Université de Bretagne Occidentale

Institut Universitaire Européen de la Mer

Mémoire d'Habilitation à Diriger des Recherches

Spécialité Océanologie Biologique

Les communautés benthiques de substrats meubles de la Manche et de la baie sud de la mer du Nord : description, fonctionnement et état écologique

Présenté par

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Annexe :

Sélection de publications scientifiques

Sélection de publications scientifiques

(classées par ordre alphabétique chronologique, les contributions des étudiants apparaissent en bleu)

1. Desroy N. & Retière C., 2001. Long-term changes in muddy fine sand community of the Rance basin: role of recruitment. *Journal of the Marine Biological Association of the United Kingdom* 81: 553-564.

2. **Desroy N**., Warembourg C., Dewarumez J.M. & Dauvin J.C., 2003. Macrobenthic resources of the shallow soft-bottom sediments in the Eastern English Channel and Southern North Sea. *ICES Journal of Marine Science* 60: 120-131.

3. **Desroy N**. & Denis L., 2004. Influence of spring phytodetritus sedimentation on the spatio-temporal variability of intertidal macrozoobenthos in the Eastern English Channel. *Marine Ecology Progress Series* 270: 41-53.

4. Dauvin J.C., **Desroy N.**, Janson A.L., Vallet C. & Duhamel S., 2006. Recent changes in estuarine benthic and suprabenthic communities resulting from the development of harbour infrastructure. *Marine Pollution Bulletin* 53: 80-90.

5. Dauvin J.C., Ruellet T., **Desroy N.** & Janson A.L., 2007. The ecological quality status of the bay and the estuary of Seine: use of biotic indices. *Marine Pollution Bulletin* 55: 241-257.

6. **Desroy N.**, Janson A.L., Denis L., Charrier G., Lesourd S. & Dauvin J.C., 2007. The intra-annual variability of soft-bottom macrobenthos abundance patterns in the North Channel of the Seine estuary. *Hydrobiologia* 188: 173-188.

7. Arbach Leloup F., **Desroy N.**, Le Mao P., Pauly D. & Le Pape O., 2008. Interactions between a natural food web, shellfish farming and exotic species: the case of the Bay of Mont Saint Michel (France). *Estuarine, Coastal and Shelf Science* 76: 111-120.

8. Blanchet H., Lavesque N., Ruellet T., Dauvin J.C., Sauriau P.G., **Desroy N.**, Desclaux C., Leconte M., Bachelet G., Janson A.L., Bessineton C., Duhamel S., Jourde J., Mayot S., Simon S., De Montaudouin X., 2008. Use of Biotic Indices in semi-enclosed coastal ecosystems and transitional waters habitats - Implications for the implementation of the European Water Framework Directive. *Ecological indicators* 8: 360-372.

9. **Desroy N.**, Dubois S.F., Fournier J., Ricquiers L., Le Mao P., Gerla D., Rougerie M. & Legendre A., 2011. The conservation status of *Sabellaria alveolata* (L.) (Polychaeta : Sabellaridae) reefs in the Bay of Mont-Saint-Michel. *Aquatic conservation: Marine and freshwater ecosystems* 21: 462-471.

10. Godet L., Fournier J., Jaffré M. & **Desroy N.**, 2011. Influence of spatio-temporal dynamic and fragmentation of worm-reefs on benthic macrofauna. *Estuarine, Coastal and Shelf Science* 92(3): 472-479.

11. Kostecki C., Rochette S., Girardin R., Blanchard M., **Desroy N**. & Le Pape O., 2011. Reduction of flatfish habitats as the consequence of the proliferation of an invasive mollusc. *Estuarine, Coastal and Shelf Science* 92: 154-160.

12. Kröncke I., Reiss H, Eggleton J.D., Aldridge J., Bergman M.J.N., Cochrane S., Craeymeersch J.A., Degraer S., **Desroy N.**, Dewarumez J.M., Duineveld G.C.A., Essink K., Hillewaert H., Lavaleye M.S.S., Moll A., Nehring S., Newell R., Oug E., Pohlmann T., Rachor E., Robertson M., Rumohr H., Schratzberger M., Smith R., Vanden Berghe E., van Dalfsen J., van Hoey G., Vincx M., Willems W. & Rees H.L., 2011. Changes in North Sea macrofauna communities and species distribution between 1986 and 2000. *Estuarine, Coastal and Shelf Science* 94: 1-15.

13. Kostecki C., Roussel J.M., **Desroy N.**, Roussel G., Lanshere J., Le Bris H., Le Pape O., 2012. Trophic ecology of juvenile flatfish in a coastal nursery ground: disentangling the influence of primary production and freshwater organic matter subsidies. *Marine Ecology Progress Series* 449: 221-232.

14. Foveau A., **Desroy N.**, Dauvin J.C. & Dewarumez J.M., 2013. Distribution pattern of benthic diversity in the eastern English Channel. *Marine Ecology Progress Series* 479: 115-126.

15. Rabaut M., Audfroid Calderon M., Van de Moortel J., van Dalfsen J., Vincx M., Degraer, S. & **Desroy N.**, *sous presse*. The role of structuring benthos for juvenile flatfish. *Journal of Sea Research*.

J. Mar. Biol. Ass. U.K. (2001), **81**, 3772/1–12
Printed in the United Kingdom

Long-term changes in muddy fine sand community of the Rance basin: role of recruitment

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Dynamics of the *Abra alba* muddy fine sand community of the Rance basin (western English Channel), initially sampled in one station by Retière at the beginning of the 1970s after the tidal power station built at the mouth of the estuary went into service, was reassessed from 1995 to 1997. Results showed a more 'mature' community in 1995–1997 with an increase in the number of species. After a short period, in spring 1995, during which the structure of the community was comparable to those described in 1972–1973, the assemblage was characterized by a great inter-annual structural stability. Densities of dominant species seem to fluctuate around a mean value comparable to the carrying capacity of the biota for these species. The recruitment of the dominant species with a long life span appears low compared to the densities of adults but seems sufficient to assure the replacement of individuals. Our results suggest that the pattern of massive recruitment followed by high mortality rates could not be the general rule and that a pattern of moderate recruitment followed by low post-settlement mortality of recruits should be more frequent.

INTRODUCTION

The Rance basin, on the northern coast of Brittany, is the only site where a full-scale evaluation of the ecological impact of a tidal power station, after 30 y of operation, has been conducted (Desroy, 1998). The damming of the estuary, during a 3-y construction phase was particularly disruptive to the environment (Retière, 1989, 1994). The estuary was effectively isolated from the open sea for three years between 1963 and 1966, with the exception of small amplitude discharges (1 m) at 2-w intervals, for flushing purposes (Rouvillois, 1967). During this period, the conversion from an estuary with a large tidal range into a constant-level basin virtually eradicated the marine fauna and flora; only several species of highly euryoecius invertebrates and fish species flourished (Retière, 1989, 1994). After the tidal power station was put into service in 1966, an increasingly diverse fauna became gradually established as determined from sampling of soft-bottom communities in 1971 (Retière, 1989), 1976 and 1995 (Desroy, 1998). Among the four major subtidal benthic communities described in 1971 (Retière, 1989), a facies within the *Abra alba–Corbula gibba* muddy fine sediment community, the *Melinna palmata* facies, was already dominant. To better understand the functioning of this assemblage, Retière (1979) carried out a quantitative study in 1972–1973 of the dynamics of the community at one station. This series was continued from 1974 to 1982 by Clavier et al. (1983) for the four dominant species. The monitoring of these principal infaunal components of the *M. palmata* facies indicated that despite a rapid stabilization of physical conditions once the power station went into operation in 1966, it took ten years to establish a stable community (Clavier et al., 1983).

As underlined by Dauvin (1993), such perturbations to natural communities represent an opportunity for observing the dynamics of a system. The present article aims to compare the recent dynamics of this system with that described between 1972 and 1973 and attempts to determine how this system functions in response to a physical regime largely controlled by humans. The approach consists of the long-term comparison of data sets, and can be regarded as intermediary to the two methods currently used to measure temporal changes in macrobenthic communities (Gremare, 1998): (i) long-term series data, which assess the temporal changes in macrofaunal composition based on regular sampling; and (ii) the long-term comparison of punctual data which compares the composition of macrobenthos at selected sites after a long interval. Although this approach allows a quick identification of faunal changes, it provides little information on the dynamics of change or on the underlying causes (Pearson et al., 1985; Reise & Schubert, 1987). Given that temporal scales of variability of benthic communities range from weeks to years, different sampling strategies were used. From monthly sampling of macrozoobenthos from 1995 to 1997, two comparisons were made: (i) inter-annual variations of the specific richness, abundance, diversity/regularity indices and structure of the community were compared to data acquired in 1972–1973; and (ii) changes in abundances of the four dominant species were compared to data collected between 1972 and 1982. Conjointly, the recruitment of dominant species was examined in 1996 from spring until autumn in 1996 to assess how short-term variability in these processes influences inter-annual variability/stability of population and community dynamics.

Table 1. *Main characteristics of macrobenthic and meiobenthic sampling techniques.*

	Macrobenthic survey				Meiobenthic survey
	1972–1973	1974–1982		1995–1997	1996
Sampling gear	1/13 m^2 orange-peel grab	1/13 m^2 orange-peel grab (until 1977)	1/55 m^2 hand corer (scuba diving) from 1977	1/10 m^2 Smith-McIntyre grab	1/470 m^2 hand corer (scuba diving)
N of replicate per series	3	3	12	2	Determined by an a posteriori test (5–9)
Sieve mesh-size	1 mm, square mesh	1 mm, square mesh	1 mm, square mesh	1 mm, square mesh	300 μm, square mesh
Sampling frequency	~2 months	~2–3 months	~2–3 months	monthly	10 d
Total N of series	8	12	12	25	16
Fauna sorted	Total macrofauna	four top rank species	four top rank species	Total macrofauna	300 μm < Meiofauna < 1 mm

MATERIALS AND METHODS

Reference site

The station (48°56′N 02°00′W) is located in the Rance Basin (northern Brittany), an estuary where the operating constraints of the installation impose highly specific 'tidal' conditions on the waters. Tidal range varies between 4.0 and 7.0 m instead of 8.0–13.5 m in the open sea. Mean water level is raised by approximately 2.5 m and there is a particularly long high water stand. Except for a relative instability period following the starting up of the station (1967–1975), fluctuations of low, intermediate and high tide mean levels are regular (Desroy, 1998). Their fall of 1.0 to 1.5 m since 1994 is linked to a protective initiative of banks and habitations (Electricité de France (EDF), personal communication). The violent sluice and turbine currents have modified the distribution of the sediments during the first few years following start-up of the installation. A map of the superficial sediment distribution, drawn in 1994, shows that, from downstream to upstream of the estuary, pebbles and coarse sands are followed by medium and fine sands, muddy sands and finally muds beyond Port-St-Jean (Bonnot-Courtois, 1997). A similar sequence is observable from the central channel to the banks.

The reference site is located in the bay of Saint-Suliac, on the centre of the distribution of the *Abra alba–Corbula gibba* community. Water depth varied between 4 and 13 m up to 1994 and between 2.5 and 12 m after 1994 since the drop of tide mean levels. After the tidal power station was brought into service, the sediment has become a muddy fine sand with median particle size comprised between 62 and 120 μm (5–7% of particles <0.63 μm). Particulate organic carbon content represents 2.4% of the dry sediment weight (Clavier, 1981). The water temperature varies between 5°C in winter and 19°C in summer, and salinity between 34 and 35 psu. Currents alternate with the tidal cycle and remain parallel to the coast. Depending on the functioning of the power station, flow speed, recorded with a Braystoke velocimeter, varies from 0 to 0.40 $m\,s^{-1}$ at the surface and from 0 to 0.25 $m\,s^{-1}$ one metre above the bottom. No major changes in the normal hydrologic conditions were noticed between 1972 and 1997 (Retière, personal communication).

Sampling technique

With the dual purpose of gathering quantitative data on the macrozoobenthic as well as on temporary meiobenthic populations, different sampling strategies were used over different spatial and temporal scales (Table 1).

Depending on the periods, macrobenthic organisms were sampled with an orange peel grab (Collignon, 1991), a 1/55 m^2 hand corer and a Smith-McIntyre grab. Although more effective than the Orange-peel grab, the Smith-McIntyre grab should produce largely the same results (Clavier, 1983). In all cases, organisms were fixed with 4.5% formalin and sieved through 1 mm mesh, sorted and counted at the laboratory. Despite the techniques used, the minimal area studied was always greater than 0.2 m^2, which samples more than 80% of species (Clavier, 1983).

The meiobenthos was sampled every 10 d from the end of May 1996 to the end of October 1996 with a small 1/470 m^2 hand corer. The sampling grid consisted of a 10×10 m topographically and edaphically homogeneous area, divided into 25 unit squares of 2×2m. Organisms were sampled by SCUBA divers who positioned the corer trap randomly inside each square. Ten samples were systematically performed on each date. The number of sub-samples necessary to sort was determined a posteriori by the test of Healy (1962). Samples were fixed with neutral formalin containing Rose Bengal stain. The samples were sieved using seawater into three size fractions (<300 μm; 300–1000 μm; and >1000 μm). As the size of recruits of the dominant species was >300 μm (Cazaux, 1970; Clavier, 1981; Lechapt, 1983; Rivain, 1983; Grehan et al., 1991), only the 300–1000 μm size fraction was examined.

Data analysis

Rank-Frequency Diagrams (RFD; Frontier, 1976), the diversity index of Shannon–Weaver, the regularity coefficient of Pielou and the summed cumulated function were used to characterize and compare long-term changes in the structure of the community and its inter-annual variability between the 1972–1973 and the 1995–1997 study periods.

Table 2. *Relative importance of number of species and individuals of different taxa in 1972–1973 and 1995–1997. Category 'Others' regrouped anthozoans, nemertans, sipunculids, lophophorids, echinoderms and urochordates.*

	1972–1973			1995–1997		
	Number of species	%	Number of individuals (%)	Number of species	%	Number of individuals (%)
Polychaetes	32	38.6	48.2	42	40.4	60.1
Molluscs	25	30.1	3.8	23	22.1	4.3
Arthropods	23	27.7	47.6	28	26.9	32.6
Others	3	3.6	0.4	11	10.6	3
Total	83			104		

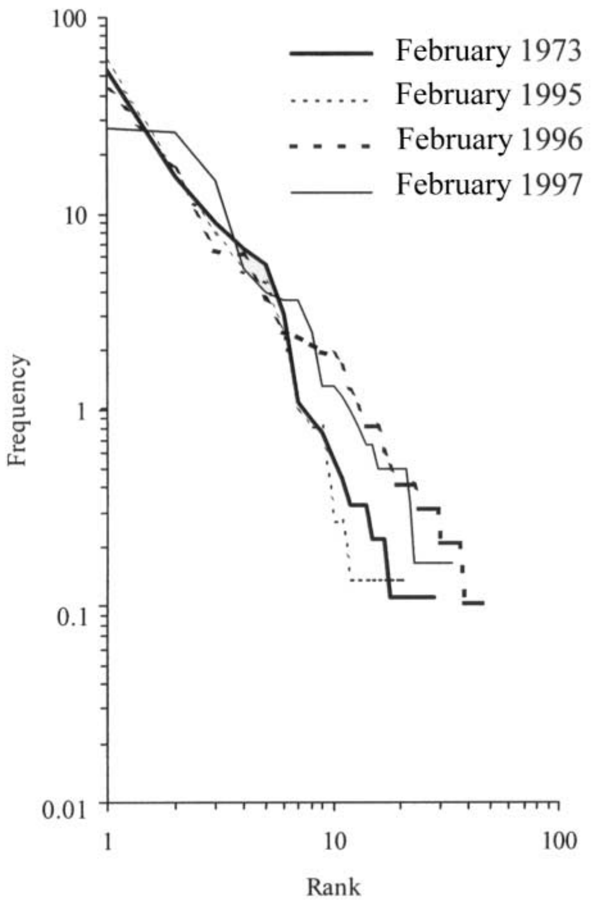

Figure 1. Winter variations of RFD of the *Abra alba–Corbula gibba* community.

To emphasize the range of inter-annual fluctuations of main species abundances in 1972–1973 and 1995–1997, two Factorial Correspondence Analysis (FCA) were performed. For greater clarity, the projection of stations on the F1×F2 plane has been shown separately from the projection of species. Analyses were done only for species with a frequency $\geqslant$12.5%. As densities of *Ampelisca brevicornis* and *A. tenuicornis* varied by several hundreds or thousands of ind m^{-2} from one month to the other and could rapidly reach values up to 7000 ind m^{-2} (Figure 6A), these species were considered to be additional elements.

Dynamics of dominant populations recorded in 1973, 1995 and 1996 were compared with each other by Spearman rank correlations calculated between original data. As successive observations were highly autocorrelated, significance of coefficients was determined with a Monte-Carlo test performed with 500 permutations (Ibanez et al., 1993).

RESULTS

General description of the benthos

A total of 83 species were found in the eight samples collected during the 1970s whereas 104 were found in the 26 samples collected during the 1990s, corresponding to a total of 133 different species. The fauna was composed almost exclusively and in comparable proportions of polychaetes, molluscs and arthropods (Table 2).

Winter structure

The RFD of February 1973 and 1995 (Figure 1) showed an intermediate situation (1′) between states 1 and 2 as defined by Frontier (1976), which correspond, respectively, to pioneer communities at the beginning of ecological succession and mature communities. The structure of the community was not substantially modified after an interval of 23 y. The RFD of February 1996, whose lower section became more convex, is distinguishable from previous curves and reflects the progressive maturation of the community. Finally, the curve of February 1997 shows the most mature state with a number of species >36.

Comparison of the inter-annual change of the assemblage: 1972–1973 vs 1995–1997

Specific richness

Despite an unequal range between 1972 and 1973, the variation of the index of specific richness is consistent, maximum (33 and 47) and minimal (26) values being recorded, respectively, at the end of summer (following the recruitment) and at the end of the winter (Figure 2A).

Although values of specific richness as well as fluctuation range observed in 1972–1973 and 1995–1997 are similar, comparison of summed cumulated densities for the two series shows different changes (Figure 2B). The

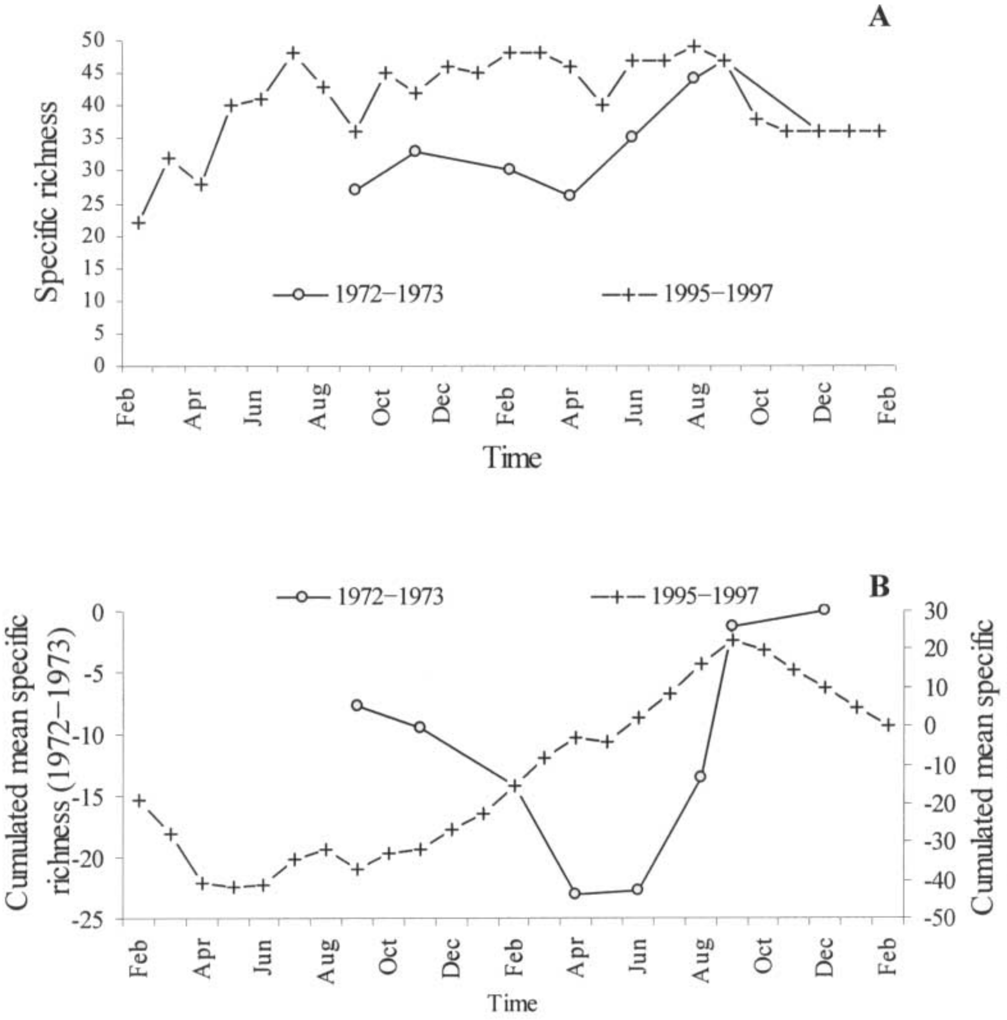

Figure 2. Change of the specific richness in 1972–1973 and 1995–1997 (A) and summed cumulated function of the mean specific richness for the two periods (B).

latter emphasized, for 1995–1997 data, a major phase (from May 1995 to September 1996), during which the number of species remained high and stable (between 36 and 49) and, for 1972–1973 observations, serrated change.

Abundance

Between 1972 and 1973 and after *Ampeliscidae* were excluded from the calculation, maximal values varied between 423.1 and 657.8 ind $0.1\,m^{-2}$ (Figure 3A). In the same way, between 1995 and 1997, the change of total abundance appears serrated, with maximal and minimal values of $\sim$800 ind $0.1\,m^{-2}$ and $\sim$300 ind $0.1\,m^{-2}$, respectively.

Function of summed cumulated densities vary differently for the two series (Figure 3B). Unlike the succession of 1972–1973 characterized by alternating short periods of increase and decrease of abundance, dynamics observed from 1995 to 1997 show a main stage of abundance increasing, from May 1995 to September 1996.

Diversity and regularity

From 1972 to 1973, without consideration of *Ampeliscidae*, diversity index varied from 1.3 to 2.9 with a mean value of 2.3 and regularity index, from 0.27 to 0.54. These last showed an unbalanced distribution of the abundances of individual species: although diverse, fauna was strongly dominated by some species (*Chaetozone setosa*, *Euclymene oerstedii*, *Melinna palmata*, *Nephtys hombergii* and *Nucula nitidosa*; Table 3).

In 1990s, higher diversity and regularity indices reflected a community more structured than in 1972–1973, fauna remaining dominated by the same group of species. After a period (February 1995–May 1995) characterized by values of diversity ranging from 2.1 to 2.7 and comparable with those observed between 1972 and 1973, the assemblage appeared stable from July 1995 to February 1997 ($2.5 <$ diversity index < 3.5). Regularity index remained constant, fluctuating from 0.5 to 0.6.

Factorial Correspondence Analysis (FCA)

A FCA was performed with all data clearly separated into observations from the 1970s and the 1990s. To better understand the mechanisms that determine community change, data from both series were analysed separately.

A new analysis was performed using data recorded in 1972–1973 (i.e. matrix of 8 observations × 83 species), with *Ampeliscidae* (i.e. *Ampelisca tenuicornis* and *A. brevicornis*) considered as supplementary species. The first two axes of the FCA accounted for 64.7% of the total inertia (axis 1: 39.6%, axis 2: 25.1%). Axis 1 opposes observations of November 1972 and September 1973 (group I, total

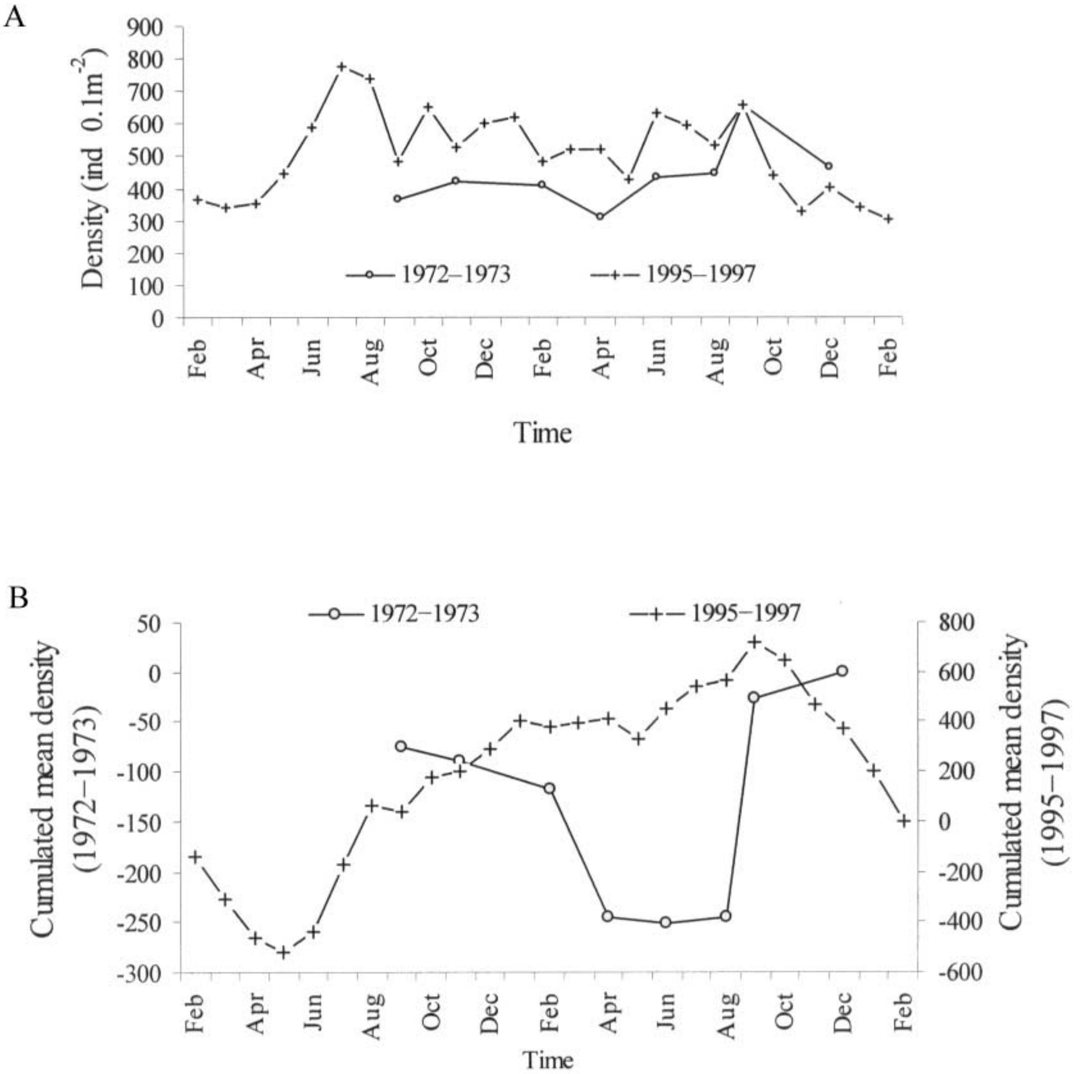

Figure 3. Change of total density (*Ampeliscidae* excluded) in 1972–1973 and 1995–1997 (A) and summed cumulated function of the mean density for the two periods (B).

contribution of 65.8%) to others (Figure 4A). This axis was determined by *Ericthonius brasiliensis*, *Amphithoe vaillanti* and *Microdeutopus versiculatus* in the negative part and *C. setosa* and *N. nitidosa* in the positive part (Figure 4B). The second axis separates observations of September and November 1972 (total contribution of 91.4%) from others (total contribution of 8.6%). This axis is determined by *Pherusa fucicola*, *Sabella pavonina* and *Nephtys hombergii* (negative part) and *E. brasiliensis* (positive part). Similarities between observations of September 1972 and February, April, June, August and December 1973 (group II) confirm the relative stability of the community over the annual cycle. Axis 1 isolates the months of September 1972 and November 1973 during which specific richness increased with recruitment, showing punctual changes to the structure and the composition of the community.

The exclusion of rare species from the 1995–1997 data resulted in a matrix of 25 observations × 63 species. The

Table 3. *Abundance of the first seven dominant species in the community (*Ampeliscidae *excluded), arranged in a decreasing order of mean density (number of ind 0.1 m^{-2}), during the two periods studied.*

September 1972–December 1973		February 1995–February 1997	
Melinna palmata	255.0	*Melinna palmata*	186.2
Chaetozone setosa	49.3	*Euclymene oerstedii*	112.0
Nephtys hombergii	44.7	*Aponuphis bilineata*	37.4
Euclymene oerstedii	43.5	*Nephtys hombergii*	25.8
Nucula nitidosa	21.8	*Chaetozone setosa*	17.2
Eudorella truncatula	9.7	*Phoronis psammophila*	15.8
Thyasira flexuosa	5.7	*Thyasira flexuosa*	12.0

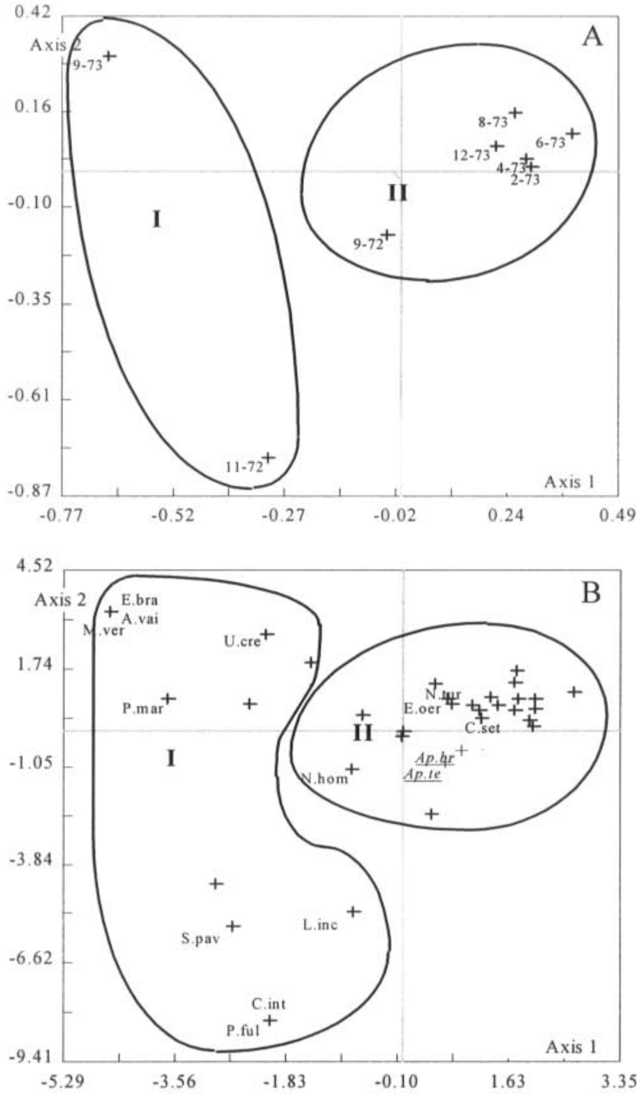

Figure 4. Stations (A) and species (B) on axes 1 and 2 of FCA performed with 1972–1973 data, with indication of the inertia groups. *Ampeliscidae* (underlined) were considered as supplementary elements. Ap.br, *Ampelisca brevicornis*; Ap.te, *Ampelisca tenuicornis*; A.vai, *Amphithoe vaillanti*; C.set, *Chaetozone setosa*; C.int, *Cheirocratus intermedius*; E.oer, *Euclymene oerstedii*; E.bra, *Ericthonius brasiliensis*; L.inc, *Leucothoe incisa*; M.ver, *Microdeutopus versiculatus*; N.hom, *Nephtys hombergii*; N.nit, *Nucula nitidosa*; P.ful, *Pherusa fucicola*; P.mar, *Phtisica marina*; S.pav, *Sabella pavonina*; U.cre, *Unciola crenatipalma*.

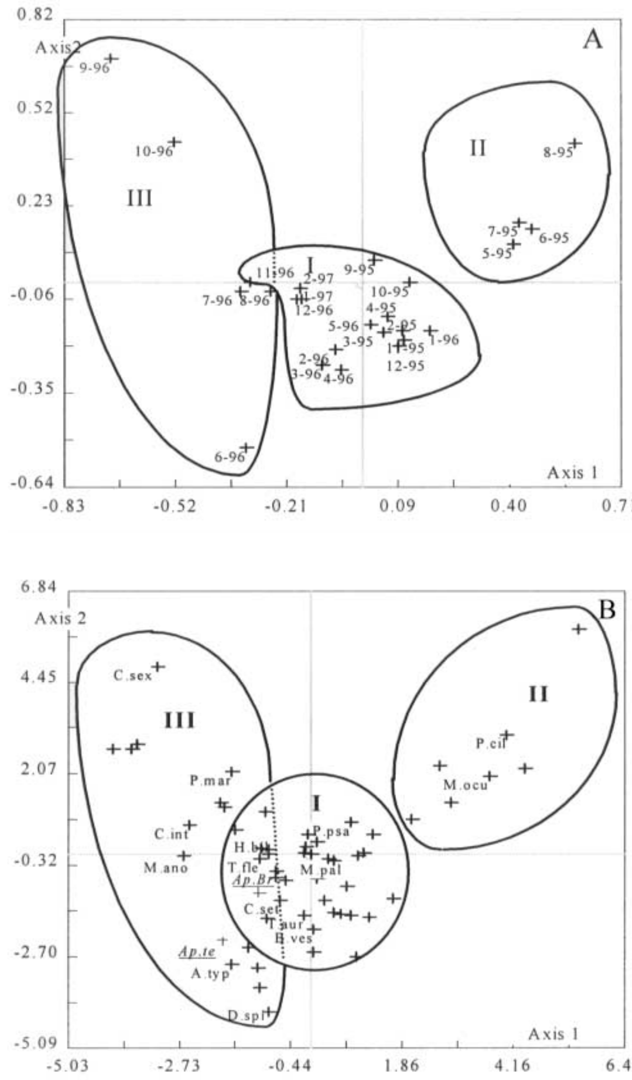

Figure 5. Stations (A) and species (B) on axes 1 and 2 of FCA performed with 1995–1997 data, with indication of the inertia groups. *Ampeliscidae* (underlined) were considered as supplementary elements. Ap.br, *Ampelisca brevicornis*; Ap.te, *Ampelisca tenuicornis*; A.typ, *Aora typica*; A.bil, *Aponuphis bilineata*; C.set, *Chaetozone setosa*; C.int, *Cheirocratus intermedius*; C.sex, *Corophium sextonae*; D.spi, *Dexamine spinosa*; M.ves, *Megalomma vesiculosum*; M.pal, *Melinna palmata*; M.ano, *Microdeutopus anomalus*; M.ocu, *Myriochele oculata*; P.psa, *Phoronis psammophila*; P.mar, *Phtisica marina*; P.cil, *Polydora ciliata*; R.aur, *Ruditapes aureus*; T.fle, *Thyasira flexuosa*.

first two axes of the FCA accounted for 40.9% of the total inertia (axis 1: 24.0%; axis 2: 16.9%). As shown by Figure 5A, axis 1 isolates observations characterized by recruitment: from May to August 1995 (group II; total contribution of 44.7%) and from June to October 1996 (group III; total contribution of 45.7%). This axis separates the species that recruited in 1995 as *Polydora ciliata* or *Myriochele oculata* (group II; total contribution of 42.7%) or in 1996 as *Aora typica*, *Cheirocratus intermedius*, *Corophium sextonae* and *Microdeutopus anomalus* (group III; total contribution of 30.2%; Figure 6B). By separating observations of 1995 and 1996, the FCA confirms the progressive evolution of community structure as indicated by diversity and regularity indices. Group I is constituted, as in 1972–1973, by a consortium of species constant and abundant: *Aponuphis bilineata*, *Diplocirrus glaucus*, *Euclymene oerstedii*, *Melinna palmata*, *N. hombergii*, *Phoronis psammophila*, *Thyasira flexuosa*, *Ruditapes aurea*, etc., with stable abundances all year long. Following massive recruitment, some species that were normally weakly represented reached high densities before disappearing more or less rapidly.

Fluctuations of abundances of dominant macrobenthic (1972–1973 and 1995–1996) and meiobenthic (1996) populations

A Monte-Carlo test shows that Spearman rank correlations calculated from the original series of 1973, 1995 and 1996 are significant (Table 4) for each of the six species considered afterwards.

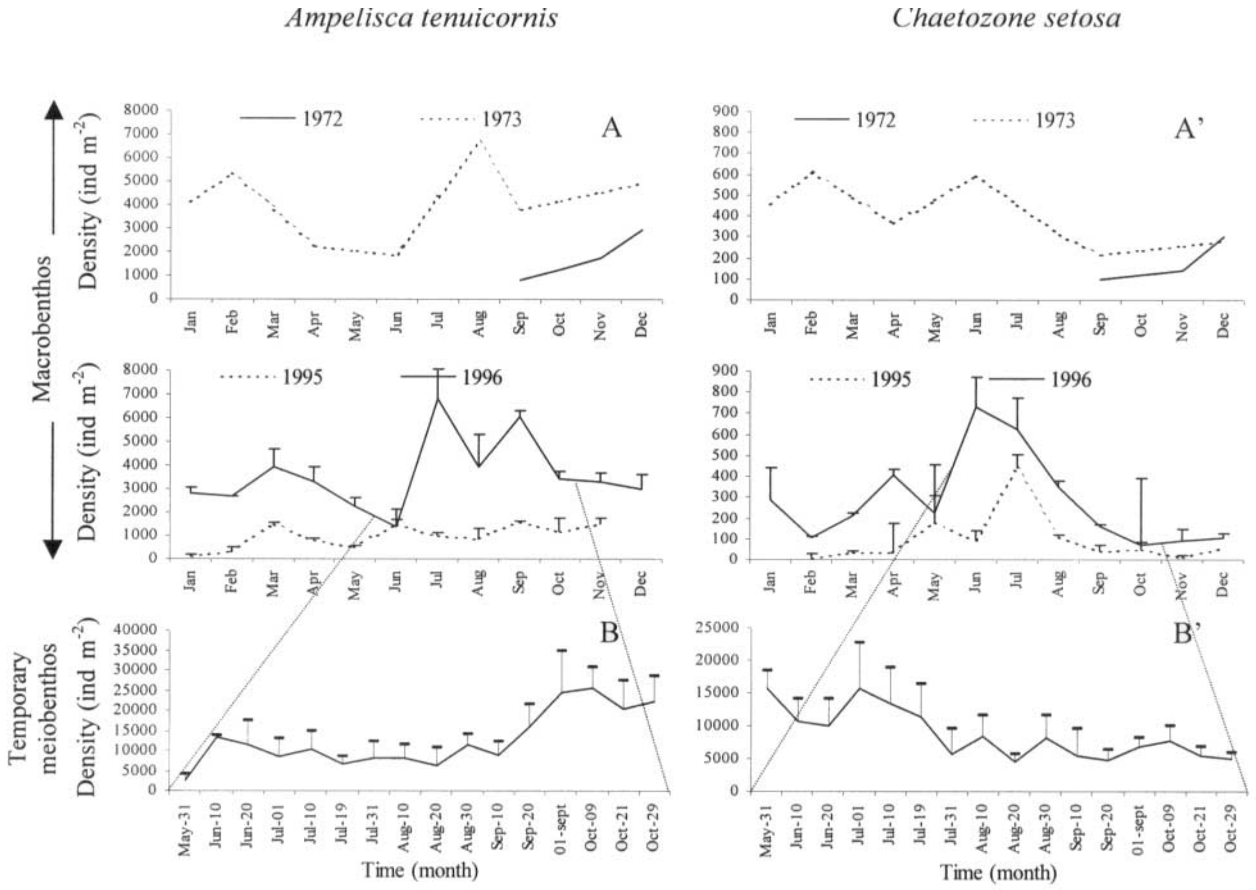

Figure 6. Changes in density (+SD) of macrozoobenthic (1972–1973 and 1995–1996) and meiobenthic (May–October 1996) populations of *Ampelisca tenuicornis* (A–B) and *Chaetozone setosa* (A′–B′).

Short life cycle species (<2y)

Ampelisca tenuicornis

Despite different ranges, annual changes in abundance of *A. tenuicornis* were comparable in 1972–1973 and 1995–1996, with main peaks observed at the end of the winter or in early spring and in summer (Figure 6A). The summer maximum of abundance observed in 1996 followed massive recruitments of June (up to 14 000 ind m^{-2}, Figure 6B): individuals from the recruitment grow rapidly whereas those settling during the autumn (September–October) slow or stop growth during winter and are integrated into the macrozoobenthos later and more gradually the following spring (Dauvin, 1987).

Chaetozone setosa

Except slight temporal lags, changes of abundances appear consistent between 1972–1973 and 1995–1996, with notably a summer peak of abundance and similar densities (from 400 to 700 ind m^{-2}; Figure 6A′). Despite the high densities of recruits (maximal values of 15 000 ind m^{-2} in May 1996; Figure 6B′) and the high summer abundance resulting from the spring recruitment (around 450 and 730 ind m^{-2} in July 1995 and June 1996 respectively), winter densities of adults remained low (<50 ind m^{-2}).

Long life cycle species (>2y)

Melinna palmata

Inter-annual changes of abundance appear variable from one year to the other (Figure 7A). Maximal abundances of *M. palmata* were observed: (i) in September 1972 (up to 3500 ind m^{-2}); (ii) in July and December 1995 (approximately 3100 and 2600 ind m^{-2}); and (iii) from

Table 4. *Spearman rank correlations from original data of 1973, 1995 and 1996.*

	1995–1996	1995–1973	1996–1973
Ampelisca tenuicornis	0.4286, **	−0.0857, **	0.3143, **
Chaetozone setosa	0.4058, **	−0.3143, **	0.2029, **
Melinna palmata	−0.1449, **	0.4857, **	−0.5798, **
Nephtys hombergii	0.2000, **	0.6571, **	−0.1429, **
Aponuphis bilineata	0.6000, **	0.3769, **	−0.0580, **
Euclymene oerstedii	0.3189, **	0.3479, **	0.7206, **

**, $P<0.01$.

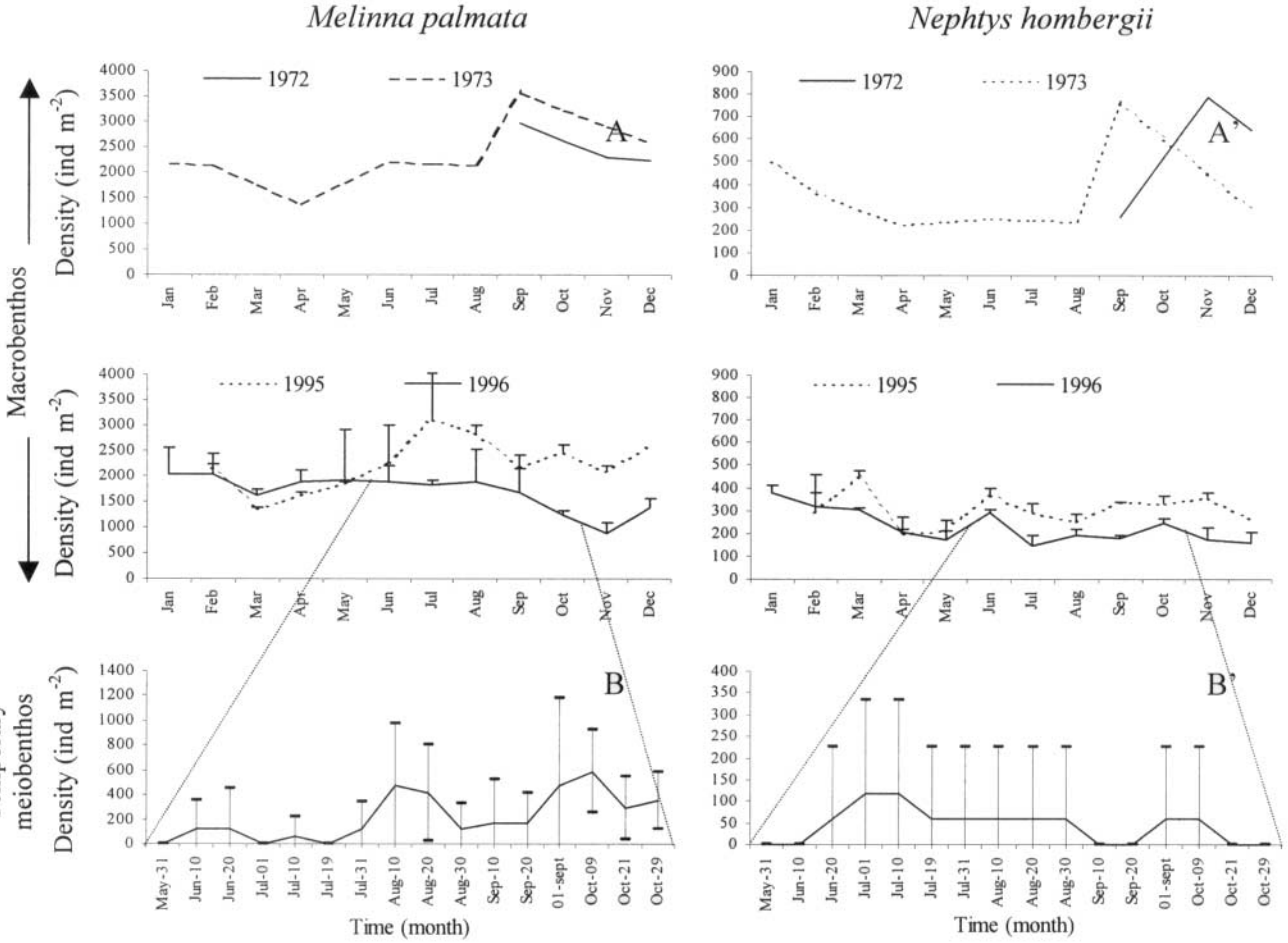

Figure 7. Changes in density (+SD) of macrozoobenthic (1972–1973 and 1995–1996) and meiobenthic (May–October 1996) populations of *Melinna palmata* (A–B) and *Nephtys hombergii* (A′–B′).

April to August 1996 and December 1996 (about 1800 and 1400 ind m^{-2}). In 1972 and 1995, the population dynamics were characterized by a main peak of abundance observed in summer or autumn, followed by secondary peaks. By contrast, any maximum was observed in 1996 as the population was supplied by small variable pulses of recruits (100–600 ind m^{-2}; Figure 7B).

Nephtys hombergii

As with *M. palmata*, densities tended to decrease from 1995 to 1996 (Figure 7A′). Despite the high variability of abundances from one month to the other, dynamics appeared inter-annually consistent between 1995 and 1996 with main peaks recorded in winter (January or March) and at the beginning of the summer (June). In 1972–1973, dynamics were characterized by one consistent peak of abundance and greater annual variation of abundances (maximal values of 800 ind m^{-2}). Recruitment, occurring in 1996 mainly in summer (July) and autumn (September–October), was low and spread over several months (Figure 7B′).

Aponuphis bilineata

Two periods of maximal abundances were observed in both 1995 and 1996 (in summer and autumn; Figure 8A). Fluctuations of densities between winter and summer periods were minor, winter abundances remaining high: 194 ind m^{-2}, 300 ind m^{-2} and 455 ind m^{-2} in February 1995, 1996 and 1997. Despite a low recruitment during summer 1996 (<150 ind m^{-2}, Figure 8B), densities of the population remained higher than 400 ind m^{-2} during the following winter, inducing the increase of the population size. Comparison of the changes observed between 1995 and 1996 to those described in 1972–1973, is difficult as *A. bilineata* was just starting to re-colonize at this time (Figure 8A).

Euclymene oerstedii

Except in February 1995, density of *E. oerstedii* fluctuated between 800 and 1600 ind m^{-2}, from 1995 to 1997, (Figure 8A′). Dynamics were characterized by a non-consistent succession of peaks of abundance. Correspondence between the two main periods of recruitment observed in 1996 (maximal values of 1500–2000 ind m^{-2}) and the dynamics of the population is not clear (Figure 8B′). Again a comparison with data acquired in 1972–1973 is not very informative because *E. oerstedii* was in recolonization stage at this time (Figure 8A′).

Comparison of the dynamics of four dominant species from 1972 to 1982 and 1995 to 1997

Dynamics of *A. bilineata*, *E. oerstedii*, *M. palmata* and *N. hombergii* observed between 1995–1997 were compared to those recorded from 1972 to 1982 (Figure 9). Between 1972 and 1982, Clavier et al. (1983) defined, for each, a

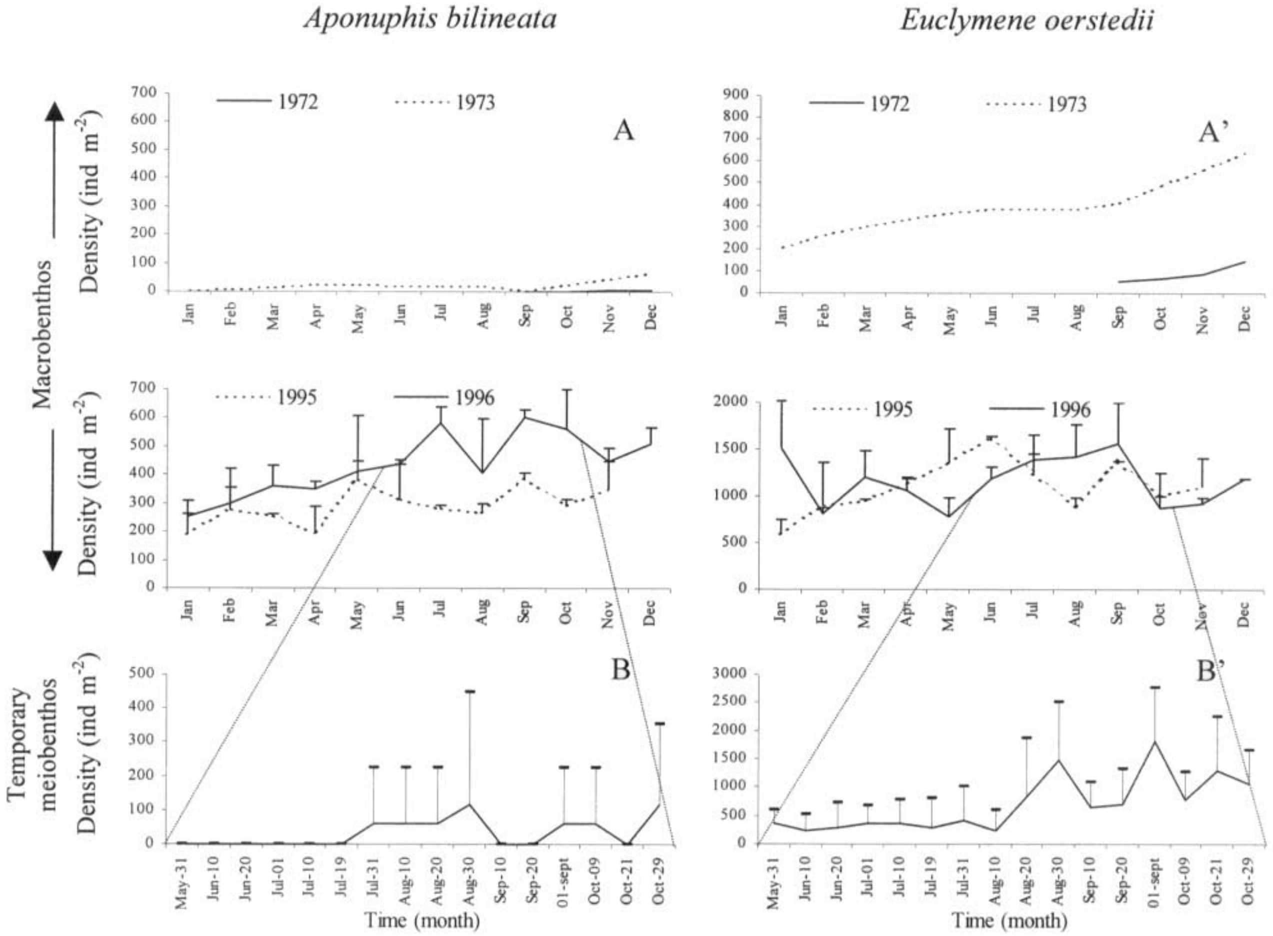

Figure 8. Changes in density (+SD) of macrozoobenthic (1972–1973 and 1995–1997) and meiobenthic (May–October 1996) populations of *Aponuphis bilineata* (A–B) and *Euclymene oerstedii* (A′–B′).

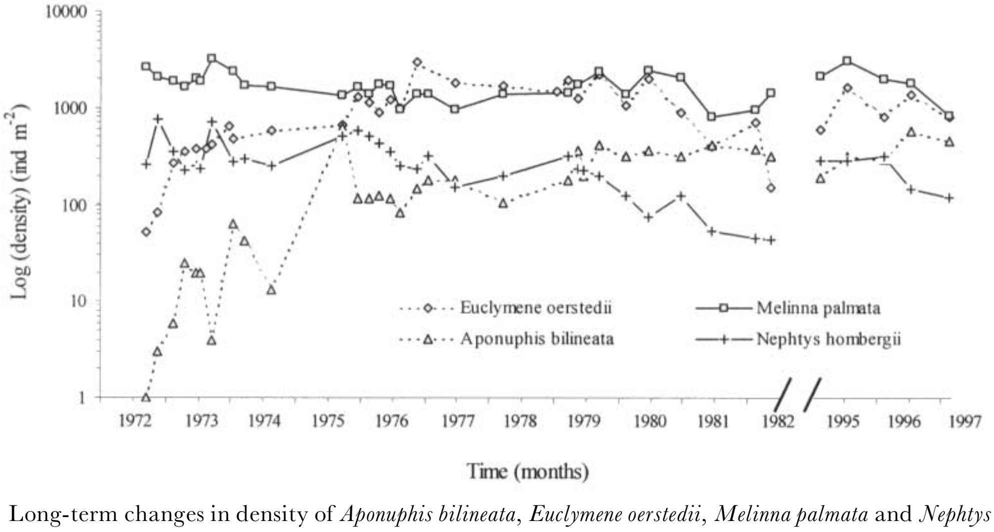

Figure 9. Long-term changes in density of *Aponuphis bilineata*, *Euclymene oerstedii*, *Melinna palmata* and *Nephtys hombergii* from 1972 to 1982 and 1995 to 1997.

type of population dynamics depending on whether their abundances remained stable (*M. palmata*), increased (*A. bilineata*), decreased (*N. hombergii*), showed a peak during the following (*E. oerstedii*). Ignoring fluctuations occurred between 1982 and 1995, it appears that mean densities of these species are comparable between both periods. Abundance of *N. hombergii*, however, slightly increased at the studied station.

DISCUSSION

Comparison of the structure and the dynamics of the community in 1972–1973 and 1995–1997

Between 1972 and 1973, the relatively high and stable values of diversity and regularity indices reflected the high degree of structure attained by the community, five years after the power station was put into service. Except the *Ampeliscidae*, three species of polychaetes played a major role in terms of density and biomass: *Euclymene oerstedii*, *Melinna palmata*, and *Nephtys hombergii*. The hierarchy of species abundances seemed relatively independent of seasonality including biological events such as recruitment.

In 1995–1997, about 20 species were newly recorded in a more 'mature' community, *sensu* Frontier & Pichot-Vialle (1991). Densities of species already established 23 years ago were comparable. Two consortia of species can be distinguished from the change in species abundances: (i) a group of constant dominant species, in which abundances increased from February to reach a maximum during the summer; and (ii) a group of temporary dominant species which are absent in winter and among the most abundant species in summer. After the period of spring 1995 and the modification in the hierarchy of the major species observed, the community was characterized by its inter-annual structural stability, easily explained by the relative stability in abundances of its main components: the seven top ranking species (*Ampelisca tenuicornis*, *Chaetozone setosa*, *Aponuphis bilineata*, *E. oerstedii*, *M. palmata*, *N. hombergii* and *Thyasira flexuosa*) represented more than 77% of individuals throughout the year.

During the winter 1995, the structure of the community was, according to the diversity/regularity indices and RFD, comparable to those described in 1972–1973. Knowing that the studied community is located on a shallow area where the physical environment is stable (Desroy, 1998), succession of periods of high and low values of density and diversity could be conditioned by the alternance of severe and warm winters as shown by Beukema (1979). However, the number of species rapidly increased during spring and was followed, from summer 1995 to autumn 1996, by a period of stability of the structure associated to a great constancy of hierarchical relationships between species. Such a rapid re-organization within the course of the season reflects the major role of recruitment which allows the colonization by new species or the increase of those already present.

Patterns of recruitment and stability of macrobenthic community

The recruitment of the dominant species with a long life span (*A. bilineata*, *M. palmata*, *N. hombergii* and *E. oerstedii*) appears low compared to the densities of adults but seems sufficient to assure the replacement of individuals. Concerning *E. oerstedii*, Clavier (1981) observed that, in the Rance basin, the variation range of density did not exceed the quarter of the size of the population. For *N. hombergii*, densities of recruits are lower than data observed by Bachelet (1990) on mudflats of the Gironde estuary (1500 ind m^{-2}), by Olive (1977) and Kirkegaard (1978) in British estuaries (around 450 ind m^{-2}) and more similar to values recorded by Mathivat-Lallier et al. (1989) in the basin of Arcachon (from 50 to 550 ind m^{-2}). The high post-settlement reductions of abundances of recruits (due to mortality and/or emigration) observed for species with a short life span (*Ampelisca tenuicornis*: 4–16 months; *C. setosa*: 2 y...) contrast with the low rates of recruit mortality and/or emigration in species with a pluri-annual life span (3 y and more). The extreme example is that of *Aponuphis bilineata* which, despite low densities of recruits (less than 150 ind m^{-2}) increased its abundance. Although it is known that species with a long life cycle can determine the long-term structure of communities, does population dynamics only depend on the recruitment? Owing to the results of Olivier et al. (1996a,b) on the role of the deposition-resuspension of recruits on the dynamics of dominant populations of an *Abra alba* muddy fine sand community, the importance of secondary settlement or recruit emigration on the stability/variability of populations cannot be ignored where hydrodynamics is particularly intense such as in the Rance basin. Moreover, biological interactions (predation, spatial and trophic competition, bioturbation) necessarily play a role in the regulation of recruit densities. Then, the *Ampeliscidae*, surface deposit feeders with densities up to 6000 ind m^{-2}, probably contributed to the mortality of recruits, by the sedimentary modifications they create at the sediment/water interface.

From the data of 1996, it appears that high and low densities of recruits correspond, respectively, to species with short life span (less than a week such as *M. palmata* (Grehan et al., 1991), *E. oerstedii* (Clavier, 1981)) and long life span (more than a month such as *Aponuphis bilineata* (Rivain, 1983), *N. hombergii* (Cazaux, 1970)). Although recruitment rates directly depend on fecundity rates of each species, the low level of recruitment could, in part, be a consequence of the exportation of larvae outside the basin especially when the larval stage is long. As the hydrodynamic conditions in the adjacent shallow areas and the basin of Rance are poorly known, any conclusion on the exact intensity of dispersion in this sector can be advanced. A hydrodynamic model covering a sufficiently large spatial scale and with a resolution enough precise to take account of the functioning rhythm of the power station would be necessary to test this hypothesis. This last could assess: (i) the relative inter-annual reproducibility of recruitment; and (ii) the persistence of high and relatively constant densities of dominant species at short and long terms on fine sediments in the basin.

Our results clearly demonstrate that the muddy fine sand community in the Rance basin functions differently from those located on the mudflats of the Gironde (Bachelet, 1990) or on subtidal fine sediments of the eastern part of the bay of Seine (Olivier, 1997) where strong recruitment was observed (up to 50,000 ind m^{-2} depending on the species considered) followed by high rates of mortalities and/or active or passive emigration (up to 99% of young settlers). Similarities can however be seen with the *M. palmata* muddy fine sediments of the Morlaix river. Ibanez & Dauvin (1988), who followed the density change of *M. palmata* in this site from 1977 to 1987, showed that densities can be stable during several years before suddenly increasing by means of a large recruitment. These maxima observed in summer or autumn, by decreasing regularly, does not fundamentally modify the global size of the population. The pattern of a large recruitment followed by a rapid decrease of the density of settlers could be not as widespread as it is thought. An alternative hypothesis suggests, without excluding the occurrence in some years of a large recruitment, that the pattern of moderate recruitment followed by low rates of mortalities should be more frequent than has been proposed.

Patterns of recruitment aforementioned could be also linked to the stability/variability of the environmental conditions. Reproduction modes of *A. bilineata*, *E. oerstedii*, *M. palmata* and *N. hombergii* can be compared to the K type demographic strategy defined by Mac-Arthur & Wilson (1967). Such a strategy is encountered for species living in physically stable environments, such as bottoms of the marine area of the Rance basin, where biotic and abiotic conditions are foreseeable for several years (Southwood, 1977). Recruitment temporarily turns the community of a 'homeostatic' state towards which it systematically tends to return, species with long life span having the greatest effect on the trends observed. Their densities seem at long term, to fluctuate around a mean value comparable to the 'carrying capacity' of the biota for these species (Pianka, 1970).

The relation between environmental parameters and the change in the community is all the more clear that the assemblage is diversified and initially submitted to low abiotic constraints. In this view, the *Abra alba–Corbula gibba* community should be further sampled to follow the dynamics of the benthic recruitment and its influence on future changes in the Rance Basin. The use of both approaches, as in this study, would permit to integrate spatio-temporal fluctuations occurring over micro- ($m^2\ w^{-1}$) and meso-scale ($100–1000\ m^2\ month^{-1}$) and to correlate them with change of abiotic parameters, natural or induced by the functioning of the scheme. A third approach, at macro-scale (several $km^2\ y^{-1}$) is also necessary to assess the drift or the stability of the ecosystem. This long-term monitoring, considering natural cycles of variability of communities (3–4 y and 7–10 y for the *A. alba* community in the English Channel) would need a sampling interval of the half period of the fluctuations (Frontier, 1983), i.e. 1.5–5.0 y. The most realistic frequency, considering the extensive effort of sampling, sorting and processing, would be every 4–5 y at the scale of the basin.

This study forms a part of the GDR 'Manche' contribution to the study of the variability of coastal systems. The authors thank Electricité de France for their support, the crew of NO'Louis Fage' for their valuable assistance in field work. Authors are also grateful for comment and corrections on the manuscript made by J.M. Dewarumez and Professor L. Johnson.

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Submitted 17 November 2000. Accepted 2 April 2001.

ICES Journal of Marine Science, 60: 120–131. 2002
doi:10.1006/jmsc.2002.1333

Macrobenthic resources of the shallow soft-bottom sediments in the eastern English Channel and southern North Sea

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Desroy, N., Warembourg, C., Dewarumez, J. M., and Dauvin, J. C. 2003. Macrobenthic resources of the shallow soft-bottom sediments in the eastern English Channel and southern North Sea. – ICES Journal of Marine Science, 60: 120–131.

To obtain a baseline for future comparisons and to assist in the conservation of marine biodiversity, the distribution patterns and faunal composition of shallow (0–15 m depth) macrobenthic assemblages were studied along the French coast of the eastern English Channel and southern North Sea from two surveys conducted in 1998 and 2000. A total of 227 sites were sampled from Cap d'Ailly to the Belgian border, from which a total of 167 species were collected. Species richness, abundance and biomass were all increased in the vicinity of outflows from harbours, major bays and estuaries. Three principal macrobenthic assemblages were defined: (i) an *Ophelia borealis* medium to fine sand assemblage; (ii) a muddy heterogeneous sediment assemblage; and (iii) an *Abra alba* muddy fine sand assemblage. The *Abra alba* assemblage covered approximately 80% of the seabed in the survey area. Sediment characteristics and a latitudinal gradient accounted for a significant proportion of the observed variability in assemblage distribution patterns. In the eastern English Channel, the distribution patterns of species diversity, abundance and biomass values were most continuous, whereas in the southern North Sea a more heterogenous distribution was observed.

Keywords: *Abra alba* assemblage, eastern English Channel, macrobenthic resources, monitoting.

Received 10 July 2002; accepted 21 October 2002.

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Introduction

Approaches to the study of marine biodiversity include the identification of spatial patterns via surveying and mapping, the description of these patterns, and the study of their relationships with, for example, ecosystem function and production (Costello, 1998). Well-informed decisions about possible uses are easier to make if information about the resource and changes over time are available. This descriptive information remains an important tool, as underlined by the Rio Convention on Biological Diversity, in the process of identifying areas of conservation importance and in providing an empirical basis for the classification of marine biotopes (Costello, 1998). However, the importance of monitoring the marine environment on large spatial scales, in order to better manage the marine habitats and resources, has only recently been recognized, especially in areas where biodiversity may be affected by human activities, such as in coastal zones. This recent awareness is paradoxical as coastal areas often support large concentrations of people, significant marine biodiversity resources, and have a higher probability of being exposed to perturbations than the open sea. Ideally, the biological components of coastal areas should be known in order to assess the consequences of man-made impacts (Bachelet *et al.*, 1996). However, Snelgrove (1999) emphasized that although soft-sediment habitats are common in coastal areas throughout the world, only a small proportion of the macrobenthos has been described, despite being considered a good bioindicator (Dauvin,

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1993). Furthermore, shallow subtidal assemblages, samplable only during high tide, are often excluded from sampling areas and remain to a large extent unknown.

