples also illustrated the phenological or phenotypic traits molluscs could develop when faced with changing environmental conditions, at a small (seasonal) vs. large (decennial) temporal scale, and their potential repercussions on shorebirds' diet choice/preference in time.

The last section of the thesis addressed larger temporal and spatial scales. The determinants of food intake rates were analysed in three connected ecosystems along the East-Atlantic flyway for over a decade. Impact of prey size, burial, quality, variability and toxicity on intake rates for red knots was assessed for every study region, using a Digestive Rate Model (Chapter 6). Results revealed environmental changes (*e.g.* decrease vs. increase in certain prey types) that were reflected by predicted diet choices over time. The same conclusion was reached thanks to an in-depth study of last decade's feeding behaviour of red knots in Banc d'Arguin. The combination of an indoors feeding experiment, isotopic analyses from blood samples, benthic monitoring and survival estimates revealed that the newly observed feeding behaviour of red knots *Calidris canutus canutus* (*i.e.* feeding on seagrass roots and rhizomes) was an adaptive response to decreasing molluscan food densities, and was correlated a decrease in survival rates of the red knot's population (Chapter 7). These two last studies revealed that diet choice is flexible, and responds to environmental change (see Fig. 7.6). However, if changes are too sudden or too severe, top predators like shorebirds may suffer irremediably, despite a change in behaviour (feeding regime, migration route or timing, or even phenotype).

The change in scales operated through these 7 studies mainly focused on bottom-up carry over effects, from environmental degradation to benthic community changes, until shorebird's behaviour. However it is necessary to keep in mind, and it is a common thing in ecology, that feedbacks (among which top-down effects) can strengthen/counteract these bottom-up effects. For instance, a change in phenotype (like bill length), or behaviour (like herbivory) could have consequences on the habitat and its resources (*e.g.* depletion of seagrass patches, burial depth of molluscs).

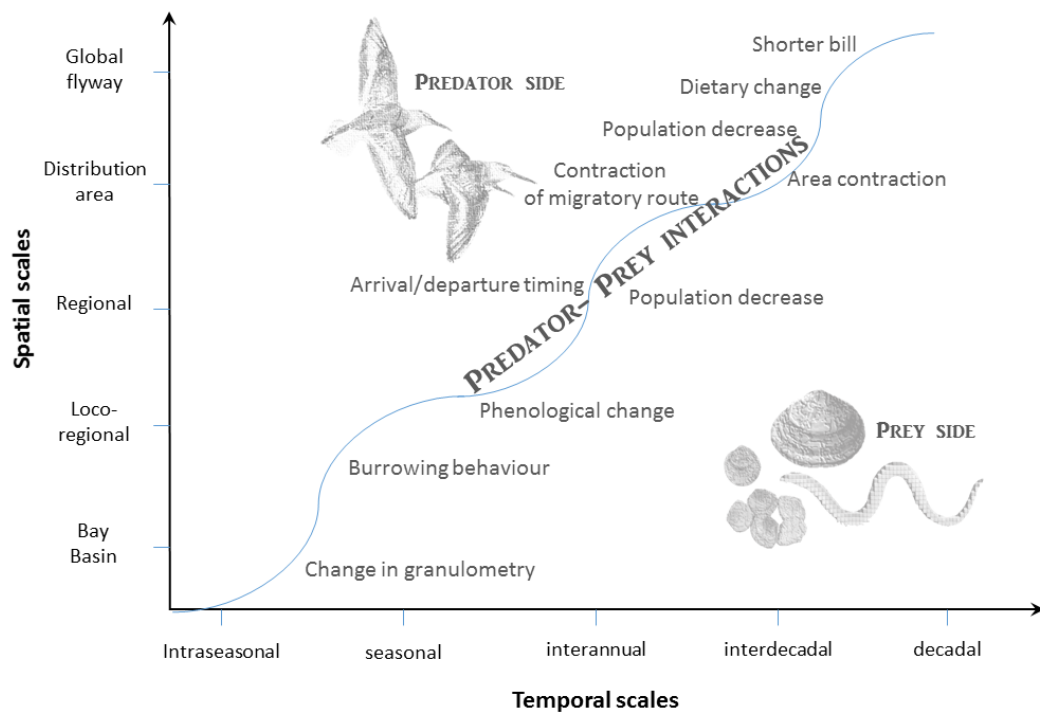
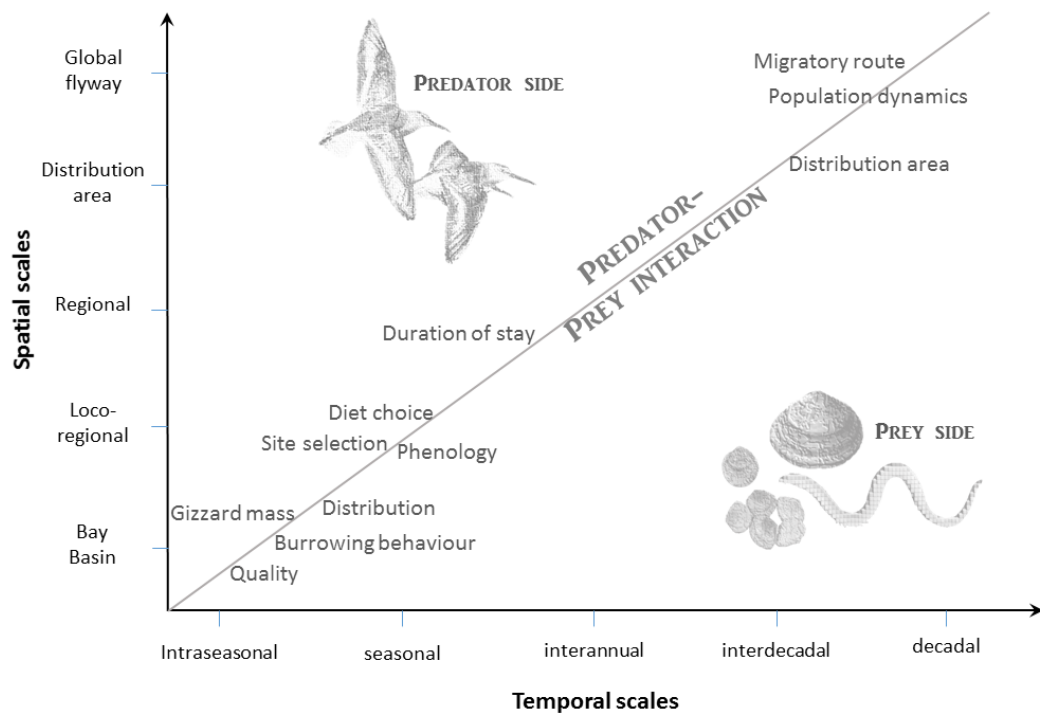


