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The conservation status of *Sabellaria alveolata* (L.) (*Polychaeta: Sabellariidae*) reefs in the Bay of Mont-Saint-Michel

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Abstract :

Reefs built by the annelid worm *Sabellaria alveolata* in the Bay of Mont-Saint-Michel (France) are the most extensive intertidal biogenic structures within Europe. Before and after mussel farming extensions, a study designed to provide a biological health index of the Sainte-Anne reef (223 ha) was carried in 2001 and 2007 to serve as an easy-to-use management tool and to ensure endangered reef portions were properly targeted and protected.

Coupled physical and biological parameters were included in a spatial Health Status Index (HI). A spatial and temporal mapping survey of the HI showed a continuous deterioration of the reef's state of health, particularly in its central part. This degradation correlates with the colonization of the Pacific oyster *Crassostrea gigas* and with increasing silt deposits on the reef.

A combination of several factors is likely to explain such rapid reef deterioration: (1) an increase in trophic competition between cultivated and wild suspension-feeders that is detrimental to the annelids; (2) a modification in the hydrodynamics and consequently in sedimentary patterns leading to an increase in silt deposition; and most importantly (3) an increase in recreational harvesting of oysters and associated reef trampling, resulting in reef fragmentation.

Understanding the parameters that influence the reef dynamics is necessary in order to help efficient and effective management and policy focusing on the conservation status of large biogenic structures.

Keywords : *Sabellaria alveolata* ; biogenic reef ; health status ; biological indicator ; shellfish farming ; recreational fishing activities

1. Introduction

Biogenic reefs offer a large diversity of micro-habitats for a wide range of sessile and vagile macrofaunal species. As specified by Holt *et al*. (1998), organisms other than cnidarians, notably sponges (de Voogd, 2006), mollusks (Rodney and Paynter 2006), polychaetes (Moore *et al*., 1998; Pawlik, 1998; Dubois, 2003) or bryozoans (Cranfield *et al*., 2003) are able to build reefs in certain environmental conditions. Many of these species form highly variable physical habitat and along a "reefiness" gradient (Hendricks and Foster-Smith, 2006) not all of them worth be calling reef. A number of *sabellariidae* (annelida: polychaeta) species are known to form extensive reefs, such as *Phragmatopoma californica* in California, *Phragmatopoma caudata* in the Atlantic coasts of the Americas, *Idanthyrsus spp.* in equatorial regions, *Gunnarea capensis* in South Africa and *Sabellaria alveolata* along European coasts (Achary, 1974; Wilson, 1971).

Biogenic reefs play key functional roles in ecosystems and contribute to physical and biological process, by (1) stabilizing the substrate and trapping sediment, (2) providing a diversity of microhabitats (e.g. crevices) and increasing available spaces for new species to colonize, and (3) accumulating faeces, pseudo-faeces and other organic deposits that may be important food sources for other organisms (Holt *et al*., 1998). As a consequence, fauna and flora associated with biogenic reefs are very often species-rich, at least in terms of macrofauna, and generally contrast with the surrounding areas where diversity and abundances are lower. Along the European coast, the largest biogenic reefs are constructed by *Sabellaria alveolata*. These bioconstructions can have two forms: encrusting colonies adhering to rocks, very common at the mid level of the intertidal zone and, more rarely, reefs developing on soft-bottom and forming large banks in the intertidal zone. The largest *Sabellaria* reef (225 ha) is found in the Bay of Mont-Saint-Michel in France (Dubois *et al*., 2002; Fournier *et al*., 2010).

Whereas historical studies focused on the biology of *S. alveolata* [reproduction, larval development and behaviour (see Wilson, 1929, 1968 and 1970), recent research works were dedicated to the ecological and functional role of the reef they constitute. As shown by Dubois *et al*., (2002) in the Bay of Mont-Saint-Michel, biodiversity associated with *S. alveolata* reefs is an order of magnitude higher than the surrounding soft bottom communities and host unique species assemblages, composed of species originated from other coastal and deeper environments.

Sabellaria reefs are also highly vulnerable structures and subject to various direct and indirect anthropogenic pressures (e.g. Dubois *et al*., 2002; 2006; Le Cam, 2011). In 2006 the mussel aquaculture concessions in the Bay of Mont-Saint-Michel were spatially extended. Consequently, the *Sabellaria* reefs were surrounded by intensive mussel cultivations, and susceptible to be indirectly degraded by smothering under *Mytilus edulis* faeces and pseudo-faeces or by the settlement of mussels on the reef, which subsequently break up the surface as they grow. In addition, reefs are exploited at spring low tides for settled oysters and mussels (Dubois *et al*., 2006) despite strong evidence that fishing and associated trampling are seriously damaging fragile intertidal habitats, such as reef (Dubois *et al*., 2002) or seagrass (Eckrich and Holmquist, 2000) habitats.

With the Council Directive 92/43/EEC on the Conservation of natural habitats and of wild fauna and flora (Habitats Directive) implementation in the Bay of Mont-Saint-Michel, the protection and conservation of *Sabellaria alveolata* reefs (habitat type 1170 "Reefs"), identified as being of rare biological and patrimonial heritage, became a major environmental issue. A better understanding of the contribution to biodiversity, and in particular the role of reef-builders as ecosystem engineers, would help to promote the conservation of biogenic reefs (Godet *et al*., 2008; Holt *et al*., 1998). The primary aim of this study is hence to determine the health status of the reef in the Bay of Mont-Saint-Michel in 2007. To address this issue, a monitoring protocol was designed and a health index was developed to determine the condition status of the reef. Results obtained in two sampling campaigns (2001 and 2007) were compared to accurately describe the reef status

evolution and provide valuable information to stakeholders when determining adapted conservation strategies.