One of the few areas for which the macrobenthos is relatively well known is the English Channel. On the French coast of the eastern English Channel, the distribution of macrobenthic fauna has been described by Cabioch and Glaçon (1975, 1977) and Davoult *et al.* (1988). More recently, benthic diversity data for the eastern part of the Channel, collected in the 1970s, has been re-evaluated by Sanvicente-Anorve *et al.* (1996). Five main sub-tidal soft sediment communities were identified (Cabioch and Glaçon, 1975, 1977; Souplet and Dewarumez, 1980): the *Abra alba–Pectinaria koreni* assemblage associated with muddy fine sands (replaced by the *Donax vittatus–Abra alba–Macoma balthica* assemblage near the shoreline); the *Ophelia borealis* assemblage associated with fine to medium sands; the *Amphioxus lanceolatus* assemblage associated with coarse sands; the pebbly and gravelly assemblage; and the muddy heterogeneous sediment assemblage. These studies complete the research efforts along the Belgian coasts, in the southern Bight of the North Sea (Govaere *et al.*, 1980; Vermeulen & Govaere, 1983). In French waters, benthic ecologists have mainly focused their efforts on describing and interpreting variability in the benthic fauna over large spatial scales and over offshore sediments. To our knowledge, few studies have been conducted on the assemblages associated with the soft bottom sediments of very shallow areas (less than 15 m depth). Data often result from previous qualitative studies carried out with dredges, or from localized impact studies such as the Dunkirk industrial area (Dewarumez, 1979), which may be followed by a time-series of data collections (Dewarumez *et al.*, 1986; Ghertsos *et al.*, 2000). The present survey aims to provide an insight into the composition and distribution of benthic assemblages located in very shallow areas along the French coast of the eastern English Channel and southern North Sea. An important challenge of this work was the choice of a spatial observation scale that would be appropriate to adequately describe benthic assemblage structure and the distribution of the dominant species (Thrush, 1991; Luczak, 1996). Although there is no single correct scale, Armonies (2001) concluded from a study of the dispersal of the American jacknife, *Ensis directus*, that benthic assemblages should be sampled at a spatial scale similar to the dispersal capabilities of the dominant taxa. In the eastern English Channel, between the Seine river and the Cap Gris-Nez, the dispersion in the coastal water is often limited seaward by a coastal front located between 3 and 5 miles of the coasts (Brylinski *et al.*, 1991). The coastal water is characterized as a transfer pathway from the English Channel to the North Sea. In order to encompass the dispersal capabilities of the most dominant macrobenthic species in the study area, sampling was conducted over a spatial area of approximately 160 × 5 km.

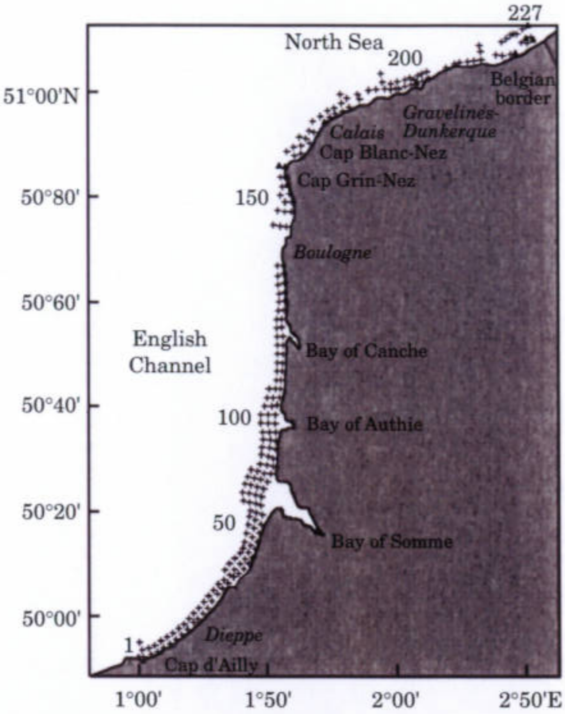

Figure 1. Location of benthic sampling stations (1 to 227); +: sampled station; ▲: hard substrate stations impossible to sample with a grab.

The objectives of the study were: (i) to estimate abundance and biomass of shallow water communities in order to obtain baseline data for future comparisons and to assist in the conservation of marine biodiversity; (ii) to describe the structure and spatial distribution of macrobenthic assemblages and their dominant species; and (iii) to identify the main environmental factors determining the distribution patterns.

Study area

The area investigated (49°92′–51°12′N 0°99′–2°51′E, Figure 1) was restricted as far as possible to water depths of less than 15 m, and extended from the Cap d'Ailly in the eastern English Channel to the Belgian border in the southern North Sea.

In the eastern English Channel, tidal current strengths increase from 1.5 to 3 knots from the south to the northeast as the narrower part of the Dover Strait is approached (Davoult *et al.*, 1988). Flow velocity decreases in the southern North Sea where it does not exceed 2 knots (Davoult *et al.*, 1988). Variations in the speed of the tidal current create a sedimentary gradient (Larsonneur *et al.*, 1982): pebbles and gravels dominate in the open sea, whereas coastal areas are dominated by large homogeneous sand banks and associated channel systems. Hard substrata and mudflats are restricted to such areas as capes, bays and harbours. In those areas of shoreline (<10 m depth) where there is a regular morphology, tidal currents decrease and wave action becomes comparatively more important (Cabioch and Glaçon, 1977). Sediments located in low energy environments (5–7 m depth) frequently consist of fine particles; a discontinuous border between muddy and fine sands is also typically observed.

The water quality of the sampling area is largely influenced by two main estuaries, namely the Seine estuary to the southwest, and the Scheldt delta to the northeast. Depending on the direction, intensity and duration of the wind, the plume of both rivers can reach the Cap Gris-Nez/Cap Blanc-Nez zone and modify the water salinity up to 2–3 miles offshore (Cabioch and Glaçon, 1975). Other smaller rivers (i.e. Somme, Authie, Canche, Liane, Aa and Yser) and runoff from sea cliffs contribute to a decrease in the salinity of the coastal waters. Although the outflows from these sources are relatively low, they may be locally significant at low tide. In the southern North Sea, water quality is also influenced by large industrial complexes surrounding Calais and Dunkerque harbours. A large variety of manufacturing industries, primarily metallurgical, chemical and petrochemical, are responsible for the input of a range of contaminants of varying significance (Dewarumez and Davoult, 1997). In contrast, the area from Dieppe to the Canche estuary is free from major industrialization, although water quality may be impacted by contaminants discharged from the Seine river.

Material and methods

The distribution of macrofauna was established from two surveys conducted in March 1998 and April 2000 (Figure 1). In March 1998, 142 sites were sampled between the cap d'Ailly and Boulogne harbour, and in April 2000, 85 sites were sampled between Boulogne harbour and the Belgian border, providing a total of 227 sites for the two surveys. Samples were collected at this time in order to describe the status of macrofauna prior to the spring recruitment. Samples were collected along transects spaced at 1 nmi intervals along the length of the study area. Between 2 to 4 samples, spaced at 1 nmi intervals, were collected from each transect.

At each site, two sediment samples for macrobenthos analysis were collected using a 0.25 m^2 Hamon grab (Dauvin, 1979). A large grab and mesh sieve (see below) were used as the aim of the study was not to quantify local biodiversity precisely but to define benthic assemblages and the distribution of adult benthic organisms. The recommendation of Ellingsen (2001) to sample a 5×0.1 m^2 surface area was followed in order to obtain a meaningful measure of local biodiversity. Sub-samples of sediment were taken from additional grab samples and subsequently analysed for grain size distribution (wet sieving) and organic matter content (loss of weight of dry sediment at 600°C during 6 h). Replicates were collected from within a 50 m range of each site, using DGPS position-fixing.

The depth of sediment in the jaw of the grab provided an indication of the sample volume. Very small samples (i.e. less than about 5 cm depth) were discarded. The contents of the grabs were gently sieved on site through a 2-mm circular mesh sieve. The retained material was preserved for analysis in 5% buffered formaldehyde with added Rose Bengal. A visual description of the sediment type was recorded, along with the depth of the water column, and the location and times at which the sample was collected. The macrofauna was identified to the lowest possible taxon and enumerated. The biomass of each taxon was determined as g of AFDW 0.5 m^{-2} (loss of weight of dry organisms after 6 h at 520°C).

Data analysis

Species diversity was calculated at each site using the Shannon–Wiener function, H'Log$_2$ (Shannon & Weaver, 1963) and Pielou's index of evenness, R (Pielou, 1975). Relationships between biological characteristics (total biomass and densities of main macrobenthic species) versus sediment parameters (median grain size and organic matter content) were tested using Spearman's rank correlation coefficient (Scherrer, 1984).

The affinity of assemblages both among species and sites were established from the stations × species matrix using factorial correspondence analysis (FCA) (Benzecri, 1973). Species occurring at fewer than five sites (i.e. 2.3%), and stations without macrofauna were omitted in data analysis procedures. Data were transformed logarithmically [$\log_{10}$ (species count + 1)] prior to analysis. From their coordinates on the axes of the FCA, station groupings were identified using the hierarchical clustering method of Ward (1963). To determine the important species of each station group, constancy [$C_{ij} = (n_{ij}/n_j) \times 100$] and fidelity [$F_{ij} = (C_{ij}/\Sigma_{j=1}^{k} C_{ij}) \times 100$] indices were calculated, where n_{ij} is the number of occurrences of species i in the station group j, and n_j is the number of stations in station group j, where $j = 1$ to k. Characteristic species were categorized as being constant ($C > 50\%$), common ($50\% > C > 25\%$), elective ($F < 90\%$), or preferent ($90\% > F < 66.7\%$) (Retière, 1979). This method was used by Cabioch and Glaçon (1975, 1977) and Davoult *et al.* (1988) to describe patterns of distribution in the benthic fauna of the eastern English Channel. It was chosen in preference to the indicative value process, which combines abundance and frequency of species for characterizing site groups (Dufrêne and Legendre, 1997), to facilitate comparison with previous studies.

Results

It was only possible to collect quantitative samples at 217 of the 227 sites as 10 stations were located over rocky substratum. The large sandbanks found in the study area, especially along the southern North Sea coast, reduce the depth of the water column substantially so that approximately 70% of sampled sites were at a low tide depth of <10 m, with approximately 90% of sites at a depth of <15 m.

Sediments

The distribution of superficial sediments was relatively homogenous throughout the study area; 80% of the sampling stations were associated with finer sediments, i.e. muds and medium to fine sands of particle sizes less than 0.5 mm (Figure 2a). Sediments distributed near the bays of Somme, Authie and Canche, and from Dunkerque harbour to the Belgian border, had a high proportion of fine sands, i.e. median particle sizes of <0.2 mm. Coarser sediments, with a gravel fraction exceeding 50%, were found at only a few stations located along the capes of Gris-Nez and Ailly. As a consequence of strong tidal currents, the organic matter content of sediments was very low, ranging from 0 to 2.03%.

General description of fauna

A total of 167 taxa were identified and consisted of 83 polychaetes (49.7% of the fauna), 35 crustaceans (20.9%), 29 molluscs (17.4%), 8 echinoderms (4.8%) and 12 in the category "diverse" (i.e. anthozoans, nemerteans, sipunculids and cephalochordates) (7.2%). In terms of the numbers of individuals, polychaetes accounted for 68.3% of all specimens recorded. Other groups were less numerous: molluscs constituted 18.6% of the total individuals, crustaceans 8.1%, echinoderms 4.0% and "diverse" 1.0% (Table 1).

The total abundance and species richness recorded from the grab samples was variable throughout the survey area. Abundance ranged from 0 to 1130 ind. 0.5 m^{-2} with a mean of 114.8 ind. 0.5 m^{-2} (s.d. 27.4; Table 1). Similarly, the species richness showed variation from a maximum of 28 species at station 55, to 0 at 3 stations. The average taxonomic diversity was 11.1 (s.d. 6.4). Values for biomass also showed considerable variations, from 0 to a maximum of 310.2 g AFDW 0.5 m^{-2} at station 68. The average for the survey area was 7 g AFDW.0.5 m^{-2} (s.d. 24.4). Most of the biomass was accounted for by molluscs and echinoderms and, to a lesser extent, by polychaetes. Total biomass was negatively correlated with both median particle size and the gravel and sand/gravel fraction, and positively correlated with the silt and clay fraction (Table 2).

Spatial distribution patterns of species richness, abundance and biomass are given in Figure 2b–d. The demographic parameters were distributed more homogenously and continuously in the eastern English Channel, from Cap d'Ailly to Cap Gris-Nez, than in the southern North Sea, where three main patches were identified: at the entrance to Calais and Dunkerque harbours and near to the Belgian border. Greatest species richness, abundance and biomass values were generally located near the main bays (i.e. Somme, Authie and Canche) and close to the Belgian border, at sites characterized by a range of small median particle sizes (<0.5 mm) and by freshwater outflows. Shannon diversity and evenness indices summarize the above observations: to the south of Cap Gris-Nez, values were homogeneously distributed, whereas to the east the distribution was patchier. Diversity values ranging from 3.0 to a maximum of 3.85, and evenness values greater than 0.8, characterized 21.2% and 30.1% of the sites respectively, all of which were situated in the vicinity of freshwater outflows.

Spatial distribution of dominant species and characteristic taxa of fine sediment assemblages

Correlation analysis suggested that the predominant influence on the structure of the benthic populations in the study area is the proportion of gravel and sand/gravel mixtures in the sediment. These factors were significantly correlated with the distribution of eight of the ten highest ranked species (Table 2). Variation in median particle size also exerted an influence, albeit to a lesser degree. However, it is recognized that these are not independent variables but are inter-correlated to a certain degree. Despite statistically significant relationships between the distributions of some dominant species and organic matter content, we do not attach much ecological significance to these because of the generally very low amounts of organic matter encountered.

The spatial distribution of the dominant taxa in the survey area is illustrated in Figure 3. In agreement with the above results, the frequency of occurrence and abundance of these species were greater to the south of Cap Gris-Nez than to the east. Three main patterns can be identified: (i) taxa associated with fine sediments influenced by freshwater outflows (*Macoma balthica* – Figure 3f); (ii) taxa associated with muddy sediments (*Abra alba* – Figure 3e); and (iii) taxa associated with sandy sediments (*Nepthys cirrosa* – Figure 3a; *Donax vittatus* – Figure 3d; *Magelona johnstoni* – Figure 3c; *Ophelia borealis* – Figure 3b).

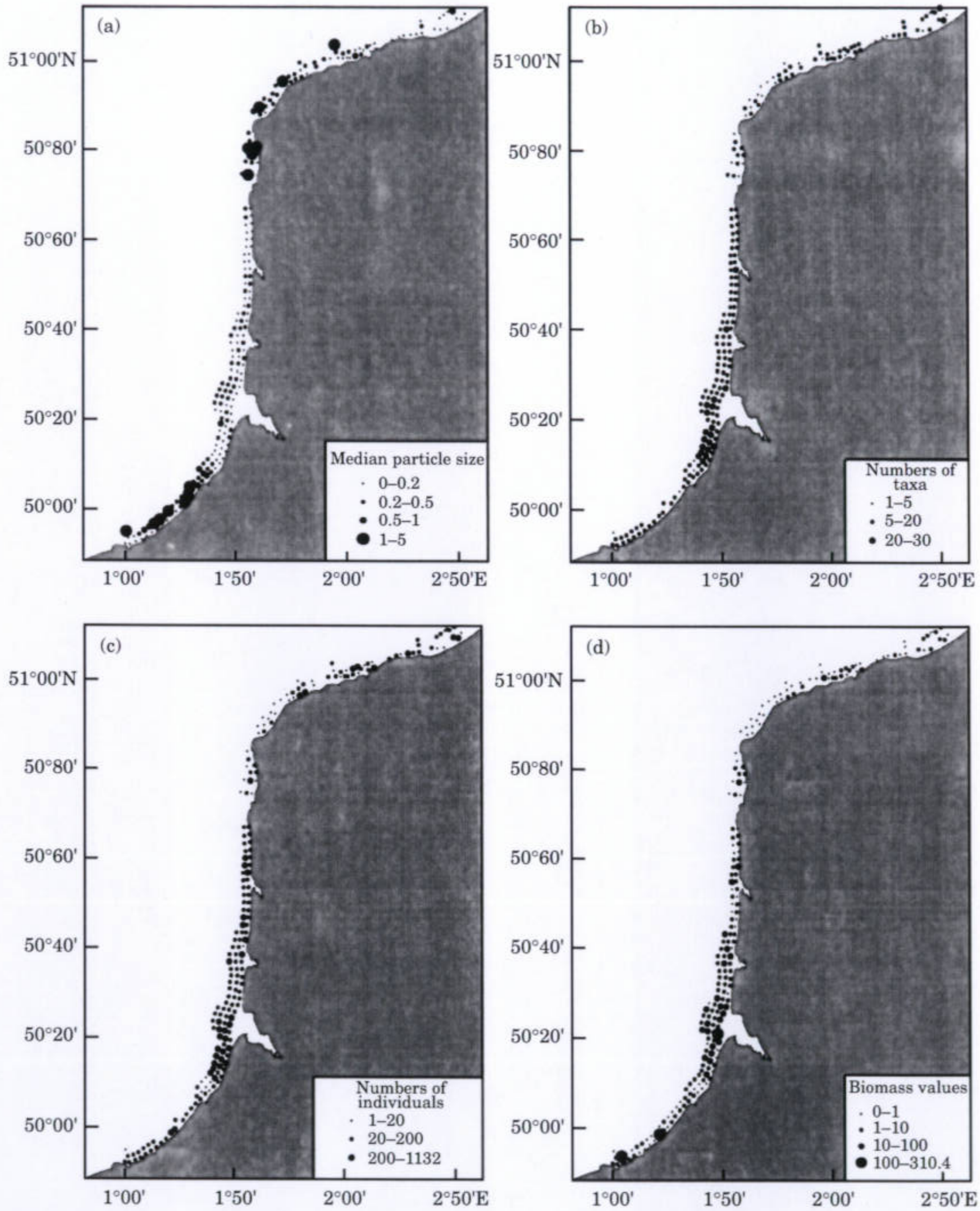

Figure 2. Distribution patterns of (a) median particle size, (b) numbers of taxa, and (c) abundances (No 0.5 m^{-2}) and (d) biomass (g AFDW 0.5 m^{-2}).

Ordination of stations

The area sampled was notable for the number of "rare" species encountered, in that 99 species were recorded at less than five stations. These rare species were excluded from further analysis. As a result, a faunal data set of 204 sites × 68 species was used as input to the FCA. The first six axes of the FCA accounted for only 34.7% of the total inertia. Hierarchical classification, performed while taking into account the inertia of all axes, separated the

Table 1. Mean abundance (ind. $0.5\ m^{-2}$) and biomass (g AFDW $0.5\ m^{-2}$) (± s.d.) of the main zoological taxa.

	Polychaetes	Molluscs	Echinoderms	Crustaceans	"Diverse"	Total
Abundance	78.4 ± 144.6	21.4 ± 44.4	4.6 ± 18.8	0.64 ± 3.4	0.6 ± 0.1	114.8 ± 27.4
Biomass	0.50 ± 0.92	3.46 ± 21.34	2.84 ± 12.26	0.18 ± 0.82	0.006 ± 0.028	6.98 ± 24.38

Table 2. Spearman rank correlation coefficients for total biomass and main macrobenthic species abundance vs. sediment parameters. Significance levels: *p<0.05; **p<0.01; ***p<0.001.

	Median particle size	% gravel (≥2 mm)	% sand/gravel (≥500 μm)	% silt/clay (<63 μm)	% organic matter
Magelona johnstoni	−0.537***	−0.364***	−0.470***	0.128	−0.152*
Nephtys cirrosa	−0.124	−0.230***	−0.239***	−0.224**	−0.251***
Cirratulus cirratus	−0.034	−0.039	−0.035	−0.05	−0.094
Tellina fabula	−0.565***	−0.337***	−0.424***	0.284***	−0.018
Donax vittatus	−0.411***	−0.203**	−0.355***	−0.072	−0.191**
Echinocardium cordatum	−0.244***	−0.276***	−0.259***	0.119	−0.059
Scoloplos armiger	−0.108	−0.154*	−0.140*	0.030	−0.026
Notomastus latericeus	0.063	0.275***	0.210**	0.160*	−0.196**
Urothoe brevicornis	0.111	−0.022	0.016	−0.234***	−0.115
Sigalion mathildae	−0.462***	−0.215**	−0.322***	0.056	−0.122
Total biomass	−0.288***	−0.140*	−0.224**	0.146*	−0.098

more ill-defined site groups, which suggests a degree ofcontinuity in the structure of the assemblage types (Figure 4). Contiguous groups contained common, dominant taxa, reflecting the high level of similarity at which they are linked. The classification of stations resulted in one major unity (Group "G"=163 sites), which accounted for approximately 80% of all stations, five small Groups ("A"=2 sites; "B"=9 sites; "C"=5 sites; "D"=4 sites; and "F"=20 sites), and an isolated site not associated with any other cluster ("E"=station 222). Excluding Group E, the distribution of classes was found to be significantly correlated with sediment distribution (Spearman rank correlation: $P<0.05$), as shown in Figure 5.

Group A sites are associated with the most oligospecific assemblage, as only five taxa in low densities were identified (Table 3). The assemblage, typified by *Mactra corallina* and *Ensis arcuatus*, occurred in medium to fine sands located off Cap Blanc-Nez and in the southeastern region of the Bay of Somme (Figure 5). Molluscs in this group were responsible for 98% of the total biomass (3.482 g AFDW $0.5\ m^{-2}$). The Group B assemblage is also mainly located near to Cap Blanc-Nez, a region where tidal currents can be locally enhanced. Associated with heterogeneous sands, the fauna of this group (18 species) is characterized by *Gastrosaccus spinifer* and dominated by typical inhabitants of mobile sandy sediments, such as *Nephtys cirrosa* and *Ophelia borealis*. As a result of the low abundance of species associated with this group, biomass values are correspondingly low (0.346 g AFDW). Group C stations are associated with various deposits ranging from fine to coarse sands, and were occasionally enriched by heterogeneous particles (shells or gravel), as indicated by the presence of *Sagartia troglodytes* and *Malmgrenia arenicolae*, which were among the five top ranked species. This assemblage of 10 species is spatially limited to those sand banks adjacent to Cap Blanc-Nez and to the southern region of the Bay of Somme. The Group D assemblage, associated with Group E by way of a similar species composition, occurs at a few sites in the southeastern Bay of Somme and off Dunkerque Harbour, and is characterized by muddy heterogeneous sands found in the channels separating the sandbanks. Of the 32 species recorded, *Crepidula fornicata*, *Abra alba*, and *Sagartia troglodytes* were the most abundant. This assemblage group could be interpreted as transitional as it also comprises fauna that are characteristic of pebbles and muddy fine sediments. Group F (90 species), typified by *Notomastus latericeus* (elective – constant), is located along the coast of Cap d'Ailly, adjacent to Boulogne and Dunkerque harbours, and near to the Belgian border where it progressively replaces the Group D assemblage. The dominant species of Group F show an affinity for muddy fine sands (*Notomastus latericeus*, *Abra alba*, *Ensis directus* and *Tellina fabula*) and heterogeneous sediments (attested by the occasional presence of *Sthenelais boa*). Group G stations occur in medium to fine sands that are sometimes enriched with silt/clay, as indicated by the presence of *Magelona johnstoni*,

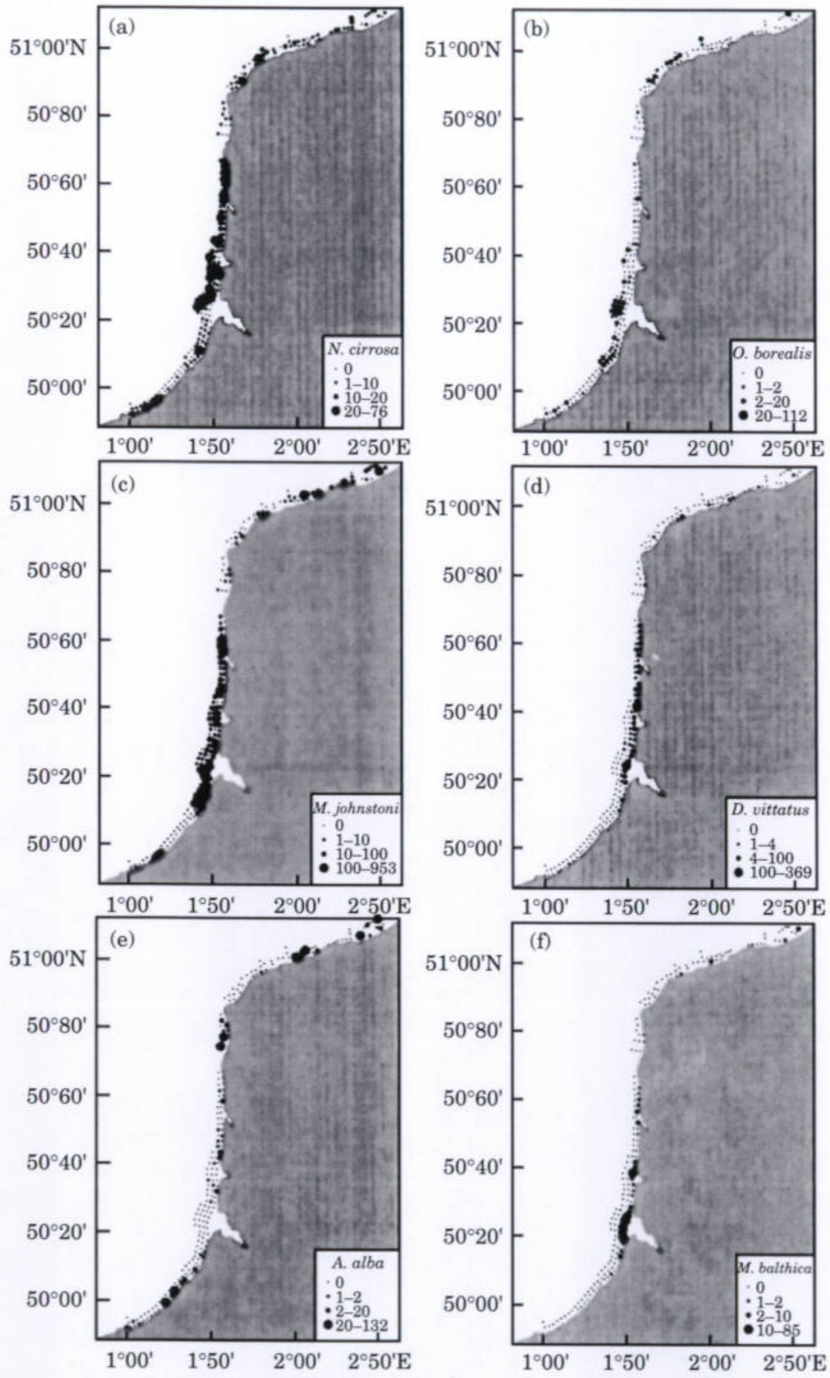

Figure 3. Distribution and abundances (ind. 0.5 m^{-2}) of (a) *Nephtys cirrosa*, (b) *Ophelia borealis*, (c) *Magelona johnstoni*, (d) *Donax vittatus*, (e) *Abra alba* and (f) *Macoma balthica* populations. Upper limits of each classes defined are excluded to intervals.

Nephtys cirrosa and *Donax vittatus*. The assemblage, characterized by the polychaetes *Magelona johnstoni* and *Sigalion mathildae* (constant – elective), accounted for 186 sites located from Cap d'Ailly to the Belgian border, and supported a greater diversity of species (133) as well as enhanced densities and biomass (average of 7.926 g

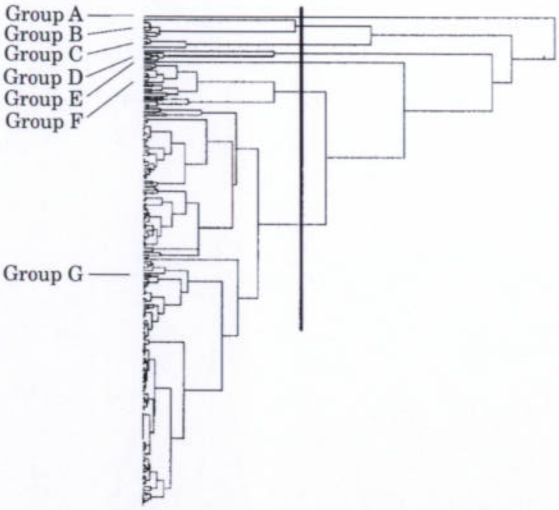

Figure 4. Dendrogram resulting from hierarchical ascendant classification of stations (Ward's method).

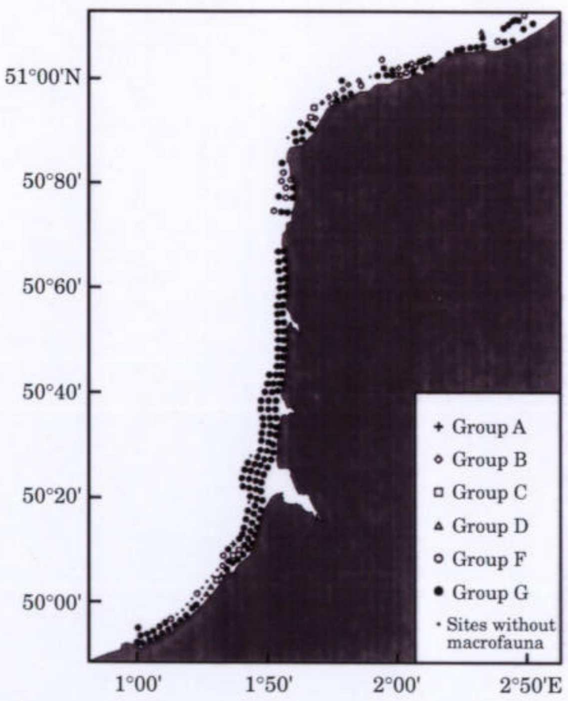

Figure 5. Spatial distribution of the faunal assemblages (Group E excluded) defined by FCA and hierarchical classification.

AFDW 0.5 m^{-2}). The fauna of Group G stations found in shallower areas was enriched by estuarine species, such as *Macoma balthica* and *Cardium edule*. Group G stations therefore comprised two subgroups, divided at a high similarity level, corresponding to coastal and offshore stations (Figure 4).

Discussion

The uniformity of the seabed environment along the French coast of the eastern English Channel and southern North Sea contrasts strongly with the heterogeneity reported in offshore sediments where various substrata are represented, such as pebbles, muddy heterogeneous sediments, fine to coarse sands, and muddy-fine sediments (Davoult *et al.*, 1988). As a consequence, about 80% of the shallow sites support a single benthic assemblage typified by species showing an affinity for sands or slightly muddy sands, such as *Magelona johnstoni* and *Nephtys cirrosa*. This well-known species association, used in the classification of biotopes by conservation workers, extends along the Belgian (Govaere *et al.*, 1980) up to the western Scheldt estuary (Vermeulen & Govaere, 1983).

Considering the large extent of the area we sampled (≈ 800 km^2), the number of taxa recorded (167) is relatively low and cannot easily be compared with data from previous studies due to differences in sieve mesh size (1 or 2 mm), the sampling gear used (Rallier du Baty dredge, Smith–McIntyre or Hamon grabs) and the surface area sampled. The large number of taxa classified as "rare" although to some extent influenced by use of a larger (2 mm) sieve mesh, indicate that the majority of large animals in the sediments encountered in the study area are present in relatively low densities and are also patchily distributed. Moreover, the survey was conducted during the winter period, which is characterized by a low abundance of benthic fauna in the English Channel (Dauvin, 1984; Thiébaut *et al.*, 1997). The analysis of long-term data series for the *Abra alba* community on the southern North Sea, adjacent to Gravelines, also highlights the difference in species richness, abundance and biomass that exists between winter and summer as a consequence of pronounced seasonal fluctuations (Ghertsos *et al.*, 2000).

Species abundance varied along the coastal survey area; several sites were strongly dominated by a few species such as *Magelona johnstoni*, which represented more than 60% of the total abundance at some sites. Depending on meteorological conditions, and after any post-settlement mortality that may occur in response to physical and biological characteristics of the habitat, new recruits can form patches of high abundances, as observed for *Ensis directus* in the southern North Sea (Luczak, 1996). Variable currents and winds can induce unpredictable changes from year to year in the abundance and structure of macrobenthic assemblages in the southern part of the North Sea (Nihoul, 1975; Belgrano *et al.*, 1995). These stochastic dispersions differ from the larval retention reported in the Bay of Seine (Lagadeuc, 1992; Thiébaut *et al.*, 1992; Thiébaut *et al.*, 1994), which is responsible for the spatio-temporal persistence of the muddy–fine sand assemblage.

Table 3. Averaged density (ind. 0.5 m^{-2}, $\bar{y}$) of the top five ranked taxa and characteristic species (in bold; C: Constant; E: Elective; P: Preferent) for assemblage (E excepted) defined by FCA. Mean, maximal and minimal values for number of taxa, abundances, biomass, median particle sizes, depths are listed with habitat types.

	A	$\bar{y}$	B	$\bar{y}$	C	$\bar{y}$
	Gastrosaccus spinifer	4.4	*Nephtys cirrosa*	7.0	*Sagartia troglodytes*	3.4
	Ensis arcuatus (C, P)	1.0	***Gastrosaccus spinifer*** (C, P)	4.4	*Ophelia borealis*	2.0
	Mactra corallina (C, E)	0.4	*Ophelia borealis*	2.4	*Tellina tenuis*	0.4
	Processa canaliculata	0.4	*Magelona johnstoni*	1.4	*Nephtys cirrosa*	0.4
	Glycera gigantea	0.4	*Urothoe brevicornis*	0.8	*Malmrenia arenicolae*	0.4
Number of taxa	2.5 (2–3)		4.7 (3–7)		2.8 (1–5)	
Number of individuals	7.0 (3.0–11.0)		19.2 (7.0–51)		8.0 (2.0–23)	
Biomass (g AFDW 0.5 m^2)	3.482 (0.114–6.854)		0.346 (0.076–0.756)		0.260 (0.026–1.006)	
Median diameter (mm)	0.35 (0.26–0.44)		0.29 (0.13–0.39)		0.32 (0.29–0.38)	
Depth (m)	9.0 (5.0–13.0)		13.2 (2.5–21)		8.8 (5–17.8)	
Habitat type	Clean medium–fine sand		Mobile clean medium–fine sand ± heterogeneous particles		Coarse to fine sand	
	D	$\bar{y}$	**F**	$\bar{y}$	**G**	$\bar{y}$
	Crepidula fornicata	52.6	***Notomastus latericeus*** (C, P)	29.6	***Magelona johnstoni*** (C, P)	58.2
	Abra alba	12.0	*Abra alba*	21.8	*Nephtys cirrosa*	10.0
	Sagartia troglodytes (C, P)	10.4	*Ensis directus*	3.2	*Donax vittatus*	6.8
	Urothoe poseidonis	4.6	*Tellina fabula*	2.8	*Cirratulus cirratus*	6.8
	Polycarpa gracilis	4.6	*Heterocirrus alatus*	2.0	*Scoloplos armiger*	5.4
	Owenia fusiformis (C, P)	1.0			***Sigalion mathildae*** (C, E)	4.2
Number of taxa	11.7 (7–17)		13.3 (4–21)		12.5 (1–28)	
Number of individuals	113.4 (25.4–196.0)		92.4 (10.0–401.0)		135.6 (1.0–1130)	
Biomass (g AFDW 0.5 m^2)	4.128 (0.270–7.718)		4.428 (0.052–23.808)		8.606 (0.005–310.258)	
Median diameter (mm)	1.81 (0.19–4.50)		0.86 (0.11–2.63)		0.28 (0.11–2.44)	
Depth (m)	7.2 (5.0–14.0)		10.5 (3.4–19.7)		7.3 (0.5–21.5)	
Habitat type	Muddy heterogeneous sand		Stable lightly muddy medium–fine sand ± heterogeneous particles		Stable lightly muddy fine sand ± heterogeneous particles	

Table 4. Biomass values (g AFDW m^{-2}) recorded for *Abra alba* community in different location in the English Channel. Values, initially expressed in dry weight (DW) were conversed in AFDW from results reported by Ricciardi and Bourget (1998): AFDW=0.75 × DW.

Study	Area	Biomass (g AFDW m^{-2})
Davoult *et al.* (1988)	From Boulogne to Dunkerque	15.0–37.5
Dewarumez *et al.* (1992)	Gravelines	45.0–187.5
Thiébaut *et al.* (1997)	Bay of Seine (1986)	23.5
Thiébaut *et al.* (1997)	Bay of Seine (1987)	27.5
Thiébaut *et al.* (1997)	Bay of Seine (1988)	24.2
Thiébaut *et al.* (1997)	Bay of Seine (1991)	26.0
Dauvin (1998)	Pierre Noire	10.6
Dauvin (2000)	Morlaix river	10.9
Ghertsos *et al.* (2000)	Gravelines	52.5–3000
Govaere *et al.* (1980)	Belgian coasts	2.7
Our study	Eastern English Channel–southern North Sea	8.1

Relative proximity to inshore waters, outflows from bays, harbours and the Scheldt estuary were all factors that enhanced the structure of the benthic community along the French coast of the eastern English Channel and southern North Sea. Increases in species diversity, abundance and biomass may indicate an increased food supply at these locations, as recently reported by Rees *et al.* (1999) for macrobenthic assemblages along the UK coast. The disparity between benthic assemblages in the eastern English Channel and the southern North Sea is clearly demonstrated; species diversity, density and biomass values are greatest and their distribution patterns more continuous in the eastern English Channel from Cap d'Ailly to Cap Gris-Nez. Beyond Cap Gris-Nez, and despite the presence of a homogeneous habitat, a biological "fragmentation" is observed as three patches were identified. It is, however, surprising that samples collected in the first survey seem to be on the whole homogeneous, while those collected in the second do not. This tendency could reflect temporal or artifactual differences rather than spatial differences, but could also be related to a decreasing trend in biomass with latitude, as reported by Heip *et al.* (1992) for North Sea macrofauna. Organic matter content, although found to be influential in determining the distribution of the *Abra alba* assemblage in the eastern Bay of Seine (Thiébaut *et al.*, 1997), cannot be considered a significant parameter in our study area as the amounts recorded are very low.

The factorial correspondence analysis revealed six major site groups, which can be associated with three main assemblages. Rather than viewing these as discrete and isolated entities, they may be better viewed as noda along a continuum, as their faunal composition progressively varies with edaphic parameters and hydrodynamics. Despite local trends in accretion and erosion that are related to hydrological changes, the comparison with previous studies of spatial distributions (Cabioch and Glaçon, 1975, 1977; Davoult *et al.*, 1988) does not suggest drastic changes. Site Groups A, B and C, characterized by species showing an affinity for well-sorted medium to fine sands, were found to occur in sediments subjected to significant physical disturbance, such as would be caused by strong tidal streams and wave action. These species associations clearly ascribed to the *Ophelia borealis* assemblage defined by Thorson (1957) are also distributed on the southeast English coasts (Rees *et al.*, 1999). Due to (i) natural deposits of mud, (ii) erosion of cliffs and (iii) *Crepidula fornicata* colonies, the shells of which modify the flow regime at the sediment/water interface, sandy substrates are progressively colonized by species living on muddy heterogeneous sediments such as *Cirratulus cirratus* and *Sthenelais boa*. As a result, the muddy heterogeneous sediment assemblage (Group D sites) progressively replaced the *Ophelia borealis* assemblage. Group F sites, which including a few components of the muddy heterogeneous sediments (e.g. *Sthenelais boa*), progressively replaced the Group D assemblage. A common group of species that characterize slightly muddy sands or slightly mixed sediments (*Notomastus latericeus*, *Owenia fusiformis*, *Pectinaria koreni*, *Ophiura texturata*) links Group F and G sites, which are both comparable with the *Donax vittatus–Macoma balthica* form of the *Abra alba–Corbula gibba* assemblage (Cabioch and Glaçon, 1975). Although the biomass distribution pattern is highly heterogeneous due to local dominance of molluscs and echinoderms, the average biomass for the study area (4.03 ± 13.08 g AFDW 0.5 m^{-2} for F and G assemblages) is respectively lower and higher to that reported in other areas in the Channel and along the Belgian coast (Table 4). The one exception is at Gravelines, where a very high biomass was observed in 1992 and 1994 as a result of mass recruitment of *Lanice conchilega* and *Ensis directus* (Luczak, 1996). Average biomass values of 0.77 g AFDW 0.5 m^{-2} from Calais to the Belgian border compared to 5.30 g AFDW $0.5\ \mathrm{m}^{-2}$ from Cap d'Ailly to Boulogne harbour confirm the contrast in benthic productivity either side of the Dover strait.

On French coasts the increasing need for coastal zone observation, brought about by a desire to enhance environment quality and public health, has led to the development of national grid systems for water quality monitoring. These grids allow an examination of changes in chemical and biological parameters in the pelagic ecosystem in relation to natural or human influences. The data are valuable in increasing our knowledge of coastal areas, for example through their use in calibrating or validating models. However, data acquisition was until recently mainly focused on water column processes and not sufficiently on benthic environments. Studies of benthic communities are, nevertheless, essential for monitoring changes in biodiversity and initiating adaptive management measures in order to preserve the integrity of shallow areas and the species of commercial interest that they support may be preserved. In the North Sea, efforts to describe and interpret variability in the benthic fauna over large geographical areas are more developed (Eleftheriou and Basford, 1989; Kunitzer *et al.*, 1992; Duineveld and Van Noort, 1990; Jennings *et al.*, 1999). The potential benefits from studying shallow benthic communities over such a wide spatial scale are clearly demonstrated. Such data provide a valuable baseline for understanding changes in benthic communities and can act as a useful tool for environmental monitoring and conservation projects.

Acknowledgements

The authors would like to thank the crew of N/O "Côtes de la Manche" and S. Baudet, L. Dauvin, L. Denis, S. Gaillard, T. Ruellet, C. Six, S. Skibinski and E. Thiébaut for participating in the sea missions. C. Luczak is gratefully acknowledged for his help in statistical treatments. Authors are also grateful for comment and corrections on the manuscript made by H. L. Rees and address their special thanks to Dr Paul Eastwood for help in correcting the English text.

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Vol. 270: 41–53, 2004

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published April 14

Influence of spring phytodetritus sedimentation on intertidal macrozoobenthos in the eastern English Channel

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ABSTRACT: The North Sea shallow waters of the eastern English Channel are recurrently affected by the high algal spring bloom of the Prymnesiophyte *Phaeocystis* spp. When the bloom has run its course, foam accumulations resulting from the release of mucilaginous polysaccharides can be observed both on the sea surface and on beaches. Four beach sites, 2 that were affected and 2 that were not, were sampled from April to December 2001 and from April to August 2001 respectively. The physical and chemical conditions of the sediment, as well as the macrofauna associated with it, were assessed in the Canche Bay before, during and after the phytodetritus sedimentation period. *Phaeocystis* spp.-derived material significantly changed the grain-size distribution in accumulation areas as shown by the resulting fine-particle input (>60%) observed. Due to the rapid decomposition of decaying colonies, organic content increased in the sediments towards the end of the bloom, marked by a single peak on sands or strong, persistent enrichment on muds. As a result of this increase in organic matter, oxygen flux increased over time. In the low-energy silty environment, severe anoxic conditions rapidly occurred whereas on areas subject to tidal or wind-induced turbulence, superficial residual crusts resulting from drying foam prevented oxygen diffusion into sandy sediment. At the impacted sites, all macrobenthic taxa were affected, and both the number of species and their densities were simultaneously reduced. Sandy assemblages showed a better recovery, starting in July, due to more suitable environmental conditions, while on muddy assemblages full recovery had still not occurred by the end of the year. Spring recruit mortality was partly responsible for the lack of faunal recovery, which was mainly dependant on the migration of adults from the surrounding area.

KEY WORDS: *Phaeocystis* spp. bloom · Organic matter input · Macrobenthos · Recovery

INTRODUCTION

In the eastern English Channel and the Southern Bight of the North Sea, high biomass algal blooms (over 20 µg chl *a* ml^{-1}) are recurrent spring events. Blooms are composed primarily of strains of the Prymnesiophycae *Phaeocystis* spp., but diatoms are also present (Adams 1987, Reid et al. 1990, Tett & Mills 1991, Boon et al. 1998). The information currently available would seem to indicate that the *Phaeocystis* spp. complex in the eastern English Channel–North Sea coastal waters includes both the dominant non-toxic alga *Phaeocystis globosa* (Baumann et al. 1994) and the toxic alga *P. pouchetti* (Lancelot et al. 1987). However, differences between the 2 species are still ill defined, and the existence of 2 species remains uncertain (Baumann et al. 1994). One of the characteristic features of *Phaeocystis* spp. blooms is the production of large amounts of mucoid colonial material, representing up to 90% of total algal biomass (Rousseau et al. 1990). Historical and contemporary records indicate that *Phaeocystis* spp. colony blooms are closely related to changes in land use and/or hydraulic and waste management systems that, over the last century, have increased the presence of nitrates in the coastal area (Lancelot 1995). Harmful events have been linked to

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the gelatinous nature of the *Phaeocystis* spp. colony matrix, which releases mucilaginous polysaccharides after disrupting senescent colonies. At the end of the spring bloom, massive sedimentation takes place, with sedimentation rates >800 mg C m^{-2} d^{-1} being reported in the Barents Sea (Wassmann et al. 1990). In intertidal areas, a spectacular consequence of the post-bloom sedimentation is the formation of large amounts of foam on the beaches (Lancelot et al. 1987, Lancelot 1995). Two to 3 wk after the *Phaeocystis* spp. bloom, massive phytodetritus deposits and associated organic material inputs result in large numbers of dead benthic or other moribund organisms in intertidal depositional areas (N. Desroy pers. obs.). Although the ecological effects of *Phaeocystis* spp. on the pelagic food web have been relatively well studied, the impact of this increase in organic matter on the intertidal fauna and on the benthic food web has received only incidental interest (Weisse et al. 1994). Sedimentation can cause changes in (1) the physical environment at the sediment-water interface by modifying the sediment characteristics (Wassmann 1994), (2) the microbiology and chemistry of the underlying sediments by inducing benthic anoxia problems through the remineralization of sedimented phytodetritus-derived organic matter (Graf et al. 1983, Wassman et al. 1996, Boon et al. 1998, 1999), and (3) benthic fauna (Boon et al. 1998).

The aim of this paper is to describe the impact of phytodetritus post-bloom sedimentation (comprised mainly of the decaying remains of *Phaeocystis* spp. colonies) on the intertidal benthic habitat and macrofauna in the Canche Bay, situated on the French coast of the eastern English Channel. As the greatest proportion of organic matter is likely to sediment out in accumulating areas, sediment characteristics are important variables in an evaluation of the possible impact of sedimentation. For this reason, standard physical parameters (granulometry, pigment concentration and sedimentary organic matter content) were measured, as were certain biological parameters (macrofauna). Given that the extent of areas exhibiting oxic and anoxic degradation provides indications of biogeochemical changes (Smetacek et al. 1991, Justic et al. 1994), oxygen profiles were also measured to emphasize the mineralization processes in superficial sediments.

MATERIALS AND METHODS

Study site and sampling strategy. The Canche Bay, whose intertidal surface covers ca. 630 ha, is situated in the eastern part of the English Channel (Fig. 1). The average tidal range is ca. 7 m for a spring tide and 3 m for a neap tide. River discharge varies seasonally, from a maximum of 100 m^3 s^{-1} in winter to a minimum of 60 m^3 s^{-1} in summer. Previous observations have shown that foam deposits resulting from sedimentation at the end of *Phaeocystis* spp. blooms are highly variable, both spatially and temporally. However, the north side of the bay is more frequently affected by foam sedimentation than the south side (L. Denis pers. obs.). The resulting sampling strategy integrated 4 intertidal sites that were daily immersed and emerged, 2 situated on either side of the upstream bay. To the north, north sand (NS) was characterized by medium to fine sands and north mud (NM) was characterized by mud; while to the south, south sand (SS) was characterized by muddy fine sands and south mud (SM) by mud (Fig. 1). The NM and SM sites emerged at high tide (HT) + 2 h, and the NS and SS sites at HT + 3 h. Benthic assemblages at these sites were the *Macoma balthica* community (Petersen 1913) at Sites NM, SM and SS, and an impoverished form of the *Abra alba–Corbula gibba* community (Cabioch & Glaçon 1975), characterized by *Donax vittatus* and *Macoma balthica*, at Site NS.

Sampling was performed with the dual purpose of gathering quantitative data concerning the physical and chemical parameters of the sediment as well as the different macrobenthic populations; the sampling periods depended on the parameters under study (Table 1). Because recovery was faster at southern than northern sites, different sampling timelines were

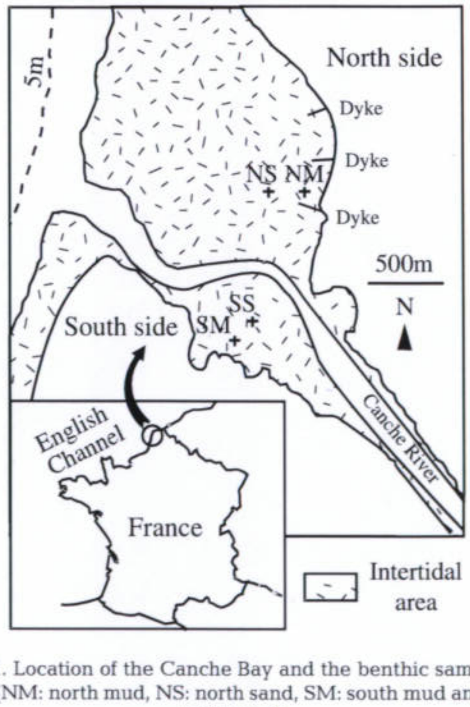

Fig. 1. Location of the Canche Bay and the benthic sampling sites (NM: north mud, NS: north sand, SM: south mud and SS: south sand)

Table 1. Sampling dates of the physical, chemical and biological parameters studied at each site (Year 2001). Foam accumulation (visual obs.) evident on 3/05, 14/05, 23/05, 4/06 and 13/06. NS: north sand; NM: north mud; SS: south sand; SM: south mud

	05/04	13/04	25/04	03/05	14/05	23/05	04/06	13/06	05/07	24/08	01/10	19/10	12/12
Sites NM and NS													
Granulometry	x					x					x		
Organic matter	x	x	x	x	x	x	x		x	x	x		
Oxygen flux	x	x	x	x	x	x	x	x	x				
Benthic pigments	x	x	x	x		x	x	x	x	x			
Macrofauna	x	x	x	x	x	x	x	x	x	x	x	x	x
Sites SM and SS													
Granulometry	x					x					x		
Organic matter	x	x	x	x	x	x	x		x	x			
Oxygen flux	x	x	x	x	x	x	x	x	x				
Benthic pigments	x	x	x	x		x	x	x	x	x			
Macrofauna	x	x	x	x	x	x	x	x	x	x			

required; the north was observed from April to December 2001 and the south from April to August 2001. A total of 13 surveys were conducted in the northern sites while 10 were done in the southern sites. An approximately 10 d sampling frequency was maintained during the main period of foam accumulation (from April to June), slowing to a monthly sample after July.

Phytoplanktonic bloom monitoring. The monitoring networks SOMLIT (Réseau National des Stations Marines–CNRS INSU) and REPHY (Ifremer) provided data concerning the chl *a* concentration and the numeration of *Phaeocystis* spp. cells in coastal waters (50° 46.190 N, 00° 13.605 E) near the Canche Bay.

Sediment samples. *Granulometry and organic matter:* Two replicate cores of sediment were taken at low tide with a hand corer (7 cm diameter) and were subsequently analyzed at the laboratory. Particle size distribution was assessed (wet sieving) before the foam began accumulating (4 April), during foam accumulation (23 May) and after it stopped (1 October, Table 1). Organic matter content was calculated from measurements of weight loss after 6h at 600°C (Luczak et al. 1997).

Oxygen content: Dissolved oxygen concentrations were measured in 2 sediment samples to take spatial heterogeneity in foam accumulation into account and to limit the time required to realize (manually) microprofiles before oxygen concentration evolved in surficial sediments. Samples were taken using a cylindrical core (2.6 cm diameter) that enclosed a 20 cm long sediment column. A sealing top valve prevented disturbance of the sampled sediment-air interface. Oxygen microprofiles were measured immediately on returning to the laboratory, under minimal light conditions. Dissolved O_2 concentrations were measured with an oxygen microelectrode that had a built-in reference and an internal guard cathode (Revsbech 1989). The O_2 microsensor had an outer tip diameter of 100 µm and a 95% response time of 5 s. The vertical resolution of the measurements was 50 µm. The position of the sediment-air interface was determined from O_2 microprofiles, using a modified version of the technique developed by Sweerts et al. (1989), which consists of assigning the interface position to a break in the oxygen concentration gradient. Because our method for measuring dissolved oxygen concentrations is non-destructive, study samples were also used to determine sediment porosity.

The flux was estimated from the oxygen microprofiles using the following formula:

$$J = \varphi \times D_s \times \left(\frac{dC}{dz}\right)_{z=0} \quad (1)$$

where J is the diffusion flux (µmol m^{-2} h^{-1}), φ is the porosity, D_s is the diffusion coefficient (cm^2 s^{-1}), dC is the estimated concentration gradient just below the sediment-water interface, and z is the depth in the sediment scale positively downward. D_s is calculated using the following formula: $D_s = D_m/\theta^2$, where D_m is the molecular diffusion rate at *in situ* temperature and θ is the sediment tortuosity. D_m was calculated according to the formula:

$$D_m = D_0 + at \quad (2)$$

where D_0 is the molecular diffusion rate at 0°C, a is a coefficient relative to the oxygen (Soetaert et al. 1996) and t is the ambient temperature. θ can be calculated from the porosity according to the formula:

$$\theta = \varphi^{(1-m)} \quad (3)$$

where m is an adjustment value depending on sediment granulometry ($m = 2$ for muddy sands and mud with $\varphi < 0.7$; Ullman & Aller 1982).

Benthic pigments: Following the bloom and the resulting phytodetritus sedimentation, pigments characterizing *Phaeocystis*, e.g. 19'-hexanoyloxyfucoxanthin (Liaan-Jensen 1985, Adams 1987, Reid et al. 1990, Tett

& Mills 1991, Boon et al. 1998, Goffart et al. 2000) are generally too degraded to be detected in the sediment (Boon et al. 1998). Consequently, quantitative estimations of the contribution of *Phaeocystis* spp.-derived material to the organic matter input in the sediment are not easily provided. The single observable indication is the depth of foam accumulations and the presence of cells or colony fragments in the sediment. Although chl *a* and phaeopigments do not characterize *Phaeocystis* spp.-derived material and do not provide evidence of a change in the composition of material reaching the benthos over the sampling season, the concentrations of these pigments were measured at all sites in order to assess the extent of phytodetritic sedimentation. Benthic chl *a* and phaeopigment concentrations were determined for each sampling date, using 2 sample cores (2.6 cm diameter × 20 cm deep) taken at each site. The top 3 centimeters were sliced and frozen (–25°C) for later analyses. Samples were thawed, and pigments were extracted, using 15 ml of 90% acetone for 4 h in the dark at 8°C. Pigment concentrations were determined before and after acidification, using standard spectrophotometric techniques (Lorenzen 1967).

Biological samples: At each site, 4 replicates for benthos analysis were collected using a 0.027 m^2 hand corer (20 cm depth), which provides a total surface of 1/9 m^2, 0.1 m^2 constituting the minimal sampling area in the bay (N. Desroy pers. obs.). The collected organisms were sieved through 1 mm mesh, fixed with 10% formalin containing Rose Bengal stain, sorted, identified and counted at the laboratory.

Data analysis. Macroinvertebrate community structure was described at each site and for each sampling date by determining the number of species and their abundance as well as the Shannon-Wiener diversity. The significance of the changes in the sedimentary variables (e.g. granulometry, organic matter content, oxygen flux and pigment content) and in the biological index over the course of the sampling period was tested using a 1-way ANOVA. Prior to completing the ANOVAs, a preliminary test for variance homogeneity (Cochran's test) was conducted in each case, and when necessary, heterogeneity was removed by performing a log $(x + 1)$ transformation.

Significance tests concerning the differences in macrobenthic community descriptors for the different sites and times were performed, using a 2-way ANOVA. Seasonal changes in community composition were visualized through non-metric multidimensional scaling (MDS) plots, based on triangular matrices of the Bray-Curtis similarities, by performing a square-root transformation of the species abundance data. The faunal groups contributing to the dissimilarity between samples, observed via MDS ordination, were investigated using the similarity percentages procedure, SIMPER (Clarke & Warwick 1994), and these results were used to help interpret the faunal changes responsible for the patterns observed in the MDS ordination. The contribution of each species to the average similarity within each group was also analyzed. Finally, the relationships between the sedimentary and biological variables were analyzed separately, using the BIO-ENV procedure developed by Clarke & Warwick (1994) to define the environmental variables (organic matter content, oxygen flux, chl *a* and phaeopigment contents) that explain assemblage structures. The BIO-ENV procedure (using Spearman's rank correlation method) was used on the untransformed environmental variables and the square root transformations of abundance data for each site. Correlations were calculated only on the data collected from 4 April to 5 July, because the oxygen flux measurements were not measured beyond this date.

RESULTS

Initiated in March, the phytoplanktonic bloom peak was observed in April/May, with values of chl *a* up to 20 µg ml^{-1} (Fig. 2). In the water column, the numeration of *Phaeocystis* spp. cells was documented from a

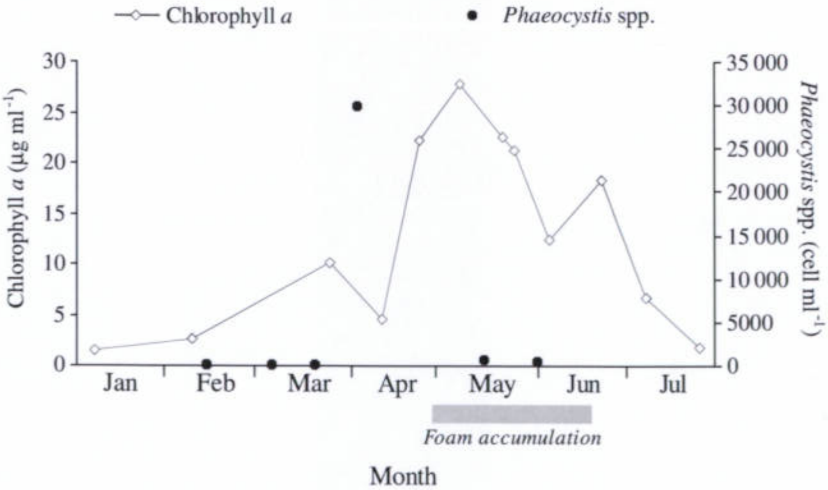

Fig. 2. Chl *a* rates (µg ml^{-1}, data provided by the SOMLIT monitoring framework) and *Phaeocystis* spp. cells ml^{-1} (data provided by the Reseau phytoplancton [REPHY] monitoring framework — Ifremer) in the nearshore coastal waters near Canche Bay from January to July 2001. The period of foam accumulation on the north side of the bay is indicated (grey bar)

Table 2. Variations in sediment granulometry (±SD) at the sampling sites in April (B: before the bloom), May (D: during the deposition) and October (A: after the deposition). Significance levels from a 1-way ANOVA are indicated: *p < 0.05; no asterisk = p > 0.05 (not significant). NS: north sand; NM: north mud; SS: south sand; SM: south mud

Site	% Silt-clay (<63 µm)			% Sand/gravel (≥500 µm)			Median particle size		
	B	D	A	B	D	A	B	D	A
NM	27.3 ± 11.5	74.8 ± 4.7*	70.0 ± 4.8*	0.5 ± 0.8	0.5 ± 0.1	0.7 ± 0.0	0.10 ± 0.0	0.03 ± 0.0	0.04 ± 0.0
NS	3.1 ± 0.6	7.58 ± 5.1	0.4 ± 0.0	1.4 ± 0.0	1.7 ± 1.3	1.6 ± 0.3	0.14 ± 0.0	0.14 ± 0.0	0.14 ± 0.0
SM	23.9 ± 2.0	27.1 ± 26.5	14.4 ± 0.3	2.5 ± 0.2	4.0 ± 5.0	1.7 ± 0.2	0.11 ± 0.0	0.09 ± 0.0	0.11 ± 0.0
SS	4.5 ± 2.1	0.3 ± 0.3	0.2 ± 0.0	0.5 ± 0.0	1.3 ± 0.6	0.2 ± 0.2	0.14 ± 0.0	0.14 ± 0.0	0.15 ± 0.0

minimal monitoring, providing 6 values from February to June. Despite their limited range, data emphasized that reaching a concentration of 30 000 cells ml^{-1} at the beginning of April, *Phaeocystis* spp. contributed heavily to this high primary production. When the *Phaeocystis* spp. bloom ended, large amounts of foam containing fine particles settled on the north side of the bay from the end of April to the middle of June. The presence of numerous decaying colony fragments in the superficial sediments underlined the significant quantities of *Phaeocystis* spp.-derived material in the phytodetritus accumulations at Sites NM and NS. The difference in bentho-pelagic coupling on the 2 sides of the bay was assessed by the absence of foam accumulation in the southern sites.

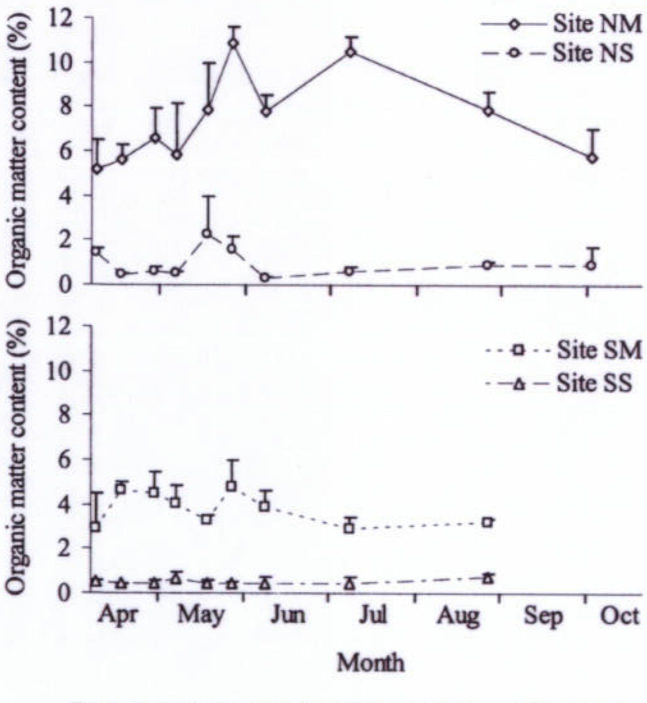

Fig. 3. Organic matter content (% dry weight) variations at north mud (NM), north sand (NS), south mud (SM) and south sand (SS) sites from March to October 2001. Error bars denote +SD

Granulometry

The north side of the bay, particularly the mudflat (Site NM), was most affected by foam accumulations. As a result, the granulometric change was obvious at Site NM, where silt-clay fractions increased significantly, e.g. up to 60 % ($p < 0.05$) in the sediment sample of 23 May (Table 2). At the other sites, changes in granulometric composition were insignificant ($p > 0.05$).

Organic matter content

As suggested by Fig. 3, the significantly highest organic matter percentages were consistently measured at Sites NM and SM (month pooled; $p < 0.001$). One-way ANOVAs indicate significant changes in organic matter over time at Sites NM ($p < 0.001$) and NS ($p < 0.01$). An increase in the organic matter content following the accumulation period was observed on 23 May and 5 July at Site NM and on 14 May at Site NS. Values reverted more rapidly to initial levels at Site NS (from 4 June) than at Site NM (from 1 October). A significant change over time was also observed at Site SM (1-way ANOVA, $p < 0.01$), despite the apparent stability of organic matter content, though no significant changes were apparent at Site SS ($p = 0.22$).

Oxygen flux

An overall significant difference between the oxygen flux in the muddy and the sandy sediments was observed from April to July (months pooled; $p < 0.001$), with mean values of 1690 ± 925 (Site NM) and 1527 ± 504 (Site SM) µmol m^{-2} h^{-1} and mean values of 356 ± 524 (Site NS) and 495 ± 286 (Site SS) µmol m^{-2} h^{-1}, respectively. Although some temporal trends were obvious, ANOVA yielded insignificant differences at each site ($p = 0.098$, Site NM; $p = 0.101$, Site NS) due to the heterogeneous replicate values of the measured flux (Fig. 4).

