Responses of spider communities to salinity and flooding in a tidal salt marsh (Mont St.-Michel Bay, France)

Реакция сообщества пауков на засоленность и затопляемость солончаков приливной зоны (бухта Монт Сан-Мишель, Франция)

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ABSTRACT. Consequent to sea couch grass (*Elymus athericus*) invasion over the last ten years, the succession of plant formations usually observed in salt marshes was suppressed in Mont Saint-Michel Bay (western France). This provided an opportunity to study the effects of salinity on arthropod communities from high to low marshes independently of vegetation changes. The specific composition of spider communities was compared along a transect from a dike to the mean tide level using complementary sampling techniques. The effects of tidal flooding were also investigated by determining species distributions and abundances along the salt marsh before and after tides. In total, one whole year of sampling resulted in the capture of 7 949 individuals representing 73 species, but only half of these were caught regularly in the marshes studied. It is hypothesized that spiders are very sensitive to soil salinity, and different groups of species can be characterized in accordance with their distribution within the marsh. Distribution ranges of spider species along the salinity gradient and their responses to tidal flooding allow us to define more precisely the status of 'salt marsh resident species'.

РЕЗЮМЕ. Как результат десятилетней инвазии пляжной травы (*Elymus athericus*) сукцессия обычно наблюдаемых растительных формаций в солончаках бухты Монт Сант-Мишель (Зап. Франция) была подавлена, давая тем самым возможность для изучения эффекта засоленности на сообщества членистоногих от приподнятых до низинных солончаков независимо от изменений растительности. Видовой состав сообществ пауков вдоль транссекты от дамбы до затопляемого уровня сравнили используя взаимодополняющие методы сбора. Эффект приливного затопления был также изучен путем определения видового распределения и видового богатства вдоль солончака до и после прилива. В целом, за год было собрано 7 949 особей 73 видов, но только половина из них регулярно ловилась в изучаемых солончаках. Предполагается, что пауки чувствительны к солености почвы, и группы разных видов могут быть охарактеризованы в соответствии с их распределением вдоль солончака. Типы распределения видов пауков вдоль градиента солености и их реакция на приливное затопление позволяют нам более точно определить статус так называемых 'резидентных видов солончаков'.

Introduction

Salt marshes are ecosystems subjected to periodical tidal flooding and are characterized by extreme conditions, with two abiotic factors affecting the structure of habitats: a regular submergence by seawater and, as a direct result, the soil salinity. The effect of salinity on the successional distribution of organisms in salt marshes is well known for vegetation [e.g., Chapman, 1940; Zelder, 1977; Rand, 2002], marine invertebrates [e.g., Kneib, 1984; La-Salle et al., 1991; Talley & Levin, 1999], gastropods [e.g., Costil et al., 2001; Gérard et al., 2004] and carabid beetles [e.g., Meijer, 1980; Descender & Maelfait, 1999]. Despite the fact that spiders constitute one the most abundant and taxonomically diverse groups in these ecosystems [Davis & Grey, 1966; Marples, 1966; Foster & Treherne, 1976], relatively few studies have been undertaken on the spider communities of European littoral salt marshes [Healy, 1975; Fouillet, 1986; Baert & Maelfait, 1999; Descender & Maelfait, 1999; Elkaim & Rybarczyck, 2000]. In these studies, the status of halophilic species is generally defined by 'the preference of the species for saline habitats' [e.g., Hänggi et al., 1995; Jacquemin, 1999; Descender & Maelfait, 1999] and a few species are actually considered to be halophilic, either in littoral or in both littoral and continental habitats. Very few studies dealt with submergence effects on spiders [e.g., Uetz, 1976; Döbel et al., 1990; Morse, 1997]. Among these, only Döbel et al. [1990] concerned spider communities in salt marshes. However, American salt marshes are submitted to daily flooding, whereas European ones are flooded monthly. Therefore, the study of Döbel et al. [1990] is not directly comparable to our study devoted to a French salt marsh.

Vegetation architecture and habitat diversity are known to strongly affect spider community structure in many ecosystems [e.g., Hatley & MacMahon, 1980; Greenstone, 1984; Canard, 1990; Wise, 1993; Ysnel et al., 1996; Ysnel & Canard, 2000], especially in salt marshes [Dö-bel et al., 1990; Descender & Maelfait, 1999], but very little is known about the influence of the main salt marsh-specific abiotic factors, viz., soil salinity and tidal flooding. In order to identify a potential link between species distribution and salinity in salt marshes, it is important to eliminate the impact of plant community variation as a confounding factor (e.g., resulting from differences along the elevation gradient). Over the past ten years, the progression of the invasive plant species *Elymus athericus* (Poaceae) in the salt marshes of the Mont St-Michel Bay (France) has suppressed the typical succession of plant communities [Bouchard et al., 1995; Valéry et al., 2004], without modifying the soil salinity gradient (present study). Therefore, by creating a more homogeneous plant community along the land–sea gradient (Fig. 1), the invasion of *E. athericus* provided an opportunity to study the effects of the salinity gradient on spider communities from the high to low marshes. The aim of this paper is to refine the status of salt marsh resident spider species by answering the following two questions: (1) does the soil salinity affect spider communities at the level of a salt marsh; and (2) how do tides affect species distributions in this salt marsh?

