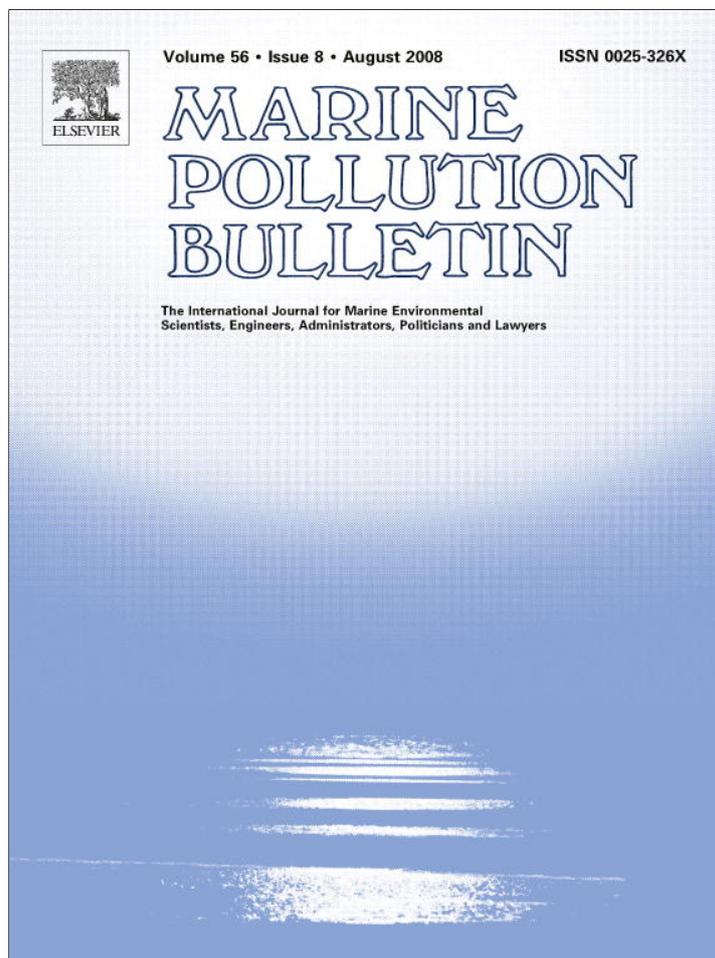


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Does Manila clam cultivation affect habitats of the engineer species *Lanice conchilega* (Pallas, 1766)?

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A B S T R A C T

The major French site of Manila clam *Ruditapes philippinarum* (Adams and Reeves, 1850) cultivation is located in the Chausey Archipelago where the associated practices are highly mechanized: every steps of production are made with tractor-driven machinery. The Manila clam concessions are concentrated on *Lanice conchilega* (Pallas, 1766) bioherms, which are known to increase alpha-diversity and to locally modify sediment dynamics. This study focus on the impacts of Manila clam cultivation on (i) the natural populations of *L. conchilega* and on (ii) the structure of the associated benthic assemblages during the different steps of the farming production cycle. We found that the *L. conchilega* populations are significantly affected within the concessions where their total abundances drastically decrease, their spatial patterns are modified and the associated benthic assemblages are significantly altered. Our results are discussed in a context of a sustainable management of the Manila clam cultivation in coastal areas.

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1. Introduction

Although the environmental hazards of shellfish farming are now well known (e.g. Crawford, 2003a, 2004), the effects of Manila clam (*Ruditapes philippinarum*, Adams & Reeves, 1850) cultivation on the benthic compartment are little documented. The few studies available have shown mostly an organic enrichment (Bendell-Young, 2006; Spencer, 1996; Spencer et al., 1996) and an increase of sedimentation rates (Goulletquer et al., 1998; Spencer, 1996; Spencer et al., 1996, 1997). Both on-growing and harvesting processes have the potential to alter benthic communities (Spencer et al., 1996, 1997), but only short-term effects have been observed (Kaiser et al., 1996). In the Chausey archipelago (Normand-Breton Gulf, English Channel, France), Manila clam cultivation is highly mechanized throughout the production cycle, including tractor-towed tolls which allow large-scale operations and increase productivity. The effects of such mechanical processes have already been assessed for cockle cultivation (Ferns et al., 2000; Hall and Harding, 1997), but not for Manila clam. In 1989, the SATMAR (Société Atlantique de Mariculture) company started cultivation of this exotic species in Chausey and nowadays it annually pro-

duces 120 tons of marketable clams (first national production). One of the major features of this shellfish farming concerns the setting up of clam concessions on the sand-mason worm *Lanice conchilega* (Pallas) habitats.

L. conchilega is one of the most common tube-building polychaetes in the Northern European sandflats. This amphiboreal species (absent from Arctic) ranges from intertidal to subtidal (up to 100 m depth) fine to coarse sediments and its populations are mainly concentrated below the low water neap tide level (Carey, 1987). This Terebellid worm has a mean life of about 3 years (Féral, 1988) and is a deposit/filter feeder changing its feeding strategy in response to density-dependant processes (Buhr and Winter, 1976). This tube-dweller has an aggregative distribution (Nicolaidou, 2003) with patches reaching densities of several thousands of individuals per square meter (extreme cases up to 20,000 ind. m⁻²; Buhr and Winter, 1976). The *Lanice* tube (diameter = 0.5 cm, total length up to 65 cm; Ziegelmeier, 1952) is prolonged by sandfringes which protrude from the sediment and modify the small-scale benthic boundary layer patterns and consequently the local hydrosedimentary environment (Eckman et al., 1981; Luckenbach, 1986). Above a threshold density, current velocities decrease within clusters, deposition of fine sediment particles is facilitated and mounds are created (Friedrichs et al., 2000). Sand-mason worms stimulate oxygen exchanges at the water-sediment interface ('piston-pumping mechanism: Forster and Graf, 1995; Zühlke et al., 1998) and promote the nutrient cycling of key elements (Bendell-Young, 2006). Moreover, *L. conchilega* clusters generate a more beneficial environment for other benthic species such as a refuge

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from predation, a source of food (Callaway, 2006; Zühlke, 2001; Zühlke et al., 1998) and a suitable surface for larval settlement (Armonies and Hellwig-Armonies, 1992; Callaway, 2003b; Gallagher et al., 1983). In fact, *L. conchilega* may be considered as an auto- and allogenic ecosystem engineer (Jones et al., 1994) with high positive effects on the diversity features of the associated benthic macrofauna, and consequently on secondary consumers (Peterson and Exo, 1999; Amara et al., 2001; Godet et al., in press).