On the north side of the bay most affected by the foam, the patterns of the changes in oxygen flux varied

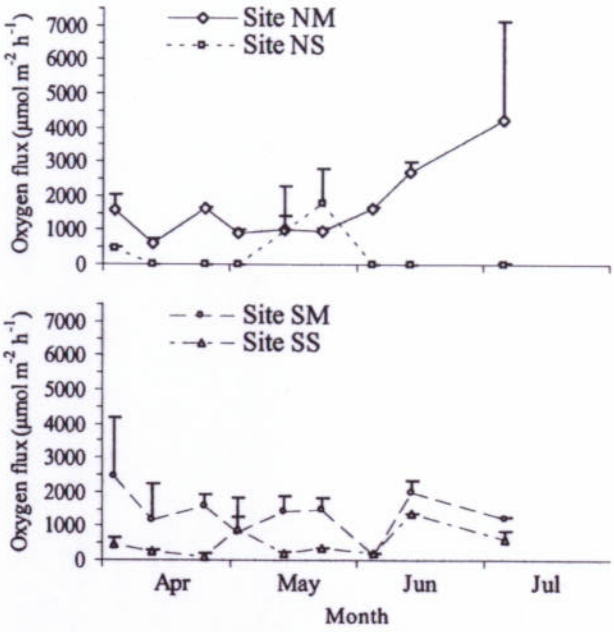

Fig. 4. Mean oxygen fluxes at north mud (NM), north sand (NS), south mud (SM) and south sand (SS) sites. Vertical bars represent +SD

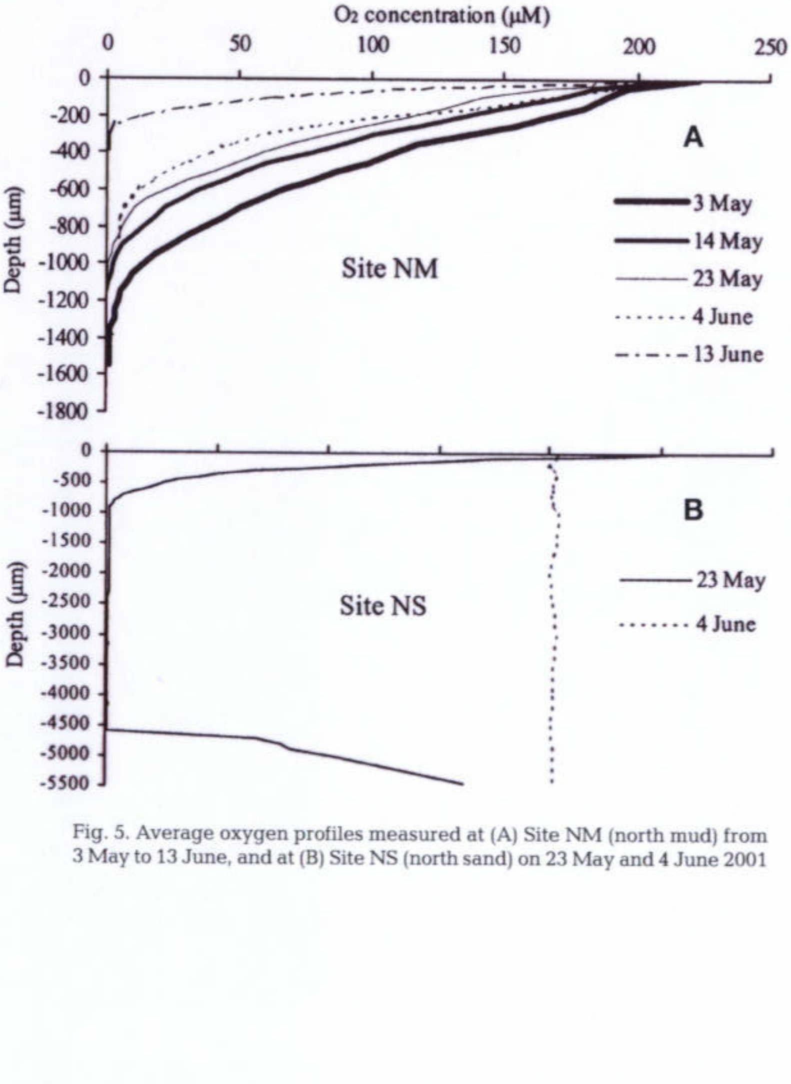

Fig. 5. Average oxygen profiles measured at (A) Site NM (north mud) from 3 May to 13 June, and at (B) Site NS (north sand) on 23 May and 4 June 2001

according to the nature of the sediment. At Site NM, oxygen flux increased consistently from 23 May (~950 µmol m^{-2} h^{-1}) to 5 July (>4000 µmol m^{-2} h^{-1}), whereas at Site NS, values were highest on 14 and 23 May, as compared to earlier and later dates where no significant oxygen gradients were detected. At Sites SM and SS, insignificant differences ($p = 0.582$ and 0.094 respectively) were obtained because too few replicates were taken to detect apparent differences shown in Fig. 4.

Fig. 5A shows the changes in average oxygen concentrations (calculated on 2 profiles) in the superficial layers of Site NM from 3 May to 13 June. During this period, the oxygen penetration depth decreased, resulting in enhanced diffusive oxygen flux. At Site NS, superficial residual crusts resulting from drying foam prevented oxygen diffusion in the sandy sediment. Although the top few centimeters were saturated by oxygen as in normal conditions, the sediment showed an oxygen deficit in the top 4 to 5 mm where dried foam existed (Fig. 5B).

Benthic pigments

Fig. 6A,B shows the temporal changes in chl *a* and phaeopigment *a* m^{-2} in the top 3 centimeters of the sediment at each site. Overall, significantly higher concentrations of both pigments were found at Sites NM and SM as compared to Sites NS and SS (month pooled; $p < 0.001$). With the exception of the high value recorded on 25 April at Site SM (1211 ± 585 mg m^{-2}), sediment chl *a* concentrations ranged between 100 and 600 mg m^{-2} during the study period at each site. Changes were significant at Sites NM ($p < 0.05$) and NS ($p < 0.05$), where the highest concentrations were found following foam accumulation in May and June, but were insignificant at Sites SM ($p = 0.074$) and SS ($p = 0.122$).

Similarly, phaeopigment concentrations changed significantly at Sites NM and NS. Values increased from April to May at Site NS ($p < 0.05$), and from May to July at Site NM ($p < 0.001$). Phaeopigment values were variable throughout the sampling period at Site NM, with maximal and minimal values of 3568 ± 96 mg m^{-2} and 651 ± 312 mg m^{-2}, respectively. Concentrations at Site SM remained stable, and decreased gradually at Site SS during the study, with respective values of $p = 0.461$ and $p = 0.728$.

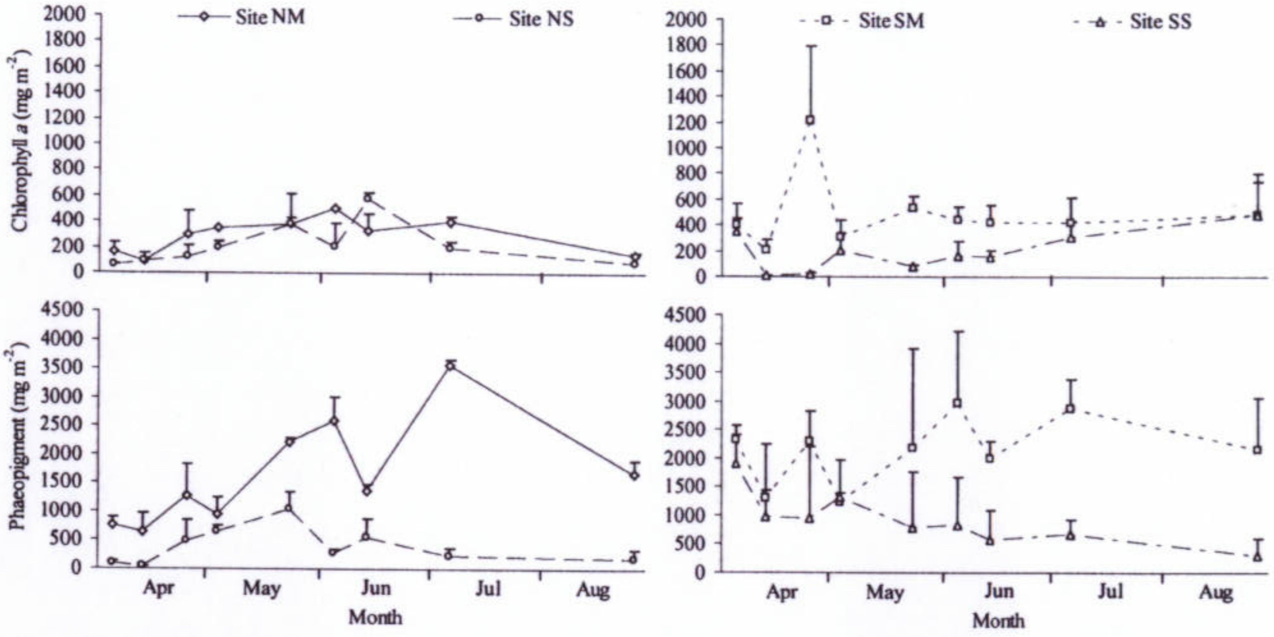

Fig. 6. (Top panels) Chl *a* (mg m^{-2}) and (bottom panels) phaeopigment (mg m^{-2}) concentrations in surficial sediments (3 cm depth integrated) at the 4 sites. NM: north mud; NS: north sand; SM: south mud; SS: south sand. Vertical bars represent +SD

Macrofauna

A total of 35 species was identified from the core samples. The fauna was composed almost exclusively of polychaetes, mollusks and crustaceans, in various proportions depending on the site (Table 3). Most of the numerically dominant taxa during the study period were estuarine species, such as *Hydrobia ulvae*, *Macoma balthica* and *Pygospio elegans* at Sites NM and SM, *Bathyporeia pilosa* and *Cerastoderma edule* at Site NS and *Hediste diversicolor*, *Heteromastus filiformis* and *Macoma balthica* at Site SS.

Two-way ANOVA conducted on data recorded from 4 April to 24 August (a common data set for each site) showed that values of community descriptors (number of species and total abundance of all species per sample) varied greatly with time ($p < 0.001$), with no significant differences among the sites (Table 4). The Shannon diversity results, however, were significantly influenced by both time and site ($p < 0.001$, Time; $p < 0.01$, Site).

Both sites located on the north and the south sides of the bay showed variations in number of species and the abundance of all species pooled, but these variations were different depending on whether the site was on the north side or the south (Fig. 7). At Sites NM and NS, the number of species changed significantly ($p < 0.001$). This trend was characterized at both sites by a strong reduction in species numbers: on 14 May, 2 and 0.25 species on average (on 1/9 m^2) were recorded at Sites NM and NS respectively, versus 7 and 8.25 on 5 April. After a peak observed on 4 June at both sites, the number of species remained low (<4 species) at Site NM and increased at Site NS, where the initial number of species was partially restored by the end of the sampling period. The significant change in total abundance at both sites ($p < 0.001$) appears consistent with variation patterns described for specific richness: after a rapid spring decrease, densities remained low throughout the season. The high densities recorded at Site NS on 4 April were mainly due to the presence of 2 species, *Cerastoderma edule* and *Pygospio elegans*, which rapidly disappeared. Changes in Shannon diversity were highly significant ($p < 0.001$) and consistent at both sites (Fig. 8).

On the south side of the bay, at Sites SM and SS, stability in the number of species was the overall trend (Fig. 7). No significant difference was detectable over the course of the sampling season at Site SM. Density, however, varied significantly ($p < 0.001$), increasing by a factor of 4 from 25 April to 13 June. At Site SS, despite a high variability from one month to the other, density varied consistently with species number. The overall stability recorded over the course of the sampling season was punctuated by one significant decrease on 4 June ($p < 0.05$). Shannon diversity changed significantly ($p < 0.01$) at both sites over the course of the sampling period (Fig. 8).

Table 3. Number of taxa (per group and total) and mean (±SD) abundances (ind. m^{-2}) of infauna at each site (4 April to 12 December for Sites NM and NS; 4 April to 24 August for Sites SM and SS). Groups are classified according to the decreasing number of species. NS: north sand; NM: north mud; SS: south sand; SM: south mud

Species	NM	SM	NS	SS
Crustacea: 12 spp.	5 spp.	6 spp.	9 spp.	8 spp.
Bathyporeia pilosa	0.7 (5)	–	239.5 (490.4)	24.9 (77.9)
Bathyporeia sarsi	–	0.9 (5.7)	–	0.9 (5.8)
Carcinus maenas	9.7 (22.7)	215.1 (309.2)	2.8 (20.0)	1.8 (8.0)
Corophium arenarium	–	–	2.8 (15.7)	–
Corophium volutator	0.7 (5.0)	1.8 (11.3)	–	–
Crangon crangon	6.2 (22.2)	45 (75.5)	2.1 (8.5)	34.2 (60.1)
Eurydice pulchra	2.1 (8.5)	13.5 (85.4)	51.9 (97.07)	0.9 (5.8)
Gammarus sp.	–	–	1.4 (7.0)	0.9 (5.8)
Haustorius arenarius	–	–	0.7 (5.0)	–
Neomysis integer	–	2.7 (17.1)	1.4 (10.0)	6.5 (21.6)
Pinnotheres pisum	–	–	0.7 (5.0)	–
Sphaeroma rugicauda	–	–	–	0.9 (5.8)
Annelida: 10 spp.	8 spp.	9 spp.	6 spp.	7 spp.
Arenicola marina	2.1 (11.1)	15.3 (29.3)	–	9.2 (22.9)
Capitella capitata	12.5 (27.5)	883.8 (1076.3)	6.2 (23.3)	129.2 (230.61)
Eteone longa	99.0 (244.8)	436.5 (767.3)	39.5 (157.7)	14.8 (24.4)
Hediste diversicolor	33.2 (87.8)	720 (535.0)	6.9 (28.6)	426.5 (217.2)
Heteromastus filiformis	29.8 (115.6)	31.5 (78.3)	42.9 (190.6)	427.4 (401.1)
Lanice conchilega	2.1 (15.0)	23.4 (131.1)	–	–
Polydora antennata	–	11.7 (62.8)	–	–
Pygospio elegans	1299.5 (2812.5)	4834.8 (4131.6)	720.0 (2716.7)	105.2 (399.1)
Scolelepis squamata	–	–	92.8 (429.7)	1.8 (8.0)
Spio martinensis	1.4 (7.0)	1.8 (7.9)	–	–
Mollusca: 7 spp.	6 spp.	6 spp.	3 spp.	7 spp.
Abra tenuis	3.5 (16.3)	29.7 (52.8)	–	2.8 (17.3)
Cerastoderma edule	330.9 (603.0)	171.9 (418.1)	337.1 (1145.1)	76.6 (243.2)
Hydrobia ulvae	1383.9 (2334.7)	10471.5 (11637.7)	68.5 (370.2)	48.0 (74.5)
Macoma balthica	222.9 (76.01)	18151.2 (20826.2)	4.8 (21.4)	520.6 (790.2)
Mya arenaria	2.8 (9.7)	8.1 (17.3)	–	1.8 (8.0)
Scobicularia plana	2.1 (15.0)	8.1 (20.8)	–	1.8 (8.0)
Tellina tenuis	–	–	–	0.9 (5.8)
Insecta: 2 spp.	2 spp.	1 sp.	2 spp.	
Chironomidae sp.	1.4 (7.0)	–	2.1 (11.1)	–
Diptera sp.	2.8 (9.7)	2.7 (9.6)	54 (90.3)	–
Pisces: 2 spp.	1 spp.	1 sp.		2 spp.
Gobidae sp.	–	–	–	0.9 (5.8)
Solea solea	1.4 (7.0)	1.8 (7.9)	–	1.8 (8.0)
Nemertean: 1 sp.	1 sp.		1 sp.	1 sp.
Nemertean sp.	1.4 (7.0)	–	0.7 (5.0)	1.8 (8.0)
Oligochaeta: 1 sp.	1 sp.	1 sp.	1 sp.	1 sp.
Oligochaeta sp.	31.2 (70.2)	649.8 (804.0)	33.2 (80.9)	12.0 (38.14)
Total	24 spp.	24 spp.	22 spp.	26 spp.

Table 4. Results of a 2-way ANOVA used to test for site and time effects on the number of taxa, the number of individuals and the diversity among sites and times (macrofaunal cores were individually considered). ns: not significant, $p \geq 0.05$; $^{*}p < 0.01$; $^{**}p < 0.001$

Source of variation	df	Number of taxa		Abundance		Shannon diversity	
		F	p	*F*	p	*F*	p
Time	3	11.34	<0.001**	15.71	<0.001**	8.82	<0.001**
Site	9	1.43	0.223ns	0.61	0.781 ns	3.59	0.005*
Residual	27						

The SIMPER analyses indicated that 11 taxa contribute most to the dissimilarities between sites (cut-off 90%; Table 5). Since most of these taxa were generally present at all sites (Table 3), differences between sites would appear to be the result of the variations in their relative abundance.

As shown by the clusters on the plot projections, assemblage structures were comparable and stable at SM and

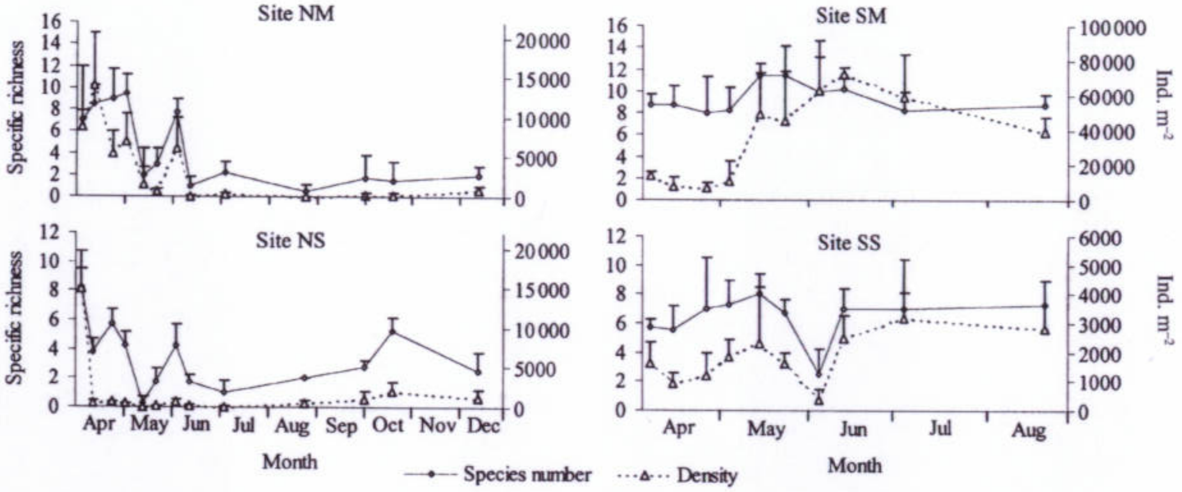

Fig. 7. Number of species (+SD) per core and number of individuals of all species per sample (m^2) (+SD) at north mud (NM), north sand (NS), south mud (SM) and south sand (SS) sites

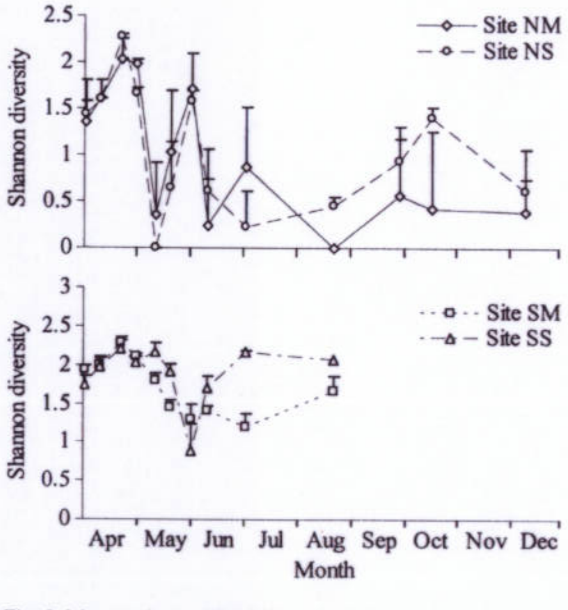

Fig. 8. Mean values +SD of Shannon-Wiener diversity at the 4 sites: north mud (NM), north sand (NS), south mud (SM) and south sand (SS)

NM sites in the early spring (Fig. 9). These structures began to change and were heavily differentiated as of mid-May, when large foam deposits began to form on the north side of the bay. Samples from Site NM became much more widely spaced in the ordination plane than those in the SM group, revealing that changes in the overall community structure and composition had occurred. The most impoverished stage was recorded on 24 August (sample NM10), when only *Hediste diversicolor* was recorded with an abundance of 0.25 ind. m^{-2}. A similar pattern was observed for Sites NS and SS. While Site SS samples during the study period show the tight plot clustering that indicates high assemblage stability, Site NS samples are much more diffusely distributed. The most disturbed stage was observed on 14 May (sample NS5) when only *Cerastoderma edule* was present (0.5 ind. m^{-2}).

At Site NM, the highest correlation ($r = 0.718$, BIO-ENV procedure) was obtained for the combination of organic matter and oxygen flux, while at Site NS, this correlation was based only on oxygen flux measurements ($r = 0.227$). At Sites SM and SS, the highest values were associated with the chl *a* content ($r = 0.239$) and the combination of organic matter, chl *a* and phaeopigment contents ($r = 0.198$).

DISCUSSION

The pronounced foam accumulation in the spring, followed by the subsequent decomposition that provokes hypoxia and increased sulphate-reduction activity, is a recurrent and dominant event on the eastern English Channel–North Sea coasts. The low grazing pressure exerted by copepods on *Phaeocystis* spp. (Gasparini et al. 2000) is likely to favour the sedimentation of algal cells or colonies ungrazed to the sea floor. Although deposits of algal matter in varying states of decay are presumed to represent the majority of the particulate organic material available to the benthos (Boon & Duineveld 1996), these deposits may adversely affect benthic ecosystems. Our study is the first to investigate the effects of foam accumulation on

Table 5. SIMPER analyses results: average Bray-Curtis % dissimilarities among sites (**bold**) and the 5 taxa contributing most to dissimilarity (%).NS: north sand; NM: north mud; SS: south sand; SM: south mud. See Table 3 legend for genus names

NM vs SM	NM vs NS	NM vs SS	SM vs NS	SM vs SS	NS vs SS
67.2	**84.6**	**73.0**	**88.4**	**69.9**	**84.3**
16.7: *M. balthica*	20.3: *H. ulvae*	12.1: *H. ulvae*	19.5: *M. balthica*	16.2: *M. balthica*	13.6: *H. diversicolor*
12.0: *H. ulvae*	14.5: *P. elegans*	9.7: *P. elegans*	18.7: *H. ulvae*	16.0: *H. ulvae*	13.0: *H. filiformis*
10.2: *P. elegans*	10.1: *C. edule*	9.3: *H. diversicolor*	14.4: *P. elegans*	12.3: *P. elegans*	12.8: *M. balthica*
5.4: *C. capitata*	7.3: *M. balthica*	8.8: *H. filiformis*	6.7: *C. capitata*	4.0: Oligochaeta	6.6: *P. elegans*
4.8: *H. diversicolor*	6.9: *B. pilosa*	8.4: *M. balthica*	6.0: *H. diversicolor*	4.0: *C. capitata*	6.4: *C. capitata*

the benthic habitat and its associated macrofauna.

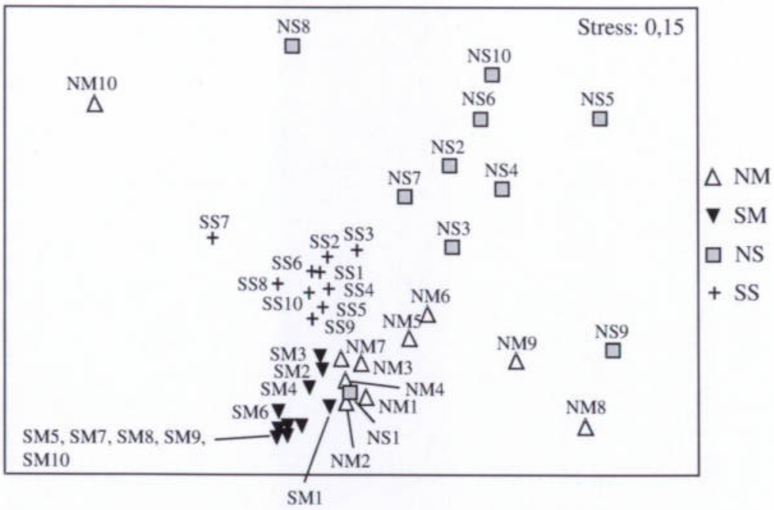

Fig. 9. Two-dimensional configuration for non-metric multidimensional scaling (MDS) ordinations of macrofaunal assemblages from north mud (NM), north sand (NS), south mud (SM) and south sand (SS) from April to August 2001 (1 = 4 April, 2 = 13 April, 3 = 25 April, 4 = 3 May, 5 = 14 May, 6 = 23 May, 7 = 4 June, 8 = 13 June, 9 = 5 July and 10 = 24 August)

The evidence regarding the effects of *Phaeocystis* spp.-derived material deposits observed at affected sites (NM and NS) are summarized in Table 6. Although chl *a* and phaeopigments do not characterize *Phaeocystis* spp.-derived material, both pigment concentrations changed significantly over the course of the sampling period at Sites NM and NS, consistent with field observations of large accumulations of decaying remains of *Phaeocystis* spp. colonies (Fig. 6). Unlike the toxic algal bloom of other Prymnesiophytes, such as *Chrysochromulina polylepis* or *Karenia brevisulcata*, which Olsgard (1993) and Wear & Gardner (2001) have respectively shown do not change the predominant sediment type pre- to post-bloom, *Phaeocystis* spp.-derived material may profoundly change post-bloom grain size distribution. The resulting fine particle input (>60%) observed at Site NM in May was significantly higher as compared to other sites, and was persistent over time. At Site NS, a major part of the sedimented phytodetritic material was resuspended by the turbulence generated by wind-waves and subsequently transported by tidal currents. Residual deposits, exposed to sunshine at low tide, developed impervious, heterogeneous distributed crusts. As a result of the rapid decomposition of decaying colonies, the organic content of the sediments at Sites NM and NS increased consistently, the presence of

Table 6. Main effects of foam accumulation on the muddy and sandy sediments of the Bay of Canche. NS: north sand; NM: north mud

	Sediment characteristics			Biological parameters
Presence of foam	Granulometry	Organic matter content	Oxygen fluxes	Number of species, abundance and diversity
Low turbulence (Mudflats—NM)				
High accumulation	Significant and lasting increase in silt-clay content	Significant enrichment (strong and persistent)	Overall insignificant increases Development of anoxic conditions	Rapid significant reduction Slow recovery Few opportunistic species
High turbulence (Sandflats—NS)				
Low accumulation	No effect	Significant enrichment (low and sporadic)	Insignificant increases Formation of crusts preventing oxygen diffusion	Rapid significant reduction Rapid recovery Few opportunistic species

organics indicated by a single peak on sand and the strong, persistent enrichment of the mud. Subsequently, oxygen flux increased at Sites NM and NS. Although insignificant, these changes were the consequence of the enhanced aerobic and anaerobic mineralization rates that resulted from the presence of increased organic matter (Soetaerts et al. 1996, Denis 1999). This condition occurred despite the advanced degradation of particulate organic matter in the foam and its associated resistance to microbial degradation (Thingstad & Billen 1994). The decomposition rate of the organic matter was high at Site NM, depleting oxygen resources during the degradation process (Bucci et al. 1992, Millet & Guelorget 1994). This depletion rapidly led to severe anoxic conditions, accompanied by a release of H_2S from the bottom.

The decrease rates of oxygen penetration in the sediment at Site NM from 3 May to 13 June were partly due to increased mineralization activity and the reduced solubility of oxygen as water temperatures increased (Rasmussen & Jorgensen 1992). On the other hand, the sediment's recolonization by macrofauna and the bioturbation activity may facilitate oxygen penetration into sediment (Nilsson & Rosenberg 2000). The average diffusion flux values calculated for muddy sediment (1690 ± 925 µmol m^{-2} h^{-1}, Site NM; 1368 ± 532 µmol m^{-2} h^{-1}, Site SM) accord with those recorded by Böttcher et al. (2000) on intertidal Weser mudflats at similar temperatures. In the Weser flats, oxygen flux ranged from 1245 to 2195 µmol m^{-2} h^{-1}, with a mean of 1630 µmol m^{-2} h^{-1}. During our survey, the oxygen flux variability observed at Site NM increased (2947 to 6294 µmol m^{-2} h^{-1} on 5 July) as a result of 'organic hotspots' produced by the small-scale spatial heterogeneity of foam distribution. At Site NS, the high concentrations of oxygen recorded downcore are due to the high permeability of the sediments and to the discontinuous character of the surficial crusts. Although lower, our average diffusive oxygen flux values (356 ± 524 µmol m^{-2} h^{-1}, Site NS; 495 ± 286 µmol m^{-2} h^{-1}, Site SS) are of the same order of magnitude as the overall oxygen flux values measured for intertidal sands in the bay of Somme (eastern English Channel, 500 to 1360 µmol m^{-2} h^{-1}) with benthic chambers in the emerging sediments (Spilmont pers. comm.).

The macrobenthic assemblages were characterized by a small total number of species, with an overall low diversity and the strong dominance of a few of the existing taxa. The MDS analyses provided evidence that foam sedimentation influenced the macrobenthic assemblages on the north side of the bay. The development of anoxic conditions affected all taxa, and both the number of species and their abundance were simultaneously reduced. The most affected taxa at Site NM were *Cerastoderma edule*, *Eteone longa* and *Pygospio elegans*, and at Site NS were *Bathyporeia pilosa*, *Eurydice pulchra* and *P. elegans*. Reductions of abundance were either due to migration as presumed for amphipods and isopods, mortality as shown for *C. edule* that rapidly die when buried below 10 cm sediment depth (Jackson & James 1979), or predation by waders. As reported by Everett (1994) during macroalgal blooms, we observed in foam accumulation areas that infaunal species such as bivalves (*C. edule*, *Macoma balthica*) and polychaetes (*Arenicola marina*, *E. longa*) were forced to the sediment surface in response to the development of anoxic conditions, increasing their chance of being eaten by waders (N. Desroy unpubl. data). Due to the increased accessibility of infauna by upward vertical migration, the combined presence of foam and predation can intensify the effects of each factor on benthic invertebrate densities. At Site NM, only the gastropod *Hydrobia ulvae* remained abundant during foam sedimentation. Since this species feeds on diatoms (Austen et al. 1999), snails were able to migrate towards sites characterized by high biomass of benthic diatoms. The abundance of opportunistic species did not increase in the northern sites, whereas they were abundant on the south side of the bay (Site SM and SS), which is unusual in coastal systems after a succession of organic enrichments. A common community response to stress, after a short period of stimulation, is a reduction in the number of species, an increase in total abundance due to an increase in the opportunistic species, and a corresponding reduction in diversity (Pearson & Rosenberg 1978). Similar situations with a reduction in both the number of species and their abundance, and the absence of opportunistic species, has already been described in studies of benthic faunal response to both heavy metal pollution (Rygg 1986) and toxic algal bloom (Olsgard 1993).

Our results show that faunal recovery essentially depended on the spatial and temporal scales of the disturbance and the hydrodynamics of the area. An increasing current decreased the negative effect of organic enrichment, most likely by increasing oxygen concentrations in the sediment (Ford et al. 2001). Sandy assemblages showed a quicker recovery as of July due to more suitable environmental conditions. The recovery at Site NS after the foam was resuspended by wind-induced waves was mainly due to *Pygospio elegans*, *Bathyporeia pilosa* and *Eurydice pulchra*. Many amphipods or isopods are highly mobile and can increase opportunistically in response to increased food supplies (Colan 1994). At Site NM, the polychaetes *Hediste diversicolor* and *P. elegans* were the first settlers, but the high organic matter content recorded at the end of the summer suggested that, at that time, the habitat was not yet fully restored. Full recovery had still not occurred by the end of the year, as witnessed by the low numbers of species and individuals. Disturbed areas may take months or years to recover (Beukema et al. 1999) but there is still the possibility of initial and rapid colonization by opportunistic species that were previously not present or not abundant in a site. In the present study, there was no sign of an initial increase in diversity following disturbance. The lengths of organisms in samples indicated that recolonization was mainly due to the migration of adults from surrounding areas. Spring recruit mortality was partly responsible for this lack of faunal recovery following sedimentation. Although macroalgal detritus are assumed to induce larval settlement or to result in enhanced survival of newly settled infauna (Renaud et al. 1999), the recruits observed on 4 June at Sites NM (*Cerastoderma edule, Hydrobia ulvae, Macoma balthica* and *P. elegans*) and NS (*C. edule, E. pulchra* and *P. elegans*) failed rapidly, maybe in response to hypoxic conditions. Observations directly relating the benthic faunal changes and nontoxic phytodetritus accumulations are lacking and no other comparable data sets are available. The closest similar event to foam accumulations is the proliferation of green macroalgae on intertidal flats, the effects of which can be either direct, due to physical interference with macroinvertebrate feeding behaviour (Raffaelli et al. 1991), or indirect, due to changes in physico-chemical characteristics of the sediment (Hull 1987).

Large amount of foam recurrently occurred at spring in the north side of the bay mainly in response to the dominant SW winds. Their persistence on depositional areas was variable from one year to another, mainly depending on winter storm intensity and on the colonization level by the polychaete *Pygospio elegans*. After a severe winter storm, part of the non-cohesive sediment layer deposed in spring and non colonized can easily be eroded, uncovering the original sediment and disturbing the recovery process. When densely colonized by *P. elegans*, sediment characterized by a higher level of physical stability was preserved from erosion. Macrofaunal assemblages that had been affected for several years had similar composition to preserved ones, but abundance of organisms remained low. The absence of long-term baseline data prevent us from quantifying environmental consequences of phytodetritus accumulation on a large time-scale. However, the recurrent disturbance involved a high level of variability in habitats and may preserve benthic assemblages in a juvenile stage.

In conclusion, the spring algal bloom dominated by *Phaeocystis* spp. had a widespread and profound impact upon the biological communities. Although the low-energy silty environment was impacted more severely than areas subjected to tidal or wind-induced turbulence, the effects documented here show that the effect of foam accumulation must be taken into account even when deposits are temporary or are limited in size, as is the case in the sandy sediments that predominate in the Canche Bay. In comparison, mudflats and depositional areas represented only 10% of the surface (i.e. 60 ha), and the sedimentation of *Phaeocystis* spp.-derived material leading to impoverished assemblages observed at Site NM primarily affects these depositional areas. Visual estimation showed that more than 50% of the sandy sediments were covered by foam, with the attendant disturbance of the benthic communities. These results will support the quantification of effects upon the community structure and dynamics on the scale of the eastern English Channel–North Sea intertidal area.

Acknowledgements. This study was done within the framework of the CPER program, which is partially supported by the 'Nord/Pas-de-Calais' Region. The authors thank C. Luczak, P. Hacquebart and Y. Jacquemin for their valuable assistance in the field and/or laboratory work. The authors address their special thanks to Dr F. Obeirn and L. E. Spencer for their comments and help in correcting the English text.

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Editorial responsibility: Otto Kinne (Editor),
Oldendorf/Luhe, Germany

Submitted: July 3, 2003; Accepted: October 21, 2003
Proofs received from author(s): March 26, 2004

Available online at www.sciencedirect.com

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Marine Pollution Bulletin 53 (2006) 80–90

MARINE POLLUTION BULLETIN

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Recent changes in estuarine benthic and suprabenthic communities resulting from the development of harbour infrastructure

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Abstract

Using a Before/During/After sampling protocol, the effects of the Le Havre harbour extension, which was started at the end of 2001, on the macrobenthic and suprabenthic communities in the eastern Bay of Seine (English Channel) were examined. As the construction phase has not yet been completed, the results presented here reflect only the data collected before and during the operations (September 2000 and 2002 for benthos sampling and March 2001, September 2001, October 2002 and March 2003 for suprabenthos sampling). Although bio-sedimentary changes did occur at the mouth of the Seine river, an analysis of benthic assemblages reveals that the dredging and construction operations do not seem to have influenced assemblage structure or the spatial distribution of organisms. Comparisons of the suprabenthic assemblages at each sampling date indicate that seasonal dynamics was mainly responsible for determining species distribution. We conclude that, 1 year into the harbour management plan, the observed changes in benthic and suprabenthic assemblage abundance do not exceed the range of spatial variability that exists naturally in the Seine estuary. Despite this compensatory actions designed to protect the aquatic habitats and to preserve a sustainable and healthy ecosystem have been added to the infrastructure development plan.

Keywords: Seine estuary; Le Havre Port 2000; Compensatory actions; Macrobenthos; Suprabenthos

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1. Introduction

Estuaries are highly variable ecosystems due to the interaction of local physical, geological, chemical and biological factors. Given their position at the ocean–continent interface, estuaries are also prime sites for the development of various human activities such as industry, marine transportation, fisheries, and tourism. The Seine estuary reflects this trend and its catchments of ≈79,000 km^2 supports 40% of the agricultural and industrial activity of France, 50% of the national river, and 30% of its population (16 million inhabitants for the watershed, of which 80% live in urban areas). As a consequence of its national and European importance, significant projects (i.e. dams, land claims and navigational channels) that have disturbed the natural environment (Dauvin, 2002; Dauvin and Desroy, 2005) have been conducted for more than 150 years, especially in the lower part of the estuary.

The most recent development of infrastructure along the Seine estuary—part of the "Port 2000" project—aims to extend the Le Havre harbour. Plans for the North Channel include (1) construction of a 16 m deep, 350 m wide, and 2800 m long channel connected to the Le Havre port's navigational channel and (2) construction of a dam-protected basin. Given their location within the North Channel marine and terrestrial habitats, these new infrastructures will have affected the local flora and fauna.

In order to assess the impact of physical disturbance on wildlife conservation, studies of habitat quality and marine fauna are important (Lewis et al., 2002). However, inter-

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0025-326X/$ - see front matter © 2005 Elsevier Ltd. All rights reserved.
doi:10.1016/j.marpolbul.2005.09.020

preting the effects of disturbance in estuaries is often complex and confusing, since dynamic physical, chemical and geologic conditions can confound the impacts of anthropogenic activity on estuarine biotic integrity (Warwick, 1988; Weisberg et al., 1997; Gaston et al., 1998). Experimental designs that include sampling before, during and after the impact event (BACI approach), on several occasions and at several control sites have been recommended to achieve the necessary spatial and temporal replication (Underwood, 1992, 1994). The determination of whether the origins of change are natural or anthropogenic is largely dependant on the choice of the parameters that are monitored. Unlike the suprabenthic fauna, which is a good source of information on short-term changes (Dauvin et al., 2000; Mouny et al., 2000), sediment and benthic fauna are good indicators of both past and present disturbances. Because of their sedentary lifestyle and their longevity (several months to a few years), macrobenthic organisms integrate the environmental changes to estuarine and marine habitats. In this study, monitoring surveys of the macrobenthic and suprabenthic assemblages were conducted in order to assess the effects of ecosystem changes on marine invertebrate fauna.

Since the construction phase has not yet been completed, the results presented here reflect only the data collected before and during the operations (September 2000 and 2002 for benthos sampling and March 2001, September 2001, October 2002 and March 2003 for suprabenthos sampling). The objectives of this paper are to present the structure and most recent changes in macrobenthic and suprabenthic communities, as observed 1 year into the port construction project.

2. Environmental characteristics of the lower part of the Seine estuary

The Seine estuary is the largest megatidal estuary in the English Channel, covering ≈150 km^2 at high tide. The average tidal range, at the mouth, is about 8.5 m for spring tides and 4 m for neap tides. The influence of marine water is increased by the estuarine morphology: the tide penetrates 70 km from the coastline (to the Barrage de Poses at PK 202; PK0: Notre Dame de Paris). Freshwater discharge to the estuary is mainly from the Seine river and varies seasonally, from a maximum of 2000 m^3 s^{-1} in winter to a minimum of 100–200 m^3 s^{-1} in summer (Guézennec, 1999).

The estuarine morphology is mostly artificial, resulting from man-made modifications. Since the mid-19th century, industrial activity and development has taken place in the lower part of the Seine. The Seine has been canalized and dredged 120 km upstream from the mouth to allow navigation from the sea to the inland port of Rouen. At the mouth, intensive dredging (≅5 millions ton y^{-1}) to a depth of 5–6 m below Chart Datum is necessary to maintain the water depth necessary for navigation to Rouen. The successive construction of dykes, has reduced the intertidal zone from 130 km^2 in the middle of the 19th century, to less than 30 km^2 in 2000. The elongated sandbars typical of tide-dominated estuaries have developed at the mouth of the estuary, superficial sediments have become more and more muddy (Lesourd et al., 2001). Mud also dominates the subtidal zones of both the North and South Channels, with the exception of two sand banks in the South and North Channels.

The mean annual particulate river discharge has been evaluated at ≈500,000 ton as suspended matter. The maximum turbidity zone is now located at the mouth of the estuary but can be pushed into the Bay of the Seine during swelling (Le Hir et al., 2001).

Although found upstream from the "Pont de Tancarville" during spring tide and periods of low freshwater discharges, the 0.5 isohaline is usually located between the "Pont de Tancarville" and the "Pont de Normandie", depending on the discharge from the Seine. The Seine estuary is well mixed although the water column can be stratified at the mouth of the estuary during ebb and low tide, when the discharge of freshwater is >500 m^{-3} s^{-1} (Mouny et al., 1998).

High levels of heavy metals, particularly cadmium and lead, make the Seine estuary the most contaminated in Europe (Miramand et al., 2001). Cadmium mainly affects benthic and suprabenthic species such as bivalves, and high concentrations of copper are found in copepods, shrimp and fish. Lead is concentrated mainly in the planktonic species living in the Seine channel, especially the dominant copepod *Eurytemora affinis*, although it is also found in benthic deposit-feeders. Elevated levels of zinc have also been measured in all species living in the Seine estuary, from benthic invertebrates to fish (Miramand et al., 2001). In addition, the level of organic contaminants such as PAHs, PCBs and pesticides, put the Seine estuary among the most contaminated European estuaries (Tronzynski, 1999). Most of these contaminants come from continental sources, although an internal source of PAHs has also been identified. The chronic, high level of organic contamination in the Seine estuary is of concern as contamination of organisms and ecological resources increases with the trophic level from benthic and suprabenthic preys to carnivorous fish. The highest concentrations have been found in the oldest sea bass individuals, and a steady-state model of PCBs bioaccumulation shows that feeding is the principal route for contamination (Loizeau et al., 2001).

3. Material and methods

3.1. Sampling

3.1.1. Macrobenthos

The distribution of macrofauna was determined from two surveys conducted in September 2000 and 2002. A total of 54 sites were sampled in September 2000, using a Rallier du Bathy dredge (qualitative sampling of about 30 L of sediment) or a 0.1 m^{-2} Smith–McIntyre grab.

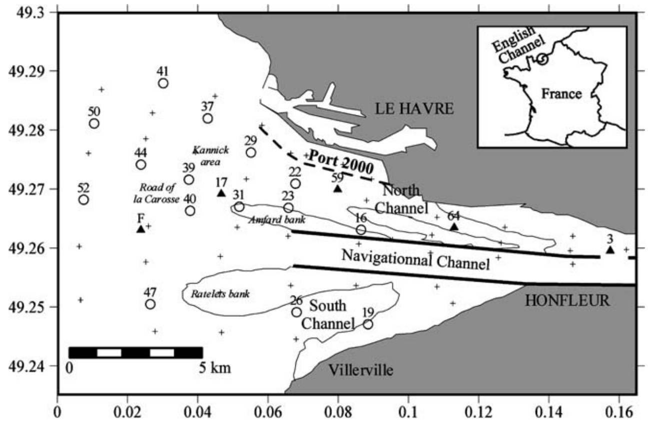

Fig. 1. Study area and sampling location. (+ and ○): benthos sampling sites visited in September 2000. (○): benthos sampling sites visited in September 2000 and 2002 (present results). (▲): suprabenthos sampling sites [visited in March and September 2001 (site 3 excepted), October 2002 and March 2003].

From this large list, 15 subtidal sites were selected for a second survey in September 2002, and sampling was done with a Smith–McIntyre grab (Fig. 1). When the grab was used, three samples were collected to define the benthic assemblages, and sub-samples of sediment, taken from additional samples, were subsequently analysed for grain size distribution (wet sieving). The sample volume provided an indication of the depth of the sediment in the jaw of the grab. Very small samples, those less than 5 cm in depth, were discarded. The contents of the grabs were gently sieved on-site, using a 1-mm circular mesh sieve. The material retained was preserved for analysis in 4% buffered formaldehyde until it could be sorted, identified in terms of species level, and finally counted in the laboratory.

3.1.2. Suprabenthos

The suprabenthos also called hyperbenthos was sampled at four sites (F, 17, 59 and 64) in March and September 2001 and at five sites (F, 17, 59, 64 and 3) in October 2002 and March 2003 (Fig. 1), using a new version of the Macer-GIROQ sledge (Dauvin et al., 1995) to study its seasonal and perennial changes. The sledge head is comprised of four 0.18 m^{-2} boxes (0.6 × 0.3 m), which are used to screen the water column in the four layers above the sea bottom: 0.10–0.40 m (net 1), 0.45–0.75 m (net 2), 0.80–1.10 m (net 3) and 1.15–1.45 m (net 4). Each box is linked to a WP2 zooplanktonic net (0.5 mm mesh size) and includes a Tsurimi–Seiki–Kosakusho (TSK) flow meter in the centre to measure the volume of water filtered. Sampling—the period during which the sledge was in contact with the seabed—lasted for 10 min at a sledge speed of approximately 1.5 knots. The sampling was made during the tidal excursion from the downstream site (F) to the upstream site (3). Towing took place against the tide. Table 1 presents the sampling dates and the hydrological conditions at each site.

Table 1
Hydrodynamic characteristics at each site and sampling dates (ND, no data); a single value at each site and at each time

	Site F	Site 17	Site 59	Site 64	Site 3
March 2001					
Temperature (°C)	7.3	7.0	6.9	6.9	ND
Salinity	25.03	19.86	19.62	17.61	ND
Turbidity	ND	ND	ND	ND	ND
Seine flow ($m^3 s^{-1}$)			1071		
September 2001					
Temperature (°C)	16.4	16.2	16.0	15.6	ND
Salinity	26.62	19.69	12.72	11.63	ND
Turbidity	ND	ND	ND	ND	ND
Seine flow ($m^3 s^{-1}$)			618		
October 2002					
Temperature (°C)	17.2	17.3	17.0	17.1	17.0
Salinity	26.6	20.6	15.48	17.68	16.5
Turbidity	44.1	60.0	61.5	72.8	82.0
Seine flow ($m^3 s^{-1}$)			183		
March 2003					
Temperature (°C)	7.0	6.8	6.8	6.8	6.7
Salinity	30.94	30.45	29.13	26.68	25.6
Turbidity	44.1	60.0	61.5	101.8	102.0
Seine flow ($m^3 s^{-1}$)			611		

Organisms were washed, fixed with 10% neutralized formaldehyde, and then transferred to a 70% ethanol solution. All the organisms were sorted, counted and identified in terms of species level under a dissecting microscope. These organisms were classified into two groups: (1) macrozooplankton (chaetognaths, the ctenophore *Pleurobrachia pileus*, and fish larvae) and (2) suprabenthos sensus stricto (peracarids and decapods crustaceans). The species richness values corresponded to the total number of species found in the four nets, and the abundance level was standardized for a volume of 100 m^{-3}.

3.2. *Neomysis integer* telson

The morphological anomalies of the mysid *Neomysis integer* telson were taken into account as an indicator of the environmental conditions in the Seine estuary. This species typically has a truncated whole telson, exhibiting an external pair of long spines and an internal pair of short spines. Chojnacki and Ciupinski (1986) suggested that aberrant telsons in *N. integer* correspond either to regeneration following predation by such estuarine predators as fish or shrimp (irregular telson), or to malformations resulting from environmental pollution (round and regular telson with modified spine lengths).

3.3. Statistical analysis

Suprabenthic and macrobenthic community structure was measured at each site and for each sampling date by determining the number of species and their abundances. Benthic assemblages in September 2002 and changes in benthic and suprabenthic community compositions were visualized through non-metric multidimensional scaling (MDS) plots based on triangular matrices of the Bray–Curtis similarities (Clarke and Warwick, 1994). Prior to ordination, $\sqrt{x}$ and $\log(x+1)$ transformations were performed respectively on the benthic and suprabenthic species abundance data, and single individuals from any species recorded at the various sampling sites were omitted from data analysis. A formal significance test for differences in benthic fauna composition between sampling dates was performed using the ANOSIM randomization/permutation test (Clarke, 1993). Kruskall–Wallis tests, followed when necessary by the multiple comparison tests described by Noether (Scherrer, 1984), were performed to test for the difference between the number of suprabenthic species and individuals for the different sites and dates. Finally, the number of suprabenthic species and individuals at each site and for each sampling date were compared to Seine flow values using a Pearson correlation test.

4. Results

4.1. Sediment

In September 2000 and 2002, five sedimentary types were observed—mud, sandy mud, muddy sand, clear coarse to fine sand and muddy heterogeneous sediment (Fig. 2A). In September 2002, the sampling sites associated with the finest sediments, ranging from mud to muddy sands, were evenly distributed in both the North and South Channels, as well as at the mouth of the Seine river. Clean coarse to fine sands were located exclusively in the North Channel around the Kannick dumping area, whereas muddy heterogeneous sediment, with pebble fractions up to 40%, were found only at site 50, located near the entrance of Le Havre harbour. Sedimentary changes from September 2000 to 2002 indicated that seven of fifteen sites (46.6%) were characterized by similar types of sediment, while three sites exhibited finer sediments and five others had coarser sediments (Fig. 2B).

4.2. Macrobenthos

Similar patterns of species richness distribution, showing an increase along the salinity gradient from the inner part of the North and South Channels towards the marine environment, were emphasized in September 2000 and 2002. At each sampling date, a total of $\cong$100 taxa represented mainly by polychaetes ($\cong$40% of the fauna), crustaceans ($\cong$30%), molluscs ($\cong$20%), echinoderms ($\cong$6%), and others ($\cong$4%) were collected. The lowest species richness values ($\cong$5 species on 0.3 m^{-2}) were observed in the Channels, whereas the highest ($\cong$55 species on 0.3 m^{-2}) were located in offshore sediments.

In terms of the numbers of individuals, polychaetes were dominant, accounting for $\cong$70% of all specimens recorded. With the exception of site 19, located in the South Channel, total abundance values also exhibited an increase along the salinity gradient, from the inner Channels to the offshore bottom. In September 2002, total abundance values ranged from 193 ind. m^{-2} (site 23) to 24,880 ind. m^{-2} (site 52), with an average value of 4290 ± 6744 ind. m^{-2}.

4.2.1. Benthic assemblage characteristics in September 2002

MDS ordination determined three groups of sites ($\text{I} = 3$ sites; $\text{II} = 4$ sites and $\text{III} = 8$ sites) in patterns related to species richness (Fig. 3A) and abundance (Fig. 3B).

Group I sites (sites 19, 50 and 52) were located in the most offshore sediments and in the South Channel. Associated with muddy sands, the fauna of these sites (53 species, average abundance of 13,974 ± 10,077 ind. m^{-2}) was dominated by the polychaete *Aphelochaeta marioni* (>50% of the individuals), the bivalves *Abra alba* and *Mysella bidentata*, as well as the polychaetes *Owenia fusiformis* and *Pectinaria koreni*. These five species, representing about 90% of the individuals, are typical components of the *A. alba–P. koreni* community.

Group II sites (sites 29, 31, 37 and 41) were spatially limited to the northern area of the estuary, on fine and coarse sands. Of the 79 species recorded, the polychaetes *Magelona johnstoni* (>52% of the individuals), *Lanice conchilega*,

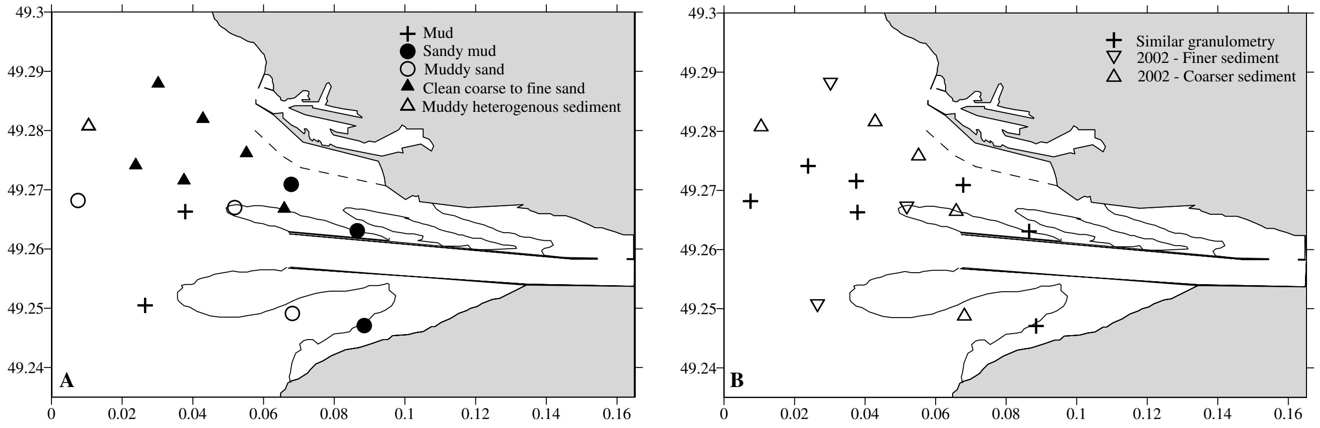

Fig. 2. Superficial sediment distribution in September 2002 (A) and sediment granulometry changes between September 2000 and 2002 (B).

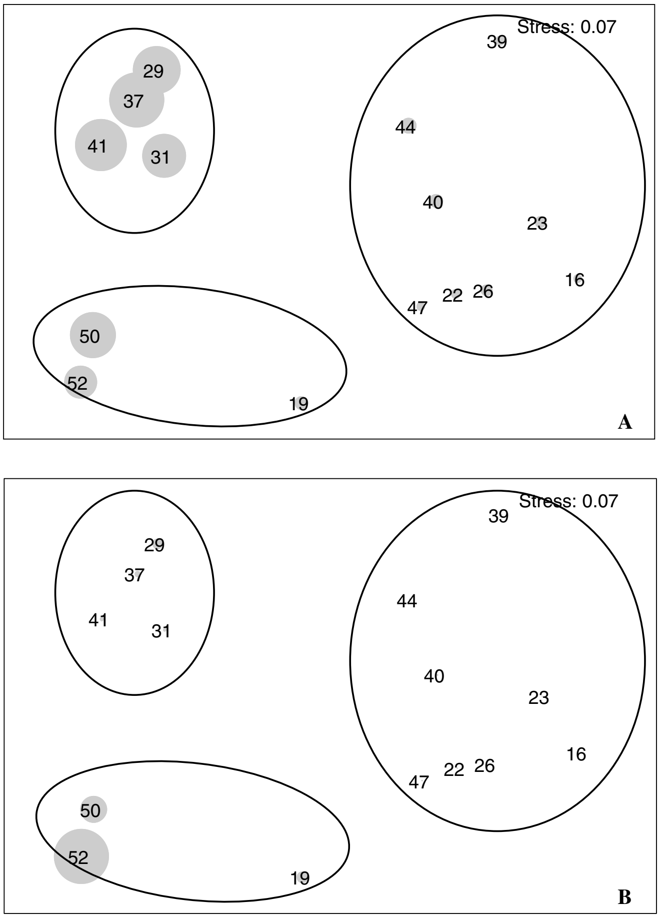

Fig. 3. MDS ordination of Bray–Curtis similarities, using $\sqrt{x}$-transformed benthic species abundance data (15 sites x 84 taxa matrix). Superimposed circles of increasing size represent the number of species (A) and the abundance levels (B).

Magelona filiformis, *Ampharete baltica* and *Eumida sanguinea* dominated. Despite their constant presence, abundance values for the species that characterise the *A. alba–P. koreni* community (*P. koreni*: 90.0 ± 105.4 ind. m^{-2}; *A. alba*: 55.8 ± 44.1 ind. m^{-2}, *M. bidentata*: 23.3 ± 46.6 ind. m^{-2} and *O. fusiformis*: 4.2 ± 8.3 ind. m^{-2}) were modest, considering the average abundance value of 4889 ± 2971 ind. m^{-2} for the assemblage.

Located downstream from the Seine mouth (sites 39, 40, 44 and 47), in the North (sites 16, 22 and 23) and South Channels (site 26), group III sites were associated with the low diverse assemblage, as only 30 species were identified, and these were present in low densities (average abundance: 351 ± 173 ind. m^{-2}). The dominant species were *M. johnstoni*, *Nephtys hombergii*, *A. alba* and *Macoma balthica*. A sub-group, associating sites 39 and 44 located near the Kannick dumping area, is recognizable by its poorly diversie fauna (18 species), a characteristic of clean fine sand (mean abundance of *M. jonhstoni* = 361.7 ± 211.7 ind. m^{-2}). Mixing species typical of the *M. balthica* (*Cerastoderma edule*, *M. balthica*…) and the *A. alba–Pectinaria koreni* (*A. alba*, *M. bidentata*, *Nucula turgida*, *P. koreni*…) communities, the group III assemblage provided a transitional unit between the estuarine *M. balthica* community established in brackish areas (North and South Channel upstream bottoms) and the marine *A. alba–P. koreni* community.

4.2.2. Benthic assemblage changes from 2000 to 2002

Since sites 37 and 41 were sampled using a Rallier du Bathy dredge in September 2000, only 13 stations were considered in the analysis of benthic assemblage changes from 2000 to 2002. Fig. 4 depicts the macrofaunal relationships between sites using MDS and identifies four groups of sites.

The macrobenthic assemblages were relatively stable between September 2000 and 2002 given that 61,5% (8/13) of the sites sampled both in 2000 and 2002 appear in the same group (Fig. 4A and B). Groups I and II combined sites were located in the inner part of the estuary and are characterized by a low number of individuals and species. Sites 39 and 44, influenced by the Kannick dumping area, stand out in-group I both in 2000 and 2002 due to their faunal

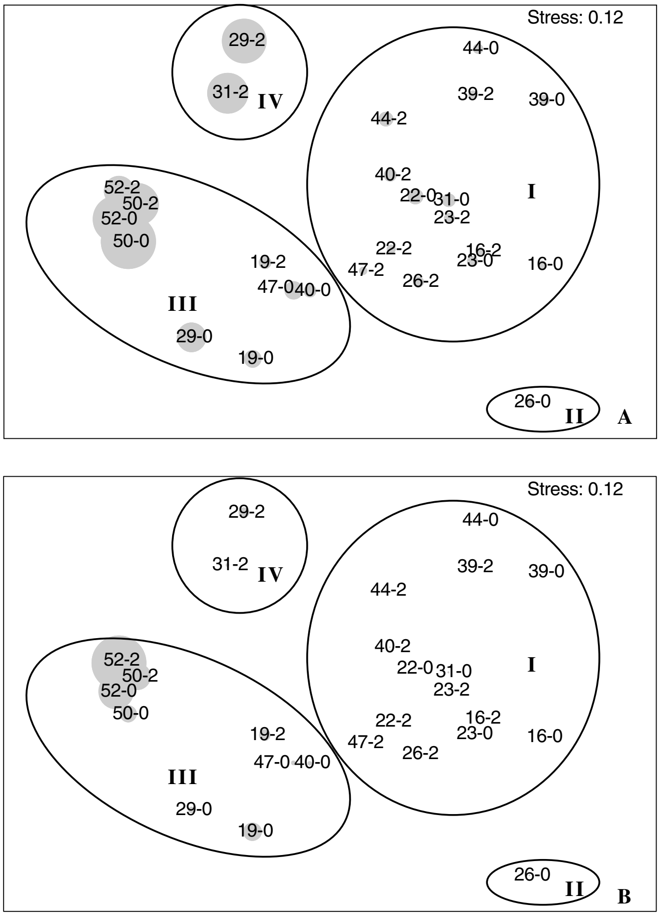

Fig. 4. MDS ordination of the 13 sites, based on $\sqrt{x}$-transformed benthic abundances and Bray–Curtis similarities (2 × 13 sites/83 taxa matrix). Superimposed circles of increasing size represent the number of species (A) and the abundance levels (B). xx-0 and xx-2 indicate sites sampled in 2000 and 2002, respectively.

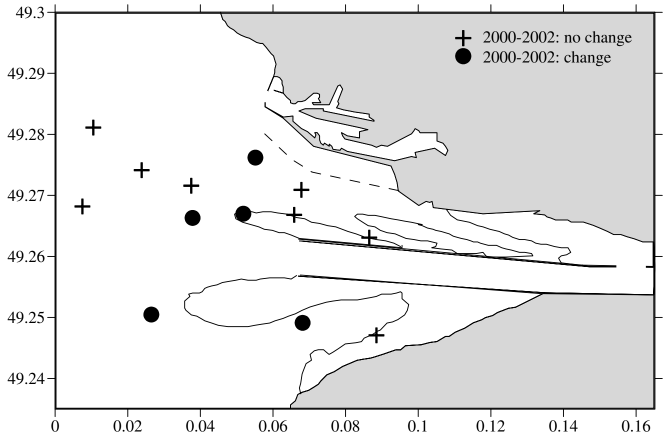

Fig. 5. The change in benthic assemblages between September 2000 and 2002.

composition, typical of clean fine sands. Group III included offshore sites that were typified by medium to high numbers of species and individuals, whereas group IV sites were characterized by medium to high numbers of species with medium to low numbers of individuals. A one-way ANOSIM randomization–permutation test for both dates at each of the 13 sites confirms the stability of macrofauna, showing insignificant differences among the sampling dates ($r = 0.056$, $P = 0.129$). Faunal changes occurred at only five sites (26, 29, 31, 40 and 47), all situated downstream from the navigation channel (Fig. 5). Comparing samples from 2000 to those from 2002 shows that sites 29 and 31, situated close to the North Channel, had an increase in the number of species and individuals, while at sites 26, 40 and 47, located downstream from the South Channel, these numbers decreased (Table 2).

4.3. Suprabenthos

A total of 70 species were collected during the four surveys. Macrozooplanctonic species (15 taxa) were mainly represented by the ctenophore *Pleurobrachia pileus*, the chaetognaths *Sagitta* spp. and larval polychaetes. The suprabenthic fauna (55 species) was dominated by amphipods, mysids, decapods and cumaceans.

In March 2003, the dominant species were *Schistomysis ornata* (51.7%) and *Pleurobrachia pileus* (32.5%) at site F; *S. ornata* (62.1%) and *Mesopodopsis slaberri* (28.9%) at site 17; *M. slaberri* (62.4%) and *S. ornata* (32.8%) at site 59; *N. integer* (82.4%) and *S. ornata* (5.9%) at site 64; and *N. integer* (61.3%) and *S. ornata* (27.0%) at site 3. Results obtained in March 2003 clearly showed that the number of species increased along the salinity gradient from site 3 (20 < bottom water salinity < 30, 18 taxa) to site F (bottom water salinity > 30, 31 taxa; Fig. 6A), whereas the number of individuals tended to decrease from site F to site 3 (Fig. 6B). However, the absence of significant differences between sites (sampling dates pooled) for the number of species ($Hc = 15.20$, $P = 0.295$) and individuals ($Hc = 0.88$, $P = 0.928$) precluded pronouncements concerning the existence of a structured distribution of suprabenthic fauna. The numbers of species and individuals were highly variable seasonally, as shown by the significant differences in the numbers of species and individuals between dates (Table 3). With the exception of site F, whose total abundance values were significantly correlated with the Seine river flow ($r = 0.996$, $P = 0.04$), the number of

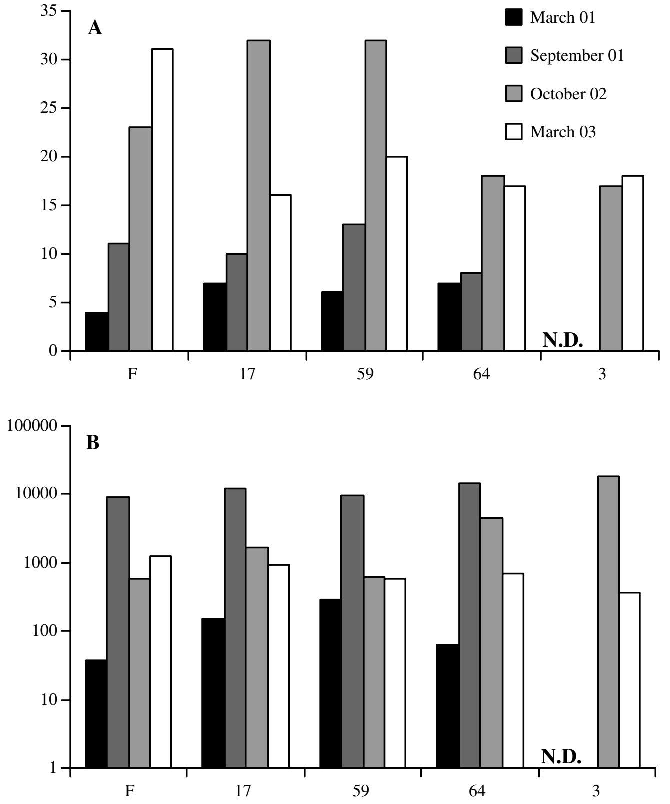

Fig. 6. The change in the number of suprabenthic species and abundance levels (ind. 100 m^{-3}, log scale) in March 2001, September 2001, October 2002 and March 2003 (ND: no data).

Table 2
Change in number of species and abundance levels (ind. m^{-2}) in sites 26, 29, 31, 40 and 47 between 2000 and 2002

	Sites									
	26		29		31		40		47	
	2000	2002	2000	2002	2000	2002	2000	2002	2000	2002
Number of species	9	11	31	47	14	43	13	13	19	8
Abundance	357	273	2610	4513	527	1250	1680	370	1820	423

Table 3
Effect of sampling date on the number of species and individuals

	Number of species ± SD	Number of individuals ± SD	N
March 2001	6.00 ± 1.22	134.90 ± 97.92	4
September 2001	10.25 ± 1.47	11335.30 ± 2202.41	4
October 2002	24.40 ± 6.52	5110.02 ± 6615.94	5
March 2003	20.40 ± 5.46	759.40 ± 299.94	5
Kruskall–Wallis	$Hc = 14.23,\ P = 0.0025^{**}$	$Hc = 13,\ P = 0.0046^{**}$	
Statistical comparison	M-01 S-01 M-03 O-02	M-01 M-03 O-02 S-01	

Horizontal lines link groups that are statistically equivalent using the non-parametric multiple comparisons test. N = number of sites sampled.
** $P < 0.01$.