Material and methods

Study site

The Mont Saint-Michel Bay is located in north-west France between Brittany and Normandy (48°40′N, 1°40′W). This 500 km² bay is unique in Europe for the extent of its salt marshes and mud flats, which together cover 250 km². The salt marshes studied were either 'natural' (i.e., ungrazed), or impacted by sheep/cattle grazing or hay-mowing. On average, the salt marshes are inundated every two hours by tides, and are flooded by approximately 43% of tidal events [Lefeuvre et al., 2000]. Only spring tides submerge the marshes. Spider communities and soil were sampled at eight stations (designated A–H) located along a transect running up the shore from the sea (1 200 m) near the Mont St-
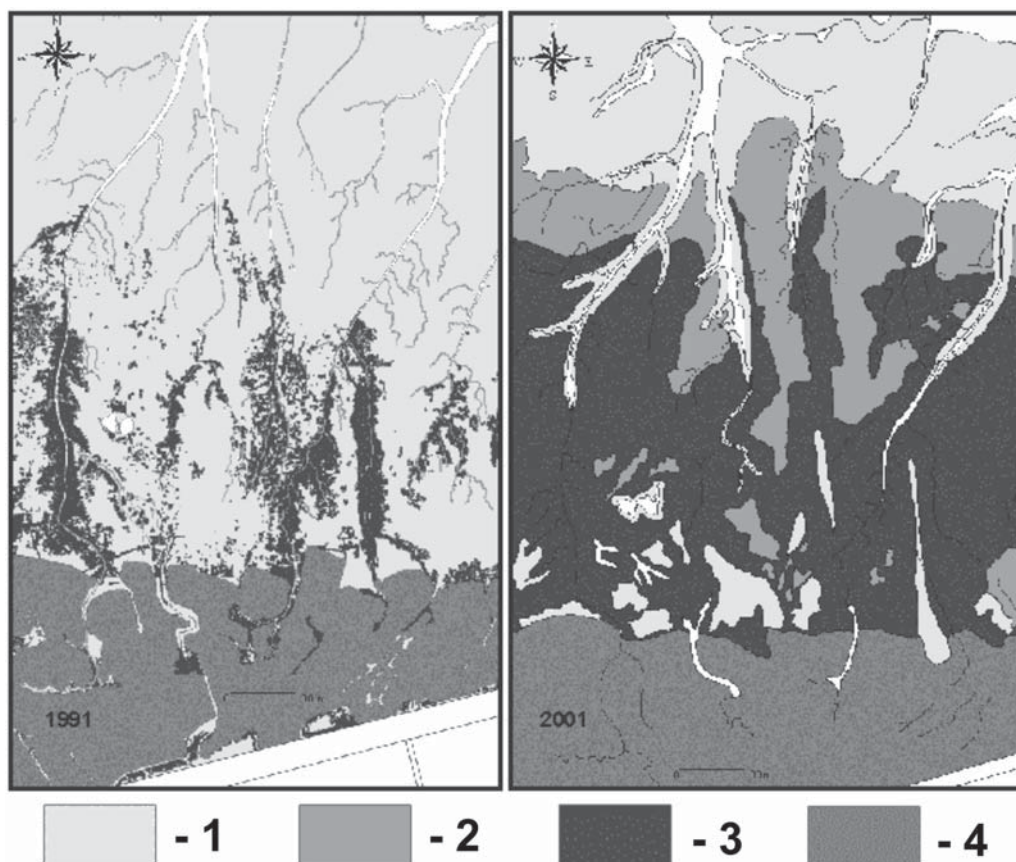
Fig. 1. Progression of *Elymus athericus* between 1991 and 2001 along the land–sea transect studied [from Valéry *et al*., 2004; with kind permission of the authors]. Legend: 1 — salt marsh without *Elymus athericus*; 2 — dominance of *Elymus athericus* mixed with other grass species; 3 — *Elymus athericus* mono-specific stand; 4 — mowed area with *Elymus athericus* (75%) and *Festuca rubra* (25%).

Рис. 1. Развитие *Elymus athericus* между 1991 и 2001 вдоль изученной приморской транссекты [из Valéry *et al*., 2004; с любезного разрешения авторов]. Легенда: 1 — солончак без *Elymus athericus*; 2 — доминирование *Elymus athericus* в смеси с другими вилами трав; 3 — *Elymus athericus* моновидовое сообщество; 4 — косимая зона *Elymus athericus* (75%) и *Festuca rubra* (25%).

Michel (Fig. 2), which traversed the *E. athericus* dominated plant communities.

Mean vegetation height did not vary along the transect (mean = 73 cm; s.e. = 6), except at station B (mown area), which was lower (mean= 55 cm; s.e. = 3). Station A was located on a dike built a century ago, which is never submerged by tides, whereas the others stations (B–H) are subjected to monthly inundation. The distance of each station from the dike was measured to the nearest metre with a geographic information system (GIS) using the extension "Distance and Bearing" of Arcview 3.1. These stations were chosen for their general homogeneity in order to avoid edge effects, especially important in small study areas [Bonte *et al*., 2002].

Habitat characteristics

SALINITY. Soil salinity was estimated at each station by measuring pore water electrical conductivity (expressed in mSiemens per metre). Conductivity was measured using a W.E.T. Sensor connected to a moisture meter HH2 (both by Delta-T Devices Ltd., Cambridge, UK). All measurements were made with a specific clay soil calibration. Salinity was measured four times around each pitfall trap. In addition, soil salinity was measured at each station, three
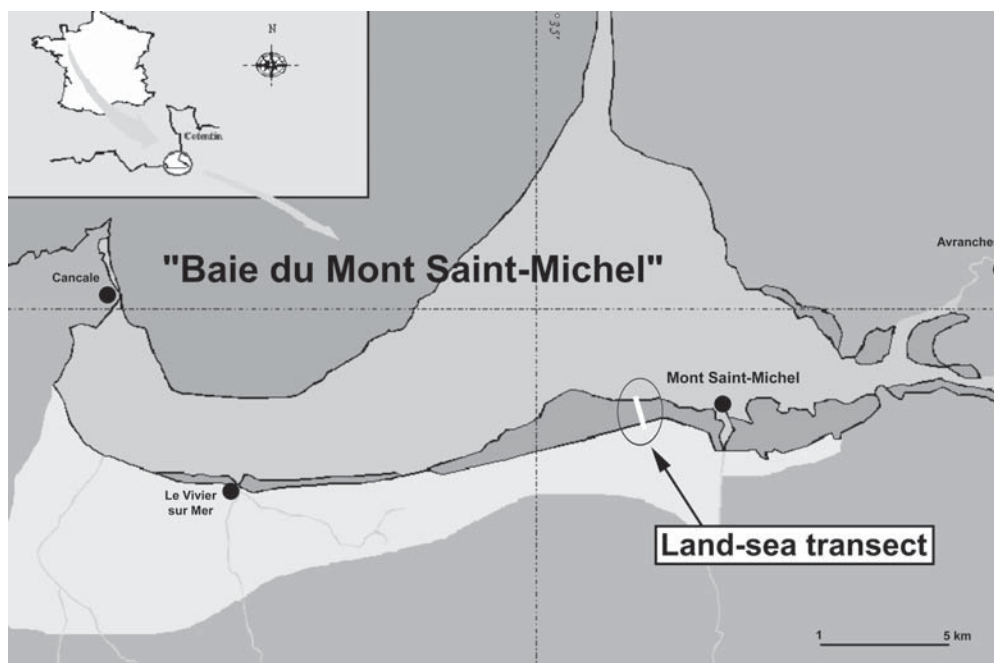
Fig. 2. Location of the sea-land transect studied (Mont St.-Michel Bay, France).
Рис. 2. Местонахождение изученной приморской трансекты (бухта Монт Сант-Мишель, Франция).

weeks after the last tidal event that had flooded the marsh in July 2003. These soil salinity measurements (mean of 16 measures) are considered to be representative of mean soil salinities in the salt marshes, independent of the direct influence of tidal flooding.

Along the land–sea transect, successive stations had significantly higher mean salinities (ANOVA, df = 31) than the preceeding one's (Table 1): B vs. A, ($F = 133.81$; P < 0.001), C vs. B ($F = 4.52$; P = 0.042), D vs. C ($F = 15.89$; P < 0.001), F vs. E ($F = 8.42$; P = 0.007) and H vs. G ($F = 5.25$; P = 0.030). The soil salinity of four stations situated at different distances from

the dike did not show any significant differences (E vs. D: ANOVA; $F = 0.02$; P = 0.881; 31df and G vs. F: ANOVA; $F = 0.26$; P = 0.611; 31df). Nevertheless, mean station salinities increased with distance from the dike (regression analysis; $y = 530 + 0.660x$; $r^2 = 61.8\%$; P = 0.007; eight data points).

