



Impact of vegetation structure dynamics and usage on the nursery function of West European tidal salt-marshes

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Abstract: An analysis of the fish community of Aiguillon bay (France) and Mont Saint-Michel bay was performed in order to identify the fish settler guild structure. Some species settled in salt marshes only in their first years when they were young-of-the-year or juveniles (“yoy salt marsh settlers” and “juvenile salt marsh settlers”). Other fish species were “resident salt marsh settlers” like gobies (*Pomatoschistus spp.*) that conduct all their life cycle in this ecosystem. Another settler guild is composed of species that show opportunistic settler behaviour. These species forage in the salt marsh at either young or adult stages (“opportunistic salt marsh settlers”). Management for bird conservation leads to modifications in vegetation structure. The halophytic community is mowed every year during spring and autumn to create favourable habitats for Anatidae and wader conservation. This management seems to have adverse effects on the nursery role for fish populations such as Seabass. A comparison between the nursery role of Aiguillon bay and Mont Saint-Michel Bay showed significant differences. This latter bay sustains preferentially young-of-the-year of pelagic species. The Aiguillon bay sustains many YoY species (Seabass, European anchovy and Clupeidae YoY). The key nursery role often described seems to be disturbed in Mont Saint-Michel bay. Low juvenile abundances were observed. Sheep grazing impact and invasion by the grass *Elytrigia spp.* seems to have modified the initial nursery function of these coastal zones.

Résumé: *Impact de la dynamique et de la gestion de la végétation sur la fonction de nourricerie des marais salés d'Europe occidentale.* L'étude du peuplement piscicole du marais salé de la baie de l'Aiguillon (France) et de la baie du Mont Saint-Michel a permis de mettre en évidence une structuration en guildes colonisatrices de ce système singulier. Certaines espèces colonisent le marais exclusivement lors de la ou des premières années (jeunes de l'année et juvéniles colonisateurs des marais salés). D'autres espèces sont résidentes comme les gobies du genre *Pomatoschistus spp.* et effectuent la totalité de leur cycle biologique aux alentours du marais (espèces résidentes colonisatrices des marais salés). Une autre catégorie d'espèces fréquente le marais de manière opportuniste en tant que zone privilégiée d'alimentation soit aux jeunes stades soit à l'âge adulte (espèces opportunistes colonisatrices des marais salés). Les activités liées à la conservation de l'avifaune induit des modifications de l'architecture végétale initialement présente pour des prairies rases à puccinellies, entraînant une raréfaction des communautés d'arthropodes proies tels que *Orchestia gammarellus*. Ces mesures de gestion semblent antagonistes avec la fonction de nourricerie de ces écosystèmes qui soutiennent les populations à caractères halieutiques comme le bar. Une comparaison des communautés piscicoles de la baie du Mont Saint-Michel et de la baie de l'Aiguillon a montré deux fonctions de nourricerie un peu différentes, centrées sur des espèces plutôt pélagiques pour la baie du Mont Saint-Michel, et autour du bar, des clupéidés et de l'anchois pour la baie de l'Aiguillon. La fonction généralement décrite

de nourricerie de bar dans le premier site semble altérée. De très faibles abondances de juvéniles ont été observées. L'impact des activités de pâturages ovins, de la fauche et de l'invasion du chiendent maritime (*Elytrigia atherica*) semble modifier la fonction initiale de nourricerie des ces espaces littoraux.

Keywords: Fish community; Nursery function; Estuarine systems; Settlers guilds; Aiguillon bay; Mont Saint-Michel bay

Introduction

The ecosystem complexes formed by European intertidal mudflats and salt marshes play an important nursery role for many species of fish (Riou, 1999; Laffaille et al., 2000a, Le Pape et al., 2000; Lefeuvre et al., 2000). Most of these species have the capacity to withstand large variations in salinity (Elie et al., 1990). They can therefore take advantage of the high production of organic matter on these coastal mudflats (Christensen & Pauly, 1998; Laffaille et al., 2002) or on their adjacent saltmarshes (Laffaille et al., 1998). Some of these species have an economic fisheries interest and also participate actively in transfers of organic matter between the tidal marshes and adjacent coastal systems (role of biotic vector). By means of these trophic transfers, these ecosystems export organic matter toward coastal waters (Teal & Teal, 1962). This process, defined as outwelling by Odum (1968) enriches the coastal zones and enables sustainable exploitation practices such as fishing and shellfish cultivation to install there (Lefeuvre et al., 2003). However, the human activities (mowing, management, fishing, etc.) conducted on the upper vegetated parts of these remarkable areas can have adverse effects on their nursery function. Laffaille *et al.*, (2001) have shown that intensive sheep grazing activities on the grasslands of the Mont Saint-Michel bay reduce the nursery value of these coastal environments. The processes related to the invasion by sea couch grass *Elytrigia atherica* (Link, 1886) which could result from agricultural land (Bockelmann & Neuhaus, 1999; Valery, 2001) change accessibility to resources of terrestrial origin thereby changing fish diets (Laffaille et al., 2005). This is notably the case for young Seabass (*Dicentrarchus labrax*, L. 1758) and gobies of the genus *Pomatoschistus* spp. (Laffaille et al., 2000a; Parlier, 2002).

Most of the salt marsh area of the Aiguillon bay is managed as two nature reserves (Office National de la Chasse et de la Faune Sauvage and Ligue de Protection des Oiseaux). These two reserves have produced a joint management plan, mainly aimed at the conservation of waders and Anatidae, the area being a RAMSAR Convention site for the knot (*Calidris canutus*, L. 1758), black-tailed godwit (*Limosa limosa*, L. 1758) and widgeon (*Anas penelope*, L. 1758). In order to improve the carrying

capacity of the salt marshes for these species, the north-west part of the area is mown (Fig. 1), whereas in another area further south in the bay, the salt marshes are not subjected to mowing or grazing activity. The highly productive vegetation is therefore organized along the standard succession observed in such habitats, from the pioneer zones dominated by *Puccinellia* spp. (Hudson, 1750) and/or *Spartina* spp., to the mature marsh areas dominated by purslane (*Halimione portulacoides* L. 1758). These management options chosen in different parts of the Aiguillon bay, probably have consequences on the structure of the characteristics fish communities of these nursery areas.

The aim of this study was therefore to analyse the effects on the annual variations in the functional structure and the abundance of the fish communities. It will rely in particular on an analysis of ecological guilds, and on a seasonal comparison with the Mont Saint-Michel bay.

Materials and Methods

Description of the study sites

The nature reserves of the Aiguillon bay situated in Vendée (north) and Charentes Maritime administrative districts (south) on the Atlantic coast of France constitute an ecological area consistent in term of spatial distribution for fish. This area consists of 3700 ha of bare mud-flats, of 1100 ha of salt marshes ("Mizottes") in the head of the bay, and of 100 ha of tidal creeks (Meunier & Joyeux, 2003). The salt marshes are the subject of a management plan involving mowing to maintain grassland suitable for Anatidae. The areas drained by the creeks flowing into the Canal de Luçon are therefore mown between May and July, favouring *Puccinellia maritima* and *Elytrigia atherica* to the detriment of the original community dominated by *Halimione portulacoides* that is much more productive and offers a suitable habitat for amphipods such as *Orchestia gammarellus* (Pallas, 1766). In addition to management activities, there is a very intensive elver fishery from mid-November to early March. The winter of 2003-2004 was notable for the large number of intrusions into the Canal de Luçon, particularly by professional fishermen (Meunier, pers. comm.). The samplings sites are situa-

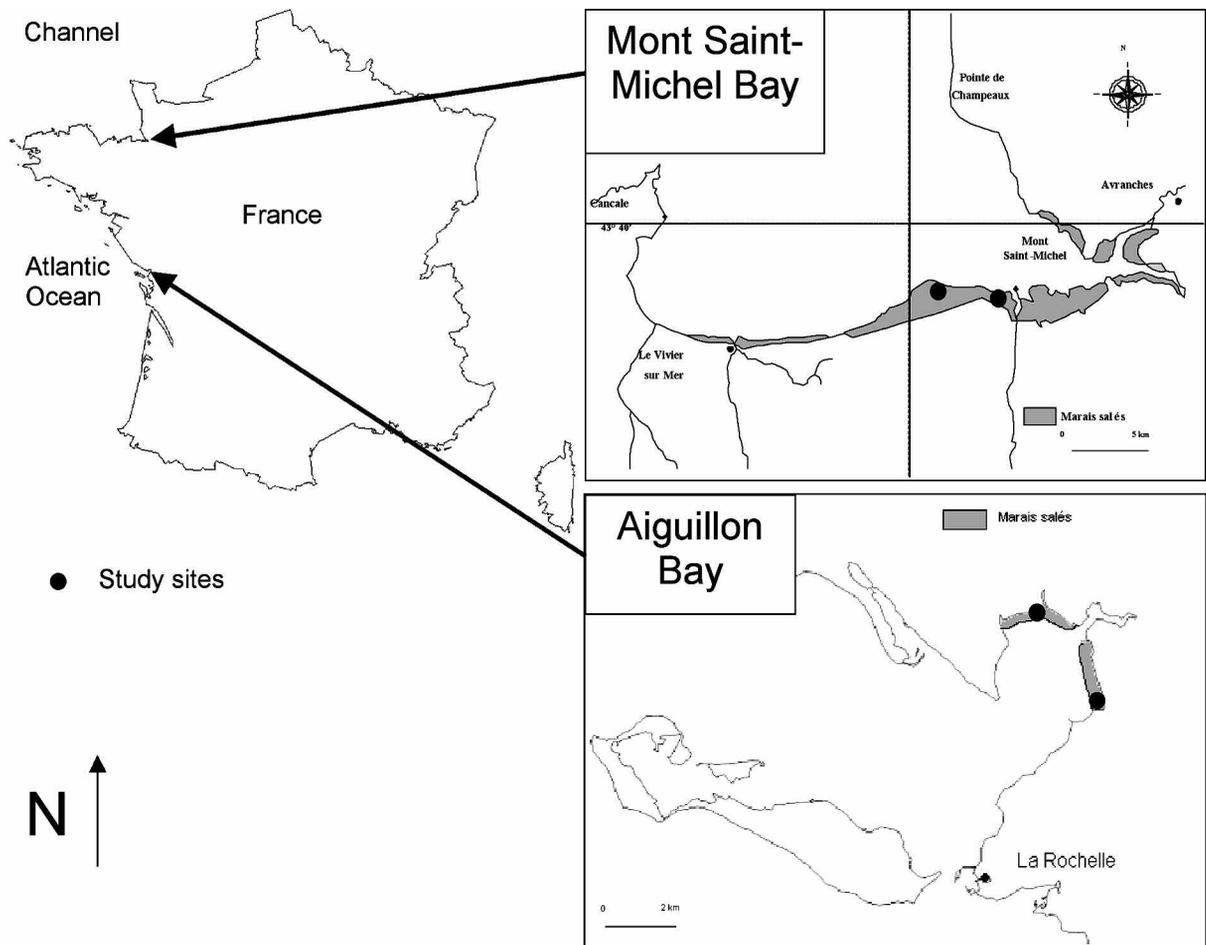


Figure 1. Location of the Aiguillon bay and the Mont Saint-Michel bay.