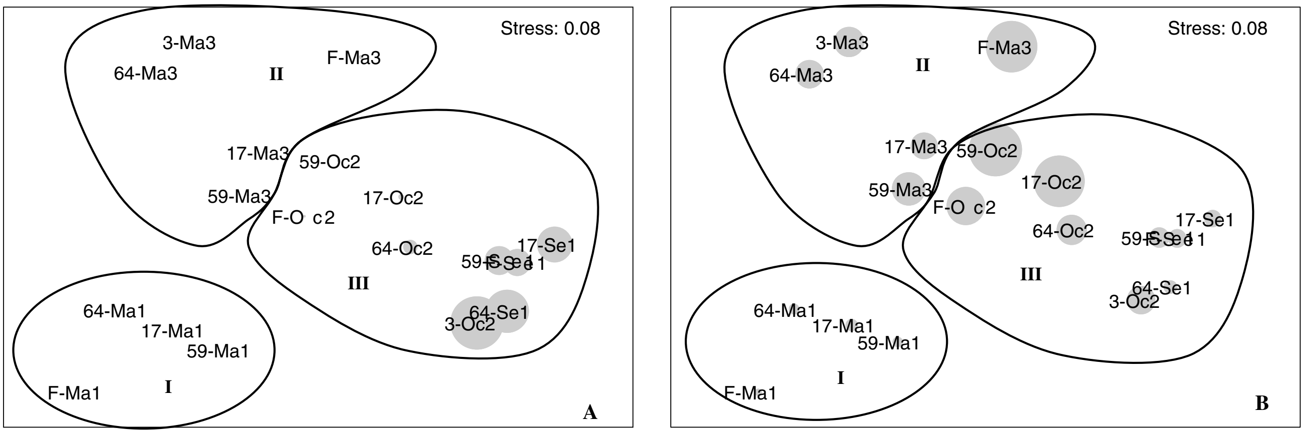

Fig. 7. MDS plot from Bray–Curtis similarities computed for $\log(x+1)$-transformed suprabenthic species abundances ($4 \times 4 + 2 \times 1$ sites/70 taxa). Superimposed circles of increasing size represent the number of species (A) and the abundance levels (B). Ma: March; Se: September; Oc: October. 1, 2 and 3: 2001, 2002 and 2003.

species and individuals never showed significant relationships with the river flow.

MDS configuration confirmed the above analyses: the clusters on global plot projections isolated three groups of sites (Fig. 7A and B), corresponding to the four sites sampled in March 2001 (group I), the sites sampled in March 2003 (group II), and the autumnal samples (group III) collected in September 2001 and October 2002. The sites are scattered according to their number of species and individuals, ranging from the lowest values, associated with group I, to the highest values, which correspond to group III.

Group I samples (March 2001) were characterized by nine species, and an average abundance value of 135 ± 113 ind. 100 m^{-3}. The mysid *M. slaberri* dominated, particularly in sites 17 and 59. Group II samples (March 2003) were more diversified (46 species), with a higher average abundance value (759 ± 335 ind. 100 m^{-3}). Upstream (64 and 3) and downstream sites (F, 17 and 59) were dominated, respectively, by the mysids *N. integer* and *S. ornata*. Characterized by 46 species and an average abundance value of 7877 ± 6368 ind. 100 m^{-3}, group III was typified mainly by the mysid *M. slaberri*, which was dominant at all sites in September 2001 but only at the upstream sites (64 and 3) in October 2002, and by the ctenophore *Pleurobrachia pileus*, at the downstream sites (F, 17 and 59) in September 2001.

4.4. N. integer telson

Three abnormal types of telson were observed: (1) broken telsons (following predation or during sampling); (2) regular telsons (the majority had lost their small terminal teeth, which were often replaced by one or two longer teeth) and (3) asymmetrical irregular telsons. Although the rate of abnormal telsons decreased from the downstream site F to the upstream site 3 (Table 4), the rate remained high in the three sites where *N. integer* was collected (F, 64 and 3). At sites F and 3, males exhibited modified telsons more frequently than females and

Table 4
Rate of the mysid *Neomysis integer* population with modified telsons in sites F, 64 and 3 in March 2003 (a single value at each site)

	StF	St64	St3
Total rate of modified telson	25.0	15.6	17.8
Male	50.00	20.10	57.57
Female	31.25	15.88	10.09
Brooding female	12.50	13.15	13.65
Juvenile	6.25	50.87	18.69

juveniles, whereas at site 64, the highest rate of abnormal telsons was observed in juveniles.

5. Discussion

The expected consequences of the port construction on the physical nature of the North Channel would be (1) an increased of the current speed in the downstream part with a bottom erosion due to a reduction of the width of the Channel and (2) a decreased of the current speed in the upstream part with a mud sedimentation (Hamm et al., 2001). Our results, stemming from data taken at a minimal number of sampling sites, do not show evidence of a clear pattern of sedimentation change. Non-impacted sites were evenly distributed over the whole estuary, from very shallow sites (19) to offshore bottom sites (52). At sites located in the northern part of the estuary, sediment grain size distribution tended to increase, probably in response to preliminary dredging operations in this area. On the contrary, sites close to the sand banks neighbouring the mouth of the Seine river silted up between 2000 and 2002, confirming observations reported by Lesourd (2000) concerning the rapid silting up in this area. In the Seine estuary, sediment dynamics are mainly influenced by the volume of river discharge and by hydrodynamic conditions (Avoine, 1981; Avoine and Crevel, 1985; Lesourd, 2000). The conditions observed in autumn 2000 and 2002 showed relatively little silt/clay content in sediments compared to the data reported in the literature (Lesourd, 2000). Given that the river discharge decreases during the season with the lowest water levels, thus confining the maximal turbidity zone upstream in the navigational channel, the rate of particles exported to the bay of Seine remains low during this autumnal period. Despite this, the lateral shifting of the northern and southern navigational channels, which induces the recycling of sediments from the riverbanks and the north tidal flat, interferes with the silting up of the estuary (Lesourd, 2000). Such contradictory data makes the impact of the harbour extension on the dynamics of the North Channel difficult to assess at this time, although it is hypothesized that it will have an influence on the bottom morphology of the estuary due to a reduction of the area of the North Channel which probably induces a decreasing of the water volume enters in this part of the estuary.

5.1. Benthic assemblages

The qualitative composition of the benthic fauna in the study area was as it should be, given the sediment characteristics and the salinity levels, both of which are major determinants of community composition in estuaries and largely determined by hydrodynamic conditions (Holland et al., 1987; Rakocinski et al., 1997; Ysebaert et al., 1998). The greatest environmental stress, due to salinity and hydrodynamic conditions in the middle and upper subtidal areas of estuaries, corresponds a lower diversity of benthic fauna (Ysebaert et al., 2000).

The Seine estuary benthic fauna exhibits strong differences, ranging from compartments with very high abundance levels to others with very low levels (Elkaïm et al., 1982). Although the number of species recorded for the *A. alba–P. koreni* was high (>100 in the eastern part of the Seine estuary, Thiébaut et al., 1997), high abundance only occurred in about 10 species (the polychaetes *A. marioni*, *M. johnstoni*, *N. hombergii*, *O. fusiformis* and *P. koreni*; the mollusks *A. alba*, *M. bidentata*, *Phaxas pellucidus* and *Tellina fabula*; and the echinoderms *Acrocnida brachiata*, *Echinocardium cordatum* and *Ophiura ophiura*). Gentil et al. (1986) attributed the high biological richness of such subtidal bottoms to their high degree of organic matter enrichment, the hydrodynamic condition that prevents the development of hypoxia. In the brackish areas with an increased silt and clay content, the *A. alba–P. koreni* community is progressively impoverished and is replaced by the low diverse *M. balthica* community (<20 species) (Dauvin, 2002).

The polyhaline subtidal zone of the Seine estuary is characterized by large fluctuations in salinity, high current velocities and high turbidity, making it difficult to assess human impact on the benthic communities. In addition to their superimposition on natural processes, human activities also interfere with such processes. This partly explains why, as previously noted for the sediments, no clear effects of the harbour infrastructure extension have been detected for macrofauna at the present time. Local changes observed at the sites close to Seine river mouth could not be directly related to the disturbance caused by the harbour extension. The inter-annual variability of assemblages at the mouth of the Seine river might result from the silting up of the outer estuary, generated by several decades of man-made modifications and natural processes (Lafite and Romana, 2001; Lesourd et al., 2001). Recent studies showed the existence of resuspension and deposit of silt sediment during the high flow river period and of fine sand during the low flow river period (unpublished data). This mechanism induced changes in superficial sedimentary environment and in composition and structure of macrobenthic assemblages at a small temporal scale (<1 month) (unpublished data). The dumping activity might also have direct effects on macrobenthos composition, as indicated by the MDS ordination. At locations where intensive dumping of sandy sediment has taken place (sites 39 and 44), typically low-diversity communities can be found, dominated by *M. johnstoni*, a well-adapted inhabitant of clean fine sands (Fiege et al., 2000).

Our findings, which show no impact on benthic communities, contradict previous studies. Harbour infrastructure development was expected to cause changes in sedimentary composition or in hydrological conditions, which would affect benthic communities, as was reported by Monbet (1997) in similar circumstances. This author showed that during the Antifer petroleum harbour construction project (English Channel, France), macrofaunal abundance and biomass levels decreased by 75% and 80%, respectively, mainly due to dredging and dumping operations. These effects were temporary, given that 3 years after the disturbance ended, average abundance and biomass levels recorded for the *A. alba–P. koreni* reached 600 ind. m^{-2} (versus 147 ind. m^{-2} before) and 29 g m^{-2} (versus 23 g m^{-2} before).

5.2. Suprabenthic communities

Although Mouny et al. (2000), using samples from marine (30 salinity) to fresh (0) waters, correlated the distribution of suprabenthic species to the salinity gradient in the Seine estuary. The suprabenthic fauna showed to be homogeneously distributed in the North Channel. Due to the large intrusion of marine waters in the North Channel, species are typical of polyhaline waters (Dauvin et al., 1995). The differences between winter (March 2001 and March 2003) and autumn samples (September 2001 and October 2002) indicate that suprabenthic assemblages are simply exhibiting a seasonal pattern that is highly variable interannually. Turbidity also influences species distribution. Species, such as the mysid *N. integer* and the decapod *Palaemon longirostris*, were confined to the upstream part of the North Channel in brackish waters with high turbidity, while the mysids *Mesopodopsis slaberri*, *Gastrosaccus spinifer* and *Schistomysis ornata*, and the ctenophore *Pleurobrachia pileus* were distributed downstream in marine water with low turbidity. Clearly, both the species distribution and the abundance values observed for each sample date were consistent with expected patterns. Thus, no significant changes in the suprabenthic assemblages can be observed 1 year after the harbour extension operations were initiated. Considering the low abundances of benthic invertebrates in the upstream North Channel, the suprabenthic fauna was and remains an important trophic resource for higher consumers (especially fish) in the food web.

As shown by sampling surveys, *N. integer* is one of the most common species in the Seine estuary (Dauvin et al., 1995; Mouny et al., 2000). Morphological analysis conducted on this species in March 2003 showed that 15–20% of individuals exhibited abnormal telson. This rate is high compared to values reported by Chojnacki and Ciupinski (1986) in the Baltic sea (1–5%) and Mees et al. (1995) in various European estuaries: the Elbe, Ems-Dollard, Scheldt and Gironde. The percentage of symmetrical telsons was higher than that of asymmetrical telsons. While the latest form is mainly the result of predation by fish and shrimp, abnormal symmetrical telsons do assess polluted environments, especially those showing metallic contamination (Chojnacki and Ciupinski, 1986). Such a result could be expected given that the Seine estuary is one of the most contaminated estuaries in Europe. A comparison of the metal concentrations found in Seine estuarine species with those found in the same species collected on contaminated et non-contaminated sites indicated that the estuary was contaminated by copper, zinc, and lead (Miramand et al., 2001). However, at the present time, it is not possible to ascribe our observations to organic or metallic contamination, and further studies would have to be undertaken concerning *N. integer* before it could be selected as a biological indicator of the water quality in the Seine estuary.

5.3. Compensatory actions to preserve the ecological role of the estuary

When the French Authorities decided to ratify the "Port 2000" extension project for Le Havre harbour in September 1998, they underlined the importance of striking a balance between the Port 2000 project's economic development objectives and the protection of aquatic habitats via an exemplary management program for the Seine estuary. Without compensatory actions upstream, the presumed effects of the high current velocities in the North Channel included (1) an oscillating water volume that would lead to the silting up of the North channel and (2) a loss of benthic fauna (Dauvin, 2002). In order to minimize these hydro-sedimentary and biological changes, and to preserve the "Grande vasière" tidal flat located in the upper part of the North Channel, several compensatory actions were planned to take place between 2004–2006 (Hamm and Viguier, 1997; Hamm et al., 2001; Fig. 8). In addition to monitoring programs that study hydro-sedimentary (bathymetry, topography, hydraulics, sedimentology), and biological components (macrobenthos, suprabenthos, ichtyofauna, avifauna) in the North Channel, these actions include:

- a new opening in the north dam, upstream from the Normandy Bridge, and the dredging of a channel connected to the north navigational channel;
- the elevation of the downstream opening to the level +3.5 m in order to allow water to flow more easily toward the new upstream opening;
- the construction of an immersed dam supported by the north dam in order to increase the circulation of seawater during ebb tide;
- a 500 m prolongation of the north dam in the direction of the sea;

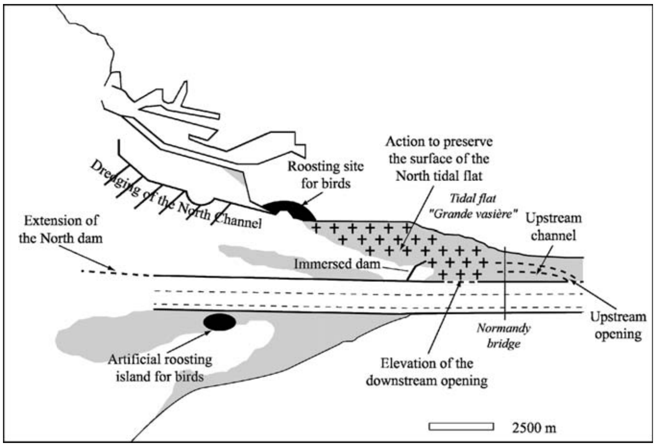

Fig. 8. Compensatory actions planned in the Seine estuary.

- the dredging of more than 5 million tons of sediment, including a new organization of dredging operations, which would change the location of the Kannick dumping site for sediment dredged in Rouen;
- the construction of artificial roosting sites for birds, on the northern bank as well as in the South Channel.

The last action constitutes one of the major challenges of the wildlife conservation plan: the preservation of the resting site capacity for birds living on/near the estuary. The Seine estuary is a site of international importance for birds like the common shelduck, the northern pintail and the piet avocet, among others. Though part of the environmental preservation plan, some of the compensatory actions will have direct effects that are as important as those caused by the harbour extension, specifically on benthic habitats, and these effects must be evaluated. Sustainability attempts to balance economic, social and environmental considerations to produce a solution that reaches the widest possible consensus (Jones et al., 2002).

This study concludes that the benthic and suprabenthic assemblage abundances in the study area are within the normal range of spatial and/or temporal variability encountered in the Bay of Seine. This is in contrast to that expected given the surface under consideration. But, as underlined by Elliott and McLusky (2002), although estuaries are habitats that man has exploited and often destroyed, the estuarine habitats remain among the most resilient habitats on earth, maintaining their attractiveness for wildlife, despite of industrialization and land claim. Despite this, further long-term studies are needed in order to distinguish meaningful change from mere local variations in the overall structure and interactions of assemblages in the Seine estuary.

Acknowledgements

This study was undertaken as part of the Seine-Aval II program ordinated by the "Haute Normandie" region. The authors are grateful to the crew of "N.O. Côte d'Aquitaine" for their help during sampling, to D. Hilde for his help in sorting the suprabenthic fauna and to L. E. Spencer for comments and help in correcting the English text. The authors would like to thank the "Port Autonome de Rouen" and the "Port Autonome du Havre" for their permission to use the data obtained while under contract to the two harbours.

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Marine Pollution Bulletin 55 (2007) 241–257

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The ecological quality status of the Bay of Seine and the Seine estuary: Use of biotic indices

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Abstract

Using recent indices developed, in part, for use under the European Water Framework Directive (AMBI, BENTIX, BOPA, BQI, I2EC and the trophic index ITI), the ecological quality status of two highly contaminated environments—the Bay of Seine and the Seine estuary (Eastern English Channel)—was determined on several spatial and temporal scales. Data from 604 observations gathered over a 14-year period (1988–2002) were analyzed, and the results used to show the relationship between biotic indices, environmental variables and classic descriptors (e.g., number of species, total abundance, dominance index, ES(50) and Shannon/Brillouin diversities). Though the specific ecological quality (EcoQ) values calculated with the various indices were different, the overall trend of the results was similar. Synthesizing the values produced by the six indices used in the study allowed attribution of a *high* to *good* EcoQ status to the Bay of Seine and a *moderate* EcoQ to the estuary. The mesh size used when processing samples was proved to have no effect in winter on the EcoQ values for either body of water.

Keywords: Seine estuary; Bay of Seine; English channel; Macrobenthos; Biotic index; Benthic index

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1. Introduction

Benthic invertebrates are frequently used as bio-indicators for marine monitoring because they respond rapidly to anthropogenic and natural stress (Pearson and Rosenberg, 1978; Dauvin, 1993; Dauer et al., 2000; Bustos-Baez and Frid, 2003). Macrobenthic organisms are good indicators because they (i) are relatively sedentary and so unable to avoid deteriorating water/sediment quality, (ii) have relatively long life-spans, (iii) include diverse species with different tolerances to stress, and (iv) play a vital role in cycling nutrients and materials between the underlying sediment and the overlying water column. Several authors have reviewed the use of biotic indices (e.g., Diaz et al., 2003; Occhipinti Ambrogi and Forni, 2004). Some of these authors accept that a biotic index is unlikely to be universally applicable, because all organisms are not equally sensitive to all types of anthropogenic disturbances and thus are likely to respond differently to different types of perturbations. Several of the indices proposed for evaluating estuarine and coastal water quality have already been used as proxies for detecting the impact of pollution on the macrobenthic communities (see Grall and Glémarec, 1997; Eaton, 2001; Borja et al., 2000, 2003a, 2004a). Given this context, macrobenthic organisms may provide the foundations for a multimetric bio-assessment method that can be adjusted for application in different geographical regions (Weisberg et al., 1997; Borja et al., 2000, 2003a,b, 2004a,b).

In order to implement the European Water Framework Directive (WFD), a series of common concepts, terminologies and tools had to be developed. The process of development has led to a certain degree of controversy within the European scientific community, particularly as concerns

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doi:10.1016/j.marpolbul.2006.04.010

the advantages of using the AZTI Marine Biotic Index (AMBI) developed by Borja et al. (2000) as compared to the BENTIX created by Simboura and Zenetos (2002), with some researchers feeling that the AMBI is more appropriate for assessing the EcoQ of transitional (estuarine) and coastal water bodies (see Borja et al., 2004a,b; Simboura, 2004; Borja and Heinrich, 2005; Muxika et al., 2005). Both indices attribute five environmental status ratings—*high*, *good*, *moderate*, *poor* and *bad*—according to the quality of the biological, hydro-morphological and physico-chemical elements present in an area, with the biological elements, especially the benthos, being particularly important. This already complex situation has been further complicated by the development of a new method, the benthic quality index (BQI), for determining marine benthic quality under the European Water Framework Directive (Rosenberg et al., 2004).

Clearly, the notion of indicators and indices has undergone considerable scientific development in a variety of domains. Many policy and management authorities interested in evaluating the quality of marine systems have endorsed indicator-based approaches to management (Link, 2005). The field of fishery management has provided a suite of indicators (Rice and Rochet, 2005), and is now working to develop ecological indicators able to detect the effect of fishing activities on the environment (Fulton et al., 2005). In short, the implementation of the WFD has provided a marvellous opportunity for those working on the benthos to gauge the efficiency of the numerous bio-indicators and biotic indices—existing and under development—for testing the quality of estuarine and marine environments (see Bricker et al., 2003; Salas et al., 2004; Marin-Guirao et al., 2005; Rogers and Greenaway, 2005).

In the study presented in this article, a variety of biotic indices were applied to data from both the Bay of Seine and the Seine estuary in order to test the pertinence of these indices for highly contaminated environments. The Seine estuary is the largest megatidal estuary in the English Channel, covering approximately 150 km^2 at high tide. Although the water column can be stratified at the mouth of the estuary (ebb and low tide), the estuary is generally well mixed when the discharge of freshwater exceeds 500 $m^3 s^{-1}$ (Mouny et al., 1998). The freshwater discharge into the estuary (mean 1975–2005: 484 $m^3 s^{-1}$; N. Bacq personal communication) comes mainly from Seine River and varies seasonally from a maximum of 2200 $m^3 s^{-1}$ in winter to a minimum of 50–100 $m^3 s^{-1}$ in summer. The mean annual particulate river discharge has been evaluated at 650 000 t of suspended matter (Avoine, 1994), and the maximum turbidity zone, located at the mouth of the estuary, can sometimes be expulsed into the Bay of Seine during swelling (Lafite and Romana, 2001).

In addition to the disturbances resulting from man-made modifications of the estuary (Dauvin and Desroy, 2005), high levels of heavy metals, particularly cadmium and lead, make the Seine estuary one of the most contaminated in Europe. While the cadmium levels mainly affect benthic and suprabenthic species (e.g., bivalves), elevated levels of zinc have been measured in all species living in the Seine estuary—from benthic invertebrates to fish (Miramand et al., 2001). Addes to these metal contaminants, the level of organic contaminants (e.g., PAHs, PCBs and pesticides) helps to place the Seine estuary among the most contaminated of estuaries (Tronzynski, 1999). The chronic, high-level organic contamination in the Seine estuary is a major concern since the contamination of organisms and ecological resources increases with the trophic level, from benthic and suprabenthic prey to carnivorous fish (Dauvin, in press). Due to the contamination mentioned above and the rapid silting up of the estuary (Lesourd et al., 2001), which will probably increase in response to the Le Havre harbor extension (Dauvin et al., 2006), the environment of the benthic communities existing in the Seine estuary and in the eastern part of the Bay of Seine can be said to be perturbed.

Given the concentration of environmental disturbances, the different areas in the Bay of Seine have been studied more or less intensively at a variety of spatial scales (Thiébaut et al., 1997; Dauvin et al., 2004). A large-scale project assessing the effect of previous dredging on the benthic communities throughout the bay was carried out in 1997 (Gentil and Cabioch, 1997), and in 2002 the first mesoscale quantitative study of the bay was conducted (Ghertsos, 2002). Beginning at the end of the 1990s, several other benthic studies were conducted at different spatial and temporal scales, often with the support of the Seine-Aval scientific program. Recently, a new database called Macrobenthos of the Bay and Estuary of Seine (MABES); available via the data administrator of the GIP Seine Aval: nbacq@seine-aval.fr) was set up to collect the benthic data from the Bay of Seine and the Seine estuary.

The data examined in this paper come from the MABES database. Through this examination, we seek (i) to evaluate the usefulness of the recent benthic biotic indices proposed for implementing the WFD, (ii) to compare their pertinence in terms of the existing indices, and (iii) based on the results produced by the various indices, to identify the response of the macrobenthic communities in the Bay of Seine and the Seine estuary to a highly contaminated environment.

2. Material and methods

2.1. The Bay of Seine

The Bay of Seine forms a roughly 5000-km^2 quadrilateral measuring ≅50 km from north to south and ≅100 km from west to east, with mostly regular morphological features (Fig. 1). Opening wide onto the central English Channel in the north, the Bay of Seine never exceeds 30 m in depth. To the north of the Pays de Caux and northwest towards the Cotentin Strait, the maximum speed of the tidal currents is 3 knots. In the eastern part of the Bay, the current is weak—less than 1.5 knots on

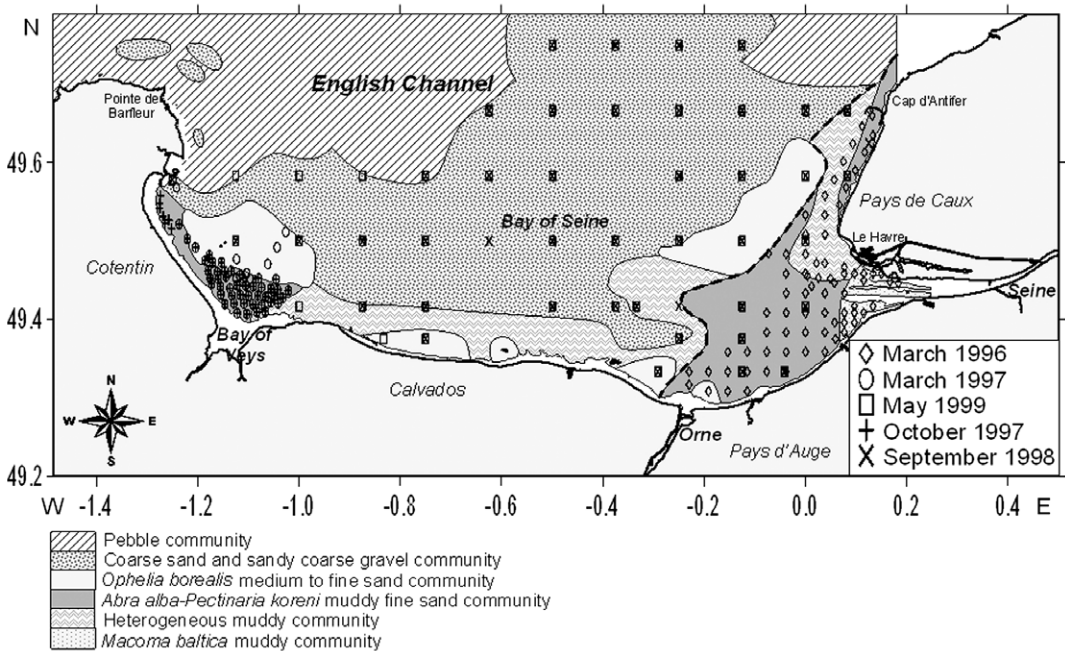

Fig. 1. Map showing the benthic sites sampled before (March 1996, March 1997 and May 1999) and after (October 1997 and September 1998) the recruitment in the Bay of Seine as well as the limits of the main benthic communities defined by Gentil and Cabioch (1997). The bold dashed line represents the limit between sites located outside (to the west) and inside (to the east) the zone influenced by the Seine River. Coordinates are expressed in decimal degrees.

the surface (average spring tide). These tidal currents, added to the general drift of the water, play an essential role in distributing both sediment and benthic communities, as well as in dispersing river input, especially from the Seine River (Gentil and Cabioch, 1997). Together, they create an offshore-inshore gradient in the Bay, with the dominant sediment offshore generally consisting of pebbles, gravel and coarse sand, and the sediment inshore in the coastal zones—especially in the western part of the Bay (Bay of Veys) and in the eastern part just in front of the Seine estuary—consisting mostly of fine sand, and silty/muddy fine sands.

In the Bay of Seine, Gentil and Cabioch (1997) identified six main macrobenthic communities: (i) an pebble-inhabiting community offshore in which strong tidal currents prevail; (ii) a coarse sand to sandy-coarse-gravel community, with dense patches of the ophiurid *Ophiothrix fragilis*, occupying the central part of the bay; (iii) a medium-to-fine sand *Ophelia borealis* community linked to hydrodynamic sand dunes; (iv) a muddy-fine sand *Abra alba-Pectinaria koreni* community; (v) a heterogeneous muddy community, and (vi) a muddy *Macoma balthica* community in the estuary and the inner part of the Bay of Veys (Fig. 1), the last four populating the eastern and western parts of the Bay.

2.2. Macrobenthic sampling

Table 1 summarizes the main characteristics of the quantitative samples taken from the subtidal macrobenthic communities in the Bay of Seine at four spatial scales.

(i) *The entire Bay of Seine.* A total of 90 sites were sampled—44 in September 1998 and 46 in May 1999—over a wide grid measuring approximately 100 km (East to West) by 50 km (North to South, Fig. 1), which encompasses the entire Bay of Seine (Ghertsos, 2002). The distance between sampling sites was about 5 nautical miles. Although two biological samples provide more than the required precision (i.e., 5%) for estimating the densities of the main populations (Thiébaut et al., 1997), four replicates were collected at each site using a Hamon grab ($0.25\ m^2$–10 cm depth, Eleftheriou and Holme, 1984). This grab, judged best suited to the varying sedimentary environments, was chosen to avoid the inevitable problems of incomparability had different grabs been used in different areas. An additional 5th sample was collected at each of the sites in order to analyze such environmental parameters as granulometry, total organic matter and pigment (chlorophyll *a*/phaeopigments, Ghertsos, 2002).

(ii) *The Bay of Veys.* The macrofaunal distribution in the Bay of Veys was determined by two surveys conducted in 1997 (Fig. 1, Dauvin et al., 2004). The first was performed in March (55 sites) before the recruitment period of the dominant species, and the second, in October (54 sites), following the main recruitment period. The distance between sampling sites was about 1 nautical mile. Most of the sites were located in the muddy/fine-sand *Abra alba-Pectinaria koreni* community, though the sampling grid was completed

Table 1
Main characteristics of the subtidal sampling sites in the Bay of Seine and the Seine estuary

Sampling zone in the Bay of Seine	Sampling dates	Number of sites	Sampling gear and total surface or volume sampled	Sieving mesh (mm)	References
Eastern part	February 1988	64[a]	Hamon grab (0.5 m^2)	2	Thiébaut et al., 1997
Eastern part	March 1991	64[a]	Hamon grab (0.5 m^2)	2	Thiébaut et al., 1997
Eastern part	March 1996	77[a]	Hamon grab (0.5 m^2)	2	Unpublished data
Bay of Veys	March 1997	55[a]	Hamon grab (0.5 m^2)	2	Dauvin et al., 2004
Bay of Veys	October 1997	54[a]	Hamon grab (0.5 m^2)	2	Dauvin et al., 2004
Bay of Seine	September 1998	44[a,b]	Hamon grab (1 m^2)	2	Ghertsos, 2002
Bay of Seine	May 1999	46[a,b]	Hamon grab (1 m^2)	2	Ghertsos, 2002
Seine estuary	November 1993	2	Smith McIntyre grab (0.3 m^2)	1	Mouny et al., 1998
Seine estuary	May and October 1995	3	Rallier du Baty dredge (30 L)	1	Mouny et al., 1998
Seine estuary	February 2001	11	Hamon grab (1 m^2)	1 and 2	Janson and Desroy, unpublished data
Seine estuary	March, May and September 2002	23	Hamon grab (0.5 m^2)	2	Janson and Desroy, unpublished data
Seine estuary	March to December 2002	4[c]	Van Veen grab (0.5 m^2)	1	Janson and Desroy, unpublished data

[a] Granulometric analyses available.

[b] Organic matter rate and pigment concentrations in the sediment available.

[c] 10 Sampling dates (excepted in one site where March sampling is missing): March (2 surveys), April (2), May (3), June (1), September (1) and December (1).

by few offshore sites located in the fine-sand *Ophelia borealis* community (Gentil and Cabioch, 1997). All benthic sampling was carried out using a Hamon grab, with two grabs collected at each site for biological analysis and one for sediment characterisation.

(iii) *The Eastern part of the Bay of Seine.* The macrofauna distribution in the eastern part of the Bay of Seine was established from three benthic surveys organized before the recruitment period of the dominant species—in February 1988, March 1991 and March 1996 (Thiébaut et al., 1997; unpublished data). Grids of 64, 64 and 77 sites, respectively, were sampled during each survey (Figs. 1 and 2). The distance between sites was about 1.5 nautical miles. Most of the sites were located in the muddy/fine-sand *Abra alba-Pectinaria koreni* community and its heterogeneous muddy/sand facies, as well as in the medium-sand *Ophelia borealis* community. Samples were collected using a Hamon grab, with three grab samples being collected at each site, two for biological analysis and one for granulometric analysis.

(iv) *The Seine Estuary.* Four different surveys were carried out in the estuary, each at a different spatial and temporal scale.

- Three replicate samples were taken in November 1993 using a 0.1 m^{-2} Smith–McIntyre grab at two sites located in the Navigational Channel of the Seine estuary, downstream from Honfleur. Later, three sites were sampled in May and October 1995 in the upper part of the Navigational Channel (Honfleur-Pont de Tancarville), using a Rallier du Baty dredge (samples containing about 30 L of sediment) (Mouny et al., 1998).
- Eleven sites situated in the Northern Channel of the estuary were sampled in February 2001 using a Hamon grab, the distance between sites being about 1 nautical mile. Four grab samples were col-

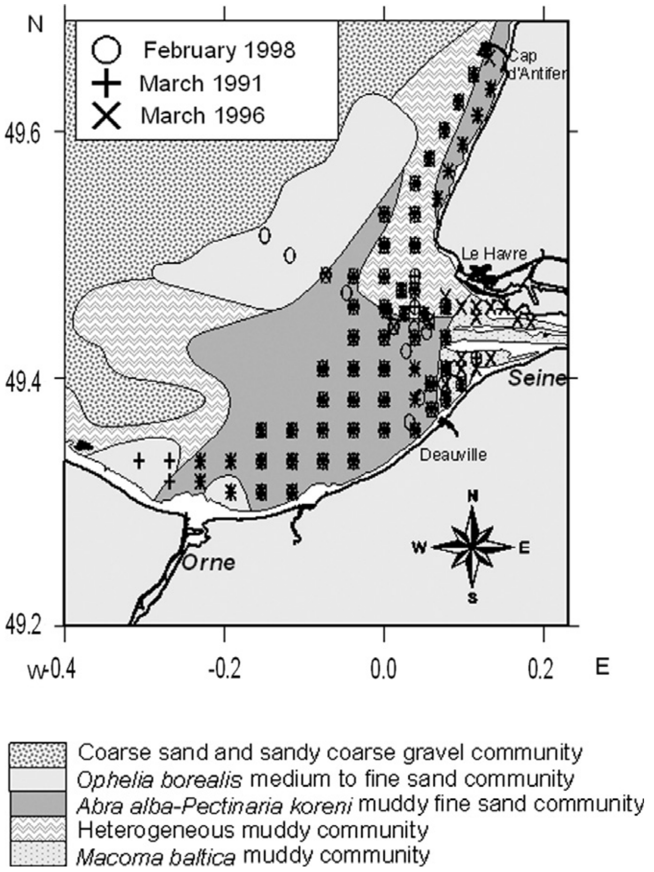

Fig. 2. Map showing the benthic sites in the eastern part of the Bay of Seine—sampled in February 1998, March 1991 and March 1996—and the limits of the main benthic communities defined by Gentil and Cabioch (1997). Coordinates are expressed in decimal degrees.

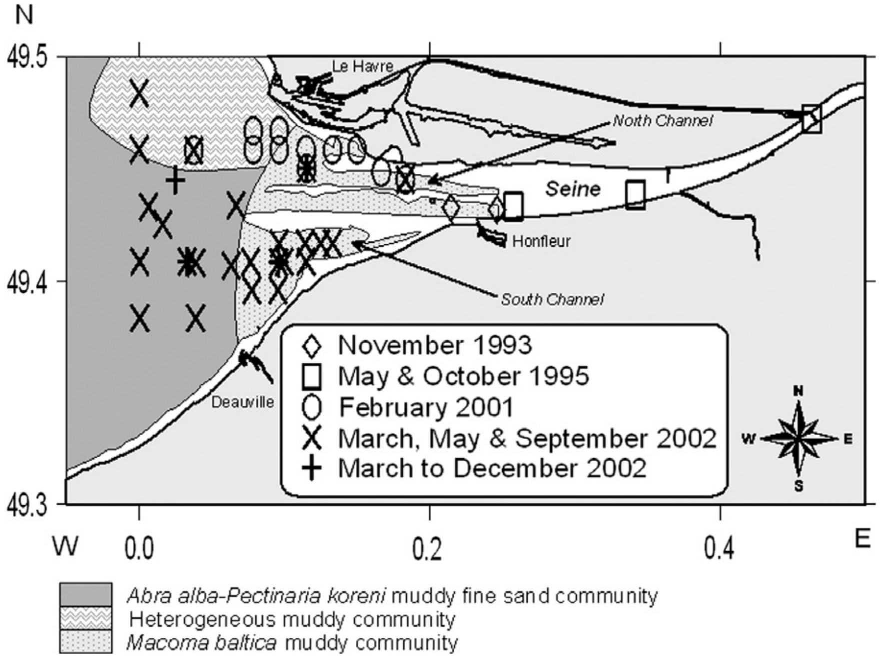

Fig. 3. Map showing the benthic sites of the Seine estuary (sampled in November 1993, May and October 1995, February 2001, March, May and September 2002 and from March to December 2002) and the limits of the main benthic communities defined by Gentil and Cabioch (1997). Coordinates are expressed in decimal degrees.

lected at each site for biological analysis, plus an additional sample for sediment characterisation.

– A total of 23 sites were sampled in March, May and September 2002 using a Hamon grab (two samples for biological analysis and one for sediment characterisation). These sites were located throughout the polyhaline zone of the estuary, the North and South Channels, and the mouth of the estuary (Janson and Desroy—unpublished data, Fig. 3).
– Four sites—one in the North Channel, one in the South Channel and two at the mouth of the estuary—were sampled regularly with a Van Veen grab from March to December 2002 (10 dates for all sites, except the North Channel site, which was sampled only 9 times) (Janson and Desroy—unpublished data). The benthic assemblages studied were the muddy/fine-sand *Abra alba-Pectinaria koreni* community that occupy the external part of the estuary and the entrance to the North and South Channels, and the *Macoma balthica* community that is spread throughout the inner subtidal bottoms in the North, South and Navigational Channels (Dauvin and Desroy, 2005).

In the above studies cited, the samples collected with the Hamon grab were sieved through a 2 mm mesh, except for those taken in February 2001, which were processed using both 2 mm and 1 mm mesh sizes. For samples collected with other gear (the Smith McIntyre or Van Veen grabs and the Rallier du Baty dredge), a circular 1 mm-mesh sieve was preferred. For all the samples in all surveys, the biological material retained by the sieve meshes (1 mm or 2 mm, see Table 1 for details) was fixed in 4% buffered formaldehyde mixed with seawater until it could be sorted, identified to the species level, and counted in the laboratory. Abundances were expressed in nb ind. 0.5 m^{-2}.

Table 1 shows the number of sites for which environmental parameters were measured and are available. The size distribution of sediment particles was analysed by wet sieving; the results in Table 1 are expressed in percentages for the five sediment grain sizes: gravel (>2 mm, denoted G), coarse sand (500 μm–2 mm, denoted CS), medium sand (200–500 μm, denoted MS), fine sand (63–200 μm, denoted FS), and silt/clay (<63 μm, denoted silt). The total organic matter rate was measured using a method of weight loss upon ignition. Using spectrophotometry, the level of chlorophylls *a*, *b* and *c*, as well as of phaeopigment values and carotenoids, was measured after dilution in acetone (results in μg/cm^3 of sediment) (Ghertsos, 2002).

All results were compiled in a database comprising 604 observations and 392 species.

2.3. Biotic indices

Numerous biotic indices have been proposed in the literature (see Gomez Gesteira and Dauvin, 2000; Diaz et al., 2003; Occhipinti Ambrogi and Forni, 2004; SGSOBS, 2004). Among the indices available, we chose to evaluate six (Table 2): the Infaunal Trophic Index (ITI) (Word, 1978) based on trophic groups; the indices AMBI (Borja et al., 2000), BENTIX (Simboura and Zenetos, 2002),

Table 2
Indices calculated from the macrobenthos database referring to the Bay of Seine and Seine estuary

Variable	Determination or calculation	References
S	Number of species	–
n_i	Number of individuals belonging to the ith species	–
N	$\sum n_i$, total number of individuals per m^2	–
Dominance	$\sum n_i \times (n_i/(N-1))$	–
H (Brillouin)	$N^{-1}\ln(N!/(N_1!N_2!\ldots N_s!))$	In SGSOBS (2004)
ES$_{(50)}$	Expected number of species for 50 individuals	Rosenberg et al. (2004)
H' (Shannon)	$-\sum[(n_i/N)\times\log_2(n_i/N)]$	In SGSOBS (2004)
BQI	$\sum[(n_i/\sum n_i)\times \mathrm{ES50}_{0.05i}]\times\log_{10}(S+1)$	Rosenberg et al. (2004)
AMBI	$0\ \mathrm{EG_I} + 1.5\ \mathrm{EG_{II}} + 3\ \mathrm{EG_{III}} + 4.5\ \mathrm{EG_{IV}} + 6\ \mathrm{EG_V}$	Borja et al. (2000)
BENTIX	$6\ \mathrm{EG_{I\&II}} + 2\ \mathrm{EG_{III–V}}$	Simboura and Zenetos (2002)
I2EC	Key of determination based on 5 EG	Grall and Glémarec (2003)
BOPA	$\log_{10}[(f_P/(f_A+1))+1]$	Gomez Gesteira and Dauvin (2000), revised in Dauvin and Ruellet (submitted for publication)
ITI	$100-33.3(\mathrm{TG}_2+2\ \mathrm{TG}_3+3\ \mathrm{TG}_4)/\mathrm{TG}_{1,2,3,4}$	Mearns and Word (1982)

AMBI: AZTI Marine Biotic Index; BOPA: Benthic Opportunistic Polychaetes Amphipods index; BQI: Benthic Quality Index; EG: Ecological Group (see text); f_A: amphipods frequency (except *Jassa* sp.); f_P: opportunistic polychaetes frequency; I2EC: Coastal Endofaunic Evaluation Index; ITI: Infaunal Trophic Index; TG: Trophic Group (see text).

I2EC (Grall and Glémarec, 2003) and BOPA[2] (Gomez Gesteira and Dauvin, 2000; Dauvin and Ruellet, submitted for publication), all based on ecological groups; and the Benthic Quality Index (BQI) (Rosenberg et al., 2004), developed specifically for use under the WFD. Other quantitative variables were also considered (e.g., number of species (S), number of individuals (N)), as were several univariate indices (e.g., dominance index, H' Shannon diversity index, H Brillouin diversity index) (Table 2). In addition, the expected number of species present for 50 individuals was also calculated (Primer version 5) to allow the BQI (Rosenberg et al., 2004) to be established (Table 2).

The ITI was determined in consideration of the feeding habits of macrobenthic species, as specified by Thiébaut et al. (1997) and Ghertsos (2002). The four main trophic groups (TG) retained were those defined by Mearns and Word (1982): (TG1) suspension feeders, (TG2) carrion feeders (e.g., carnivorous, omnivorous and necrophagous), (TG3) surface deposit feeders and those species that are both suspension feeders and surface deposit feeders, and (TG4) subsurface deposit feeders that feed on sedimentary detritus and bacteria.

The indices based on ecological groups all refer to the same five ecological groups. These groups are ranked according to their sensitivity to an increasing stress gradient as per the regularly updated list published by the AZTI Laboratory (www.azti.es): Group I (species very sensitive to organic enrichment), Group II (species indifferent to enrichment), Group III (species tolerant of excessive organic enrichment), Group IV (second-order opportunistic species) and Group V (first-order opportunistic species). Less than 8% of the taxa observed in the Bay of Seine and the Seine estuary could not be assigned to an ecological group. The AMBI was calculated following the guidelines of Borja and Muxika (2005).

To use the BQI, it was first necessary to calculate the expected number of species present in 50 individuals (Table 2). This ES(50)$_{0.05}$ was calculated for 90 of the 392 taxa, using the thresholds proposed by Rosenberg et al. (2004) for species present at least in 20 observations where the total abundance is higher than 50 individuals.

2.4. Data analyses

Since the database encompasses different spatial and temporal scales, several patterns were considered for the distribution of biotic indices in the Bay of Seine.

(i) Large spatial scales were available for two periods: (1) prior to the recruitment period of the principle benthic species (see Thiébaut et al., 1997; Dauvin et al., 2004)—based on 176 observations from the March 1996, March 1997 and May 1999 surveys, and (2) following the recruitment period—based on 98 observations from the September 1998 and October 1997 surveys.
(ii) Inter-annual temporal changes were detected in the eastern part of the Bay of Seine based on 203 observations from three surveys: February 1988, March 1991 and March 1996.
(iii) The influence of the salinity gradient was observed from the polyhaline to the oligohaline zones based on eight observations at five sampling sites in the Navigational Channel.
(iv) Seasonal changes were detected in the estuary based on 69 observations from surveys conducted at 23 sites in March, May and September 2002 and on 39 observations from three sites sampled 10 times and one site sampled 9 times in a single year.

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[2] The BOPA index is an improved version of the Opportunistic Polychaetes/Amphipods ratio proposed by Gomez Gesteira and Dauvin (2000). It takes into account the total number of individuals collected, the frequency of opportunistic polychaetes, and the frequency of amphipods, except the genus *Jassa* (Dauvin and Ruellet, submitted for publication).

(v) The effect of mesh size (1 mm versus 2 mm) was evaluated based on 44 observations from 11 sites in the Seine estuary sampled in February 2001.

Only a selection of some indices was shown for each scale, but in the discussion all the indices were integrated to establish the EcoQ status of the studied area (see Fig. 7 for the range of the 12 variables).

2.5. Statistical analysis

The relationships between number of species and abundance versus sediment parameters and biotic indices were tested using Spearman's rank correlation coefficients (Scherrer, 1984) with XLSTAT-Pro version 5.1.4 (© Addinsoft).

3. Results

3.1. Large spatial scales

For both sampling periods, AMBI produced very low values, indicating a *high* or *good* ecological status for the whole Bay of Seine, independent of the recruitment phenomenon (Fig. 4). Still, the general status does appear to be slightly better in autumn than in spring. Since no values attained the threshold of 3.3 (corresponding to *moderate* status), no gradient could be identified. Zones with values ranging between 1.2 and 2.3 (*good* status) were located both near the Seine estuary and offshore prior to the recruitment period, and near the Bay of Veys after the recruitment period.

On the other hand, according to the BQI, the situation was both worse and more contrasted for both seasons, with status values varying from *good* to *poor*. Despite these unpromising ratings, the general EcoQ status in the Bay of Seine improved between the two periods. Prior to the recruitment period, several *poor* status zones were identified just in front the Seine estuary and offshore in the northern and western parts of the bay; moderate status zones were found throughout the central section of the Bay, with good status zones appearing along the southern coast. After the recruitment period, the EcoQ for the shallow waters of the bay was generally *good*, except locally near the Seine estuary. Only one site, located in the northwestern part of the bay could be ranked as *poor*, while the rest of the northwestern section attained *moderate* status.

3.2. Inter-annual temporal changes in the eastern part of the Bay of Seine

During the three-winter/spring periods, the general status indicated by the AMBI index was *high* or *good* (Fig. 5). However, AMBI also underlined an improvement in the water quality over time, with the majority of the sites that attained *good* status in 1988 and 1991 evolving toward *high* status by 1996. Although the Bay of Seine obtained a worse rating from the BQI for the same three years, with a gradient ranging from *poor* in front of the Seine estuary to *good*

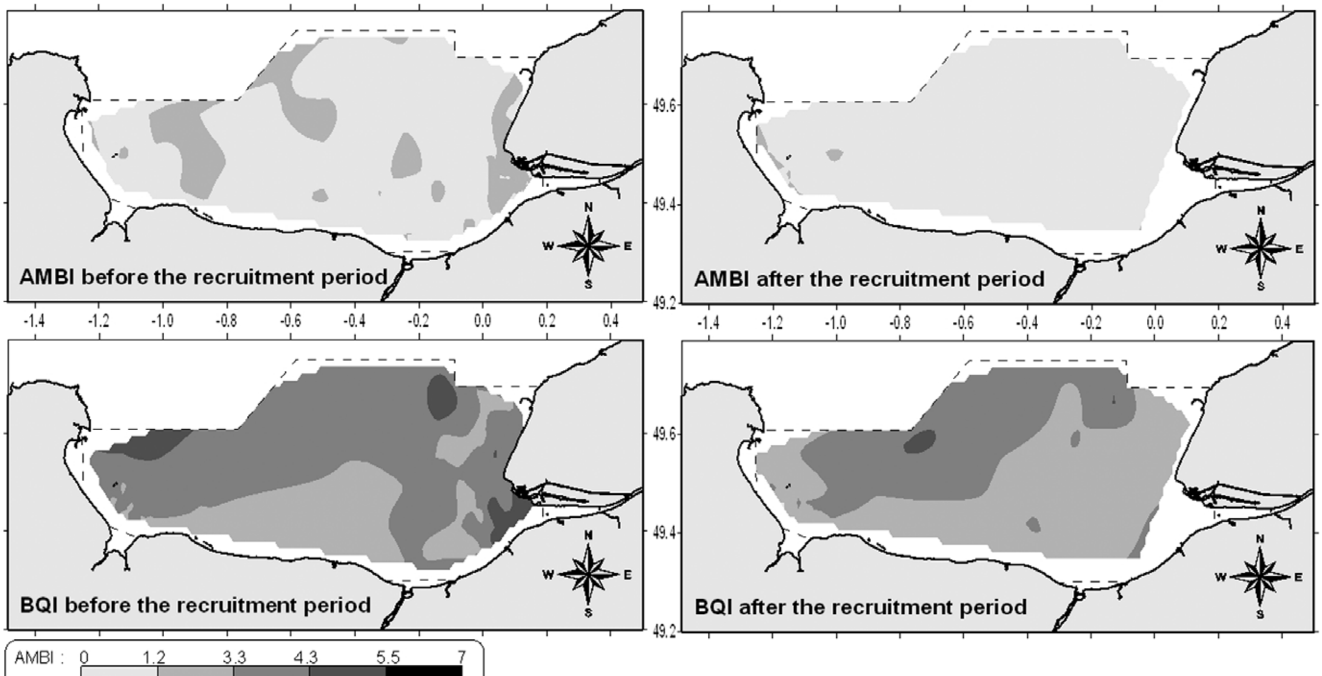

Fig. 4. AMBI and BQI values in the Bay of Seine before and after the recruitment period. Dashed lines represent the limits of the area studied. Coordinates are expressed in decimal degrees.

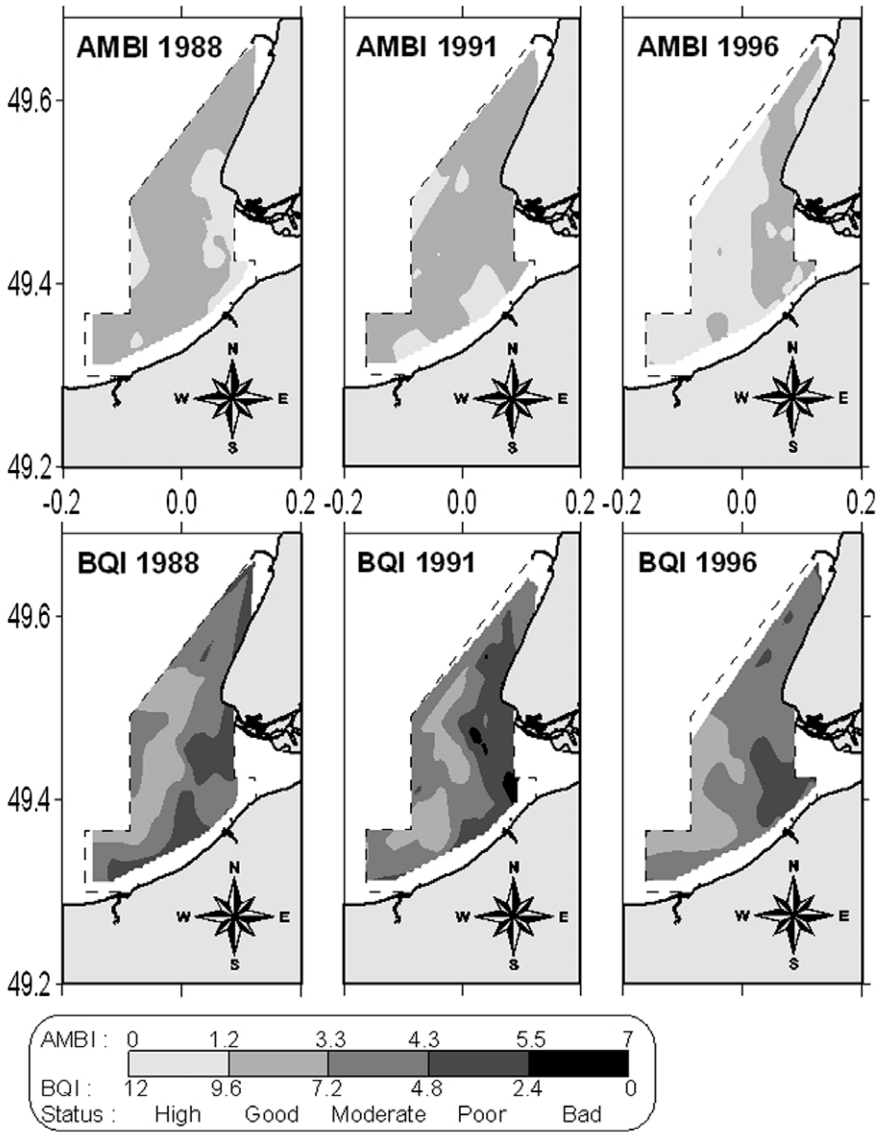

Fig. 5. Inter-annual evolution of AMBI and BQI values in the Eastern part of the Bay of Seine: February 1988, March 1991 and March 1996. Dashed lines represent the limits of the area studied. Coordinates are expressed in decimal degrees.

in the offshore bottoms, the overall trend with the BQI was also towards improved water quality over time (Fig. 5).

3.3. *Effects of the salinity gradient*

Based on data collected in 1993 and 1995 (not presented in this study), the EcoQ status of the Seine estuary as defined by the AMBI ranged from *good* to *high*, while the status calculated with the BQI ranged from *bad* to *good* (Fig. 5). The ITI classified the Seine estuary and the Bay of Veys as *modified* zones ($30 < \text{ITI} < 60$, data not shown), according to the definitions proposed by Bascom et al. (1978). This classification can be explained by the presence of a small *degraded* zone ($\text{ITI} < 30$) in the middle of the channel between Honfleur and Le Havre and a larger such zone in the Bay of Veys. The ITI classification for the other sections of the Bay of Seine was predominantly *normal* or *slightly modified*.

3.4. *Annual temporal changes in the estuary*

Surveys of 23 sites located in the Seine estuary done in March, May, and September 2002 indicate small seasonal changes. Using the AMBI index produced a predominance of *good* status ratings, while using the BQI resulted in an inshore-offshore gradient ranging from *poor* to *good* status, with an occasional *bad* status rating (Fig. 6).

3.5. *Relationship between demographics, sediment parameters and the biotic indices*

Fig. 7 presents the range of variations and the median value of each index for the 11 datasets tested. Although each of the 12 indices produced a range of widely varying values, calculating the median values allows some general trends to be highlighted. Overall, the S, N, H' and Brillouin diversity values were higher in the Bay of Seine than in the

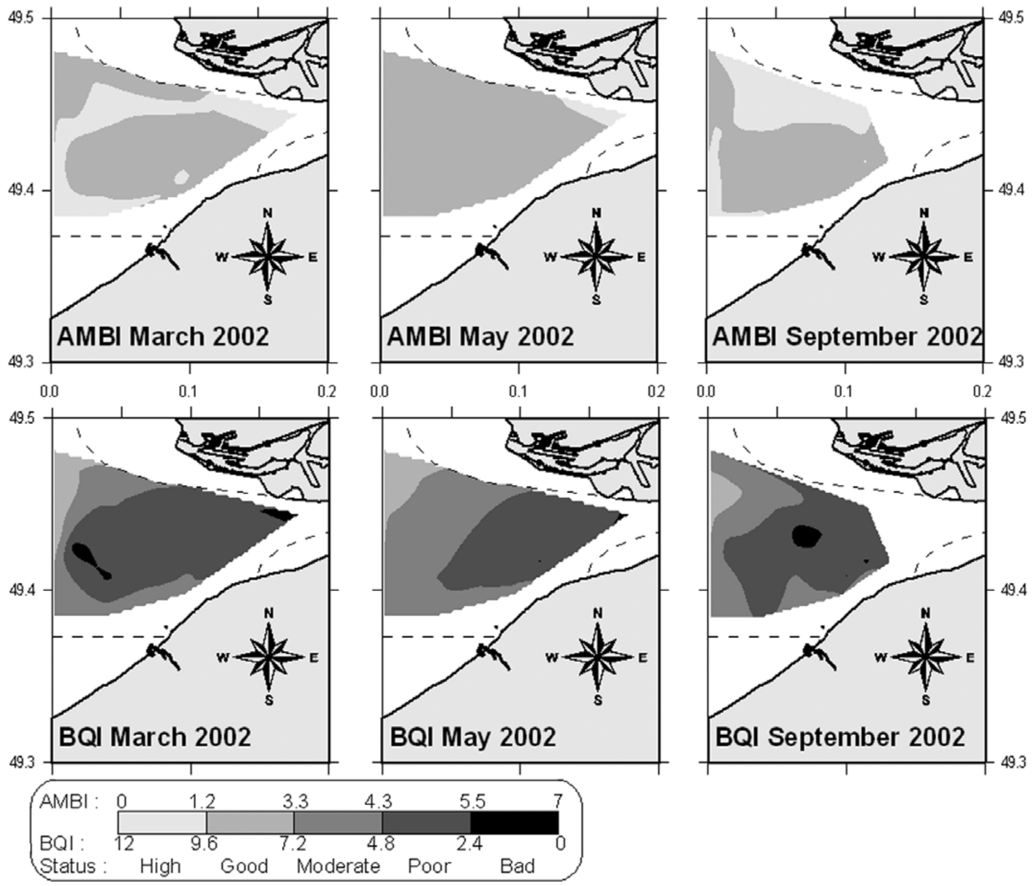

Fig. 6. Seasonal evolution of AMBI and BQI values in the Seine estuary: March, May and September 2002. Dashed lines represent the limits of the area studied. Coordinates are expressed in decimal degrees.

Seine estuary, reflecting the more diverse communities of the Bay of Seine (Fig. 1). Nevertheless, due to presence of numerous polychaetes in samples, the 2002 survey of four sites in the Seine estuary (9 or 10 sampling dates) indicated high abundance values at the end of spring and at the beginning of autumn at the same sites (data not shown).

Fig. 8 presents the results of the Spearman correlations between the environmental variables (e.g., organic matter and pigments in the sediment, percentages of the five grain sizes) and the various indices and descriptors measured. Absolute values are used because the sign of the relationship between two indices has no biological signification; it shows only that these indices used scales that vary in opposite directions. The expected number of species, the actual number of species, the BQI, the Shannon diversity and the dominance index were significantly correlated ($0.42 \leqslant |r_s| \leqslant 0.97$, $p < 0.01$). Since the classification of the benthic species into ecological groups is taken into account the calculation of all the indices, correlations were also significant ($p < 0.01$) between the benthic Biotic Indices—AMBI, BENTIX, I2EC and BOPA. Similarly, the BOPA index and BQI, S, ES(50) and H' were also significantly correlated. The correlation between the biotic indices and sedimentary organic matter and pigment content was weak ($|r_s| \leqslant 0.28$, $p < 0.01$), indicating that these variables do not influence the EcoQ status in the Bay of Seine. The ITI was weakly correlated with the other indices ($|r_s| < 0.20$), but was significantly ($p \leqslant 0.01$) correlated with granulometry ($|r_s| < 0.30$ for three fractions of sediment) and slightly correlated with pigment content ($r_s = -0.24$), though not with the concentration of organic matter in the sediment ($p = 0.12$). All the biotic indices calculated were significantly correlated ($|r_s| < 0.25$ $p < 0.05$) with the sediment grain size, except for medium sand with AMBI ($r_s = -0.30$, $p < 0.01$).

3.6. A comparison of AMBI and BQI

Fig. 9 shows the relative frequency of the AMBI and BQI values inside (respectively 419 and 372 values) and outside (respectively 185 and 148 values) the Seine estuary. Curves were computed using classes of 0.25 for AMBI and two for BQI and smoothed for a 0.05 step with Table Curve 2D software (© SPSS). The AMBI revealed similar quality status ratings for both areas (inside and outside the estuary), though estuary sites had higher values than those outside of the estuary (mode = 1.35 for inner sites compared to 0.80 for outside sites). The AMBI/BQI

Fig. 7. Range of variations observed in the data set used to calculate the 12 indices for the Bay of Seine before (a) and after (b) the benthic recruitment period, for the eastern part of the Bay of Seine in February 1988 (c), March 1991 (d) and March 1996 (e), and for the Seine estuary in 1993 and 1995 (f), in March (g), May (h) and September 2002 (i). The variations in the data set used to study the effect of the mesh size 1 mm (j) versus 2 mm (k) in February 2001 are also shown (Black: 2 mm; grey: 1 mm). Minimum, median and maximum values are indicated. See text and Table 2 for the meaning of the abbreviations.

comparison revealed the strong divergences within the BQI values, highlighting two distinct areas: the estuary sites, with low values (mode = 2.7), reflecting the *bad* to *poor* status of the estuary; and the offshore sites, with high values (mode = 7.6), indicating the *moderate* to *high* status that prevails in areas less influenced by the input from the Seine River.

3.7. The effect of mesh size

To assess the effects of the mesh size on the EcoQ of the water bodies studied, the values of the six selected indices, calculated for the 11 sites sampled in February 2001, were compared after the biological samples had been sieved through a 2 mm or a 1 mm mesh (Fig. 10). After sieving with a 1 mm mesh, the values for S, N or H' increased moderately, except at one site (60) located in the upper part of the estuary. The AMBI, BQI and BOPA also exhibited moderate changes depending on which mesh size was used. Specifically, when a 1 mm mesh was used instead of a 2 mm mesh:

- the AMBI revealed a change in status from *good* to *moderate* at one site (59);
- the BQI showed that two sites (16 and 57) improved from *moderate* to *good*, while two others (17 and 62) degraded from *moderate* to *poor*;
- the BOPA indicated a change from *moderate* to *good* at site 60 and from *good* to *moderate* at site 64.

Clearly, the size of the mesh used does not influence the value ranges or the medians for the 12 indices (Fig. 7(j) and (k)). For several indices (the $ES(50)_{0.05}$, the dominance index, the Shannon and Brillouin diversities and the I2EC index), the mesh size made absolutely no difference. AMBI and BENTIX values span a wider range with the 2 mm mesh than with the 1 mm mesh, which was the opposite of the results for the BQI, BOPA and ITI. The median value for I2EC was often equal to the minimum or maximum values because I2EC uses a discontinue scale. The median BOPA value was often near or equal to 0 because the opportunistic polychaetes and the amphipods are lightly represented in the Bay of Seine.

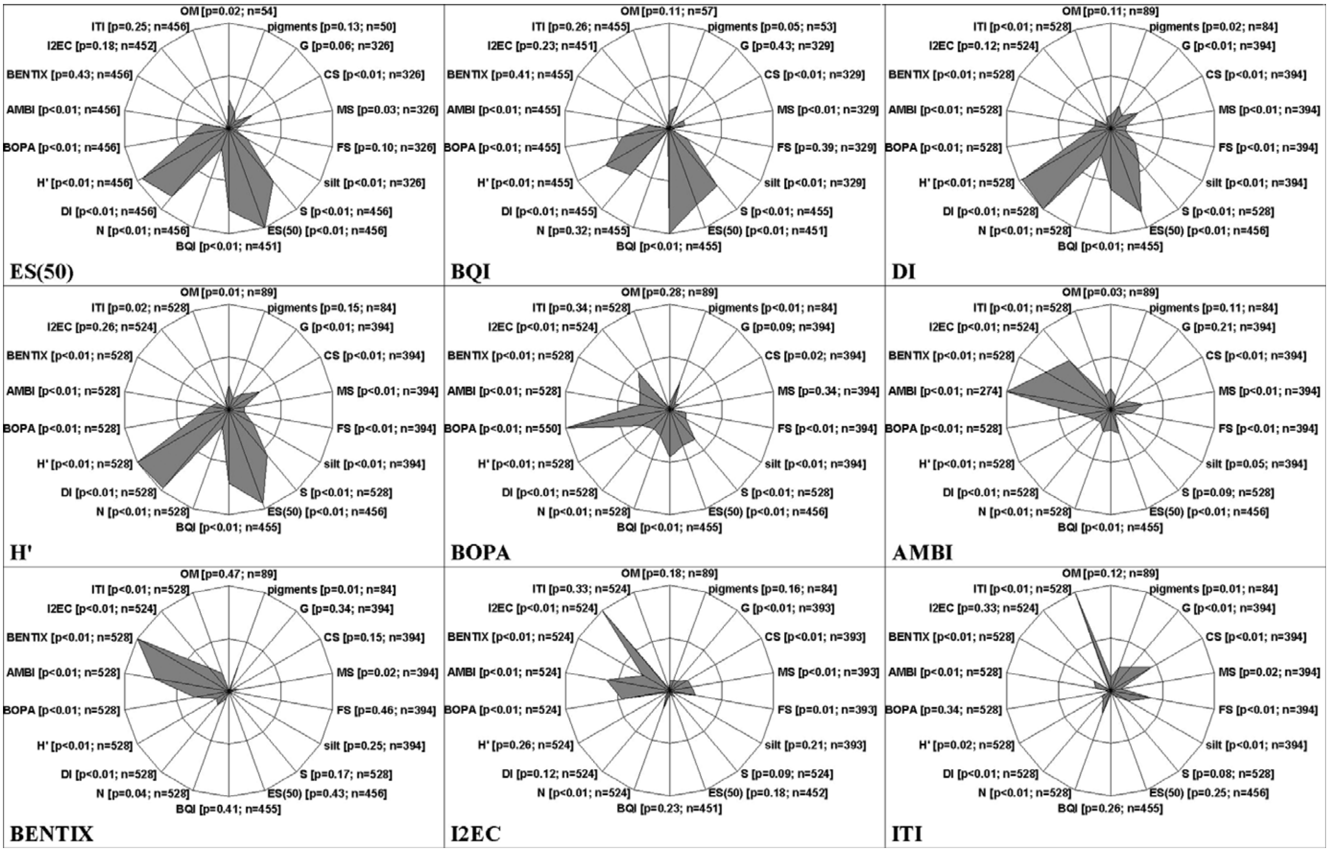

Fig. 8. Relationships between sediment parameters, biotic indices, and macrobenthic abundance and diversity indices. Absolutes values of Spearman's rank correlation coefficients are represented on a circle whose centre is 0 and whose range is 1. Probability (*p*) of the coefficients and number of data (*n*) are also indicated. See text for the meaning of the abbreviations.