2. Material and methods

2.1. Study area

The *Sabellaria alveolata* reefs reach their maximum size in the Bay of Mont-Saint-Michel. There are two main *Sabellaria* reefs in this Bay: the Champeaux reef (29 ha, as measured in 2001) and the Saint-Anne reef (225 ha, as measured in 2001). The current study focused on the larger reef (Saint-Anne), situated in the southern part of the Bay at 48°38'700N and 1°40'100W (Figure 1).

The reef complex formed by *S. alveolata* is located at the edge of the two joint hydro-sedimentary systems. The central part of the Bay, which is characterized by high bioclastic content (25% to 95%), shows a gradual decrease of mean grain size from the subtidal to the intertidal zone. Sedimentation rates are higher (3mm to 25mm/year) in the intertidal zone and tend to decrease seawards (Bonnot-Courtois *et al.*, 2004, 2008).

The Saint-Anne reef is made up of three main sub-reefs (named A, B and C) aligned in parallel to the 0m line and facing intensive mussel cultures (Figure 1). Since 2003, new concessions were granted, in an effort to restructure the activity in close proximity to the reef.

2.2. Reef dynamics

Different morphological stages, as defined in Dubois *et al.* (2002) characterise the reef dynamics. The settlement of young recruits leads to isolated ball-shaped structures, which fuse as they grow to form barriers (named coalescent ball-shaped structures) and then platforms, which are considered the climax status. Through natural or anthropogenic disturbance, structures can regress toward degraded forms (named degraded ball-shaped structures or degraded platforms depending on the initial stage).

2.3. Sedimentary and biological data collection

In order to assess differences between the reef and the surrounding sediments, we used a stratified sampling design for sediment samples. We collected sediment samples in the fore-reef (2001: $n = 11$; 2007 $n = 11$), inside the reef (2001: $n = 15$; 2007 $n = 15$) and the back-reef (2001: $n = 12$; 2007 $n = 12$) area both in March 2001 and February 2007. The fore-reef corresponds to the sand bank and the sand ridge (sea ride) located in front of the reef (Figure 1). The reef area corresponds to the sand bodies located within the reef complex. The back-reef area corresponds to the sedimentary extent located behind the reef (landward). Sediment samples were collected over a short period of time (3 days in 2001 and 1 day in 2007) during low water spring tides. Each sediment samples consisted of a core for sediment characterisation (10 cm², 10 cm deep), and a positioning information from a GPS, plotted into a GIS (Geographic Information System).

A coupled complementary sampling protocol was applied in 2001 and 2007 for biological sampling. A regular grid consisting of 196 squares (each 75x75 m) was drawn from an aerial orthophotograph of the reef (the 2001 and 2007 studies used images from 1999 and 2002, respectively) (Godet *et al.*, 2009). Each grid cell was visited during field studies carried out in spring 2001 and 2007, during low water spring tide. New squares were added when the reef extension differed from the aerial view. For each grid cell, several parameters related to the physical structure of the reef were scored: the percentage of the total reef cover (scoring from 0 for

absence to 10 for 100% of cover), the ratio of each developmental stage of the reef (scoring 0 for absence to 10 for 100% of cover) from the pioneer isolated ball-shaped structures to the degraded forms, and the fragmentation level (scoring from 0 to 10, as detailed in Figure 2). The sediment feature associated to each grid was also recorded. Moreover, within each 75x75 m mesh, three quadrats of 1 m² were used to randomly collect additional information from the reef surface, including the reef elevation as well as the density and percent cover (scoring from 0 for absence to 10 for 100%) of the two main epibionts colonizing the reef, *i.e.* oysters *Crassostrea gigas* oysters and mussels *Mytilus galloprovinciallis.*

2.4. Data analysis

In order to simplify the result analysis, the reef was divided into three sub-reefs (A, B and C, Figure 1). Sediment samples were washed with distilled water, given 24 hours for particle settlement, and decanted. Sediments were then dried at 70 °C for 24 h and approximately 100 g were sieved through AFNOR standard sieves (with mesh sizes of 2.5, 2, 1.6, 1.25, 1, 0.8, 0.63, 050, 0.40, 0.315, 0.25, 0.20, 0.16, 0.125, 0.100 mm, 80, 63, 50, 40 and <40 µm). Each size fraction was weighed and the results expressed as a percentage of the total sample weight. Sedimentary parameters were determined by performing grain-size analyses on raw data through the Gradistat v. 4.1. program (Blott and Pye, 2001) modified by Fournier for AFNOR use (unpublished data), based on the Moments method using the Folk and Ward (1957) classification.

Differences of mean grain-size ($M_G = \exp (\ln P_{16} + \ln P_{50} + \ln P_{84})/3$) and mud (<63µm) between years and sites (fore-reef, reef, back-reef) were tested by using parametric tests with R v. 2.13.0. (R Development Core Team, 2011). The assumptions of normality and homogeneity of variances were verified by the Shapiro and Bartlett tests, respectively.

Biological and reef physical and morphological data collected to characterize the reef status were processed with the software Surfer 8. For the reef elevation and the density/degree of epifaunal covering, , mean values were used to draw distribution maps and to test for statistical differences. The relationships between reef parameters measured in 2007 were tested using the Spearman rank correlation coefficient (Scherrer, 1984) and changes between 2001 and 2007 were analysed with a non-parametric Wilcoxon test for dependant samples (Scherrer, 1984). Basic parameters were tested for all squares of the grids defined in 2001 (n=213) and 2007 (n=198) and health status change was considered only for common grid cells (n=160).

2.5. Definition of Health status index (HI)

To define the vitality status of the reef and its change since 2001, we suggest here a Health Status Index (HI), integrating physical characteristics of the reef and reflecting its dynamics :

HI = FD + (IB+CB+P-DIB-DP-OC-MC) x RC

where FD = Fragmentation degree score, IB = Isolated Ball-shaped structure cover score, CB = Coalescent Ball-shaped structure cover score, P = Platform cover score, DIB = Degraded Isolated Ball-shaped structure cover score, DP = Degraded Platform cover score, OC = Oyster Cover score, MC = Mussel Cover score and RC = total Reef Cover score (necessarily >0). The dominance of IB, CB and P as well as a high RC value and a low fragmentation are a sign of extension and of positive reef dynamics.