Figure 1. Situation de la baie de l'Aiguillon et de la baie du Mont Saint-Michel.

ted on either side of the tidal channel of the Sèvre Niortaise river. The Canal de Luçon site ($46^{\circ}18'57\text{N}$; $01^{\circ}09'53\text{W}$) was chosen for its position as a tributary of the canal (10 m wide). It drains the water of an artificial catchment of 10 ha that is cut for hay as part of the management plan. The vegetation is dominated by *Elytrigia atherica*. The second study site is a tributary of the Canal du Curé ($46^{\circ}15'49\text{N}$; $01^{\circ}07'09\text{W}$) that drains about 10 ha of *H. portulacoides* salt marshes.

A complementary study consisting of two fishing surveys (at the same time as those conducted in the Aiguillon bay) was conducted in two sites in the Mont Saint-Michel bay ($48^{\circ}40'\text{N}$, $1^{\circ}40'\text{W}$) already studied for many years (Laffaille et al., 2000a; Parlier, 2002; Laffaille et al., 2005). The two creeks studied were a few hundred metres apart and both drained an area of salt marshes of about ten hectares. The plant community had the normal vegetation succession typical of a salt marsh in one of the sites (Ponton), whereas the other (Tesnière) had been subject to severe changes in plant structure as a result of invasion by *E. atherica* (see Parlier, 2002).

Sampling methods

In the Aiguillon bay, the catches were conducted between April 2003 and April 2004 (except in January) with one sampling per month for the Canal du Curé site, and two samplings per month for the Canal de Luçon site between April and August 2003, then one monthly sampling until the rest of the study. The sampling dates were always timed to coincide with tidal coefficients greater than 85 (i.e. more than 85% of the height of spring tides, or a tidal range of 6 m), after which fish could enter the drainage creeks. The salt marshes are covered by the tide when the coefficient is over 95. Particular care was taken to conduct the fishing in weather conditions that were as similar as possible, and whenever possible when the tide was increasing from neap to spring. The fishing gear used was a combination of a fyke net (4 mm mesh, 20 m long and 1.80 m tall) and two gill nets (30 and 70 mm mesh, 30 m long and 2 m tall) in accordance with methods proven in such environments to reduce the selectivity of each type of gear (Duhamel et al.,

2002; Parlier, 2002). The fishing gear was set at slack high water and left in place until the creeks had almost emptied. The drainage creeks were almost empty at half-tide. Samplings lasted for 20 min at intervals of 5 min throughout the duration of the ebb tide. The fish catches were stored at -18°C in the laboratory until identification to species level. Once identified, the total length in mm (TL), fork length (FL) and fresh weight to the nearest mg (FW) were measured. Measurements were conducted on subsamples when the samples were too large (there was a pronounced shoaling effect in the juvenile stages of some species). Estimates of the numbers and biomass were then made using length-weight relations (Table 1).

Two additional seasonal sampling campaigns (spring and autumn) were conducted at the same time in Mont Saint-Michel bay. They consisted of 7 catches in June and 7 in September using the same sampling methods, and in similar conditions. A comparison in spring and autumn between the two bays was then made to assess any latitudinal differences that could exist between these two salt marshes on the west coast of France.

In order to estimate the share of each age group present in our samples, two analyses are carried out in the same time. Firstly, individuals of each species are old near at the year using length frequency diagram. Secondly, a validation is carried out thanks to a scalimetric analysis under binocular magnifying glass.

A numerical distribution of each cohort is practiced in order to estimate the percentages of each cohort (G_0 , G_1 and G_2 & +). Thus, various groups are describe by using the respective percentages of YoY (G_0), of G_1 and of G_2 and +. This classification in guild is related then to these percentages. Four behaviours of colonization of the estuarine complexes can be identified and gathered in colonizing guilds:

(i) Only the first stage is present (Young-of-the-Year or YoY). These species then are qualified young of the year settlers (*YoY Salt Marsh Settlers*). (% $G_1 < 10\%$; % $G_2 < 5\%$).

(ii)) Secondly, the young-of-the-year and the youthful ones are present in the studied zone. One will then speak about youthful or juvenile settlers (*Juvenile Salt Marsh Settlers*). (% $G_1 > 10\%$; % $G_2 < 5\%$).

(iii) Thirdly, when various cohorts are present but that all the ecophases are not indexed, one speaks about opportunist saltmarsh settlers (*Opportunistic Salt Marsh Settlers*). (% $G_1 10\%$; % $G_2 5\%$).

(iv) Lastly, when all the cohorts are present, in spite of the temporary side of these mediums undergoing marling one will speak about resident settlers (*Resident Salt Marsh Settlers*).

Analyses

The Catch Per Unit Effort (CPUE) (number or biomass per min of fishing) was calculated for each species from the

numbers and biomasses captured (Laffaille, 2000).

$$N_{i-i+1} = \frac{\frac{N_i}{t_i} + \frac{N_{i+1}}{t_{i+1}}}{2} \times t_{i-i+1} \quad CPUE = \frac{\sum N_{i+1} + \sum N_i}{\sum t_{i+1} + \sum t_i}$$

Where CPUE = number or biomass of fish per species per minute,

t_i = sampling duration in minutes

t_{i-i+1} = time in minutes between samples i and $i+1$,

N_i = quantity of fish captured per species (in numbers or biomass) during sampling i .

N_{i-i+1} = estimation of the quantity of fish per species (in numbers or biomass) which colonized the salt marshes between samplings i and $i+1$.

The temporal variations in the structure of the community were analysed by cluster analysis (Euclidian distance, Ward's method), the CPUE values were log (x+1) transformed as recommended by Field et al. (1982). Species only recorded a single time or in a single sample were excluded from the cluster analysis

An analysis of the size frequency distribution was conducted on the fish populations captured in the salt marshes of the Aiguillon bay (Fig. 2 & Table 3). Three size classes were used: young-of-the-year (YoY), juveniles and adults. A cluster analysis was conducted on the percentages of these classes. The values were log (x+1) transformed as recommended by Field et al. (1982).

Results

Composition of the fish population of the Aiguillon bay

A total of 16 302 fish belonging to 22 species were captured during the samplings (20 genera) with a total biomass of over 115 kg. More than 60% of the species occurred in both sites (Table 1). Four different ecological guilds were present (Elie et al., 1990; Laffaille et al., 2000a). Three transient species (amphihaline catadromous) were captured (Eel, *Anguilla anguilla* L. 1758). They frequent the estuarine zone during their migrations. Two strict marine species were caught during the sampling (Garfish (*Belone belone*, L. 1761), and Transparent goby (*Aphia minuta*, Risso 1810)). More than half of the population was composed of marine euryhaline species (Sandeel (*Ammodytes tobianus*, L. 1758), Silverside (*Atherina presbyter*, Cuvier 1829), Atlantic her-ring (*Clupea harengus*, L. 1758), Seabass (*D. labrax*), Golden grey mullet (*Liza aurata*, Risso 1810), Pilchard (*Sardina pilchardus*, Walbaum, 1792), European anchovy (*Engraulis encrasicolus*, L. 1758), European sprat (*Sprattus sprattus*, L. 1758), Common sole (*Solea solea*, L. 1758), Gilt head (*Sparus aurata*, L. 1758)). The rest of the

