Renewal and accumulation of a *Lanice conchilega* (Pallas) population in the baie des Veys, western Bay of Seine

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Abstract – Since the mid-1980s, an increase in abundance of the annelid polychaete *Lanice conchilega* (Pallas) (Annelida: Polychaeta, Terebellidae) has been observed in the Bay des Veys (western Bay of Seine). The first particularity of this population is that it is strictly limited to the eastern side of the bay, in an oyster aquaculture area. Its proliferation (over 7 000 ind.m^{-2}) has had a significant impact on the local aquaculture. Several studies have been carried out since 1993; monthly monitoring of population densities and size structure has demonstrated the lack of significant juvenile recruitment between 1993 and 1996. In terms of geographical occupation, maps of population spatial distributions were drawn in 1995 and 1998. They showed an increase in colonised surface of 18%, with a slight reduction of abundance. The consequence was a remarkable biomass stability which represented 3 500 tons of fresh weight excluding worm tubes (against 1 400 tons for the cultured oysters). A topographic survey was carried out in order to better understand the colonisation strategy developed by this population. A survey was also made in order to assess the extension of this species in the subtidal area. Overall, results suggest that population renewal can occur by transfer of benthic populations from offshore towards the coast, allowing the intertidal population to maintain high abundance levels in the absence of recruitment of juveniles. © 2000 Ifremer/CNRS/IRD/Éditions scientifiques et médicales Elsevier SAS

Polychaeta / *Lanice conchilega* / accumulation / renewal / adult transport

Résumé – Recrutement et prolifération de la population de *Lanice conchilega* (Pallas) en Baie-des-Veys, baie de Seine Occidentale. Depuis le milieu des années 1980, une population intertidale de *Lanice conchilega* (Pallas) (Annélide polychète térébellidé) se développe en baie des Veys (baie de Seine occidentale). La particularité majeure de cette population vient du fait qu'elle se limite strictement au flanc est de la baie sur un secteur conchylicole. Son caractère proliférant (densités pouvant dépasser 7 000 ind.m^{-2}) affecte l'aquaculture locale. Depuis 1994, différentes actions ont été menées. Un suivi mensuel des densités de population et de la structure en taille montre l'absence de recrutement significatif de juvéniles entre 1993 et 1996. En terme de colonisation, deux cartographies de répartition spatiale de la population, réalisées en 1995 et 1998, mettent en évidence une augmentation de la surface colonisée, de 18 % en trois ans, compensée par une légère diminution des densités. Il en résulte une remarquable stabilité des biomasses qui représentent 3 500 t de poids frais hors tube (contre 1 400 t pour les huîtres en élevage). Pour comprendre la stratégie de colonisation développée par cette population, une étude topographique a été effectuée. Des campagnes de prospection en mer au large de la baie ont été menées afin d'évaluer l'extension de l'espèce au niveau subtidal. Les résultats suggèrent que des

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phénomènes de transfert, du large vers la côte, permettent à la population intertidale de maintenir son abondance en l'absence de recutement de juvéniles.

Polychète / *Lanice conchilega* / prolifération / recrutement / transports adultes

1. INTRODUCTION

The terebellid polychaete *Lanice conchilega* (Pallas) represents the principal species of the genera *Lanice*. Marcano and Bhaud [28] suggest the existence of a second non-determined species: *Lanice sp.*, after observations of aulophora larval stages in the Bassin d'Arcachon; however differentiation has not been observed in the adult stages. This amphiboreal species [41] is present in a continuous distribution within the tropics. It has been observed on all the coasts of Europe, in the Pacific and in tropical waters, but is absent from arctic waters. The species colonises estuarine sediments until the mid-tide level. In the subtidal zone it is found in depths of up to 100 m. The population densities of *L. conchilega* can reach several thousand individuals per square metre [1] until 20 000 ind·m^{-2} just after a period of recruitment [8].

Since 1985, a population of *L. conchilega* has developed in the Baie des Veys (western part of the Bay of Seine) (*figure 1*) [39]. This intertidal population has

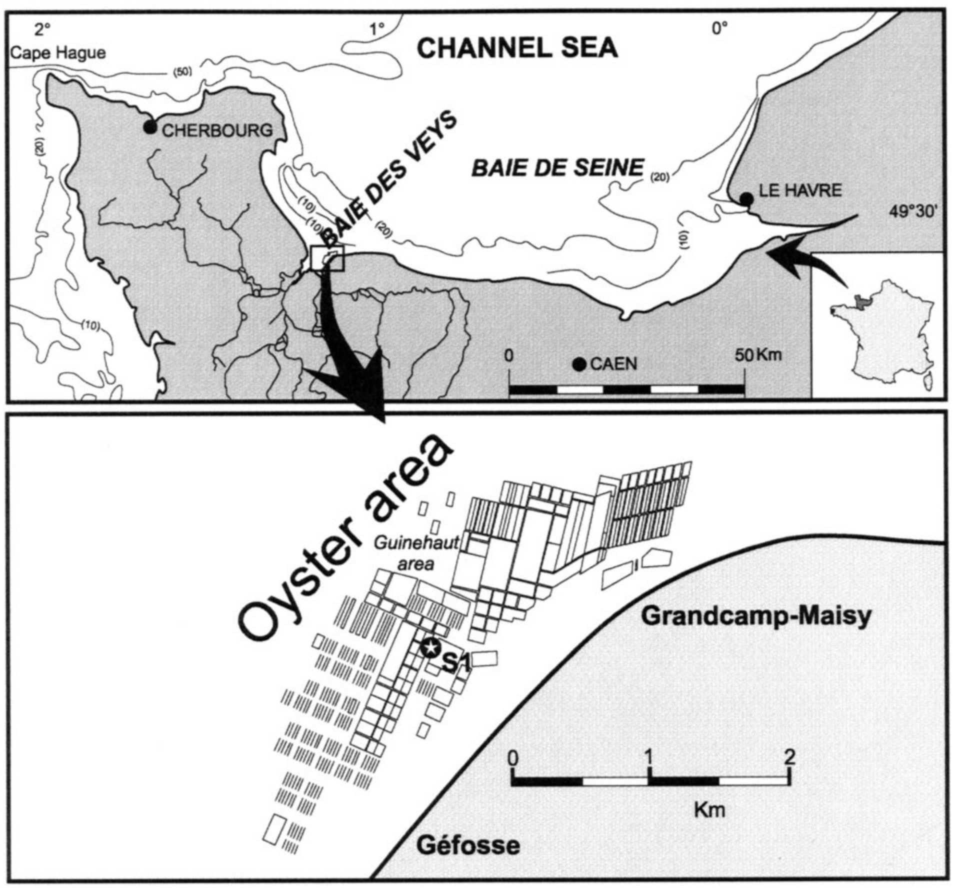

Figure 1. Location of the Baie des Veys in the Channel Sea (eastern part of Bay of Seine) and oyster culture area (S1: Position of survey population point).

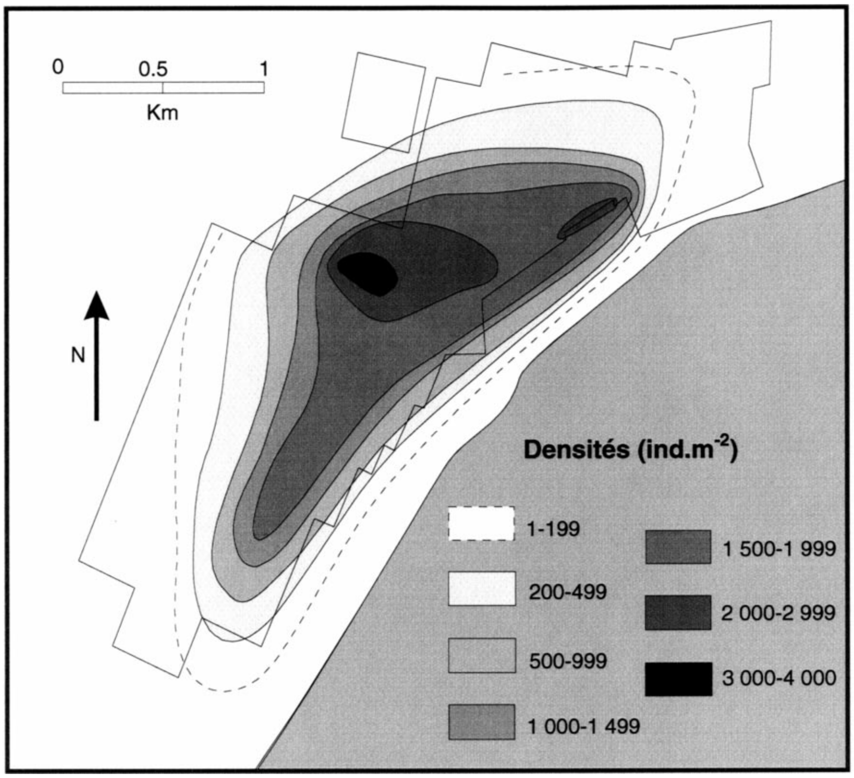

Figure 2. Spatial cartography of *Lanice conchilega* population on the oyster-beds areas in 1992 (adapted from [39]).