FIGURE 7.6: General scheme of the factors that may affect predator-prey interactions under natural conditions (top) and in the context of a disrupted environment (below), depending on spatio-temporal scales

SOME MISCELLANEOUS THOUGHTS

Birds out of their shell

In this thesis we addressed predator-prey interactions essentially with a bottom-up point of view. Only because we had long-term benthic surveys, and extended knowledge about the effects of food resources especially on red knots (gizzard, spatial distribution, prey selection...) could we adopt this point of view. However shorebirds can also induce changes on their prey: by harvesting specific size classes, inducing responses that can impact individuals body condition etc. In this thesis, benthos allowed us to make small things bigger in the sense that from benthic data, which is nothing more than a huge accumulation of small tasks on small invertebrates, we reached a deeper understanding of the behaviour of a vertebrate predator, connecting continents.

This is how you end up having knots in the loop

Ecology science must be apprehended first as a fundamental science (Courchamp et al., 2015). However now research is orientated internationally and nationally towards society needs (inc. conservation and economy), and less space is given to fundamental research. This new era has advantages, and claims to bring research back into society, and even save money. However such a guidance of fundamental research can have negative consequences. This trend could result in more money being invested in research concentrating on 'useful' species (because they are cultivated, or bring ecological services for humans), or more research effort would be made on the study of flag predators species (common in the greening of firms), not to mention climate change and other trendy subjects. The consequence would be to orientate science through the selection of topics, but also to orientate debate and writing, and even careers.

Top predators are studied because their behaviour and fitness reflect ecosystem state. The red knot is an incredible species to study in that respect, and this thesis is another demonstration of the importance of studying these migratory species, at the origin of the benthic monitorings used in this research and many findings concerning the ecosystem functioning of its migratory areas. However, I hope I helped the small things (macrofauna, but the same would apply for meio- or microfauna) speak louder by making them bigger...as it is interesting to consider benthic macrofauna not only as passive prey, but as model species in themselves for the study of distribution, behaviour, adaptation, variability and as proven macro-indicators of ecosystem state/change.

Into the shoes of a wader

Benthic monitorings are labour intensive and it can take time until they become essential. Most benthic surveys supporting this thesis are more than a decade old. In the recent years, they have become key elements advocating state shifts in ecosystems, describing species invasions, or explaining variability in secondary production for instance. Only thanks to these long-term databases, are we able now to understand the effects of climate change on ecosystems (van Gils et al., 2016). Benthic monitorings often rely on a handful of persons whose field knowledge and dedication must be welcomed. Monitoring is at the very basis of ecology science: observing, describing, counting, sorting, identifying etc. Like any other mission of observation, monitorings require perseverance and in the case of mudflat ecology, physical effort. When performed over large scales, monitorings enable large spatio-temporal relevant studies, and allow a deeper understanding of the functioning of ecosystems.

When prey fit the bill

This thesis was another occasion to unravel the various traits that make a prey suitable for its predators. Starting with the early technique of reconstruction from faeces until reconstruction from blood samples, or modelling, diet reconstruction is a key tool in the study of predator prey interactions. All these techniques are complementary and allow us to understand better what is the share of each species in the diet, and to compare it with ecosystem densities in order to assess prey selection, intake rates and trophic segregation. Multiple studies have demonstrated that when habitats are faced with regime shifts, these changes do cascade on prey and predators, and result in lower fitness and population decrease (Kraan et al., 2010b; Bowgen, Stillman, and Herbert, 2015; de Fouw, 2016). Our results highlighted the tendency of shorebirds to be more flexible and generalist in their diet composition, when faced with competition from other species or because of human disruption of the ecosystems (Fuller, 2012, section 'Ability to adapt: a shift towards generalisation?'). Shorebirds turn to lower energetic food in times of food shortage, but their flexibility, we all hope, will help them survive the Sixth Extinction. The inclusion of a new item in their diet in Mauritania (*i.e.* *Zostera noltei*) is puzzling. We suppose this item bring them energy, but obviously it seems to be correlated with a decrease in survival rate in the population *C. c. canutus*. More knowledge is needed concerning isotopic fractionation for this new prey, as well as metabolization processes and efficiency.

Do not try to catch a fly with a bazooka when tweezers are sufficient

Because ecosystems are so complex, it is impossible to capture all the feedbacks and indirect consequences of the smallest disturbance. In the past decades, models of habitat, game theory, energy budgets and trophic network analysis have flourished, which aimed at capturing this complexity. It has now become impossible to be an ecologist and publish results without using advanced statistical tools and computer coding. Thanks to this evolution, ecology has certainly acquired more recognition from other science fields as well as from society. However, we should all keep in mind that the worst and the best can arise from complexity as well as simplicity. In ecology science, it seems essential '*not to extrapolate conclusions or derive models beyond the realm in which they were established*' (quoted from Fuller, 2012), and to match properly the study question and the habitat grain (Fuller, 1994).