Table 1. Characteristics of the community structure and population structure in Aiguillon bay between April 2003 and April 2004. Total length, numerical abundance and %N: Relative numerical abundance. Biomass and %B: Relative abundance in terms of biomass, %FO: Frequency of occurrence, Frequency class.
Tableau 1. Composition du peuplement de poissons capturée en baie de l'Aiguillon entre avril 2003 et avril 2004 et indicateurs de la structure en taille des populations. Longueur totale, contribution numérique %N: Abondance numérique relative. %B: Biomasse relative, %FO: Fréquence d'occurrence et classe de fréquence d'occurrence

| Species | Common name | Mean | Total length (mm) | | N | % N | Biomass (g) | % B | % FO | Frequency class (Fc) | |
|--------------------------------|--------------------------|-------|-------------------|------|---------------|-------|------------------|-------|------|----------------------|---------------|
| | | | Min | Max | | | | | | error (se) | Standard |
| <i>Liza aurata</i> | Golden grey mullet | 51.2 | 34.3 | 15.0 | 2 853 | 17.5% | 14 374.3 | 12.5% | 92.6 | Frequent | 75 < Fc ≤ 100 |
| <i>Pomatoschistus microps</i> | Common goby | 26.9 | 8.7 | 10.0 | 1 495 | 9.2% | 285.3 | 0.2% | 85.2 | | |
| <i>Liza ramada</i> | Thihip mullet | 120.6 | 132.8 | 13.0 | 2 572 | 15.8% | 93 476.0 | 81.1% | 77.8 | Common | 50 < Fc ≤ 75 |
| <i>Dicentrarchus labrax</i> | Seabass | 33.0 | 23.2 | 10.0 | 5 464 | 33.5% | 6 053.7 | 5.3% | 66.7 | | |
| <i>Pomatoschistus minutus</i> | Sand goby | 36.3 | 9.5 | 14.0 | 1 007 | 6.2% | 186.7 | 0.2% | 59.3 | | |
| <i>Sprattus sprattus</i> | European sprat | 34.5 | 9.6 | 21.0 | 515 | 3.2% | 112.2 | 0.1% | 51.9 | | |
| <i>Clupea sp.</i> | Clupeidae yoy | 31.7 | 6.0 | 17.0 | 960 | 5.9% | 91.2 | 0.1% | 44.4 | Occasional | 25 < Fc ≤ 50 |
| <i>Egervallus encrasicolus</i> | Anchovy | 32.6 | 7.8 | 12.0 | 1 063 | 6.5% | 200.9 | 0.2% | 44.4 | | |
| <i>Anguilla anguilla</i> | European eel | 124.5 | 55.7 | 64.0 | 26 | 0.2% | 128.9 | 0.1% | 37.0 | | |
| <i>Gasterosteus aculeatus</i> | Three-spined stickleback | 27.3 | 3.5 | 18.0 | 117 | 0.7% | 21.0 | 0.0% | 29.6 | | |
| <i>Mugilidae sp.</i> | Mugilidae yoy | 22.0 | 6.9 | 12.0 | 102 | 0.6% | 162.5 | 0.1% | 25.9 | | |
| <i>Atherina presbyter</i> | Silverside | 55.6 | 45.1 | 16.0 | 34 | 0.2% | 152.5 | 0.1% | 22.2 | Rare | 10 < Fc ≤ 25 |
| <i>Platichthys flesus</i> | Flounder | 18.3 | 5.4 | 10.0 | 52 | 0.3% | 2.9 | 0.0% | 14.8 | | |
| <i>Syngnathus rostellatus</i> | Nilsson's pipefish | 102.0 | 50.6 | 44.0 | 4 | 0.0% | 2.2 | 0.0% | 14.8 | | |
| <i>Sardina pilchardus</i> | Pilchard | 55.5 | 17.7 | 45.0 | 4 | 0.0% | 4.3 | 0.0% | 11.1 | | |
| <i>Solea solea</i> | Common sole | 19.6 | 8.7 | 9.0 | 25 | 0.2% | 1.3 | 0.0% | 11.1 | | |
| <i>Pomatoschistus sp.</i> | Gobiidae yoy | 23.5 | 3.3 | 19.0 | 4 | 0.0% | 0.3 | 0.0% | 7.4 | Accidental | Fc ≤ 10 |
| <i>Ammodytes tobianus</i> | Sandeel | 70.0 | - | 70.0 | 1 | 0.0% | 0.7 | 0.0% | 3.7 | | |
| <i>Aphia minuta</i> | Transparent goby | 18.0 | - | 18.0 | 1 | 0.0% | - | 0.0% | 3.7 | | |
| <i>Belone belone</i> | Garfish | 54.0 | - | 54.0 | 1 | 0.0% | 0.1 | 0.0% | 3.7 | | |
| <i>Clupea harengus</i> | Atlantic herring | 43.0 | - | 43.0 | 1 | 0.0% | 0.2 | 0.0% | 3.7 | | |
| <i>Sparus aurata</i> | Gilt head | 33.0 | - | 33.0 | 1 | 0.0% | 0.4 | 0.0% | 3.7 | | |
| Total | | | | | 16 302 | | 115 257.6 | | | | |

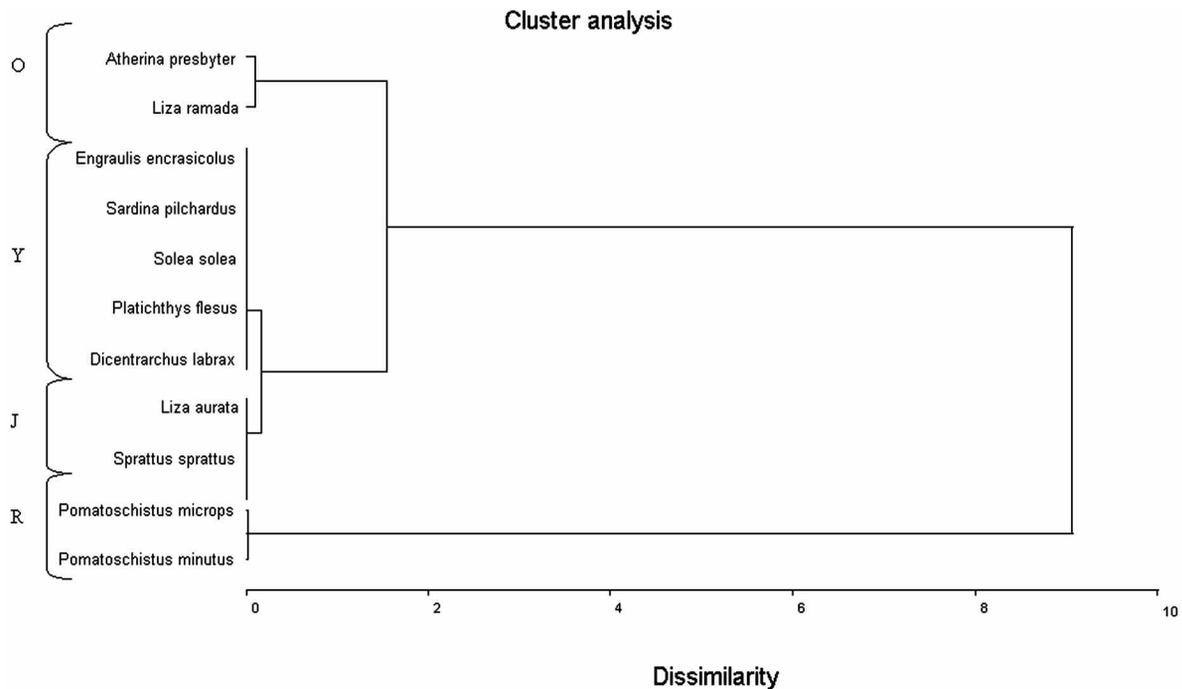


Figure 2. Cluster analysis (Ward's method, Euclidian distances) on fish population structures in Aiguillon bay (classification by percentage of each age class: young-of-the-year, juvenile, adult). Data have been log (x+1) transformed (Field et al., 1982).

Figure 2. Classification Ascendante Hiérarchique (Méthode de Ward, distance euclidienne) des pourcentages de chaque classe d'âge (jeune de l'année, juvénile, adultes) pour les poissons capturés entre avril 2003 et avril 2004 dans les marais salés de la baie de l'Aiguillon. Les données sont transformées en log (x+1) (Field et al., 1982).

population (about 20%) was composed of resident autochthonous species (Three-spined stickleback (*Gasterosteus aculeatus*, L. 1758), Gobies of genus *Pomatoschistus* spp. and Nilsson's pipefish (*Syngnathus rostellatus*, Nilsson 1855)).

The fish population was dominated in terms of biomass by Mugilidae, accounting for 93.6% of the total biomass captured (81.1% for Thinlip mullet and 12.5% for Golden grey mullet). Eight species accounted than 93% of total numbers, in order of importance they were Seabass, Golden grey mullet, Thinlip mullet, Common goby (*Pomatoschistus microps*, Krøyer 1838), European anchovy, Sand goby, Clupeidae yoy and European sprat. However, these species did not colonize the salt marsh creeks in the same way and at the same frequency. The species occurring in the largest number of samples were classified as frequent (Table 1). These were mullets of the genus *Liza* (Golden grey mullet, %FO = 92.6%, Thinlip mullet, %FO = 77.8%), and the Sand

goby (%FO = 85.2%). Seabass occurred in 66.7% of catches. Six species were captured accidentally (%FO < 10%), either as a single individual (Sandeel, Transparent goby, Garfish, Atlantic herring, Gilt head).

Size structure and colonizing guilds

Examination of the mean sizes showed that catches (Table 1) show that young stages were present for almost all species. Some species only occurred in the marsh at the juvenile stage. This was the case for Seabass, European anchovy, Common sole, Pilchard and Flounder. For these species only young-of-the-year were present. Other species occupied the salt marshes for a longer period (i.e. several years in succession). In this case several cohorts could be recorded at the same time, as with the European sprat and Golden grey mullet that inhabit the salt marsh exclusively during their first years of life, before breeding. In contrast, some species such as the gobies (*Pomatoschistus microps* and *Pomatoschistus*

Table 2. Comparison of the fish communities sampled in Aiguillon bay and Mont Saint-Michel Bay in spring and autumn 2003. CPUE numerical (nb of fish per min) and CPUE biomass (g of fish per min), total number of fish, total weight of the catches.