This index can then be expressed as an ecological status, as defined in ecological quality ratios (EQR) by expert judgement (Table 1). Three ecological statuses were used: good (up to 20), intermediate (between 20 and 2.5) and bad (below 2.5) Extreme values [positive (110) and negative (-200)] remain theoretical and have never been observed on *S. alveolata* reefs.

3. Results

3.1. Sedimentary changes

In the whole reef area, the mean grain size of surrounding sediment was significantly higher in 2001 (595 µm, n=38) than in 2007 (464 µm, n=38) (t-test: $t_{(75)}$= -32.3261, p=2.2e-16). The percentage of silt (<63 µm) in 2001 was significantly lower (4.66%, n=38) than in 2007 (8.74%, n=38) (t-test: $t_{(75)}$ = -1183.975, p=2.2e-16) (Figure 3). The heterogeneity of the sediments in the reef area was confirmed with an one-way ANOVA computed among the fore-reef, reef and back-reef zones ($F_{(2,73)}$=7.6246, p=0.0009). A HSD Tukey test showed that the fore-reef zone was significantly different from the back-reef zone (p=0.02) and that the reef zone was significantly different from back-reef zone (p=0.0008), which validated the hypothesis that the reef had a barrier effect.

The decrease in mean grain-size for surrounding sediments and the silting-up of each sub-unit was also significant. The fore-reef, reef and back-reef zones were compared separately between 2001 and 2007 (Table 2) with paired t-tests. In the fore-reef zone, sediments were coarser in 2001 (753 µm) compared to 2007 (369 µm, p=2.2 10^{-16}). The percentage of silt in 2001 (3.00%) was significantly lower than in 2007 (8.39%) (p=2.2 10^{-16}). More subtle differences were found in mean grain-size and silt percentage in the central reef zone. The mean grain size was 703 µm in 2001 and 693 µm in 2007. The difference was significant (p=8.37 10^{-16}). A significant but weak increase of silt occured in this zone (4.25% in 2001 and 5.19% in 2007; p=2.2 10^{-16}). For the back-reef zone, we found a significant decrease of mean grain size between 2001 (313 µm) and 2007 (265 µm) (p=2.2 10^{-16}) and a significant increase of in silt percentage between 2001 (6.69%) and 2007 (13.50%) (p=2.2 10^{-16}). The evolution of the reef environment between 2001 and 2007 showed an increase in the size of the sand banks in the back-reef zone but a spectacular decrease of the sand sheet in the fore-reef zone.

3.2. Biological and morphological changes

3.2.1. Reef general characteristics

The mean reef coverage in 75x75m grid cell increased significantly between 2001 and 2007 (36.0%±14.1% in 2007 versus 27.6±16.8 in 2001; t=4.91, p=1 10^{-4}). In 2007, elevation of the reef was at an average of 35.3±9.1 cm, with the highest structures reaching around 75 cm. Reef height was homogeneous between zones A, B and C in 2007, with 87% of values ranging between 25 and 50 cm. Mean value (35,3±9,1 cm) did not significantly change from 2001 (38,6±15.2 cm; Z=0.742, p=0.457). The highest levels of fragmentation were observed in 2007, with the most severely fragmented located on the south-east zones of the reefs, facing the coast (Figure 4). The zone A was the most fragmented part of the reef, with 68% of the grid squares having a fragmentation score equal to 0 or 2.5. Although the least fragmented zones were facing the mussel cultures, which was also the case in 2001, fragmentation levels significantly increased over the last years across the entire reef (Z=5.03, p=1 10^{-4}). When sub-reefs were examined individually though, fragmentation was found to have significantly increased only on zone B (Z=4.46, p=1 10^{-4}).

3.2.2. Colonisation by epifauna

Despite the presence of blue mussel culture (*Mytilus edulis*) adjacent to the reef, mussels colonizing the structure belong to the species *M. galloprovincialis*. In 2007, the extent of spatial mussel coverage was significantly higher (22% of the grid squares, localized primarily in the south-east parts of sub-reefs B and C, compared to 9% in 2001, Z=2.16 and p=0.030). With the exception of one grid square, *M. galloprovincialis* was totally absent of sub-reef A in 2007. However, mussel density significantly decreased between 2001 (11.5±41.7 ind.m^{-2}, with a

maximum of 450 ind.m^{-2}) and 2007 (2.0±4.8 ind.m^{-2}, with a maximum of 33 ind.m^{-2}; Z=2.54 and p=0.010) for the benefit of the Pacific oyster *Crassostrea gigas*. Spatial distribution patterns of these two mollusks looked opposite since high mussel densities were associated with low oyster densities, and *vice-versa*.

In 2001, oyster banks were essentially located in the south-west region of the reef, with densities reaching up to 40 ind.m^{-2} (Figure 5). In 2007, their occurrence spread from sub-reefs A (Z=1.15, p=0.249, ns) to B (6.68, p=1 10^{-4}). Sub-reef C remained largely free of oysters, although rare spots were colonised by oysters, reaching densities of 60-90 ind.m^{-2}.

3.2.3. Health status

In 2001, 35.2, 38.5 and 26.3% of total grid squares referred to bad, intermediate and good ecological statuses respectively, against to 38.9, 25.7 and 35.4% in 2007. When all grid cells were considered, the average HI was 8.1 and 2.6 in 2001 and 2007 respectively (Z=1.50, p=0.132), both intermediate ecological statuses. In 2001, sub-reefs B and C were in a better status (*i.e.* intermediate - average HI=9.6 and 16.5 respectively) than sub-reef A (bad status - average HI=-16.7, Figure 6). In 2007, health status decreased for sub-reefs A and B (overall bad status – average HI= -26.3 and -18 respectively). Conversely, sub-reef C reached a good status (average HI=22.0) in 2007. In 2007, degradation status was highly correlated with the density of *Crassostrea gigas* (-0.723)

Statistical comparisons of HI, performed between the two years (2001 and 2007) on common grid squares (*i.e.* 160) for each sub-reef, showed that changes were not statistically significant.