This thesis mainly used basic tools to describe the spatio temporal evolution of benthic invertebrates (Chapters 1, 2 and 3). As mentioned earlier, this thesis would have benefited from models including top-down effects of predators on their prey (e.g. include depletion trajectories in Chapter 6, Chapter 4 and Box 3), or interference calculations between dunlins and red knots (Chapters 1 and 2, and Box 3). Such models should be applied in future research.

Free as a bird? Tipping the scales

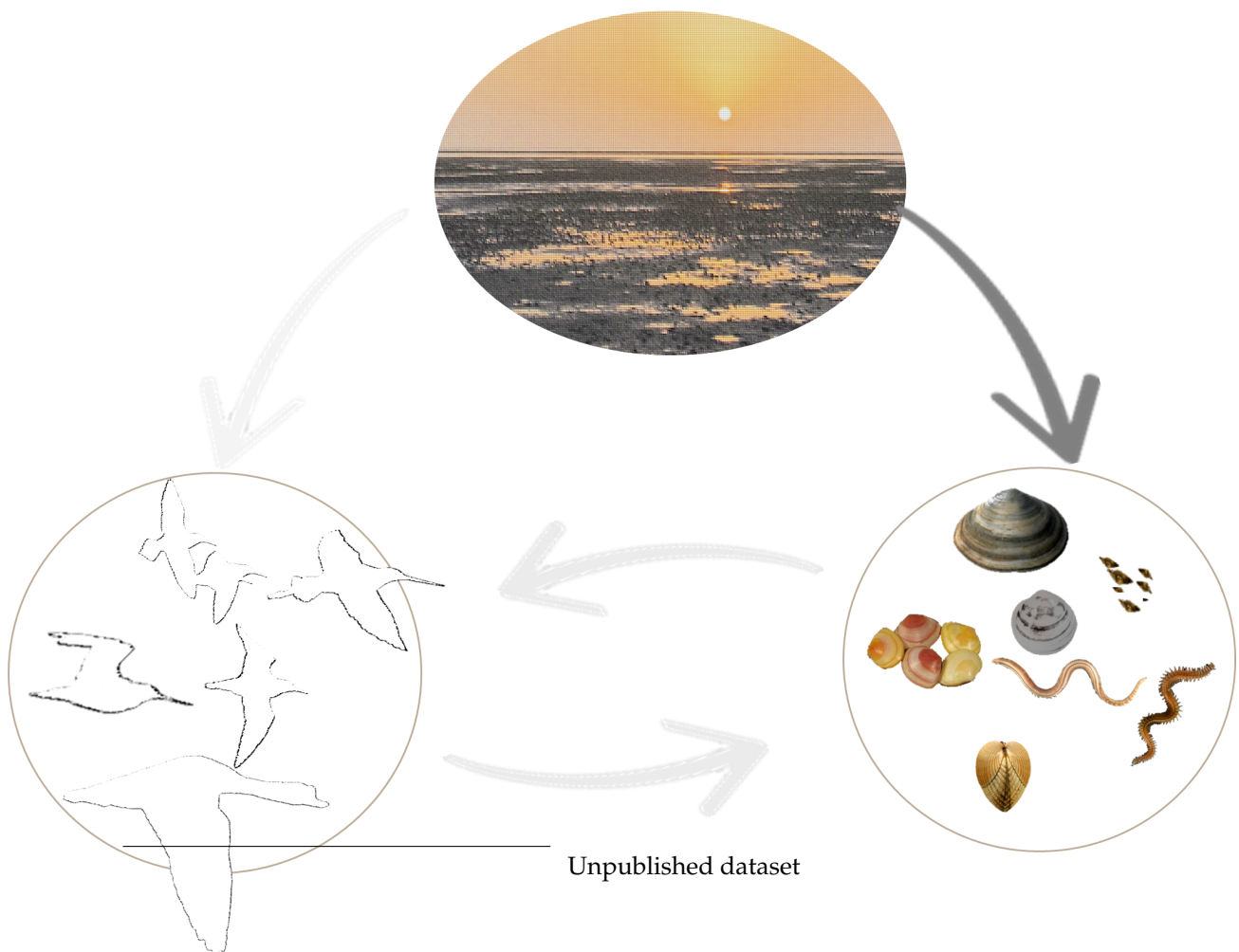
As mentioned in the Introduction, it is fundamental to choose the right scale depending on the research question we address in ecology. In this PhD, different temporal (month, season, annual, inter-annual, decadal) and spatial scales (biomorpho-sedimentary habitat, mudflat, regional, flyway) were used to address the topics of diet choice or distribution. In general, '*the nature of the predator assemblage is frequently linked with characteristics of the wider landscape*' (Chapter 6, Box 3), whereas the '*ability of a species to reduce the risk of predation is more typically determined by fine scale habitat quality*' (Chapter 1), Fuller, 2012.

Sometimes if the behaviour seems not optimal, it may be because the scientist did not consider the right scale, but we argue that there can be maladaptive behaviour that lead to a loss of fitness and survival when changes occur at a spatial or temporal scale that is not natural and which is unpredictable. In such cases, what is called "ecological trap" occurs (Chapter 7, Fuller, 2012). Anthropogenic disruption of ecosystems is currently causing maladaptive behaviours. We can question ourselves whether in such modified conditions, the Optimality paradigm should still govern our reasoning, and if we should still think that birds are free.