TIDAL FLOODING. Sampling before and after a spring tide was achieved in April 2003 to determine which species were still present after the tidal flooding (i.e., those able to resist the flooding) or not found after flooding (i.e., those potentially able to re-colonize the marsh). The transects were the same as in Table 1, with the

Table 1.
Change in soil salinity along the salt marsh and significance by ANOVA (* = P < 0.05; ** = P < 0.001).
Таблица 1.
Изменение солености почвы вдоль солончака и значимость по ANOVA (* = P < 0.05; ** = P < 0.001).

| | **Stations** | | | | | | | |
	A	**B**	**C**	**D**	**E**	**F**	**G**	**H**
Distance from embankment (metres)	0	110	350	350	890	350	800	1140
Mean salinity (mS.m⁻¹)	142	683	796	945	953	1044	1074	1237
(standard deviation)	(27)	(188)	(99)	(113)	(155)	(133)	(191)	(314)
Comparison with previous station		**	*	**	n.s.	**	n.s.	*
Maximum salinity (mS.m⁻¹)	175	821	967	1215	1333	1241	1448	2029
Minimum salinity (mS.m⁻¹)	105	510	602	777	808	838	810	935

addition of a ninth station. This station, designated A', was localized 50 m away from the dike, but had an altitude similar to station A. Consequently, station A' was not affected by tidal flooding, and alongside station A represented a reference station for studying the changes in species distribution in the non-immersed locations. Station E could not be sampled, because it drained slowly and thus remained flooded between the series of studied tides. The 32 pitfall traps (four pitfall traps per station: see below for details) were sampled during three consecutive days: the traps were checked the day before the tides and two days (the time necessary to drain the sea water) after the tides and catches were completed by time-standardized hand collecting. Sediment salinity was measured as described above. All statistical analyses were carried out using MINITAB 12.1 for Windows.

Spider community structure

The community of cursorial spiders was sampled using pitfall traps from April 2002 to April 2003. Traps consisted of polypropylene cups (10 cm diameter, 17 cm deep) set into the ground with the lips level with the soil surface. Ethylene-glycol was used as a preservative because of its non-effects on spider catches [Granström, 1973; Topping & Luff, 1995]. Each trap was covered with an elevated wooden roof to keep out the rain. The traps were checked weekly in accordance with the tides. Catches in pitfall traps were related to trapping duration and pitfall perimeter and were then transformed into 'activity densities' of hunter species [Luff, 1975; Curtis, 1980]. Four pitfall traps were installed at each station, which represents a sufficient number of replicates to estimate spider communities in herbaceous areas [Bonte *et al.*, 2000]. Pitfall traps were set up ten metres away from each other; this distance is considered minimal for avoiding interference between traps for spider catches [Topping & Sunderland, 1992; Churchill & Arthur, 1999]. In order to sample web-building species, collecting by pitfall traps during their periodical migrations [Canard, 1981; Churchill, 1993] and time-standardized hand collecting were conducted monthly during May, June, July, September 2002 and

March, April 2003. Each station was visited for one hour during the afternoon for hand-collecting. Spiders were preserved in 70% ethanol. Adult spiders were identified using Roberts [1985a,b, 1987, 1995] and Heimer & Nentwig [1991], nomenclature follows Canard [2004].

Results

Community structure and salinity gradient

In total, 7 964 spiders belonging to 86 taxa (including 13 immatures and 73 species; see Appendix) in 21 families were trapped along the salt marsh over the 2002–2003 sampling period. The majority of spiders (i.e., 7 240 individuals from 54 species) were caught in the pitfall traps. Only 724 individuals were hand-collected, which represented 39 species, including 17 species absent in the pitfall traps. Catches by pitfall traps in the salt marsh (stations B–H) were strongly dominated by the halophilic species *Pardosa agrestis* (all specimens were similar to *Pardosa purbeckensis* as described by Locket & Millidge [1951]; see Table 2). The relative abundance of *P. agrestis* was always greater than 50% and reached very high values, for example, more than 80% of the cursorial communities at stations C and D. *Arctosa fulvolineata* and *Pachygnatha degeeri* were, after *P. agrestis*, the two co-dominant species. Station H, the lowest one, was characterized by a high relative abundance of the linyphiid species *Erigone longipalpis*. Of the six dominant species caught by pitfall traps (Table 2), two, viz., *P. degeeri* and *Agroeca lusatica*, are not usually considered to be halophilic. Only six species, which have been considered to be halophilic in the literature (given in bold in the Appendix), were found during the survey; therefore, species richness measured in the salt marsh was due mainly to the presence of others species.

Based on our sampling protocol, three groups of spider species can be characterized, both from their distribution ranges and their relative abundance along the salt marsh (Table 2). The first group (type I) contains 15 species found in stations F or H and hence able to withstand a

Table 2.
Changes in spider abundances along the salt marsh (data from pitfall traps only; bold: dominant species).

Таблица 2.
Изменение видовой численности вдоль солончака (только данные из почвенных ловушек; полужирным: доминантные виды).