4. Discussion

There is a high contrast in biodiversity between the *Sabellaria alveolata* reefs, now recognized as a biodiversity hot-spot (Dubois *et al.*, 2002), and the *Macoma balthica* sand community bordering these formations in the Bay of Mont-Saint-Michel which is known for its low species richness (Thorin, 2001). The argument for effective conservation management of *S. alveolata* reefs is therefore strongly supported, considering the vulnerability of the reef (Dubois *et al.*, 2002).

4.1. Evolution of the sedimentary environment

The evolution of the reef environment is summarised in Figure 7. Additional field observations showed that the back-reef sand banks (called "la Grande Bosse" and "la Dune Plate", see Figure 3) rapidly grew and shifted landwards (50 to 100m.year^{-1}, Bonnot-Courtois *et al.*, 2004). Also, organic-rich mud deposits and moderately well sorted coarse-grained sands partly derived from the reef were accumulated in the back-reef zone. Associated reef-derived sand bodies were depleted in bioclasts contrary to the worm tubes forming the reef that play an actual role in storing of carbonate bioclasts (Noernberg *et al.*, 2010). On the other hand, a slight south-westward expansion of the reef was noted. Sabellariid reefs generate sand bodies which consist of reef-derived loose sands and the shape and distribution of these sand bodies are then controlled by local wave and current patterns (*e.g.* by tidal currents in the Bay of Mont-Saint-Michel). These elongated sand bars or spits (also figuratively named "tails") build out across tidal flats and ultimately connect with the main shore.

The Sainte-Anne reef here illustrates how organisms that do not produce carbonate may nevertheless form reefs in a siliclastic environment. The distribution and geometry of reef-related

sand bodies are similar to those found in other regions (e.g. the Bay of Bourgneuf in the most southern part of Brittany). The *S. alveolata* colonies as well as the associated sand mound – colonised by *Lanice conchilega* (another tube-building polychaete), indicate that annelids may modify the texture and the distribution of intertidal sediments because of their ability to trap and/or concentrate particles of specific mineralogy and grain-size (Callaway *et al.*, 2010; Godet *et al.*, 2011).

4.2. Evolution of the reef health status

In line with the observed sedimentary changes, the different descriptors of the reef health status, integrated in the HI calculus, suggest a degradative trend from 2001 to 2007. The average HI value decreased only moderately from 8.1 to 2.6 between the sampling periods, but the trend differed between the reef sections. Sub-reefs A and B are strongly degraded and were therefore assigned bad statuses whereas sub-reef C evolved towards a better health status (from intermediate to good). Paradoxically, investigations of biodiversity associated to the different reef stages showed that the higher species richness is observed on the degraded sub-reef area, as well as completely different species assemblages, essentially because of the habitat fragmentation associated with changes in surface topography and increase in available space for new species to colonize the reef (Dubois *et al.*, 2002). However, while degraded areas should not be considered as dead reef, the density of *S. alveolata* individuals is very low and not high enough to provide a basic maintenance of the reef. Biodiversity level is obviously not the only issue in terms of reef management objectives, especially knowing that the lower species richness occurs on platforms, when the reef reach its maximal height and higher tube density. In that perspective, a combination of all reef evolution stages is a way of assuring enough *Sabellaria* densities to allow maintenance and a proper renewal and evolution in reef structures. If the number of individuals is high enough to allow the *Sabellaria* population to grow and develop, degraded structures could then be the preferential substratum for *S. alveolata* larvae, also creating in the mean time an extension of the reef contours. Recent modelling results from Ayata *et al.* (2009) obtained from a 3D biophysical coupling developed in the Bay of Mont-Saint-Michel indicated that despite actual very low settlement rates (*i.e.* <0.004%), its hydrodynamic specificities could allow larval retention at the Bay scale and facilitate larval exchanges between the reef of Sainte-Anne and the one of Champeaux. In this context, any decrease in the reproductive outputs of the Sainte-Anne reef could adversely affect the sustainability of both reefs within the Bay of Mont-Saint-Michel. If the Sainte-Anne reef disappears, the larval supply from Champeaux might not be sufficient enough to both sustain itself and recolonise the Sainte-Anne reef (Ayata *et al.*, 2009). The reef status in 2007 should then be considered as its minimal condition status and should not fall below this limit without jeopardizing its short-term survival.

4.3. Understanding main factors adversely affecting reef health status

Beyond the natural dynamics of the reef, several hypotheses are likely to explain the observed changes in the reef dynamics and its associated health status. Those factors relates to the colonization of the reef surface by epibionts and their recreational fishing as well to the implantation of new mussel farming structures their consequences on trophic competition within suspension-feeding species.

4.3.1. Influence of reef colonisation by epibionts

The stability of *Sabellaria* reefs is influenced not only by the stability of the substratum on which they settled, but also by their interactions with other species. Mussels, oysters and *S. alveolata* often occur together, and in many areas, one of them may be dominant at different times. Factors

affecting this competitive interaction remain unclear. It has been reported by Perkins (1988) on reefs in Cumbria (North West England) that mussel recruitment was able to change the physionomy of the reef, and Cunningham *et al.* (1984) reported the existence of a *Sabellaria*/*Mytilus* succession. The development of shellfish farming in the Bay of Mont-Saint-Michel, leads to high abundances of cultivated oysters (5000 tons) and mussels (12 000 tons) spatially concentrated in close areas to the reef. Such anthropogenic activities could indirectly affect *Sabellaria* reefs evolution by inducing high larval mortality and subsequently reducing larval supply because of filtration pressure as hypothesised in Dubois *et al.* (2007) and evidenced in wild mussel beds by Lehane and Davenport (2004) or Troost *et al.* (2008).