strict geographical limits to the eastern side of the bay on a zone characterized by oyster culture activity. For several years the abundances did not increase [24, 33, 39]. Recently the most densely colonised areas showed evidence of proliferation with abundances exceeding 7 000 ind·m^{-2}. Since the beginning of the 1980s the development of this population has been accompanied by major impacts at numerous levels (e.g. trapping of particles, acceleration of the siltation process, loosening of the substrate, trophic competition, difficulties in the exploitation of oyster culture) [33–35].

To identify the origin and reasons for the development of this *L. conchilega* population in the Baie des Veys, a research program has been developed since 1994: the temporal dynamics of this species are investigated by a monthly survey of the population to determine the periods of recruitment. In parallel, several maps of spatial distribution have been constructed and related to a topographic study of the area. Maps of the subtidal population at the opening of the Baie des Veys, made on two occasions in 1997, complete the information gathered on the intertidal area. The objectives of this work are i) to evaluate the spatio-temporal dynamics of this species at the local scale of the Baie des Veys; ii) to characterize the relationship between the population and its physical environment; iii) to formulate different hypotheses relative to the improved renewal strategy of this species with a strong colonisation capability.

2. MATERIALS AND METHODS

2.1. Population survey

The *Lanice* population survey site (S1) was located in the central part of the oyster culture park corresponding to the sector of appearance of this population in the 1980s (*figures 1, 2*). Situated outside all the oyster farming concessions, the sampling stations avoided direct disturbance linked to fisheries activities. Between June 1994 and March 1998 the surveys were carried out bi-monthly to monthly. Samples were taken with the aid of a TASM corer of 0.02 m^2 and 30 cm depth [39]. They were carefully sieved through a 1 mm mesh. However, the animal can retract into its tube and/or disappear rapidly into depths of more than 40 cm [14]. For this reason it was very difficult to sample *L. conchilega* correctly, and some tubes were not occupied by the animal. Contrary to the observations of Smith [37], no 'U-shaped' were found. Thus the estimation of densities was assessed by the number of sand tubes bearing fringed ends and/or which were fairly rigid in their first 15 cm [14]. The minimum number of samples necessary for a good estimation of abundance was evaluated by the method of Healy [21]:

$$t_h = \frac{m \times \sqrt{n}}{\sigma} \qquad (1)$$

where m represents the mean abundance of *L. conchilega* in the sample, n the number of replicates and σ is the standard deviation.

The test is valid at a given significance level by comparison with Students' 't' table, for n − 1 degrees of freedom. For the purpose of our survey two samples were recognised as systematically efficient for the estimation of the population abundance of *L. conchilega* at a significance level of 95 %. Nevertheless the sampling effort was extended to five replicates to have a greater number of individuals, necessary for the determination and analysis of the size structure of the population. Under these conditions the estimation of abundance was very highly significant ($P <$ 0.01 %).

2.2. Size structure

Buhr [7] and Féral [14] used the interior diameter of the *Lanice* tube as a parameter representative of the mass of the individual as a consequence of size. The diameter of the tube was measured by introducing a cone-shaped stainless steel gauge into the opening of the tube. The diameter of the instrument varied from 1.2 to 5.4 mm by steps of 0.2 mm. A preliminary study confirmed the relationship between the individual dry weight, assessed by freeze-drying (48 h) and the inner diameter of the sand tube. This relationship was of a log-linear shape and expressed as:

$$\mathrm{Log(D)} = 0.25\ \log(\mathrm{W}) + 0.025$$
$$(N = 102;\ r^2 = 0.93) \qquad (2)$$

where D is the inner diameter of the sand tube and W the dry tissue weight after freeze-drying for 48 h. This technique has the advantage of not altering organic material and so avoids in this way underestimation of dry tissue weight [17].

All the tubes sampled were subject to measurements of the diameter and were classified according to the progression of the scale of measurements. The smaller tubes were pooled in the class of less than 1.2 mm. The histograms of size class were subject to modal analysis with the help of the software NORMSEP [40] adapted by [19]. The normal components (mean, standard deviations) of frequency size distributions were identified for each campaign.

2.3. Cartography of spatial distribution

Changes in the spatial distribution of the intertidal *L. conchilega* were determined by two mapping approaches carried out in September 1995 and March 1998. A stratified sampling strategy of two factor [16], inspired by oyster farm evaluation techniques used by Ifremer [24] was selected. The zone was divided into three strata parallel to the coast, according to a high level/low level theoretical gradient. These three strata were themselves sub-divided according to a south west/northeast direction corresponding to the estuarine-marine gradient (*figure 3*). In situ observations two months prior to the survey allowed the further delimitation of these strata as a function of the relative homogeneity of abundances. In each of the sub-strata, two to twelve points were sampled randomly (respectively 135 stations in 1995 and 143 in 1998). The sampling effort was estimated as a function of local conditions (heterogeneity of abundances, presence of oyster-beds influencing the distribution).

At each station two samples were taken with the help of a TASM corer at depths of about 20 to 30 cm. A systematic counting of fringed ends present at the surface of the sample was made. When the number of fringed ends was less than 25 (500 ind·m^{-2}), the abundance of the population was evaluated by systematic counting on two quadrants of 1 m^2.

The interpolation technique used for cartography was based on the method of triangulation of Delaunay [25]. This precise interpolation method showed both the advantages of: i) being perfectly adapted to a grid of relatively regular sampling stations; and ii) allowing an accurate representation of marked clines in abundance that characterize the population. The results were plotted from digitised aerial photographs of the zone using the geodesic Lambert I system.

2.4. Topographic study

To complete the cartography of the population a topographic survey was carried out in September 1995. The topography of the oyster-bed area in Grandcamp-Maisy was made with the help of a Wild Ti1000 electro-optical theodolite. Ten stations distributed over the whole study area were used to establish a polygonal base. The survey was spread out according to a regular grid of 50 m interval, and the elevation was corrected with reference to an IGN (*Institut Géographique National*) reference milestone located near the oyster-beds. The 1 500 points of elevation allowed the development of an in situ numerical model, using SURFER software (covering more than 300 ha with a grid resolution of 20 m). The technique used was krigging, with a linear, no drift variogram model removing the 'nugget' effect [12].