| | | Stations |
		A	B	C	D	E	F	G	H	Total
Type Ia	***Arctosa fulvolineata***	0	68	102	139	46	196	31	28	**610**
	Erigone longipalpis	0	0	0	1	2	1	0	86	**90**
	Pardosa agrestis	52	944	742	1355	331	599	352	451	**4826**
	Pachygnatha degeeri	11	61	0	52	275	51	81	12	**543**
Type Ib	***Agroeca lusatica***	2	14	3	49	2	39	5	0	**114**
	Argenna patula	0	3	6	9	15	15	1	4	53
	Clubiona stagnatilis	0	0	0	3	1	5	3	0	12
	Enoplognatha mordax	0	0	0	2	2	2	3	3	12
	Pachygnatha clercki	0	8	0	2	1	8	0	0	19
	Oedothorax fuscus	0	4	6	1	0	0	0	6	17
	O. retusus	0	5	4	1	0	0	0	4	14
	Silometopus ambiguus	0	5	0	2	14	2	3	0	26
	Stemonyphantes lineatus	0	2	1	6	1	15	4	0	29
	Tenuiphantes tenuis	3	4	1	2	3	14	4	4	35
	Zelotes latreillei	4	1	1	2	0	17	0	0	25
Type II	***Alopecosa pulverulenta***	157	53	1	2	0	1	3	0	**217**
	Bathyphantes gracilis	10	2	1	2	0	1	1	1	18
	Erigone atra	1	24	5	0	0	0	0	5	35
	Oedothorax apicatus	0	0	9	0	0	0	0	0	9
	Ozyptila simplex	15	10	0	1	0	0	0	0	26
	Pardosa prativaga	43	10	0	2	0	0	0	0	55
	P. proxima	0	8	4	0	0	0	0	0	12
	P. pullata	20	16	2	4	0	1	0	0	43
	Tiso vagans	4	0	0	1	0	0	0	0	5
	Trochosa ruricola	5	2	0	0	0	0	0	0	7
Type III	*Agroeca inopina*	1	0	0	0	0	0	0	0	1
	Centromerus sylvaticus	1	0	0	0	0	0	0	0	1
	Diplostyla concolor	14	0	0	0	0	0	0	0	14
	Dysdera crocata	1	0	0	0	0	0	0	0	1
	Enoplognatha latimana	1	0	0	0	0	0	0	0	1
	Episinus truncatus	1	0	0	0	0	0	0	0	1
	Ero furcata	1	0	0	0	0	0	0	0	1
	Euophrys petrensis	1	0	0	0	0	0	0	0	1
	Gongylidiellum vivum	1	0	0	0	0	0	0	0	1
	Pardosa nigriceps	9	0	0	0	0	0	0	0	9
	Robertus lividus	2	0	0	0	0	0	0	0	2
	Scotina celans	2	0	0	0	0	0	0	0	2
	Tegenaria picta	13	0	0	0	0	0	0	0	13
	T. sylvestris	1	0	0	0	0	0	0	0	1
	Theridion bimaculatum	1	0	0	0	0	0	0	0	1
	Zelotes pusillus	1	0	0	0	0	0	0	0	1
	Zodarion italicum	18	0	0	0	0	0	0	0	18
	Zora spinimana	1	0	0	0	0	0	0	0	1
Undetermined type	*Agyneta conigera*	0	1	0	0	0	0	0	0	1
	Alopecosa accentuata	0	1	0	0	0	0	0	0	1
	Arctosa leopardus	0	1	0	0	0	0	0	0	1
	Crustulina sticta	0	0	0	0	0	1	0	0	1
	Erigone dentipalpis	1	1	2	0	0	0	0	1	5
	Larinioides cornutus	0	0	1	0	0	1	1	0	3
	Pirata latitans	0	0	0	0	0	0	0	1	1
	P. piraticus	0	0	1	0	1	0	0	3	5
	Thanatus striatus	0	0	0	0	0	0	0	1	1
	Tibellus maritimus	1	1	0	0	0	0	0	0	2
	Trachyzelotes pedestris	1	1	0	0	0	0	0	0	2
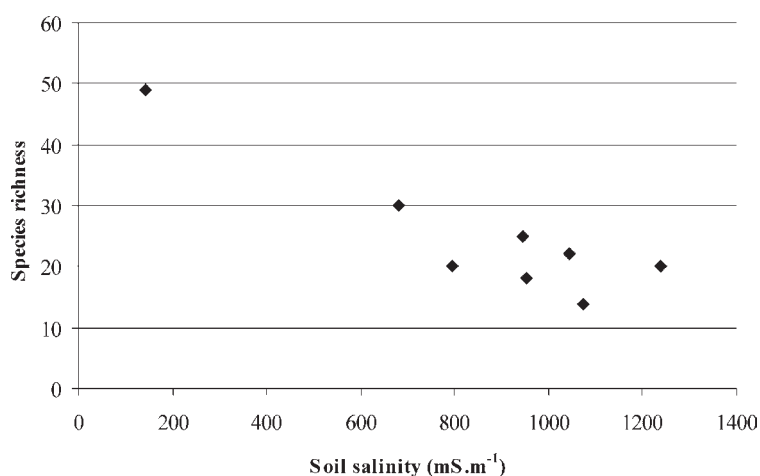
Fig. 3. Species richness in relation to soil salinity.
Рис. 3. Видовое богатство относительно солености почвы.

large range of salinities (Table 1). Within this group, in addition to *P. degeeri*, three halophilic species: *E. longipalpis, P. agrestis* and *A. fulvolineata* were captured in high proportions in the low marsh stations (where maximum salinity reaches 2 029 mS.m⁻¹). The relative abundance of other species of type I (type Ib), including only non-typical halophilic species, increases in the middle areas of the salt-marsh where soil salinity values are intermediate (between 945 and 1 044 mS.m⁻¹; Table 1). Type II species were absent or very poorly represented in the middle and low marsh areas. The maximum abundance was often found on the dike and the number of individuals collected rapidly decreased along the salinity gradient. These species seem to be present mainly in the stations with low mean soil salinity (i.e., less than 683 mS.m⁻¹). The third group (type III) contains species strictly localized at the dike and consequently not found in the areas with a mean soil salinity above 142 mS.m⁻¹. The remaining species ('undetermined type') were collected in one/several stations in very small numbers.

The results of time-standardized hand collecting (Table 3) follow the same classification for all species also caught by pitfall traps, except for *Oedothorax apicatus* and *Bathyphantes gracilis*, previously in group I. Three orb-web species were found at all stations and had a type I distribution, but *Araneus diadematus* was found primarily on the dike and was therefore regarded as a 'type II species'. The majority of species collected by hand only were restricted to the dike and regarded as 'type III species'.

As a general trend, the species richness decreased with increasing soil salinity (Fig. 3). Thus, the soil salinity is revealed to be a good predictor of species richness (regression analysis; $y = 50.1 + 0.0295x$; $r^2 = 82.5\%$; $P = 0.002$; eight data points).

Effects of tidal flooding

Apart from doubtful distribution changes, the two types of species distribution can be distinguished based on changes following a sea tide (Table 4): the relatively unmodified species distribution and the reduced species distribution. Most species from group I (*Agroeca lusatica, Arctosa fulvolineata, Argenna patula, Larinioides cornutus, Pachygnatha degeeri* and *Pardosa agrestis*) were still similarly distributed following the sea tide and consequently appear able to resist tidal flooding. Three species, *A. fulvolineata, P. degeeri* and *P. agrestis*, were even of comparable abundance before and after the sea tide (Table 4). Only in the last station, did the mean abundance of *P. agrestis* decrease after the sea tide (Table 5), but the difference was not significant (ANOVA; $F = 3.31$; $P = 0.119$; df = 7). Apparently *Tibellus maritimus* and *Pardosa proxima* were able to resist sub-

Changes in spider abundances along the salt marsh (data from hand catches only; * = species only or mostly hand collected).

Таблица 3.
Изменение видового богатства вдоль солончака (только данные ручных сборов; * = вид собран в основном или только ручным сбором).