**Appendix 1: Seasonal dynamics of macro- and meiofauna in Aiguillon Bay
(May 2014 - July 2015)**

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ABSTRACT

To understand the dynamics of the mudflat on a fine temporal scale, a benthic monitoring has been conducted on 20 stations in South-East Aiguillon Bay. Samples were taken by foot every month at low tide during the spring tides from May 2014 to July 2015. Our dataset includes abundances and biomass densities of all mollusc species and principal annelids as well as mean lengths, flesh mass and shell mass when appropriate or available. This sampling was also the occasion to follow reproductive investment in the dominant bivalve species: *Scrobicularia plana*. The dataset includes meiofauna densities, primary production as well as temperatures and water content of the mud at two stations every month. This dataset has supported Chapter 4 of the present thesis, using the data of the species *S. plana* only. This dataset can support future studies concerning spatial and temporal changes in species abundance, interspecific or even meio-macrofauna interactions as well as the effects of environmental factors (T° , Chl a and water content) on the communities. It can also be linked to the long term benthic monitoring (Chapter 3) to understand what are the causes of interannual variability in benthic resources.

INTRODUCTION

Genesis of the project

This monitoring was designed after the long-term winter monitoring in the Pertuis Charentais (see Chapter 3), following a similar protocol. The idea was to better understand the factors influencing inter-annual variability in benthic resources for shorebirds, by focusing on seasonal changes within one study year (2014-2015). The objective was also to verify if all the major macrobenthic species were in a relative steady state during winter months (*i.e.* no growth, no recruitment, no reproduction), one of the prerequisites of our long-term winter benthic monitoring (Chapter 4).

Description: The Design was inspired by Ahmedou Salem et al., (2014) in the Mauritanian Banc d'Arguin, where authors applied a depletion model to monthly benthos data to explain the evolution of densities under predation pressure by shorebirds. A monthly sampling is the occasion to understand predator-prey interactions, biological development, and interactions between species in a changing ecological context. It is labour intensive, and to our knowledge there is only one dataset in the world that proposes a monthly sampling larger than a year or two: the one developed at the NIOZ laboratory by Dr. Jan Beukema. As illustrated by the studies based on this dataset, monthly sampling allows a large set of environmental studies, for example: Beukema, 1974; Beukema, 1989; Beukema, 1993a; Beukema et al., 1993; Beukema et al., 2001; Beukema and Dekker, 2005; Beukema et al., 2014.

Novelty: We decided to include the meiobenthic compartment as well as additional environmental variables (T° , Chl a and water content) to describe the dynamics of the various compartments of the mudflat, starting at the basis of the trophic chain (primary production) to the study of the resources available of the top-predator in this ecosystem: shorebirds.

Objectives: The objective of this benthic sampling is to describe the variability of environmental variables and benthic compartments (primary production, meio and macrofauna as well as shorebirds numbers) to explain the community dynamics and interactions throughout 15 consecutive months. The various traits measured in macrofauna specimens (*e.g.* length, shell mass, flesh mass, depth, numbers) will support studies on the seasonal dynamics of growth, densities, phenotype, or even burial behaviour in relation to predation and/or other environmental variables.

MATERIALS AND METHODS

Sampling design:

Sampling occurred every month for 15 months (starting in May 2014 until July 2015 included) during spring tides. Macrobenthic sampling took place in South-East Aiguillon Cove, on 20 semi-randomly selected stations distributed in a 400 m diameter circle area (Fig. 7). Sampling design was inspired by Ahmedou Salem et al., (2014).

Macrobenthos sampling: Coring was performed using corers of 1/56 m². The fraction accessible to sandpipers (*Calidris canutus* and *Calidris alpina*) representing more than 2/3 of the birds during winter was analysed separately (*i.e.* first 4 cm of the sediment core, hereafter the “top”).

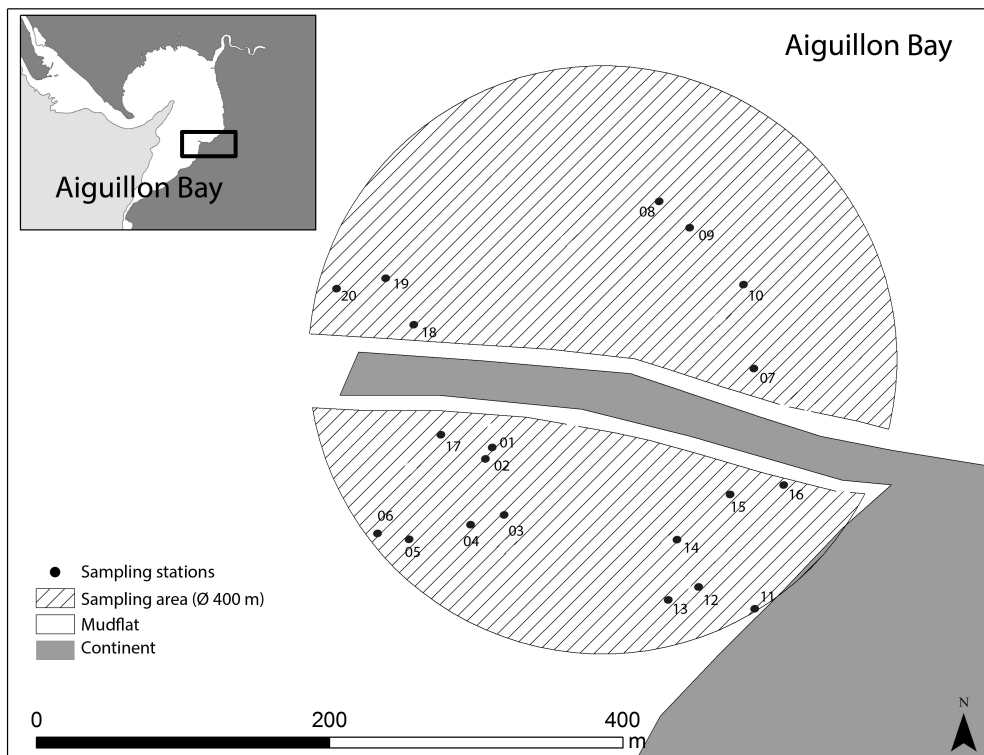


FIGURE 7: Sampling stations in Aiguillon Bay

Each station was located using a handheld GPS device using WGS84 geodetic datum. We took an additional core (70 mm diameter) covering 0.0038 m² to a depth of 4 cm for sampling exclusively the very abundant mudsnail *Hydrobia ulvae* (Pennant) (Bocher et al. 2007). The cores were sieved over a 1 mm mesh, except for the *H. ulvae* cores, which were sieved over a 0.5 mm mesh. All living molluscs were collected in plastic bags and frozen (-18 °C) until laboratory treatment. Polychaetes were preserved in 70% ethanol.