Tableau 2. Composition des peuplements de poissons captures en baie de l'Aiguillon et en baie du Mont Saint-Michel au printemps et en automne 2003. CPUE numériques et pondérales, captures totales (nb et masse).

| Species | Guild | Settlers guilds | Common name | Mont Saint-Michel Bay | | | | | | | |
|-------------------------------|---|-------------------------|------------------------|-----------------------|-------------|-------------------|---------------|------------------|-------------|------------------|----------------|
| | | | | Spring | | Autumn | | | | | |
| | | | | CPUe num. BM. Spr | N | CPUe mass BM. Spr | Biomass (g) | CPUe num. BM. Au | N | CPUe mass BM. Au | Biomass (g) |
| <i>Ammodytes tobianus</i> | (Elle et al. 1990) Euryhaline marine | this study Dieltrons | Common name Sandeel | 0.00 | 2 | 0.00 | 0.4 | - | - | - | - |
| <i>Anguilla anguilla</i> | Dieltrons | Resident | Eel | 0.00 | 1 | 0.00 | 1.5 | - | - | - | - |
| <i>Aphia minuta</i> | Marine | Resident | Transparent goby | - | - | - | - | - | - | - | - |
| <i>Atherina presbyter</i> | Euryhaline marine | Boy Settler | Silverside | - | - | - | - | - | - | - | - |
| <i>Belone belone</i> | Marine | Boy Settler | Garfish | - | - | - | - | - | - | - | - |
| <i>Clupea harengus</i> | Euryhaline marine | Boy Settler | Atlantic herring | - | - | - | - | - | - | - | - |
| <i>Clupea sp.</i> | Euryhaline marine | Boy Settler | Clupeidae yoy | 2.07 | 1174 | 0.20 | 112.7 | 0.01 | 4 | 0.00 | 0.1 |
| <i>Dicentrarchus labrax</i> | Euryhaline marine | Boy Settler | Clupeidae yoy | 0.17 | 92 | 0.02 | 8.5 | 0.02 | 5 | 0.08 | 22.2 |
| <i>Ergasilus encrasicolus</i> | Euryhaline marine | Boy Settler | Sebass | - | 0 | 0.00 | 0.0 | 0.00 | 0 | 0.00 | 0.0 |
| <i>Gasterosteus aculeatus</i> | Estuarine | Resident | European anchovy | 0.06 | 34 | 0.01 | 3.9 | 0.01 | 2 | 0.00 | 0.7 |
| <i>Lea aurata</i> | Euryhaline marine | Juvenile Settler | Golden grey Mulllet | 0.81 | 437 | 2.26 | 1206.6 | 0.16 | 59 | 2.46 | 1065.3 |
| <i>Lea ramada</i> | Dieltrons | Opportunistic Settler | Thimble mullet | 2.45 | 1413 | 0.00 | 2530.9 | 6.05 | 2012 | 19.43 | 7950.2 |
| <i>Mugilidae sp.</i> | Euryhaline marine | Opportunistic Settler | Mugil yoy | - | 0 | 0.00 | 0.0 | 0.02 | 9 | 0.00 | 1.0 |
| <i>Plutichthys fleuss</i> | Dieltrons | Resident | Flounder | 0.02 | 21 | 0.01 | 8.2 | 0.00 | 0 | 0.00 | 0.0 |
| <i>Pomatoschistus microps</i> | Estuarine | Resident | Common goby | 1.86 | 941 | 0.14 | 66.7 | 7.13 | 3764 | 2.00 | 899.3 |
| <i>Pomatoschistus minutus</i> | Estuarine | Resident | Sand goby | 0.00 | 1 | 0.00 | 0.9 | 0.00 | 1 | 0.00 | 0.3 |
| <i>Pomatoschistus sp.</i> | Estuarine | Resident | Goby yoy | - | - | - | - | - | - | - | - |
| <i>Sarbaia pilchardus</i> | Euryhaline marine | Boy Settler | Pilchard | - | - | - | - | - | - | - | - |
| <i>Solea solea</i> | Euryhaline marine | Boy Settler | Common sole | - | - | - | - | - | - | - | - |
| <i>Sparus aurata</i> | Euryhaline marine | Boy Settler | Gill head | - | - | - | - | - | - | - | - |
| <i>Sparus sprattus</i> | Euryhaline marine | Boy Settler | European sprat | 0.32 | 176 | 0.24 | 137.0 | 0.32 | 165 | 0.15 | 77.1 |
| <i>Syngnathus rostellatus</i> | Estuarine | Resident | Nilsson's pipefish | - | - | - | 0.0 | - | - | - | - |
| <i>Trachinus draco</i> | Euryhaline marine | Boy Settler | Greater weever | 0.00 | 1 | 0.00 | 0.0 | - | - | - | - |
| Total | | | Total | 7.8 | 4293 | 4.9 | 4077.4 | 13.7 | 6023 | 24.2 | 10024.7 |

| Species | Guild | Settlers guilds | Common name | Aiguillon Bay | | | | | | | |
|-------------------------------|---|-------------------------|--------------------------|-------------------|-------------|-------------------|----------------|------------------|------------|------------------|---------------|
| | | | | Spring | | Autumn | | | | | |
| | | | | CPUe num. BA. Spr | N | CPUe mass BA. Spr | Biomass (g) | CPUe num. BA. Au | N | CPUe mass BA. Au | Biomass (g) |
| <i>Ammodytes tobianus</i> | (Elle et al. 1990) Euryhaline marine | this study Dieltrons | Common name Sandeel | - | - | 0.20 | - | 0.00 | 1 | 0.00 | 0.7 |
| <i>Anguilla anguilla</i> | Dieltrons | Resident | Eel | 0.03 | 18 | 0.00 | 121.7 | - | - | - | - |
| <i>Aphia minuta</i> | Marine | Resident | Transparent goby | 0.00 | 1 | 0.00 | 0.0 | - | - | - | - |
| <i>Atherina presbyter</i> | Euryhaline marine | Boy Settler | Silverside | 0.03 | 18 | 0.00 | 2.0 | - | - | - | - |
| <i>Belone belone</i> | Marine | Boy Settler | Garfish | 0.00 | 1 | 0.00 | 0.1 | - | - | - | - |
| <i>Clupea harengus</i> | Euryhaline marine | Boy Settler | Atlantic herring | - | - | - | - | - | - | - | - |
| <i>Clupea sp.</i> | Euryhaline marine | Boy Settler | Clupeidae yoy | 1.61 | 725 | 0.10 | 50.7 | 0.00 | 1 | 0.00 | 0.1 |
| <i>Dicentrarchus labrax</i> | Euryhaline marine | Boy Settler | Clupeidae yoy | 5.31 | 2245 | 4.26 | 3352.5 | 0.80 | 252 | 4.81 | 1482.1 |
| <i>Ergasilus encrasicolus</i> | Euryhaline marine | Boy Settler | Sebass | 0.00 | 0 | 0.00 | 0.0 | 0.03 | 7 | 0.01 | 2.4 |
| <i>Gasterosteus aculeatus</i> | Estuarine | Resident | European anchovy | 0.23 | 113 | 0.04 | 19.3 | 0.00 | 0 | 0.00 | 0.0 |
| <i>Lea aurata</i> | Euryhaline marine | Juvenile Settler | Three-spined stickleback | 1.84 | 685 | 2.62 | 1223.6 | 0.93 | 194 | 1.55 | 377.8 |
| <i>Lea ramada</i> | Dieltrons | Opportunistic Settler | Golden grey Mulllet | 3.66 | 1387 | 9.138 | 58112.0 | 0.70 | 212 | 20.92 | 6836.0 |
| <i>Mugilidae sp.</i> | Euryhaline marine | Opportunistic Settler | Thimble mullet | 0.10 | 46 | 0.19 | 93.5 | - | - | - | - |
| <i>Plutichthys fleuss</i> | Dieltrons | Resident | Flounder | 0.54 | 13 | 0.00 | 1.6 | - | - | - | - |
| <i>Pomatoschistus microps</i> | Estuarine | Resident | Common goby | 0.07 | 276 | 0.09 | 43.8 | 0.31 | 93 | 0.20 | 58.0 |
| <i>Pomatoschistus minutus</i> | Estuarine | Resident | Sand goby | 0.07 | 44 | 0.04 | 22.5 | 0.02 | 4 | 0.04 | 8.7 |
| <i>Pomatoschistus sp.</i> | Estuarine | Resident | Goby yoy | - | - | - | - | - | - | - | - |
| <i>Sarbaia pilchardus</i> | Euryhaline marine | Boy Settler | Pilchard | 0.00 | 2 | 0.00 | 1.1 | - | - | - | - |
| <i>Solea solea</i> | Euryhaline marine | Boy Settler | Common sole | 0.02 | 7 | 0.00 | 0.4 | - | - | - | - |
| <i>Sparus aurata</i> | Euryhaline marine | Boy Settler | Gill head | 0.07 | 1 | 0.00 | 0.4 | - | - | - | - |
| <i>Sparus sprattus</i> | Euryhaline marine | Boy Settler | European sprat | 0.43 | 237 | 0.08 | 51.3 | 0.01 | 3 | 0.02 | 5.4 |
| <i>Syngnathus rostellatus</i> | Estuarine | Resident | Nilsson's pipefish | 0.00 | 2 | 0.00 | 0.2 | - | - | - | - |
| <i>Trachinus draco</i> | Euryhaline marine | Boy Settler | Greater weever | - | - | - | - | - | - | - | - |
| Total | | | Total | 14.0 | 5821 | 99.0 | 63096.7 | 2.8 | 767 | 27.6 | 8771.2 |

minus, Pallas 1770), that are resident, colonize the marsh throughout their life cycle. Another type of salt marsh colonization is observed, especially in the Silverside and Thinlip mullet, since juvenile and mature fish are present at the same time in the marsh, but intermediate age classes are absent. The high biomasses of the latter species can also be explained by the presence of very large individuals weighing over a kilogram.

A cluster analysis was conducted on the three previously defined size classes: young-of-the-year, juveniles and adults (Table 3). Figure 2 showed a discrimination of organisation into four groups. An O group (“*Opportunistic salt marsh settlers*”) for which the species were present during most stages, but which were not resident species (Silverside and Thinlip mullet). A Y group (“*Young-of-the-year salt marsh settlers*”) including the European anchovy, Pilchard, Common sole, Flounder and Seabass. These are species for which only the young-of-the-year were present in the salt marshes. Other cohorts can be encountered but much less frequently. The Golden grey mullet and European sprat constituted the third J group (“*Juvenile salt marsh settlers*”). These two species are frequent for more than one year in the salt marshes, but the older stages are not encountered. The two species of gobies constitute the last R group (“*Resident salt marsh settlers*”). All stages of these species occur because they are resident.