		Stations								
		A	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**Total**
Type Ia	*Arctosa fulvolineata*	0	2	0	2	1	27	1	6	39
	Pachygnatha degeeri	0	6	0	0	15	3	9	8	41
	Pardosa agrestis	2	8	2	10	31	24	34	53	164
Type Ib	*Agroeca lusatica*	0	1	0	2	0	4	1	0	8
	Argiope bruennichi *	9	4	2	2	3	12	5	2	39
	Argenna patula	0	16	0	10	5	77	1	0	109
	Bathyphantes gracilis	0	3	0	1	2	7	3	0	16
	Crustulina sticta	2	0	0	0	0	5	0	0	7
	Clubiona stagnatilis	0	0	0	0	5	4	2	0	11
	Enoplognatha mordax	0	0	0	0	4	6	4	1	15
	Erigone atra	0	7	1	3	1	0	0	2	14
	Larinioides cornutus *	13	9	7	3	2	15	4	2	55
	Tenuiphantes tenuis	3	12	0	0	11	22	18	1	67
	Neoscona adianta *	1	3	4	2	2	4	0	0	16
	Oedothorax apicatus	0	0	0	0	0	0	0	6	6
	Silometopus ambiguus	0	7	0	7	21	1	3	1	40
Type II	*Araneus diadematus* *	11	0	0	0	0	1	0	0	12
	Enoplognatha ovata *	3	1	0	0	0	0	0	0	4
Type III	*Bathyphantes parvulus* *	1	0	0	0	0	0	0	0	1
	Centromerus sylvaticus	1	0	0	0	0	0	0	0	1
	Crustulina guttata *	2	0	0	0	0	0	0	0	2
	Dysdera crocata	1	0	0	0	0	0	0	0	1
	Enoplognatha latimana	3	0	0	0	0	0	0	0	3
	Episinus truncatus	2	0	0	0	0	0	0	0	2
	Ero furcata	1	0	0	0	0	0	0	0	1
	Hypsosinga sanguinea *	2	0	0	0	0	0	0	0	2
	Lepthyphantes pallidus *	3	0	0	0	0	0	0	0	3
	Neriene clathrata *	2	0	0	0	0	0	0	0	2
	Pisaura mirabilis *	3	0	0	0	0	0	0	0	3
	Salticus scenicus *	1	0	0	0	0	0	0	0	1
	Tegenaria silvestris	2	0	0	0	0	0	0	0	2
	Theridion bimaculatum	1	0	0	0	0	0	0	0	1
	Tibellus oblongus *	2	0	0	0	0	0	0	0	2
	Zora spinimana	6	0	0	0	0	0	0	0	6
Undetermined type	*Erigone dentipalpis*	0	1	0	0	1	0	1	0	3
	E. longipalpis	0	0	0	0	1	0	0	1	2
	Oedothorax fuscus	0	0	0	0	0	0	0	2	2
	O. retusus	0	1	0	0	0	0	0	0	1
	Ozyptila simplex	0	3	0	0	0	0	0	0	3
	Pachygnatha clercki	0	1	0	0	3	0	0	0	4
	Pardosa pullata	0	0	0	0	0	1	0	0	1
	Stemonyphantes lineatus	0	1	0	1	0	1	1	1	5
	Tetragnatha extensa *	1	0	0	0	0	2	0	0	3
	Tibellus maritimus	1	3	0	0	0	0	0	0	4
	Tiso vagans	0	1	0	0	0	0	0	0	1
	Zelotes latreillei	0	1	0	0	0	0	0	0	1

mergence, whereas they seemed unable to withstand mean soil salinities above 683 mS.m^{-1} and 796 mS.m^{-1} respectively (Tables 1 and 2).

Only one species from group I, *Silometopus ambiguus*, disappeared from the low stations (i.e., stations F–H), but it remained in the high stations (Table 4). This distribution change may be explained by lower water levels in stations B–D. *Alopecosa pulverulenta* disappeared from the high marsh (stations B and D, respectively) and the abundance of *A. pulverulenta* in the dike increased (Table 5) significantly (ANO-

Table 4.

Distribution of species before (upper line) and after (lower line) spring tide (April 2003, tidal range: 13.80 metres; dotted line: less than five individuals collected).

Таблица 4.

Распределение пауков до (верхняя линия) и после (нижняя линия) весеннего прилива (Апрель 2003, размах прилива: 13,80 метров; прерывистая линия: собрано менее пяти особей).

Distance from embankment (m) and stations	0 (A)	50 (A')	110 (B)	350 (C)	350 (D)	800 (F)	890 (G)	1 140 (G)	Total number of individuals Before tide	After tide
Species distribution and abundance not or little affected by tide										
Pardosa agrestis									195	131
Pachygnatha degeeri									58	53
Arctosa fulvolineata									41	36
Agroeca lusatica									3	5
Larinioides cornutus									23	24
Argenna patula									4	10
Pardosa proxima									5	3
Tibellus maritimus									2	2
Species distribution reduced										
Silometopus ambiguus									5	3
Stemonyphantes lineatus									6	0
Clubiona stagnatilis									6	0
Alopecosa pulverulenta									47	18
Doubtfull distribution										
Erigone atra									2	1
Tenuiphantes tenuis									2	1
Tetragnatha extensa									2	0
Crustulina sticta									1	1
Pachygnatha clercki									1	0
Species richness Before tide	5	6	10	7	10	5	8	5		
After tide	6	6	9	5	7	4	3	4		

VA; $F = 5.96$; $P = 0.050$; $df = 7$). This species probably disappeared from the salt marsh, but not from the dike. Two species, *Clubiona stagnatilis* and *Stemonyphantes lineatus*, were present in the salt marsh before tidal flooding but disappeared afterwards (Table 4). It may be assumed that these species were unable to resist submergence in sea water, nor did they manage to seek refuge in the high marsh or the dike.

Discussion

The year round sampling protocol, yielded numerous species in low numbers, probably due to the high soil salinity, which is well known to be a highly constraining factor for osmotic regulation [Foster & Treherne, 1976; Verschoor & Krebs, 1995a,b; Levin & Talley, 2000]. Despite the low numbers of individuals caught, we hypothesize that the observed distributions can primarily be attributed to soil salinity because (1) the vegetative cover was homogenous along the transect, and (2) several samples were taken until five weeks after salt marsh submergence. Tidal flooding and fluctuations in the vegetation architecture cannot then be considered as restricting factors to explain species presence/absence along the transect during one year. Data

| Species | Distance from the dike | | | | | | | | | | | | | | |
| | 0 m (station A) | | | 110 m (station B) | | | 350 m (station C) | | | 800 m (station F) | | | 1 140 m (station H) | | |
	Before	After	Code	Before	After	Code	Before	After	Code	Before	After	Code	Before	After	Code
Alopecosa pulverulenta	1.75	8.50	*	2.00	0	B	0	0		0	0		0	0	
Pardosa proxima	1.00	0	*	0.25	0.50	n.s.	0	0		0	0		0	0	
Agroeca lusatica	0.25	0	B	0	0		0	0.25	A	0	0.75	A	0	0	
Arctosa fulvolineata	0	0.25	A	0.75	1.75	n.s.	2.5	2.5	n.s.	0.50	1.50	n.s.	1.00	?	C
Pachygnatha degeeri	0.25	0.50	n.s.	0.50	1.75	n.s.	3.50	3.00	n.s.	5.75	5.25	n.s.	0.50	?	C
Pardosa agrestis	1.25	0.75	n.s.	10.25	10.50	n.s.	3.50	5.75	n.s.	3.5	3.75	n.s.	12.50	4.75	n.s.

from pitfall traps have to be considered very carefully, especially when comparing 'activity-densities' of individuals at different stations. Variations in the local micro-environment around each trap can lead to variations in the number of individuals caught. However, high variations in species caught at the different stations can be considered to give new interpretations on the status of halophilic species.