The objective of this study was to assess the effects of this cultivation on the high value habitats of *L. conchilega* (Godet et al., in press) by testing the following hypotheses:

- (1) The spatial distribution and the structure of *L. conchilega* populations are modified in the shellfish farming concessions when compared to a control site and they develop along the production cycle.
- (2) The total abundance and the structure of the benthic assemblages associated to the *L. conchilega* habitats are altered within the Manila clam concessions.

2. Materials and methods

2.1. Study site

The study was carried out in the Normand-Breton Gulf (English Channel), whose main characteristic is an extreme tidal range (up to 15.5 m for highest spring tides in the Mont-Saint-Michel's bay). At the Northern limit of the bay, the Chausey archipelago (11 km long and 5 km wide, Fig. 1) comprises tidal flats of 2000 Ha, among which 1500 Ha are soft-sediments including various highly fragmented habitats. Due to its high patrimonial value, this archipelago is protected by several conservatory measures including the 'Natura 2000 site' in 2005 (from the European Network).

2.2. Farmers' procedures along the production cycle

In 2005, the Manila clam concessions covered 24 Ha of mean to coarse sediments, principally restricted to a central place in the 101 Ha *L. conchilega* habitats (Godet et al., in press; Fig. 2).

Each step of the production cycle is performed using tractor-towed machines: (i) seeding and anti-predators nets setting, (ii) nets brushing, (iii) nets removing and (iv) harvesting (Fig. 3). Monthly maintenance (ii) is performed to prevent high rates of

sedimentation and to avoid macroalgae settlement. Nets are removed when shell lengths exceed 1 cm and clams were harvested at marketable-size (>4 cm), 3 years later. Shellfish farmers exploit pools of parcels in order to provide marketable clams all the year.

The practices associated with Manila clam cultivation have strong mechanical effects on the bottom, mixing the superficial sediments during the harvesting phase (the first 10 cm) and generating particular topographic features (pers. obs.). Sedimentary "bumps" occur in the areas previously covered by nets (seeded areas) and are separated by "furrows", where nets were burrowed (inter-seeded areas). The persistence of such features seems to be related to the local hydrodynamic regime.

2.3. Sampling design

In order to assess the influence of the production practices on the population dynamics of *L. conchilega* and the structure of the associated benthic assemblages, we sampled in April 2005 five contiguous sites corresponding to particular stages of production: (i) site 'A' was just seeded (10th April 05), (ii) site B was seeded 1 year ago, (iii) sites C and Cbis were seeded 2 years ago, (iv) site D was just harvested (9th April 05), and (v) site control was colonized by dense natural clusters of *L. conchilega* and constituted the non-impacted area (Fig. 2). Site Cbis was submitted to more intense hydrodynamical stress than C (pers. obs.).

2.4. Impacts on the populations of *L. conchilega*

Spatial distributions of the *Janice* populations were examined on 1.28 Ha areas (80 × 160 m) located in three Manila clam parcels (A, B, C) and in the Control. Densities were estimated on 26th and 27th April 2005 on 50 regularly distributed stations (cell = 16 m) by taking numerical pictures of three 0.25 m² random quadrats (3008 × 2000 pixels, Nikon D70). The number of intact sand-fringes was counted on the pictures because this parameter is highly correlated to the number of individuals burrowed in the sediment (Callaway, 2003a; Ropert and Dauvin, 2000; Strasser and Pieloth, 2001; Zühlke, 2001; Bendell-Young, 2006) and the error associated does not exceed 3% (Ropert, 1999). An overestimate has been noticed in the low density areas due to the presence of U-shaped tubes (Bendell-Young, 2006; Strasser and Pieloth, 2001), but these shaped tubes are not systematically present in intertidal populations of *L. conchilega* (Jones and Jago, 1993; Ropert and Dauvin, 2000).

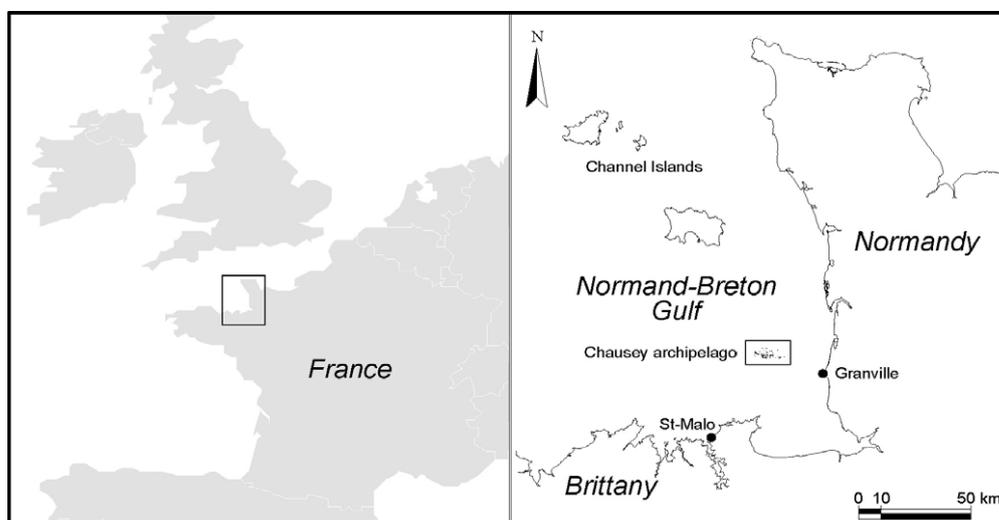


Fig. 1. Localization of the study site.

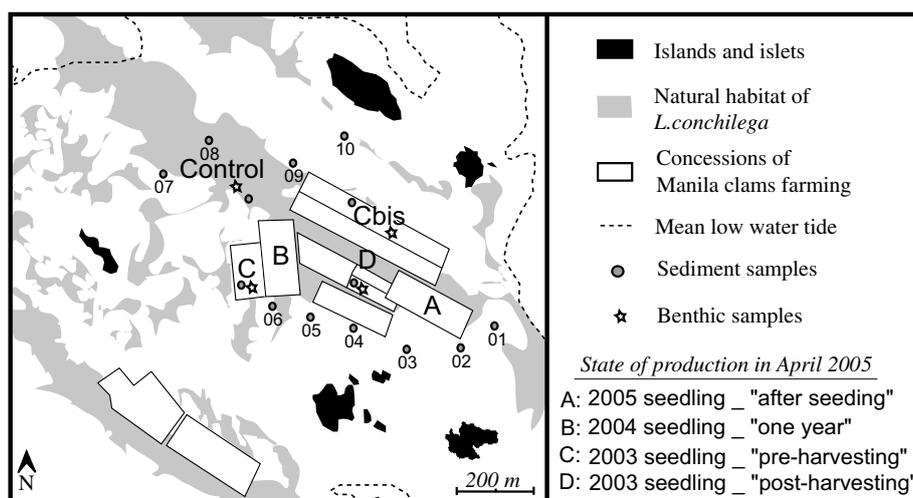


Fig. 2. Map of the Chausey farming site showing the layout of Manila clam concessions, the location of the Control area and of the natural *Lanice conchilega* bioherms. The parcels studied in April 2005 (A, B, C, Cbis and D) are detailed according to their step of production. Stars and rounds locate the sampling plots of, respectively, benthic macrofauna and sediment.