Temporal variations in the fish population of the Aiguillon bay

The biomass of mullets accounted for nearly 94% of the total biomass (Table 1). Since a previous analysis had shown a structure that was dominated by whether these species were present simultaneously or not, we decided to conduct the

cluster analysis without these two species (Table 2). The study of numerical CPUE (Fig. 3) showed a division into two major periods: winter (A) and summer (B). The winter period is characterized by the small number of species and low numbers. In contrast, the summer period is characterized by a very high abundance of juveniles and a high diversity (especially in early summer). The months of August and September, however, stand out from this grouping. The structure in terms of biomass (Fig. 4) is relatively similar, with relatively low biomasses in winter (A) and higher biomasses in summer (B).

Spatial variations in the fish population of the Aiguillon bay

The structure generally encountered, with high numerical abundances in summer and low ones in winter was only evident for the Canal du Curé (Fig. 5). The Canal de Luçon site had a relatively stable pattern with time (the summer peak in abundance was absent). The CPUE in terms of numbers in May, June and July were significantly different between the two sites (Mann-Whitney, $p < 0.05$) with means for the Canal du Curé of $32.24 \text{ fish.min}^{-1}$ (± 16.05) and of $3.05 \text{ fish.min}^{-1}$ (± 1.63) for the Canal de Luçon.

In terms of biomass (Fig. 6) the mean annual catches at the two sites showed no significantly different values (Mann-Whitney, $p > 0.05$, NS), because of the very great variation between months ($62.85 \text{ g.min}^{-1} \pm 56.90$ vs $36.51 \text{ g.min}^{-1} \pm 66.45$). However, the sum of biomass CPUE values for the Canal du Curé was two times higher than that of the Canal de Luçon (365.1 g vs 628.5 g). The high biomasses were caused by the presence of large individuals of detritivorous/benthic-feeding species. The Thinlip mullet could account for up to 98% of the monthly biomass, as in May (175.9 g.min^{-1}) or in November (78.8 g.min^{-1}).

| Species | Common name | Aiguillon bay | | | | N | Parlier et al. (this study) | Elie et al. 1990 |
|-------------------------------|--------------------|-----------------|-----------------|---------------------|-------|------------------|--------------------------------|------------------|
| | | %G ₀ | %G ₁ | %G ₂ et+ | | | | |
| <i>Atherina presbyter</i> | Silverside | 100 | - | - | 34 | YoY Settler | Euryhaline marine | |
| <i>Dicentrarchus labrax</i> | Seabass | 98.6 | 0.8 | 0.6 | 5 464 | YoY Settler | Euryhaline marine | |
| <i>Engraulis encrasicolus</i> | Anchovy | 100 | - | - | 1 063 | YoY Settler | Euryhaline marine | |
| <i>Liza aurata</i> | Golden grey mullet | 95.6 | 3.8 | 0.6 | 2 853 | YoY Settler | Euryhaline marine | |
| <i>Liza ramada</i> | thinlip mullet | 66.3 | 11.5 | 22.2 | 2 572 | Juvenile Settler | Diadromous | |
| <i>Platichthys flesus</i> | Flounder | 100 | - | - | 52 | YoY Settler | Diadromous | |
| <i>Pomatoschistus microps</i> | Common goby | 29.37 | 70.63 | - | 1 495 | Resident | Estuarine | |
| <i>Pomatoschistus minutus</i> | Sand goby | - | 100 | - | 1 007 | Resident | Estuarine | |
| <i>Sardina pilchardus</i> | Pilchard | 100 | - | - | 4 | YoY Settler | Euryhaline marine | |
| <i>Solea solea</i> | Common sole | 100 | - | - | 25 | YoY Settler | Euryhaline marine | |
| <i>Sprattus sprattus</i> | European sprat | 100 | - | - | 515 | YoY Settler | Euryhaline marine | |

Table 3. Percentage of each maturity class (young-of-the-year, juvenile, adult) of fish species caught in Aiguillon bay between April 2003 and April 2004.

Tableau 3. Pourcentage de chaque classe de maturité (jeune de l'année, juvénile, adultes) des espèces de poissons capturées en baie de l'Aiguillon entre avril 2003 et avril 2004.

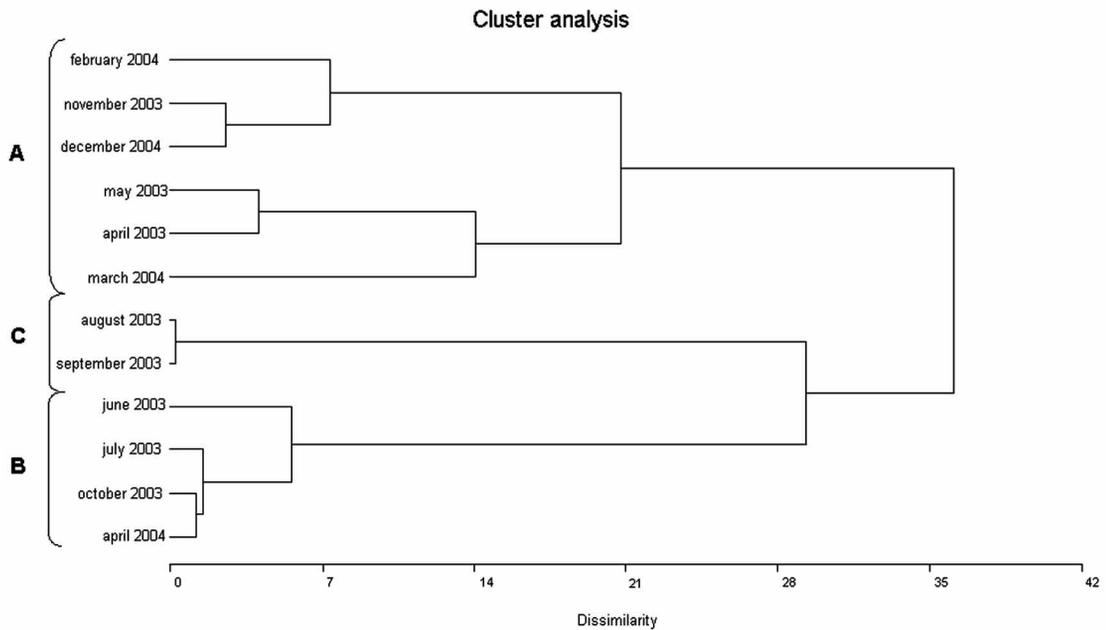


Figure 3. Cluster analysis (Ward’s method, Euclidian distances) on numerical CPUE values for fish caught between April 2003 and April 2004 in the Aiguillon salt marshes. CPUE values have been log (x+1) transformed (Field et al., 1982).

Figure 3. Classification Ascendante Hiérarchique (Méthode de Ward, distance euclidienne) des CPUE numériques du peuplement de poissons capturé entre avril 2003 et avril 2004 dans les marais salés de la baie de l’Aiguillon. Les données sont transformées en log (x+1) (Field et al., 1982).

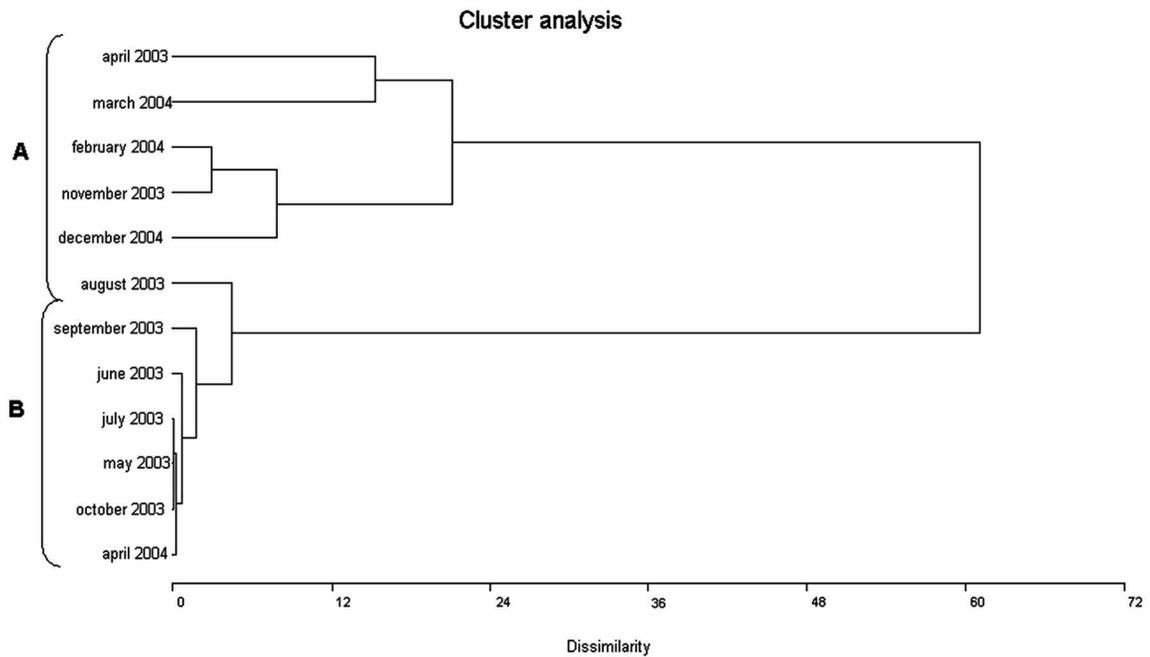


Figure 4. Cluster analysis (Ward’s method, Euclidian distances) on mass CPUE values for fish caught between April 2003 and April 2004 in the Aiguillon salt marshes. CPUE values have been log (x+1) transformed (Field et al., 1982).

Figure 4. Classification Ascendante Hiérarchique (Méthode de Ward, distance euclidienne) des CPUE pondérales du peuplement de poissons capturé entre avril 2003 et avril 2004 dans les marais salés de la baie de l’Aiguillon. Les données sont transformées en log (x+1) (Field et al., 1982).