Processing of polychaetes: Everytime a polychaete head was encountered in a

sample, it was counted as one individual, determined to the species level (using Hayward and Ryland, (1995) determination key) and measured. The measure taken depended on the species. For Nereididae species (*i.e.* *Hediste diversicolor* and *Alitta succinea*), the length of the first three paragnaths was considered, and for Nephtyidae species (*i.e.* *Nephtys hombergii*), the width of the 10th setiger was measured, see Fig. 8. When the individual was still in one piece, we also measured total body length, and weighed the individual to constant dry mass and, after burning it in an oven (550 °C) we calculated ash-free dry mass (for more details on the protocol see Chapter 4). When individuals were not entire, we used extrapolation curves based on the data from entire individuals to estimate total body length, dry mass and AFDM; Whenever possible, and depending on the number of entire individuals we had, these extrapolation curves were species and month-specific.



FIGURE 8: Specific measure for *Hediste diversicolor* (and *Neanthes succinea*) (on the left) et *Nephtys hombergii* (on the right)

Processing of bivalves: Living bivalves were determined, counted and measured (width and maximum length of the shell) to the nearest 0.01 mm. For small bivalves (individuals <8 mm), we distinguished between three species essentially: *Macoma balthica*, *Scrobicularia plana* and *Abra tenuis* (Fig. 9). When individuals were smaller than 2 mm, identification was not possible using the bionucular, especially between the two scrobicularidae species (*i.e.* *Abra tenuis* and *Scrobicularia plana*), and we identified them as 'biv' standing for bivalve species. Because in some months the number of small spat (<8 mm) was so high, we only weighed them (flesh and shell together, pooled by size class) at 5 stations (4, 10, 13, 14, 15) to get total AFDM values ($AFDM_{flesh+shell}$). DM_{shell} and $AFDM_{flesh}$ were then extrapolated from total AFDM using regression curves, see Chapter 3 for more details. Total AFDM of small bivalve spat at the other

stations were obtained using month-species-specific curves based on the values of these 5 stations. Only for these 5 stations again, a precise measure of the shell length of each individual was taken using a Vernier caliper (to 0.01 mm), to be able to assess growth rate.

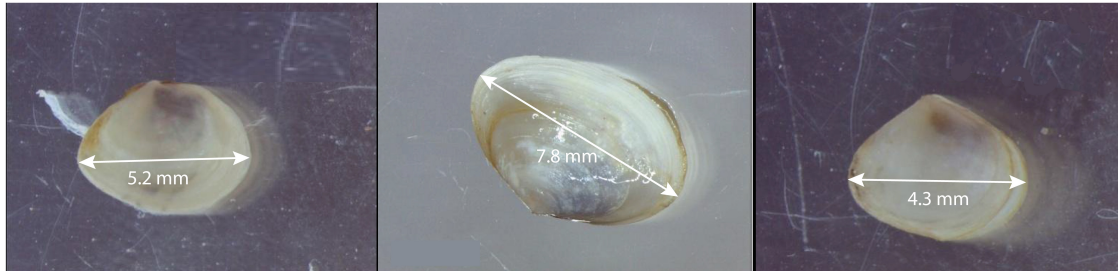


FIGURE 9: From left to right: spat of *Macoma balthica*, spat of *Scrobicularia plana* and spat of *Abra tenuis*.

Processing of *Hydrobia ulvae*: For *Hydrobia ulvae* individuals, precise measures of maximum shell height (from the aperture to the apex) were taken using a Vernier caliper (to 0.01 mm), for all individuals of 6 stations each month: (stations 3, 4, 10, 13, 14, 19). For all other stations, individuals were size-categorized to the nearest mm only (Fig. 10). Then individuals were pooled by size class into crucibles and weighed to obtain total AFDM values. DM_{shell} and $AFDM_{flesh}$ were extrapolated from total AFDM using regression curves, see Chapter 3 for more details.

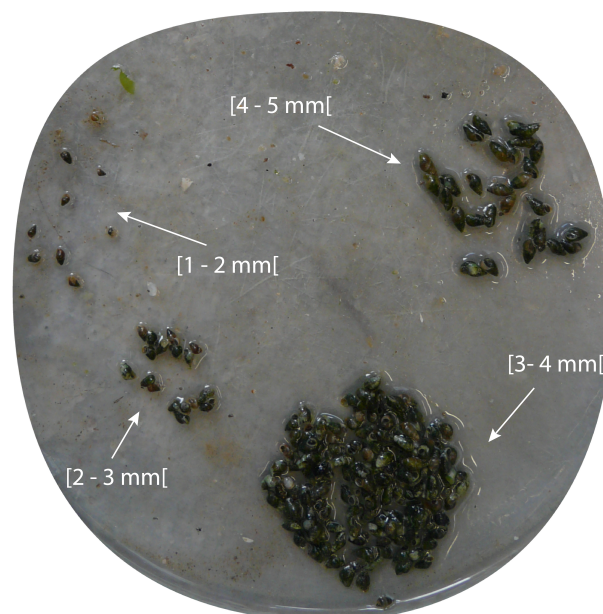


FIGURE 10: *Hydrobia ulvae* individuals, categorized by mm class-sizes

Gonadic status of *Scrobicularia plana*:

Reproduction investment was measured from the observation of maturation stages (Caddy, 1967; Zwarts, 1991; Mouneyrac et al., 2008; Santos et al., 2011a) on freshly collected animals. Maturation stages were determined by visual inspection using a binocular dissecting scope. Scores were given to each individual depending on the relative importance of the gonads (as a fraction of the digestive gland covered by gonad tissues): (0) gonads absent, (1) sexually undifferentiated ($\frac{1}{4}$ or less), (2) development ($\frac{1}{2}$), (3) ripe ($>\frac{3}{4}$), or (4) absent after spawning, see Fig. 11. Individuals larger than 17 mm were referred to as adults considering that the smallest individual with a reproductive stage larger than 1 measured 17 mm. Individuals with reproductive stages larger than 2 were considered active since their gonads were developing. Another index was calculated to evaluate reproduction investment in adult *S. plana*: Gonado-somatic ratio (GSR). GSR reflected the relative investment in reproduction and was calculated after separating gonadal tissues from somatic tissues (*i.e.* $Gonadal_{AFDM}$ divided by $AFDM_{flesh+shell}$, after Santos et al., (2011a)).



FIGURE 11: Reproduction stages in *Scrobicularia plana*. From left to right, stage 1 (undifferentiated), 2 (developing), 3 (ripe) and 4 (spawned).

For further details concerning measurements, weighing of macrofauna species as well as reproduction status of *Scrobicularia plana*, refer to Chapters 3, and 4.

Meiofauna:

Meiobenthic sampling was performed at stations 3 and 14, (Fig. 7). We chose these two stations because our sampling area was potentially divided into two different habitats: one dominated by *Macoma balthica* individuals (on the west, including station 3) and the other one by *Scrobicularia plana* (on the east, including station 14). Samples were taken approximately in the first 200 to 300 μm of the sediment, scraping the surface of the mud and inserting a ruler in this surface layer before extracting 60 mL of mud using a syringe, in triplicates for both stations. Densities were expressed per cm^3 , since it was not possible to accurately estimate sampling area. Samples were first preserved in 70% ethanol (final concentration) until they were sieved under water over a 63 μm mesh. The oversize

fraction was collected and preserved in 70 % ethanol. Identification and counting was performed using a binocular dissecting scope. The living fraction (at the time of sampling) was determined using the traditional Rose bengal staining method (Walton, 1952). Various Operational Taxonomic Units (OTU) were determined: two foraminifera species (*i.e.* *Ammonia tepida* and *Haynesina germanica*), copepods and ostracods. 'Temporary' meiofaunal taxa were also counted: gastropods (mainly *Hydrobia ulvae*), bivalves (mainly spat of *Scrobicularia plana*) and polychaetes (mainly *Hediste diversicolor* and *Nephtys hombergii*) as well as individuals from the phylum Platyhelminthes. Extremely abundant nematods were only counted over a fraction of the samples, obtained after a dilution factor between 1/8 and 1/32.

Shorebird counts:

Shorebird counts were performed by the Nature Reserve of Aiguillon Bay following the protocol detailed in Chapter 4.

Primary production:

Primary production was measured following the protocol detailed in Chapter 4.

Water content:

50 mL of sediment were inserted in previously weighed pots at stations 3 and 14, in triplicates, to assess water content (interstitial water, from the top 4 cm). Back in the laboratory, the pots filled with humid sediment were weighed to obtain Humid weight (w_h). Then, pots were placed in ventilated ovens during 3 days (60°C) to get Dry weight (w_d). To assess water content the following formula was applied: $\frac{w_h - w_d}{w_h}$

Temperature:

Temperature was measured every month at station N °7. Three temperature probes (HOBO U23 prov2 data loggers) were inserted in the sediment at three different depths: 0 cm, 2 cm and 10 cm during sampling sessions. To insure representativity, we will use mean temperatures of each sampling session for the analyses.

Median grain size:

Sediment samples were taken at every station in August 2014, October 2014, December 2014 and April 2015. Samples were analysed for grain size distribution after removal of salts and organic matter, using a Malvern Mastersizer 2000

(Malvern Instrument Ltd, Works, R.U.) diffraction laser (particle sizes analysed from 0.04 to 2,000 μm).

DATABASE ARCHITECTURE

A relational database was built following similar rules as the database presented in Chapter 3, under MS Access, using primary and foreign keys, see Fig. 12.