4. Discussion

4.1. EcoQ status of the Bay of Seine and the Seine estuary

In general, the results of our study suggest that the indices perform satisfactorily. It is true, however, that the ecological quality status of the Bay of Seine and the Seine estuary appears to be different, depending on which the biotic index was used.

- AMBI produced EcoQs that were generally *high* in the bay and *good* in the estuary.
- BENTIX, on the other hand, attributed a *high* status rating to both the bay and the estuary, except for a couple of sites just offshore of the Seine estuary that had a *good* to *moderate* EcoQ.
- The BOPA index assigned a *high* EcoQ to the bay, while the estuary's status rating ranged from *high* to *poor*, with a predominance of *good* and *moderate* ratings.
- The BQI produced values that indicate that all five-status ratings exist in the Bay of Seine and Seine estuary; this finding is consistent with the definition of the EcoQ status ratings proposed by Rosenberg et al. (2004), which supposes that extremes (*high* and *bad*) exist in each data set (Labrune et al., 2006). Despite this wide distribution, *good* and *moderate* EcoQ dominate in the bay, while *poor* and *bad* EcoQ exist primarily near the Seine River, providing evidence of the benthic degradation in this part of the Seine estuary.
- The I2EC results are more disparate: *high* EcoQ were produced for offshore areas, *high* to *good* EcoQ for areas near the coast, and *poor* and *bad* EcoQ for some estuary sites.
- The ITI values indicate that the Bay of Seine is primarily *normal* or *slightly modified* and that the Seine estuary and the Bay of Veys were generally *modified* but *locally degraded*.

Despite differences in EcoQ ratings, the overall general trend is similar: offshore areas have better EcoQs (*high* or *good*) than the estuarine areas, which are more contaminated. However, the variations between the indexes underline the need to calibrate the thresholds between the classes defined for each index and seasonal variations detected by indices must be integrated for the assessment of the EcoQ classification (Borja, personal communication).

Our results are consistent with those published by Simboura (2004), which show that the EcoQ produced with AMBI and BENTIX do not totally agree and that EcoQ ratings

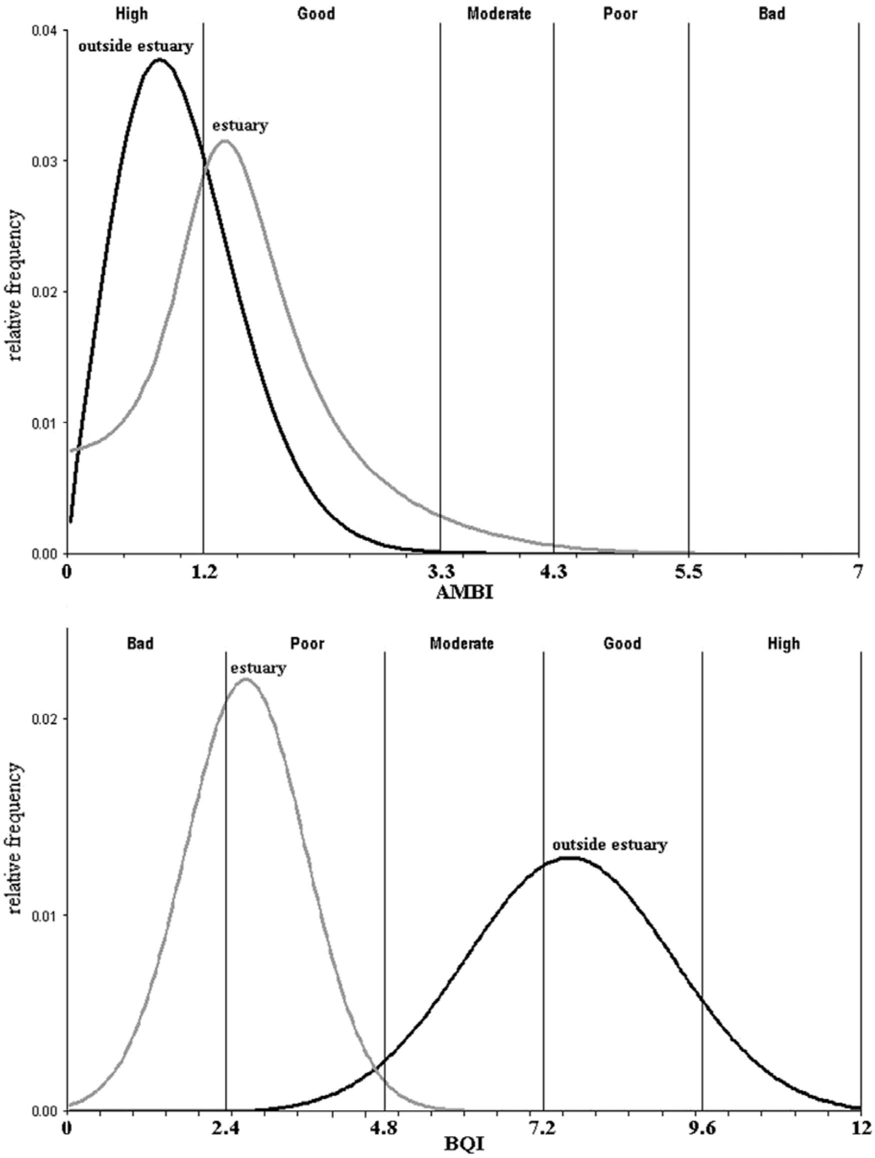

Fig. 9. Relative frequency of the AMBI and BQI values inside and outside the Seine estuary (see limits in Fig. 1).

may differ when calculated using the classic univariate and multivariate methods in vogue prior to the development of the newer WFD-inspired indices. Thus, the question that needs to be answered appears to be two-fold: what benthic indices are best suited to evaluating contaminated coastal areas and estuaries, and is it best to use a single index, a set of indices, or a multimetric approach?

4.2. Single index versus multimetric approach

According to Dale and Beyeler (2001), a useful ecological disturbance indicator is one that is easily calculated, sensitive, anticipatory, and integrative across key environmental gradients. However, although a single index may provide a good overview of the gradient status of a benthic environment, choosing one that will definitively establish the true status of a specific site is difficult. Some of the practical problems related to using a single index include questions about classifying species as indicators for different disturbance levels, sensitivity to dominance, and lack of objectivity when setting stress effect thresholds (Salas et al., 2004). Several studies have underlined the inconsistencies between diversity indices, stemming from the biological characteristics of the area being studied. The AMBI index, for example, sometimes appears to be more appropriate for the Atlantic ecosystems and estuarine areas with low biodiversity, few species and high densities; the BENTIX index, on the other hand, seems better suited to determining EcoQ in Mediterranean coastal ecosystems with high biodiversity (Simboura, 2004).

In addition, sometimes the source of the disturbance must be identified in order to choose the appropriate index. For instance, AMBI, as probably others indices, is not always able to differentiate between the origins of the

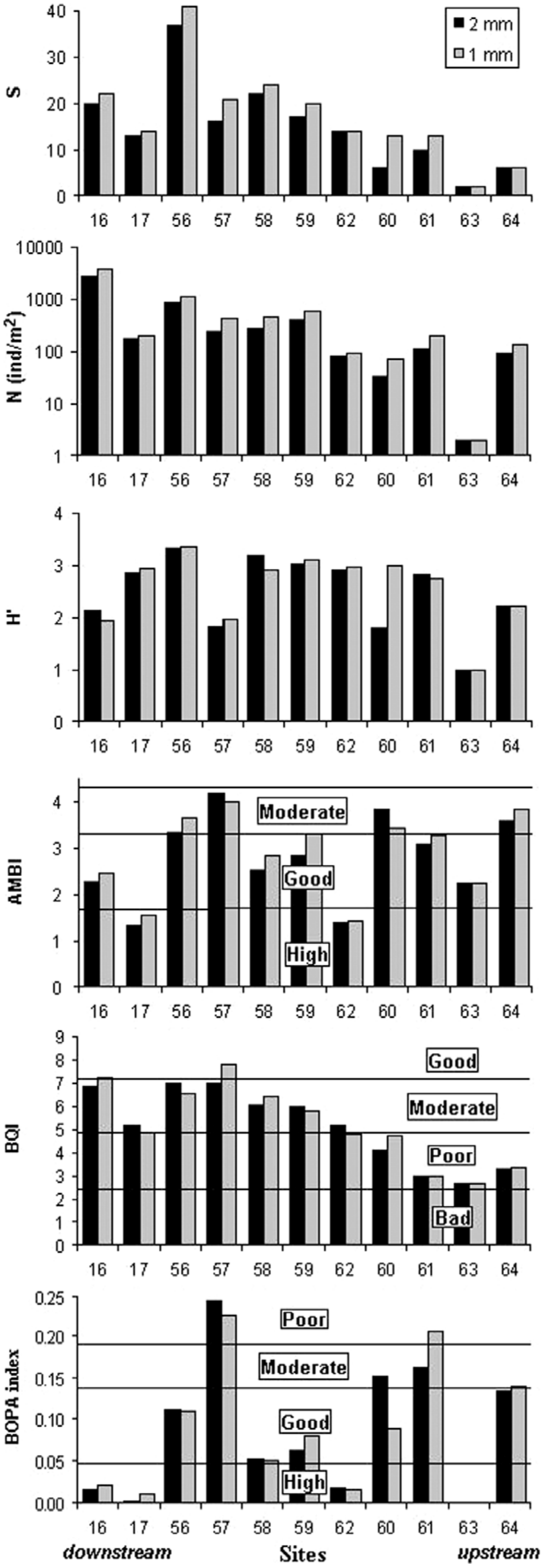

Fig. 10. Comparison of community status for 11 sites, based on the sampling done with a 1 mm mesh and a 2 mm mesh in February 2001.

diverse stresses and thus can produce similar values for differing stress factors (Salas et al., 2004). Added to the difficulties mentioned above, as Marin-Guirao et al. (2005) recently remarked, neither AMBI nor BENTIX—to be fair, probably none of the existing indices—are suitable for monitoring all the purely toxic pollutions. In response to this shortcoming, these authors have suggested developing a new indicator list, with each indicator adapted to a specific type of contamination (e.g., metals, pesticides, hydrocarbons). For all of these reasons, though it is always possible to choose a single index that, like AMBI, has been tested in a variety of situations (Muniz et al., 2005), it seems preferable to combine several indices when assessing the EcoQ status of an area in order to take the complexity of the ecosystem into consideration and to minimize errors (Dale and Beyeler, 2001; Alden III et al., 2002; Borja et al., 2003a; Borja and Muxika, 2005; Muniz et al., 2005; Rogers and Greenaway, 2005).

Dale and Beyeler (2001) echo Dauer et al. (1993) when they suggest the complementary use of an appropriate succession of indices, matched to the characteristics of the environment in question, for determining the environmental quality of ecological systems. However, in order to properly evaluate this suggestion, the practical limits of the various indices must be acknowledged.

As in all indices, and despite its excellent properties, AMBI clearly appears to have certain limitations, though their extent is not yet apparent. For example, unsatisfactory results have been obtained using AMBI in situations with low abundance and/or low specific richness values (Muniz et al., 2005). Regardless, Simboura (2004) recommends using AMBI rather than BENTIX in sites where specific richness is low and total abundance is high, considering that AMBI more exactly defines the ecological groups of the sampled species (five groups for AMBI versus only two for BENTIX). This said, Simboura (2004) also feels that, in some situations, AMBI is less discriminating than BENTIX and the older methods. Since the percentage of taxa not assigned to an ecological group is an important factor in correct AMBI use (for that matter, in the use of BENTIX and I2EC also), AMBI's own creator recommends choosing an index other than AMBI when this rate exceeds 20% (Borja and Muxika, 2005). In our data set, this threshold was not reached since only 7.65% of the taxa were not assigned to an ecological group.

Based on a different approach of ecological grouping, the BQI remains a highly empirical index, which requires the analysis of individual data sets. This index, which is highly sensitive to dominance and has a tendency to classify dominant species as tolerant (Labrune et al., 2006), requires samples with a minimum abundance of 20 individuals (Rosenberg et al., 2004) and a large data set in order to improve the accuracy of the $ES(50)_{0.05}$ used to calculate the BQI. Thus, habitats falling short of such requirements should be evaluated with another index. Others alternatives include the ITI, the B-IBI (Benthic-Index of Biotic Integrity; Llanso et al., 2002a,b) or the BOPA index; however, using these last three indexes optimally also requires meeting certain environmental specifications. For example, the ITI works better at depths under 20 m (Donath-Hernadez and Loya-Salinas, 1989), and so another index would be more appropriate for higher depths. Similarly, since Llanso et al. (2002b) exclude amphipods from the calculation of the B-IBI in the oligohaline areas, using the BOPA index would appear judicious in areas with salinity levels greater than 5. Since managers require indicators that vary only slightly over the seasons and/or years, using such benthic indices can be problematic because they vary seasonally and depend on the different environmental conditions for the various marine regions, as Reiss and Kröncke (2005) have underlined.

Taking the known limitations of each index into account would make it possible to choose one index for the offshore areas, and another one for coastal and transitional waters. Such a process would not be a problem in terms of WFD application as long as the final results are expressed as ratios (comparison to a state of reference) ranging from 0 to 1. Unfortunately, for the moment, such states of reference remain undefined at the European level due to insufficient spatio-temporal data. However, they already exist for Basque Country in Spain (Borja et al., 2004b) and for Denmark, Norway and UK (Borja, personal communication).

In order to fulfil the WFD requirements for water quality assessment, Vincent et al. (2002) thought that methods combining composition, abundance and sensitivity might be the most promising. If their reasoning is accepted, the knowledge of the indices' limitations could be applied to develop a multimetric approach. The B-IBI—which takes into account, in a single cumulative value, several indices (H', N, percentage of sensitive and opportunistic species, percentage of TG_2 and TG_4, and others metrics, including biomass)—is one example of such a combinatory approach (Llanso and Dauer, 2002; Llanso et al., 2002b; Dauer and Llanso, 2003). The Ecological Quality Ratio (EQR) (Borja et al., 2003b)—which combines the Shannon–Wiener Index, the species richness and the AMBI in one cumulative index—is another, although Reiss and Kröncke (2005) have already shown in their study of different areas in the North Sea (the German Bight, the Oyster Ground and the Dogger Bank) that the ecological status rating produced by this EQR is generally one or two categories below the other indices and consequently recommended to use a multivariate analysis to determine a best EQR (see Borja et al., 2004b).

To determine EcoQ status ratings under the WFD, we propose that the results produced by each index be scored from 1 (*high*) to 5 (*bad*), with all scores being averaged to determine the definitive ecological quality of an area. This proposition is consistent with the recommendations of Dauer et al. (1993) and Salas et al. (2004), who advise using a variety of indices based on different approaches. That differs to the possibility offer by the WFD to use different metrics and methods following the Member States and then to intercalibrate the metrics (Borja et al., 2004b). The relationships between the indices calculated with our data set suggest that three parameters should be taken into account: species diversity, the proportions of the various ecological groups, and trophic structure. Since the indices based on the first two were highly correlated, it would seem sensible to use at least one index for each parameter. Using this approach, the Bay of Seine earns a *high* to *good* EcoQ, while the estuary garners a*moderate* EcoQ.

4.3. Relationship between the indices and the environmental variables

Our results show that the Seine estuary and the Bay of Veys (at least, according to certain indices) are more degraded than the Bay of Seine, probably due to the severity of the disturbances that prevail in estuarine areas. Still, these results must be interpreted with prudence because the classification method is less efficient in low salinity areas, including both tidal freshwater and polyhaline areas (Llanso et al., 2002b). Benthic indices often have trouble differentiating between the effects of salinity and the effects of pollution due to river discharge (Alden III et al., 2002). The AMBI and BQI indices, for example, have different discriminating capacities, depending on whether the site is estuarine or non-estuarine (Fig. 9). If this difference is due to a pollution gradient, then the BQI would appear better suited to detecting anthropogenic responses than AMBI. If not, it would mean that the BQI is more sensitive to the salinity gradient than is AMBI.

Clearly, salinity has a strong influence on the index values. Thus, in order to compare the results obtained, ecological assessments of estuarine habitats—which are often irregular, silted-up, and rich in organic matter—can best be accomplished using data detrending methods (Dauer et al., 2002). However, salinity is not the only influencing factor. Sediment type, as well as salinity, defines benthic habitats and their faunistic assemblages, and the qualitative and quantitative compositions of these benthic habitats modulate the values of benthic indices (Llanso et al., 2002a). In addition, Maurer et al. (1999) have shown that granulometry can affect the infaunal trophic index. This proved true in the Bay of Seine and the Seine estuary, where the ITI values increased as the proportion of suspension feeders increased, in relation to increases in offshore coarse sediment.

According to our results, the organic matter content in the sediment did not play a determining role in the ecological status of the Bay of Seine and the Seine estuary, nor did the structure of the benthic fauna (Thiébaut et al., 1997). Though this is not the first time that no correlation has been found between organic matter content in the sediment and biotic indices (see Muxika et al., 2005 for AMBI), it seems clear that indices based on ecological groups (e.g., AMBI, BENTIX and I2EC) are rooted in a model that predicts a succession of species along an organic matter gradient (Borja et al., 2000). This model does not correspond with our observations may be because indices values were used instead of ratios due to the absence of reference conditions, as underlined previously, and because the estuarine and coastal environments of the Seine have been largely modified by human activities for many decades. Despite a general disturbance, a benthic community can be considered in good status in the frame of the WFD (Borja et al., 2006).

Presumably, the benthic communities in the Bay of Seine and the Seine estuary have adapted progressively to the high organic content in the sediment of a megatidal area with high tidal currents. The eastern part of the Bay of Seine and the Seine estuary exhibit widely contrasting features, with some areas displaying abundance and biomass values that are among the highest for all European and North American estuaries, and other areas that are quite impoverished (Dauvin, in press). The subtidal macrobenthic community near the Seine estuary presents a paradox: despite the relatively low numbers of opportunistic species, such as polychaetes, and despite being located in a zone with high levels of dissolved contaminants, very high abundance and biomass values have been recorded. This paradox might be due to the delay in this area between the periods with the maximum runoff and the maximum contaminant input (at the end of autumn and during the winter) and the period of recruitment for the principle abundant species (throughout the spring and summer) (Thiébaut et al., 1997). The absence of anoxic conditions, especially in the summer when temperatures reach their maximum (>20 °C), might also explain the high abundance and biomass values found in the Seine estuary, despite the highly contaminated environment (Dauvin, in press). Nevertheless, it should be noted that, probably in response to the contamination of the environment, the number of species sensitive to pollution (e.g., amphipods) is relatively low in the entire Bay of Seine and Seine estuary (Dauvin and Ruellet, submitted for publication).

In their work on the Chesapeake Bay, Dauer and Llanso (2003) have suggested that studying the effect of decreases in oxygen content requires sampling on a smaller spatial scale than does studying overall contamination in sediment. In light of the relationship between the indices and environmental variables, it would seem that the scale of observation must be adapted to the type of natural and anthropogenic perturbations.

4.4. Future researches

A long-term global observation strategy is needed for the Bay of Seine and the Seine estuary. The mesh size used has few effects on the EcoQ classification in our results (2 mm versus 1 mm). Nevertheless our comparison takes into account only winter samples, a period outside the recruitment of the main benthic species of the Bay of Seine (Ghertsos, 2002). A smaller mesh (0.5 mm) could give other results because opportunistic species have often-smaller size than sensitive species. Thus, it is necessary to take into account special attention on this point for the future. As part of the WFD coastal zone implementation, an inshore/offshore transect should be chosen for observation and a variety of benthic indices selected for use in periodic assessments. In addition, an integrated ecosystem approach similar to the one adopted by the Bergen Declaration for managing human activities in the North Sea (http://odin.dep.no/archive/mdvedlegg/01/11/Engel069.pdf, Carlberg, 2005) should be applied in the offshore zone of the defined transect.

Acknowledgements

This study was undertaken as part of the Seine-Aval program, which is coordinated by the *Haute Normandie* region and the French National Coastal Environment Program (PNEC 'Chantier Baie de Seine'). It was supported financially by the CNRS-INSU and IFREMER. The authors are grateful to the crews of N.O. 'Côte d'Aquitaine' and N.O. 'Côtes de la Manche' for their help during sampling; to the co-organizers of the sampling surveys—L. Cabioch, F. Gentil, K. Ghertsos, M. Ropert, and C. Retière; to the numerous students who participated in the surveys and in the development and use of the benthic sampling data, to A. Borja for his comments on the first version of this paper, and to L.E. Spencer for her comments and help in correcting the English text.

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Hydrobiologia (2007) 588:173–188
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The intra-annual variability of soft-bottom macrobenthos abundance patterns in the North Channel of the Seine estuary

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Sandric Lesourd · Jean-Claude Dauvin**

Abstract Temporal and spatial variability of the *Abra alba–Pectinaria koreni* and *Macoma balthica* communities was examined in the northern part of the Seine estuary (North Channel) over different space and time scales in order to assess the role that the hydrologic regime and/or anthropogenic influences play in defining benthic communities over time. Sediment in the North Channel displayed strong spatial and temporal variability, sustained by intense sediment transport episodes. Total macrobenthic abundances ranged widely on the course of the year and there was no evidence of a seasonal signal for the density fluctuations, whatever the spatial scale considered. The bio-sedimentary dynamics can be divided into two periods: the first corresponds to the high flow rate period (January–May) during which fauna is influenced by fine silt/clay deposition, and the second to the low flow rate period (June–December) during which sandy deposits prevail. Despite the absence of significant correlations between sediment composition and abundance, episodes of sediment transport seem to be an important structuring mechanism in the Seine estuary. As a consequence, the faunal composition varied throughout the year. The winter and spring fauna, characterised by species living on muddy fine-sands or muds, were enriched during the summer and autumn by species living in clean fine sand, such as *Donax vittatus*, *Nephtys cirrosa* or *Spio decoratus*, mainly represented by adult individuals. Secondary settlement of drifters may explain the rapid structuration of assemblages a few days after the sandy deposits. Our results suggest the importance of the bentho-pelagic coupling, primarily induced by the sedimentary instability, on the macrobenthic fauna dynamics. The intra-annual variability of assemblages at the

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Guest editors: R. Lafite, J. Garnier & V. De Jonge
Consequences of estuarine management on hydrodynamics and ecological functioning

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mouth of the Seine river and the silted situation of the North Channel might simply be the result of the silting up and alteration of the inner estuary, generated by several decades of man-made modifications and natural processes.

Keywords Temporal variability · Bentho-pelagic coupling · Sediment · *Abra alba* community · Anthropogenic impacts · Port 2000

Introduction

Since the mid-19th century, industrial activities have been taking place in the lower part of the Seine estuary, with the attendant negative impact on the environment. The extensive management operations that have been carried out to "subdue" the estuary–including land reclamation, dyke construction, waste water drainage, and the dredging and sediment disposal needed to keep the navigable waterways accessible–have led to a decrease in the river channel width, a lessening of the seawater exchanges, and the progressive silting up of the inner part of the estuary (Lesourd et al., 2001). The estuary is also affected by the heavy input of organic matter in the sediment and industrial effluents. For example, the concentrations of heavy metals in the Seine estuary are among the highest found in the European estuaries, particularly with regard to cadmium and lead (Chiffoleau et al., 2001; Miramand et al., 2001).

In the eastern part of the bay of Seine, in response to hydrodynamic and sedimentary gradients, two communities are distributed from the open sea to the coast: a muddy fine sand *Abra alba-Pectinaria koreni* community and a muddy *Macoma balthica* community (Cabioch & Gentil, 1975). Although the macrobenthic communities along the inner estuary are well known (Elkaim et al., 1982; Thiébaut et al., 1997, Dauvin & Desroy, 2005), data about the intra-annual changes in macrobenthos abundances are completely absent. However, according to Lesourd et al. (2003), such data is crucial to understanding how the estuary functions since sediment distribution is governed by seasonal meteorological and hydrologic variations and divided into two main successive periods. During winter, the fine-grained sediment supply is the result of high river discharge periods, amplified by ebb currents during spring tides. The mud deposit areas are then limited to the proximal outlet part of the estuary. The associated mean silt and clay content generally exceeds 75% in the topmost 10 cm of the superficial sediment. During low river flow, the fine-grained sediment accumulated in the estuary outlet are reworked by waves and tidal currents. A fraction of this material is scattered away to the Bay of Seine, the other part being transported landward into the estuary where it contributes to the deposition of estuarine mud. Suspended particulate matter has a tendency to settle in the lateral zones and in some sink holes. These residual deposits make up a superficial cover that contributes to the filling of the Seine outlet. These seasonal variations mainly depend on the intensity of the river discharge, but are also linked to wave activity. Such variability may strongly affect the magnitude of the processes which regulate benthic macrofauna from season to season (Seitz, 1998).

To this highly heterogeneous pattern of physical and chemical factors will be added the effects of the most recent infrastructure development along the Seine estuary, the extension of Le Havre harbour (Port, 2000 project) near the mouth of the Seine river. Begun in 2002, plans for the North Channel include the construction of a channel (16 m deep, 350 m wide, and 2,800 m long) connected to the habour's navigational channel, as well as the construction of a dam-protected basin (Dauvin et al., in press). Simulations have predicted that the harbour extension will have consequences on sedimentation in the estuary by increasing fine particle accumulation, thus reducing the intertidal zone in the North Channel and causing further damage to the Seine estuary as a whole (see Dauvin, 2002). Some compensatory measures, such as the construction of an artificial island for wild birds, and the dredging of a new canal in the upper part of the North Channel to maintain seawater circulation, are planned in order to limit the negative ecological effects of this new man-made modification of the Seine estuary (Hamm et al., 2001, Dauvin et al., in press).

Given this context, the present study had several objectives. The first, based on the sampling of the Northern Channel soft-bottoms in 2001 (i.e. before the extension of Le Havre harbour began), was two-fold: to determine whether or not the density, biomass and composition of benthic communities were subject to seasonal fluctuation or any other significant temporal variation, and to assess the ecological importance of this area in the estuary's functioning. The second objective was to examine the role of hydrologic regime and anthropogenic influence in defining benthic communities over time, using data from a 2002 study of a single site located in the centre of the Channel.

Materials and methods

Study area

The Seine estuary is the largest megatidal estuary in the English Channel, covering about 150 km^2 at high tide. As a result of extensive activities/public works operations, over the last hundred years, the river channel has shrunk and the seawater exchanges in the estuary have greatly decreased (see Lesourd et al., 2001; Dauvin & Desroy, 2005 for details). The average tidal range at the mouth is about 8.5 m for spring tides and 4.0 m for neap tides. The influence of seawater is increased by the estuarine morphology: the tide penetrates 70 km in from the coastline (to the Poses dam). River discharge (mean flow rate of 400 m^3 s^{-1}) varies seasonally, from a maximum of 2,000 m^3 s^{-1} in winter to a minimum of 100–200 m^3 s^{-1} in summer (Guézennec, 1999). Like many European macrotidal estuaries, the Seine estuary is characterized by a zone of maximal turbidity with suspended matter concentrations from 1 to 10 g l^{-1}, generally located in the upper part of the estuary.

Sampling designs

Temporal changes in the composition and abundance of the macrobenthic invertebrate communities were studied in the Northern Channel before the work for the harbour extension began, from surveys conducted in February (26–28), June (5–7), September (26–28) and December (3–5) 2001. The macrobenthos was sampled at 11 sites in February, June and September and 10 sites in December (4<water depth<10 m), site 61 being inaccessible due to harbour maintenance work (Fig. 1). Four sediment samples were collected using a 0.25 m^2 Hamon grab, with replicates collected within a 50 m range of each site, according to DGPS positioning. Sub-samples of

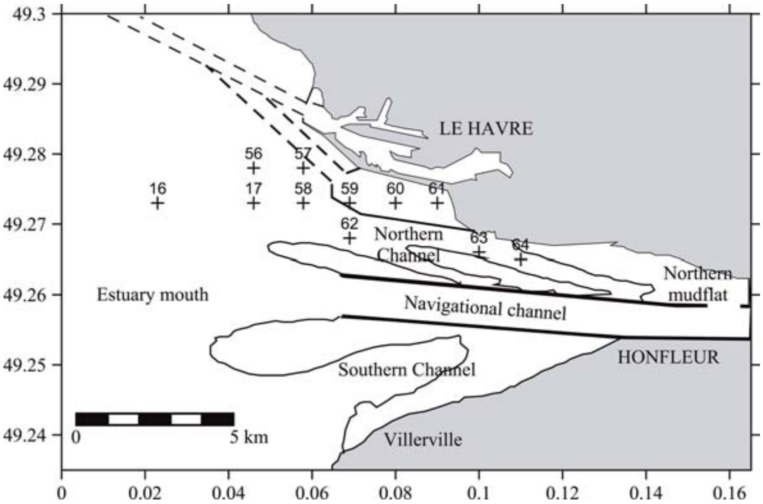

Fig. 1 Location of sampling sites. All sites were sampled in February, June, September and December (excepted site 61) 2001 and site 62 was sampled during the year 2002 (see Fig. 2 for frequency). Fine full lines: intertidal banks, full bold lines: dykes embanking the Seine river and location of the future dock (completion in 2005), doted lines: Main channel to Le Havre harbour (fine) and channel dredged to go to the future dock (bold)

sediment (5 superficial cm) were taken from additional grab samples and subsequently analysed for grain size distribution (wet sieving) and organic matter content (weight loss of sediment dried at 600°C for 6 h).

Site 62, which was sampled during 2002, was chosen in order to determine whether the benthic abundance patterns observed in the Channel were influenced mainly by natural factors (such as hydrology) or mainly by the disturbances associated with the harbour extension, and to classify the factors responsible for the observed changes. Its location at the centre of the North Channel and its distance from the harbour extension work, had protected the estuary bottoms from direct influence. To assess the influence of the high and low flow rate periods of the Seine river, the sampling frequency was ≈15 days from March to June 2002 and 2–3 months from June to December (Fig. 2). Unfortunately, a different sampling gear, a Van Veen grab, has to be used in 2002. To avoid doubt on inter-annual differences due to the use of these two grabs, species area curve specifications were considered. The minimal areas to sample 80% of species depended on the gear used (0.3–0.4 m^2 for the Van Veen grab depending on the season and 0.75 m^2 for the Hamon grab). As a result, to allow a meaningful measurement of local biodiversity because of the habitat heterogeneity, a minimal number of four replicates (whatever the gear considered) was necessary. Then, five replicate sediment samples were collected with a 0.1 m^2 Van Veen grab for the benthos study. At each date, an additional grab was used to determine grain-size distribution (5 top cm of sediment), and a Reineck box core (1/58 m^2), from which one rectangular sub-core (14 cm × 8 cm × 10–35 cm deep depending on the sediment) was taken, was used for the lithological description.

In all cases (both the 2001 and 2002 surveys), the benthic samples were sieved through a 1-mm mesh in the field and preserved in buffered formalin. In the laboratory, samples were sorted after staining with Rose Bengal, identified to species level and counted.

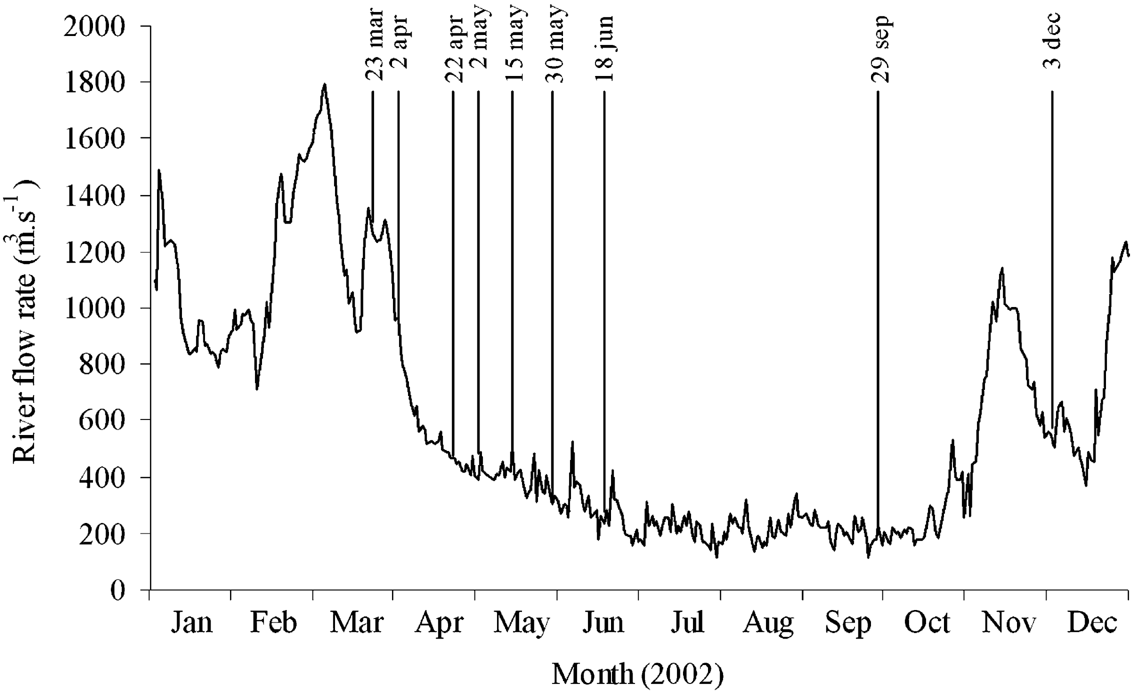

Fig. 2 Sampling design conducted at site 62 with regard to the Seine flow rate (recorded at Poses at the entrance of the Seine estuary)

Data analysis

A formal significance test for differences in sediment and benthic fauna compositions between seasons was performed using either the ANOSIM randomisation/permutation test implemented in the PRIMER package (Clarke, 1993) or the variance analysis (ANOVA) following Bartlett test for variance homogeneity (Scherrer, 1984). Two granulometric classes, dominant in the Seine estuary sediments (Lesourd et al., 2003), were chosen for graphic representations and data analysis. According to the Larsonneur (1977) classification, these sediments belong to the silt/clay class (particles<63 μm) and the upper fraction of fine sand class (100 μm<particles<200 μm). Changes in assemblages and in sediment characteristics were visualized through non-metric multidimensional scaling (MDS) plots based on triangular matrices of the Bray-Curtis similarities implemented in PRIMER (Clarke & Warwick, 1994). Prior to ordination, Log(x + 1) transformations were performed on the benthic species abundance data. Patterns in the fauna distribution were linked to the environmental variables using the BIOENV routine in PRIMER. Finally, a t-test for paired samples was used to assess the inter-annual changes at site 62 and the summed cumulated function was used to characterize the bio-sedimentary dynamics in 2002. This last method consist of substracting a reference value (here, the mean of the series) from each of the data, and to successively add residuals to form a cumulative function [see Ibanez et al. (1993) for more details]. The graph of this function gives directly dates, intensity and duration of any changes.

Results

Seasonal changes in the North Channel (year 2001)

Patterns of sediment distribution

Fine sediments, globally ranging from muds to fine sands depending on the season, were dominant in the North Channel throughout the year. Although silt/clay (<63 μm) and fine sand (100 μm<particles<200 μm) were the principal granulometric classes, the high mud content of sediments, reaching values of up to 50% in 45% of the sites in February, June and September, underlined the general silted situation of the channel (Fig. 3). Spatial changes in the overall sediment composition were significant (ANOSIM, $r = 0.458$; $P < 0.001$). Independently of any longitudinal gradient, mud and fine sand distribution patterns exhibited a high spatial heterogeneity, given that the percentages of mud or fine sand in sediment ranged from 5%–25% to more than 80% in adjacent sites. The sediment composition also varied temporally, as shown by changes in silt/clay or fine sand content in the sediment throughout the year (Fig. 3). Seasonal changes in silt/clay and fine sand content were drastic and asynchronous from one season to another; for example, at site 16 or sites 61 and 62, large sand deposits were observed in December and in September, respectively. Some sites were also characterised by the temporary presence of pebbles (site 60 in February and December and site 56 in September). The overall statistical analysis (North Channel scale, *i.e.* sites pooled) of seasonal variability did not integrate the changes occurring at each site and thus was not significant (ANOSIM, $r = –0{,}06$; $P > 0.05$).

Despite seasonal variations, the organic matter content of sediments remained less than 6%, except at sites 56 and 59 where values reached 9% in June and 11% in February, respectively.

Patterns of faunal abundance

A total of 115 taxonomic groups were collected from the samples (62 sp.–February, 56 sp.–June, 61 sp.–September, and 80 sp.–December). With 60 species (52.2% of the macrobenthic species), the polychaetes were the most diverse taxon. Mollusks comprised 23 species (20.1%); crustaceans, 22 species (19.1%); echinoderms, 5 species (4.3%); and anthozoans, nemertineans, phoronidians and sipunculids comprised 5 species. The species with the highest occurrence frequency included the polychaetes *Nephtys hombergii* (present in 97.7% of samples) and *Aphaelochaeta marioni* (77.2%), and the mollusc *Abra alba* (77.2%).

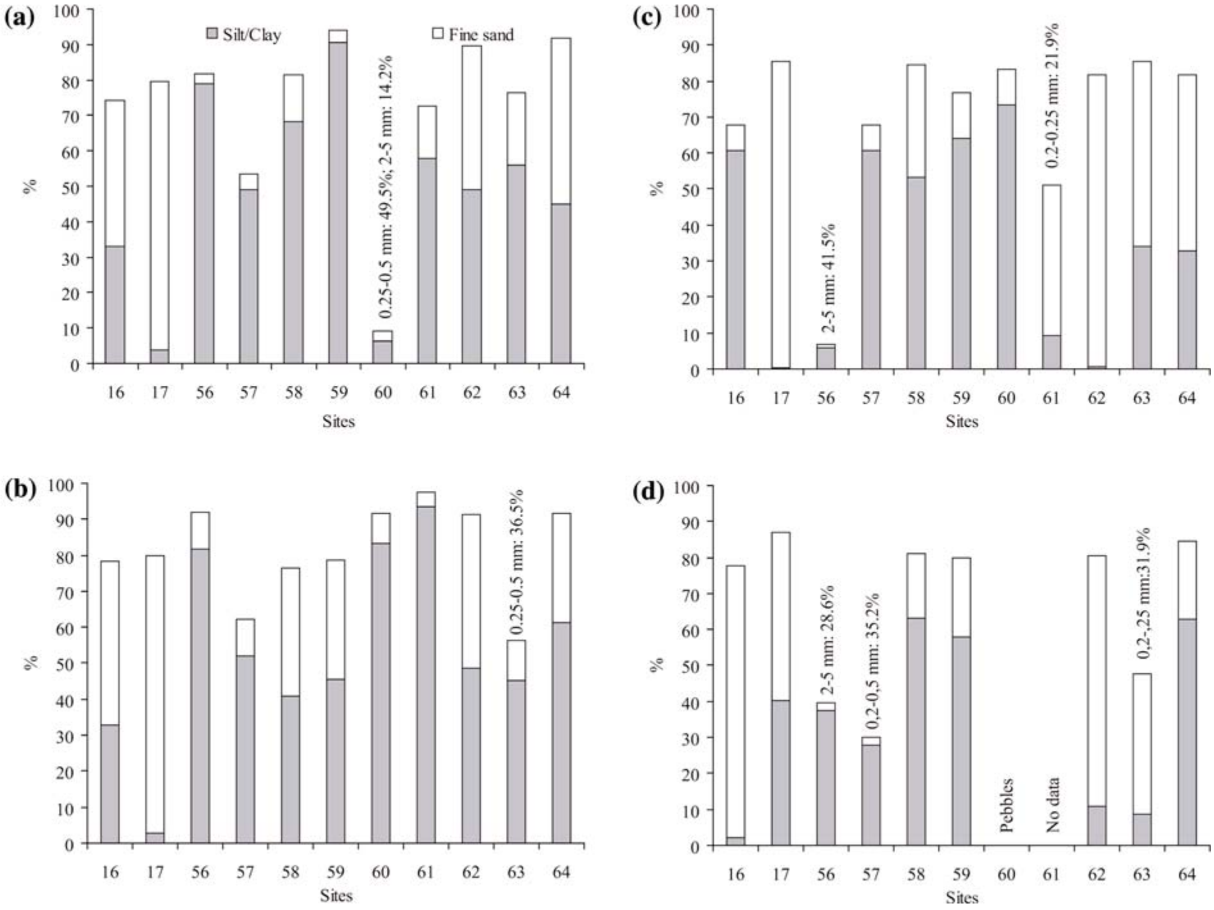

Fig. 3 Seasonal variations in silt/clay (<63 μm) and fine sand (100 μm<size particle<200 μm) contents in (**a**) February, (**b**) June, (**c**) September and (**d**) December 2001 in the North Channel. Contribution of other granulometric classes were presented when necessary

Total macrobenthic abundances varied from 0.5 to 942.6 ind. 0.25 m^{-2} in February, 2.2–462.7 ind. 0.25 m^{-2} in June, 1.0–752.5 ind. 0.25 m^{-2} in September, and 1.2–834.5 ind.0.25 m^{-2} in December (Fig. 4). Molluscs (especially *Abra alba* and *Mysella bidentata*) were the dominant fauna in every season (59.4%–February, 51.0%–June, 69.7%–September and 57.5%–December).

In spite of a marked intra-site variability due to the patchily distribution of dominant species as the polychaete *Aphaelochaeta marioni* and *Owenia fusiformis* or the molluscs *Mysella bidentata*, in February, June and September, species richness and abundances tended to increase along an upstream–downstream gradient in the Channel, with site 16 exhibiting the highest densities [from 462.7 to 942.6 ind. 0.25 m^{-2} (Fig. 4)]. No clear seasonal trend was observed in abundance; values were stable in February, June and September and highly varied from September to December, with the highest abundances being observed in the central part of the Channel (Fig. 4). The Shannon diversity index remained low (between 0.2 and 1.1) at each site throughout the year, reflecting the unbalanced distribution of individual species abundances. A relatively small number of species (*Abra alba*, *Aphaelochaeta marioni* and *Mysella bidentata*) strongly dominated a fairly diverse fauna.

Congruently with the spatial heterogeneity of sediment distribution, the structure of invertebrate assemblages also exhibited differences along the Channel, regardless of the season (ANOSIM, $r = 0.674$; $P < 0.001$). A MDS analysis of the variability of the benthic faunal abundances

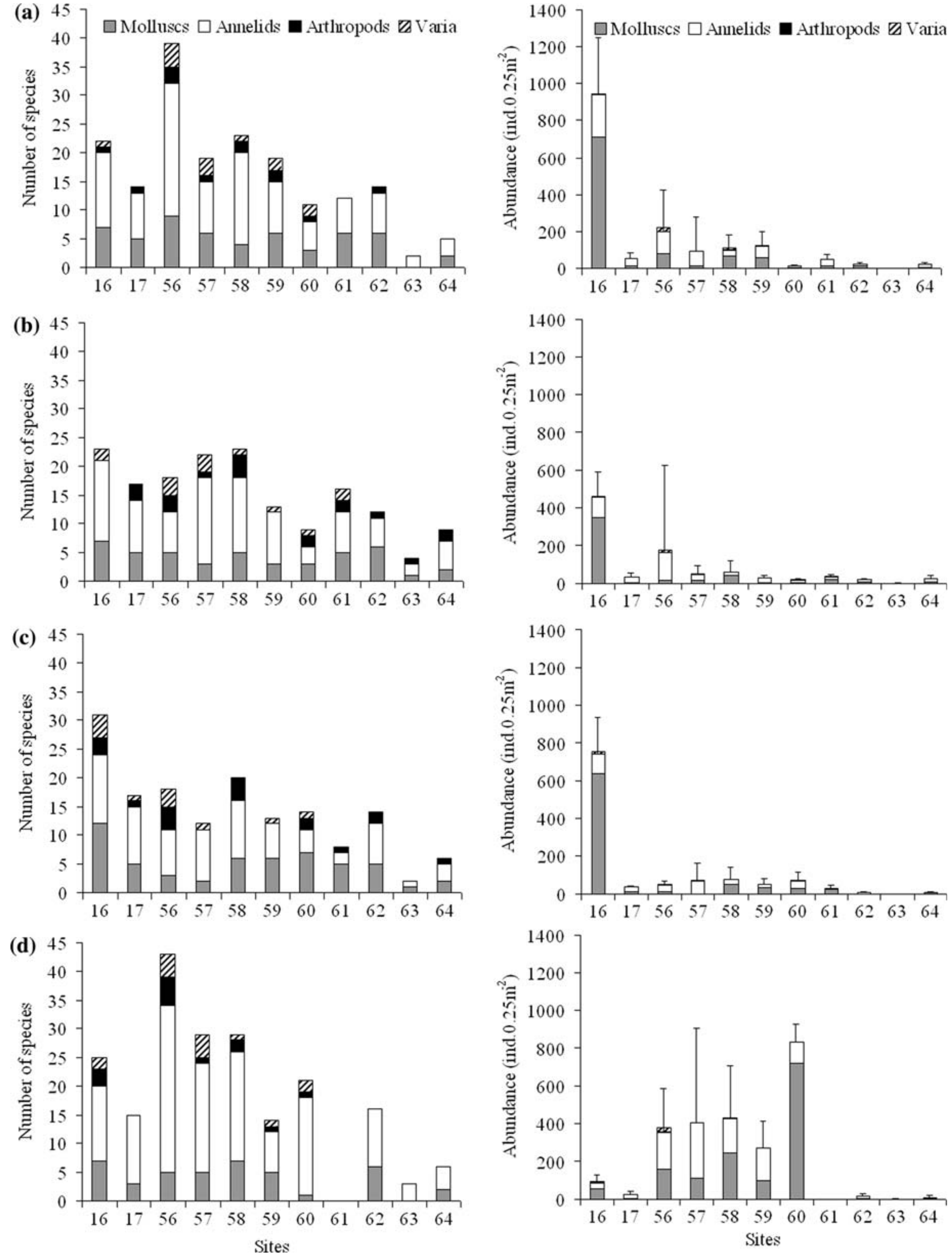

Fig. 4 Seasonal variations in (1) number of species and (2) abundances (+SD) of macrobenthos in (**a**) February, (**b**) June, (**c**) September and (**d**) December 2001 in the North Channel

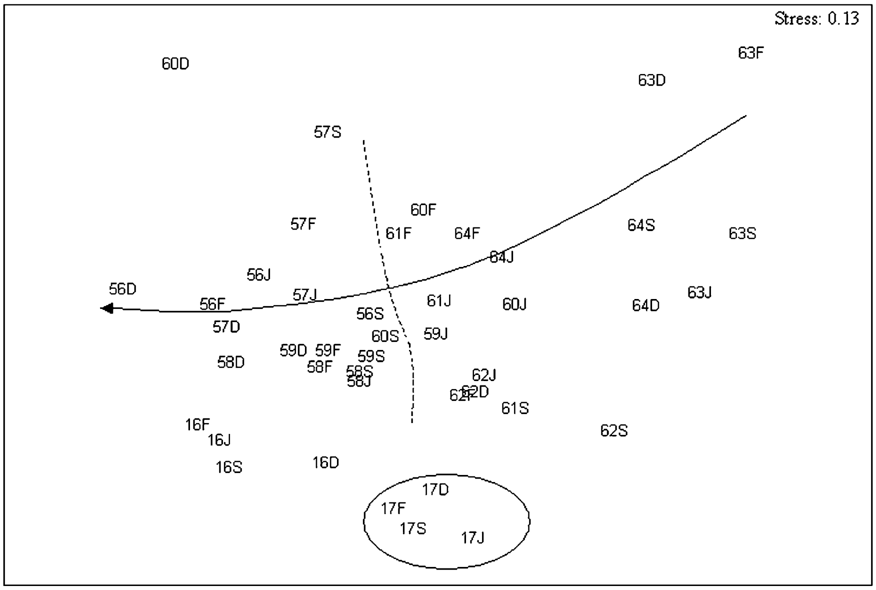

Fig. 5 Two-dimensional configuration for MDS ordination of macrofaunal assemblages (F: February samples, J: June samples, S: September samples and D: December samples)

highlighted a *continuum* within the muddy fine sediments, from an upstream zone (sites 61, 62, 63 and 64) characterized by a depauperate fauna, regardless of the season considered (usually <50 ind. 0.25 m^{-2}) to a downstream zone (sites 16, 56, 57, 58, 59 and 60) in which faunal density was higher and time-dependent. Site 17, which is a continuation of the intertidal sandbanks, and whose sediment sheltered low abundances of fine sand preferring species, is isolated (Fig. 5). However, due to the high variability of the samples, no significant seasonal differences could be determined (ANOSIM, $r = 0.005$; $P > 0.05$).

Despite the absence of significant correlations between abundance values and sedimentary composition (BIOENV analysis), sediment dynamics, especially the rapid deposition/erosion phenomena, need to be taken into account to understand the changes in abundance. The abundance decrease observed at site 16 from September to December can be explained by the fine sand content, which increased from 7.1% to 75.7% in sediment. Similarly, following the change from fine sand to pebbles at site 60 between September and December, the benthic community changed radically from a sand-preferring infauna to a large mussel bed.

Seasonal changes at site 62 (year 2002)

Sediment composition

Whatever the date considered, silt/clay and fine sand granulometric classes at site 62 comprised more than 90% particles, with silt and clay being dominant [content >70%, except 18 June (Table 1)]. No trend can be detected from the high to the low flow rate periods since, excepted the value of 65 µm reached on 18 June, the mean grain size remained stable through the year, ranging from 15.4 µm to 24.0 µm. Grain size stability was sometimes punctuated by rapid changes, as witnessed by the important and

Table 1 Change in silt/clay (<63 µm) and fine sand (100 µm>size particle>200 µm) contents in sediment at site 62 in 2002

Date	23 March	2 April	22 April	2 May	15 May	30 May	18 June	29 September	3 December
% of fine sand	7.55	2.85	0.57	3.61	0.68	0.40	31.71	7.11	18.25
% of silt/clay	83.61	91.28	95.05	90.82	94.48	93.43	50.67	85.39	70.19

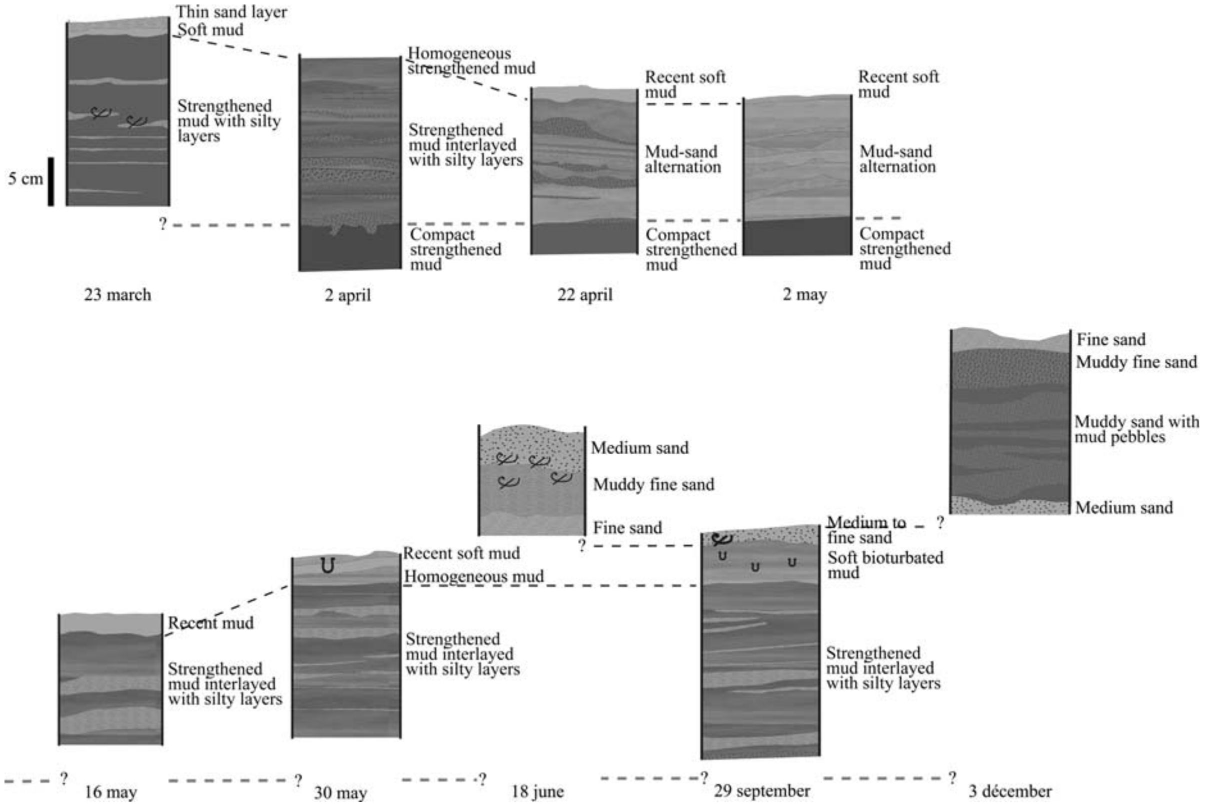

Fig. 6 Lithofacies variations, with correspondence between layers (specified by the symbol "?" when hypothetic), at site 62 from March to December 2002. Considering the basal compacted strengthened mud as a reference layer, cores were arranged one compared to the others. Upward lines suggest deposition events and downward lines, compaction and/or erosion phenomena. Symbols show the presence of shells (∽) and burrows (U).

temporary (since the initial conditions were rapidly recovered) deposition of sand observed on 18 June.

Lithofacies

Due to flood deposits, site 62 was influenced in the spring by thin (2 cm max.) deposits (i.e. after strengthening processes). As shown in Fig. 6, the sediment on 23 March was characterized by a 1-cm surficial deposit of mud, probably eroded during the highest levels of flooding (22–28 March), since the mud had disappeared by 2 April. On 22 April, the core, collected on an eroded surface, exhibited a recently deposited layer of mud (1-cm thick), still present on 2 May though reduced in thickness. This layer was topped by new deposits of homogeneous soft mud on 16 May (2 cm) and 30 May (<1 cm). These muddy sediments were covered by a heavy deposit of three grades of sand (fine, muddy fine and medium) on 18 June. This sandy deposit was presumably eroded over the summer, since only a fine layer of medium to fine sand with shells (probably deposited in June) covered the layer of stiff mud and interlaminated silty beds observed on 30 May. The autumnal period (from 29 September to 3 December) was characterized by a thick deposit of sand (≈15 cm).

Patterns of faunal abundance

A total of 36 species was collected at site 62 over the year. The fauna was composed of annelids (17 sp.), arthropods (10 sp.), molluscs (9 sp.) and cnidarians (1 sp.) and was dominated, in number of individuals, by polychaetes (63.0%) and molluscs (34.2%).

Total abundances remained low throughout the year [minimal and maximal values of 5.8 ± 5.1 and

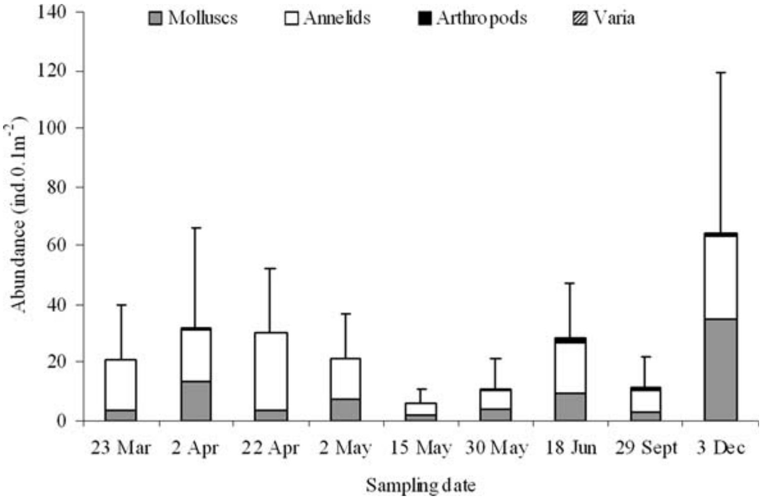

Fig. 7 Change of the total macrobenthic density at site 62 along the year 2002

63.8 ± 55.8 ind. 0.1 m^{-2}, respectively (Fig. 7)]. As noticed previously in 2001, the variability between replicates may be pronounced depending on the sampling date, evidencing the existence of a small-scale heterogeneity due to local sediment deposits. Although values varied significantly over the year (ANOVA, $P < 0.001$), total abundance values revealed no seasonal trend since the maximal values were observed in April, June and December. Changes in abundance were related to the sand deposits occurring during the period with the lowest flow rate level. The function of the summed cumulated densities and the silt/clay and fine sand particle contents indicated that the bio-sedimentary dynamics could be divided into two periods: the first from March [and maybe January (pers. obs.)] to May during which fauna was influenced by fine silt/clay deposits (usually associated with a sediment compaction phenomenon), and the second, from June to December during which sandy deposits prevailed (Fig. 8). As a consequence, the faunal composition changed over the year. The March to May fauna, characterised by an impoverished form of the *Abra alba-Pectinaria koreni* muddy fine sand community, was enriched from June to December by species living in clean fine sand, such as *Donax vittatus*, *Nephtys cirrosa* or *Spio decoratus* (Table 2). These latter species,

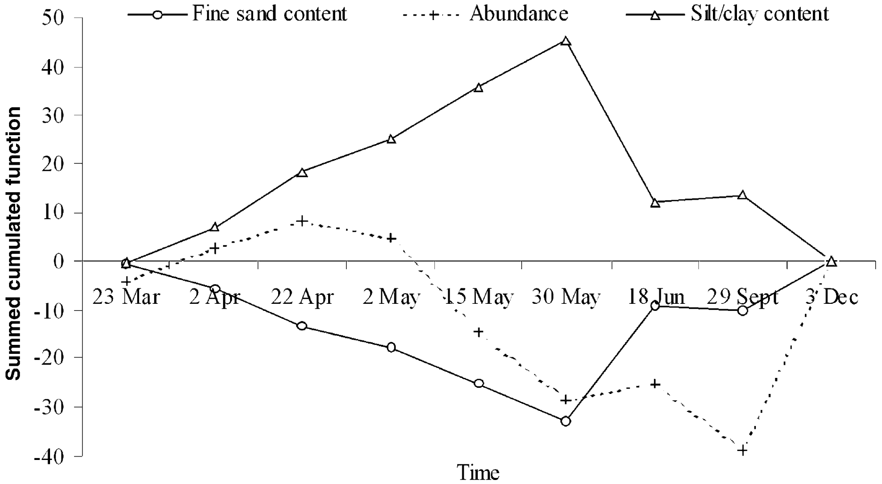

Fig. 8 Summed cumulated function of the mean fine sand and silt/clay contents and the mean abundance

Table 2 Average abundances (ind. 0.1 m^{-2}) ± SD of the first three most abundant macrobenthic species observed at site 62 between 23 March and 3 December

Sampling date	Three top ranked species	Abundance (mean ± SD ind. 0.1 m^{-2})
23 March	*Aphaelochaeta marioni*	9.4 ± 9.4
	Nephtys hombergii	6.6 ± 3.8
	Macoma balthica	1.8 ± 1.8
2 April	*Mysella bidentata*	7.2 ± 15.5
	Pectinaria koreni	6.6 ± 5.2
	Nephtys hombergii	5.8 ± 2.9
22 April	*Aphaelochaeta marioni*	15.0 ± 6.2
	Nephtys hombergii	7.4 ± 4.8
	Streblospio shrubsolii	4.6 ± 3.9
2 May	*Aphaelochaeta marioni*	6.2 ± 5.3
	Nephtys hombergii	5.8 ± 2.6
	Macoma balthica	5.2 ± 2.5
16 May	*Nephtys hombergii*	2.8 ± 2.0
	Macoma balthica	1.8 ± 0.8
	Aphaelochaeta marioni	1.0 ± 1.7
30 May	*Macoma balthica*	3.4 ± 1.8
	Nephtys hombergii	3.2 ± 1.8
	Heterocirrus alatus	1.4 ± 2.6
18 June	*Nephtys cirrosa*	7.2 ± 2.3
	Donax vittatus	5.8 ± 2.8
	Spio decoratus	5.0 ± 4.8
29 September	*Pectinaria koreni*	3.4 ± 2.9
	Nephtys hombergii	2.4 ± 0.9
	Macoma balthica	1.2 ± 1.1
3 December	*Mysella bidentata*	15.0 ± 20.7
	Pectinaria koreni	13.4 ± 10.4
	Nephtys hombergii	7.8 ± 1.6

mainly represented by adult individuals (pers. obs.), were the top three taxa on 18 June. Changes in fauna occurred very rapidly during this period, given that ≈15 days were enough to replace a mud-preferring fauna by species with an affinity for clean fine sands. In December, a mixed assemblage, combining species of the *A. alba* and the *N. cirrosa* clean fine sand communities, was observed.

Interannual variability at site 62

We compared sedimentary and faunal changes observed in 2002 at site 62 to those observed in 2001 (Figs. 9a and b). The proportion of sand was significantly higher in 2001 (*t*-test, $P < 0.05$), with maximal proportions observed in September (81.7%) and December (69.8%). Such differences did not influence total abundance values, which, with the exception of the high values recorded in December 2002 (63.8 ± 55.7 ind. 0.1 m^{-2}), remained significantly consistent over the two years and displayed the same order of magnitude (*t*-test, $P > 0.05$), although varying greatly from one replicate to another.

Discussion

The soft-bottom macrobenthic communities in this study are comparable both in density and composition to other shallow-water communities of temperate estuaries (Warwick & Uncles, 1980; Dittmer, 1981; Elkaïm et al., 1982; Ysebaert et al., 1998; 2000; 2003). They evolve from the *Abra alba-Pectinaria koreni* muddy fine sand community, located in the downstream part of the North Channel, to the *Macoma balthica* oligospecific community, spread over the inner bottoms (Cabioch & Gentil, 1975; Elkaïm et al., 1982, see Dauvin & Desroy, 2005 for details). In this study, a permanently impoverished sandy facies (site 17), characterised by the mollusc *Donax vittatus* and part of the *Abra alba* community, was identified for the first time in the Seine estuary in response to locally enhanced hydrodynamics.

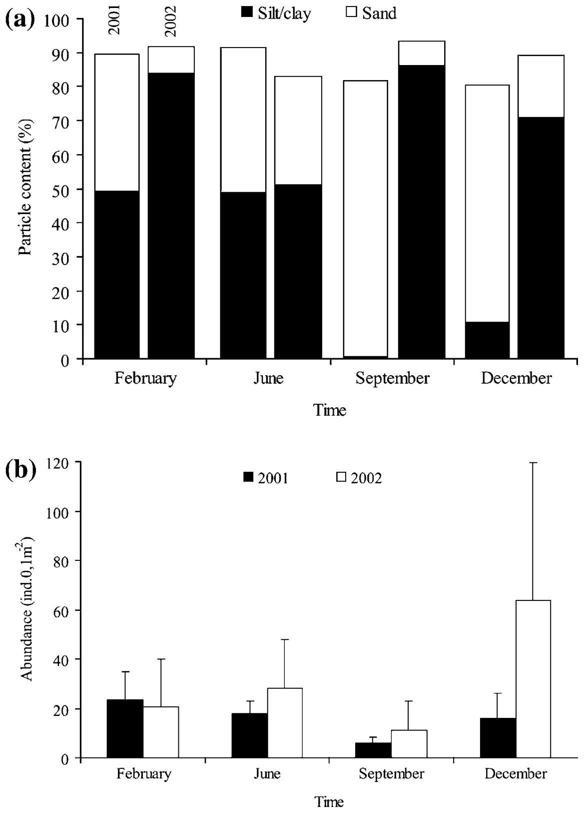

Fig. 9 Inter-annual changes in fine sand and silt/clay contents (%, **a**) and in average macrobenthic abundance ±SD (ind. 0.1 m^{-2}, **b**) in 2001 and 2002 at site 62. Abundances values recorded in 2001 were standardized to 0.1 m^{-2}.