The Sainte-Anne reef is structurally heterogeneous, with healthy areas in close proximity to degraded zones. The degradation status of the reef in the south-western part is correlated with the presence of *Crassostrea gigas*, which has increased considerably in sub-reef B. Coming from the west part of the Bay where they are cultivated, oysters can easily colonise the Saint-Anne reef via the hydrodynamic circulation seeding larvae in this reef area. The Pacific oyster is not only a trophic competitor for *S. alveolata* (Dubois *et al.*, 2003) but the high quantities of pseudo-faeces produced by oysters contribute to the increase in fine particles in the sediment. A study carried out on similar reefs in the Bay of Bourgneuf (France) showed however that the highest microphytobenthic biomass values are related to the presence of filter feeders (*Mytilus sp* or *Crassostrea gigas*, Barillé, unpub. data).

Accumulations of oysters on the reef surface induce structural weakness due to their weight and ultimately contribute to the dislocation of balls and platforms (Dubois *et al.*, 2002). But oyster's occurrence also comes with direct anthropogenic pressure generated oysters collection (*e.g.* destruction of reef blocs and surface scrapping) and associated trampling. Managing anthropogenic activities close to the reef is a major issue that needs to be address by decision-makers. The collection of species such as *Venerupis saxatilis* or the scallop *Chlamys varia* which live in reef crevices, ultimately leading to reef alteration, should be managed too. Gleaning with gears such as iron bars, chisels…, evidently break ball-shape structures and platforms and alter the reef structure. The destruction of the reef induces a fragmentation of the habitat. The conservation challenge is to avoid an irreversible habitat alteration and the decline of the reef which would induce a loss of biological diversity at large scale, and have dramatic consequences for other marine habitats as reported by Thrush *et al.* (2008).

4.3.2. Implantation of new mussel farming structures

A modification of the shellfish farming scheme was completed in 2006. Farming sites along the western portion were abandoned on behalf of more productive sites located to the North of Sainte-Anne reef. A pre-impact study of this new scheme has shown that the current speed would decrease downstream of the new installations facing the reef (Salomon, 2000). A few years after the change in shellfish structure, as modelled, we observed a decrease of mean grain-size, higher in the fore-reef area. The new scheme induced several problems. Firstly, the increase of suspended particulate matter (organic and inorganic) disturbs the filtration rate of *S. alveolata* (Dubois *et al.*, 2009) inabrading feeding organs and clogging up the tubes. Secondly, the decrease of current velocity increases the sedimentation and decreases the sand grain re-suspension. This leads to a decrease in tube-building activity, since the tubes are built by the polychaetes by catching sand particles drifting near their tube aperture.

4.3.3. Influence of trophic depletion

To understand the functioning of the trophic food wed in the Bay of Mont-Saint-Michel, an ecological model of the Bay was developed by Cugier *et al.* (2010) to couple a 2D hydro-sedimentary model with two biological models for primary production and filter-feeder filtration

activity. Results dealing with *S. alveolata* reef of Sainte-Anne showed that, after the implantation of new structures for mussel cultivation from 2004 to 2006 in front of the reef, a large decrease of mussel growth would occur due to a lack of food which persists just in front of the reef. This depletion may also affect directly *S. alveolata* growth and fecundity and could explain part of the reef regression.

5. Conclusion

Reef-forming organisms are recognized as keystone species which provide complex structural habitats of high biodiversity [*e.g. S. alveolata* (Dubois *et al.*, 2002); mussel beds (Saier, 2002); *Limaria hians* (Hall-Spencer & Moore, 2000)…]. As shown in *S. spinulosa* aggregations (Hendricks & Foster-Smith, 2006), *S. alveolata* aggregations enhance biodiversity compared to the surrounding sediment and contribute to the distinctness of the reef habitat as well as imparting a greater significance to the habitat in terms of conservation.

Contrary to the United Kingdom, where *S. alveolata* reefs have benefited from a Biodiversity Action Plan (BAP) since 1994 (http://www.ukbap.org.uk/UKPriorityHabitats.aspx), no global measures for protection or management of this habitat were taken in France. The unique extension of these reefs in the Bay of Mont-Saint-Michel is responsible for the recent rise in awareness of the necessity of their conservation within the region. However, the conservation of *Sabellaria* reefs only became a priority when the structures were included in a designated Natura 2000 site in the Bay (FR 2500077). Measures to achieve favourable conservation status (FCS) according to the Habitats Directive were drafted in 2009 and include: (1) regulation of the pedestrian and motorised circulation on the reefs and (2) promotion of sustainable gleaning techniques on the reefs and their vicinity. These measures will need environmental monitoring and information to make users aware of this exceptional biological heritage.

Acknowledgements

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Tables

Table 1: Ecological Quality Ratio (EQR) values and ecological status associated with the HI index. Theoretical minimum and maximal values are of -200 and 110.

Values for recorded parameters	FD=0, IB+CB+P=0, DIB-DP=10, OC-MC=10, RC=10	FD=2.5, IB+CB+P-DIB-DP-OC-MC=0, RC= unnecessary to determine	FD=5, IB+CB+P=7, DIB-DP=3, OC-MC=1, RC= 5	FD=10, IB+CB+P=10, DIB-DP=0, OC-MC=0, RC= 10
EQR	-200	2.5	20	110
Ecological status		BAD	INTERMEDIATE	GOOD