As expected, the so-called 'halophilic species' can tolerate high soil salinities (from 1 333 to 2 029 mS.m⁻¹). However, this study clearly demonstrates that several 'non-halophilic' species, such as *Agroeca lusatica* or *Pachygnatha degeeri*, can withstand the median to high soil salinities. Considering the whole spider community of the salt marsh area, with regards to soil salinity, three types can be defined: 'halophilic species' (type I: able to withstand strong soil salinity values), 'halotolerant species' (type II: species restricted to areas with low salinity values) and 'salinity intolerant species' (type III). It can be noted that the linyphiids form an important proportion of type I and II (40% of species: 10/25), whereas this family only represents 23% (6/26) of type III species. Species of this family are considered to be more frequent in temporary habitats [Southwood, 1962]. This poses the problem of aerial dispersal of the linyphiids (i.e., capacity for ballooning) that may result in accidental presence along the

entire salt marsh. Conversely, the high proportion of individuals of the nocturnal cursorial species *Agroeca lusatica* and *Zelotes latreillei*, and of the non aeronaut species *Pachygnatha degeeri* and *Stemonyphantes lineatus* in the high-salinity stations, is more likely to be related to a halophilic or halotolerant reaction than to accidental presence. In fact, it may be that mean soil salinity decreases between two sea tides, allowing occasional or regular incursions of halotolerant species from adjacent habitats (e.g., from the dike). The third group contained species strictly localized on the dike and consequently not found in areas even with very low mean soil salinities. This is supported by the whole-year sampling, assuming that the absence in the salt marsh of species restricted to the dike is due to a real avoidance reaction, rather than a failure to collect individuals there. The presence on the dike of several species such as *Centromerus sylvaticus*, *Scotina celans* or *Tegenaria silvestris*, which normally occur in woody habitats [Hänggi *et al.*, 1995; Roberts, 1995], supports the salt marsh avoidance hypothesis by some species intolerant of salinity.

A comparison of salinity tolerance and resistance to tidal flooding provides a distinction between: (1) the species intolerant of salinity and unaffected by tidal flooding (type III); (2) the halotolerant species unable to resist sea tides (type II in part); (3) the halotolerant spe-
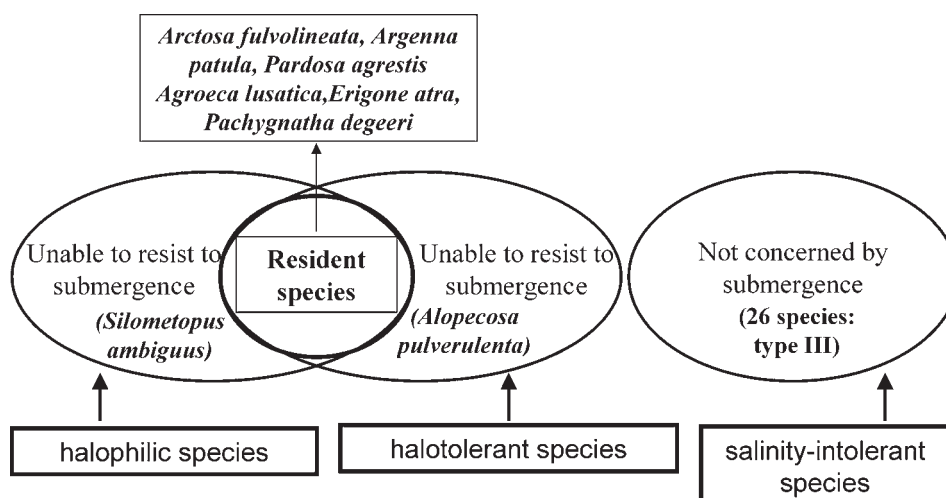
Fig. 4. Proposed status of salt marsh resident species in relation to halotolerance and tidal resistance.

Рис. 4. Предлагаемый статус резидентных видов солончаков относительно галотолерантности и устойчивости к приливам.

cies able to resist to sea tides (type II in part); (4) the halophilic species unable to resist to sea tides (type I in part); and (5) the halophilic species able to resist to sea tides (type I in part). Species of the first and second groups clearly appear to be unadapted to the salt marsh ecosystem and the presence of halotolerant species unable to resist sea tides in the high marsh can be considered the result of occasional/accidental incursion (see for example, *A. pulverulenta*). Species of the third and fifth groups can be regarded as salt marsh resident species (Fig. 4). These two groups contain the species usually regarded as 'halophilic' (e.g., *A. fulvolineata*, *P. agrestis* and *A. patula*), even if tidal resistance has yet to be demonstrated for some of them (e.g., *Erigone longipalpis* and *Enoplognatha mordax*, which were absent during our tidal flooding study), but these groups also contain other species, such as *Agroeca lusatica*, *Erigone atra* and *Pachygnatha degeeri*. These species are resistant both to high soil salinity values (mean soil salinity above $1\,000$ mS.m^{-1}) and to sea tides, and can consequently be considered as salt marsh resident species. This classification also poses the question of salt marsh resident status for species of the fourth group (Fig. 4). For example, *Silometopus ambiguus* can tolerate high soil salinities (up to $2\,000$ mS.m^{-1}), which is in accordance with its halo-

philic status as suggested by its distribution over the marsh, but it seems to be unable to withstand tidal flooding in the low marsh.

The salt marsh can be considered a constraining ecosystem with high soil salinities induced by periodical sea tides, and supporting a few species physiologically capable of tolerating them [e.g., Foster & Treherne, 1976; Levin & Talley, 2000]. These disturbances result in a quite low species richness, and in a strong dominance of one spider species, *Pardosa agrestis* in this study. This species is also reported as the most abundant species in central European agroecosystems [Samu & Szinetár, 2002]. However, all specimens caught during this study were similar to the poorly known species *Pardosa purbeckensis* [as described by Locket & Millidge, 1951], which was supposed to occur only in salt marshes and to be capable of osmoregulation [Heydemann, 1970].

Finally, it can be noticed that the relative importance of sheet-web and cursorial spider species in the invaded salt marsh, was probably associated with the litter of *Elymus athericus*. These spider species seem to have benefited from the *E. athericus* invasion to the salt marsh, which began ten years ago. Comparison with data available for the time prior to *E. athericus* invasion [cf. Fouillet, 1988] revealed a comparable number of halophilic species, but an in-

crease in the number of halotolerant spider species in the salt marsh following the invasion. Consequently, the *E. athericus* invasion has probably altered the halophilic character of arthropod communities in the salt marshes of Mont Saint-Michel Bay.

References

Baert L. & Maelfait J.-P. 1999. The spider fauna of the Belgian salt marshes // Bull. Instit. R. Sci. Nat. Belg. Entomol. Vol.65. P.5–18.

Bonte D., Maelfait J.-P. & Hoffmann M. 2000. The impact of intensive cattle grazing on the spider communities Araneae in a mesophytic dune grassland // J. Insect Conserv. Vol.6. P.135–144.

Bouchard V., Digaire F., Lefeuvre J.C. & Guillon L.M. 1995. Progression des marais salés à l'ouest du Mont-Saint-Michel entre 1984 et 1994 // Mappemonde. Vol.4. P.28–34.

Canard A. 1981. Utilisation comparée de quelques méthodes d'échantillonnage pour l'étude de la distribution des araignées des landes // Atti Soc. Toscana Sci. Nat. Vol.88. P.84–94.

Canard A. 1990. Heathland spider communities, a functional group study // Acta Zool. Fenn. Vol.190. P.45–50.

Canard A. 2004. Catalogue of spider species from Europe and the Mediterranean basin // Revue Arachnol. (in press).