Intra-annual variability of macrobenthic fauna

Understanding the patterns of estuarine systems is difficult because variations in both physical forcing functions and biota occur at all scales (Dethier & Schoch, 2005). In many coastal systems, the main community structure parameters fluctuate according to the typical yearly cycle of coastal temperate waters, as has been shown by Bachelet et al. (2000) for the lagoons of Arcachon, Certes (French Atlantic coast) and Prevost (French Mediterranean coast); by Desroy & Retière (2001) for the Rance estuary (French Channel coasts); and by Nonnis Marzano et al. (2003) for the Lesina lagoon (southern Adriatic Sea). Contrary to expectations, our study found no evidence of a clear seasonal signal, integrating spring and summer recruitment, for the abundance changes in soft-bottom communities in the North Channel. At the scale of the North Channel, the principal faunal variations occurred during the autumnal period: abundance values were consistent between sites in February, June and September 2001 and highly variable between September 2001 and December 2001, with the highest abundances observed in the central part of the Channel. In addition, benthic fauna exhibited strong differences: some sites had very high abundance levels while others displayed very low levels, this inter-site variability being supplied by a small scale heterogeneity which may be responsible for patchily distribution of the fauna. According to Elkaïm et al. (1982), our observation for the North Channel is also true for the Seine estuary. These fluctuations are probably related to the dynamics of superficial sediments, which, in the Seine estuary, depends mainly on tidal currents, which control the dispersion of fine sediment and especially fluid muds (Lesourd et al., 2003), river discharge as well as short but intense events like storms and the intensity of wave action associated (Lesourd et al., 2003). However, the lack of information about the intra-annual variability of subtidal benthic assemblages at scales higher than a single site, both for the Seine and for the other major Northern European estuaries prevents us from making comparisons that would improve understanding of estuarine functioning.

Sediment in the North Channel was characterised by a strong spatial and temporal variability, sustained by intense episodes of sediment transport. Deposition events, often temporary and mainly observed during low flow rate periods, appear to have disturbed community structure and possibly community functioning. However, the consequences for benthic assemblages depended on the sites and the periods considered; for example, abundance decreased at site 16 in December 2001 and increased at site 62 in June 2002. When abundance decreased after sediment deposition, it was impossible to determine whether these decreases were due to organisms dying after being buried (Elmgren et al., 1986; Bouma et al., 2001) or resuspended in the water column (Armonies, 1994; Olivier et al., 1996a). Studies on the polychaete *Pectinaria koreni* in the Seine estuary have shown that unsuitable sediments or the presence of bioturbators induce the active resuspension of recruits (Olivier et al., 1996b), thus decreasing abundances. On the other hand, the deposition of sandy sediments may also contribute to increases in species diversity and abundance by allowing settlements of new species that prefer fine sands. The sudden presence in our samples of adult individuals of sedentary or small species (*Donax vittatus*, *Magelona johnstoni*, *Spio decoratus*...) suggests the existence of secondary settlements of individuals on adjacent sandbanks from which resuspension and drifting is possible due to strong currents.

Physical versus biological determinism

The results concerning bio-sedimentary dynamics can be divided into two periods: the first from March (and maybe January) to May, during which fauna is influenced by fine silt/clay depositions (with an associated compaction phenomenon), and the second from June to December, during which sandy deposits prevail and mean particle size increases. Edaphic conditions were globally more stable during the period of maximal river discharge, with lithofacies showing the prevalence of strengthening phenomena (or sometimes erosion as shown by the presence of eroded surfaces) on silt/clay deposits; nonetheless, the impact of these phenomena on the fauna remained minor. Maximal disturbances, due to the succession of sandy deposition events, occurred during the low flow rate period. Such events can lead to rapid and drastic changes in composition and abundances, like those observed at site 62 on 18 June 2002. These results complete the observations of Elkaïm et al. (1982), who observed seasonal (winter/summer) differences within benthic assemblages at the scale of the estuary.

Examining the periods of maxima and minima in terms of total macrofaunal abundance values showed no consistent pattern that would suggest a relationship between the intensity of river discharge (highest flood values: 2280 $m^3 s^{-1}$ in 2001 and 1800 $m^3 s^{-1}$ in 2002) and faunal abundances. No relationships or significant correlations could be established between the river flow rate (peak flood value, lowest flow rate value, instantaneous/average flow rate values) and the changes in silt/clay or sand content in the North Channel in 2001 or at site 62 in 2002. Despite the absence of significant correlations, episodes of sediment transport and deposition emerged as a primary community structuring variable with respect to benthic community density and composition. This absence of relationships underlines a major problem associated with relating environmental variables to biological variables: the lack of knowledge about how environmental factors affect the biota, and whether upper or lower extremes, or mean values must be considered (Edgar & Barrett, 2002). Our results confirm those of McCarthy et al. (2000), who after studying the intra-annual variability of soft-bottom macrobenthic communities over a period of 25 months in shallow Hawaiian waters, concluded that there was no relationship between the macrofaunal density fluctuations and periods of increased runoff. As they reported, ‘‘each station studied, taken in isolation, could tell its own unique story’’, the common thread being the existence of sediment transport episodes as a key community structuring factor.

The effect of wind and wave events on the dynamics of benthic fauna could be more important than previously hypothesized. This seems especially likely given that, after strong storms, from 200,000 to 400,000 tons of sediments can be resuspended and redistributed throughout the estuary (Lesourd et al., 2003). A modeling of the fine sediment transport in the Seine estuary, showing that (1) wave resuspension is partially responsible for the northern drift of fine particles in the Eastern bay of the Seine, and (2) the residual flux of fine particles advected out of the Seine mouth is more correlated to meteorological events than to the river flow discharge (Le Hir et al., 2001), confirms this hypothesis.

On the basis of a grid of 40–67 sites sampled in 1986, 1987, 1988 and 1991, Thiébaut et al. (1997) emphasized the spatio-temporal persistence of the *Abra alba-Pectinaria koreni* community in the eastern bay of Seine and underlined the importance of larval retention and sediment stabilization by the polychaete *Owenia fusiformis* to explain this persistence. Post settlement processes (e.g. food limitation and post-larval drifting) were presumed to greatly modify the primary settlement pattern, generating the spatial reorganization of the whole community (Olivier et al., 1996a; Thiébaut et al., 1996). For example, studies of *Pectinaria koreni* and *Owenia fusiformis* recruitment have shown that the larval settlement of both species is relatively independent of edaphic conditions and can not generate the distribution patterns of adult populations (Lambert, 1991). Such conclusions are not inconsistent with our results and suggest the importance of bentho-pelagic coupling–via the post-settlement processes primarily induced by sedimentary instability–on the macrobenthic fauna dynamics.

Despite the variability existing at small scales of time and space, the *Abra alba* community remains stable at large spatial and temporal scales in the Seine estuary compared to other sites in the English Channel (Bays of Veys and of Morlaix) or in the south bight of the North Sea (Gravelines) where fluctuations are more pronounced (Dauvin, 2002). Paradoxically to the strong disturbing factors existing in the Seine estuary, the *Abra alba* community remains characterized by the absence of long term trend (Fromentin et al., 1997).

Human impact

Results from this study will also serve as a baseline for future studies examining the impact of the extension of Le Havre harbour on benthic communities and drawing conclusions about the abilities of the estuary to restore itself. However, assessing the human impact on benthic communities and on this communities' evolutionary trend is difficult since the polyhaline subtidal zone of the Seine estuary is characterized by large fluctuations in salinity, high current velocities and high turbidity. Moreover, rather than being superimposed on natural processes, human activities interfere with them. Although estuaries are known to be variable systems, the situation in the Seine estuary is exacerbed especially by the embankment of the Seine river and the the reduction in surface of the estuary. The high variability prevailing in the estuary makes it impossible to determine whether or not the harbour extension that began in January 2002 (essentially dredging/dumping operations) has modified the functioning of the benthic ecosystem. As observed in the Schelde estuary (Ysebaert et al., 2000), processes of sedimentation and resuspension will probably be enhanced by dredging (45 million tons for the shipping channel and 5 million tons for maintenance dredging). The inconsistent sediment dynamics observed at site 62 between 2001 and 2002 certainly reflects the industrial equipment in the North Channel but also the initial effects of the engineering work (dredging and enrockment) associated with the harbour extension. Despite the sedimentary variability, benthic fauna remain relatively unaffected and resilient. Congruently, studies carried out in 2002 by Dauvin et al. (in press) to assess effects of harbour infrastructure development show that one year into the harbour management plan, changes in benthic and suprabenthic assemblage abundance do not exceed the range of spatial variability that exists naturally in the Seine estuary, whereas the plan was expected to cause rapid changes. The intra-annual variability of the assemblages at the mouth of the Seine river and the silted situation of the North Channel might result from the silting up and the alteration of the inner estuary, which has been generated by several decades of man-made modifications and natural processes (Lafite & Romana, 2001; Lesourd et al., 2001). Like the subtidal zone of the Zeeschelde (Ysebaert et al., 2000), the low abundance of the macrobenthos provides evidence of the fact that the North Channel is a highly stressed environment. The Shannon diversity index (less than 1.1 whatever the season considered) clearly showed that communities remain in the early stages of succession and under disturbance (Frontier, 1976).

Although being an important juvenile fish feeding ground in the past, the subtidal bottoms in the North Channel have progressively became an area of little ecological interest, as illustrated by the low abundances of benthic invertebrates and mesozooplankton upstream. The main ecological highlight is the suprabenthic fauna, which was and remains an important trophic resource for higher consumers (especially fish) in the food web (Dauvin et al., in press). The adjacent intertidal mudflats, although known to be an important feeding ground for birds and juvenile fish, continue to regress due to increased silting up and colonization by halophytes. Expected modifications over the next few years, connected to the reduction of the width of the North Channel, include an erosion of the estuarine bottoms located between the new dock dam and the north dyke embanking the Seine river, and an accumulation of particles in the upper part of the North Channel, leading to the continued silting up of the intertidal mudflats. Initial field observations, conducted from 2002 to 2004, already confirm the erosion of downstream sediments in the North Channel and the emergence of pebbles on which large mussels beds are now settled. In order to minimize these hydro-sedimentary and biological changes, and to preserve the ''Grande vasière'' tidal flat located in the upper part of the North Channel, several compensatory actions are planned, to be implemented between 2004 and 2006 (Hamm et al., 2001). To be efficient, compensatory actions must integrate objective standards for these resources, which are independent of the existing altered condition. The objective must be restoring habitat and fauna diversity rather than maintaining the current conditions, since impact measurements that do not distinguish between changes to the existing environment and the desired condition of resource will fail to account for the cumulative decline of the quality of estuarine habitats (McCold & Saulsbury, 1996).

Acknowledgements This study was undertaken within the framework of the Seine-Aval programme, coordinated by the *Haute Normandie* Region, which supported A. L.J. by a doctoral fellowship. The authors are grateful to the crew of ''R. V. Côte d'Aquitaine'' for their aid during sampling, to L. Gomez-Gesteira for his valuable assistance in the laboratory, and to L. E. Spencer for comments and help in correcting the English version of this text.

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Estuarine, Coastal and Shelf Science 76 (2008) 111–120

ESTUARINE COASTAL AND SHELF SCIENCE
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Interactions between a natural food web, shellfish farming and exotic species: The case of the Bay of Mont Saint Michel (France)

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Received 9 March 2007; accepted 15 June 2007
Available online 9 August 2007

Abstract

To ensure sustainable uses of the coastal zone, an integrated ecosystemic approach and ecosystem models are required to frame ecological processes and evaluate environmental impacts. Here, a mass-balance trophic (Ecopath) model of the Mont Saint Michel Bay (MSMB) was developed, to analyze the bay's functioning as an ecosystem. This bay, intensively exploited by fishing and for shellfish farming, is also suffering from the proliferation of the gastropod *Crepidula fornicata*, an exotic species.

The MSMB model has 18 compartments, from the primary producers to top predators, and emphasizes the large biomass of filter feeders. The model identified the MSMB as a highly productive ecosystem controlled largely from the bottom-up, and strongly impacted by huge biomasses of filter feeders. However, the low transfer efficiency rates imply that a large part of the primary production is not transferred upward to higher trophic levels, but is lost in high hydrodynamic exchanges and in the trophic impasse represented by a large biomass of *Crepidula fornicata*.

Keywords: Ecopath; trophic model; shellfish farming; invasive species; *Crepidula fornicata*; Mont Saint Michel Bay

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1. Introduction

Coastal areas are productive ecosystems that host a large part of the world's living marine resources and have the highest biological diversity of any part of the sea (Costanza et al., 1997). Despite of these ecological (Beck et al., 2001; Hugues et al., 2005), economical and social (Balmford et al., 2002) largely irreplaceable benefits, these ecosystems have been increasingly subjected to a large number of human pressures, leading to major environmental problems, such as, eutrophication and pollution, over-exploitation, invasions by alien species, etc. (Antunes and Santos, 1999; Costanza, 1999; Hugues et al., 2005).

In this context, ecosystem models may be used as a tool for resolving patterns, indicative of the key ecosystem responses (Fulton et al., 2005). Using such models, analysis of the effects of disturbance and measure of the ecosystem stability and resilience become possible (Perez-Espana and Arreguin-Sanchez, 2001). Within the last few decades, the number of ecosystem models in existence has rapidly grown (Fulton et al., 2003), especially trophic or food web models, notably through the wide availability and acceptance of the Ecopath with Ecosim (Ewe) software (Christensen and Walters, 2004).

Here, Ecopath was used to organize information on the functioning of the food web of the Mont Saint Michel Bay (MSMB), located on the north coast of France. The site is famous for its abbey, built on a hill in the intertidal zone, so that both the buildings and the vast productive mudflats surrounding it have been recognized for their cultural and ecological interest and, since 1979, is listed in the World Heritage Sites

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doi:10.1016/j.ecss.2007.06.011

(UNESCO). The MSMB hosts intensive shellfish farming enterprises. Also, for the last decades, it has been facing an invasion of the American slipper limpet *Crepidula fornicata* (Blanchard, 1997). Measures designed to mitigate these various problems became unavoidable to ensure the conservation of wildlife and associated habitats (Lefeuvre and Bouchard, 2002), and the sustainable development of local economical activities (e.g. tourism, shellfish farming and fishing; Le Mao et al., 2004). Therefore the MSMB was selected, in 2001, as a study site by the French national program of coastal environment (PNEC).

The present study, carried out in the framework of the PNEC, examined the trophic functioning of the MSMB with regards to human activities and recent environmental changes. The ultimate objective was to analyze different interactions between the biological components of the MSMB, and to assess the values of consumption and production fluxes of its food web. An Ecopath model, representing a mass-balance budget of production, consumption, fish farming and fishing in the food web was constructed. It considers all functional groups in this system, from primary producers to apex predators, including the large biomass of natural, farmed and exotic filter feeders. Information on ecosystem structure and function provided by inferred biomass transfers between functional groups can then be used to evaluate the likely impact of changes in the abundance of selected groups, and examine how such changes are impacting the whole ecosystem via different links of the food web (Ulanowicz, 1986).

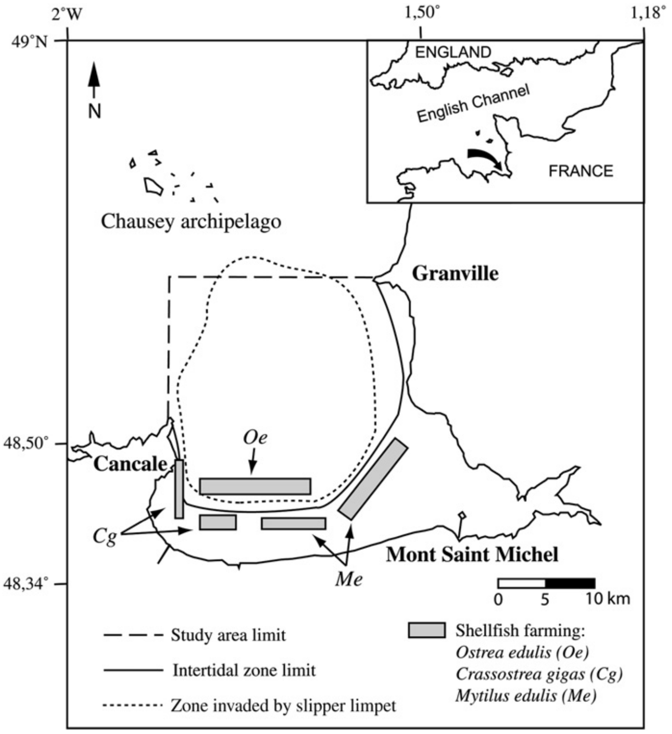

Fig. 1. General location and details of the study area within the Mont Saint Michel Bay, France (geographic coordinates are in decimal degrees).

2. Materials and methods

2.1. Study site

The MSMB is located in France, in the western part of the English Channel (48°30′N–1°40′W; Fig. 1). This bay is a semi-diurnal macrotidal system characterized by the second highest tidal range in Europe (10–11 m on average, with a maximum of 15.5 m). The intertidal zone covers 250 km^2 and includes 210 km^2 of mudflats and 40 km^2 of salt marshes.

The MSMB is host to a high biodiversity (Lefeuvre and Bouchard, 2002), notably:

- one of the largest salt marshes of the French coast;
- one of the main nurseries of the English Channel coast for many fish species of commercial interest (Lafaille et al., 2000) such as sea bass (*Dicentrarchus labrax*), whiting (*Merlangius merlangius*), flatfishes (common sole *Solea solea* and plaice *Pleuronectes platessa*), clupeids (*Sardina pilchardus*, *Clupea harengus* and *Sprattus sprattus*), and elasmobranchs (*Raja* spp.);
- thousands of over-wintering birds and birds resting while on their migrations;
- honeycomb reef-like structures built by the polychaete *Sabellaria alveolata*.

This site also hosts activities such as tourism, fishing and shellfish farming (Le Mao et al., 2004). Three bivalves are farmed (Fig. 1): (1) the Japanese oyster (*Crassostrea gigas*) in the intertidal mudflat of Cancale Bay (about 345 ha), (2) the European flat oyster (*Ostrea edulis*), farmed in the subtidal domain (880 ha) and (3) the common mussel (*Mytilus edulis*) reared on poles arranged in linear rows on the intertidal mudflat (total length of the rows: 272 km). The American limpet, *Crepidula fornicata*, which was introduced about 60 years ago, is now increasingly found, and currently represents the highest biomass of filter feeders within the bay (Loomis and VanNieuwenhuyze, 1985; Blanchard, 1997; Blanchard and Ehrhold, 1999).

2.2. Model approach

A mass-balanced trophic model was constructed using EwE (Christensen and Walters, 2004). The core Ecopath routine of EwE, derived from Polovina (1984), was applied to balance the energy budget of the different compartments of the system. The model is structured around a system of linear equations for ensuring mass-balance, which can be expressed (Christensen and Walters, 2004) as follows:

$$B_i \times \left(\frac{P}{B}\right)_i \times \mathrm{EE}_i = Y_i + \sum_{j}^{n} B_j \times \left(\frac{Q}{B}\right)_j \times \mathrm{CR}_{ij} \tag{1}$$

where, for $i = 1$ to n functional groups and $j = 1$ to n predators, B is the biomass in a given period of time; P/B the production/biomass ratio, which is equivalent to the instantaneous rate of total mortality, Z, under equilibrium (Allen, 1971); EE the ecotrophic efficiency (the fraction of production consumed, fished or exported out the system); Y the fishery yield; Q/B the consumption/biomass ratio and CR_{ij} the fraction of i in the diet of j.

Ecopath sets up a system containing as many linear equations as groups present within a system (n). The model can estimate one of the four parameters (n equations for n unknown parameters) as long as any three of these parameters are known, *viz*, B, P/B, Q/B or EE.

After the missing parameters have been estimated (with respect to the mass-balance between groups), consumption by predators can be described by the energy-balance equation:

$$\text{Consumption} = \text{production} + \text{respiration} + \text{unassimilated food} \quad (2)$$

2.3. Input data and model structure

The study area of the model included 380 km^2 of subtidal domain and 210 km^2 of intertidal mudflats (Fig. 1). To simplify the model, the salt marshes, connected to trophic network in the bay by the organic matter exported to the tidal system (Lafaille et al., 1998), were included in the model only as imported production.

The food web of the MSMB was described through 18 trophic groups, with the grouping of taxa being based on their similar trophic properties (preys, predators, turnover rate; Christensen and Walters, 2004). This resulted in two primary producer compartments (phytoplankton and microphytobenthos), three groups of cultivated filter feeders (European flat oyster, Japanese oyster and common mussel), *Crepidula fornicata*, zooplankton, meiofauna, small fishes (small species and other juvenile fish), three groups of macrobenthic fauna (carnivorous and necrophagous macrobenthic fauna, intertidal and subtidal filter feeders), mullets, three groups targeted by fisheries (cephalopods, large crustaceans and adult fishes), birds and marine mammals (Table 1).

The major part of data related to biomass, production and consumption (Table 2) were collected from studies conducted within the framework of the PNEC on the MSMB during the reference year 2003 (Table 1), taken as reference because several sampling surveys were performed in the bay during that year. When they were not available from this program, data were collected from various other sources (Table 1), particularly a model developed on the western Channel (Stanford and Pitcher, 2004). Commercial yields were taken from producer statistics for all cultivated species and from official records on statistical rectangle 28E6 of the ICES system, used for European fisheries data collection. Diet compositions (Table 3) were compiled from available literature but mainly from expert knowledge, after discussion with the specialists who provided the survey data (Table 1). Biomasses for each group are averaged on an annual period: if a group is present only during a part of the year, and eats elsewhere during the rest of the time, its biomass when present is multiplied by the proportion of time of presence to estimate the average annual biomass. It is the reason why no imported food is mentioned in the diet matrix (except for detritus that include organic matter coming from the salt marshes). Trophic fluxes between the different compartments of the trophic model were estimated in tonnes (t) of fresh weight of flesh per km^2.

2.4. Network analysis

Once the model was balanced, various parameters and indices were generated using the EwE software (Christensen and Walters, 2004). Trophic interactions between groups and the effects of exploitation were compared using EE, trophic levels (TL, computed from the mean TL of prey + 1; Christensen and Pauly, 1998), consumption rates, predation mortality and the primary production required (PPR) to sustain consumption by the various compartments of the model, and the extraction by humans.

Direct and indirect trophic interactions were analyzed using the mixed trophic impact routine of EwE, inspired by the Leontief matrix (Ulanowicz and Puccia, 1990), and which reflect both the impact of prey over their predators and predators over their preys (Pace et al., 1999).

Finally, the system was examined as a whole using the model's global parameters. With Ecopath, functional groups are aggregated into discrete trophic levels *sensu* Lindeman (1942) as suggested by Ulanowicz (1995), which allows estimation of flows to detritus and upper trophic levels, and of transfer efficiencies. Some network attributes (Ulanowicz, 1986; Ulanowicz and Kay, 1991) and flow indexes were analyzed to describe holistic properties of the system, i.e., total system throughput (T, sum of all flows through all compartments), Finn's (Finn, 1976) cycling index (FCI, fraction of ecosystem's throughput that is recycled), and Finn's mean path length (average size of the path length following for these transfers). The ratio of Net Primary Production to Total Biomass (PP/B) and to Total Respiration (PP/R) was also examined, as it is an important index of system maturity (Odum, 1969).

3. Results

3.1. Balancing the model

The Ecopath Eq. (1) states that each group must be mass-balanced, i.e., for one group, catches, consumption, biomass accumulation and export must not exceed production. Balancing an Ecopath model requires to adjust the input parameters such that none of the EE values exceeds 1 (Christensen and Walters, 2004; Kavanagh et al., 2004).

Here, the biomasses of many predator groups (cephalopods, large crustaceans, carnivorous and necrophagous macrobenthic fauna, adult fishes and small/juveniles fishes) were preliminarily adjusted according to expert estimates. A first attempt at balancing the model showed that the demand from these predator groups exceeded the production of most of the prey groups (meiofauna, carnivorous and necrophagous macrobenthic fauna, intertidal and subtidal filter feeders). Thus, to achieve mass-balance, an ecotrophic efficiency of 0.9 was applied to these groups, and the biomass of predator groups targeted by fisheries was left to be estimated by the model (Table 2).

Table 1
Input data values for the Mont Saint Michel Bay Ecopath model obtained mostly from the French national program of coastal environment on the Mont Saint Michel Bay (PNEC). The model refers to the year 2003, as most of the data used for its construction were based on sampling conducted in 2003. Choices of parameter values were also informed by the February 17–20, 2000. Ecopath workshop conducted in the Agrocampus, Rennes (D. Pauly and G. Fontenelle, unpublished data)

Trophic group	Biomass	Production/biomass (*P*/*B*)	Consumption/biomass (*Q*/*B*)	Production/consumption (*P*/*Q*)
Birds	Le Mao et al. (2006)	Stanford and Pitcher (2004)	Stanford and Pitcher (2004)	
Marine mammals	G. Gautier, DIREN Basse Normandie,[a] (PNEC); C. Liret, Océanopolis (unpublished data)	Stanford and Pitcher (2004)	Stanford and Pitcher (2004)	
Cephalopods	Model estimate	Stanford and Pitcher (2004)	Stanford and Pitcher (2004)	
Large crustaceans	Model estimate	D. Latrouite, IFREMER (unpublished data)	Stanford and Pitcher (2004)	
Adult fishes	Model estimate	Stanford and Pitcher (2004)	Stanford and Pitcher (2004)	
Small and juvenile fishes	Model estimate		Lafaille et al., 1998	Palomares et al. (1993)
Mullets	Model estimate	Stanford and Pitcher (2004)	Stanford and Pitcher (2004)	
Zooplankton	QUADRIGE II database, IFREMER	Christensen (1995)	Christensen (1995)	
Carnivorous and necrophagous macrobenthic fauna	Model estimate	Stanford and Pitcher (2004)	Stanford and Pitcher (2004)	
Intertidal filter feeders	J. Trigui and E. Thiebaut, Univ. Paris 6 (PNEC); N. Toupoint, Museum National d'Histoire Naturelle (unpublished data); Zwarts et al. (1996), Dubois (2002), Dubois et al. (2006)	Dauvin (2000), Ropert and Dauvin (2000)		Stanford and Pitcher (2004)
Subtidal filter feeders	F. Olivier, MNHN (PNEC); E. Thiebaut and C. Guichardière, Univ. Paris 6 (PNEC); Zwarts et al. (1996)	Dauvin (2000), Ropert and Dauvin (2000)		Stanford and Pitcher (2004)
Meiofauna	K. Seznec, Univ. Paris 6 (PNEC)	Le Loc'h (unpublished data)		Le Loc'h (unpublished data)
Slipper limpets	Blanchard and Ehrhold (1999)	Blanchard and Ehrhold (1999)	Blanchard and Ehrhold (1999)	
European flat oyster	Y. Thomas and J. Mazurié, IFREMER (PNEC)	Y. Thomas and J. Mazurié, IFREMER (PNEC)		Stanford and Pitcher (2004)
Japanese oyster	Y. Thomas and J. Mazurié, IFREMER (PNEC)	Y. Thomas and J. Mazurié, IFREMER (PNEC)		Stanford and Pitcher (2004)
Common mussel	Y. Thomas and J. Mazurié, IFREMER (PNEC)	Y. Thomas and J. Mazurié, IFREMER (PNEC)		Stanford and Pitcher (2004)
Phytoplankton	QUADRIGE II database, IFREMER	C. Struski, IFREMER (PNEC)		
Microphytobenthos	D. Davoult, Univ. Paris 6 (PNEC)	D. Davoult, Univ. Paris 6 (PNEC)		

[a] Institutional affiliation of data providers (unpublished data) are all located in France.

Table 2
Input and calculated (in **bold**) parameters for the Ecopath model of the Mont Saint Michel Bay. Catches and biomasses are expressed in t km^{-2} (fresh weight). The production/biomass (P/B) and consumption/biomass (Q/B) ratios are in year^{-1}. The production/consumption (P/Q) ratio, trophic level (TL) and ecotrophic efficiency (EE) are dimensionless. Data in *italics* originate from 2003 studies of the French national program of coastal environment on the Mont Saint Michel Bay (PNEC). Values in bold are computed from the Ecopath with Ecosim software

Trophic group	Catch	Troph	Biomass	*P*/*B*	*Q*/*B*	EE	*P*/*Q*
Birds	0.002	**3.01**	*0.263*	0.400	*14.000*	**0.019**	**0.029**
Marine mammals		**4.12**	0.027	0.310	13.900	**0.000**	**0.022**
Cephalopods	0.480	**3.79**	**0.230**	2.5	15.000	0.900	**0.167**
Large crustaceans	0.450	**2.69**	**1.767**	0.500	4.000	0.900	**0.125**
Adult fishes	0.150	**3.16**	**3.501**	0.800	6.000	0.900	**0.133**
Small and juvenile fishes	0.160	**2.82**	**1.088**	**6.600**	22.000	0.900	0.300
Mullets	0.002	**2.10**	**0.088**	0.500	5.000	0.900	**0.100**
Zooplankton		**2.00**	2.460	18.000	60.000	**0.257**	**0.300**
Carnivorous and necrophagous macrobenthic fauna	3.000	**2.08**	**13.615**	1.300	**6.500**	0.900	0.200
Intertidal filter feeders		**2.00**	*12.350*	1.300	**13.000**	**0.877**	0.100
Subtidal filter feeders	1.500	**2.00**	*6.450*	1.300	**13.000**	**0.808**	0.100
Meiofauna		**2.00**	*0.700*	10.000	**50.000**	**0.348**	0.200
Slipper limpets	3.050	**2.00**	*91.100*	0.300	*4.500*	**0.140**	**0.067**
European flat oyster	0.150	**2.00**	*0.410*	*0.400*	**4.000**	**0.915**	0.100
Japanese oyster	0.760	**2.00**	*1.350*	*0.630*	**6.300**	**0.894**	0.100
Common mussel	6.150	**2.00**	*4.600*	*2.000*	**20.000**	**0.854**	0.100
Phytoplankton		**1.00**	*24.055*	*166.000*	–	**0.166**	–
Microphytobenthos		**1.00**	*16.000*	*27.000*	–	**0.382**	–

3.2. Trophic structure of the MSMB

3.2.1. A large proportion of filter feeders

Input values and output estimates after balancing the model were summarized in Table 2 and ecosystem statistics in Table 4. The MSMB is characterized by a high productivity, with an overall production of about 4600 t km^{-2} year^{-1}, and the large biomass of filter feeders (65% of total biomass), with *Crepidula fornicata* as most dominant species (51% of total biomass). Fig. 2a, representing biomasses at different trophic levels, illustrates that there is a substantial lower biomass above the filter feeders (TL = 2).

3.2.2. Contrast in efficiencies of trophic transfers

In the model, the productions (Fig. 2b) and EE values (Table 2) showed a wide range of variation, reflecting the unequal trophic roles of various compartments.

Table 3
Predator–prey matrix of the ecosystem in the Mont Saint Michel Bay. Data in *italics* originate from 2003 studies of the French national program of coastal environment on the Mont Saint Michel Bay (PNEC)

Prey/predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1. Birds																
2. Marine mammals																
3. Cephalopods		0.1														
4. Large crustaceans			0.1						0.1							
5. Adult fishes		0.8	0.6	0.1					0.2							
6. Small and juvenile fishes					0.3				0.1							
7. Mullets		0.1														
8. Zooplankton					0.2	0.3										
9. Carnivorous and necrophagous macrobenthic fauna	*0.15*		0.3	0.3	0.2	0.2										
10. Intertidal filter feeders	*0.6*				0.1	0.2			0.05							
11. Subtidal filter feeders				0.1	0.1	0.1										
12. Meiofauna						0.1	0.1									
13. Slipper limpets				0.1												
14. European flat oyster																
15. Japanese oyster																
16. Common mussel	*0.25*			0.1												
17. Phytoplankton								0.4		0.8	0.8		*0.8*	*0.8*	*0.8*	*0.8*
18. Microphytobenthos							0.5	0.4	0.15	0.1	0.1	0.8	*0.05*	*0.15*	*0.15*	*0.1*
19. Detritus				0.3	0.1	0.1	0.4	0.2	0.4	0.1	0.1	0.2	*0.15*	*0.05*	*0.05*	*0.1*

Table 4
Summary statistics for the Mont Saint Michel Bay model

Parameter	Units	Value
Sum of all consumption	$t\,km^{-2}\,year^{-1}$	1090
Sum of all exports	$t\,km^{-2}\,year^{-1}$	3700
Sum of all respiratory flows	$t\,km^{-2}\,year^{-1}$	730
Sum of flows into detritus	$t\,km^{-2}\,year^{-1}$	3880
Total system throughput	$t\,km^{-2}\,year^{-1}$	9400
Sum of all production	$t\,km^{-2}\,year^{-1}$	4570
Mean trophic level of catch		2.11
Gross efficiency (catch/net P.P)		0.00358
Calculated total Net Primary Production	$t\,km^{-2}\,year^{-1}$	4430
Total primary production/total respiration		6.1
Net system production	$t\,km^{-2}\,year^{-1}$	3700
Total primary production/total biomass		24.6
Total biomass/total throughput		0.019
Total biomass (excluding detritus)	$t\,km^{-2}$	180
Total catches	$t\,km^{-2}\,year^{-1}$	15.9
Connectance index		0.17
System omnivory index		0.058
Finn cycling index	%	0.64
Finn mean path length		2.1

First, a large break in the pyramid of production is observed between TL1 and 2 (6%), indicating that little of the primary production in the system is utilized. This is matched by low EE values for phytoplankton and microphytobenthos, which indicate that only a small proportion of their production is grazed within the water column, or in the benthic domain.

In contrast, in the next step of the trophic chain (TL2/TL3), the transfer efficiency is quite high (18%). This corresponds to high values of EE for farmed and 'natural' inter- and subtidal filter feeders, whose production is largely used by shellfish farming (70% of the mortality for oysters and mussels) or consumed by predators (89% of the mortality of 'natural' filter feeders is caused by predators).

The slipper limpets (*Crepidula fornicata*) is an exception: only 14% of its production is utilized by higher trophic level animals and the fisheries. Moreover, even this is too high, as the catch of slipper limpets is discarded as it is due to dredging operations to limit its extend. The consumption of primary production by slipper limpets is four times higher than for cultivated mollusks. When the surface areas covered by the organisms are taken into account, the impact of farmed shellfish remains 2.5 times lower than those due to the slipper limpet. Requiring the highest PPR in the model (17%), slipper limpets appear as a large trophic impasse in the system: although this species represents 41% of the total consumption of primary production and detritus, its trophic efficiency when discards are removed is lower than 3%.

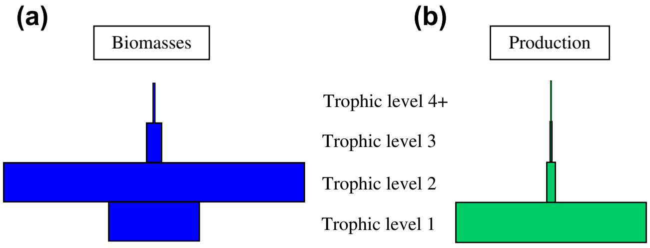

Fig. 2. Pyramids of (a) biomass and (b) productivity characterizing the Mont Saint Michel Bay ecosystem (relative scales).

Hence, in the MSMB, the trophic chain is shorten at TL2 by two different processes, extraction by shellfish farming but, mainly, large production of slipper limpets, not exploited by higher trophic levels (Fig. 3).

Finally, in the residual natural trophic chain, transfers to top predators are efficient (12%), as also indicated by high EE values.

3.2.3. Influence of shellfish farming on yields

PPR for current total catches (15.9 $t\,km^{-2}\,year^{-1}$) corresponds to 15% of the Net Primary Production; the 'catch' has a mean trophic level of 2.11. This low value is due to the intensity of shellfish farming, which contributes the major part of withdrawals by humans. However, the trophic role due to fishing activities proper is far more important than that due to shellfish farming: the PPR to sustain fishing activities is seven times higher than for shellfish farming.

3.2.4. Convergent signals indicating a bottom-up, productive immature system

Results of Leontief matrix routine underline the positive impacts of phytoplankton and microphytobenthos on the other groups of the system (Fig. 4). Primary producers provide a key food supply for filter feeders (second trophic level), which constitute the preys of higher-order consumers.

Total system throughput (Table 4) reached 9400 t $km^{-2}\,year^{-1}$, of this, 12% is devoted to consumption, 8% to respiration, 41% to flows to detritus and 39% to exports (equivalent to yield and/or net system production).

Total primary production/total biomass ($PP/B = 25\ year^{-1}$) and total primary production/respiration ($PP/R = 6$) had high values. The omnivory index of the MSMB model, of about 0.06, identifies the food web as very simple; consistently, the FCI is very low (0.64%) and the Finn's mean path length very short (2.1; Table 4).

4. Discussion

The model developed in this study was mainly based on the data collected from studies conducted on the MSMB during the reference year 2003. After that the biomass of predator groups targeted by fisheries was left to be estimated by the model, this Ecopath model was equilibrated. As (1) input data were based on *in situ* surveys, (2) none of the EE values exceeds 1 (Christensen and Walters, 2004) and (3) estimated annual productions ($B \times P/B$) were realistic with regards to catches and fishing pressures for groups in which biomasses are calculated from the mass-balance procedure, this model was considered as realistic. Even if this model is based on an annual mass-balance, and does not reproduce the large seasonal variations, and seasonal contrasted trophic situations, it can be used to analyze the system on this annual scale.

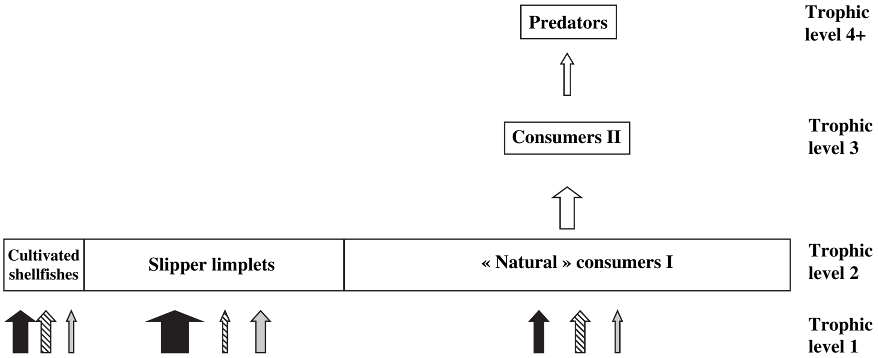

Fig. 3. Pyramids of consumption characterizing the Mont Saint Michel Bay with details on trophic level 2 (respective levels of consumption by farmed shellfish, slipper limpet and ‘‘natural’’ consumers, and origin of this consumption (primary production by phytoplankton (black arrow) or phytobenthos (cross-hatched arrow), or detritus (grey arrow))).

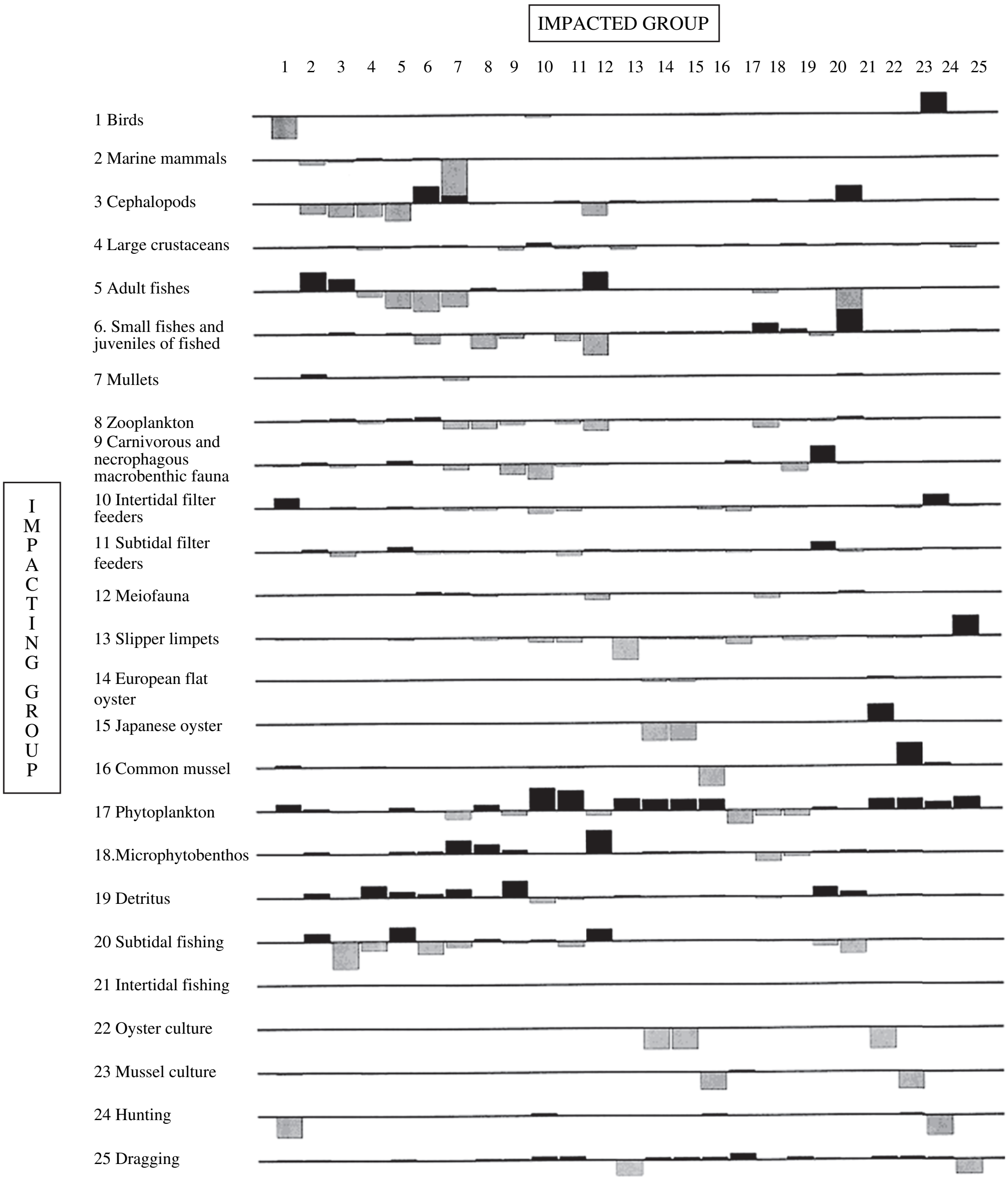

Fig. 4. Mixed trophic impacts between groups of the Mont Saint Michel Bay ecosystem. Bars represent the direct and indirect trophic impacts that the groups’ lines have on the columns groups. Black bars indicate a positive impact and white bars a negative impact. The impacts are relative and comparable to each other.

This model has highlighted the main features of the MSMB: a very high production, associated with a low efficiency of transfer from primary production to higher trophic levels, partly due to a large biomass of filter feeders not available for consumption within the system. Also, the system is profoundly impacted by the invasive mollusk *Crepidula fornicata*.

4.1. A general description of the trophic web

4.1.1. Low rate of transfer of the high primary production in the trophic chain

In spite of a moderate production of microphytobenthos, MSMB is highly productive, the primary production being essentially supported by phytoplankton, whose concentration remains high through the summer (Hoch and Garreau, 1998). As in coastal lagoons, the strong tidal currents in this bay enhance the production rate (Comin and Valiela, 1993), by injecting regenerated nutrients into the euphotic zone (Hoch and Garreau, 1998).

However, an adverse effect of hydrodynamics in the MSMB is that the tidal currents lead to exchanges with adjacent shelf waters and to huge loss of organic matter via phytoplankton export (Le Pape and Menesguen, 1997). As a consequence, the primary production cannot be fully exploited by the bay's consumers (Le Pape et al., 1999; Rybarczyk et al., 2003; Riera, 2007).

4.1.2. The large influence of filter feeders

The model highlights the importance of filter feeders in the trophic network in the MSMB, which is locally called "filter feeders' bay." Such role for filter feeders frequently occurs in highly productive coastal systems, as high primary production results in higher food availability favorable to filter feeding (Le Pape et al., 1999; Grall and Chauvaud, 2002).

However, one of the specific features of the MSMB is that a large proportion of these filter feeders consists of *Crepidula fornicata*: its consumption reaches more than 40% of consumptions at TL2, but it is not exploited by human nor by the food chain; hence, it represents a large trophic impasse (Fig. 3).

4.2. A global evaluation of the system

The model identified the MSMB as a highly productive ecosystem and the Leontief matrix routine demonstrated that it is largely controlled from the bottom-up. However, global indicators (high PP/B and PP/R, low omnivory and low Finn cycling index and mean path length) suggest that the MSMB ecosystem is immature, in line with Odum (1969), Finn (1976) and Ulanowicz (1986, 1995). Low maturity status is common in megatidal coastal and estuarine systems, as the bay of Somme (Rybarczyk et al., 2003), or the Seine estuary (Rybarczyk and Elkaim, 2003), with relation to the low rate of transfer of primary production (Le Pape and Menesguen, 1997). Even if it is sometimes difficult to compare different systems from different degree of compartments aggregation in models, very low values of cycling index in the MSMB reflect an especially immature system.

The immaturity of the MSMB trophic network may be explained, if partly, by the intensive human exploitation of the bay, through shellfish farming and fishing activities. Yields represent 15% of the Net Primary Production in the MSMB, i.e., a high rate of exploitation (Pauly and Christensen, 1995; Christensen and Pauly, 1998), especially when the large losses of primary production due to hydrodynamic exchanges (Le Pape et al., 1999) are considered.

However, the immaturity status is also due to the high biomass of *Crepidula fornicata*, which represents 50% of the biomass at TL = 2, and 40% of the consumption of the primary production, but which causes a trophic impasse and reduces the efficiency of overall trophic interactions in the system.

In conclusion, the MSMB trophic network appears to be segmented in three trophic sub-systems, partly disconnected (Fig. 3):

- A short shellfish farming chain (TL2), whose trophic influence on the system is moderate;
- A short chain (TL2), based on *Crepidula fornicata*, which consumes a large part of the, mainly planctonic, primary production (Riera, 2007);
- A residual 'natural' exploited system, with a high transfer efficiency.

4.3. The determining influence of Crepidula fornicata

Coastal and estuarine areas are among the most biologically invaded systems in the world, especially by mollusks (Grosholz, 2002; Reise et al., 2006), with grave consequences for the invaded ecosystems. Cloern (1982) demonstrated the large influence of the exotic clam *Potamocorbula amurensis* in San Francisco Bay, which now diverts to itself the major part of primary production. Ecological consequences of invasions into coastal habitats can affect the entire ecosystem (Grosholz, 2002) and, in several cases, as in the San Francisco Bay after the introduction of *P. amurensis* (Bax et al., 2003), the collapse of fisheries.

However, Crooks and Khim (1999) suggested that the effects of habitat structural changes could compensate for the effect of invasive species on food webs. Thus, *Crepidula fornicata* modifies physical characteristics of benthic habitats: (1) by accumulating chain-shaped colonies which carpet the sea bottoms (Thieltges et al., 2003), and (2) as other filter feeding invasive species do (Daunys et al., 2006), by the excessive sedimentation associated with its excretion and by modification of hydrodynamics in the boundary layer flow (Ehrhold et al., 1998). Such habitat changes have been demonstrated to alter the nursery function of coastal areas (Le Pape et al., 2004).

Reise et al. (2006), who reviewed the problem of introduced species in European coastal ecosystems, are globally less alarmist, asserting that there is no evidence that alien species generally impair biodiversity and ecosystem functioning.

Similarly, de Montaudouin and Sauriau (1999) found that biomass, abundance and species richness of benthic macrofauna were enhanced in the presence of *Crepidula fornicata*, whose shells increase the heterogeneity of the substrate (Attrill et al., 1996). MSMB hence appears as an inverse example, where the consequences of the massive invasion of slipper limpet appear very important with, as in the San Francisco Bay, a large (40%) diversion of the consumed primary production.

4.4. Investigation of future changes in the system and management measures

One aim of the PNEC program in the MSMB was to develop knowledge in order to create reliable tools for management. Since the present study is not predictive, the question of the future of the bay remains open. Possible scenarios include: (1) changes in shellfish farming distribution and intensity, and/or (2) changes in the distribution of *Crepidula fornicata* including those due to control measures. These changes could be in part simulated using Ecosim (Christensen and Walters, 2004), which simulated biomass dynamics based on the parameters derived from the Ecopath model. However, this procedure implies the setting of a vulnerability rate to simulate the top-down versus bottom-up control; the problem is that the results are very sensitive to the vulnerability values chosen (Christensen and Walters, 2004). Without time series data, it was not possible to tune these parameters and the simulations will remain very sensitive to the initial settings, particularly the spatial biogeochemical dynamics. Nevertheless, additional mass-balance sub-models, as the one used to analyze the consumption of primary production by slipper limpets in the area covered by cultivated mollusks (cf. Section 3.2.2.) can provide information on contrasted situations. This sub-model has allowed to demonstrate that the impact of the slipper limpet is still higher than this of farmed shellfish when farming areas only are taken into account. It would be possible to develop comparable sub-models to investigate other questions.

The next steps in this study should thus involve developing an alternative spatial biogeochemical dynamic model, taking into account the filtering pressure of mollusks. An alternative approach would consist of assembling suitable time series, taking into account possible changes in biomass and diet matrix, and also investigating the use of Ecospace, which also uses parameters from Ecopath (Walters et al., 1998; Pauly et al., 2000).

Acknowledgements

We would like to thank (in France) G. Fontenelle (Agrocampus Rennes) who initiate this project, D. Nicolas (Agrocampus Rennes), for her contribution to the redaction and the numerous contributors in data collection: P. Berthou, M. Blanchard, D. Gerla, D. Latrouite, J. Mazurié and C. Trutski (IFREMER), E. Thiébaut (Université Pierre et Marie Curie – Paris VI, France), F. Olivier (Muséum National d'Histoire Naturelle, Dinard), A. Radureau and P. Lafaille (Université de Rennes I) and J.P. Robin and B. Dubois (Université de Caen). The project which led to this contribution was funded by the French National program for coastal ecology (PNEC). This model is a follow-up of an Ecopath workshop held at the Agrocampus Rennes April 17–20, 2000, run by D. Pauly and G. Fontenelle. D. Pauly wishes to thank the Pew Charitable Trusts (Philadelphia, USA) funding through the *Sea Around Us* Project and M.L.D. Palomares for help with the manuscript. The authors are also grateful to the two anonymous referees for their pertinent comments on the draft version of the manuscript.

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ECOLOGICAL INDICATORS 8 (2008) 360–372

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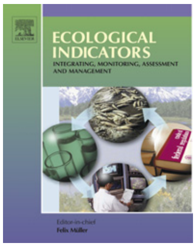

Use of biotic indices in semi-enclosed coastal ecosystems and transitional waters habitats—Implications for the implementation of the European Water Framework Directive

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ARTICLE INFO

Article history:
Received 20 October 2006
Received in revised form
19 January 2007
Accepted 22 January 2007

Keywords:
Biotic index
European Water Framework Directive
Benthic invertebrates
Semi-enclosed coastal ecosystems
Transitional waters

ABSTRACT

This study deals with the application of macrozoobenthos-based biotic indices (BI) within the frame of the implementation of the European Water Framework Directive. More precisely, this study aimed at assessing the performance of five recently developed methodologies (BI) for the assessment of ecological quality status (EcoQ) in two semi-enclosed, sheltered coastal ecosystems and in one transitional water body situated along the Western French coast, namely Marennes-Oléron Bay, Arcachon Bay, and the Seine Estuary. This study showed that these five indices rarely agreed with each other, describing very different pictures of the overall EcoQ of the three study sites. This work also clearly underlined the limitations of these approaches, notably the dependency of most of these BI and the resulting EcoQ classifications on habitat characteristics, more particularly to natural levels of sediment silt–clay content and the location of stations in the subtidal or the intertidal. The implication of our observations concerning the use of these BI for implementation of the WFD is discussed in terms of definition of habitat-specific reference conditions and necessity to adjust thresholds to the particular habitat occurring in semi-enclosed ecosystems. Meanwhile, the unmodified use of these BI severely impaired accurate assessment of EcoQ and decision-making on the managers' point of view.

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doi:10.1016/j.ecolind.2007.04.003

1. Introduction

Since the publication in 2000 of the European Water Framework Directive (WFD), the interest of European marine ecologists for the bio-assessment of human impact on littoral ecosystems has been renewed (Simboura, 2004; Borja, 2005; Borja and Heinrich, 2005; Dauvin, 2005, 2007). Indeed, European Union countries are now bound to assess and monitor the quality of their surface and ground-water bodies through the survey of a set of physical, chemical and biological quality elements defined in the Annexure V of the WFD. Among these biological quality elements, benthic invertebrates are used for assessing the ecological quality status (EcoQ) of surface water bodies including coastal and transitional (estuaries) water bodies. As a consequence, numerous bio-assessment tools have been developed or adapted to the WFD requirements in recent years (Borja et al., 2000; Simboura and Zenetos, 2002; Rosenberg et al., 2004; Dauvin and Ruellet, 2007), notably in the field of benthic invertebrate ecology (Diaz et al., 2004) because these organisms are generally considered as potentially powerful indicators of aquatic ecosystems health (Beukema and Cadée, 1986; Warwick, 1986; Dauvin, 1993). Indeed, they are situated at the interface between sediment and water column and thus integrate the characteristics of both sub-systems. Moreover, they may give evidence of environmental changes because of their sedentary life preventing them to escape unfavourable conditions and their relatively long lifespan permitting to discriminate between accidental and chronic disturbances (Dauvin, 1993; Reiss and Kröncke, 2005). Finally, in comparison to a chemical approach which consists in measuring pollutant concentrations in water or sediments and comparing them to existing norms, studying benthic invertebrate community can detect real ecological impact of disturbances at the community and ecosystem levels (Fano et al., 2003). Although a large corpus of synecological methodologies has been developed throughout the world to describe community structure and dynamics (Diaz et al., 2004), the current study only concerns a set of univariate biotic indices (BI) supposed to be adapted to fulfil the requirement of the WFD. In this paper, the behaviour of these BIs was tested in semi-sheltered littoral ecosystems. Indeed, most of the BIs proposed to the WFD and addressed in this paper are based on works which concern open marine subtidal areas and their sensitivity to increasing organic matter inputs (Pearson and Rosenberg, 1978; Bellan, 1993; Grall and Glémarec, 1997). Consequently, one can wonder whether these BIs would correctly perform in freshwater-influenced, semi-enclosed environments where sediments are naturally dominated by mud and/or organic carbon, and where intertidal areas can represent a dominant part of the whole area.

The objectives of this study were (1) to test the applicability of a set of currently available univariate BIs for the EcoQ status assessment of three semi-enclosed (two coastal and one estuarine) ecosystems and (2) to evaluate BI dependency on sediment characteristics and immersion/emersion.

2. Materials and methods

2.1. *Study sites*

The three study sites are situated along the western French coast (Fig. 1). Two sites (Arcachon Bay and Marennes-Oléron Bay) are located in the Bay of Biscay and one (Seine Estuary) in the Eastern English Channel. All sites were characterised by the dominance of soft bottoms, shallow depth and tidal regime.

2.2. *Seine Estuary*

The Seine Estuary is a 50 km^2 macrotidal estuary (maximum tidal range: 8.5 m). It opens into the English Channel (Fig. 1a). This estuary ranks among the three largest estuaries in France together with the Loire (60 km^2) and the Gironde (625 km^2). Mean flow rate is 410 $m^3\ s^{-1}$ with a maximum of 2000 $m^3\ s^{-1}$ (decennial flood) and a minimum of 81 $m^3\ s^{-1}$ during low river flow (Mouny et al., 1998; Dauvin et al., 2005, 2007). Turbidity reaches up to 100 $g\ L^{-1}$. A salinity gradient can be observed from polyhaline waters (salinity: 30–18) at the opening of the estuary toward oligohaline waters (Desroy and Dauvin, 2003). Sampling stations were situated in the polyhaline and downstream mesohaline zones with a majority of stations (99 out of 111) restricted to the polyhaline zone. Intertidal flats do not reach extended areas in this estuary. This estuary is highly industrialised and urbanised gathering 26% of the French population and 40% of national industrial activities together with areas of intensive agriculture in its 79,000 km^2 catchment area. Moreover, it has been heavily modified by the development of two major harbours (Le Havre and Rouen) and the estuarine part has been channelled and is regularly dredged (Dauvin et al., 2005). The level of various contaminants is high in water and sediments, classifying this estuary as one of the most contaminated in Europe (Dauvin et al., 2005, 2007).

2.3. *Marennes-Oléron Bay*

The Marennes-Oléron Bay is a 175 km^2 macrotidal semi-enclosed coastal system which is situated between the Oléron Island to the West and the continent to the East (Fig. 1b). The bay presents shallow depth (<20 m depth) and is characterised by large intertidal mudflats covering 60% of the total area. These flats are mostly unvegetated except on the east coast of the Oléron Island where *Zostera noltii* seagrass beds occur. The bay communicates with the ocean by two openings situated at its southern (Maumusson Pertuis) and northern (Antioche Pertuis) parts. It also receives freshwater inputs ($3 \times 10^9\ m^3\ year^{-1}$) by the Charente river which gives 90% of total freshwater inputs (Héral et al., 1978, 1984). Marennes-Oléron Bay is a major French site for oyster and mussel cultures. The level of contamination is relatively low; however, Cd concentrations may be problematic (Pigeot et al., 2006).

2.4. *Arcachon Bay*

Arcachon Bay is a 180 km^2 meso- to macrotidal (maximum tidal range: 4.9 m) coastal lagoon situated in the south-eastern Bay of Biscay (Bachelet et al., 1996) (Fig. 1c). This triangular-

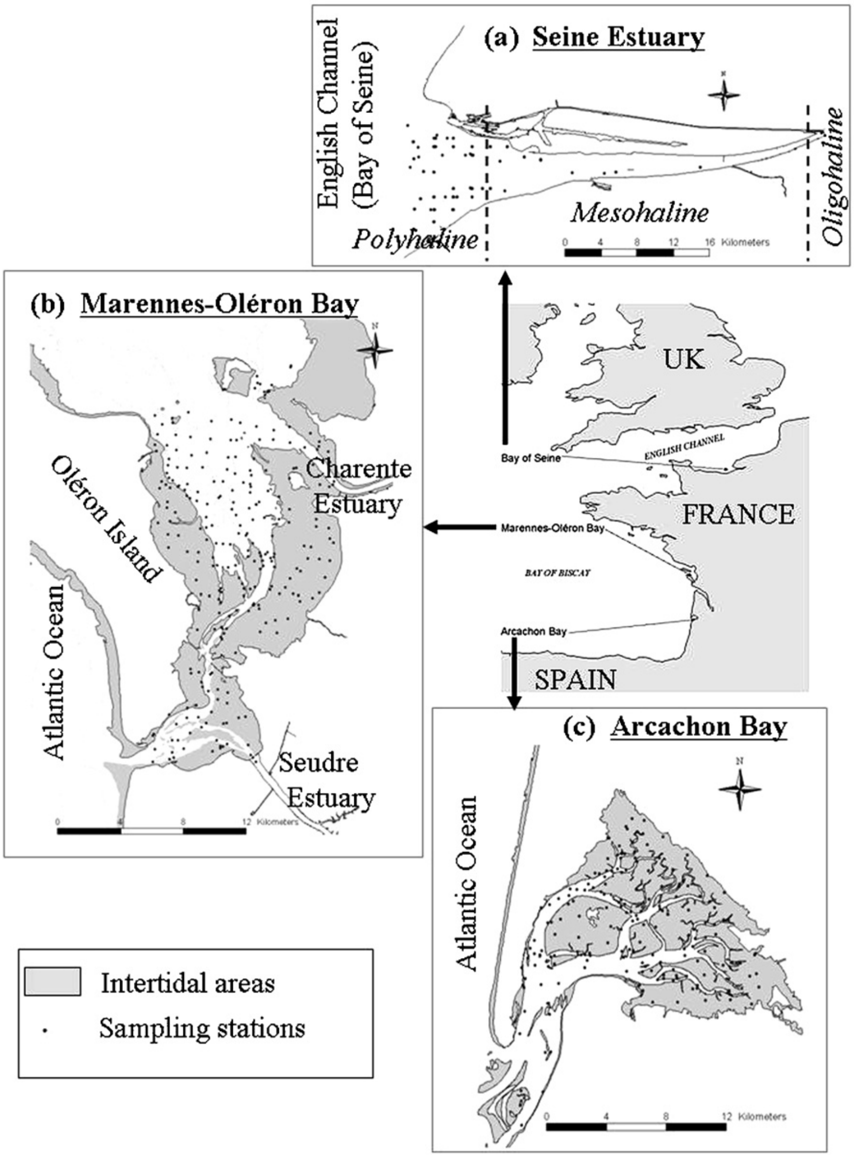

Fig. 1 – Map of the studied sites showing their locations along the French west coast and the sampled stations used in the three datasets (a) within the Seine Estuary, (b) within Marennes-Oléron Bay and (c) within Arcachon Bay.

shaped lagoon communicates with the Atlantic Ocean through a natural channel and receives its main freshwater inputs by a small river (L'Eyre) situated on its south-eastern corner (Fig. 1c). The maximum depth reaches about 24 m at the entrance of the lagoon; however, most channels displayed shallower depth (<20 m). Salinity varies from the fully marine waters at the entrance and western part of the Bay to more briny waters (salinity 22–32) toward the inner parts of the lagoon. As the Marennes-Oléron Bay, this lagoon is characterised by large intertidal flats covering 70% of the bay area. The largest and most flourishing *Z. noltii* seagrass bed of Europe (Auby and Labourg, 1996) covers these flats. The lower part of the intertidal is generally devoted to oyster culture, which constitutes a major activity at this site. Owing to the building in the late 1960s of a large sewage collector system that connects the towns and industries situated on its coast, and of the low level of industrialisation of its catchment area, the waters of the lagoon are relatively clean. Despite some signs of moderate eutrophication (e.g. large development of green macroalgae in the early 1990s) the overall water quality of the lagoon is considered as satisfying (Castel et al., 1996; Bachelet et al., 2000).

2.5. *Databases*

Three databases, each corresponding to one of the study sites, were used in this study. Each database gathered data on soft-bottom macrofauna sampled with a 1-mm mesh sieve during different studies and scientific programs (except some stations sieved on 2-mm mesh in the Seine Estuary). The characteristics of the datasets are shown in Table 1.

Concerning the Seine Estuary, data were extracted form the MABES database which gathers data from the Bay of Seine and the Seine Estuary collected during various sampling

Table 1 – Characteristics of the three datasets used in this study: number of stations, sampling device, mesh size, and years of sampling

	Arcachon Bay	Marennes-Oléron Bay	Seine Estuary
Number of stations	177	262	111
Sampling device	Ekman grab and box corer (0.045 m^2)	Smith-McIntyre grab and box corer (0.1 m^2)	Various grabs
Mesh size	1 mm	1 mm	1 or 2 mm
Location of stations	89 subtidal, 88 intertidal	135 subtidal, 127 intertidal	111 subtidal
Sampling years	2002	1995	1993–2002

All stations were sampled once.

campaigns (Dauvin et al., 2007). The dataset consisted of 111 subtidal stations located throughout the estuary and sampled on a single occasion (Table 1). The datasets from Marennes-Oléron Bay and Arcachon Bay consisted of 262 and 177 stations, respectively, each set from one sampling campaign (Table 1). In contrast with the data from the Seine Estuary, these two latter datasets included stations located on intertidal and subtidal areas.

2.6. Biotic indices and derivation of EcoQ

Five different BIs were calculated when possible for each station of the databases, namely the AMBI (Borja et al., 2000), BENTIX (Simboura and Zenetos, 2002; Simboura et al., 2005; Simboura and Reizopoulou, 2007), BQI (Rosenberg et al., 2004), Shannon-Wiener diversity (Simboura and Zenetos, 2002; Labrune et al., 2005) and BOPA (Dauvin and Ruellet, in press). These BIs were chosen because they are proposed to be used in the WFD.

AMBI, BENTIX and BOPA indices are based on the classification of species (or groups of species) into several ecological groups representing species level of sensitivity to pollutions. The number of ecological groups varied according to each index (five for the AMBI, two for the BENTIX and the BOPA). AMBI identifies five ecological groups corresponding to most sensitive species (ecological group 1) to most opportunistics/tolerant species (ecological group 5). BENTIX only recognised two groups (sensitive and opportunistic species), corresponding to ecological groups 1 and 2; and ecological groups 3–5, respectively, of the AMBI. BOPA considers the ratio between opportunistic polychaetes (i.e. polychaetes from ecological groups 4 and 5 of the AMBI) and amphipods (except those from the genus *Jassa*) as an indicator of environment quality. Full computational details can be found in Borja et al. (2000), Simboura and Zenetos (2002), Dauvin and Ruellet (2007) and are reported in Table 2.