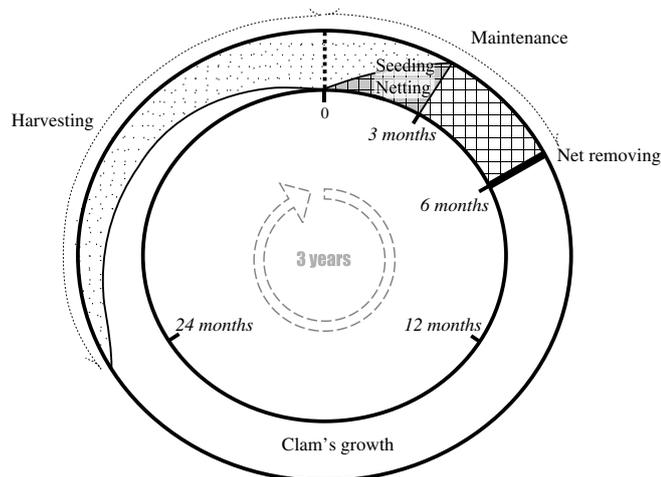


Fig. 3. Typical production cycle of the Manila clam cultivation in Chausey. For each step (seeding/netting, maintenance, net removing and harvesting), specific mechanized tractor-towed tool is used. Parcels are let without any practices during the bivalve growing phase (18–30 months).

To compare size structures of *Lanice* populations in C vs Control parcels, we randomly collected 100 tubes per treatment and measured their internal tube perimeter (ITP). On the basis of preliminary measurements of 50 complete individuals and their tubes, we chose this criterion because it was best correlated to total dried weight (DW) of the individual (Formula 1).

Formula 1 : $DW(g) = 2.12 \times 10^{-5} (ITP(mm))^3 .531, (R^2 = 0.80)$.
The acquisition method consists of sampling a 5 mm wide part of the tube at a distance of 5 cm from the fringe basis whose section is cut to obtain a nearly flat tape. A picture of the tape is then acquired under a dissecting microscope via a 2 megapixel Spot Insight™ camera and its length is further assessed through the Image Pro Plus© software.

2.5. Impacts on the benthic macroinfauna

Macroinfaunal assemblages were examined on 11th April 2005, in the centre of (i) the C and Cbis pre-harvesting parcels, (ii) the D post-harvesting parcel and (iii) the Control area. For each

20 × 20 m studied area, four cores were randomly collected (0.1 m², 15 cm deep) for biological analysis and one for sediment characterization (10 cm², 10 cm deep). Benthic samples were sieved in the field through a circular 2 mm mesh size and the biological material retained was then directly preserved in 4.5% buffered formalin. Once in the laboratory, samples were sorted twice, the second time after Rose Bengal staining. Macrozoobenthos was identified to the lowest taxonomic level as possible, mainly species.

Sediment samples were cleaned with distilled water and following decanting was allowed during 24 h. Sediments were then dried at 70 °C for 24 h and approximately 100 g was then sieved through AFNOR standard sieves (meshes of 2.5, 2, 1.6, 1.25, 1, 0.8, 0.63, 0.50, 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 has been weighted and the associated results are expressed as percentages of the total sample weight. Dried samples were combusted at 550 °C for 60 min in order to determine the organic content (Dean, 1974) in each sampling station but also in 10 others located around the shellfish farming concessions (Fig. 2).

2.6. Data analysis

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 (unpublished data) based on the Moments method using the Folk and Ward (1957) classification.

Differences between *L. conchilega* mean densities were tested either using one-way ANOVA or non-parametric Kruskal–Wallis tests (KW). The assumptions of homoscedasticity and normality were verified by direct observation of residuals (Quinn and Keough, 2002). In case of significant global analysis, post-hoc comparisons were performed through LS means or non-parametric multiple comparison tests (Scherrer, 1984). *L. conchilega* spatial distributions were studied by interpolating the mean abundances and the variation coefficients (VC = SE/mean abundance * 100) by the linear kriging method using Surfer© software. Differences of mean ITP were tested by using *t*-tests or Mann–Whitney *U*-tests depending on homoscedasticity and normality conditions. Intervals of size-classes were chosen according to the Sturge and Yules rules (Scherrer, 1984). Differences between the size-classes distributions were tested by the Kolmogorov–Smirnov test (KS).

The mean values of the number of species (*S*), total abundance (*N*), Shannon diversity (H' loge) and Pielou evenness (*J*) were compared as for the *Lanice* mean densities data (see above) and *K*-dominance plots (Warwick, 1986) were created. To compare the structure of macrozoobenthic assemblages sampled in each area, we followed Clarke and Warwick (1994) and used the Plymouth Routines in Multivariate Research (PRIMER) version v5.2.2 software (Clarke and Gorley, 2001). Non-metric multidimensional scaling ordinations (nMDS) and analysis of similarity (One-way ANOSIM: Clarke and Green, 1988) were performed after a computation of a Bray–Curtis similarity matrix. Stress values related to nMDS plots indicate the goodness of representation of 'distances' between samples (Clarke, 1993). Moreover, species accounting for the similarity within and between treatments were identified by the SIMPER sub-routine of the PRIMER software (Clarke, 1993). For each previous analysis, densities of the two dominant

species *L. conchilega* and *R. philippinarum* were excluded from the database.

3. Results

3.1. Impacts of Manila clam cultivation on the *L. conchilega* populations

Mean density of *L. conchilega* was significantly higher in the Control area (458.4 ind. m⁻²) than in Manila clam concessions (less than 150 ind. m⁻²) where abundances increased significantly along the production cycle ($p < 0.05$). Conversely, mean variation coefficient (VC) was significantly lower in the Control (VC = 11.5%) than in shellfish parcels (VC > 56.5%) where it decreased significantly along the production cycle ($p < 0.05$; Table 1).