Chapman V.J. 1940. Succession on the New England salt marshes // Ecology. Vol.21. P.279–282.

Churchill T.B. 1993. Effects of sampling method on composition of a Tasmanian coastal heathland spider assemblage // Mem. Queensland Mus. Vol.33. P.475–782.

Churchill T.B. & Arthur J.M. 1999. Measuring spider richness: effects of different sampling methods and spatial and temporal scales // J. Insect Conserv. Vol.3. P.287–295.

Costil K., Dussart G.B.J. & Daguzan J. 2001. Biodiversity of aquatic gastropods in the Mont St-Michel basin (France) in relation to salinity and drying of habitats // Biod. Conserv. Vol.10. P.1–18.

Curtis D.J. 1980. Pitfalls in spider community studies (Arachnida, Araneae) // J. Arachnol. Vol.8. P.271–280.

Davis L.V. & Gray I.E. 1966. Zonal and seasonal distribution of insects in North Carolina salt marshes // Ecol. Monogr. Vol.36. P.275–295.

Descender K. & Maelfait J.-P. 1999. Diversity and conservation of terrestrial arthropods in tidal marshes along the River Schelde: a gradient analysis // Biol. Conserv. Vol.87. P.221–229.

Döbel H.G., Denno R.F. & Coddington J.A. 1990. Spider (Araneae) community structure in an intertidal salt marsh: effects of vegetation structure and tidal flooding // Environ. Entomol. Vol.19. P.1356–1370.

Elkaim B. & Rybarczyck H. 2000. Structure du peuplement des invertébrés des zones halophiles de la Baie de Somme // Cah. Biol. Mar. Vol.41.P.295–311.

Foster W.A. & Treherne J.E. 1976. Insects of marine saltmarshes: problems and adaptations // Cheng L. (ed.). Marine insects. Amsterdam: North-Holland Company. P.5–42.

Fouillet P. 1986. Evolution des peuplements d'Arthropodes des schorres de la Baie du Mont Saint-Michel: influence du pâturage ovin et conséquences de son abandon. PhD Thesis, University of Rennes 1, 330 p.

Gérard C., Blanc A. & Costil K. 2004. *Potamopyrgus antipodarum* (Mollusca: Hydrobiidae) in continental aquatic gastropod communities: impact of salinity and trematode parasitism // Hydrobiologia. (in press).

Granström U. 1973. Pitfall traps for studying the activity of ground living spiders (Araneida) // Aquilo Ser. Zool. Vol.14. P.93–98.

Greenstone M.H. 1984. Determinants of web spider diversity: vegetation structural diversity vs. prey availability // Oecologia. Vol.62. P.299–304.

Hänggi A., Stocklie E. & Nentwig W. 1995. Habitats of central European spiders. Série Miscellanea Faunistica Helvetiae, volume 4. Neuchâtel: Centre suisse de cartographie de la faune. 460 p.

Hatley C.L. & MacMahon J.A. 1980. Spider community organization: seasonal variation and the role of vegetation architecture // Environ. Entomol. Vol.9. P.632–639.

Healy B. 1975. Fauna of the salt marsh, North Bull Island, Dublin // Proc. R. Iri. Acad. Vol.75. P.225–244.

Heimer S. & Nentwig W. 1991. Spinnen Mitteleuropas. Berlin: Verlag Paul Parey. 529 S.

Heydemann B. 1970. Ökologische Untersuchungen zum problem der Halophilen und Haloresistenten Spinnen // Bull. Mus. Nat. Hist. Nat. (Paris). Vol.41. P.226–232.

Jacquemin G. 1999. Les marais salés de Lorraine : premier bilan entomologique // Robert J.-C. *et al.* (eds.). Inventaire et cartographie des invertébrés comme contribution à la gestion des milieux naturels français [Actes du séminaire tenu à Besançon les 8, 9 et 10 juillet 1999]. Paris: Muséum National d'Histoire Naturelle / Service du Patrimoine Naturel – Office pour l'Information Eco-entomologique. P.91–97.

Kneib R.T. 1984. Patterns of invertebrate distribution and abundance in the intertidal salt marsh: causes and questions // Estuaries. Vol.7. P.392–412.

La Salle M.W., Landin M.C. & Sims J.G. 1991. Evaluation of the flora and the fauna of a *Spartina alterniflora* marsh established on dredged material in Winyah Bay, South Carolina // Wetlands. Vol.11. P.191–209.

Lefeuvre J.-C., Bouchard V., Feunteun E., Grare S. &

Laffaille P. 2000. European salt marshes diversity and functioning: the case of the Mont Saint-Michel Bay, France // Wetlands Ecol. Manag. Vol.8. P.147–161.

Levin L.A. & Talley T.S. 2000. Influence of vegetation and abiotic environmental factors on salt marsh invertebrates // Weinstein M.P. & Kreeger D.A. (eds.). Concepts and controversies in tidal marsh ecology. Dordrecht: Kluwer Academic Publishing. P.661–707.

Locket G.H. & Millidge A.F. 1951. British spiders (volume I). London: The Ray Society. 310 p.

Luff M.L. 1975. Some features affecting the efficiency of pitfall traps // Oecologia. Vol.19. P.345–357.

Marples T.G. 1966. A radionucleide tracer study of Arthropod food chains in a *Spartina* salt marsh ecosystem // Ecology. Vol.47. P.270–277.

Meijer J. 1980. The development of some elements of the arthropod fauna of a new polder // Oecologia. Vol.45. P.220–235.

Morse D. 1997. Distribution, movement, and activity patterns of an intertidal wolf spider *Pardosa lapidicina* (Araneae, Lycosidae) // J. Arachnol. Vol.25. P.1–10.

Rand T.A. 2002. Variation in insect herbivory across a salt marsh tidal gradient influences plant survival and distribution // Oecologia. Vol.132. P.549–558.

Roberts M.J. 1985a. The Spiders of Great Britain and Ireland. Volume 1. Atypidae – Theridiosomatidae. Colchester: Harley Books. 229 p.

Roberts M.J. 1985b. The Spiders of Great Britain and Ireland. Colchester: Harley Books. Volume 3. Colour plates. Colchester: Harley Books. 256 p.

Roberts M.J. 1987. The Spiders of Great Britain and Ireland. Volume 2. Linyphiidae and check list. Colchester: Harley Books. 204 p.

Roberts M.J. 1995. Spiders of Britain and Northern Europe. London: HarperCollins Publishers. 383 p.

Southwood T.R.E. 1962. Migration of terrestrial arthropods in relation to habitat // Biol. Rs. Vol.37. P.171–214.

Talley T.S. & Levin L.A. 1999. Macrofaunal succession and community structure in *Salicornia* marshes of southern California // Estuar. Coast. Shelf Sci. Vol.49. P.713–731.

Topping C.J. & Luff M.L. 1995. Three factors affecting the pitfall trap catch of linyphiid spiders (Aranea: Linyphiidae) // Bull. Br. Arachnol. Soc. Vol.10. P.35–38.

Topping C.J. & Sunderland K.D. 1992. Limitations to the use of pitfall traps in ecological studies exemplified by a study of spiders in a field of winter wheat // J. Appl. Ecol. Vol.29. P.485–491.