2.5. Subtidal distribution

To estimate the extent of the population beyond the intertidal flat, a grid of 64 stations was set up in subtidal area of the Baie des Veys, covering an area of 80 km^2. Sampling stations were located along 13 northeast transects (1–13), implemented according to a regular grid of about 1 mile and at depths of 0–15 m. Three supplementary transects were added in the outer zone: 1) towards the east (E) along the east Calvados coast; 2) towards the northeast (N); 3)

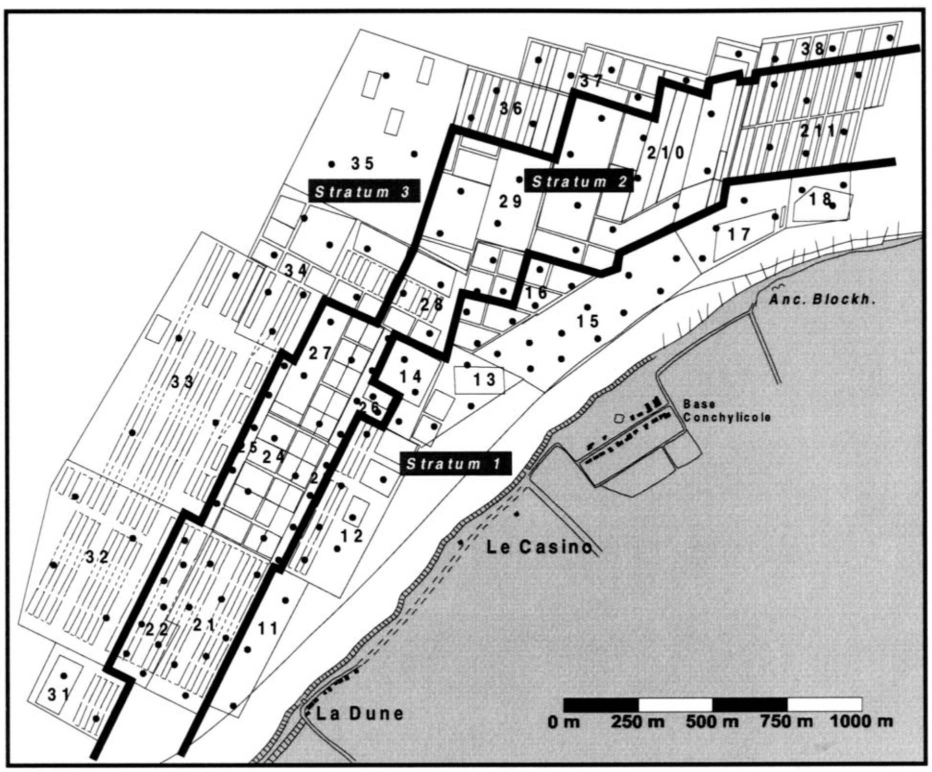

Figure 3. Stratified sampling strategy of two hierarchic factors for the *Lanice conchilega* spatial cartography in Baie des Veys. ("Stratum 1": number of stratum; "11": number of under-stratum; ●: sample point).

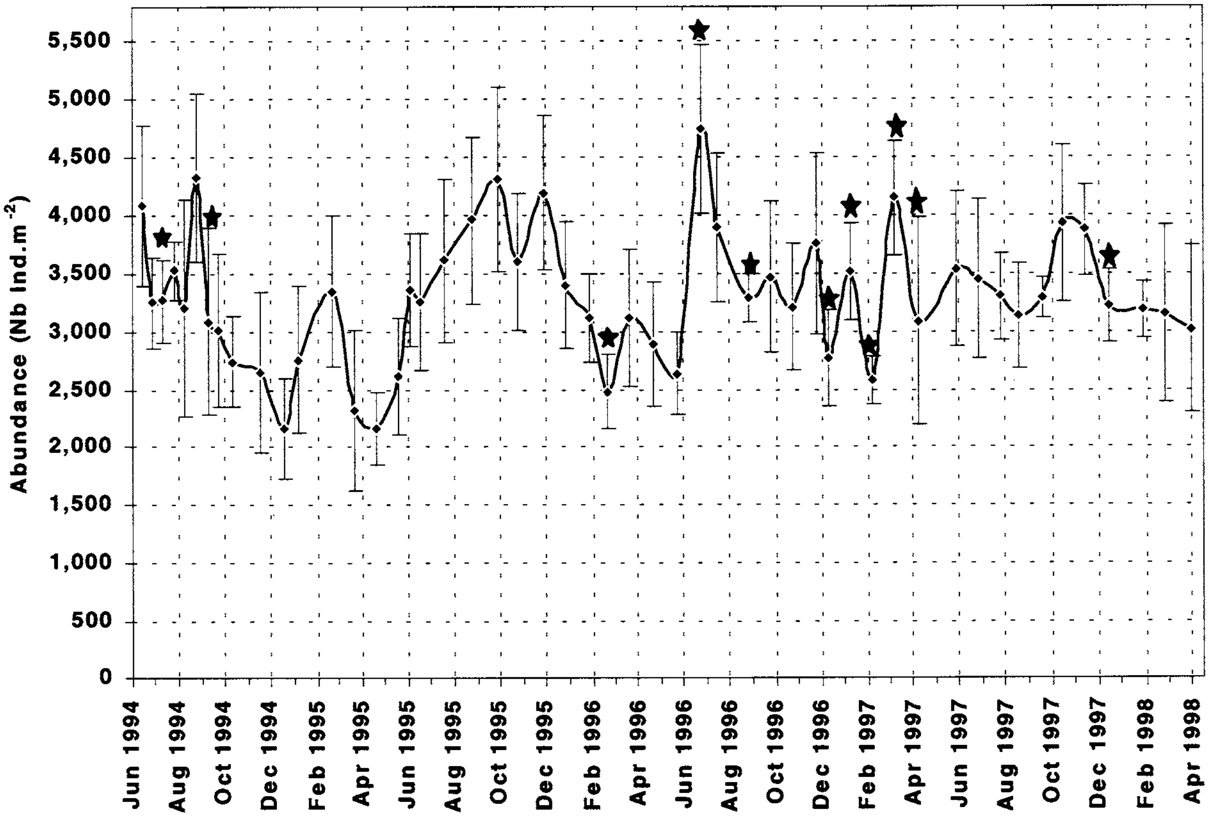

Figure 4. Change of *Lanice conchilega* abundance between June 1994 and March 1998 (mean ± standard deviation). ★: Abundance significantly different from the one preceding it [α = 0.05 threshold (test U-Mann-Whitney)].

towards the northwest (W) along the Cotentin east coast to St. Vaast-La-Hougue.

The campaigns were carried out in March and October 1997 (only 57 stations were sampled). Samples were collected using a Hamon grab of 0.25 m^{-2} surface area and 15 cm depth [13]. At each station two replicates were taken to analyse the benthic macrofauna. After sieving through a 2 mm mesh and preservation with buffered formalin solution (10%), macroinvertebrates were identified to the lowest practical taxonomic level, usually species. The depth of the sampling (10–20 cm), did not permit to collect all the live *L. conchilega* individuals, so the population abundance was estimated using the number of fringed tube ends counted. After the counts, maps were drawn using the SURFER software package.

3. RESULTS

3.1. Population Survey

The mean abundance at the S1 station fluctuated around 3 300 ind·m^{-2} (*figure 4*). The minimum abundance (2 100 ind·m^{-2}) was observed between December 1994 and April 1995. In June 1996, the abundance reached over 4 500 ind·m^{-2}. Nevertheless the population was permanent and showed a high level of abundance with multi-annual changes during the four years of surveying. During the first part of the survey (June 1994 to June 1996) the changes were progressive and the delay between increase and decrease of the population was several months. The mean abundance during this period was 3 240 ind·m^{-2} with a standard deviation of 663 ind·m^{-2}. Between the months of April and August 1995, the population doubled its abundance in four months. In the second part of the survey (July 1996–April 1998), densities varied around a mean of 3 373 ind·m^{-2}, with less variability (standard deviation of 391 ind·m^{-2}). Overall abundance changed rapidly from one month to the next with statistically significant differences between measurements (*figure 4*).

Together with these fluctuations during the four years of surveying, the population was also characterized by the absence of a well-marked seasonal cycle. The changes in abundance observed at the beginning of the survey with an autumnal decrease and a spring increase were not observed in the second part of the survey. On the contrary, during the winter of 1995/1996 the population maintained a high abundance (up to 4 000 ind·m^{-2}).