Table 1
Mean abundances (±SE) and mean variation coefficients (±SE) of *L. conchilega* populations in each sampling parcel (the control and 3 steps of production) (S: whole test significant; *: multiple comparison tests significantly different)

Parcels	Control	A	B	C	Means comparisons
Step of production	Natural conditions	Just after seeding	1 year after seeding	2 year after seeding	
Mean abundance (ind. m ⁻²)	458.3 (277.0)	32.1 (31.2)	68.9 (77.9)	142.7 (91.9)	Kruskall–Wallis S *Ctrl. *C *A *B
Ratio (%) (concessions/control)		7.0	15.0	31.1	
Mean variation coef. (%)	11.5 (10.3)	84.1 (38.2)	72.2 (48.1)	56.5 (27.6)	Kruskall–Wallis S *A *B *C *Ctrl.

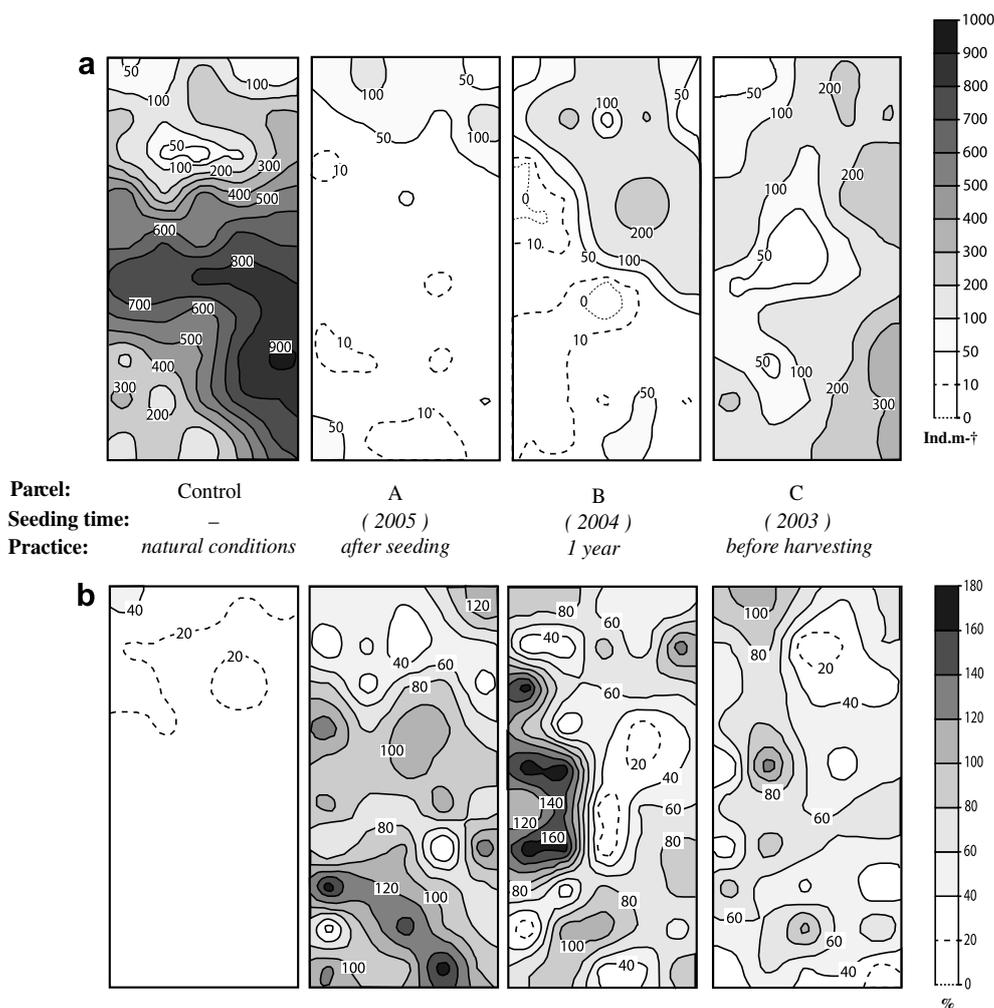


Fig. 4. Maps of the spatial distributions of *Lanice conchilega* populations in 3 steps of production (A, B and C) and in the control. The first series (a) results from the kriging of the abundances and the second one (b) from the kriging of the variation coefficients.

Observations of *L. conchilega* density maps reveal that the spatial distributions were more heterogeneous in Control than in the cultivated areas (Fig. 4a). Conversely, the spatial distribution of VC values was more homogeneous in Control than in the concessions where VC often exceeded 100% (Fig. 4b).

Mean *Lanice* ITP and therefore mean individual DW were significantly larger in C ($ITP_C = 10.6 \pm 2.3$ mm; $DW_C = 106.3 \pm 71.3$ mg) than in Control ($ITP_{control} = 9.3 \pm 1.4$ mm; $DW_{control} = 61.8 \pm 33.5$ mg) (*U*-test, $p < 0.0001$). Distributions of size frequencies (class interval of 1.4 mm) were also significantly different between the two sampling areas (KS, $p < 0.001$; Fig. 5). The mean total *Lanice* biomasses (dry weight) corresponding to each studied area (1.28 Ha) was therefore estimated to 363 and 194 kg for Control and C respectively.

3.2. Impacts of Manila clam cultivation on benthic assemblages

Grain-size distribution of the fine sands collected in parcel D differed from the other sites (medium sands; Table 2). A slight organic enrichment was observed within the concessions (sites C, Cbis, D) and within the control site when compared to the other peripheral sandflats (Table 3).

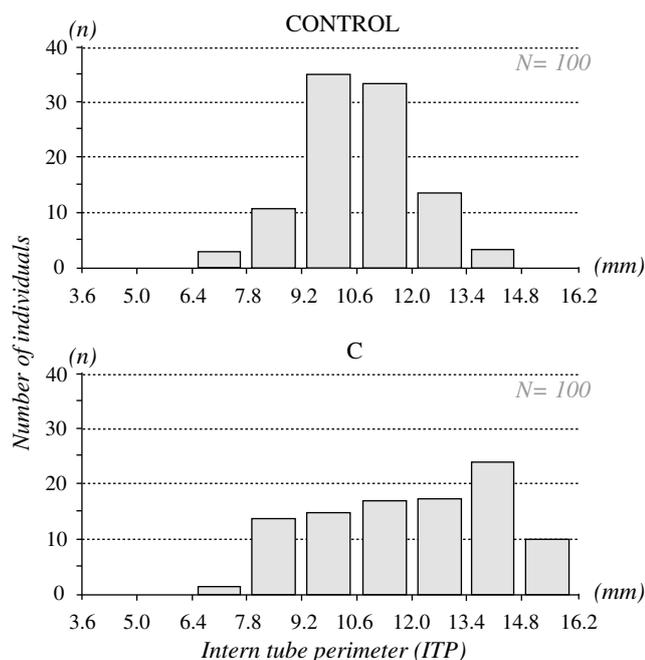


Fig. 5. Histograms of size frequencies distributions of *Lanice* tubes sampled in the control and in C ("before harvesting" step).