Table 2: Results of paired *t*-tests between reef sectors and between years for surrounding sediments of the Sainte-Anne reef with *p* value

	x	σ	*t*	dl	*p*
Fore-reef					
M_G µm (2001)	753.52	310.45	-19.3511	21	=7.246e-15
M_G µm (2007)	369.45	276.89			
% <63 µm (2001)	3	6.23	-822.664	21	<2.2e-16
% <63 µm (2007)	8.39	15.28			
Reef					
M_G µm (2001)	703.91	483.45	-15.8254	29	=8.37e-16
M_G µm (2007)	693.14	434.76			
% <63 µm (2001)	4.25	13.58	-768.4201	29	<2.2e-16
% <63 µm (2007)	5.19	14.91			
Back-reef					
M_G µm (2001)	313.56	191.27	-38.3135	23	<2.2e-16
M_G µm (2007)	265.12	249.61			
% <63 µm (2001)	6.69	13.79	-552.492	23	<2.2e-16
% <63 µm (2007)	13.50	21.52			

Figures

Figure 1: Overview of the Bay of Mont-Saint-Michel and location of the Sainte-Anne reef. Mussel culture areas represented by dotted lines correspond to recently added plots (2003)
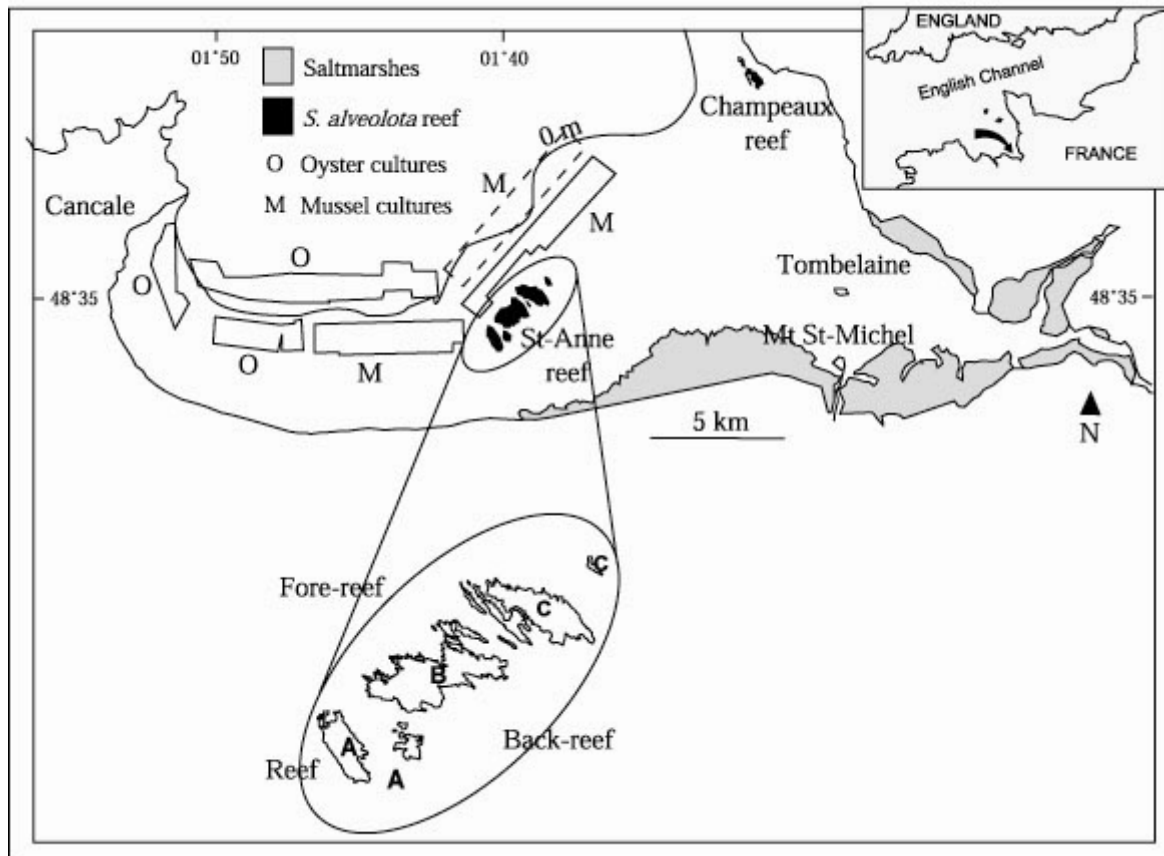