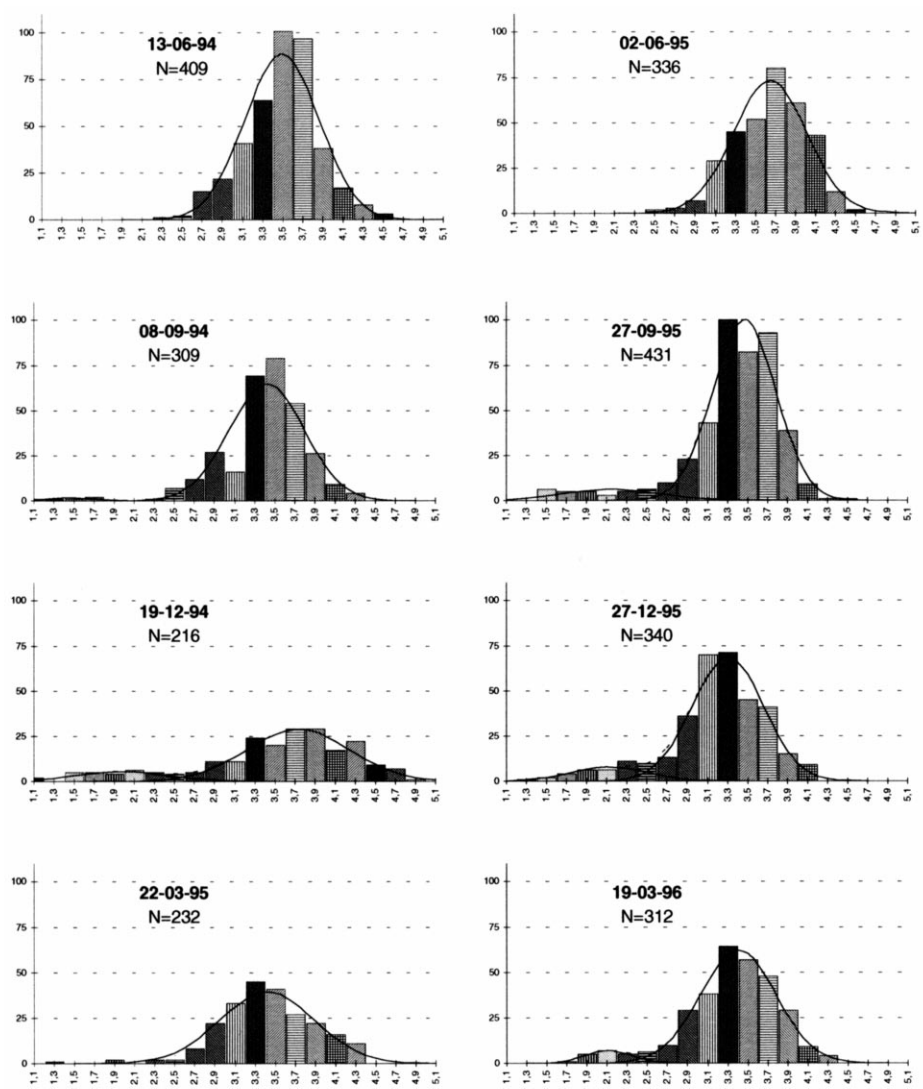

Figure 5. Quarterly size distribution change of *Lanice conchilega* population between June 1994 and March 1998 on point S1. The normal component associated was determined by NORMSEP software. [Y axis: number of individuals by 0.1 m^2; X axis: Tube diameter (mm)].

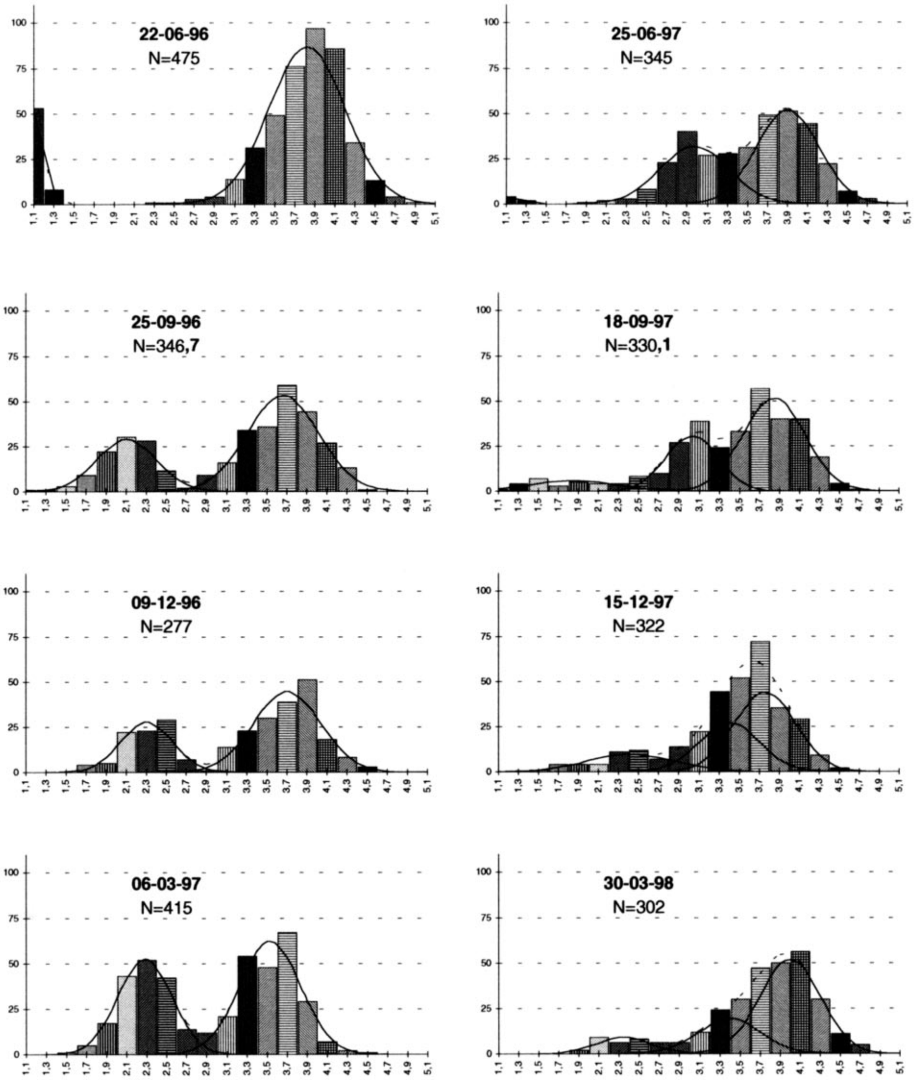

Figure 5. (*Continued*)

3.2. Size structure of the population

The temporal change of the demographic structure of the *Lanice conchilega* population showed two main characteristics (*figure 5*).

1) During the two first years of the survey, the population was constituted mainly of adults with sizes between 3.3 and 4.2 mm. No meaningful recruitment of juveniles was observed. The numbers of individuals of a size less than 2 mm (less than eight percent of the population) did not allow the identification of a new cohort.

2) In June 1996 recruitment started which accounted some months later for about 40% of the population. This 1996 cohort remained clearly identified until September 1997 (15 months). In June 1997 new juveniles were observed but their numbers never reached beyond 10 % of the population.

3.3. Cartography

The first cartography of the spatial distribution of the *L. conchilega* population was achieved in March

1992, on the eastern side of the bay [39] (*figure 2*). This work constituted the only initial reference to the state of the colonisation. The population was limited to mean densities of 1 500 ind·m^{-2}. A single small zone, in the centre of the oyster beds, showed high abundance with a maximum over 3 000 ind·m^{-2}.

3.3.1. 1995

With reference to 1992 (*figure 2*), the zone characterized by a high abundance (exceeding 3 000 ind·m^{-2}) extended to the whole area (*figure 2, 6A*). The maximum abundance observed in 1995 reached 7 748 ind·m^{-2}, as opposed to 4 000 ind·m^{-2} in 1992 [39].