A total of 71 macroinvertebrate taxa were identified from the 16 samples including 62% of Annelids Polychaeta, 24% of Crustaceans and 11% of Molluscs. Species richness, mean total abundance and Shannon value were significantly higher in the Control area than in shellfish concessions ($p < 0.05$) within which species richness and mean abundance were significantly higher in C ($p < 0.05$).

Table 3

Results of the sediment organic contents analyses (expressed in%). Data were obtained for 4 parcels (C/Cbis, D and control), and 10 other sampling sites located in the shellfish farming surroundings

Stations	Organic content
01	1.21
02	0.00
03	1.32
04	1.49
05	0.72
06	0.49
07	0.86
08	1.12
09	0.42
10	2.95
C	11.11
D	10.25
Cbis	10.01
Control	10.00

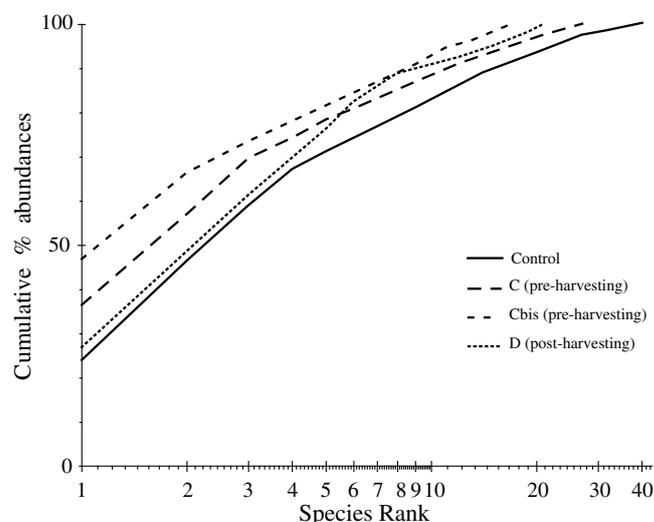


Fig. 6. K-dominance curves of the invertebrates assemblages sampled in each sampling parcel (C, Cbis, D and the control). Data for *Lanice conchilega* and *Ruditapes philippinarum* are not included in this graphic.

Table 2

Mean diversity parameters (\pm SE) of the benthic assemblages expressed for each sampling parcel (control, C/Cbis and D) and results of multiple comparisons tests (Anova/KW: $S: p < 0.05$; NS: $p > 0.05$; Lsmean or SNK post-hoc comparisons)

Parcels	Control	C	Cbis	D	Means comparisons				
Steps of production	Natural conditons	2 years after seeding	2 years after seeding	after harvesting					
Species number ($n\ m^{-2}$)	25.8 (6.4)	14.5 (1.0)	9.8 (3.3)	10.8 (1.7)	Anova	S	*Ctrl.	*C	Cbis D
Abundance ($ind.\ m^{-2}$)	1347.5 (118.1)	642.5 (97.1)	292.5 (90.0)	325.0 (37.0)	Kruskall-Wallis	S	*Ctrl.	*C	D Cbis
Shannon index ($H' \log_e$)	2.5 (0.2)	2.0 (0.2)	1.7 (0.3)	2.0 (0.3)	Anova	S	*Ctrl.	C	D Cbis
Pielou index (J')	0.8 (0.0)	0.7 (0.1)	0.8 (0.0)	0.8 (0.1)	Anova	NS	Ctrl.	Cbis	D C
Sediment mean feature (Folk and Ward method)	Medium sand	Medium sand	Medium sand	Medium sand					

The mean sediment feature of each sampling parcel was obtained using the Folk and Ward method.

Mean Pielou evenness values reflected a good equitability of the benthic assemblages (J' mean = 0.8) but did not differ between treatments ($p > 0.05$; Table 2). The K -dominance curve associated to the control assemblage show a more even distribution of numbers of individuals among species than do the cultivated ones (Fig. 6).

The dendrogram of the hierarchical cluster analysis and the corresponding nMDS plot revealed two or four groups isolated at similarity levels of respectively 40% or 45% (Fig. 7). At a 40% similarity threshold, the non-impacted (Control) and the post-harvesting (D) treatments were separated from the pre-harvesting treatments (C and Cbis). At a 45% similarity level, all treatments differed significantly from each other (ANOSIM $p = 0.1\%$, global $R = 0.9$). ANOSIM pairwise comparisons showed that the four assemblages were sig-

nificantly different (ANOSIM $p = 2.9\%$, $0.719 < R < 0.979$, $\sqrt{\sqrt{\text{transformed-data}}}$).

The dominant species of the benthic assemblages were found in both Control and cultivated areas. The SIMPER analysis shows that the dissimilarities between these two treatments (average diss. $\geq 58.5\%$) were mainly attributed to three common species: *Euclymene oerstedii*, *Lucinoma borealis* and *Marphysa bellii* (total contribution in Control = 50.7%); and to differences in the occurrence of three other species: *Exogone gemmifera*, *Notomastus latericeus* and *Scoloplos armiger* (Table 4). Some deposit-feeding species like *Ampelisca brevicornis*, *Chaetozone setosa*, *Mediomastus fragilis*, *Phoronis* sp., *Polydora flava* and *Spiophanes bombyx* were restricted to the Control whereas one species, the necrophageous *Nassarius reticulatus*, was found exclusively in the shellfish concessions.