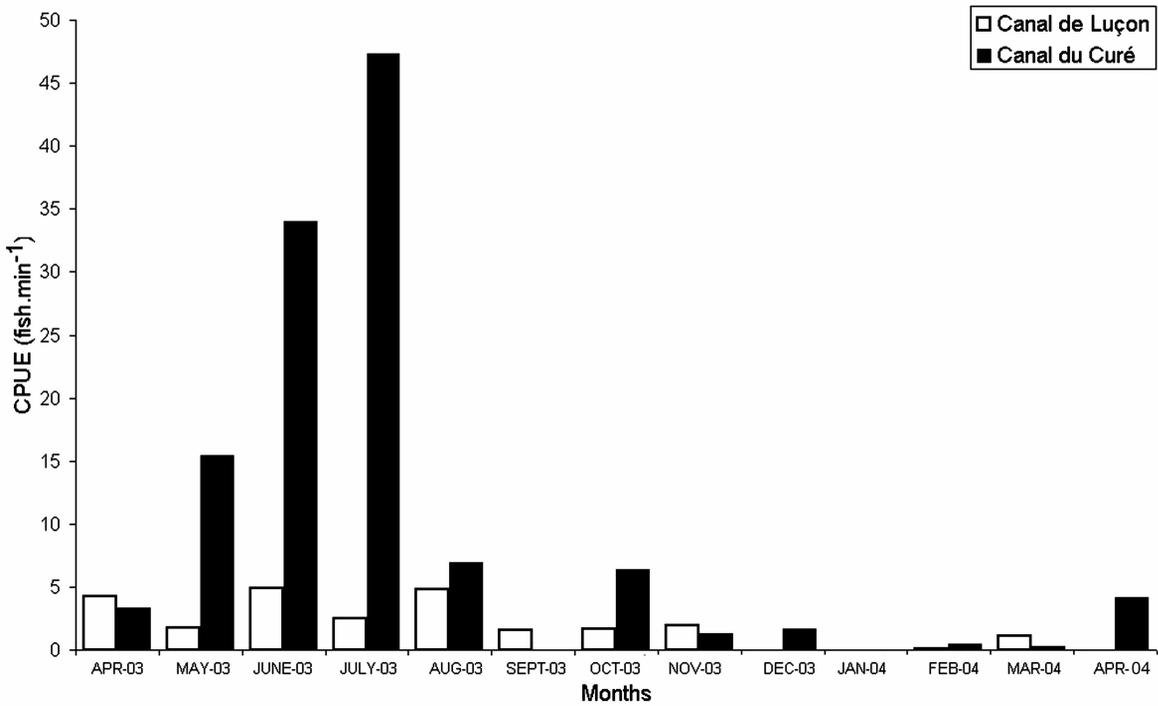


Figure 5. Numerical CPUE (ind/min) for catches made in Aiguillon bay from April 2003 to April 2004.

Figure 5. CPUE numériques (ind/min) des captures effectuées en baie de l’Aiguillon entre avril 2003 et Avril 2004.

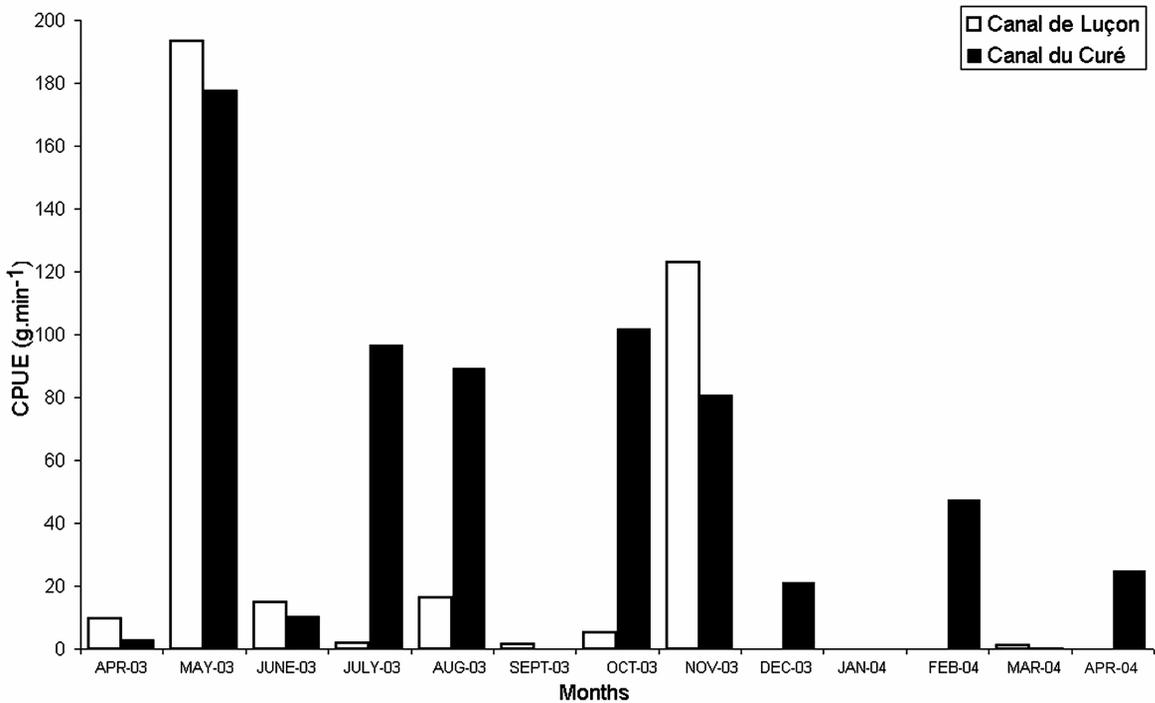


Figure 6. Biomass CPUE (g/min) for catches made in Aiguillon bay between April 2003 and April 2004.

Figure 6. CPUE pondérales (g/min) des captures effectuées en baie de l’Aiguillon entre avril 2003 et Avril 2004.

Composition of the fish population of the Mont Saint-Michel bay

The spring and autumn surveys in Mont Saint-Michel bay enabled the capture of 10 316 fish with a total biomass of 14 kg (Table 2). Fifteen species belonging 13 genera were recorded. The same ecological guilds that were defined above were present. With the exception of the Greater weever all the species captured also occurred in the Aiguillon bay. On the other hand, 7 species were not captured in Mont Saint-Michel bay during this survey (Transparent goby, Silverside, Pilchard, Common sole, Nilsson's pipefish, European anchovy and Gilt head). The latter two species have not been recorded in Mont Saint-Michel bay (this is situated outside the distribution range of the Gilt head and the European anchovy prefers to colonize saline waters rather than salt marshes). The great majority of the fish captured belonged to juvenile stages, and in particular to the young-of-the-year group (European sprat, Clupeidae yoy, Seabass, Flounder, Greater weever). Mulletts accounted for nearly 91% of the total biomass (Thinlip mullet %B = 74.32% and Golden grey mullet %B = 16.11%). The mullet species and the Common goby were the most frequently encountered species (%F > 75%). Next came the European sprat (%F = 71.4%), Clupeidae yoy and Seabass with a frequency of occurrence of 57.1% (Table 2). The numbers were largely dominated by the Sand goby (%N = 45.61% i.e. 4705 fish) and the Thinlip mullet with 3425 individuals (Thinlip mullet %N = 33.20%).

The structure of the colonizing guilds was also investigated in the species present in Mont Saint-Michel bay (not presented).

Seasonal comparison of the two fish communities (Aiguillon compared to Mont Saint-Michel)

The analysis of the CPUE in spring and in autumn revealed different structures in Mont Saint-Michel bay compared to the Aiguillon bay (Fig. 7). The seasonal (temporal) variability was lower than the variability between the two sites (latitudinal gradient) both for the numbers (Fig. 7a) and for the biomasses (Fig. 7b). The spring colonization of the creeks in the Mont Saint-Michel bay (Table 3) mainly involved the Thinlip mullet (1413 ind., 2531 g) and Clupeidae yoy (1174 ind., 113 g). Golden grey mullet (437 ind., 1206 g), Common goby (941 ind., 67g) and Seabass (92 ind., 8.5 g) came next. In contrast, in the Aiguillon bay, in addition to the Thinlip mullet (1387 ind., 58 112 g), the Golden grey mullet (685 ind., 1224 g), the European sprat (237 ind., 51 g), Clupeidae yoy (725 ind., 51 g) and the Common goby (276 ind., 44 g), it was the Seabass that had the highest numbers (2245 ind., 3352 g). In autumn, the numbers of Thinlip and Golden grey mullets were high in the Mont Saint-Michel bay with 2012 ind. (7950 g) and 59 ind. (1065 g), respectively. The

Common goby then had very high numbers with 3764 ind. (899 g). In the Aiguillon bay, as in spring, Seabass had the highest numbers with 252 ind. (1482 g), followed by Thinlip mullet (212 ind. for 6836 g) and Golden grey mullet (194 ind., 378 g), then to a lesser extent the Common goby (93 ind., 58 g).

From this comparison it is evident that there is a major colonization of the salt marshes in both sites by the detritivorous species (Mugilidae) whatever the season. However, the high numerical abundance of Clupeidae yoy in Mont Saint-Michel bay suggests a nursery role based mainly on pelagic species, whereas the Aiguillon bay mainly supports the population of young-of-the-year Seabass. Clupeidae yoy and the European sprat also occur to a lesser extent. An asymmetry in colonization was observed for the Common goby with a higher abundance in spring in the Aiguillon bay (0.54 ind.min⁻¹ compared to 0.31 ind.min⁻¹), whereas the highest abundance was observed in autumn in Mont Saint-Michel bay (1.86 ind.min⁻¹ compared to 7.13 ind.min⁻¹).