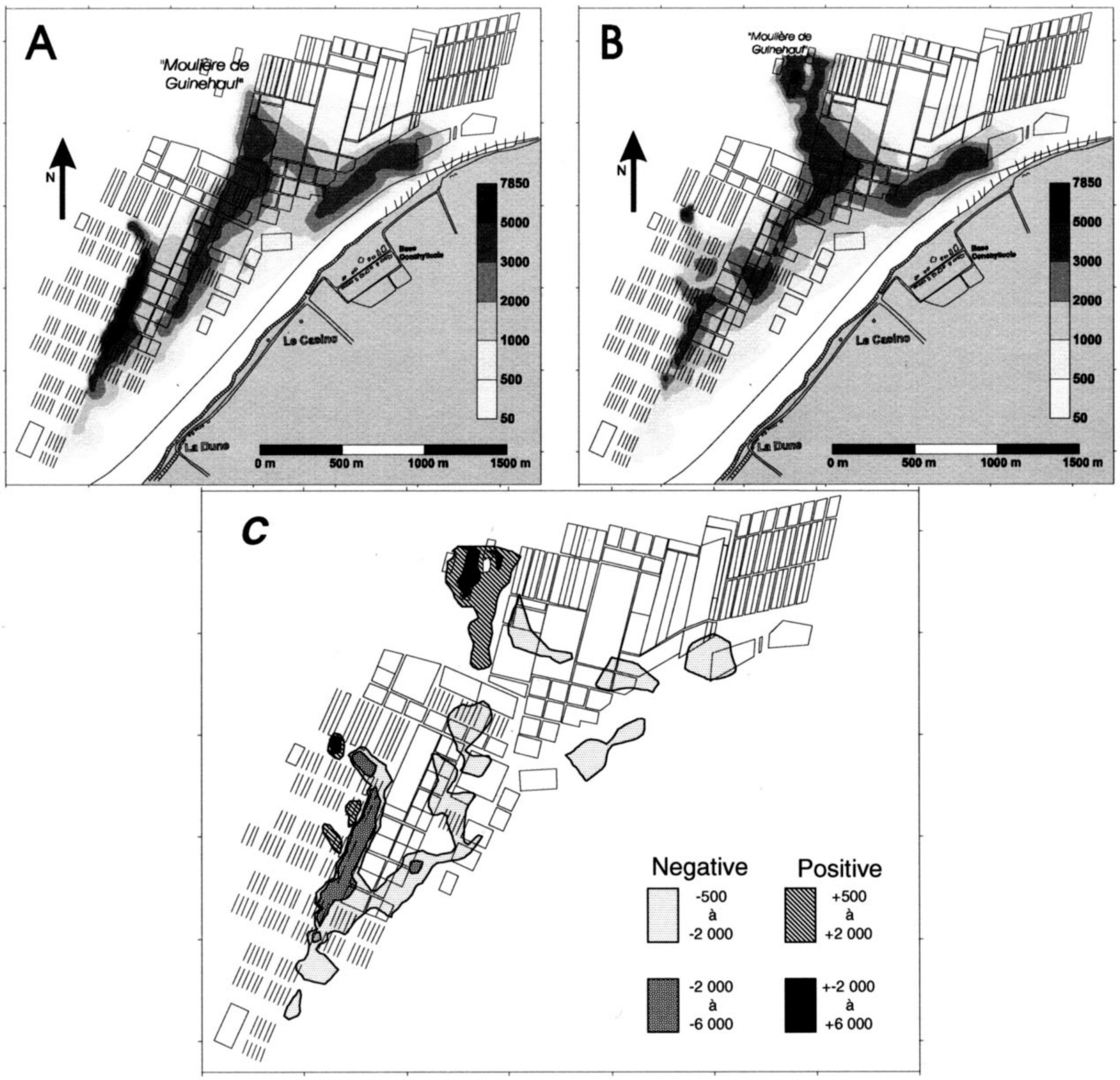

Figure 6. Spatial distribution of the *Lanice conchilega* population on the oyster-bed area in Baie des Veys. ("A": September 1995; "B": March 1998; "C": Differential balance sheet of loss and gain between September 1995 and March 1998. (Abundances: Number individuals by meter square).

Table I. Colonised surfaces distribution by abundance groups in September 1995 and March 1998, and differential balance sheet of the colonised surface.

	1995			1998			
Abundance group	Surface (ha)	% of all surface		Surface (ha)	% of all surface		Differential balance sheet
50–100	**11.26**	5.61 %	47.24 ha	**25.48**	10.77 %	72.87 ha	**+54.25 %**
100–250	**14.85**	7.40 %	(23.55 %)	**24.14**	10.20 %	(30.80 %)	
250–500	**21.14**	10.54 %		**23.25**	9.83 %		
500–1,000	**29.00**	14.46 %	29.00 ha	**33.35**	14.09 %	33.35 ha	**+14.99** %
1,000–1,500	**28.77**	14.35 %	51.43 ha	**27.65**	11.69 %	54.53 ha	**+6.02** %
1,500–2,000	**22.66**	11.30 %	(25.64 %)	**26.88**	11.36 %	(23.05 %)	
2,000–2,500	**20.26**	10.10 %	37.06 ha	**23.72**	10.03 %	43.86 ha	**+18.35** %
2,500–3,000	**16.80**	8.37 %	(18.48 %)	**20.14**	8.51 %	(18.54 %)	
3,000–3,500	**18.92**	9.43 %		**17.18**	7.26 %		
3,500–4,000	**7.70**	3.84 %	31.80 ha	**9.91**	4.19 %	31.64 ha	**−0.50** %
4,000–4,500	**3.75**	1.87 %	(15.85 %)	**4.03**	1.70 %	(13.37 %)	
4,500–5,000	**1.43**	0.71 %		**0.52**	0.22 %		
5,000–5,500	**1.11**	0.55 %		**0.24**	0.10 %		
5,500–6,000	**1.08**	0.54 %	4.03 ha	**0.13**	0.05 %	0.37 ha	**−90.86** %
6,000–6,500	**0.86**	0.43 %	(2.01 %)	**0.00**	0.00 %	(0.16 %)	
6,500–7,000	**0.48**	0.24 %		**0.00**	0.00 %		
7,000–7,500	**0.50**	0.25 %		**0.00**	0.00 %		
Total	**200.57**	100.00 %		**236.61**	100.00 %		**+17.97** %

A total of 200 hectares were occupied by more than 50 ind·m^{-2} (*table I*), with a mean abundance of 1 727 ind·m^{-2}. More than 17 % of the area was colonised (35.8 ha) by abundances higher than 3 000 ind·m^{-2}. These high abundances were distributed in three patches between the eastern border of the concessions, the central zone, and the south (*figure 6A*). An extrapolation from observed abundance of the colonised area allowed the estimation of the total biomass for the whole population to about 3 450 tonnes of fresh weight excluding the sand tube (702 tonnes in dry weight).

3.3.2. 1998

In 1998 the main characteristic of the population distribution was the persistence of the three patches observed in 1995 (*figure 6B*). On the border of the area the first patch showed no remarkable change. The central patch extended considerably to the north, the sector of the "Moulière de Guinehaut", which showed no colonisation by *L. conchilega* in 1995. On the contrary the third patch (southwest) was reduced, as much in surface area as in abundance. In a general manner, the surface colonised by more than 50 ind·m^{-2} reached 236 hectares in 1998, with a mean abundance of 1 489 ind·m^{-2} (*table I*). Abundances higher than 3 000 ind·m^{-2} occupied an area of nearly 32 ha (13 % of the total colonised surface). In biomass, the population of *L. conchilega* represented 3 500 tonnes fresh weight (714 tonnes dry weight) in 1998.

Between 1995 and 1998, the *L. conchilega* population evolved following two trends: the first was that the total biomass of the population remained steady, with only an increase of 1.8 % observed between 1998 and 1995. The second trend showed that the colonised surfaces were extended by 18 % (36 ha). The extension of the colonisation was balanced by a reduction in the total abundance, in particular on the third patch of proliferation (southwest). The main population extension occurred in the recently colonised area of the "Moulière de Guinehaut" in the north of the oyster beds. This area was not colonised in 1995, and displayed high densities (7 100 ind·m^{-2}) three years later in 1998.

The most important differences observed between 1995 and 1998 concerned the areas of extreme high and low abundances (*figure 6C*). The surface occupied by 50 to 500 ind·m^{-2} extended enormously (by 54 %). By contrast the area colonised by more than 5 000 ind·m^{-2} was reduced by 90 % despite the important colonisation of the ''Moulière de Guinehaut'' (to the north of the main population). For the intermediate classes of abundance a slight extension of the area was observed (lower than 10 %).

3.4. Topographic study

The topography of the oyster beds of the Baie des Veys was characterized by a pronounced difference in relief between the northeastern and the southwestern areas. The lowest northeastern part of the area lay on a horizontal rocky flat. These outcrops, oriented north–south, progressively receded due to an increase in sedimentary cover on the high shore.