Figure 2: Fragmentation scale of *Sabellaria alveolata* reef and associated score. Values assigned to stages are used for the HI estimates
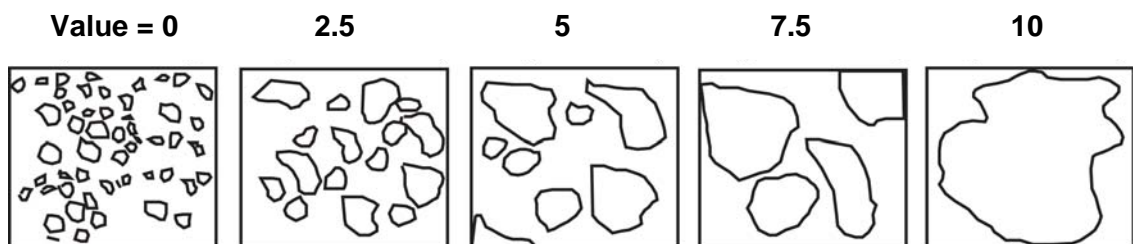
Figure 3: Sedimentary changes between 2001 and 2007 observed at the Sainte-Anne reef
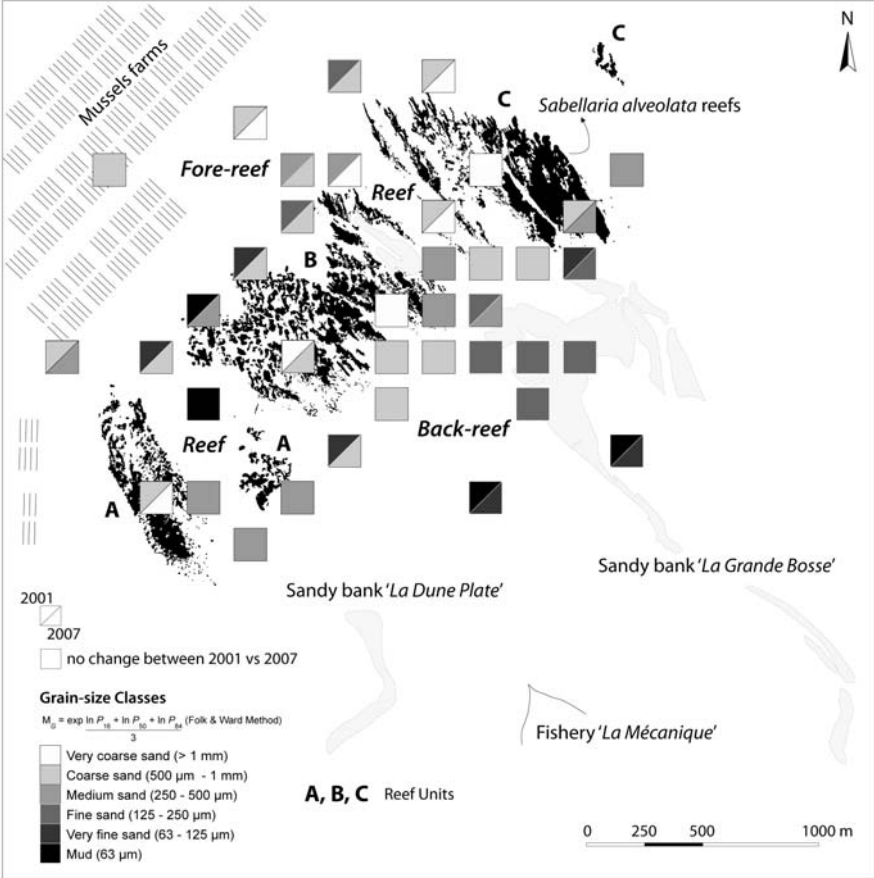
Figure 4: Fragmentation levels observed in 2001 and 2007 (ND= no data). Dotted lines (top left corner) represent mussel bouchots.
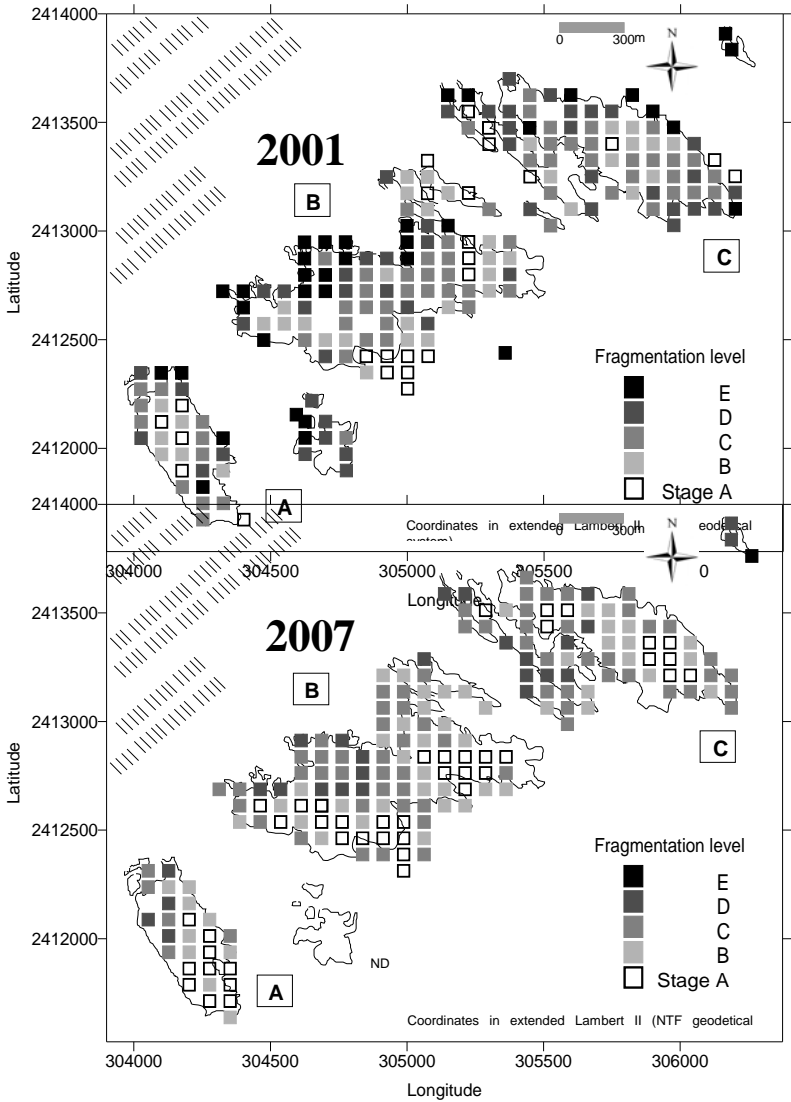