Discussion

Methodological perspectives

Studies of coastal nursery areas usually use fishing gear such as beam trawls (Le Pape et al., 2003; Parlier & Feunteun, 2004). However, in order to study the colonization mechanisms of European salt marshes, a combination of fyke nets and gill nets is generally used because of the temporary flooding conditions and the water depths rarely exceeding a few tens of centimetres (Laffaille et al., 2000a; Parlier, 2002). It is also impossible to use even small boats on the drainage creeks. The capture technique used in this study was designed to decrease the selectivity of the fishing gear by using a combination of different gears. The gill nets placed upstream of the mixed gear were intended to catch large-sized fish rather than pelagic species which are capable of jumping over the barriers formed by gill nets, whereas the fyke nets were intended to catch small-sized benthic or pelagic fish.

The Aiguillon bay and the Mont Saint-Michel bay, two models of nurseries

The fish population sampled in the Aiguillon bay was broadly similar in its structure to that described in the salt marshes on the west coasts of France (Laffaille, 2000; Duhamel et al., 2002; Parlier, 2002). 25 species were recorded in the Aiguillon bay (Table 1). A previous study conducted in the Aiguillon bay mentioned 15 species (Gascuel & Legault, 1989), including migratory species (*Petromyzon marinus*, *Alosa alosa*, *Salmo trutta*), but this was not conducted in the same conditions as it was a study

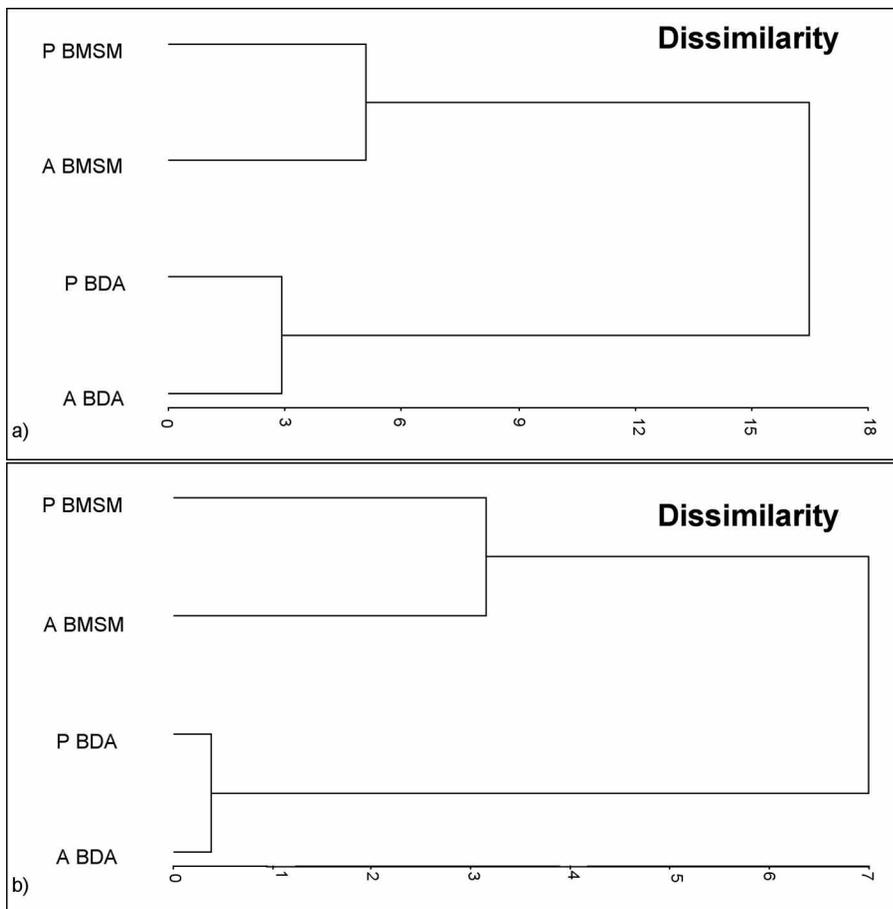


Figure 7. Cluster analysis (Ward's method, Euclidian distances) of community structure of spring and autumn in the Mont Saint-Michel bay and Aiguillon bay. a) Numerical CPUE b) Biomass CPUE. Data have been $\log(x+1)$ transformed (Field et al., 1982).

Figure 7. Classification Ascendante Hiérarchique (Méthode de Ward, distance euclidienne) de la structure printanière et automnale des peuplements en baie du Mont Saint-Michel et en baie de l'Aiguillon. a) CPUE numériques b) CPUE pondérales. Les données sont transformées en $\log(x+1)$ (Field et al., 1982).

of the trash fish discards from the nets of elver fishermen further upstream in the estuary of the Sèvre Niortaise river.

The population of the Aiguillon bay is dominated in terms of biomass by the species detritivorous feeding species (Mugilidae) that account for up to 96% of the biomass captured, as is often the case in this type of coastal area (Feunteun et al., 1999; Laffaille et al., 2000a). Golden grey mullet, Thinlip mullet and Common goby are the most frequent species with frequency of occurrence values of 92.6%, 77.8% and 85.2%, respectively. These three species enter the salt marshes for feeding. The detritivorous species characteristic of intertidal mudflats take advantage of the high production of benthic micro-algae on the mudflats adjoining the salt marshes (Laffaille et al., 1998; Almeida, 2003). Common goby and Sand goby conduct the whole of their life cycle in these intertidal zones and consume the prey occurring in the marsh when it is submerged (Laffaille

et al., 1999; Parlier, 2002). The high numbers of Seabass (5464), Clupeidae yoy (960), European sprat (515) and European anchovy (1063) composed almost exclusively of juveniles demonstrates the nursery function of these ecosystems, even if it is preferable to rely on more criteria to describe this function (Beck et al., 2001), such as use of the biomass produced in situ, or the migration towards the sites frequented at the adult stage. The colonization of salt marshes is the result of a passive transport of the larvae (Dame & Allen, 1996), undoubtedly from adjacent creeks and channels. These areas therefore play a fundamental role in the growth and survival of young fish by providing them with the trophic resources that contribute up to 50 to 90% of the growth of young Seabass (Laffaille et al., 2001). The patterns of salt marsh colonization are similar to those described in Mont Saint-Michel bay, where three periods were described (Laffaille et al., 2000a). The spring period

(April to June) had a lower abundance in terms of numbers and biomass than in the Aiguillon bay. This difference could be due to the more northerly location of this large bay, where temperature conditions may be less favourable.

The population described in Mont Saint-Michel bay in spring and in autumn (Table 2) shows a similar structure centred on benthic-feeding and resident species (Mugilidae and Gobiidae) associated with an assemblage of species that colonize the marsh during their first year of life, such as Seabass or Clupeidae yoy. An accessory fish fauna (occasional, rare or accidental species) composed of non-characteristic species is also described that consists of marine euryhaline, migratory or freshwater species. Laffaille (2000) described 47 species in Mont Saint-Michel bay, including 31 species in the richest site. The catches conducted in 2003 only recorded 15 species, but these only took place in spring and autumn and with a small number of fishing efforts (13). A more intensive and longer fishing effort would undoubtedly have caught more species, and especially species present earlier in the year.

The seasonal comparison of the populations of these two nursery areas revealed a different organisation of the species and of their colonization. The Mont Saint-Michel bay seemed to preferentially support a population of juvenile Clupeidae. These occurred exclusively in spring in both sites.

In the Aiguillon bay, they only accounted for 5.90% of total numbers, whereas they represented nearly 12.0% in Mont Saint-Michel bay, where the Seabass had the highest numbers, accounting for nearly 35.0% (compared to 0.94%). The nursery function of the Aiguillon bay salt marshes therefore seems to be less mono-specific and more diverse. The presence of European anchovy yoy in August (Table 1) seems to support this contention (1063 ind.).

Management activities, disturbance and the nursery function of Aiguillon bay

The low abundance of juvenile Seabass in Mont Saint-Michel bay indicates a weak colonization of this area that is nevertheless known to be an important nursery ground. It would however be useful to assess and monitor the nursery function described in recent years (Laffaille et al., 2001; Parlier, 2002). The combination of the invasion by *Elytrigia atherica* and intensive grazing is known to disturb the trophic function (Laffaille et al., 2000b), that is so important for young-of-the-year fish, and could lead to a decrease in the numbers of young Seabass, or lead to selective survival, resulting in later recruitment.

An asymmetrical colonization of Aiguillon bay was demonstrated in the summer period. This period that is generally suitable for strong recruitment had a low abundance at

| Mont Saint Michel Bay | | | | | | |
|------------------------------|----------------------|----------------------|---------------------|---------------------|-----------------------|-----------------------|
| | Spring | | Autumn | | All year | |
| | CPUE num. BM. Spr | CPUE mass BM. Spr | CPUE num. BM. Au | CPUE mass BM. Au | CPUE num. BM. Year | CPUE mass BM. Year |
| <i>YoY Settler</i> | 2.56 | 0.46 | 0.35 | 0.26 | 1.51 | 0.31 |
| <i>Juvenile Settler</i> | 0.81 | 2.26 | 0.16 | 2.46 | 1.54 | 1.31 |
| <i>Diadromous</i> | 0.02 | 0.01 | - | - | 0.02 | - |
| <i>Resident</i> | 1.92 | 0.14 | 7.14 | 2.00 | 1.03 | 4.57 |
| <i>Opportunistic Settler</i> | 2.45 | 2.00 | 6.07 | 19.43 | 2.23 | 12.75 |
| Somme totale | 7.75 | 4.88 | 13.72 | 24.16 | 6.32 | 18.94 |

| Aiguillon Bay | | | | | | |
|------------------------------|----------------------|----------------------|---------------------|---------------------|-----------------------|-----------------------|
| | Spring | | Autumn | | All year | |
| | CPUE num. BM. Spr | CPUE mass BM. Spr | CPUE num. BM. Au | CPUE mass BM. Au | CPUE num. BM. Year | CPUE mass BM. Year |
| <i>YoY Settler</i> | 7.48 | 4.44 | 0.86 | 4.85 | 5.96 | 2.85 |
| <i>Juvenile Settler</i> | 1.84 | 2.62 | 0.93 | 1.55 | 2.23 | 1.24 |
| <i>Diadromous</i> | 0.07 | 0.20 | - | - | 0.13 | - |
| <i>Resident</i> | 0.85 | 0.17 | 0.33 | 0.24 | 0.51 | 0.28 |
| <i>Opportunistic Settler</i> | 3.76 | 91.58 | 0.70 | 20.92 | 47.67 | 10.81 |
| Somme totale | 14.00 | 99.00 | 2.81 | 27.56 | 56.50 | 15.18 |

Table 4. Abundance of the guilds composing the fish community in Mont Saint Michel and Aiguillon bays calculated from table 3. CPUE nb = nb fish.min⁻¹ ; CPUE mass= g fish.min⁻¹.