The south-western area showed more complex features and a marked relief (*figure 7*). Two perfectly isolated channels characterized this sector. To the west an important hydraulic dune isolated the oyster beds from the Isigny channel. This accumulation of

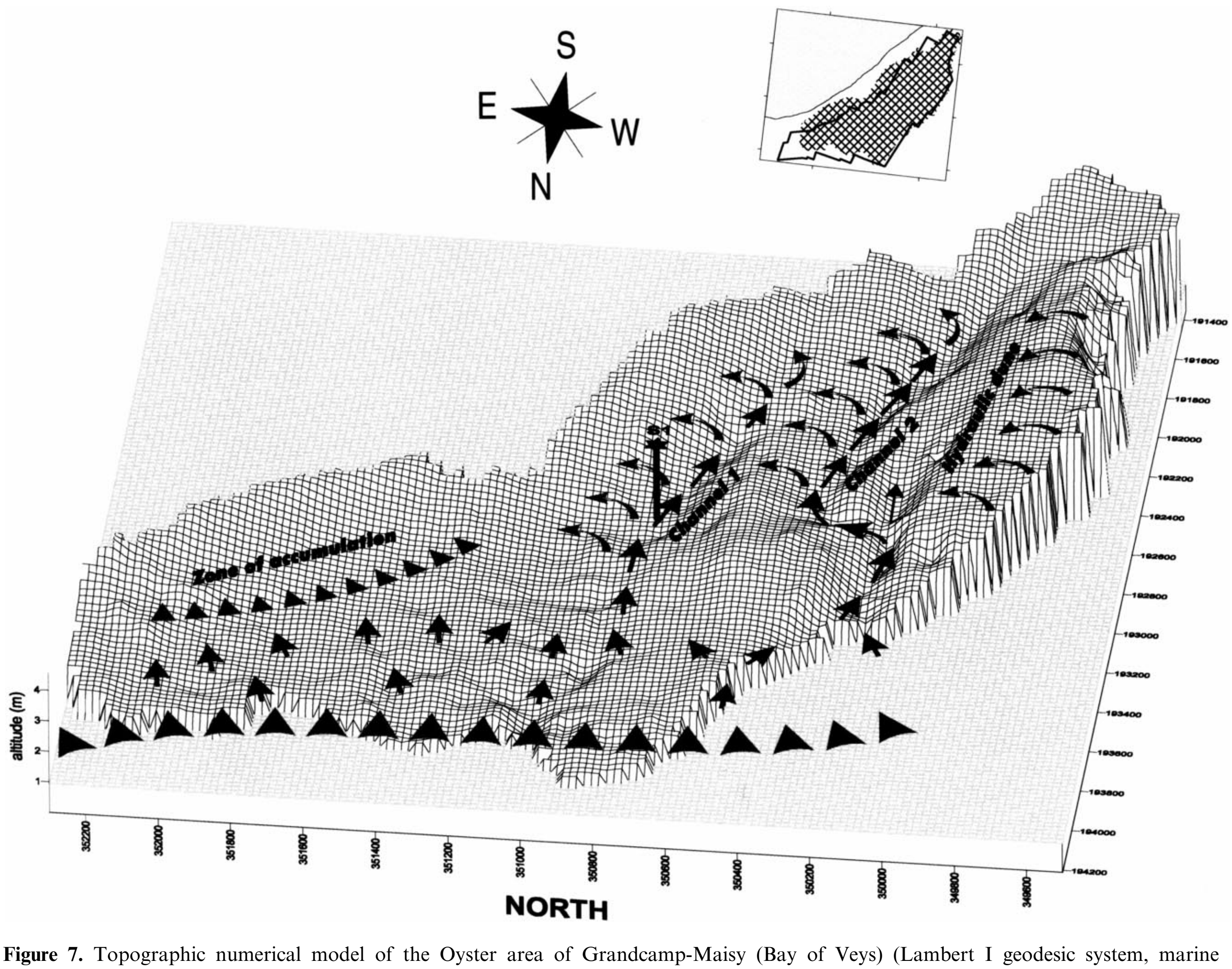

Figure 7. Topographic numerical model of the Oyster area of Grandcamp-Maisy (Bay of Veys) (Lambert I geodesic system, marine elevation, grey arrows represent flood tide progress). To facilitate the visualisation of 3D surface the area has sudden a 170° rotation.

Table II. *Lanice conchilega* total abundances obtained during each campaign of March and October 1997, off Baie des Veys ("-": no sample).

	March 1997		October 1997			
Radiales	Nb stations	Total effective	Nb stations	Total abundance	Adult abundance	Juvenile abundance
Rad. 01	2	**1**	2	**15**	4	11
Rad. 02	2	**0**	2	**27**	13	14
Rad. 03	3	**0**	3	**40**	17	23
Rad. 04	3	**0**	3	**106**	60	46
Rad. 05	4	**2**	3	**241**	139	102
Rad. 06	4	**0**	3	**146**	73	73
Rad. 07	5	**1**	4	**494**	250	244
Rad. 08	4	**1**	4	**261**	152	109
Rad. 09	5	**3**	5	**376**	202	174
Rad. 010	4	**0**	4	**280**	192	88
Rad. 011	5	**4**	5	**506**	289	217
Rad. 012	4	**1**	4	**48**	27	21
Rad. 013	3	**0**	3	**20**	4	16
Rad. N	4	**0**	0	**–**	–	–
Rad. W	3	**0**	10	**345**	120	225
Rad. E	0	–	0	**–**	–	–

sediments was explained by a difference in height of 3.62 m between the two extreme altitudes of the zone (with a relative slope of 0.13 %). During flood tide, a large amount of water is canalised by the two channels to the south, and converges towards a "zone of accumulation" (*figure 7*) to the north. At the beginning of the flood tide, the water brutally engulfs the channels at speeds reaching 3 $m \cdot s^{-1}$ [39]. When the channels are completely full, the remaining area is gradually immersed by slow overflows from the two channels. During ebb tide, the inverse process occurs. The particles brought by the flood are then exported gradually during the ebb tide when the oyster beds are drained. Over a tidal cycle, the two channels are immersed for a continuous period of eight hours on spring tide, and up to twelve hours on neap tide.

3.5. Undertidal distribution

The March cruise was characterized by a very low abundance of *L. conchilega* over the whole area (*table II*). Only 13 individuals were found during this cruise. The results found during the autumnal cruise (October) were very different. In fact, *L. conchilega* was present over the entire zone, and abundance was multiplied by a factor of 300 at some stations when compared to the in March cruise. This progression indicated a real colonisation of the subtidal area situated off the Baie des Veys during the summer of 1997. The most meaningful growth was observed between the transects 3 and 11, situated at the mouth of the bay (*figure 8*), as well as on the western transect along the coast of the Cotentin.

Half the individuals of these populations (48.6 %) can be classified as juveniles (of a size smaller than 2 mm), which originate from the recruitment of the summer of 1997 while the other half (51.4 %) are of a size that corresponds to them being more than a year old (> 2 mm and up to 5.3 mm). These two fractions of the population are not distributed in an even manner: juveniles are distributed in a relatively homogeneous way over the whole of the study area (*figure 8B*), with more than 40 % of stations showing abundances of more than 50 juveniles$\cdot m^{-2}$. Adults appear to be more geographically restricted to the mouth of the bay, with less than 35 % of stations having adult densities of more than 50 ind$\cdot m^{-2}$ (*figure 8A*).

4. DISCUSSION

Buhr and Winter [8] reported mean densities of around 5 200 ind$\cdot m^{-2}$ for a subtidal population of

L. conchilega on the Weser estuary (West Germany). During the recruitment period, abundances could reach 20 000 ind·m^{-2}. Even if this species is widespread, such levels of intertidal colonisation have never to our knowledge been described for northeastern Atlantic waters.

However, since 1994 monthly surveys of the intertidal population of the Baie des Veys have established the presence of very high abundance levels (average 3 300 ind·m^{-2}) in that area. But it is also characterized by pluriannual changes of abundances, with annual means between 2 100 and 4 750 ind·m^{-2}. From the 1994 and 1996 results, these changes, like those observed during the winter of 1994–1995 (*figure 4*), could not be due to juvenile recruitment. Indeed the population was mainly constituted of adults (size > 2 mm), and juveniles (size < to 2 mm) were present to a much lesser extent and in a discontinuous manner. Juveniles constitute, on average, less than 8 % of the total population during the two first years of the survey. However their almost permanent presence during the course of the monitoring shows a very steady reproductive ability over the course of the year [27]. It was during June 1996 that the appearance of a new cohort in the population indicated the success of a significant juvenile recruitment in the survey station. (*figure 5*). This new cohort remained perfectly identified for more than 15 months after its appearance (until September 1997). The unimodal character of the population at the beginning of the study (June 1994) reflected therefore an absence of juvenile recruitment during the previous year (in 1993). This intertidal population had therefore maintained high abundance levels during at least three years in the absence of significant recruitment of juveniles, even though Féral [14] and Buhr [7] indicate that the maximum life span for this species could not exceed three years. How, under these conditions, did the population of the Bay of the Veys maintain such levels of densities between 1993 and 1996?