Shannon index was also used as an indicator of EcoQ by Simboura and Zenetos (2002) and Labrune et al. (2005) and corresponding EcoQ classes from these studies were used. BQI calculation incorporates two measures: (1) the species' specific tolerance value ($ES(50)_{0.05}$) which is a measure of each species sensitivity or tolerance to pollutions, and (2) the diversity of the benthic assemblage estimated through the number of species collected in the sample. The index computes the relative abundance of each species together with their own tolerance value to the sample number of species. Computational details can be found in Rosenberg et al. (2004) and are also reported in Table 2. To apply this index to our study sites, the expected number of species in a random sample of 50 individuals (ES(50); Hurlbert, 1971) was calculated for each sampled station and the tolerance value ($ES(50)_{0.05}$) of each species was determined separately for each of the three study sites as recommended by Rosenberg et al. (2004) and Labrune et al. (2005). The EcoQ assessed by BQI was determined by taking the highest BQI value as a reference value and by defining five classes of equal size between 0 and this reference value (Rosenberg et al., 2004). Due to the difference in the range of index values between intertidal and subtidal stations, a separate scale was used for intertidal and subtidal sites following the same trend than Rosenberg et al. (2004). These

Table 2 – Indices calculated from macrobenthos databases

Biotic index	Algorithms	References
AMBI	$[(0 \times \%GI) + (1.5 \times \%GII) + (3 \times \%GIII) + (4.5 \times \%GIV) + (6 \times \%GV)]/100$	Borja et al. (2000)
BENTIX	$(6 \times \%GS + 2 \times \%GT)/100$	Simboura and Zenetos (2002)
Shannon index	$-\sum\left[\left(\frac{n_i}{N}\right)\log_2\left(\frac{n_i}{N}\right)\right]$	Pielou (1975)
BOPA	${}^{10}\log\left[\frac{fp}{fa+1}+1\right]$	Dauvin and Ruellet (2007)
BQI	$\left(\sum_{i=1}^{s}\left(\frac{A_i}{totA}\,ES(50)_{0.05i}\right)\right){}^{10}\log(S+1)$ with $ES(50) = 1-\sum_{i=1}^{s}\frac{(N-N_i)!(N-50)!}{(N-N_i-50)!N!}$	Rosenberg et al. (2004)

For the AMBI: %GI, relative abundance of disturbance-sensitive species; %GII, relative abundance of disturbance-indifferent species; %GIII, relative abundance of disturbance-tolerant species; %GIV, relative abundance of second-order opportunistic species; %GV, relative abundance of first-order opportunistic species. For the BENTIX: %GS, relative abundance of sensitive species = %GI + %GII; %GT = relative abundance of tolerant species = %GIII + %GIV + %GV. For the Shannon index: n_i, number of individuals belonging to the ith species; N, total number of individuals. For the BOPA: fp, opportunistic polychaetes frequency; fa = amphipods frequency (except *Jassa* sp.). For the BQI: S, number of species in the sample; A_i, total abundance of ith species in the sample; $ES(50)_{0.05i}$, $ES(50)_{0.05}$ of the ith species; totA, total abundance of the individuals belonging to the species for which $ES(50)_{0.05}$ can be computed.

separate scales permitted to avoid classifying all intertidal sites as severely degraded. The EcoQ classes in which index values were classified are shown in Table 3.

2.7. Data analysis

Agreement/disagreement between the five BIs was determined by considering only two EcoQ status: ‘Acceptable’ or ‘Not acceptable’. ‘Acceptable’ status was determined for each BI when the derived EcoQ status was ‘High’ or ‘Good’, and scored as ‘1’. This means that, on the managers point of view, no action has to be taken to restore the ecosystem. ‘Not acceptable’ status corresponded to ‘Moderate’, ‘Poor’ or ‘Bad’ EcoQ status, and was scored as ‘0’. When such an EcoQ status is derived from the biotic index, restoration measures are to be taken in order to reach ‘Good’ status by 2015 as stated by the WFD. The scores given to each of the five BIs used were summed for each station (range: 0–5). This sum of scores allowed measuring the level of agreement/disagreement between BIs (Table 4).

A non-parametric sign test was also used to assess agreement or disagreement between the different BIs on the ‘Acceptable’–‘Not acceptable’ status of stations on a statistical basis. This non-parametric test was particularly adapted to our data as it allowed comparing related sample classifications based on nominal data (‘Acceptable’–‘Not acceptable’) (Siegel, 1956).

Correlation between indices-derived classifications of EcoQ was studied in order to assess whether the different indices displayed similar tendency in the classification of stations. In summary, it permitted to assess if two indices ranked the stations from worst to best in the same way regardless of the precise classes of EcoQ. Indeed two given indices may not classify stations along the same range of EcoQ classes: one index may assess a given set of stations in EcoQ ranging from ‘High’ to ‘Moderate’ whereas another may assess the same set along a ‘High’ to ‘Bad’ range. For this test, EcoQ classes were ranked from 1 which corresponded to ‘High’ EcoQ, to 5, corresponding to ‘Bad’ EcoQ. Owing to the nature of data (five EcoQ classes), correlations between indices-based classifications were tested on the basis of ranks through the use of the non-parametric Kendall’s rank-correlation coefficient τ. Ties were taken into account in the computation of τ by using the correction factor recommended by statisticians (Siegel, 1956; Scherrer, 1984). The significance of τ was tested according to Siegel (1956).

For Marennes-Oléron Bay and Arcachon Bay, the non-parametric Kruskal–Wallis test was used to detect significant differences in environmental conditions between stations classified into the different EcoQ classes by the five BIs. Variables used in the analysis were duration of emersion (in number of days per year) and sediment silt–clay content (%). The test was first performed on the full site database to assess significant variations in environmental conditions between EcoQ classes. On a second run, subtidal and intertidal stations were analysed separately to circumvent correlation between sediment silt and clay content and the tidal location of stations. For each tidal location, the linear regression between indices value and silt–clay content was calculated and the significance of the linear coefficient of determination (R^2) was tested. This approach could not be used with the Seine Estuary because sediment characteristics were not systematically studied at all sampled stations.

Table 3 – Ecological quality (EcoQ) status classes and thresholds used to classify index values in this study

	EcoQ status					
	High	Good	Moderate	Poor	Bad	References
Shannon diversity	>4	4–3	3–2	2–1	<1	Labrune et al. (2005)
AMBI	0–1.2	1.2–3.3	3.3–4.3	4.3–5.5	>5.5	Muxika et al. (2005)
BENTIX for sands	6–4.5	4.5–3.5	3.5–2.5	2.5 – 2	0	Simboura and Zenetos (2002)
BENTIX for muds	6–4	4–3	3.0–2.5	2.5–2	0	Simboura and Zenetos (2002)
BOPA	0–0.04576	0.04576–0.13966	0.13966–0.19382	0.19382–0.26761	0.26761–0.30103	Dauvin and Ruellet (in press)
BQI Seine Estuary	11.5–9.2	9.2–6.9	6.9–4.6	4.6–2.3	2.3–0	This study, Rosenberg et al. (2004)
BQI Marennes-Oléron Bay (intertidal)	10–8	8–6	6–4	4–2	2–0	This study, Rosenberg et al. (2004)
BQI Marennes-Oléron Bay (subtidal)	17.9–14.3	14.3–10.7	10.7–7.1	7.1–3.6	3.6 – 0	This study, Rosenberg et al. (2004)
BQI Arcachon Bay (intertidal)	13–10.4	10.4–7.8	7.8–5.2	5.2–2.6	2.6–0	This study, Rosenberg et al. (2004)
BQI Arcachon Bay (subtidal)	12.8–10.2	10.2–7.6	7.6–5.0	5.0–2.4	2.4–0	This study, Rosenberg et al. (2004)

Table 4 – Levels used for the measurement of agreement/disagreement between biotic indices for each station

Sum of scores	Interpretation	
0	Full agreement of the five biotic indices on ‘Moderate’ or worse EcoQ status (‘Not acceptable’)	[a]
1	Partial agreement (four agreements out of five biotic indices) of the five biotic indices on ‘Moderate’ or worse EcoQ status (‘Not acceptable’)	[b]
2	Disagreement between the five biotic indices on the EcoQ status of the station	[c]
3	Disagreement between the five biotic indices on the EcoQ status of the station	[d]
4	Partial agreement (four agreements out of five biotic indices) of the five biotic indices on ‘Good’ or higher EcoQ status (‘Acceptable’)	[e]
5	Full agreement of the five biotic indices on ‘Good’ or better EcoQ status (‘Acceptable’)	[f]

Overall, full agreement was measured as [a] + [f], partial agreement was measured as [b] + [e] and disagreement as [c] + [d].

3. Results

3.1. EcoQ classifications

Use of the different BIs gave a different pattern of the overall EcoQ of the investigated sites (Fig. 2). The BOPA classified a large majority of stations (>97%) as ‘Acceptable’ in both coastal systems and in the Seine Estuary. In the same way, the AMBI classified the Seine Estuary, Marennes-Oléron Bay and Arcachon Bay stations as ‘Acceptable’ in 100, 95 and 88% of cases, respectively. However, the AMBI classified a majority of stations as ‘Good’ (86 and 76% for Marennes-Oléron Bay and Arcachon Bay, respectively) whereas BOPA classified stations predominantly as ‘High’

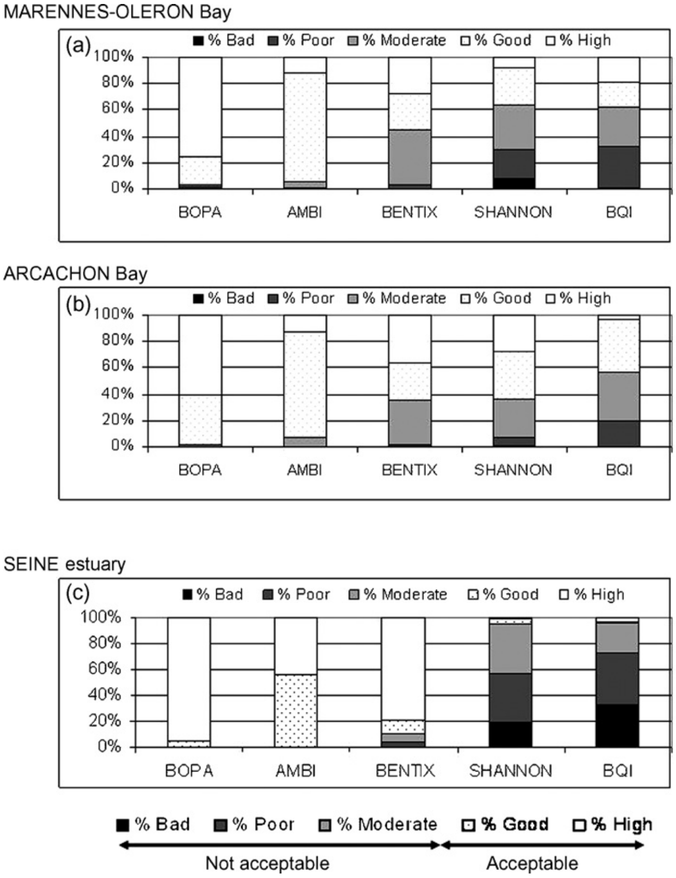

Fig. 2 – Percentage of stations of the three study sites (a) Marennes-Oléron Bay; (b) Arcachon Bay; (c) Seine Estuary classified as ‘High’, ‘Good’, ‘Moderate’, ‘Poor’ and ‘Bad’ by the five different biotic indices used: BOPA, AMBI, BENTIX, BQI and Shannon indices. The thresholds between ‘Acceptable’ and ‘Not acceptable’ ecological quality status is indicated at the bottom of the figure.

(with 65–60% of stations in both coastal systems) (Fig. 2a and b).

The classification of stations by the BENTIX index was more ‘Severe’ with 43 and 36% of stations considered as ‘Not acceptable’ (i.e. ‘Moderate’ EcoQ status or worse) in Marennes-Oléron Bay and Arcachon Bay, respectively. In the Seine Estuary, the percentage of stations considered as ‘Not acceptable’ was only 10%. ‘Bad’ and ‘Poor’ status rarely occurred (Fig. 2).

Shannon diversity classified 37% of the stations in Arcachon Bay, 53% in Marennes-Oléron Bay, and 95% in the Seine Estuary as ‘Not acceptable’ (Fig. 2). In both coastal ecosystems, the Shannon index identified as ‘Poor’ or ‘Bad’ 7 and 12% of the stations in Arcachon Bay and Marennes-Oléron Bay, respectively (Fig. 2a and b). In the Seine Estuary, the Shannon index classified 58% of stations as ‘Poor’ or ‘Bad’, whereas BOPA and AMBI never identified such status in this estuary.

The proportion of stations classified as ‘Not acceptable’ by the BQI was similar to that of the Shannon index, with 57% of the stations in the coastal systems and 95% in the Seine Estuary classified as ‘Moderate’ or worse. BQI assessed ‘Poor’ status in 19 and 20% of stations in Marennes-Oléron Bay and in Arcachon Bay, respectively. No station was considered as ‘Bad’ by the BQI in these two coastal sites whereas 33% of stations of the Seine Estuary were classified as ‘Bad’ and 40% as ‘Poor’.

3.2. *Agreement/disagreement between indices*

When considering spatial variations, the different BIs disagreed on the status of 65–90% of the stations (Fig. 3). The different BIs fully agreed on the ‘Acceptable’ or ‘Not acceptable’ status in less than 2% of stations. Partial agreement (i.e. four indices out of five agreed on ‘Acceptable’ or ‘Not acceptable’) occurred in 33% of stations in Marennes-Oléron Bay, 36% in Arcachon Bay and only 8% in the Seine Estuary (Fig. 3). The general disagreement between indices was confirmed by the sign test (Table 5). Nevertheless, there was no significant disagreement between BOPA and AMBI classifications in Marennes-Oléron Bay and the Seine Estuary and only a significant difference (at a level of significance = 0.05) in Arcachon Bay. BENTIX and BQI moreover significantly agreed

Table 5 – Significant, very significant and highly significant results of the non-parametric sign test conducted on the datasets of Arcachon Bay, Marennes-Oléron Bay and the Seine Estuary

	BENTIX	BOPA	BQI	Shannon index
Arcachon Bay				
AMBI	***	*	***	***
BENTIX		***	***	ns
BOPA			***	***
BQI				***
Marennes-Oléron Bay				
AMBI	***	ns	***	***
BENTIX		***	ns	***
BOPA			***	***
BQI				***
Seine Estuary				
AMBI	**	ns	***	***
BENTIX		**	***	***
BOPA			***	***
BQI				ns

Level of significance is indicated.

ns Not significant, $p > 0.05$.

* Significant, $p < 0.05$.

** Very significant, $p < 0.01$.

*** Highly significant, $p < 0.001$.

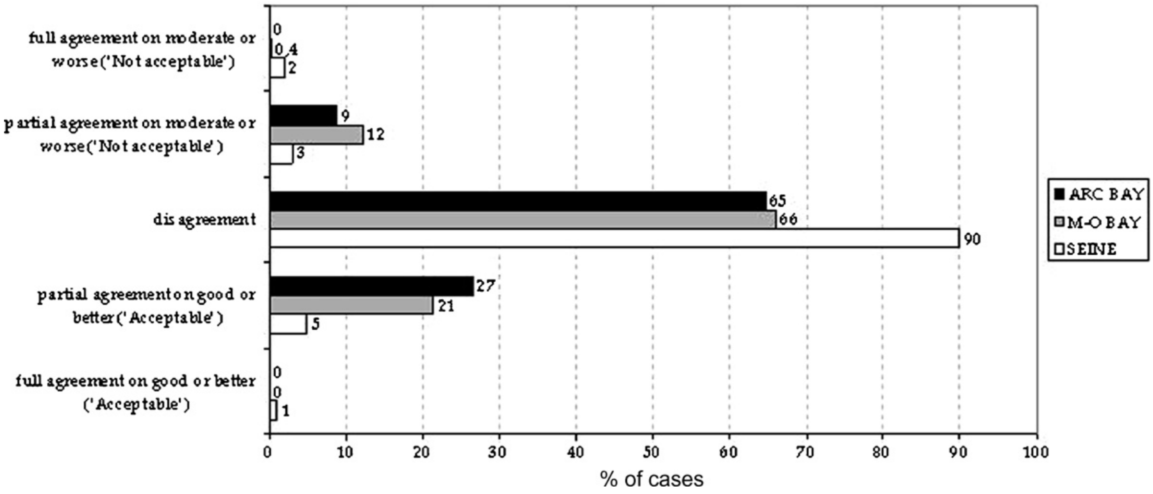

Fig. 3 – Percentage of stations of the three study sites (M-O.BAY: Marennes-Oléron Bay; ARC BAY: Arcachon Bay; SEINE: Seine Estuary) where the five biotic indices: (1) fully agreed in assessing ‘Good’ or better EcoQ status (all five indices classified the station as ‘Good’ or better); (2) partially agreed on assessing ‘Good’ or better EcoQ status (four indices over five classified the station as ‘Good’ or better); (3) fully agreed in assessing ‘Moderate’ or worse EcoQ status (all five indices classified the station as ‘Moderate’ or worse); (4) partially agreed in assessing ‘Moderate’ or worse EcoQ status (four indices over five classified the station as ‘Moderate’ or worse) or (5) disagreed on the EcoQ classification of the station (three (or two) indices classified the station as ‘Good’ or better EcoQ status whereas the two (or three) other classified the same station as ‘Moderate’ or worse).

Table 6 – Results of the non-parametric Kendall's rank correlation coefficient-test between biotic indices-derived ecological quality (EcoQ) status classifications (with the five EcoQ classes defined by the WFD namely 'High', 'Good', 'Moderate', 'Poor' and 'Bad')

$n = 231$	BENTIX	BOPA	BQI	Shannon
AMBI	$+0.911^{***}$	ns	$+0.458^{***}$	$+0.393^{***}$
BENTIX		ns	$+0.477^{***}$	$+0.709^{***}$
BOPA			ns	-0.365^{***}
BQI				$+0.522^{***}$

These tests were conducted on the pooled data of the two coastal systems (Arcachon and Marennes-Oléron Bays). Level of significance is indicated.

ns Not significant, $p > 0.05$.

*** Highly significant, $p < 0.001$.

in Marennes-Oléron Bay, BENTIX and Shannon in Arcachon Bay and BQI and Shannon in the Seine Estuary (Table 5).

When considering the five EcoQ classes, most indices, with the noteworthy exception of the BOPA, showed significant correlations with each others (Tables 6 and 7). It meant that the BENTIX, BQI, Shannon diversity and AMBI indices basically ranked stations in the same way from worst EcoQ to best EcoQ. However, these results showed that BENTIX, BQI, AMBI and Shannon index basically differed in the range of EcoQ assessed to stations. As an example, using the same set of stations, AMBI would classify these stations from 'High' to 'Good' whereas BENTIX, Shannon index or BQI would classify this same set from 'High' to 'Bad' and that stations classified as 'Bad' by the latter BI corresponded to stations classified as 'Moderate' by the first BI. As a result, a manager's decision is highly dependent on the BI used to assess the EcoQ.

3.3. *Sources of variations in semi-enclosed coastal ecosystems*

Kruskal–Wallis' test showed that there was a significant difference of both sediment silt–clay content and duration of emersion between EcoQ classes assessed by the AMBI, the BENTIX and the Shannon index (Table 8). There was a significant linear positive correlation ($p < 0.05$) between AMBI values and silt–clay content. However, this hardly modified the decision between 'Acceptable' and 'Not acceptable'. In Arcachon Bay, the index values were also higher and the EcoQ classification worsened (Kruskal–Wallis test, $p > 0.05$, Table 8) in the intertidal compared to the subtidal. As a consequence, stations situated on the muddy sediments associated to *Z. noltii* seagrass beds displayed poorest EcoQ (Fig. 4).

Table 7 – Results of the non-parametric Kendall's rank correlation coefficient-test between biotic indices-derived ecological quality (EcoQ) status classifications (with the five EcoQ classes defined by the WFD namely 'High', 'Good', 'Moderate', 'Poor' and 'Bad')

$n = 231$	BENTIX	BOPA	BQI	Shannon
AMBI	$+0.999^{***}$	ns	ns	ns
BENTIX		ns	ns	$+0.325^{*}$
BOPA			ns	-0.873^{**}
BQI				$+0.679^{***}$

These tests were conducted on the data of the Seine Estuary. Level of significance is indicated.

ns Not significant, $p > 0.05$.

* Significant, $p < 0.05$.

** Very significant, $p < 0.01$.

*** Highly significant, $p < 0.001$.

The behaviour of BENTIX was similar to that of AMBI, except that duration of emersion played a significant role in both coastal ecosystems. Intertidal sites were indeed considered as more degraded by this BI than in the subtidal leading to the classification of many intertidal stations as 'Moderate' or worse (Fig. 4). Moreover, BENTIX was more sensitive to vegetation cover, placing the *Z. noltii* stations in a 'Not acceptable' situation (Fig. 4).

Shannon index displayed a non-linear response to sediment silt and clay content (Fig. 4). Indeed, the EcoQ status slightly improved (although R^2 remain low) with silt and clay content but its value dropped with highest sediment silt and clay content (Fig. 4).

Except for the intertidal stations of Marennes-Oléron Bay where sediments did not modify the index value, BQI roughly behaved as BENTIX (and, to a lesser extent, as AMBI) but with this BI generally assessed poorer EcoQ than the two latter BI (Fig. 4).

In contrast with the other indices, BOPA assessed High EcoQ to the majority of stations in both bays, with hardly any correlation with silt–clay content (Fig. 4).

4. Discussion

The overall pattern of ecological quality status was very different according to the biotic index selected. As an example, according to the BOPA, most sites should be considered as displaying 'High' ecological quality status while Shannon index or BQI provided a much more degraded situation in all three sites, especially in the transitional waters of the Seine Estuary when considering the entire databases. With such a simplistic approach, the use of the five different biotic indices to describe the EcoQ added more complexity than clarity, impairing the accurate assessment of the EcoQ status of the benthic invertebrate communities. Such a problem was also identified by Quintino et al. (2006) in a study including three estuarine and coastal areas of the western coast of Portugal and by Labrune et al. (2005) in the Gulf of Lions. Indeed, our data showed that the classifications of EcoQ status derived from each index rarely agreed on a managerial point of view (i.e. 'Acceptable' versus 'Not acceptable' situations). However, when considering the five EcoQ classes of the WFD, correlations were generally significant with the noteworthy exception of the BOPA. It means that the AMBI, BENTIX, Shannon and BQI indices generally ranked stations in the same way but disagreed on the precise level of EcoQ assessed to each station by the different indices. Correlations between AMBI and BENTIX variations could be easily explained by the computational details of these indices. Both indices are based on the classification of species into ecological groups reflecting species sensitivity, tolerance or opportunism. AMBI considered five groups whereas BENTIX considered only two groups

Table 8 – Results of the non-parametric Kruskal–Wallis test comparing the environmental characteristics of stations (sediment silt and clay content, duration of emersion) between EcoQ classes derived from the five biotic indices for Arcachon Bay and Marennes-Oléron Bay stations

	n	Range of EcoQ	% Silt and clays *p*-level (K–W test)	Emersion *p*-level (K–W test)
Arcachon Bay (whole bay)				
AMBI	176	1–4	***	***
BENTIX	177	1–4	***	***
BOPA	176	1–3	ns	ns
BQI	94	1–5	***	***
Shannon	177	1–5	*	***
Arcachon Bay (intertidal only)				
AMBI	84	2–4	**	
BENTIX	85	1–4	***	
BOPA	85	1–4	ns	
BQI	65	1–5	***	
Shannon	85	1–4	**	
Arcachon Bay (subtidal only)				
AMBI	89	1–3	**	
BENTIX	89	1–4	**	
BOPA	89	1–3	*	
BQI	29	1–4	*	
Shannon	89	1–4	***	
Marennes-Oléron Bay (whole bay)				
AMBI	261	1–4	***	ns
BENTIX	261	1–4	***	***
BOPA	261	1–3	ns	ns
BQI	133	1–5	ns	ns
Shannon	262	1–5	***	***
Marennes-Oléron Bay (intertidal only)				
AMBI	126	1–3	**	
BENTIX	126	1–4	***	
BOPA	125	1–3	ns	
BQI	68	1–4	ns	
Shannon	126	1–5	***	
Marennes-Oléron Bay (subtidal only)				
AMBI	135	1–4	***	
BENTIX	135	1–4	***	
BOPA	133	1–3	ns	
BQI	64	1–5	*	
Shannon	135	1–5	***	

In a first approach the full dataset was used, on a second approach tests were performed dividing the datasets into subtidal and intertidal stations. Range of EcoQ is indicated with '1' corresponding to 'High' EcoQ, 2 to 'Good', 3 to 'Moderate', 4 to 'Poor' and 5 to 'Bad' EcoQ. Level of significance is indicated.

[ns] Not significant, $p > 0.05$.

[*] Significant, $p < 0.05$.

[**] Very significant, $p < 0.01$.

[***] Highly significant, $p < 0.001$.

with ecological groups 1 and 2 of the AMBI in the first group, and groups 3–5 of the AMBI in the second group (Borja et al., 2000; Simboura and Zenetos, 2002). Conversely, BQI and Shannon index are more or less directly based on alpha diversity measures, namely ES(50) and number of species, and the Shannon-Wiener diversity index, respectively. As a consequence, BQI values are closely related to diversity measures including dominance as stated by Labrune et al. (2005). When using our data, relationships between BQI and ES(50) values also proved to be very strong with a highly significant R^2 value of 0.753 between ES(50) and BQI, and a highly significant R^2 value of 0.618 between Shannon index values and BQI (not shown). Disagreement between the BQI and Shannon index mainly consisted into a different definition of thresholds between EcoQ classes. Correlation between BENTIX and Shannon index was more surprising as both indices do not account for the same variables. This correlation could be explained by the numerical dominance of a few species (such as *Hydrobia ulvae*) in intertidal muddy sites. The dominance pattern lowers the value of the Shannon index and the EcoQ derived from BENTIX as these dominant species belong to the tolerant/opportunist species considered by the BENTIX (ecological group 3 of the AMBI).

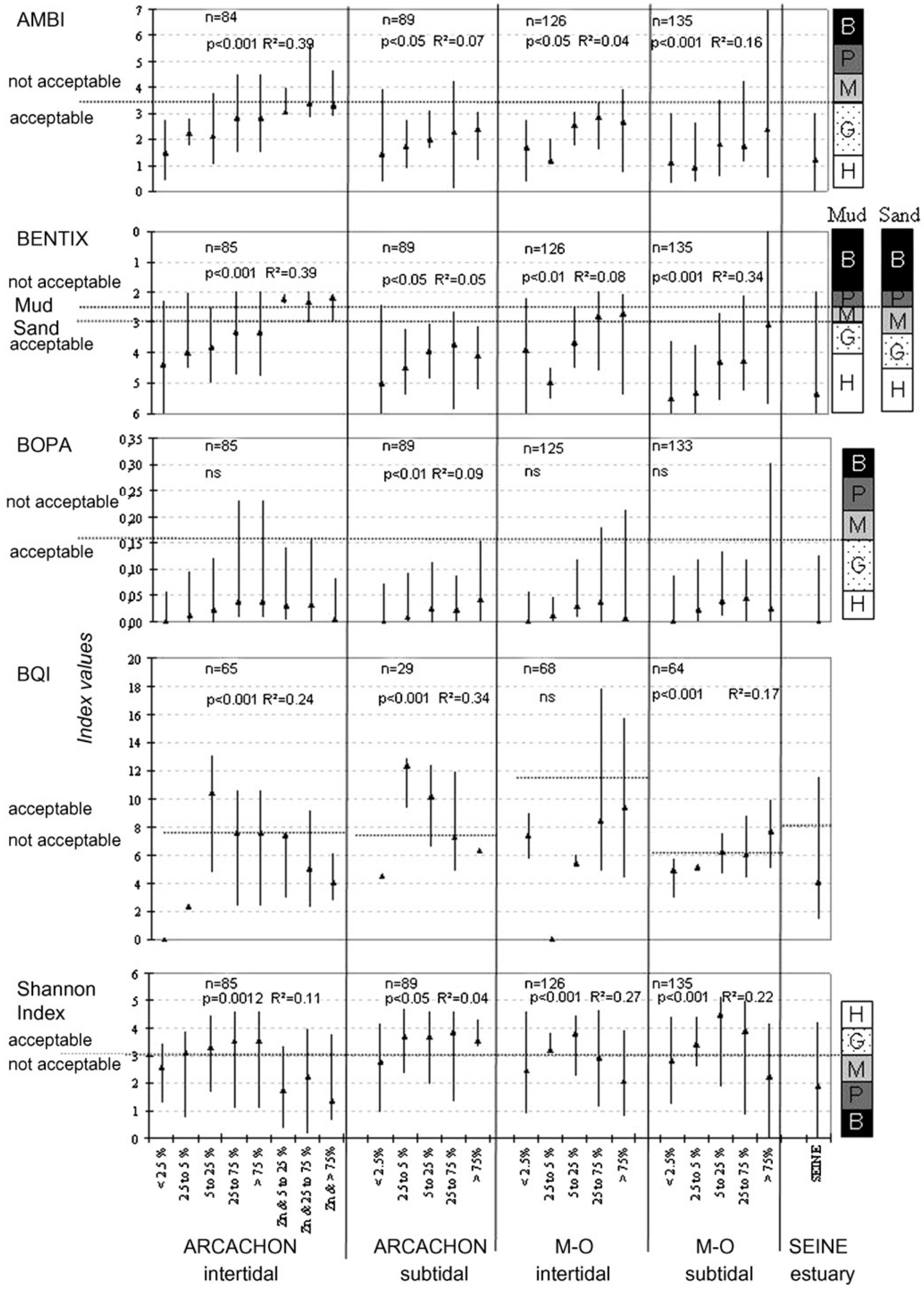

Fig. 4 – Median and range (minimum, maximum) of the biotic indices values by location (study site, intertidal, subtidal), sediment silt and clay content (for legibility, silt–clay content was divided into four classes of increasing silt and clay content: <2.5, 2.5–5, 5–25, 25–75 and >75%) and presence of the seagrass *Zostera noltii* (in Arcachon Bay only). Except for the BQI, EcoQ classes boundaries are indicated on the right side of the figure together with the threshold (dashed line) between 'Acceptable' and 'Not acceptable' status (see text for explanations). For the BENTIX, two scales are shown corresponding to M: muddy sites and S: sandy sites. For each location (intertidal or subtidal) the parameters of the linear regression (*n* = number of stations, *p*-level and R^2 coefficient of determination) between sediment silt and clay content and index values are given.

As a general result our study showed that habitat characteristics such as sediment silt and clay content and the intertidal or subtidal location of stations had significant influence on the EcoQ classification of stations by most of the BI studied here. In particular, intertidal and muddy stations were ranked as more degraded by most indices with the noteworthy exception of the BOPA. These parameters are known as key-factors structuring the benthic macrofauna and should thus be taken into account in any attempt of EcoQ assessment through the use of benthic community structure and composition. This study showed that habitat-related specificity must be taken into account, especially the sediment silt–clay content and the intertidal or subtidal location of habitat. In semi-enclosed environment, biotic index classifications varied according to the silt–clay content of the sediment. This result was not really surprising considering the historical development of the studied indices. BQI, AMBI and BENTIX development was based on the relationship between macrofaunal communities and gradients of increasing organic matter input related to either urban effluents or eutrophication processes (Pearson and Rosenberg, 1978; Glémarec and Hily, 1981; Grall and Glémarec, 1997; Borja et al., 2000; Rosenberg et al., 2004). It was thus not surprising that in muddy environments, where sediment organic matter is naturally high, such indices displayed limitations despite their wide applicability to various sources of impact (Borja et al., 2003; Salas et al., 2004; Muniz et al., 2005; Muxika et al., 2005). As a consequence, these indices express worse quality in naturally muddy environments. The fact that Shannon index had a slight tendency to increase in finer sediments is due to the importance of species richness and to the lack of ecological considerations in the formulae. This index will always increase with species richness, although such tendency is not necessarily correlated with good water quality. This phenomenon was noted by different authors (e.g. Dauvin, 2005; Quintino et al., 2006) but few studies have addressed this particular issue. With regard to these observations, the case of *Z. noltii* beds where the sediment silt–clay content is high (Blanchet et al., 2004) and which were classified as ‘Moderate’ or even ‘Poor’ (Fig. 4) by most indices was particularly demonstrating. Indeed, extensive intertidal seagrass beds are considered elsewhere as indicators of a good environmental quality with respect to eutrophication (Tagliapietra et al., 1998; Sfriso et al., 2001; Salas et al., 2004).

Finally, our study evidenced the effect of emersion on these biotic index values and classification (Fig. 4). This environmental factor is a source of natural stress for aquatic species (Cottet et al., in press). Species adapted to emersion usually become dominant in such an environment and biotic indices such as AMBI, BENTIX or BQI classify these communities as of a low EcoQ status. It is also important to highlight that most BI used in this study were originally developed for subtidal communities. For intertidal environments, the thresholds between EcoQ classes should be revised and ‘Acceptable’ and ‘Not acceptable’ redefined.

The assessment of the EcoQ status of the Seine Estuary was problematic, as we were unable to determine which part of biotic index variability was attributable to pollution-induced perturbations and which part to habitat characteristics. Moreover, using the BOPA, AMBI and BENTIX classifications, the Seine Estuary appeared in a less degraded condition than the two coastal lagoons studied here. This is in complete contradiction with what is known about the low pollution levels of these sites compared to that of the Seine Estuary (Dauvin et al., 2005, 2007). In contrast, the BQI and Shannon indices classified the Seine Estuary as of lower ecological quality status, which was more consistent with the pollution level of this site. However, in such transitional waters, the salinity variation effect has to be taken into account as shown by Zettler et al. (2007) in the Southern Baltic Sea.

In contrast with the other BIs tested here, the BOPA showed relative independence to the habitat characteristics studied here. Indeed this index is not based on the same ecological model of sensitivity/tolerance of species to increasing organic matter input. This index was primarily developed to assess the impact of oil spills on benthic invertebrate communities, as amphipods, the main component of BOPA, are recognised to be sensitive to hydrocarbons (Gomez Gesteira and Dauvin, 2000, 2005; Dauvin and Ruellet, 2007). As a consequence, it did not carry the same bias than the AMBI, BENTIX and BQI for its adaptation to naturally muddy sites.

5. Conclusions and recommendations

This study highlighted some limitations of currently available biotic indices for the implementation of the WFD in particular biotopes occurring in semi-enclosed coastal ecosystems and transitional waters and the need to adapt these biotic indices to habitat specificity. This implies that (1) reference conditions should be determined for each type of habitat and (2) thresholds between EcoQ classes should be adjusted. The definition of reference condition is required by the WFD. The type of habitat and habitat-specific definition of reference conditions is gradually being included in current development of bio-assessment tools. It is the case with the AMBI with the recent development of the Multivariate AMBI (M-AMBI). This tool accounts for reference conditions and includes Shannon-Wiener diversity index, number of species and AMBI for assessing EcoQ (Borja et al., 2007; Muxika et al., 2007). Concerning the definition of thresholds, one main issue deals with the definition of intervals between EcoQ classes. As an example, Rosenberg et al. (2004) used equal sized intervals for the definition of their EcoQ classes based on BQI. This way of defining classes remains highly subjective and cannot be considered as satisfactory because it carries very few ecological meaning. On the other hand, Muxika et al. (2005) defined EcoQ classes on a more ecologically meaningful basis. AMBI was indeed scaled according to the shifts in dominance pattern of the five ecological groups they defined. However, the new M-AMBI defines EcoQ classes in a different way with the risk of losing the ecologically meaning of the former classification of the AMBI (see Muxika et al., 2005; Borja et al., 2007). Moreover, on a more practical approach, scientists have to carefully assess the threshold between what is an ‘Acceptable’ state for benthic communities and what is not (Dauvin, 2007) which should be translated, on a manager point of view, as: where do we need to spend resources to restore the ecosystem and where do we do not? It means that, following the WFD, the threshold between the ‘Good’ EcoQ status and the ‘Moderate’ EcoQ status has to be very carefully defined by the scientists. We think that some of these problems may be partially solved by integrating several of the BIs used here (e.g. the AMBI and the BOPA, which seem to generally perform better in the case of our study sites) into a multi-criteria approach such as those developed in the United States (Weisberg et al., 1997; Eaton, 2001; Llansó et al., 2002a,b; Ranasinghe et al., 2002). These approaches, like the M-AMBI, would better fit the WFD requirements (Muxika et al., 2007) because they include other metrics describing the benthic community integrity (e.g. abundance, biomass, diversity or tropic guilds). In such an approach, one may be able to define, for each metric or BI, what is not significantly different or do not depart from natural background variability and classify it as 'Acceptable'. 'Not acceptable' state would be defined for each metric when measured values would be significantly different or depart from natural background variability. Combining the results for each metrics properly would ease to define than the five-level EcoQ classes of the WFD (Llansó et al., 2002b; Aubry and Elliott, 2006; Dauvin, 2007) based on the EcoQ ratio required by the WFD (Borja et al., 2007). Finally, we think that bimodal response of metrics and BIs have to be considered. This means that one should not always interpret the direction of variation of a given metric (e.g. AMBI, H') as a degradation (if the index increases (AMBI)/decreases (H')) or a restoration (if the index decreases (AMBI)/increases (H')) but instead use the different metrics as indicators of change. This last point may allow, in theory, to assess habitat change in a given ecosystem, which is one of the perturbation that has not yet receive much attention despite its importance, particularly in estuarine ecosystems (Dauvin, 2007).

Acknowledgements

Authors wish to thank every people who, at one moment or another, provided valuable help in the sample collection in the field. We would also like to thank two anonymous referees for their critical review of the first version of the manuscript and for their useful comments. We would also like to thank J.-C. Granger for helping us to improve the quality of the first version of the manuscript. Benthos sampling was financed by Syndicat Mixte du Bassin d'Arcachon and UMR EPOC for Arcachon Bay, by Conseil Général de la Charente-Maritime and Ifremer for Marennes-Oléron Bay and through the Seine-Aval programme coordinated by the *Haute Normandie* Region for the Seine Estuary. This work was supported by the French Ministry of Ecology and Sustainable Development (MEDD) through the QuaLiF project ("Directive Cadre Européenne sur l'Eau", resp.: X. de Montaudouin) from the LITEAU 2 scientific programme.

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AQUATIC CONSERVATION: MARINE AND FRESHWATER ECOSYSTEMS

Aquatic Conserv: Mar. Freshw. Ecosyst. **21**: 462–471 (2011)

DOI: 10.1002/aqc.1206

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

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ABSTRACT

1. 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.

2. 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.

3. 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.

4. 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.

Received 28 October 2010; Revised 6 June 2011; Accepted 8 June 2011

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

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), molluscs (Rodney and Paynter 2006), polychaetes (Moore *et al.*, 1998; Pawlik, 1998; Dubois, 2003) or bryozoans (Cranfield, 2003) are able to build reefs in certain environmental conditions. Many of these species form highly variable physical habitat and along a 'reefiness' gradient (Hendrick and Foster-Smith, 2006) not all of them justify being classed as a 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 (Wilson, 1971; Achary, 1974).

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Biogenic reefs play key functional roles in ecosystems and contribute to physical and biological processes 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* (i.e. reproduction, larval, development and behaviour; Wilson, 1929, 1968, 1970), more recent studies have investigated the ecological and functional roles of the reefs. 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 more typical of other coastal and deeper water environments.

Sabellaria reefs are also highly vulnerable structures and subject to various direct and indirect human pressures (Dubois *et al*., 2002, 2006; Le Cam *et al*., 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 being 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 (Holt *et al*., 1998; Godet *et al*., 2008). The primary aim of this study was 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 describe the reef status evolution accurately and to provide valuable information to stakeholders when determining adapted conservation strategies.

MATERIAL AND METHODS

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 (3 mm to 25 mm year^{-1}) 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 parallel to the 0 m line and facing intensive mussel cultures (Figure 1). Since 2003, new concessions have been granted in an effort to restructure the activity in close proximity to the reef.

Reef dynamics

Different morphological stages, as defined in Dubois *et al*. (2002) characterize 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 human disturbance, structures can regress towards degraded forms (named degraded ball-shaped structures or degraded platforms depending on the initial stage).

Sedimentary and biological data collection

In order to assess differences between the reef and the surrounding sediments, a stratified sampling design for sediment samples was used. Sediment samples were collected 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, $n = 12$) areas 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 sample consisted of a core (10 cm^2, 10 cm deep) for sediment characterization, with its position determined using a GPS, plotted into a GIS (Geographic Information System).

Biological sampling was carried out using a regular grid consisting of 196 squares (each 75 × 75 m), 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

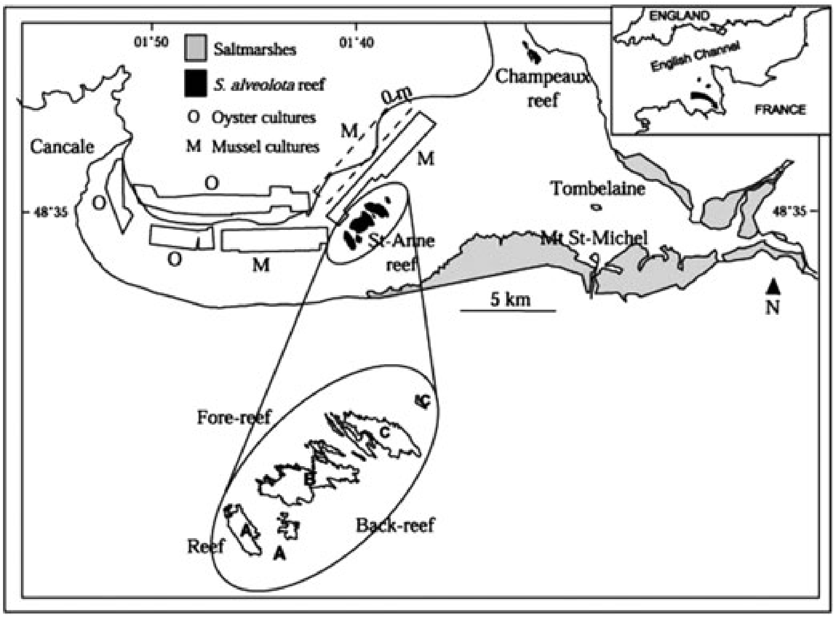

Figure 1. Overview of the Bay of Mont-Saint-Michel and location of the Sainte-Anne reef. Mussel culture areas represented by dotted lines correspond to recently added plots (2003).

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% cover), the ratio of each developmental stage of the reef (scoring 0 for absence to 10 for 100% 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 characteristics of each grid cell was also recorded. Moreover, within each 75 × 75 m grid cell, 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 percentage cover (scoring from 0 for absence to 10 for 100%) of the two main epibionts colonizing the reef, i.e. oysters, *Crassostrea gigas* and mussels, *Mytilus galloprovinciallis*.

Data analysis

In order to simplify the results analysis, the reef was divided into three sub-reefs (A, B, and C, Figure 1). Sediment samples were washed with distilled water, given 24 h 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, 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 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 (<63 µm) 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 coverage, 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 dependent 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 ($n = 160$).

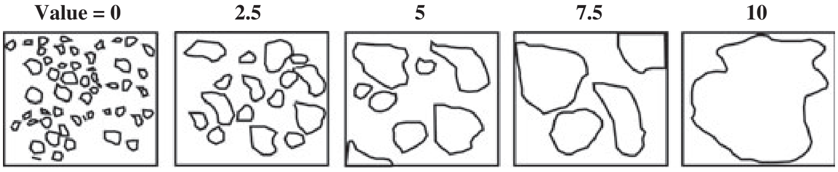

Figure 2. Fragmentation scale of *Sabellaria alveolata* reef and associated score. Values assigned to stages are used for the HI estimates.

Definition of Health Status Index (HI)

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

$$\mathrm{HI} = \mathrm{FD} + (\mathrm{IB} + \mathrm{CB} + \mathrm{P{-}DIB{-}DP{-}OC{-}MC}) \times \mathrm{RC}$$

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 (>20), intermediate (between 20 and 2.5) and bad (<2.5) Extreme values (positive (110) and negative (−200)) remain theoretical and have never been observed on *S. alveolata* reefs.

RESULTS

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: $t_{(75)} = -32.3261$, $P = 2.2 \times 10^{-16}$). The percentage of silt (<63 μm) in 2001 was significantly lower (4.66%, $n = 38$) than in 2007 (8.74%, $n = 38$) (t-test: $t_{(75)} = -1183.975$, $P = 2.2 \times 10^{-16}$) (Figure 3). The heterogeneity of the sediments in the reef area was confirmed with a 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 with 2007 (369 μm, $P = 2.2 \times 10^{-16}$). The percentage of silt in 2001 (3.00%) was significantly lower than in 2007 (8.39%) ($P = 2.2 \times 10^{-16}$). 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 ($P = 8.37 \times 10^{-16}$). A significant but weak increase of silt occurred in this zone (4.25% in 2001 and 5.19% in 2007; $P = 2.2 \times 10^{-16}$). For the back-reef zone, a significant decrease in mean grain size was found between 2001 (313 μm) and 2007 (265 μm) ($P = 2.2 \times 10^{-16}$) and a significant increase in silt percentage between 2001 (6.69%) and 2007 (13.50%) ($P = 2.2 \times 10^{-16}$). 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.

Biological and morphological changes

Reef general characteristics

The mean reef coverage in 75 × 75 m grid cells increased significantly between 2001 and 2007 (27.6 ± 16.8 in 2001 versus 36.0% ± 14.1% in 2007; $t = 4.91$, $P = 1 \times 10^{-4}$). 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 parts located on the south-east zones of the reefs, facing the coast (Figure 4). 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 in both 2001 and 2007, fragmentation levels had significantly increased over the years across the entire reef ($Z = 5.03$, $P = 1 \times 10^{-4}$). When sub-reefs were examined individually, however, fragmentation was found to have significantly increased only on zone B ($Z = 4.46$, $P = 1 \times 10^{-4}$).

Colonization 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, primarily in the south-east parts of sub-reefs B and C, compared with 9% in 2001, $Z = 2.16$ and $P = 0.030$). With the exception of one grid square, *M. galloprovincialis* was totally absent from 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 $P = 0.010$) to the benefit of the Pacific oyster *Crassostrea gigas*. In places with high mussel densities there was low oyster densities, and vice versa.

Table 1. Ecological quality ratio (EQR) values and ecological status associated with the HI index. Theoretical minimum and maximum values are −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	

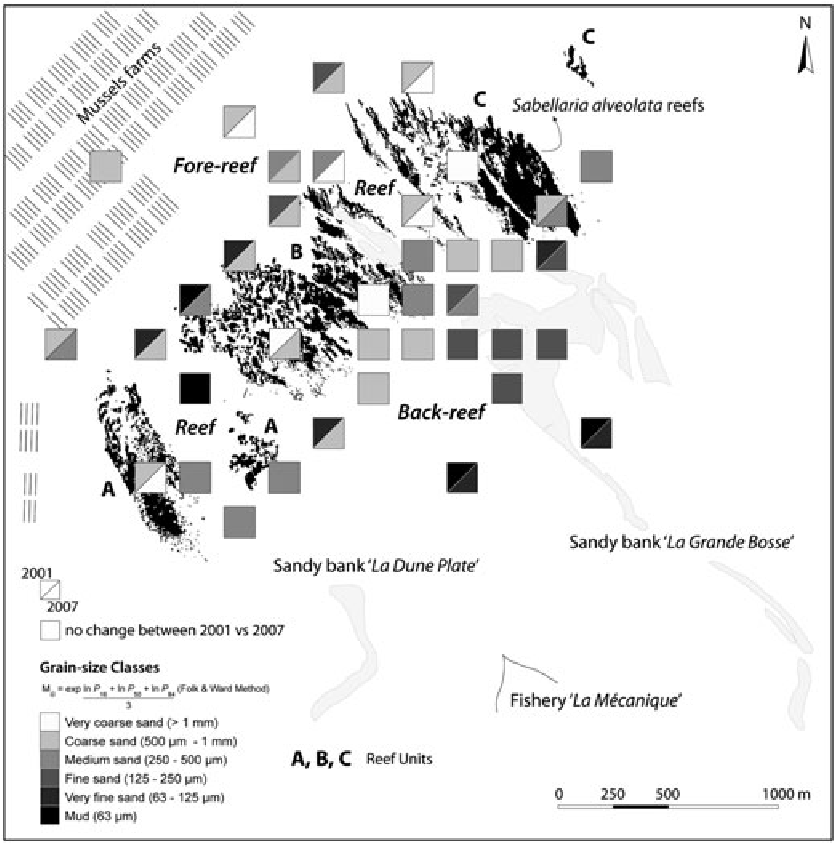

Figure 3. Sedimentary changes between 2001 and 2007 observed at the Sainte-Anne reef.

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 had spread from sub-reef A ($Z = 1.15$, $P = 0.249$, ns) to B (6.68, $P = 1 \times 10^{-4}$). Sub-reef C remained largely free of oysters, although rare spots were colonized by oysters, reaching densities of 60–90 ind m^{-2}.

Health status

In 2001, 35.2, 38.5 and 26.3% of total grid squares were classified as bad, intermediate, and good ecological status, respectively, against 38.9, 25.7, and 35.4% in 2007. When all grid cells were considered together, the average HI was 8.1 and 2.6 in 2001 and 2007, respectively ($Z = 1.50$, $P = 0.132$), i.e. both were of intermediate ecological status. In 2001, sub-reefs B and C were in a better state (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 good status (average HI = 22.0) in 2007. In 2007, degradation status was highly correlated with the density of *Crassostrea gigas* (−0.723)

Table 2. Results of paired *t*-tests between reef sectors and between 2001 and 2007 for sediments surrounding the Sainte-Anne reef

	x	σ	t	dl	P
Fore-reef					
M_G µm (2001)	753.52	310.45	−19.3511	21	$=7.246 \times 10^{-15}$
M_G µm (2007)	369.45	276.89			
% <63 µm (2001)	3	6.23	−822.664	21	$<2.2 \times 10^{-16}$
% <63 µm (2007)	8.39	15.28			
Reef					
M_G µm (2001)	703.91	483.45	−15.8254	29	$=8.37 \times 10^{-16}$
M_G µm (2007)	693.14	434.76			
% <63 µm (2001)	4.25	13.58	−768.4201	29	$<2.2 \times 10^{-16}$
% <63 µm (2007)	5.19	14.91			
Back-reef					
M_G µm (2001)	313.56	191.27	−38.3135	23	$<2.2 \times 10^{-16}$
M_G µm (2007)	265.12	249.61			
% <63 µm (2001)	6.69	13.79	−552.492	23	$<2.2 \times 10^{-16}$
% <63 µm (2007)	13.50	21.52			

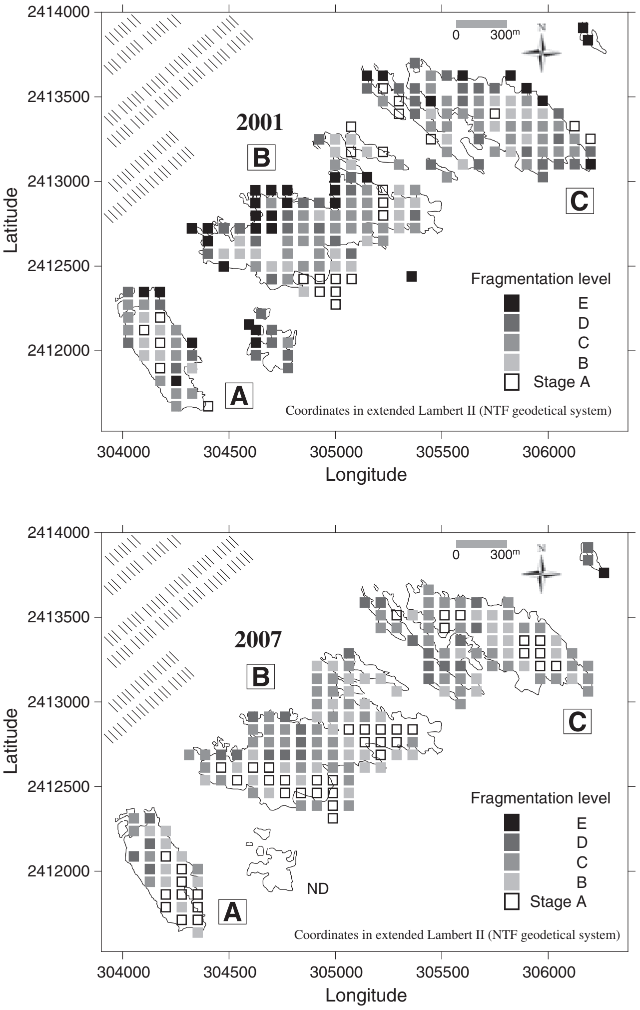

Figure 4. Fragmentation levels observed in 2001 and 2007 (ND = no data). Dotted lines (top left corner) represent mussel bouchots.

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.

DISCUSSION

There is a great 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 *et al*., 2001). The case for effective conservation management of *S. alveolata* reefs is therefore strongly supported, considering the vulnerability of the reef (Dubois et al., 2002).

Evolution of the sedimentary environment

The evolution of the reef environment is summarized in Figure 7. Additional field observations showed that the back-reef sand banks (called 'la Grande Bosse' and 'la Dune Plate'; Figure 3) grew rapidly and shifted landwards (50 to 100 m 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 important role in storing 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 – colonized by *Lanice conchilega* (another tube-building polychaete) – indicate that annelids may modify the texture and the distribution of intertidal sediments because of

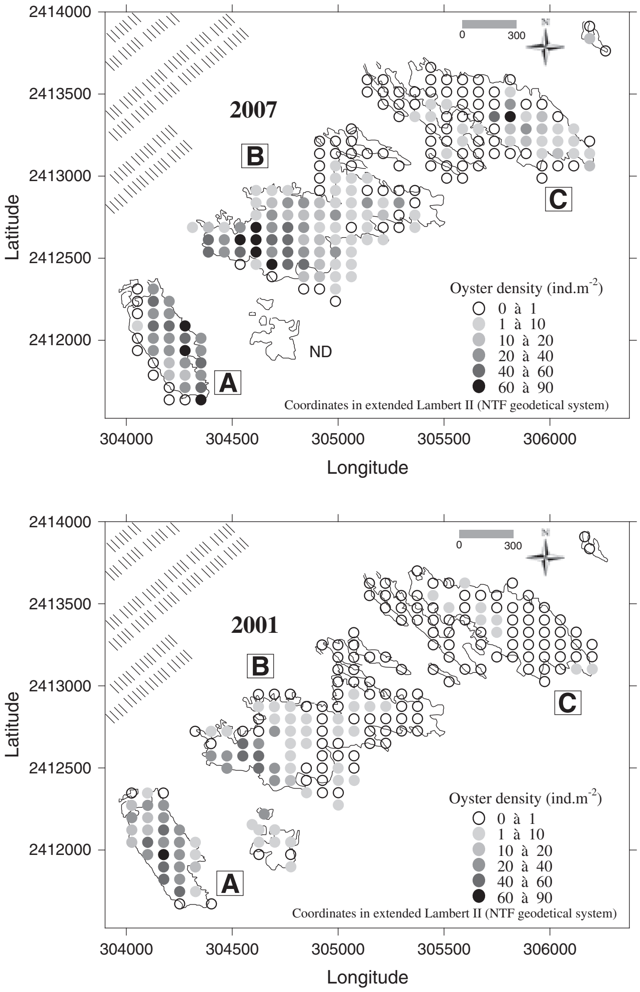

Figure 5. Oyster density (ind.m^{-2}) in 2001 and 2007 (ND = no data). Dotted lines (top left corner) represent mussel bouchots.

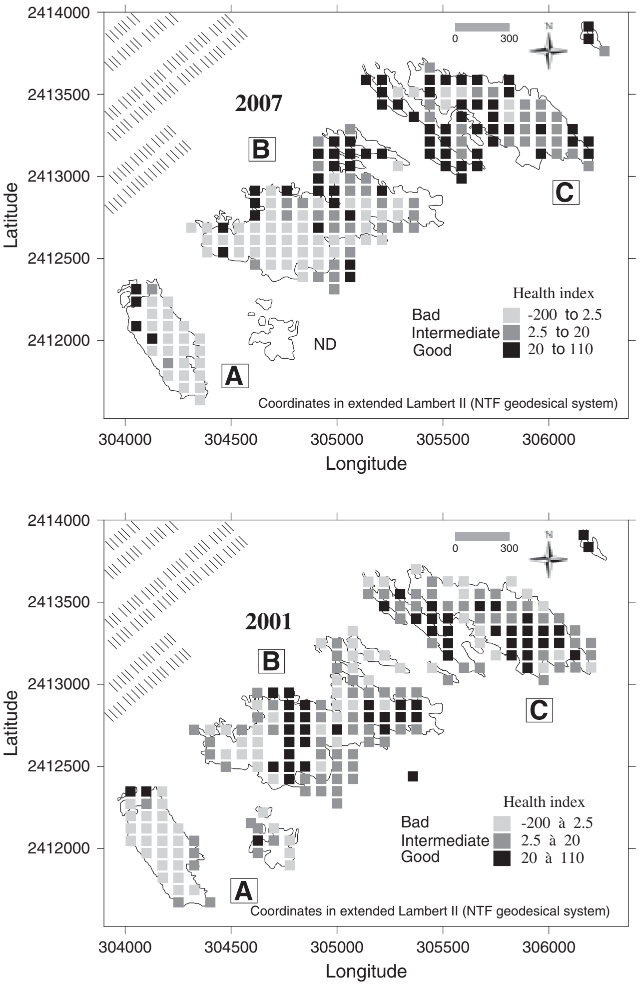

Figure 6. Health index observed in 2001 and 2007 (ND = no data). Dotted lines (top left corner) represent mussel bouchots.

their ability to trap and/or concentrate particles of specific mineralogy and grain size (Callaway *et al*., 2010; Godet *et al*., 2011).

Evolution of the reef health status

In line with the observed sedimentary changes, the different descriptors of reef health status, integrated in the HI equation, 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 were strongly degraded and were therefore assigned bad status whereas sub-reef C evolved towards a better health status (from intermediate to good). Paradoxically, investigations of biodiversity associated with 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 for the 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 reaches its maximum height and higher tube density. In that perspective, a combination of all reef evolution stages is a way of assuring enough *Sabellaria* density to allow maintenance and the proper renewal and evolution of 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 over 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 characteristics allowed larval retention at the bay scale and facilitated larval exchanges between the reef of Sainte-Anne and that 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 to both sustain itself and recolonize 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.

Understanding the main factors adversely affecting reef health status

Beyond the natural dynamics of the reef, several hypotheses may explain the observed changes in the reef dynamics and its associated health status. These factors relate to colonization of the reef surface by epibionts and their recreational fishing and to the implantation of new mussel farming structures and their consequences for trophic competition within suspension-feeding species.

Influence of reef colonization 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) for 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 has led to high abundances of cultivated oysters (5000 tons) and mussels (12 000 tons) spatially concentrated in areas close to the reef. Such human activities could indirectly affect *Sabellaria* reef evolution by inducing high larval mortality and subsequently reducing larval supply owing to filtration pressure, as hypothesized in Dubois *et al*. (2007) and recorded in wild mussel beds by Lehane and Davenport (2004) and 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

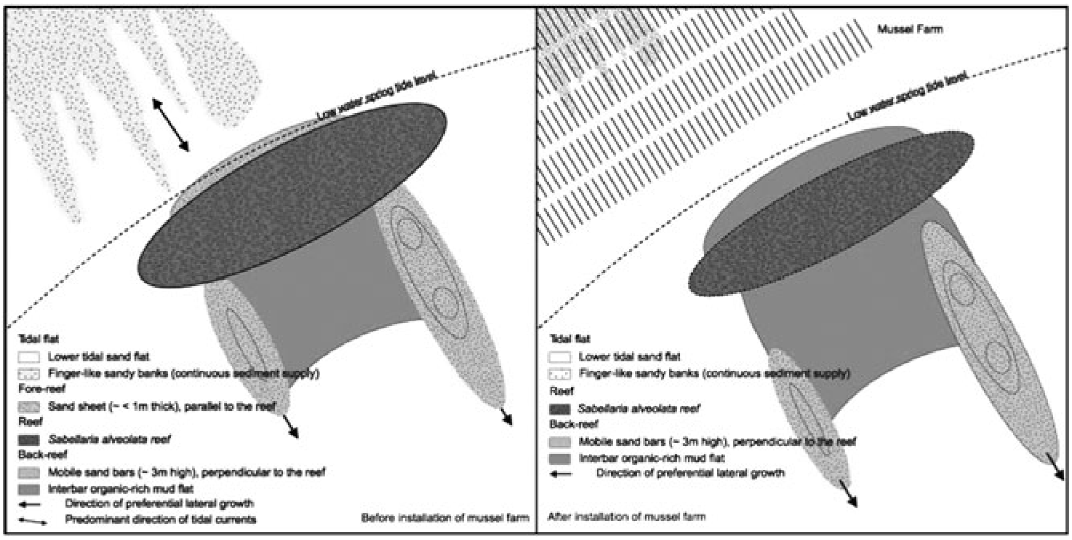

Figure 7. Biosedimentological model of a *Sabellaria alveolata* reef as based on the Sainte-Anne reef of the Bay of Mont-Saint-Michel.

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 colonize 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 occurrence also results in direct human pressure generated by oyster collection (e.g. destruction of reef blocks and surface scrapping) and associated trampling. Managing human activities close to the reef is a major issue that needs to be addressed by decision-makers. Furthermore the collection of species such as *Venerupis saxatilis* and the scallop *Chlamys varia* that live in reef crevices, which can also lead to reef alteration, should be subject to management measures. Gleaning with gears such as iron bars, chisels, etc., breaks ball-shaped structures and platforms and alters the reef structure. Such destruction of the reef induces fragmentation of the habitat. The conservation challenge is to avoid irreversible habitat alteration and decline of the reef, which would induce a loss of biological diversity on a large scale and potentially have dramatic consequences for other marine habitats, as reported by Thrush *et al*. (2008).

Implantation of new mussel farming structures

A modification of the shellfish farming scheme was completed in 2006. Farm 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, a decrease of mean grain-size was observed, higher in the fore-reef area. The new scheme has resulted in several problems; first, an increase of suspended particulate matter (organic and inorganic) has affected the filtration rate of *S. alveolata* (Dubois *et al*., 2009) by abrading feeding organs and clogging up the tubes. Second, the decrease of current velocity has increased the sedimentation and decreased sand grain re-suspension leading to a decrease in tube-building activity, since the tubes are built by the polychaetes by catching sand particles drifting near their tube aperture.

Influence of trophic depletion

To understand the functioning of the trophic food web 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 the *S. alveolata* reef at 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 in mussel growth would occur because of 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 observed reef regression.

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

Contrary to the UK, where *S. alveolata* reefs have benefitted 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 extent 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 motorized traffic 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

We wish to thank Carey G. Gelpi (Louisiana State University) and Amelia Curd (IFREMER) for English editing as well as anonymous reviewers and Prof. S. Hawkins for their helpful comments.

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Estuarine, Coastal and Shelf Science 92 (2011) 472–479

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Influence of stability and fragmentation of a worm-reef on benthic macrofauna

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ARTICLE INFO

Article history:
Received 21 June 2010
Accepted 13 February 2011
Available online 18 February 2011

Keywords:
reefs
zoobenthos
stability
fragmentation
tidal flats
Bay of the Mont-Saint-Michel

ABSTRACT

In coastal areas, reef-builder worms often are bio-engineers by structuring their physical and biological environment. Many studies showed that this engineering role is determined by the densities of the engineer species itself, the highest densities approximately corresponding to the most stable areas from a sedimentological point of view, and hosting the richest and the most diverse benthic fauna. Here, we tested the potential influence of the spatio-temporal dynamics and the spatial fragmentation of one of the largest European intertidal reefs generated by the marine worm *Lanice conchilega* (Pallas, 1766) (Annelida, Polychaeta) on the associated benthic macrofauna. We demonstrated that the worm densities do have a significant positive role on the abundance, biomass, species richness and species diversity of the benthic macrofauna and that the reef stability also significantly influences the biomass and species diversity. Moreover, the reef fragmentation has significant negative effects on the abundance, biomass and species richness. In addition to *L. conchilega* densities, the stability and the spatial fragmentation of the reef also significantly structure the associated benthic assemblages. This study demonstrates the interest of "benthoscape ecology" in understanding the role played by marine engineer species from a spatial point of view.

1. Introduction

If landscape ecology has been traditionally restricted to terrestrial systems (Hinchey et al., 2008), few authors have demonstrated the interest of this discipline for marine systems (e.g. Robins and Bell, 1994; Garrabou et al., 1998; Teixidó et al., 2002; Zajac et al., 2003). In 2008, in a special issue of *Landscape Ecology* on marine and coastal applications in landscape ecology, the interest of this discipline for benthic systems has been highlighted through the concept of "benthoscape ecology" (Zajac, 2008). Benthoscape ecology is an application of Landscape Ecology to the benthic compartment, using remote sensing methods adapted to the marine realm (mainly sonar or aerial photogaphs and satellite imagery for intertidal or shallow-water areas) to identify and delineate different seascape units at the bottom of the ocean. These spatial units are then quantified using geometric or topological indices (McGarigal et al., 2002) and can be linked with ecological patterns or processes. Such an approach has potential for studying benthic habitats that can be easily mapped and monitored, including intertidal structured habitats (Godet et al., 2009a). Here, we used this method to understand the importance of spatio-temporal characteristics on the benthic biodiversity associated with an intertidal worm-reef.