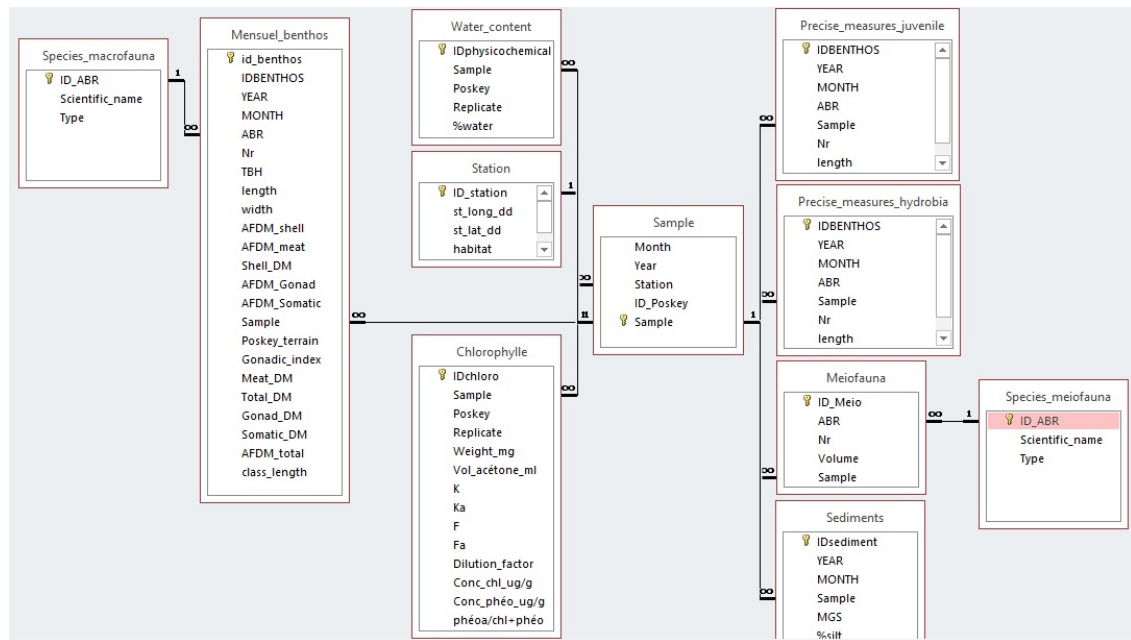


FIGURE 12: Architecture of the monthly sampling database

TABLE 4: Operational taxonomic units (OTU) present in the database

Species	Phylum	Class	Family	Genus	Abr.	AfiaID
MOLLUSCS						
<i>Abra sp.</i>	Mollusca	Bivalvia	Semelidae	Abra	abr	138474
<i>Abra tenuis</i>	Mollusca	Bivalvia	Semelidae	Abra	abt	141439
<i>Cerastoderma edule</i>	Mollusca	Bivalvia	Cardidae	Cerastoderma	cer	138998
<i>Haminoea hydatis</i>	Mollusca	Gastropoda	Haminoeidae	Haminoea	ham	141439
<i>Hydrobia ulvae</i>	Mollusca	Gastropoda	Hydrobiidae	Peringia	hyd	151628
<i>Kurtiella bidentata</i>	Mollusca	Bivalvia	Montacutidae	Kurtiella	mys	345281
<i>Macoma balthica</i>	Mollusca	Bivalvia	Tellinidae	Macoma	mac	141579
<i>Nucula nitidosa</i>	Mollusca	Bivalvia	Semelidae	Abra	abn	141435
<i>Retusa obtusa</i>	Mollusca	Gastropoda	Retusidae	Retusa	ret	141134
<i>Ruditapes sp.</i>	Mollusca	Bivalvia	Veneridae	Ruditapes	tapsp	231748
<i>Scrobicularia plana</i>	Mollusca	Bivalvia	Semelidae	Scrobicularia	scr	141424
POLYCHAETES						
<i>Alitta succinea</i>	Annelida	Polychaeta	Nereididae	Alitta	nsu	234850
<i>Hediste diversicolor</i>	Annelida	Polychaeta	Nereididae	Hediste	hdi	152302
<i>Heteromastus filiformis</i>	Annelida	Polychaeta	Capitellidae	Heteromastus	het	129884
<i>Melinna palmata</i>	Annelida	Polychaeta	Melinninae	Melinna	mpa	129808
<i>Nephtys hombergii</i>	Annelida	Polychaeta	Nephtyidae	Nephtys	nho	130359
<i>Nereis sp.</i>	Annelida	Polychaeta	Nereididae	Nereis	neresp	129379
<i>Notomastus latericeus</i>	Annelida	Polychaeta	Capitellidae	Notomastus	nla	129898
TEMPORARY MEIOFAUNA						
<i>Bivalvia sp.</i>	Mollusca	Bivalvia	-	-	biv	105
<i>Gastropoda sp.</i>	Mollusca	Gastropoda	-	-	gas	101
<i>Platyhelminthes sp.</i>	Platyhelminthes	-	-	-	pla	793
<i>Polychaeta sp.</i>	Annelida	Polychaeta	-	-	pol	883
PERMANENT MEIOFAUNA						
<i>Ammonia tepida</i>	Foraminifera	Globothalamea	Rotaliidae	Ammonia	amt	112857
Copepoda sp.	Crustacea	-	-	-	cop	1080
Foraminifera sp.	Foraminifera	-	-	-	for	1410
<i>Haynesina germanica</i>	Foraminifera	Globothalamea	Rotaliidae	Haynesina	hay	113294
Nematoda sp.	Nematoda	-	-	-	nem	799
Ostracoda sp.	Crustacea	Ostracoda	-	-	ost	1078

PRELIMINARY RESULTS

Taxonomic coverage:

The dataset compiles data on all mollusc species in the study area (to the species level) for 15 consecutive months, as well as two dominant families of annelids: Nereididae (corresponding to *Hediste diversicolor* and *Neanthes succinea*) and Nephtidae (corresponding to *Nephtys hombergii* only). This dataset also compiles data on the different taxa composing 'permanent' meiofauna (animals that are part of the meiofauna during all their development, *i.e.* sizes ranging between 50 μm and 1000 μm) and 'temporary' meiofauna (animals that are part of the meiofauna only during their juvenile stages, *e.g.* macrofauna larvae) of two sampling stations during 15 months, (Fig. 4). Epibenthic species were not considered (*e.g.* crustaceans) because the sampling method was inadequate for these mobile

species.

Some results:

Temporal variations of the main meiofauna taxa tended to differ between the two sampling stations (13).

Results seem to describe a negative correlation between the number of dunlins counted in the study area and the densities of one of their main prey species: *Hediste diversicolor* (Fig. 14).

A growing phase is detected in spring 2015 for juvenile *Scrobicularia plana* individuals, as a result of a successful recruitment (Fig. 15).

Additional results concerning temperature, primary production, and especially the bivalve *Scrobicularia plana* can be found in Chapter 4.