As the population is not maintained by regular juvenile recruitment, it must be maintained by other means. The observed changes in abundance (*figure 4*) and in population size structure (*figure 5*), such as

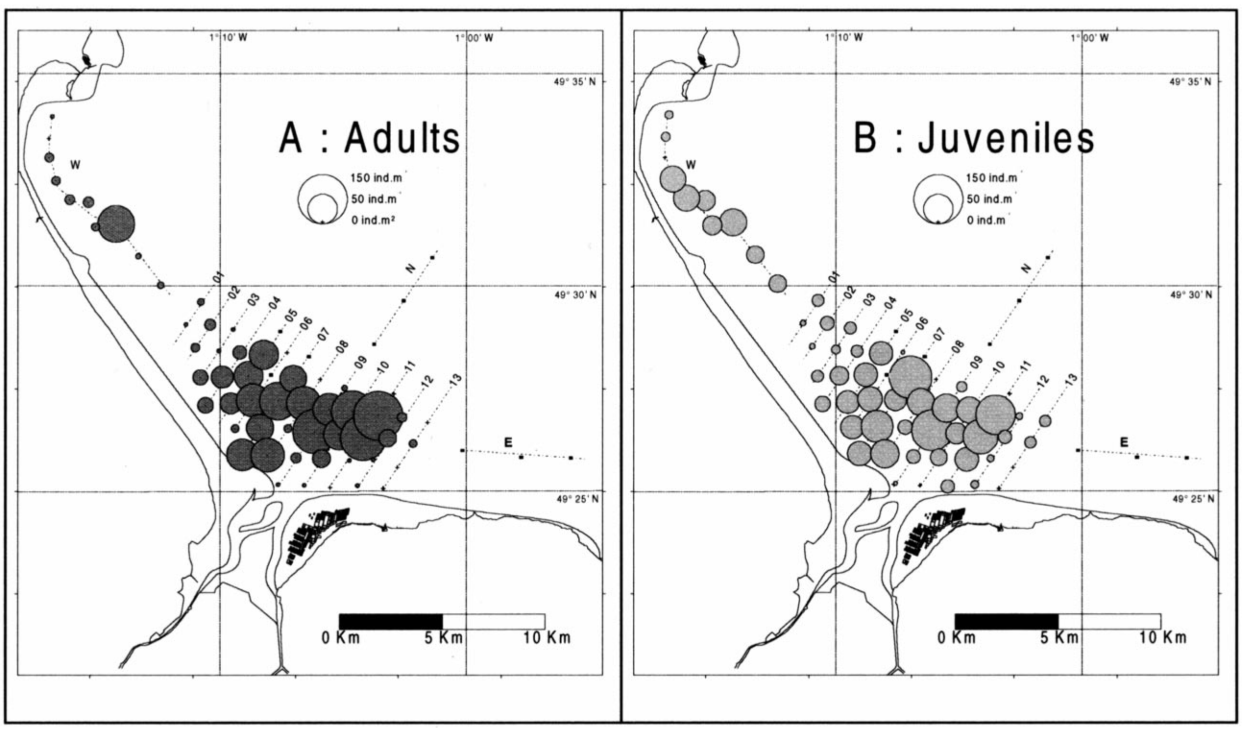

Figure 8. Abundance of *Lanice conchilega* population in October 1997, off Baie des Veys. [**A**]: Adults (size > 2 mm); [**B**]: juveniles (size < 2 mm). "01 to 13". Transect number (between 49° 24' N and 49° 30' N lat. and 1° 01' W and 1° 11' W long.); "W, N, E"; supplementary transects west, north, east.

were seen during successive winters between 1994 and 1996, showed that the increase in abundance was associated by an enrichment of the population by adult individuals.

In February 1995, during the course of a violent northeasterly storm, the observations of an important quantity of wreckage accumulated on the high shore was made. It was constituted mainly by *L. conchilega* tubes, which could reach several tens of centimeters in length. Numerous tubes were occupied by living animals, which did not show any morphological deterioration. This observation suggests that under particular hydrodynamic conditions, it is possible for *L. conchilega* individuals to be dislodged and transported intact to a different area.

The results of the population survey (maintenance of abundance), change of size structure (absence of juveniles), associated with field observations, suggests the existence of an external process allowing the input of adult individuals, therefore maintaining a high level of abundance in this intertidal population, despite a lack of regular juvenile recruitment.

The undertidal campaigns beyond the Baie des Veys have demonstrated the existence of open sea populations. Around 70 % of the 80 km^2 explored showed abundances greater than 50 $ind \cdot m^{-2}$. More than half of this population was constituted by adult individuals, with similar sizes to those observed in intertidal areas. This part of the population could potentially constitute an important reservoir for the maintenance of the *L. conchilega* stock of the eastern side of the Baie des Veys.

Since 1992, the intertidal population of the Baie des Veys had increased considerably. However in the course of the last three years, it seems to have reached an equilibrium level. Our cartography in 1998 showed an increase of 18 % of the colonised area, compensated by a reduction in abundance. This last point could however have a seasonal origin: in 1995 the cartography was established at the end of summer (September), whereas the one of 1998 occurred at the end of winter (March). However, the population was characterized by a remarkable stability more in terms of biomass than spatial distribution. Between 1995 and 1998, the increase in total biomass was lower than 2 %. At present the intertidal *Lanice conchilega* population has a biomass of about 3 500 tons (fresh tissue weight). For comparison, the total biomass of reared oysters has never reached more than 1 400 tons (fresh tissue weight) [23], i.e. a 2.5 times difference in biomass in favour of *Lanice*.

Between 1995 and 1998, from a spatial point of view, the population extended itself towards the north, within a similar pattern in both cartographies. The areas of proliferation (abundance over 3 000 $ind \cdot m^{-2}$) were always located in three isolated patches, each covering a few hectares. This particularity reflected the stable and persistent character of the intertidal *L. conchilega* population in the Baie des Veys. The evidence that the colonisation was progressing towards the north (Guinehaut area), gained in 1998, demonstrated again that this species is able to rapidly colonise its surrounding area [6, 42].

This population seems to extend over the whole of the oyster beds, however its spatial distribution does not present a homogeneous distribution at intermediate scales (100 to 1 000 m). Because of the sedentary nature of this species, this heterogeneity could be induced at the time of settlement of individuals in the sediment by concentration and accumulation during the colonisation period. Therefore, at local and medium scales (hundreds of metres) there are processes operating which influence this heterogeneity of colonisation. It is known that hydrodynamics constitute the fundamental control parameter of the colonisation processes by spatial structuring and homogenisation of the larval distributions [9]. But in the absence of juveniles, the heterogeneity observed in the population once more raises questions about the displacement of adult individuals.