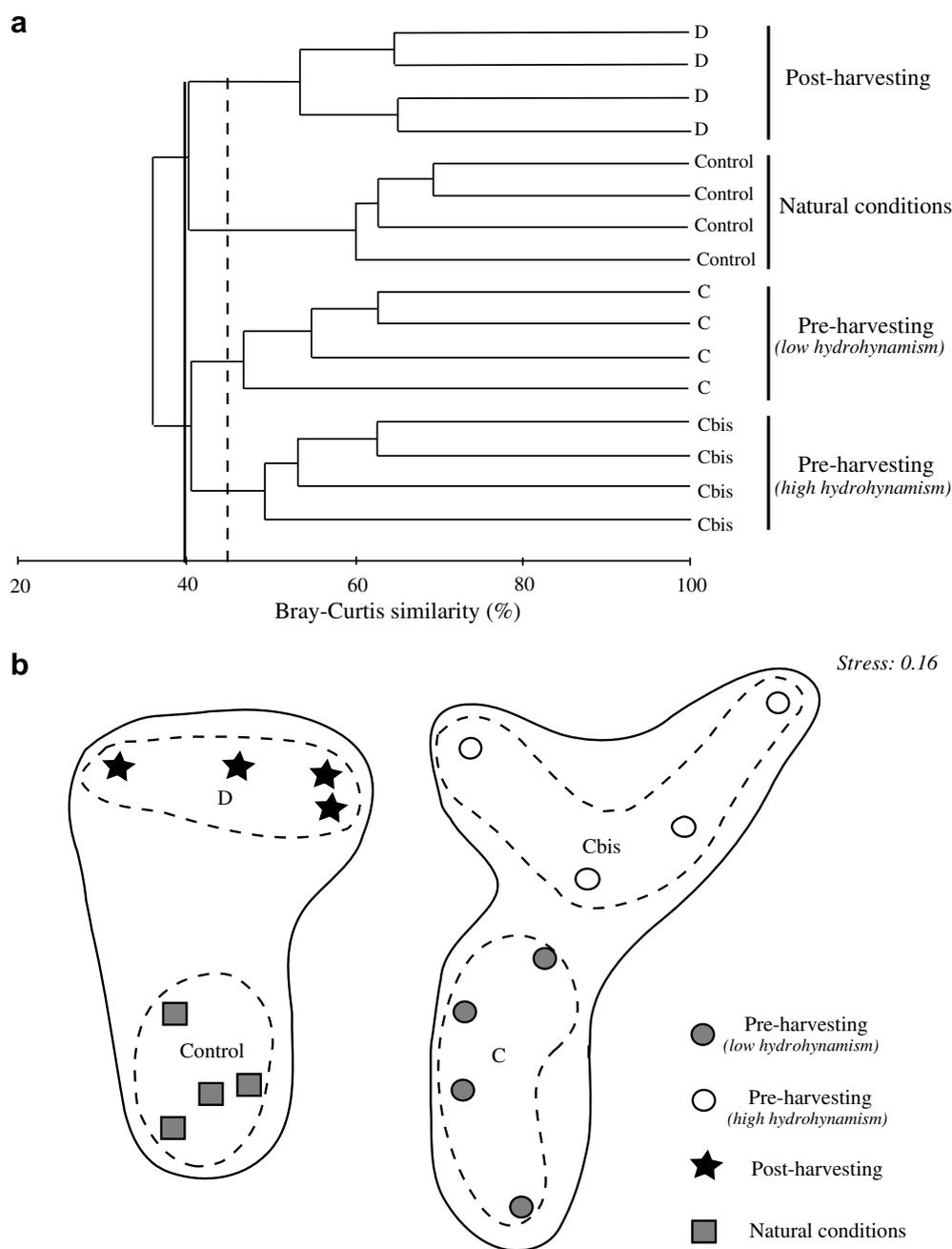


Fig. 7. Ordination plots of the macroinvertebrate abundance data (fourth root-transformed) obtained in 4 stations (C, Cbis, D and the control) in which 4 replicates have been sampled. (a) The dendrogram of the hierarchical cluster analysis and (b) the nMDS ordination plots are based on the Bray-Curtis similarity; 2 thresholds of similarity are presented: 40% (full line) and 45% (stippled line).

Table 4

Results of the SIMPER analysis: list of species contributed to a minimum of 80% of the intra-group similarity; mean abundances (ind. m⁻²) and relative contribution (%) of each species are detailed for each sampling parcel

Species	Control		C		Cbis		D	
	Mean abund.	Cont. %						
<i>M. bellii</i>	302.5	27.2	15.0	–	52.5	22.3	10.0	–
<i>E. oerstedii</i>	287.5	28.0	0.0	–	2.5	–	67.5	31.5
<i>N. latericeus</i>	160.0	11.2	125.0	24.3	10.0	–	25.0	8.4
<i>S. armiger</i>	105.0	8.6	220.0	46.4	127.5	59.6	42.5	13.2
<i>Syllidae sp.1</i>	62.5	4.6	32.5	–	7.5	–	7.5	–
<i>L. borealis</i>	50.0	4.1	10.0	–	5.0	–	20.0	8.6
<i>L. lucinalis</i>	7.5	–	15.0	–	2.5	–	87.5	31.7
<i>S. martinensis</i>	7.5	–	30.0	6.5	0.0	–	0.0	–
<i>P. elegans</i>	2.5	–	75.0	7.9	2.5	–	0.0	–
		83.7		87.9		81.9		93.4

4. Discussion

4.1. Shellfish farming impacts

As described by Crawford (2003a, 2004), traditional environmental impacts associated to the shellfish farming are mostly linked to three causes: (i) organic enrichment of the sediment, (ii) negative interactions with natural species and (iii) alteration of the habitat. Of course, the probabilities and the degree of detrimental environmental impact roughly depend on the cultivation location and practices. For example, Crawford (2003a,b) has rated the risks of the Pacific oyster farming as low to moderate and strictly localized to the inside of the cultivated site.

4.2. Organic enrichment of the sediment

In bivalve farms, the reared species produce relatively large volumes of faeces and pseudofaeces which could cover the substratum and subsequently alter the macroinvertebrate assemblage composition (Hartstein and Rowden, 2004; Stenton-Dozey et al., 1999). Moreover, anti-predator nets covering the sea-bottom are known to increase the organic contents of the sediment (Bendell-Young, 2006; Spencer, 1996; Spencer et al., 1996, 1997). But the organic enrichment of the sediment surface decreases in relatively high energy sites (De Grave et al., 1998; Hartstein and Rowden, 2004).

Our sedimentary results reveal an increase of fine particles only in parcels just harvested. The relatively small increase of organic contents in the whole site may be due to (i) high local tidal currents in Manila clam concessions and/or (ii) the short period of the net-covering on the substratum (1/6 of the total production cycle duration). Nevertheless, this organic supply could benefit individuals of the filter-/deposit-feeder *L. conchilega*, which were bigger in the concessions than in natural conditions. This mean individual mass increase may also result from the global decrease of the *Lanice* density, reducing conspecific competition for food and space and stimulating deposit-feeding (Buhr and Winter, 1976).