Valéry L., Bouchard V. & Lefeuvre J.-C. 2004. Impact of the invasive native species *Elymus athericus* on carbon pools in a salt marsh // Wetlands (in press).

Verschoor B.C. & Krebs B.P.M. 1995a. Successional changes in a saltmarsh carabid beetle (Coleoptera, Carabidae) community after embankment of the Markiezaat area // Pedobiologia. Vol.39. P.385–404.

Verschoor B.C. & Krebs B.P.M. 1995b. Diversity changes in a plant and carabid community during early succession in an embanked saltmarsh area // Pedobiologia. Vol.39. P.405–416.

Wise D.H. 1993. Spiders in ecological webs. Cambridge: Cambridge University Press. 315 p.

Ysnel F. & Canard A. 2000. Spider biodiversity in connection with the vegetation structure and the foliage orientation of edges // J. Arachnol. Vol.28. P.107–114.

Ysnel F., Canard A. & Tiberghien G. 1996. The shrub layer spider communities: variation in composition and structure of the gorse clump communities in western France // Rev. Suisse Zool. (Vol. Hors Série). P.691–700.

Zelder J.B. 1977. Salt marsh community structure in the Tijuana Estuary, California // Est. Coas. M. Vol.5. P.39–53.

Appendix.

Taxonomic list of spiders caught in the salt marsh investigated
(Data collection from April 2002 to April 2003; Mont St. Michel Bay, France)

AGELENIDAE
1. *Tegenaria picta* Simon, 1870
2. *T. silvestris* L. Koch, 1872
3. *Tegenaria* sp.
AMAUROBIIDAE
4. *Amaurobius ferox* (Walckenaer, 1830)
ARANEIDAE
5. *Araneus diadematus** Clerck, 1757
6. *Argiope bruennichi** (Scopoli, 1772)
7. *Hypsosinga sanguinea** (C.L. Koch, 1844)
8. *Larinioides cornutus** (Clerck, 1757)
9. *Neoscona adianta** (Walckenaer, 1802)
CLUBIONIDAE
10. *Clubiona terrestris** Westring, 1862

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* = species only or mostly collected by hand; names in **bold** are the halophytic species according to the literature.

DICTYNIDAE
11. *Argenna patula* (Simon, 1874)
DYSDERIDAE
12. *Dysdera crocata* C.L. Koch, 1838
13. *Dysdera* sp.
GNAPHOSIDAE
14. *Micaria* sp.
15. *Scotina celans* (Blackwall, 1841)
16. *Trachyzelotes pedestris* (C.L. Koch, 1837)
17. *Zelotes latreillei* (Simon, 1878)
18. *Z. pusillus* (Koch, 1866)
19. *Zelotes* sp.
LINYPHIIDAE
20. *Agyneta conigera* (O. Pickard-Cambridge, 1863)
21. *Bathyphantes gracilis* (Blackwall, 1841)
22. *B. parvulus** (Westring, 1851)
23. *Centromerus sylvaticus* (Blackwall, 1841)

24. *Diplostyla concolor* (Wider, 1834)
25. *Erigone atra* (Blackwall, 1841)
26. *E. dentipalpis* (Wider, 1834)
27. **E. longipalpis (Sundevall, 1830)**
28. *Gongylidiellum vivum* (O. Pickard-Cambridge, 1875)
29. *Lepthyphantes pallidus** (O. Pickard-Cambridge, 1871)
30. *Microlinyphia impigra* (O. Pickard-Cambridge, 1871)
31. *Neriene clathrata** (Sundevall, 1829)
32. *Oedothorax apicatus* (Blackwall, 1850)
33. *O. fuscus* (Blackwall. 1834)
34. *O. retusus* (Westring, 1851)
35. **Silometopus ambiguus (O. Pickard-Cambridge, 1905)**
    = *S. curtus* (Simon, 1926)
36. *Stemonyphantes lineatus* (Linnaeus, 1758)
37. *Tenuiphantes tenuis* (Blackwall, 1852)
38. *Tiso vagans* (Blackwall, 1834)
LIOCRANIDAE
39. *Agroeca inopina* O. Pickard-Cambridge, 1886
40. *A. lusatica* (L. Koch, 1875)
LYCOSIDAE
41. *Alopecosa accentuata* (Latreille, 1817)
42. *A. pulverulenta* (Clerck, 1757)
43. **Arctosa fulvolineata (Lucas, 1846)**
44. *A. leopardus* (Sundevall, 1833)
45. **Pardosa agrestis (Westring, 1861)**
    = *P. purbeckensis* (F.O. Pickard-Cambridge, 1895)
46. *P. nigriceps* (Thorell, 1856)
47. *P. prativaga* (L. Koch, 1870)
48. *P. proxima* (C.L. Koch, 1847)
49. *P. pullata* (Clerck, 1757)
50. *Pardosa* sp.
51. *Pirata latitans* (Blackwall, 1841)
52. *P. piraticus* (Clerck, 1757)
53. *Pirata* sp.
54. *Trochosa ruricola* (DeGeer, 1778)
55. *Trochosa* sp.

MIMETIDAE
56. *Ero furcata* (Villers, 1789)
PHILODROMIDAE
57. *Thanatus striatus* C.L. Koch, 1845
58. *Tibellus maritimus* (Menge, 1875)
59. *T. oblongus** (Walckenaer, 1802)
60. *Tibellus* sp.
PISAURIDAE
61. *Pisaura mirabilis** (Clerck, 1757)
SALTICIDAE
62. *Euophrys* sp.*
63. *Myrmarachne formicaria** (DeGeer, 1778)
64. *Salticus scenicus** (Clerck, 1757)
65. *Talavera petrensis* (C.L. Koch. 1837)
TETRAGNATHIDAE
66. *Pachygnatha clercki* Sundevall, 1823
67. *P. degeeri* Sundevall, 1830
68. *Pachygnatha* sp.
69. *Tetragnatha extensa** (Linnaeus, 1758)
THERIDIIDAE
70. *Crustulina guttata** (Wider, 1834)
71. *C. sticta* (O. Pickard-Cambridge, 1861)
72. *Enoplognatha latimana* Hippa & Oksala, 1982
73. **E. mordax (Thorell, 1875)**
    = *E. crucifera* (Thorell, 1875)
74. *E. ovata** (Clerck, 1757)
75. *E. thoracica** (Hahn, 1833)
76. *Episinus truncatus* Latreille, 1809
77. *Episinus* sp.*
78. *Robertus lividus* (Blackwall, 1836)
79. *Theridion bimaculatum* (Linnaeus, 1767)
THOMISIDAE
80. *Ozyptila praticola* (C.L. Koch, 1837)
81. *O. simplex* (O. Pickard-Cambridge, 1862)
82. *Ozyptila* sp.
83. *Xysticus cristatus* (Clerck, 1757)
84. *Xysticus* sp.
ZODARIIDAE
85. *Zodarion italicum* (Canestrini, 1868)
ZORIDAE
86. *Zora spinimana* (Sundevall, 1833)