This hypothesis was supported by the relationship between the spatial distribution of the intertidal population and the topography (*figure 9*). The colonisation strategy developed by *L. conchilega* in the Baie des Veys, seemed to reflect some environmental constraints directly associated with the field relief. The first two areas of proliferation, in the interior of the parks (densities over 3 000 $ind \cdot m^{-2}$), were located in the two channel areas supported by the field numeric model (*figure 7*). The third patch, on the border of the parks, was located at the point of convergence of the water masses during flood tide. These three sectors had in common comparable hydrodynamic characteristics. They were characterized importantly by

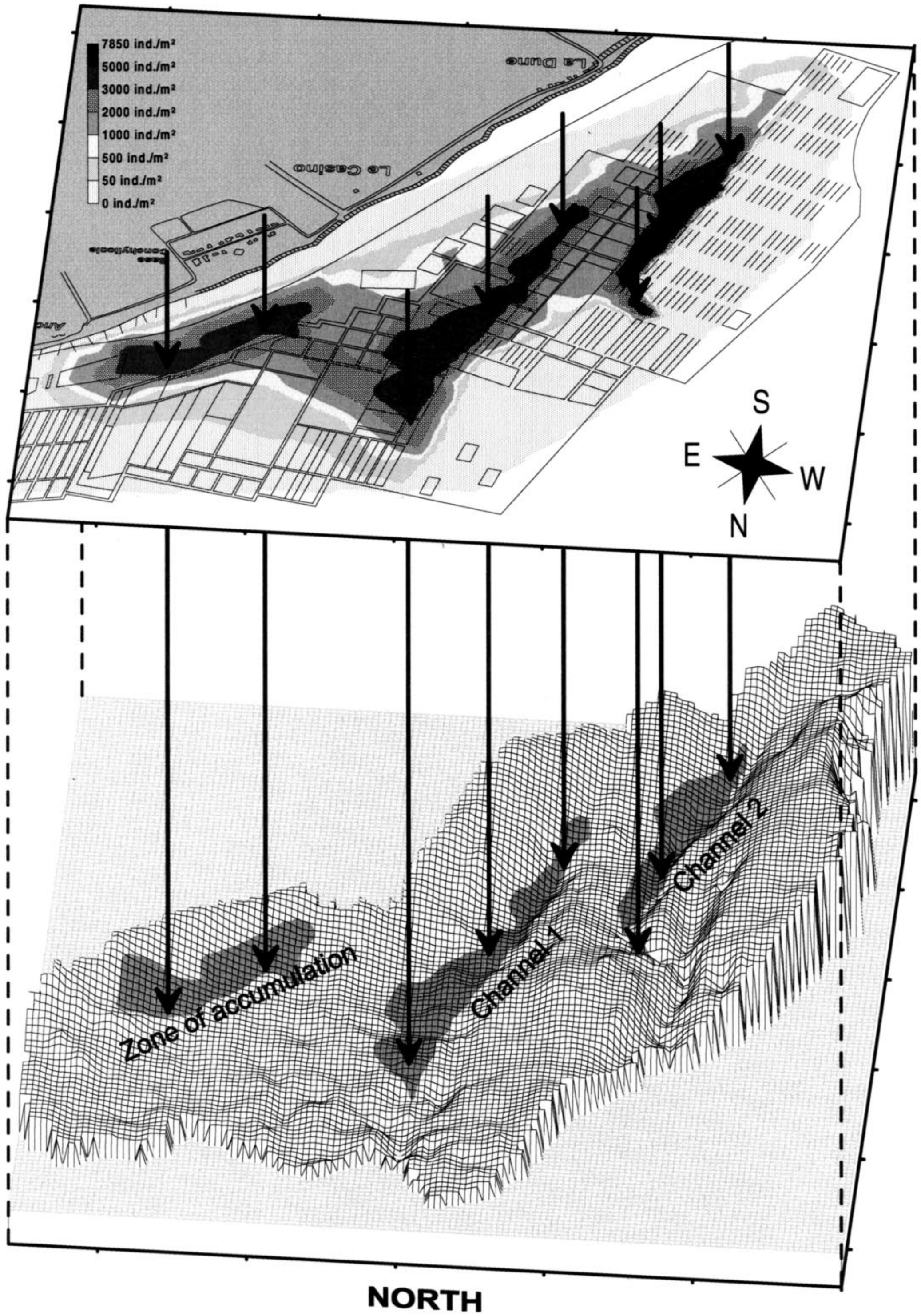

Figure 9. Correlation between topography and population cartography in 1995. Densities greater than 3 000 ind·m^{-2} are coloured grey in the topography.

flow rate, which can reach 3 $m \cdot s^{-1}$ [39] at the beginning of the flood tide. In a second period, after replenishment of the channels, current speed was considerably reduced, causing the sedimentation of suspended particles. This phenomenon allows an explanation for the population aggregation processes in the channels. When hydrodynamically violent conditions occur (spring tide, north east storms, swell…), some tubes, resulting from dislodgement of the *L. conchilega* population, can be transported by bottom currents. The combined presence of the channel, canalising the progression of the water masses, and of oyster tabular structures then create a hydrodynamic brake [38], allowing the tubes to accumulate in these deposition areas. After several hours it was possible for *L. conchilega* to re-colonise the substratum, as was observed in aquarium studies [14].

This hypothesis of adult dislodgement with subsequent transport into the intertidal and settlement influenced by hydrodynamics/topography, is reinforced by the temporal changes of the population in 1998 (*figure 6*). Indeed, two sectors presented a positive balance. On the western side, on the border of the parks, a patch of proliferation appeared at the entrance of channel no 2. It continued towards the south in an intact perimeter in 1995. This new colonisation was in fact associated to a drift of the channel of about 200 m towards westward, during the last three years. On the other side, the "Moulière of Guinehaut" (north) corresponds with the entrance channel no 1. This sector, also intact in 1995, was the centre of a colonisation progression associated with the channel. In the third proliferation area (accumulation area), the absence of morphosedimentary change allowed the population to maintain itself at a level equivalent to what it was in 1995.

Numerous studies have revealed the influence of physical processes (wind, tide), on the benthic population regulation by larval distribution control ([9] for a consequent bibliography). But rarer have been those dealing with the transfer of populations after settlement [20]. Armonies [2, 3] and Heiber [22], provided evidence for the secondary recruitment of polychaetes after a first benthic phase. Beukema and De Vlas [5] and Armonies and Hellwig-Armonies [4] showed important dispersion of post-larvae *Macoma balthica* by re-suspension. Meixner [29] observed similar patterns for *Cerastoderma edule* during violent storms. Some experimental studies demonstrated also the role of juvenile and/or of adult transport in the recolonisation process [10, 11, 15, 18, 32, 36]. For a defaunated site characterized by an elevated flow speed (between 10 and 20 $cm \cdot s^{-1}$), Levin and Dibacco [26] found evidence of a recolonisation by both juvenile and adult endofauna. The importance of the hydrodynamic factors, and in particular of swell, in re-suspending benthic organisms was confirmed by Olivier et al. [31] for some bivalves (*Abra alba*, *Mysella bidentata*, *Tellina fabula*) gastropods (*Nassarius reticulatus*, *Natica alderi*) and polychaetes (*Owenia fusiformis*, *Pectinaria koreni*) in the eastern part of the Bay of Seine. For *L. conchilega* hydrodynamic conditions may be particularly important to facilitate the dislodgement of both tube and animal. Thereafter, the cylindrically-shaped tube certainly may facilitate the transport by tidal currents.

Günther [20] studied the relationship between the scale of the disturbance and the type of dispersal induced (larval, post-larval or adult). She concluded that the scale of disturbance is the main factor affecting the size of organism being dispersed and limiting the scale of dispersal. On a large scale (10^6 m^2), planktonic larvae were dispersed. On a meso-scale (10^3 m^2), post-larvae and the permanent meiofauna could be affected. Dispersion of adults would be conceivable mostly on a small scale (1 m^2). Our results showed that the Günther assumption should be revised. Indeed, larval dispersion processes controlled the *L. conchilega* population on a large-scale (western Bay of Seine). Subtidal recruitment observed off the bay reflected this process, but the transport of adults was not limited to small scales. On the contrary, the spatio-temporal change of the population and the appearance of adults in the subtidal population off the bay between the months of March and October 1997, suggests that this phenomenon emerges at a scale of several kilometres. These mechanisms are directly bound to hydrodynamic environmental conditions and are strictly independent of the natural seasonal reproduction cycle of the species. The development of such a colonisation "strategy" allows the intertidal population to escape the constraints of the classic annual larval recruitment process (failure of larval fixing, absence of metamorphosis, post-larvae mortalities). The colonisation of tidal flats is ensured by individuals which have passed the most crucial phases of their biological cycle. Imported individuals possess an acquired resistance, which may prompt a greater stability and persistence in the development of their subpopulation.

The life history of the intertidal *L. conchilega* subpopulation of the Baie des Veys suggests the hypothesis that the modification of sediment grain size in the oyster culture area was related to the accumulation of imported tubes [34]. The results allow the characterization of transport processes, but it is not possible to quantify the input of adults. Future studies could be considered in two ways: firstly, in situ measurements associated with flume studies [11, 30, 32] should be carried out in order to comprehend the necessary limited conditions that induce the dislodgment and/or transport of individuals. Secondly, a tidal flow survey, combined with trapping of particles [10] and drifting specimens [20] could allow the assessment and quantification of the magnitude of transport processes in the regulation of the population.

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