4.3. Interactions with natural species

The stocking of high densities of bivalves generally negatively impacts infauna (Beadman et al., 2004). Shellfish farmers should carefully consider sustainable densities of cultivated bivalves (Bartoli et al., 2001) which are generally considered as “sinks” of oxygen and particulate organic matter (Nizzoli et al., 2005; Richard et al., 2007a,b). The introduction of large stocks of *R. philippinarum* could alter the trophic network through filter-feeding competition for primary production and could lead to a food shortage for the other macrozoobenthic species. Ropert and Gouletquer (2000)

suggested that the cultivated oyster *C. gigas* and *L. conchilega* could be competitors, but Dubois et al. (2007) have demonstrated that these co-occurring suspension-feeding species had a different diet. Moreover, bivalve populations may control the densities and size of future benthic generations (Lindgarth et al., 2002).

In our study, the significant increase of the mean individual biomass of *Lanice* with the clam production cycle supports the hypothesis of non-competitor species. But, the switch from benthic assemblages dominated by tube-dwellers to assemblages dominated by bivalves could induce a change of the biogeochemical fluxes at the water-sediment interface. It would reduce the efficiency of ‘piston-pumping’ and thus decrease the quantity of O₂ (Forster and Graf, 1995) and the recycled nutrients in the adjacent sediment along its tube (Bendell-Young, 2006). In addition, the filtering activity of *R. philippinarum* could inhibit the recruitment of other species population by ingesting pelagic larvae (André and Rosenberg 1991; Davenport et al., 2000; Lehane and Davenport, 2002).

Farmers have introduced *R. philippinarum* for cultivation because its growth rate was better than the endemic European clam *Ruditapes decussatus* (Spencer et al., 1991). Following a 6-years trial of Manila clam rearing in the Arcachon Basin, a ‘neo-natural’ population has colonized the site and supplanted the European clam (Auby, 1993). Ten years later, it represented 98% of the total abundances of the benthic macrofauna (Caill-Milly et al., 2003). In Chausey, through ‘natural’ reproduction or bedload transport, small populations of the non-native species Manila clam have colonized the whole archipelago. We can therefore wonder about the durability and on the future proliferation of ‘pseudo-natural’ populations in the site.

4.4. Disturbance and alteration of the habitat

Spencer (1996), Spencer et al. (1996, 1997), Gouletquer et al. (1998) have shown an increase of the sedimentation rate under the nets compared to a previous unaltered situation, with or without modifications of the associated infaunal community. Bendell-Young (2006) has still demonstrated a simplification of the intertidal benthic community within netted parcels after 3 years. In the present study, the sediment stability was increased under the nets and the induced relief (bump/furrow) persisted along the production cycle only in relatively low energy concessions (pers. obs.). Bumps provide more beneficial conditions than furrows for the installation of *L. conchilega* but not for the associated benthic macrofauna (unpublished data). However, within netted parcels, which have sustained different practices using tractor-towed machine (harvesting, seeding and net brushing), the abundances of *L. conchilega* are still reduced than in natural clusters. Its more homogeneous spatial distribution confirms the aggregative nature of the *L. conchilega* at high densities (Nicolaidou, 2003).

Among the few studies dealing with the impacts of the Manila clam cultivation, Spencer (1996) synthesized the results of small-scale field trials monitored to study the ecological change at each stage of the production process. During the first 2 years of production, authors concluded there were major changes of community structure but underlined that the effects were similar in other marine culture practices (Spencer et al., 1996, 1997). The effect of the harvesting phase was assessed to be the most important for benthic communities but to cause large short-term changes to the intertidal habitat (Kaiser et al., 1996). In our study, the populations of the engineer species are negatively impacted and can not recover because of the short duration of the production cycle. The associated benthic macrofauna is also altered along the whole production cycle and the scraping of the superficial sediment is the most negative practice. The presence of the necrophagous *Nassarius reticulatus*, restricted to recently harvested parcels, could reveal deleterious effects on the infauna.

The harvesting phase may be equivalent to dredging in subtidal areas. For example, the towed bottom-fishing gear negatively affects the benthic communities (Collie et al., 2000) and such practices alter the seabed structure and thus involve deep changes in the community structure (Blyth et al., 2004; Dolmer et al., 2001). Even hand-raking harvesting of bivalves damages non-target species (Kaiser et al., 2001; Spencer, 1996) and one suction-dredging event could have a significant negative impact on the subsequent settlement of the main bivalve species. The tractor-dredging method is known to induce high levels of mortality on non-target benthic fauna (Hall and Harding, 1997) and the structurally complex (like habitats of *L. conchilega*) and relatively stable habitats are more adversely affected by fishing than those on unconsolidated sediment (Ferns et al., 2000; Kaiser et al., 2002). In a long-term study, Piersma et al. (2001) showed that the recovery of initial conditions has appeared only 8 years after the harvesting process. Nevertheless, the recolonization rate varies according to local hydrodynamics, exposure to natural physical disturbance and sediment stability (Spencer et al., 1998). A modification of the benthic macrofauna could also be linked to physical disturbance by heavy vehicle traffic (De Grave et al., 1998), but within Chausey concessions tractors roll only nine times per 3 years.

4.5. Vulnerability of an engineer species

Manila clam cultivation has important impact on the *L. conchilega* populations and decreases their positive effects on the associated benthic macrofauna, which are proportional to the local densities of burrow-tubes (Callaway, 2006). Nevertheless, populations of this engineer species still persist since the start of this culture in the archipelago in 1989. Farmers have assumed that the presence of this species was an indicator of stable substrate, more appropriate for the mechanized practices. In our study, a rapid recolonization of *L. conchilega* is observed during each step of the Manila clam production cycle and it takes place preferentially in the periphery of the impacted areas.

On the one hand, the persistence of *L. conchilega* populations under anthropogenic pressure might be explained by their resistance to physical constraints and to a high recolonization ability. Strasser and Pieloth (2001) have noted a full recovery of a previously altered population 3 years after its destruction. *L. conchilega* individuals can be dislodged and transported intact to a different area (Ropert and Dauvin, 2000) where they can re-establish when washed out from the sediment, building a new tube within 48 h (Nicolaidou, 2003). They may resist increases of sedimentation rates under nets by elongating their tubes to protrude from the sediment surface. The population of *L. conchilega* surrounding Manila clam concessions could also constitute a natural reserve for the renewal of the impacted populations. The presence of adult

tubes facilitates the settlement of recruits (Callaway, 2003a; Günther, 1999) and the population renewal can occur through transfer of adults from the offshore towards the coast (Ropert and Dauvin, 2000).