Figure 5: Oyster density (ind.m^{-2}) in 2001 and 2007 (ND= no data). Dotted lines (top left corner) represent mussel bouchots.
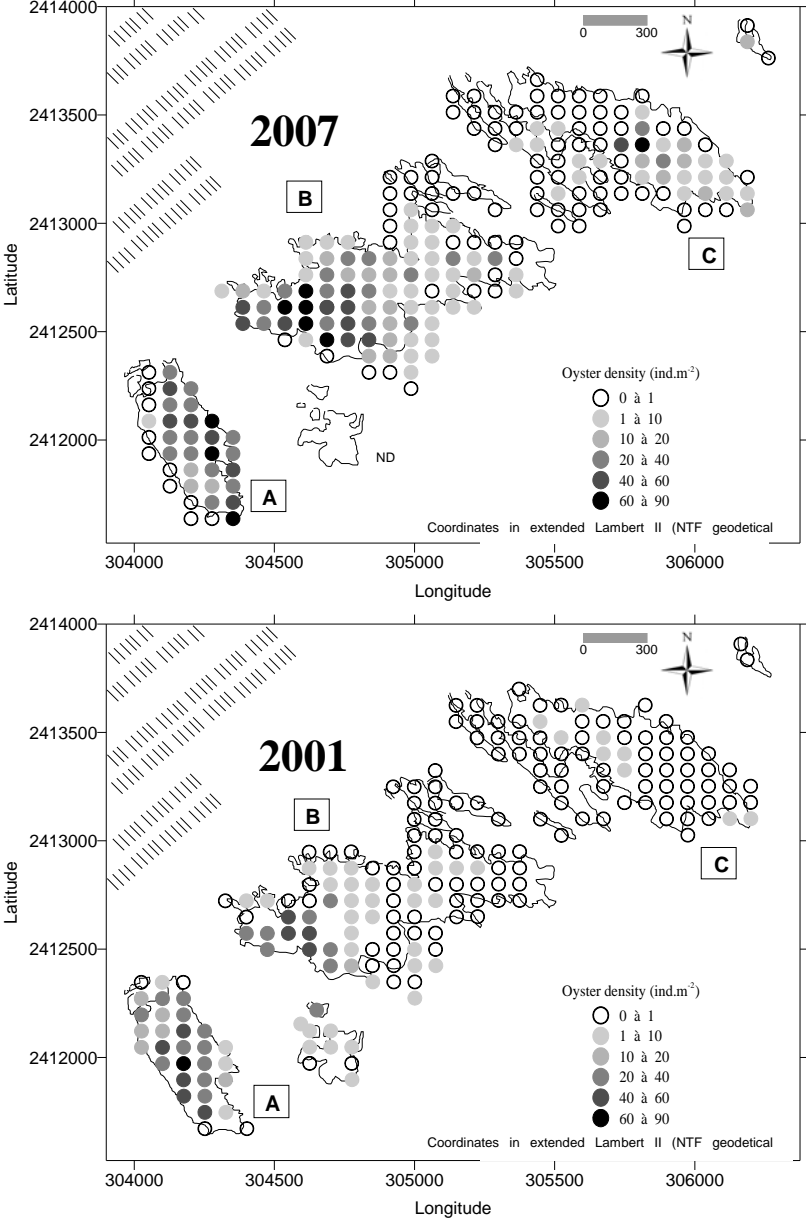
Figure 6: Health index observed in 2001 and 2007 (ND= no data). Dotted lines (top left corner) represent mussel bouchots.
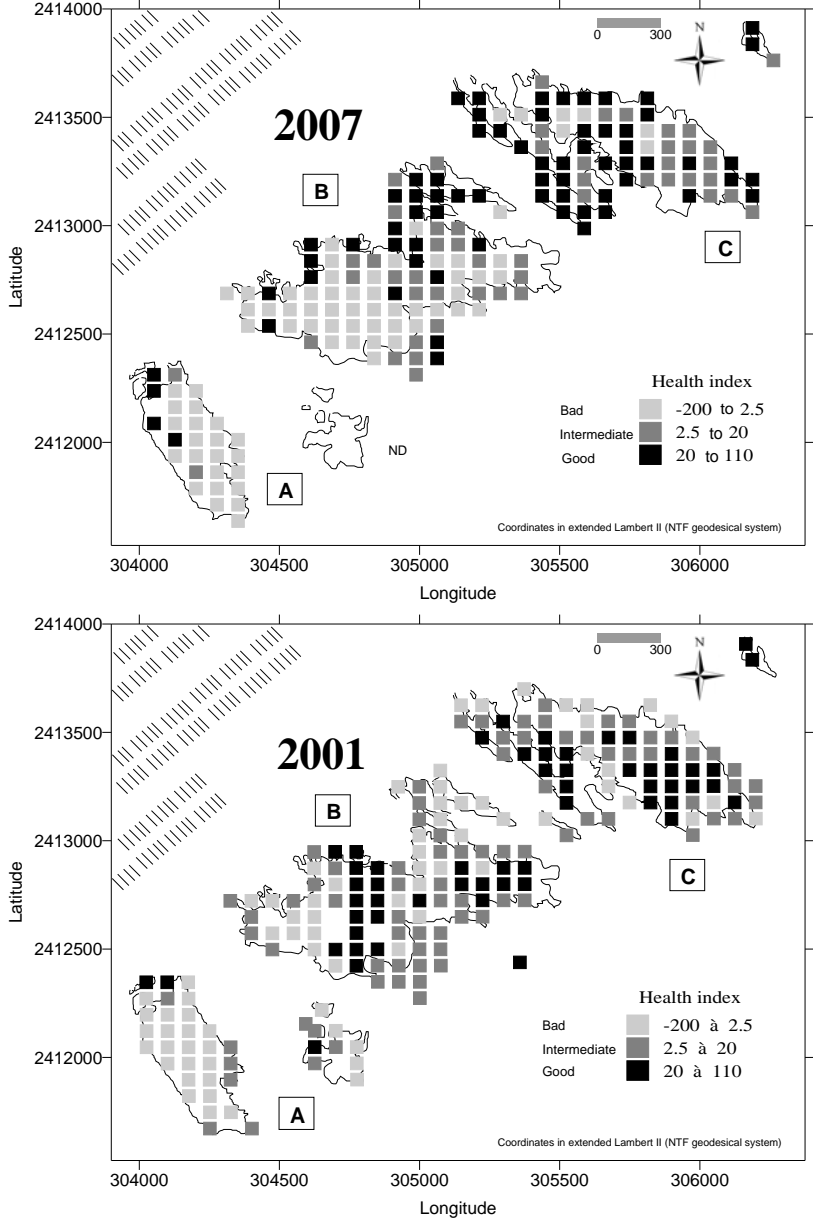
Figure 7: Biosedimentological model of a *Sabellaria alveolata* reef as based on the Sainte-Anne reef of the Bay of Mont-Saint-Michel.