FIGURE 13: Monthly variations in abundances of meiofauna (histograms), with associated group composition (pie plots)

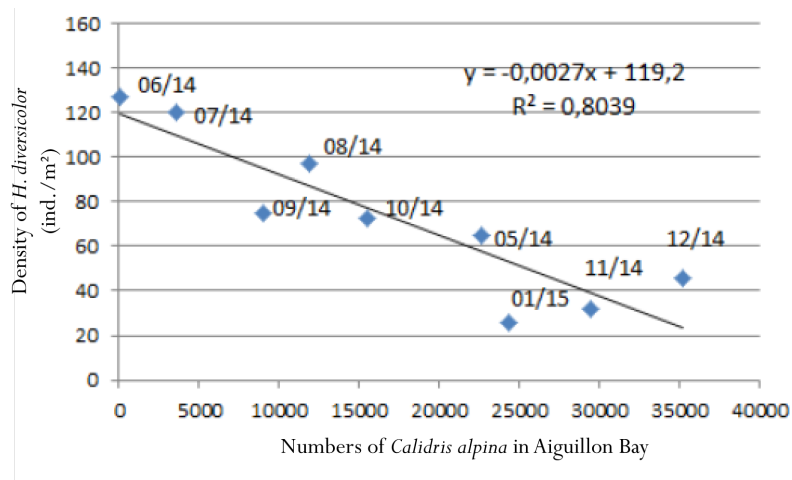


FIGURE 14: Correlation between the number of predators (*Calidris alpina*), based on monthly counts by the Nature Reserve of Aiguillon Bay, and densities of *Hediste diversicolor*

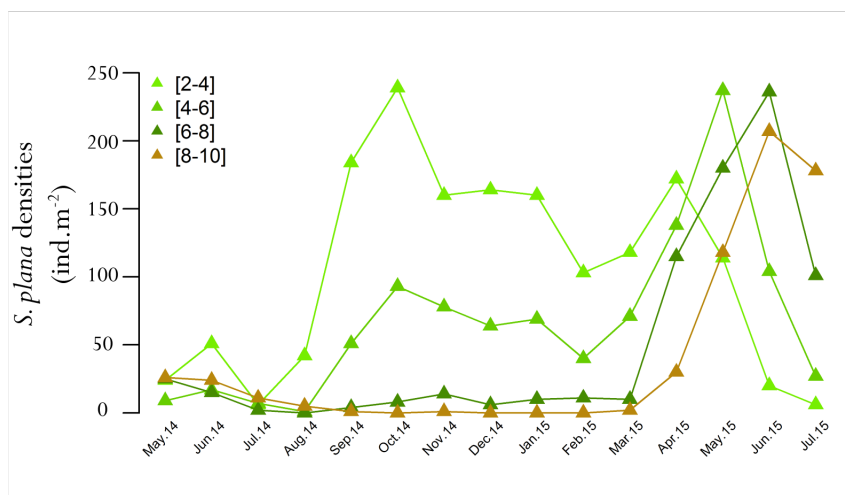


FIGURE 15: Variations in mean *Scrobicularia plana* densities (ind.m²) between May 2014 and July 2015, depending on the size considered ([2-4mm], [4-6mm], [6-8mm], [8-10mm])

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Interactions spatio-temporelles entre oiseaux limicoles et macrofaune benthique: une approche multi-échelles

Résumé :

Les vasières intertidales sont des environnements complexes et changeants, qui abritent des invertébrés enfouis dans le sédiment (la macrofaune benthique) et sont visités de manière saisonnière par de grands migrateurs : les oiseaux limicoles. Ce travail de recherche s'intéresse aux relations proie-prédateur entre les oiseaux limicoles et leur ressource alimentaire : la macrofaune benthique. La thèse est articulée en 8 chapitres qui présentent des études à différentes échelles spatio-temporelles : des saisons à la décennie, et de la baie à la route migratoire. Ces études sont basées sur un échantillonnage régulier des vasières intertidales du Golfe de Gascogne (France) ainsi que d'échantillonnages en mer des Wadden (Pays-Bas) et au Banc d'Arguin (Mauritanie). Les données de macrofaune (qualité, taille, densité, biomasse) sont couplées aux données de comptages de leurs prédateurs ainsi qu'à leur comportement alimentaire (reconstruction du régime alimentaire d'après les isotopes, les fèces, la modélisation ou l'observation de vidéos). Ces huit études apportent un éclairage sur l'écologie de leurs interactions (en intégrant des variables environnementales telles que le temps d'inondation, la granulométrie, la température, la production primaire, ou encore la latitude). Une attention particulière est portée à la variabilité des proies et du comportement alimentaire de leurs prédateurs, dans l'espace et le temps. Des encarts viennent illustrer pour l'un les techniques de reconstruction du régime alimentaire, pour l'autre les défenses développées par les mollusques marins, ou encore la relation entre énergie à disposition et sélection du site pour les limicoles.

Mots clés : macrofaune benthique, vasières intertidales, oiseaux limicoles, relations proies-prédateur

Interactions between shorebirds and benthic macrofauna: Making small things bigger

Summary :

Intertidal mudflats are complex ecosystems undergoing constant changes, home to infaunal invertebrates (benthic macrofauna), and migratory sites for particular birds: shorebirds. This research focuses on predator-prey interactions between shorebirds and their macrobenthic prey. The present thesis is composed of 8 chapters which illustrate different spatio-temporal scales: from seasons to the decade, and from the Bay to the migratory flyway. These studies are based on regular benthic sampling of intertidal flats along the Bay of Biscay (France), as well as sampling data from the Dutch Wadden Sea and the Mauritanian Banc d'Arguin. Macrobenthic data (quality, sizes, densities, biomass) are linked with shorebird counts and data about their feeding behaviour (diet reconstruction from isotopes, faeces, modeling and video observations). These eight studies shed light on particular relationships between some prey and their predators, and the ecology of these interactions (including environmental variables such as inundation time, grain size, temperature, primary production, or even latitude). Particular attention is given to the variability of prey and predator behaviour in time and space. Inserts are included in between chapters to illustrate for instance different diet reconstruction techniques, anti-predation traits in marine molluscs, or relation between energy available and site selection in shorebirds.

Keywords : benthic macrofauna, intertidal mudflats, shorebirds, predator-prey interactions

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