On the other hand, the populations of *L. conchilega* are known to be very dynamic at a short temporal scale following a seasonal cycle (Bartholoma, 2006; Carey, 1987; Zühlke, 2001) but also at a longer scale, according to a pluri-annual cycle (Dauvin, 2000). Extreme conditions such as sediment discharge (Witt et al., 2004), winter storms and low temperatures (Beukema et al., 1993; Ropert and Dauvin, 2000; Strasser and Pieloth, 2001) could reduce *Lanice* densities and could conduct to its extinction. When *L. conchilega* populations reach low densities, sediment is destabilized (Eckman et al., 1981; Friedrichs et al., 2000; Luckenbach, 1986), mounds rapidly disappear (Carey, 1987) and there is no resilience of the positive effect on benthic macrofauna (Zühlke, 2001). Thrush et al. (1996) have assessed that the removal of organisms which played a role in stabilizing the sediment increased the susceptibility of the habitat for further disturbance. Moreover, the decline of high densities clusters may have strong consequences on secondary consumers. This species is recognized to be a preferred prey for birds in the Wadden Sea (Beukema et al., 1993). The food supply on *L. conchilega* dominated flats is also favourable for birds, especially shorebirds and gulls (Petersen and Exo, 1999). Ferns et al. (2000) have demonstrated that bird feeding activity increased and subsequently declined in cockle tractor-towed harvested parcels when compared to unaltered control areas. In Chausey farming, birds have been demonstrated to significantly select *L. conchilega* clusters over other available habitats for feeding (Godet et al., in press). Moreover, clusters of *L. conchilega* constitute a large feeding area for 0-group flatfishes like plaices or soles (Amara et al., 2001).

We present a synthesis of anthropogenic and environmental factors affecting the *Lanice* populations through a simple conceptual scheme including their consequences on the ecosystem functioning (Fig. 8). We underline the probable negative impact of shellfish farming on secondary consumer species which are often integrated in conservative plans. In fact, the most relevant European Commission Directives includes the management of the environmental impacts of marine aquaculture. Among these, the Species and Habitats Directive (92/43/EEC), the Wild Birds Directive (79/409/EEC) and the Water Framework Directive (2000/60/EC) aim to protect natural biodiversity (Read and Fernandes, 2003). A single management scheme may be necessary for each site and the relevant authority has to ensure that habitat integrity and favourable conservation status of species and habitat are not compromised.

4.6. Management proposals

The negative effects of Manila clam cultivation described in this study have been assessed for a three year cycle of production in an energetic hydrodynamic environment on intertidal *L. conchilega* habitats. A variation in only one of the features of the shellfish activity (related to structures or practices) or different environmental conditions (low hydrodynamic regime, other benthic habitats) could lead to different damage. The areas regularly cultivated likely have to be maintained in a permanently altered state (Collie et al., 2000) and farm managers are usually advised to select the cultivation site carefully and to create fallow areas (through rotational practices). But inappropriate use of fallow areas may transfer farming activities into previously non-impacted habitats, which could be more vulnerable to disturbance than those currently cultivated by farmer.

L. conchilega seems to recolonize altered areas from the periphery of the concessions; this may be explained by both concepts of

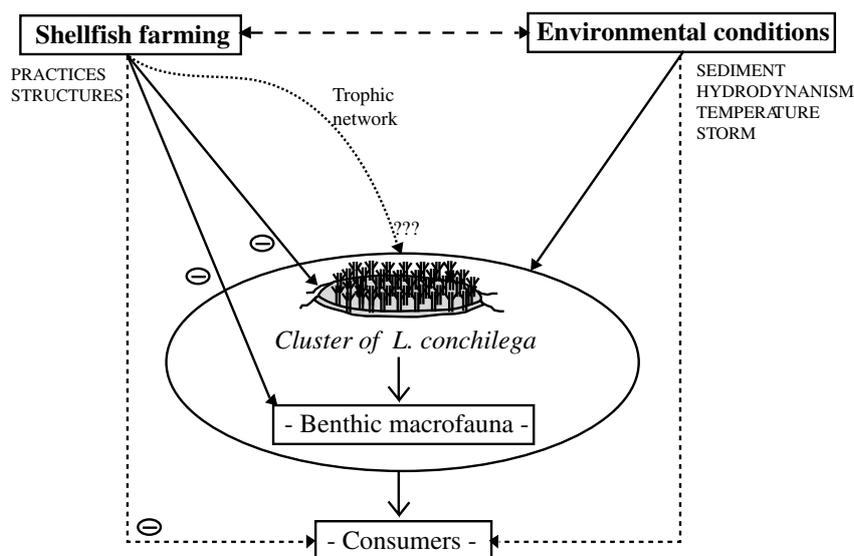


Fig. 8. Synthetic conceptual scheme: the clusters of *Lanice conchilega* have a positive effect on the associated benthic macrofauna and this assemblage promotes the presence of secondary consumers like birds and fishes. The environmental and anthropogenic factors affect directly (full line) the *Lanice* bioherm but also indirectly (stippled line) the secondary consumers population. In this study we demonstrated that, via its practices and its structures, the shellfish farming negatively impacts this ecosystem. Submitted to the environmental conditions, the farming could conversely modify this previous factor and thus have additional indirect effects on this ecosystem. Moreover, we wonder about the consequences of Manila clam cultivation on the *Lanice conchilega* bioherms by modifying the trophic network.

adults carriage, juvenile's attachment to adults and patch recolonization. The process of recolonization is related to the perimeter of the patch to be recolonized rather than the area available and to the presence of already established individuals at the border of the area (Alvarado et al., 2001; Littorin and Gilek, 1999). The recolonization in sandflat habitats is scale-dependent: the increase of the distance to the centre from the edges of the disturbed area led to reductions in the rate of colonization of common species (Thrush et al., 1996). In order to promote a bedload recolonization, fragmentation on the cultivated parcels has to be increased in a view to moderate the environmental impact of the Manila clam cultivation.

From a management perspective, the positive effect of this ecosystem engineer worm could make the *Lanice* habitat a particularly useful conservation target. Through managing high density clusters of this species, the entire community can be influenced. Actually, the durability of *Lanice* populations depends exclusively on the good will of the farmers. We therefore have to promote legal protection of dense *Lanice* beds which do not benefit from any legal protection status (Godet et al., in press).

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