Tableau 4. Abundance des guildes colonisatrices composant les communautés de poissons des marais salés calculés à partir du tableau 3. CPUE nb = nb de poissons.min⁻¹. CPUE mass = g de poissons.min⁻¹.

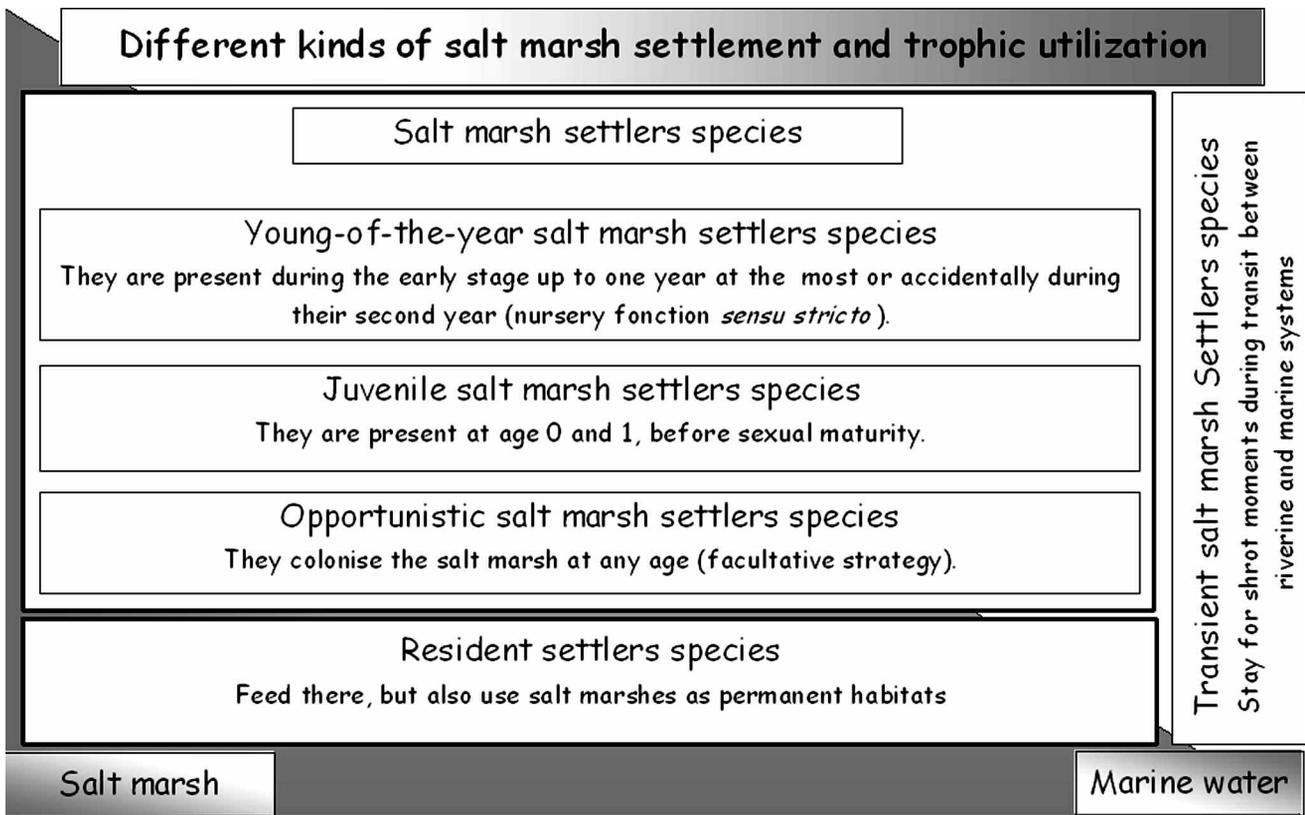


Figure 8. Conceptual diagram of settlement behaviours and food resource use of European salt marshes by different fish populations.

Figure 8. Schéma conceptuel du comportement colonisateur et de l'utilisation trophique des marais sales européens par différentes populations de poissons.

the Canal de Luçon site, but this is also the period when the salt marsh grasses are cut for hay. The impacts of sheep grazing on the availability of prey of terrestrial origin, and on the feeding of young Seabass and gobies of the genus *Pomatoschistus* sp. have been demonstrated in Mont Saint Michel bay (Laffaille et al., 2000b). But these practices have to be put into the perspective of the exceptional heat wave that occurred in August and September 2003, which led to a decrease in the colonization on both sites (Fig. 4). A high abundance of juvenile anchovies was however observed during August but only in the Canal de Luçon site (11.79 ind.min⁻¹). This pelagic species feeds on prey of marine origin (Plounevez & Champalbert, 2000; Tudela et al., 2002) and therefore does not use the marshes as a nursery ground in the full sense of the term (*sensu* Beck et al., 2001). The winter numbers seemed to be similar in both sites, although there was a general tendency for colonization to be greater in the Canal du Curé (Fig. 4). The study of the total biomasses (table 2) showed that these were two times higher in the Canal du Curé (365.1 g compared to 628.5 g).

The Canal de Luçon is subject to a very high level of fishing pressure in winter when nearly 10 boats exploit this

site at each tide (Meunier, comm. pers.). Low values in terms of weight and biomass were observed during this period. It would be useful to study the by-catches discarded from the nets in the manner of Gascuel & Legault (1989), to estimate the impact of these fishing practices on the fish communities.

Salt marshes, nursery function and colonizing guilds

This inventory of the fish population demonstrated the different strategies of colonizing the salt marshes that were affected by temporary access. The classifications into ecological guilds described in the literature do not provide any information on the uses made of salt marshes during the life cycle of the fish. This is why we proposed a revised classification of the species:

The resident (autochthonous) species colonize the salt marshes for the whole of their life cycle at all stages. This is the case of the gobies of the genus *Pomatoschistus* sp. The trophic resources used by these fish therefore support the whole population. This ecosystem therefore plays an exclusively feeding role. These feeding species can therefore be classified as resident salt marsh settlers. Other species colonize the marsh during precise stages in their life

cycle. The Thinlip mullet colonizes the salt marshes in the first years of its life. It then stops its colonization, so that sub-adults are absent. A re-colonization by older fish then occurs. In terms of predation, the marsh provides the young stages with physico-chemical protection because of the very strong constraints that any potential predators would face (salinity, temperature, dissolved oxygen, etc.). The ability of some species to withstand these conditions is a considerable evolutionary advantage. However, the shallowness and temporary nature of these habitats obliges the fish either to be of small size or have good swimming abilities, allowing them to actively swim out of the creeks before they dry out. The colonization process used by Thinlip mullet enables it to optimise the use of an unlimited food resource, the benthic micro-algae. Two hypotheses could therefore be proposed in terms of the frequentation of these marshes. Firstly, these food resources could allow the fish to build up energy reserves needed for reproduction (ovogenesis). Secondly, the return to these ecosystems after spawning in the sea could allow those fish exhausted by this stage in the life cycle to recover essential energy reserves. The species colonizing the marsh for one or other of these purposes could be called Opportunistic salt marsh settlers. Here again the food resources support the whole population.

Two other salt marsh colonization behaviours can also be identified. These differ in terms of the timing of colonization. Some species such as the European anchovy, Seabass and Common sole only occur during their first year (young-of-the-year), or accidentally during their second year. The nursery function *sensu stricto* as defined by Beck et al. (2001) applies to these species. The salt marshes only actively support the young-of-the-year, so that these species are called Young-of-the-year salt marsh settlers. Another less restrictive strategy is that adopted by the Golden grey mullet and European sprat. These species occur during the first few years of their life cycle. This is therefore an extended form of the nursery function since several cohorts are maintained by the production produced *in situ*.

Access to the salt marshes is temporary, because of the tides. At another temporal scale (that of the year), the regularity and/or fidelity of frequenting these productive ecosystems enables various populations of fish to survive. They have developed various colonizing strategies enabling them to use the food resources of salt marshes and improve their growth performance and their survival. The trophic role of coastal salt marshes is therefore fundamental for supporting coastal stocks and in the production of the breeding stock.

Conclusion

Since European salt marshes are declining in area and number, the remaining ones play a crucial role in the

survival of coastal fish populations. This study of the colonization of the salt marshes of the Aiguillon bay showed that there has been a change in the distribution of the young stages of some species of high fisheries value such as the Seabass. Salt marshes are often managed to maintain populations of breeding, passage or wintering birds (Meunier & Joyeux, 2003), or for traditional activities such as elver fishing, but these seem to have endangered the initial nursery function of these areas (Laffaille et al., 2000b). The invasion of the initial vegetation structure by couch grass (*Elytrigia atherica*) also alters this function, obliging the fish to turn to prey of marine origin instead of terrestrial original, such as *Orchestia gammarellus* (Parlier, 2002). If these imbalances persist, the whole of the trophic networks in coastal zones are going to be altered because of adverse changes in recruitment. The whole outwelling process (Odum, 1968) could also going to be affected, with the fish no longer being able to play their role of biotic vector. The understanding of colonization phenomenon of coastal areas subjected to strong human pressures or biological disturbances through the fish communities and the study of the use of food resources of interface ecosystems must be continued. It will then be possible to draw lessons from activities relating to the conservation and sustainable management of these estuarine ecosystem complexes – European salt marshes.

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