Lanice conchilega (Polychaeta, Terebellidae) is a widespread marine species over Europe (Fauvel, 1927; Holthe, 1986) which occurs locally in high densities from a few hundreds to several thousands individuals per square metre (see Buhr and Winter, 1976), both in intertidal and subtidal areas. The habitats structured by *L. conchilega* are named *L. conchilega* aggregations (e.g. Zühlke, 2001), *L. conchilega* beds (e.g. Godet et al., 2008) or *L. conchilega* reefs (e.g. Rabaut et al., 2009). At high densities, the species is considered as an "engineer species" (*sensu* Jones et al., 1994) because it has a structuring effect both on the physical and the biological compartments (Godet et al., 2008). Above a threshold density, current velocities decrease within the aggregations, deposition of fine sediment particles is facilitated (Friedrichs et al., 2000) and the species produces its own sedimentary structures constituted of mounds and depressions (Carey, 1987; Féral, 1989). The presence of *L. conchilega* aggregations is also positively

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doi:10.1016/j.ecss.2011.02.003

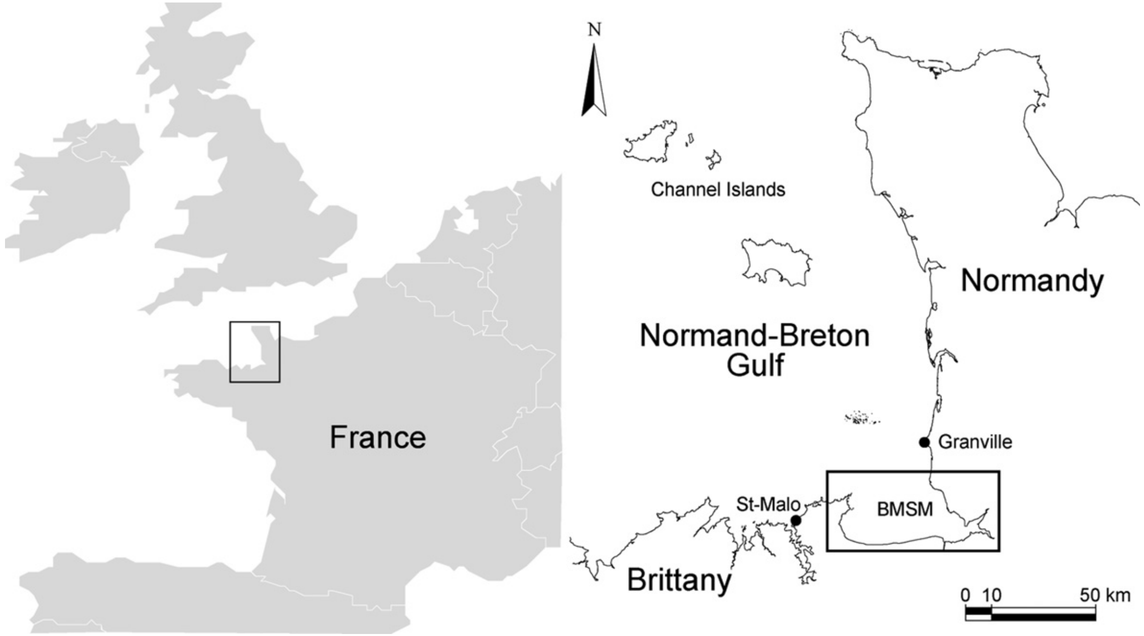

Fig. 1. Location map of the study site (BMSM, Bay of Mont-Saint-Michel).

correlated with the abundance and the specific richness of the associated macrofauna (Zühlke et al., 1998; Zühlke, 2001; Callaway, 2006; Rabaut et al., 2007; Van Hoey et al., 2008). Rabaut et al. (2007) recently developed the concept of a Russian-doll-like organisation pattern of the associated benthic communities: they found that similarity between individual samples of benthic macrofauna increases as the densities of *L. conchilega* increase as *L. conchilega* tends to restructure the species assemblages by expanding the available niche of several species.

Until now, the previous studies on the relationship between this engineer species and its physical and biological environment essentially focused on the influence of the densities of *L. conchilega* itself. No studies tested the potential influence of the stability of the reefs and their spatial structures on the associated fauna. In this paper, we tested together the potential influence of: (1) *L. conchilega* densities in the reef, (2) stability of the reef, (3) spatial structures of the reef both on: (1) the abundance, biomass, species richness and species diversity of the associated benthic macrofauna, and (2) the structure of the macrozoobenthic assemblages.

2. Methods

2.1. Study site

We selected one of the largest intertidal *Lanice conchilega* reefs in Europe, located in the Bay of Mont-Saint-Michel (BMSM), France (Fig. 1). The Bay is subjected to an extreme megatidal regime (tidal range up to 15.5 m during spring tides). Combined with very low beach slopes, the tides provide large intertidal sandflats, covering more than 250,000 ha. The study was carried out on the main reef of *L. conchilega* in the BMSM, close to the main reef of *Sabellaria alveolata*, which is located in the central part of the bay. The sedimentary environment of the bay is mainly controlled by tidal residual current patterns, typically characterized by an anticyclonic gyre off Cancale (NW of the Bay), a large cyclonic gyre around the Channel Islands and reduced drift of water masses to the north along the coast of Normandy. Gyres are partly disrupted under high wind velocity (Bonnot-Courtois et al., 2002). The reef of *L. conchilega* is located at the edge of the two juxtaposed hydrosedimentary systems, i.e. where the roughness is strongest. The central part of the bay is characterized by high bioclastic content (25–95%) and shows a gradual decrease in mean grain size from the subtidal to the intertidal zone (Bonnot-Courtois et al., 2004; Billeaud et al., 2007). In this area, the tidal flat is mainly formed by very fine sand to coarse carbonate-rich sand, with superficial deposits of silt. Sedimentation rates are higher (3–25 mm year^{-1}) in the intertidal zones and tend to decrease seawards.

2.2. Reef mapping

The reef was mapped on a Geographical Information System (GIS) (Arcview 3.2, ESRI, Redlands, CA, USA) via photo-interpretation processing (see Godet et al., 2008). The 1:10,000 colour aerial photographs come from surveys carried out in 1973, 1982, 2002 and 2008 by the French Geographic Institute (IGN). Each date corresponds to a specific map and to a specific layer in the GIS. The high quality of aerial photographs allowed for an accurate manual mapping of the reefs even without geoprocessed methods by an operator with a strong field control based on Ground Control Point acquisition

Table 1
Calculation of the stability level of the reef. "X" means that the reef is present.

1973	1982	2002	2008	Level of stability
				0
X				1
	X			1
		X		1
			X	1
X			X	2
X		X		3
	X		X	3
X	X			4
	X	X		4
		X	X	4
X	X		X	5
X		X	X	5
X	X	X		6
	X	X	X	6
X	X	X	X	7

Table 2
Class metrics ($n = 4$) used to quantify the landscape structure of the reef (from McGarigal et al., 2002).

Indice	Definition	Formula	Interpretation
Total area (ca)	Sum of the areas (m^2) of all patches of the corresponding patch type, divided by 10,000 (to convert to hectares).	$\sum_{j=1}^{n} a_{ij}(1/10,000)$ $a_{ij} =$ area (m^2) of patch ij	The area covered by the reef.
Patch density (pd)	Number of patches of the corresponding patch type divided by total landscape area (m^2), multiplied by 10,000 and 100 (to convert to 100 ha).	$(n_i/A) \times (10{,}000) \times (100)$ n_i, Number of patches in the landscape of patch type (class) i. A, total landscape area (m^2).	A simple measure of the reef fragmentation.
Mean perimeter-area fractal dimension (frac)	Two times the logarithm of patch perimeter (m) divided by the logarithm of patch area (m^2); the perimeter is adjusted to correct for the raster bias in perimeter.	$(2 \ln(0.25\, p_{ij}))/(\ln a_{ij})$ p_{ij}, Perimeter (m) of patch ij. a_{ij}, area (m^2) of patch ij.	A measure of the degree of complexity of *L. conchilega* patch forms.
Patch cohesion index (coh)	1 minus the sum of patch perimeter (in terms of number of cell surfaces) divided by the sum of patch perimeter times the square root of patch area (in terms of number of cells) for patches of the corresponding patch type, divided by 1 minus 1 over the square root of the total number of cells in the landscape, multiplied by 100 to convert to a percentage.	$(1 - (\sum_{j=1}^{n} p_{ij} / \sum_{j=1}^{n} p_{ij}\sqrt{a_{ij}})) \times (1 - 1/\sqrt{A})^{-1} \times 100$ p_{ij}, Perimeter of patch ij in terms of number of cell surfaces. a_{ij}, area of patch ij in terms of number of cells. A, total number of cells in the landscape.	A measure of the physical relationship between each patch of *L. conchilega*.

(dGPS). Densities of *Lanice conchilega* from ±250 ind m^{-2} can be detected on such aerial photographs (Callaway et al., 2010), so that the areas with densities equal or higher to this threshold were mapped as *L. conchilega* reef. All output maps are to a scale of 1:10,000 even if we zoomed up to 1:1,000 for the mapping process.

2.3. Quantifying stability

For a given ecological system, different types of stability can be distinguished (Callaway et al., 2010; modified from Grimm et al., 1999): constancy (the duration a system remains essentially unchanged); resistance (the capacity of a system to remain unchanged despite the presence of disturbance which could potentially change the system); resilience (the property to return to a reference state after a disturbance); and persistence (the property of a system to exist over long periods of time, and, contrary to the constancy, even with intermittent absence). Here, we quantified the stability of the reef through its persistence from 1973 to 2008. The four 1:10,000 maps of the reef (1973, 1982, 2002, 2008) were superimposed as different layers in the GIS to distinguish between seven levels of stability (Table 1) resulting in a 'stability map'. Then, this 'stability map' was divided into cells of 1 ha, and for each cell a 'stability index' was computed (stability index = % of the cell covering a specific stability level × specific level number). For example, in a cell for which 20% is covered by a stability index of 2 and 80% of a stability index of 5, its stability index will be: $20 \times 2 + 80 \times 5 = 440$. This index thus ranges theoretically from 0 (0×0 = no *Lanice conchilega* reef present in the cell from 1973 to 2008) to 700 (100×7 = *L. conchilega* reef covering the full cell in 1973, 1982, 2002 and 2008).

2.4. Quantifying L. conchilega densities

Lanice conchilega densities were examined within the reef in 2005, 2006, 2007 and 2008. Densities were estimated by taking numerical pictures of three 0.25 m^{-2} random quadrats in the middle of the 1 ha cells of the same grid used to quantify the stability of the reef. The number of intact tube-tops was counted on the pictures; the number of tube-tops is highly correlated with the number of individuals burrowed in the sediment (Ropert and Dauvin, 2000; Strasser and Pieloth, 2001; Zühlke, 2001; Callaway, 2003; Bendell-Young, 2006) and the error associated does not exceed 3% (Ropert, 1999).

2.5. Quantifying spatial structures

The spatial structures of the reef were examined with the 2008 map. In this map, two classes were considered: *Lanice conchilega* reef and sand. Spatial metrics were calculated only for the *L. conchilega* class within the cells of the same 1 ha grid used to quantify the stability of the reef. The same process was then performed for three different spatial extents: 0.75 ha, 0.50 ha and 0.25 ha cells (with the same cell centres). For each cell, and for each spatial metric, we calculated a mean metric for the three spatial extents. Calculations of spatial metrics were performed using the public domain software FRAGSTATS version 3.3 (McGarigal et al., 2002). While FRAGSTATS provides a large number of spatial metrics, we selected a subset of them (Table 2). We selected these metrics because: (1) they are not correlated with each other, (2) they correspond both to geometric and topologic indices, (3) their interpretation is easy and corresponds to ecological realities.

2.6. Sampling, sorting, identifying and weighting benthic macrofauna

Benthic macrofauna was sampled along the same 1 ha grid used to quantify the stability of the reef, but only one out of every two stations of each row of the grid was sampled + every station with *Lanice conchilega* densities ≥200 ind m^{-2} in 2008 (i.e. 80 stations). In each station, one core was collected (1/40 m^{-2}, 30 cm deep). Benthic samples were sieved in the field through a 1 mm mesh size and the biological material retained was then directly preserved in 4.5% buffered formalin. Once in the laboratory, samples were sorted and macrozoobenthos was identified to the highest taxonomic separation possible, usually species level. The values of the species richness (S), total abundance (N) and species diversity (H′) were calculated from the final macrozoobenthic database, excluding the species *L. conchilega* itself. Total biomasses were estimated by weighting their dry weight (60 °C for 48 h). The ash-free dry weight (AFDW) was calculated as a difference between the dry weight and the ashes (500 °C for 3 h).

2.7. Statistical analysis

All the statistical analyses were performed with R version 2.10.0 (R Development Core Team, 2009).

The relation between (1) biodiversity indices (abundance, biomass, species richness and species diversity of the benthic

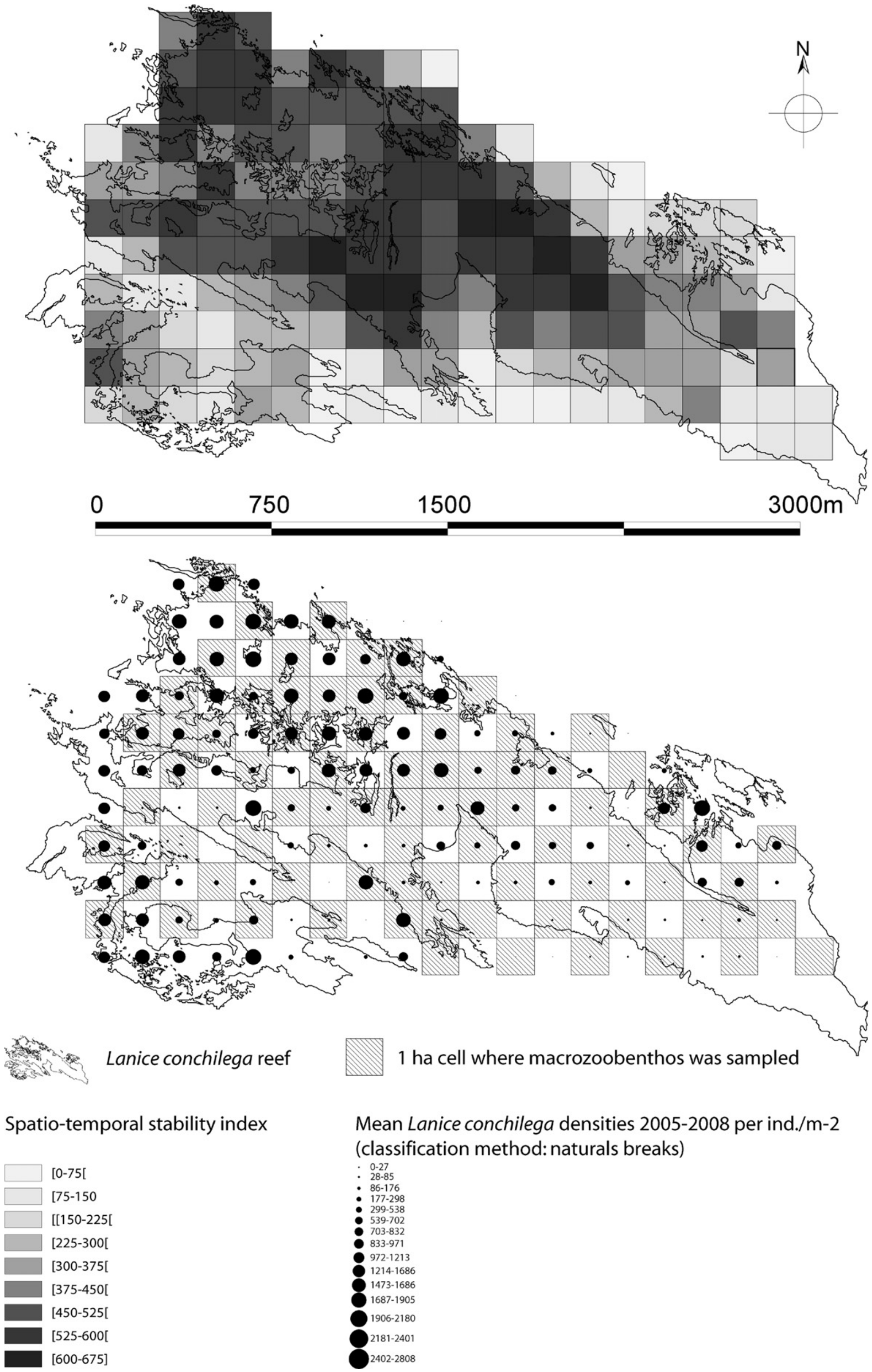

Fig. 2. Map of the *L. conchilega* reef, stability, *L. conchilega* densities and macrozoobenthic sampling design.

macrofauna), and (2) *L. conchilega* densities, spatio-temporal index, and spatial metrics, were analysed with multiple linear regression models. The best linear models were selected with the "regsubsets" function of the R package "leaps" which plots a measure of fit against subset size (see Miller, 2002). In other words, regsubsets is an algorithm that enables to select the best combination of factors that best 'explains' the variance of a variable.

To test the influence of *Lanice conchilega* densities, spatio-temporal index, and spatial metrics on macrozoobenthic assemblages, we used the R "MASS" and "vegan" packages. After a log $(x+1)$ transformation of the macrozoobenthic matrix, non-metric multidimensional scaling ordinations (nMDS) were performed after a computation of a Bray–Curtis similarity matrix, using the "metaMDS" function of the "MASS" packages (Oksanen, 2009). The "envfit" function ("vegan" package) was used to test the influence *L. conchilega* densities (log $(x+1)$ transformed, as macrozoobenhtic abundances), spatio-temporal index and spatial metrics of the macrozoobenthic asemblages (Oksanen, 2009). Factors were then plotted on the nMDS with the function "ordisurf" of the "vegan" package (Oksanen, 2009).

3. Results

3.1. Spatial and biological characteristics of the reef

In 2008, the reef covered 105 ha (Fig. 2), 134 ha in 1973, 68 ha in 1982, 193 ha in 2002. The mean *Lanice conchilega* densities from 2005 to 2008 were 1311.71 ind m^{-2} (±sd 1411.78), and maximal densities of 6700 ind m^{-2} were reached in the middle of the reef in 2007. The stability of the reef is positively correlated with the *L. conchilega* densities (R^2: 0.33, 316 DF, $p < 0.0001$) and the most stable parts of the reef are located approximately in the core area and vice versa (Fig. 2). Only one cell has a stability index of 0 (i.e. no *L. conchilega* present during the period).

A total of 13,806 macroinvertebrates representing 61 different species were recorded. The mean biomass is 49.69 g AFDW m^{-2} (±sd 50.43) including the species *Lanice conchilega*, and 26.81 g AFDW m^{-2} (±sd 36.22) without the species *L. conchilega*. One single benthic assemblage was identified (average similarity of the assemblage based on a Bray-Curtis similarity matrix, after a log$(x+1)$ transformation: 49.70%), dominated by the two bivalve species *Macoma balthica* (occurrence: 100%) and *Cerastoderma edule* (70%), and the two polychaetes *Nephtys hombergii* (96%) and *L. conchilega* (90%).

3.2. Influence of reef stability and spatial characteristics of the reef on the macrozoobenthic biodiversity

Lanice conchilega densities are positively correlated with macrozoobenthic abundance, biomass, species richness and diversity (Table 3). Reef stability is positively correlated with macrozoobenthic species diversity, and negatively correlated with biomass. Patch density is negatively correlated with macrozoobenthic abundance, biomass and species richness.

3.3. Influence of stability and spatial characteristics of the reef on the macrozoobenthic assemblage structure

The fitting factors ($R^2 > 0.25$) most explaining the macrozoobenthic assemblage structure are the stability of the reef, *Lanice conchilega* densities, then the total area index ($R^2 = 0.17$), the cohesion index ($R^2 = 0.16$), and, finally, the fractal dimension index ($R^2 = 0.08$) (Fig. 3; Table 4).

4. Discussion

4.1. Dense, stable and non-fragmented reefs host a higher biodiversity

The first new result comes from the positive effect of the stability of the reef on the species richness. This agrees with Zühlke (2001), Toupoint et al. (2008) and Godet et al. (2009b) demonstrating the low resilience of the macrozoobenthic assemblages associated with *Lanice conchilega* reefs. However, regression or disappearance of *L. conchilega* reefs – even for a short time – involves a rapid biodiversity loss, even if benthic fauna is able to recover quickly after a perturbation of a *L. conchilega* reef (Rabaut et al., 2008; Callaway et al., 2010). These previous studies had suggested that the biodiversity associated to the reef could be controlled by the stability of the reef itself, and probably more by the constancy of the reef (i.e. the duration a system remains essentially unchanged) than its persistence (i.e. the property of a system to exist over long periods of time, and, contrary to the constancy, even with intermittent absence). However, assessing the constancy of the reef requires a constant monitoring of the reef over time to be able to detect any potential modification or disappearance of the reef, an almost impossible task. Hence, in our study, we

Table 3
Best regression models for macrozoobenthic abundance, biomass, species richness and diversity in relation to *L. conchilega* densities, reef stability and reef spatial structures. $0 < p < 0.001$ (***); $0.001 < p < 0.01$ (**); $0.01 < p < 0.05$ (*). lan, mean *L. conchilega* densities 2005–2008 log$(x+1)$ transf.; stab, stability index; ca, total area; pd, patch density; coh, patch cohesion index.

Macrozoobenthic abundance (log$(x+1)$ transf.).
Residual standard error: 0.8362 on 75 degrees of freedom.
Multiple R-squared: 0.1982, adjusted R-squared: 0.1555, F-statistic: 4.635 on 4 and 75 DF, p-value: 0.002129.

	Estimate	Std. error	t value	Pr(>|t|)
(Intercept)	3.1895944	0.5572506	5.724	2.03e−07***
pd	−0.0002356	0.0001011	−2.330	0.02250*
coh	0.0085041	0.0065025	1.308	0.19493
stab	−0.0013106	0.0007544	−1.737	0.08646
lan	0.1833671	0.0552522	3.319	0.00140**

Macrozoobenthic biomass (log$(x+1)$ transf.).
Residual standard error: 0.355 on 75 degrees of freedom.
Multiple R-squared: 0.1726, adjusted R-squared: 0.1284, F-statistic: 3.91 on 4 and 75 DF, p-value: 0.006143.

	Estimate	Std. error	t Value	Pr(>|t|)
(Intercept)	1.280e−01	2.366e−01	0.541	0.59022
pd	−9.124e−05	4.294e−05	−2.125	0.03688*
coh	4.111e−03	2.761e−03	1.489	0.14063
stab	−9.674e−04	3.203e−04	−3.020	0.00345**
lan	6.666e−02	2.346e−02	2.842	0.00578**

Macrozoobenthic species richness (log$(x+1)$ transf.).
Residual standard error: 0.394 on 74 degrees of freedom.
Multiple R-squared: 0.2767, adjusted R-squared: 0.2278, F-statistic: 5.662 on 5 and 74 DF, p-value: 0.0001787.

	Estimate	Std. error	t Value	Pr(>|t|)
(Intercept)	1.585e+00	2.680e−01	5.915	9.54e−08***
ca	−9.125e−01	7.166e−01	−1.273	0.20687
pd	−1.346e−04	5.417e−05	−2.484	0.01525*
coh	5.321e−03	3.424e−03	1.554	0.12442
stab	4.228e−04	3.720e−04	1.137	0.25930
lan	7.368e−02	2.630e−02	2.802	0.00648**

Macrozoobenthic species diversity.
Residual standard error: 0.3634 on 76 degrees of freedom.
Multiple R-squared: 0.2548, adjusted R-squared: 0.2254, F-statistic: 8.662 on 3 and 76 DF, p-value: 5.146e−05.

	Estimate	Std. error	t Value	Pr(>|t|)
(Intercept)	1.004e+00	1.274e−01	7.887	1.81e−11***
pd	−5.571e−05	4.380e−05	−1.272	0.2073
stab	6.940e−04	3.043e−04	2.280	0.0254*
lan	4.913e−02	2.395e−02	2.051	0.0437*

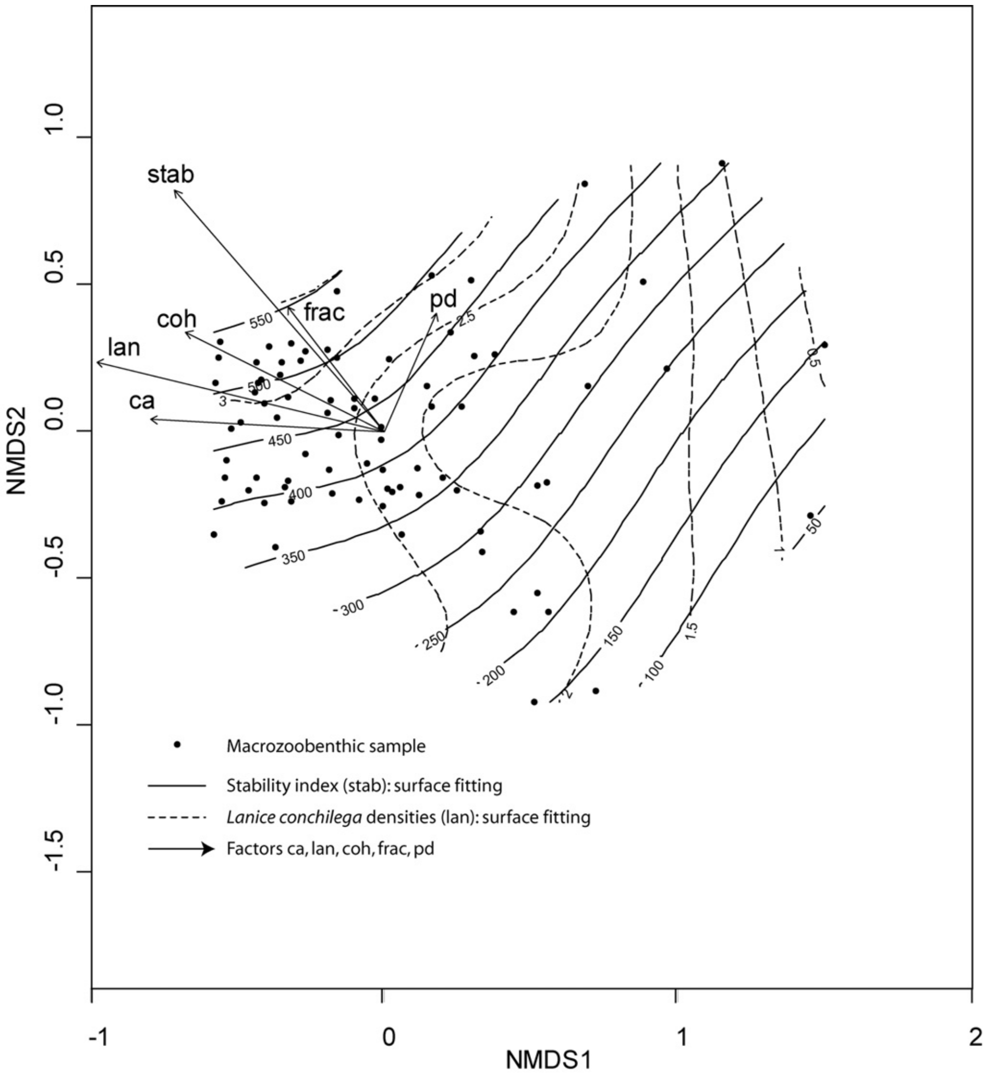

Fig. 3. nMDS plot of the macrozoobenthic abundance data ($\log(x+1)$ transformed) obtained in 80 samples and based on the Bray-Curtis similarity. Arrows represent the 6 factors significantly explaining the ordination and surface fitting represents the 2 factors best explaining the ordination ($R^2 > 0.25$). lan = mean *L. conchilega* densities 2005–2008 ($\log(x+1)$ transformed); stab, stability index; ca, total area; pd, patch density; coh, patch cohesion index; frac, mean perimeter-area fractal dimension.

used persistence as a proxy for the general stability of the reef as it is almost the only index that can be assessed using remote sensing methods (aerial photographs in our study). We expect that long-term persistence of the reef is highly correlated with long-term constancy of the reef as the most stable areas over long-term period are also likely to be the most stable over short-term periods. In the future, in addition to inter-annual persistence, it would be also interesting to assess the potential effects of the intra-annual persistence (seasonal changes) of the reef on benthic fauna.

The second new result is the negative influence of patch densities on the macrozoobenthic abundance, biomass and species richness. Patch densities can be viewed as a proxy of the reef fragmentation which is thus negative for the benthic macrofauna. This result has to be explored more thoroughly, in the context of a rapid development of human activities fragmenting *Lanice conchilega* reefs in European coastal areas. Beam-trawling (Rabaut et al., 2008) and clam cultivation (Toupoint et al., 2008; Godet et al., 2009b) are among human activities for which negative impacts on the fauna associated to *L. conchilega* reefs have been demonstrated. Such activities leading to a spatial fragmentation can thus also have an impact on non-directly impacted *L. conchilega* reefs by fragmenting them.

An unexpected result is the negative influence of the stability of the reef on the biomass although an additional analysis showed that this effect is mainly due to *Cerastoderma edule* biomass. By excluding *C. edule* from the total biomass we found no significant relation between the stability of the reef and macrozoobenthic biomass. The sampled *C. edule* corresponded to juveniles, which can form very mobile aggregations. In the Wadden Sea, Zühlke et al. (1998) also showed that the only macrofaunal species whose densities were not linked with *Lanice conchilega* aggregations was another species of bivalve (*Mya arenaria*), at a juveline stage.

4.2. Reef stability and benthoscape structures have a structuring effect on benthic assemblages

The structuring effect of *Lanice conchilega* on benthic fauna was demonstrated by several authors (Zühlke et al., 1998; Zühlke, 2001; Callaway, 2006; Rabaut et al., 2007; Van Hoey et al., 2008). Here, we highlighted that the stability of the reef can have a more structuring effect on benthic assemblages than *L. conchilega* densities. The other factors best explaining macrozoobenthic assemblages are mainly the total area index and the cohesion index, positively explaining the homogeneity of the assemblages. The most stable,

Table 4
Factors best explaining macrozoobenthic assemblages. The first two columns give direction cosines of the vectors, and R^2 gives the squared correlation coefficient. p-Values are based on 999 permutations: $0 < p < 0.001$ (***); $0.001 < p < 0.01$ (**); $0.01 < p < 0.05$ (*); $0.05 < p < 0.1$ (.). lan, mean *L. conchilega* densities 2005–2008; stab, stability index; ca, total area; pd, patch density; coh, patch cohesion index; frac, mean perimeter-area fractal dimension.

	NMDS1	NMDS2	R^2	Pr(>r)
stab	−0.646702	−0.762743	0.3278	0.001***
lan	−0.962755	−0.270377	0.2727	0.001***
ca	−0.996319	−0.085719	0.1692	0.001***
coh	−0.873883	−0.486135	0.1563	0.01**
frac	−0.584034	−0.811729	0.0809	0.042*
pd	0.400895	−0.916124	0.0545	0.121

dense, extended and cohesive parts of the reef thus host the most homogeneous assemblages.

4.3. Comparison with other benthic structured habitats

The positive effect of tube-building polychaete aggregations on benthic fauna is a well-known phenomenon, demonstrated for other species, such as *Owenia fusiformis* (Fager, 1964; Somaschini, 1993; Barnay, 2003) or *Diopatra cuprea* (Woodin, 1978). However, to our knowledge, Dubois et al. (2002) were the only authors demonstrating an effect of three discrete spatial structures of a worm-reef on the associated fauna (corresponding to three stages of the reef evolution: degraded reef stage, ball-shaped structures, platform stage). Thus, the quantification of benthoscape structures and their influence on the associated fauna applied to coastal worm-reefs is new.

In addition to kelp beds (e.g. Dayton, 1994), coral reefs (e.g. Aronson and Precht, 1995; Murdoch and Aronso, 1999; Grober-Dunsmore et al., 2008), mussel and oyster beds (DeAlteris, 1998; Smith et al., 2001), the major biogenic habitats studied from a benthoscape perspective concerned seagrass habitats (see the review of Boström et al., 2006). However, it is very difficult to compare our results on worm-reefs with the results obtained on seagrass. According to Boström et al. (2006) no clear patterns emerged when seagrass habitat patch size were tested among the most studied faunal groups, and seagrass habitat fragmentation effects on decapods, bivalves and fish have been inconclusive.

Coastal worm-reefs, such as *Lanice conchilega* reefs, but also those generated by *Sabellaria alveolata*, *Sabellaria spinulosa* or *Serpula vermicularis* seem to be convenient models to understand the influence of spatial characteristics of aggregative engineer species on the associated fauna. Consequently, contrary to soft-sediment benthoscapes without biogenic patches that are difficult to map and define (Zajac, 1999), such structured habitats can be easily mapped, monitored and their spatial structures can be easily quantified.

5. Conclusions

This study provides first results on the application of benthoscape ecology to worm-reefs and highlights the importance of stable and non-fragmented parts of the studied reef for macrozoobenthic biodiversity. However, these results cannot be directly generalised for all types of coastal worm-reefs and this approach should be also tested in the future on subtidal reefs (including subtidal *Lanice conchilega* reefs, the species being rather subtidal), less dense reefs or on other reef-building species. Benthoscape ecology applied to such coastal habitats is a promising approach in a conservation perspective. Yet, it enables to select the best areas to be conserved, including for example the most stable or less fragmented parts of a reef, and the quantification of the stability of *L. conchilega* aggregations is one of the key points to classify them as biogenic reefs (see Rabaut et al., 2009; Callaway et al., 2010). It may justify their potential conservation in Europe as, from a conservation perspective, long-lived and stable biogenic concretions should have a greater value than comparable ephemeral habitats (Callaway et al., 2010). Moreover, benthoscape ecology approach is a suitable methodology to better investigate the indirect impacts of human activities on the fragmentation of coastal habitats. In the future, it would be of value to test for the potential effects of stability and spatial structures of structured coastal habitats: (1) at different time scales to understand how temporal changes in spatial structures may influence biodiversity, (2) at different spatial scales and different taxonomic groups to assess how different species may be influenced by different fragmentation levels at different spatial scales. Moreover, the influence of spatial structures of coastal habitats could be investigated in the future on functional diversity, this component of biodiversity being recently investigated for the macrozoobenthic compartment (see Bremner, 2008). Finally, it would also be of value to test the potential effects of 3D benthoscape structures of structured coastal habitats, for example using accurate remote sensing tools such as the LIDAR (Noernberg et al., 2010).

Acknowledgements

Thanks to all volunteers who helped us for field sampling: Amélia Curd, Jézabel Lamoureux, Alexandre Carpentier, Matthieu Beaufils, Christophe Boinet, Julien Guillaudeau and Sébastien Provost. Special thanks to Amélia Curd for improving the English of this manuscript and Pierre Godet for helpful comments on a first version of this manuscript.

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Estuarine, Coastal and Shelf Science 92 (2011) 154–160

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Reduction of flatfish habitat as a consequence of the proliferation of an invasive mollusc

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A R T I C L E I N F O

Article history:
Received 12 May 2010
Accepted 24 December 2010
Available online 7 January 2011

Keywords:
spatial competition
flatfish habitat
Crepidula fornicata
invasive species
Mont Saint-Michel Bay

A B S T R A C T

Coastal bays provide habitats for juveniles and adults of many marine species. Mont Saint-Michel Bay (MSMB, France) hosts a highly diversified fish community and constitutes one of the most important nursery grounds for many commercially exploited marine species, such as sea bass, flatfish, clupeids and rays in the English Channel. Besides, MSMB also suffers from the massive invasion of an exotic mollusc, the American slipper-limpet (*Crepidula fornicata*, L.). This species arrived four decades ago and now represents the main filter-feeder biomass in the bay (150 Mt), an order of magnitude larger than local farmed and natural shellfishes. Recent analyses underlined the impact of this small gastropod on the trophic structure of this bay and its negative influence on juvenile sole densities in the nursery grounds. The present study uses a geostatistical approach to explore the effect of the extension of the slipper-limpet on flatfish (common sole *Solea solea*, L.; plaice *Pleuronectes platessa*, L.; brill *Scophthalmus rhombus*, L. and flounder *Platichthys flesus*, L.) spatial distribution. Data collected during survey of the MSMB at the end of the 1970s and three decades later have been used to build interpolated maps of (1) slipper-limpet and (2) flatfish spatial distributions. Slipper-limpets were concentrated in a small area, in the western part of the MSMB, in the 1970s while today they occupy half of the bay. This rapid proliferation led to the decrease of available surface for flatfishes, which previously occupied the whole bay and are now restricted to its eastern part. The present study highlighted that the negative influence on fish habitat in MSMB is apparently more related to changes in the substratum than to trophic interactions. This invasion has possible consequences on flatfish population renewal at a large scale and may also damage other benthic or demersal species, such as rays.

1. Introduction

Coastal and estuarine systems are the most productive environments in the world and represent half of the oceanic production (Costanza et al., 1997). They are essential fish habitats for many marine species since they provide nursery grounds for their juveniles (Van der Veer et al., 2000; Beck et al., 2001) and also because they constitute feeding grounds for adults (Peterson, 2003). The available coastal and estuarine habitats and their quality have a considerable influence on the renewal of marine population (Rijnsdorp et al., 1992; Gibson, 1994). Because of the very high human pressure in these areas, juveniles, but also significant numbers of adults, confined within these coastal and estuarine habitats can be affected by habitat degradation and related populations can be reduced (Johnson et al., 1998; Peterson et al., 2000; Le Pape et al., 2007; Rochette et al., 2010).

The introduction of alien species, either natural (*via* dispersion) or human induced (during transplanting organisms for aquaculture or transport in ship ballasts), is now considered as a major threat for marine biodiversity (Bax et al., 2003). Indeed, introduction of non-native species may have biological effects on native species and a variety of cascading effects in the marine environment (Grosholz, 2002). Coastal and estuarine habitats are considered as the environments most heavily impacted by invasions (Grosholz, 2002; Paavola et al., 2005).

In order to maintain the ecological functions of essential fish habitat and to facilitate decision-making concerning their management, it is thus fundamental to estimate the consequences of disturbance in these systems (Rubec et al., 1999; Beck et al., 2001) and especially to analyse how alien species disturb native populations.

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0272-7714/$ – see front matter © 2011 Elsevier Ltd. All rights reserved.
doi:10.1016/j.ecss.2010.12.026

The Mont Saint-Michel Bay (MSMB, France), located on the western part of the English Channel (Fig. 1), is a very large and productive coastal area with a very high ecological value. Since 1979, this bay has been listed in the World Heritage Sites (UNESCO) and its environment is protected by the international Ramsar convention (1971) and by the European nature conservation network "NATURA 2000". The bay is affected by human pressures and especially from the introduction of an invasive species, the American slipper-limpet *Crepidula fornicata* (L., 1758). This small gastropod, native of the North American Atlantic coast (Walne, 1956), was unintentionally imported along with American oysters (*Crassostrea virginica*) in the 1970's (Blanchard, 1997). Slipper-limpets can have a wide distribution but individuals prefer soft bottoms and particularly muddy areas (Barnes et al., 1973; Montaudouin and Sauriau, 1999). Soft bottom areas are also the most appropriate for many fishes species, and especially flatfishes (Gibson, 1994). In coastal areas of the Bay of Biscay (France), Le Pape et al. (2004) showed that the slipper-limpet decreased juvenile common sole abundance inside the nursery grounds, even if there was no observed incidence on the nursery function. As habitat structure governs the distribution of demersal and benthic species because of their influence on the amount of prey and shelters (Stoner and Titgen, 2003; Shucksmith et al., 2006; Nordström and Booth, 2007; Katsanevakis et al., 2009), the question here is to analyse whether the slipper-limpet, by modifying benthic communities, trophic dynamics and habitat structure, influences flatfish distribution in the MSMB. The link between the distributions of four flatfish species (common sole *Solea solea*, L.; plaice *Pleuronectes platessa*, L.; brill *Scophthalmus rhombus*, L. and flounder *Platichthys flesus*, L.) and the spread of slipper-limpet was thus analysed in the MSMB. The main goal was to map flatfish distribution in MSMB at the end of the 1970's and thirty years later in order to compare their distributions with slipper-limpets extent for the three last decades.

2. Material and methods

2.1. Study site

The MSMB is located in North-West France, in the western part of the English Channel (latitude 48°40'N, longitude 1°35'W; Fig. 1). This bay is a semi-diurnal system with a high tidal range, reaching 14 m during the highest spring tides (Larsonneur, 1994). About half of this wide and shallow bay (500 km^2, depth < 20 m) consists of mudflats (210 km^2) and intertidal salt marshes (40 km^2), which make the MSMB the most important salt marsh area in Europe (Lefeuvre et al., 2000).

This bay is one of the most important nurseries in the English Channel for several fish species of commercial interest such as sea bass *Dicentrarchus labrax*, whiting *Merlangius merlangius*, flatfishes (common sole and plaice) and elasmobranchs (*Raja* spp) (Legendre, 1984; Laffaille et al., 1998). The MSMB also represents an important site for migration and wintering of many birds and waterbirds (Le Drean-Quenec'h Du et al., 1995).

This highly productive area provides important ecological services and many activities such as tourism, fishing and shellfish farming are carried out in the bay (Le Mao et al., 2004). Since the late 1970s, the bay has hosted the invasive slipper-limpet (Blanchard, 1995) with a biomass reaching 150,000 t at the beginning of the XXI century (Blanchard, 2006). This species is the most numerous filter feeders within the bay (Loomis and VanNieuwenhuyze, 1985; Blanchard, 1997; Blanchard and Ehrhold, 1999; Arbach Leloup et al., 2008).

2.2. Sampling methods

2.2.1. American slipper-limpet

At the end of the 1970's, Aubin (1979) conducted a survey on slipper-limpets in the western part of MSMB. The benthic fauna was sampled with a Smith MacIntyre grab (0.1 m^2) in December 1978, January and February 1979. As slipper-limpets were known to be only present in this part of the bay, the sampling scheme focused on a restricted area (Fig. 2a). All grab samples (36 samples) were sieved on a 1 mm mesh and organisms were preserved in formaldehyde 10%. Species were identified in the laboratory. At each station, slipper-limpets were counted and data are expressed in densities (ind. m^{-2}).

A new slipper-limpet population survey was undertaken in May 2003 and 2004 in MSMB (Blanchard, 2009). This study was carried out on stations using sonar and video observations associated with benthic samples (Fig. 2b). Sonar first allowed the exclusion of areas without limpets. Then, in the limpet area, three samples (0.25 m^2 each) were taken at each station (65 stations) using a Hamon grab

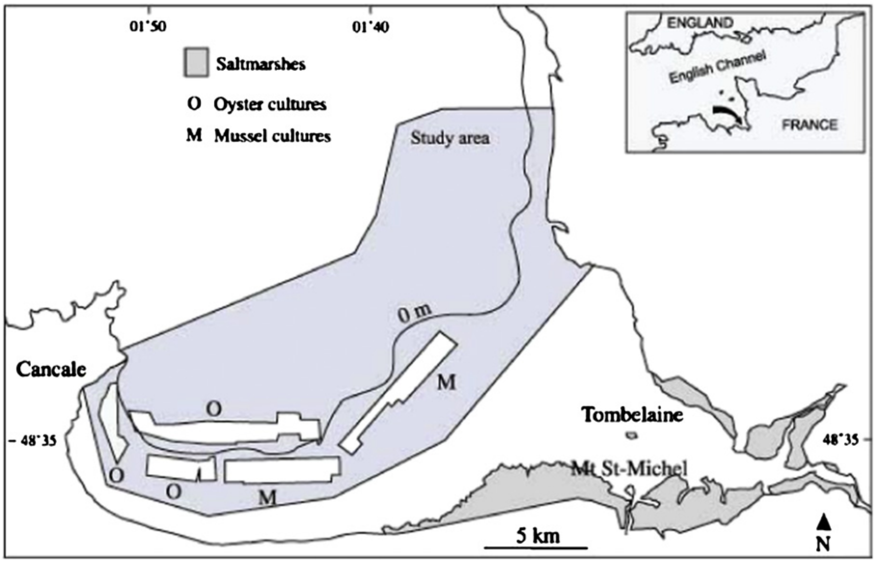

Fig. 1. Map of the Mont Saint-Michel Bay with the location of the study area (light grey), the oyster (O) and mussels (M) cultures and the salt marshes. In the upper right corner of the figure: general location.

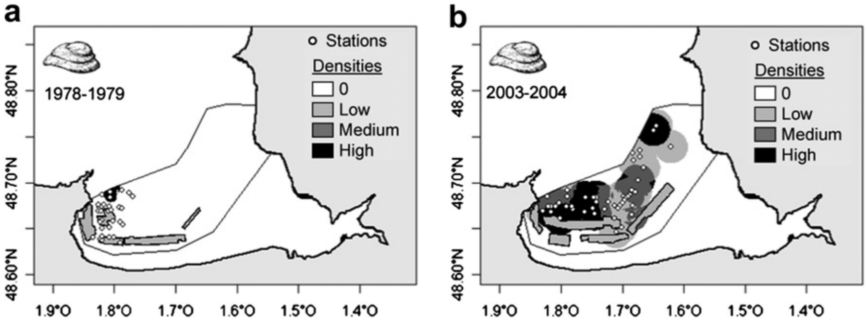

Fig. 2. American slipper-limpet distribution in 1978–1979 (a) and in 2003–2004 (b). Polygons inside the studied area represent oyster and mussels cultures of the respective studied period. No predictions were calculated within these cultures.

or by diving. The samples were sieved on a 2 mm mesh and animals were frozen. Back to the laboratory, the limpets were brushed to remove epibionts, cleaned, drained and weighed. The biomass for a station corresponded to the mean value of the three samples expressed in g m^{-2} (total fresh weight).

To compare data from 1978 to 1979 with those from 2003 to 2004, densities from the first survey were transformed into biomass, using a mean weight per individual of 5.18 g (calculated from Blanchard, 2005).

2.2.2. *Flatfish*

Trawl surveys were carried out in October, in 1979 and in 1980. Hauls were performed with a 12 m wide and 10 m high opening otter trawl using a 24 mm stretched mesh net cod end. A total of 43 trawls hauls in 1979 and 15 in 1980 were conducted at 3 knots during 30 min and 20 min respectively (Fig. 3a), covering approximately 29,000 m^2.

Another survey was performed in August 2008. Flatfish were caught with a 2.9 m wide and 0.5 m high opening beam trawl using a 20 mm stretched mesh net cod end. Forty-two beam-trawl hauls were carried out (Fig. 3b) at 2.5 knots for 15 min, each covering approximately 3400 m^2.

During all surveys, all flatfish were identified, measured and counted and then catch densities were expressed as number of individuals per 10,000 m^2.

2.3. *Data analysis*

2.3.1. *Preliminary analyses and validation of data*

2.3.1.1. Slipper-limpet. In 2003, the sampling survey was performed in the south and in the east of the BMSM while in 2004, stations were located in the western part of the bay. Data were compiled in one database to map a unique recent repartition of slipper-limpet within the entire BMSM. We assumed that there are little variations in limpet distribution between the two years, considering its lack of mobility (Blanchard, 1997).

2.3.1.2. Flatfish. Dab (*Limanda limanda*) and turbot (*Psetta maxima*) were very scarce in flatfish sampling (less than 5 individuals), which led us to study only 4 of the 6 fished flatfish species: common sole, plaice, flounder and brill. Regarding these species, most of common sole, plaice, and brill were juveniles (Table 1). On the contrary, both juvenile and mature flounders were caught in 1979–1980.

Sampling schemes (stations sampled) were different in 1979 and 1980 but the patterns of flatfish distribution were equivalent, which allowed pooling these data.

To make sure that a comparison between August 2008 and October 1979–1980 was possible, ie to avoid any seasonal biases, data from another survey performed in August 1978 and focused on common sole and plaice only were compared with observations made in October 1979–1980. For these two species, no seasonal variations were observed between August and October suggesting the same conclusions for all the flatfish species of this Bay.

Use of different sampling gears in 1979–1980 (large otter trawl) and 2008 (small beam trawl) could have biased a comparison between densities, even if these two gears did not seem to have significantly different efficiency for juvenile sole (Dorel et al., 1991). For this reason the present study mainly focused on the analysis of changes in the distribution of flatfishes, from the following mapping approach.

2.3.2. *Mapping*

Spatial boundaries of the mapping area were chosen as a compromise between the amount of sampling stations and their distribution in the different flatfish trawl surveys (Fig. 3a,b); few external stations, specific of each survey and located outside the area studied during the two periods, were removed from the dataset.

Comparison between current and historical distributions of species required interpolated densities within the studied area. Interpolation was performed using ordinary kriging (Kitanidis, 1997; Christakos, 2000). This geostatistical technique examines spatial structure in the dataset to determine interpolation parameters. This structure is established with the construction of semivariograms (Matheron, 1971) fitted to a theoretical model (e.g. linear, spherical, gaussian or exponential). Modelling was performed with R software (library "gstat").

To minimise skewing of distributions, raw data were transformed using $Z = \log(x + 1)$. As patchiness of flatfishes was assumed to be constant over time, spatial structure of recent (2008) and historical (1979–1980) data were combined to fit a common variogram, however different for each species. Best fits were found using the exponential theoretical model. To map interpolated densities of each species for recent and historical periods, models were applied to a regular grid of points covering the study area. Considering the spatial distribution and the variability in densities of samples, interpolations were made with a minimum of 3 stations until a distance of 2 km for slipper-limpet and 5 km for flatfish. Despite these constraints, interpolations covered 96% and 100% of the study area for flatfishes in 1979–1980 and 2008 respectively.

Predictions of the regular grid for each map were ranged in classes to distinguish gradients of densities. The first class contained all stations of the grid where the species is not present. Other interpolated densities (i.e. positive) of the regular grid were classed in 3 quantiles, each containing 33% of the remaining stations. Resulting maps of predicted densities were thus represented with a 4-level (absence, low, medium and high densities) grey scale whose limits were different from a species to another and between periods. These maps thus represented relative densities and avoid

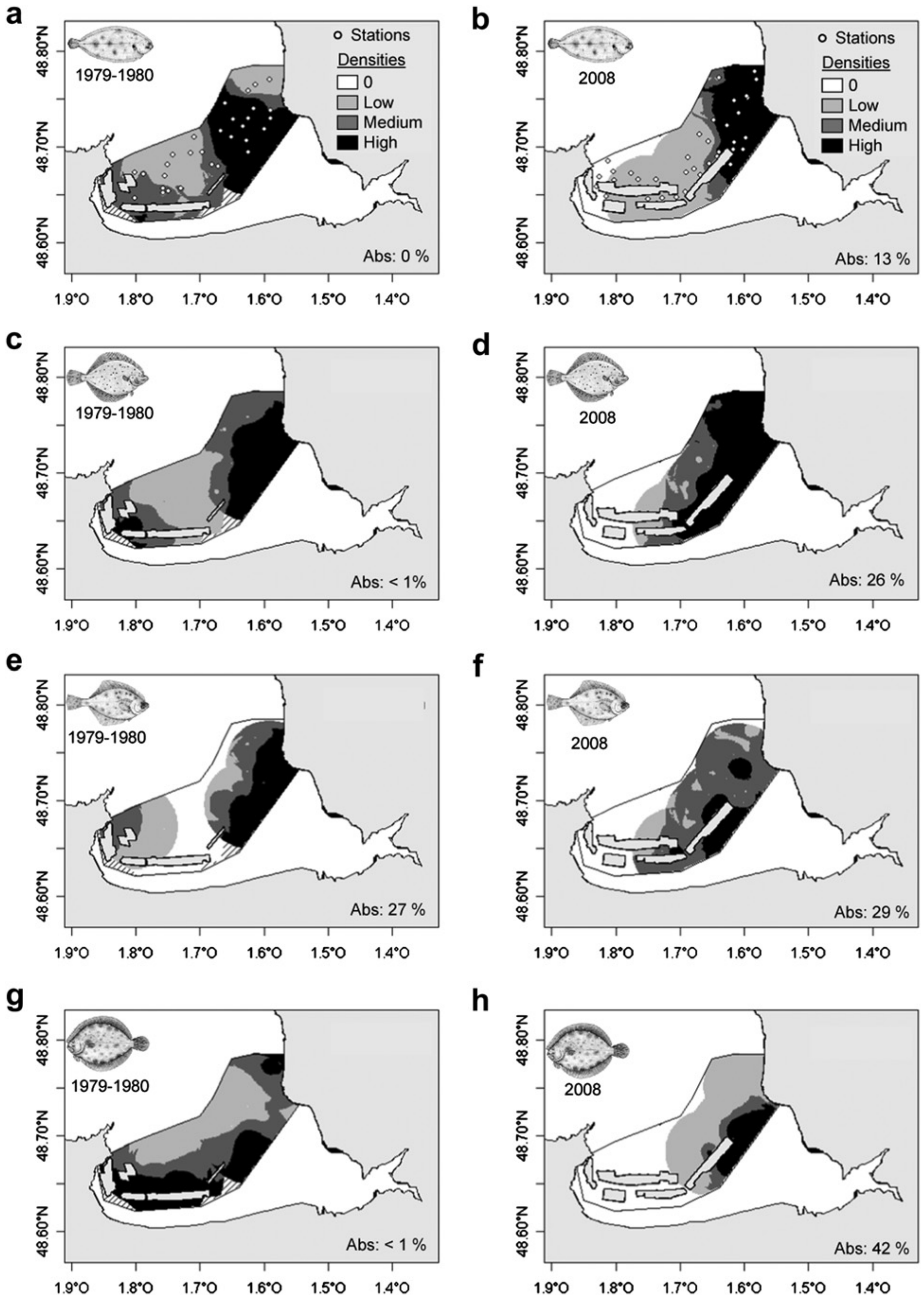

Fig. 3. Flatfish distribution in 1979–1980 and in 2008 for common sole *Solea solea* (a and b), plaice *Pleuronectes platessa* (c and d), flounder *Platichthys flesus* (e and f) and brill *Scophthalmus rhombus* (g and h). Polygons inside the studied area represent oyster and mussels cultures of the respective studied period. No predictions were calculated within these cultures. The proportion of absence is indicated in the right lower corner.

bias related to different trawl efficiency. Changes in slipper-limpet extent and flatfish distribution in the three last decades were analysed from these maps. In addition, proportions of null densities (absence) were calculated and differences between the two periods were statistically compared. The western limit of the distribution was reported for each period and the distance between the two limits was also calculated.

Finally the relation between limpet biomass and flatfish densities was analysed on the recent period. Raw survey data were 0-inflated and were not appropriate for graphical analysis nor for parametric tests (Le Pape et al., 2003). Thus, for each flatfish species, the proportion of interpolated density in the different quartile was compared for the different levels of limpet biomass and tested with a χ^2 test.

3. Results

In 1978–1979, American slipper-limpets were only located in two stations with very low densities: 5 and 24 ind. m^{-2}, which correspond to an approximate biomass of 26 and 124 g m^{-2} respectively (Fig. 2a). Experts knowledge considers that in 1978–1979, this mollusc was not present elsewhere in the bay (Blanchard, 1995). In 2003–2004, slipper-limpets distribution was very much larger: they were not only located in the western part of

Table 1
Information on flatfish catches for each period.

		Total catches	Juveniles (%) and reference
1979–1980	Common sole	5523	99% (<25 cm; Dorel et al., 1991)
	Plaice	936	96% (<30 cm)
	Flounder	383	37% (<25 cm; Van der Land, 1991)
	Brill	95	74% (<25 cm; Quéro and Vayne, 1997)
2008	Common sole	648	99% (<25 cm; Dorel et al., 1991)
	Plaice	199	99% (<30 cm)
	Flounder	12	83% (<25 cm Van der Land, 1991)
	Brill	15	100% (<25 cm Quéro and Vayne, 1997)

the bay, but spread also towards the centre and the northeast. The maximum biomass reached more than 11,500 g m^{-2} and slipper-limpets cover approximately half of the bay (Fig. 2b).

Changes in flatfish distribution between the two periods have also been determined. Common sole was widely distributed in the entire bay at the end of 70's with a peak distribution in the eastern part (Fig. 3a). In 2008, common sole was absent from the western part but maximum densities were located in the same place, in the east (Fig. 3b). Plaice spread throughout almost the entire bay in 1979–1980 and maximum densities were reached in the northeast (Fig. 3c). In 2008, plaices were totally absent from the west and highest densities were found in the east (Fig. 3d). Flounder were only present at a few stations in 1979–1980, in the southwest and in the east (Fig. 3e); they were totally absent from the western part of the bay in 2008 (Fig. 3f). The brill situation was extreme: while it was present in the entire bay in 1979–1980 (Fig. 3g), it is now only found in the east (Fig. 3h). Thus, the flatfish spatial range has changed and reduced while the slipper-limpet was extending its distribution.

The western limit of the common sole distribution has moved eastward by 5.6 km between 1979–1980 and 2008. This limit has also moved eastward by 8.9 km, 10.0 km and 14.5 km for plaice, flounder and brill respectively. This shift in the flatfish distribution western limit is also shown by the highly significant (χ^2 test p-value $<10^{-12}$) increase in zero in flatfish densities (Fig. 3).

When analysing the co-occurrence between slipper-limpet and flatfish during the recent period, for the four studied species found in the MSMB, densities are lower when the slipper-limpet biomass increases (Fig. 4). These gradients in densities are significantly different for all flatfish (χ^2 test, p-value $<10^{-12}$ in all cases).

4. Discussion

4.1. Slipper-limpet distribution

The American slipper-limpet, a small gastropod native of the North American Atlantic coast, greatly invaded the Western Europe coastal area since the beginning of the 20th century (Minchin et al., 1995). The first observation of this gastropod in the MSMB was reported in 1976 (Retière, 1979) in the western part of the bay, in the Corbière bank in front of Cancale (Fig. 2a). Slipper-limpet propagation in the bay began in the western sector to reach the centre and east of the bay in 2003–2004 (Fig. 2b). A recent study comparing data from 1996 to 2003–2004 showed that during this period, the slipper-limpet population grew by 50%. As a consequence, in 2003–2004, 25% of the bay was covered by slipper-limpets at their highest density levels (Blanchard, 2009). Blanchard (2009) considered that the MSMB has not reached its saturation level, suggesting that slipper-limpet propagation in the MSMB has not reached a stable state and may progress eastward. Different explanations for this extension are expressed (Blanchard, 2009). For example, slipper-limpets benefit from several biological advantages and from favourable environmental conditions in the bay: water circulation and weak currents in the bay of Cancale favour larvae settlement whereas high productivity prevents food limitation. Temperature in the MSMB is within the optimal range for slipper-limpet and in the context of climate change and increasing temperature, the dispersion of *Crepidula fornicata*, only sensitive to cold winters (Thieltges et al., 2004), would be stimulated. Human activities are also involved since oyster farming enhance slipper-limpet development, and shellfish dredging/fish trawling facilitate slipper-limpet spread (Blanchard, 2009). Moreover natural predation rate is low in Europe (Blanchard, 1997). Experimental tests performed in the northern Wadden Sea showed that the slipper-limpet natural predators, the crab *Carcinus maenas* and the sea star *Asteria rubens*, preferred blue mussels to slipper-limpets (Thieltges et al., 2004). Predation by waterbirds has not been studied in the BMSM but appeared limited elsewhere in Europe (Thieltges et al., 2004).

4.2. Flatfish spatial distribution

4.2.1. Current state and evolution

In the present study, a direct comparison of flatfish densities between the two periods was not quantitatively possible: fishing gears and their related efficiency changed from a period to another and interannual recruitment variability could not be taken into account from a single year survey (2008). This induced the present semi-quantitative approach using relative distribution of flatfish densities. Almost all flatfish distributions have changed between the late 1970's and the late 2000's: flatfishes have left the western part of the bay and their spatial ranges have significantly decreased (Fig. 3).

4.2.2. Cause

Habitat suitability for flatfish, a mix between abiotic and biotic factors, is especially governed by food availability, predation pressure and temperature (Gibson, 1994). Slipper-limpets can disturb flatfish at different levels. Slipper-limpet shells accumulation deeply modifies the habitat structure and these modifications have different consequences. The first consequence of the substratum nature modification is in preventing bentho-demersal species to bury in the sediment. The substratum preferences of the four flatfish species in this study are soft bottoms, sand or mixed sand and mud (Gibson, 1994; Elliott and Dewailly, 1995). On the contrary slipper-limpet shell mats are not a suitable habitat for bentho-demersal species. By covering the substratum and modifying its nature, slipper-limpets prevent juvenile and adult flatfish to settle and to bury, which may indirectly increase their vulnerability to predation (Gibson, 1994). On the other hand, slipper limpets, by changing benthic fauna and catching a large part of the primary production, change the trophic structure (Arbach-Leloup et al., 2008), which can affect food availability for flatfish.

4.2.3. Slipper-limpet consequences on nursery size

The MSMB is an important nursery ground for flatfishes: during the sampling surveys, the major part of flatfish catches concerned immature fish (Table 1). As predation strongly influences juvenile mortality (Van der Veer and Bergman, 1987; Johnson, 2007; Juanes, 2007), flatfish juveniles that settle in an inappropriate substratum (i.e. cover with shells) cannot bury, are vulnerable for their predators and have low chance to survive. High biomasses of slipper-limpet were already known to strongly reduce densities of juvenile sole (Le Pape et al., 2004). The present study reinforces this previous knowledge and demonstrates that juvenile flatfish distribution is reduced in the MSMB. Flatfish distributions are significantly

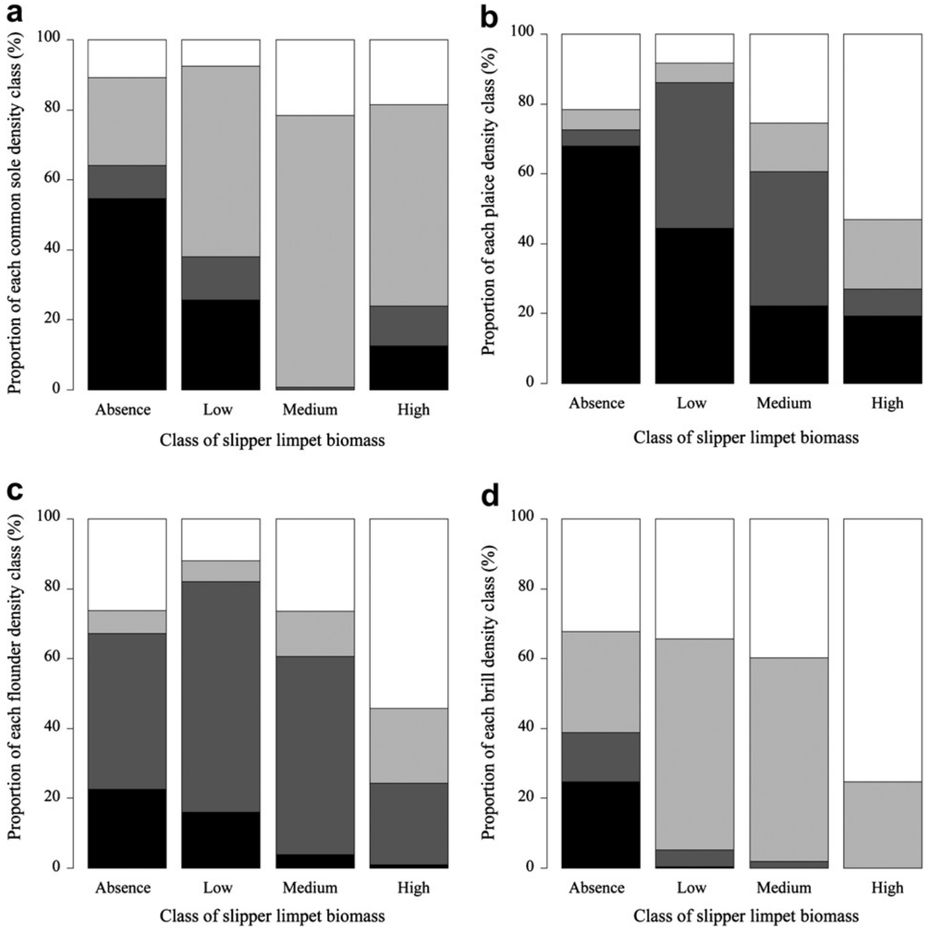

Fig. 4. Proportion of interpolated stations of the regular grid in each density class with relation to slipper-limpet biomass for common sole *Solea solea* (a), plaice *Pleuronectes platessa* (b), flounder *Platichthys flesus* (c) and brill *Scophthalmus rhombus* (d) for the recent period. The increasing grey gradient distinguishes classes of increasing densities of the flatfishes distributions: white for absence, light grey for low densities, dark grey for medium and black for high densities. Limits for the slipper-limpets biomass classes are: low [0; 920], medium [920; 2655] and high >2655 g m^{-2}.

reduced while co-occurrence is observed with slipper-limpet and quite no flatfish are found at the highest density of slipper-limpet (Fig. 4). As demonstrated from xenobiotics exposure (Moles et al., 1994) or stable isotopes footprints (Kostecki et al., 2010), juvenile flatfish migrations are very limited and they cannot move far from unfavourable settlement area. Thus, the settlement suitable area and the related nursery size are reduced in response to limpet extent.

4.2.4. Slipper-limpet consequences on residual flatfish habitat

By changing the habitat structure, limpets compelled flatfish adults to move eastward in the bay. This induces a shift in flatfish distribution to suitable sediment which leads to a concentration of remaining flatfish in the eastern part of the BMSM. The presence of slipper-limpet shells, by reducing the suitable habitat size, should limit this avoiding strategy on residual suitable slipper-limpet free habitat.

In the remaining habitat, food limitation could result from slipper-limpet invasion. Primary production would be higher in the BMSM without the slipper-limpet filtering activity (Cugier et al., 2010). This primary production is consumed by the slipper-limpet and is not yet available for the other suspension feeder benthic invertebrates, which are also common preys for flatfishes (Elliott and Dewailly, 1995; Arbach Leloup et al., 2008). Food availability and growth could decrease in the residual habitat in the MSMB because of density dependent competition in a smaller area.

4.2.5. Possible long-term consequences on population size and renewal

In flatfish populations, post-settlement mortality, linked to nursery habitat capacity, affects recruitment strength and population size (Gibson, 1994; Johnson, 2007). Both the nursery ground area and suitable habitats for remaining juvenile and adult flatfish in MSMB are reduced due to changes in habitat structure linked to slipper-limpet extent. Thus, the slipper-limpet can damage flatfish populations in the Western English Channel and have consequences on related fisheries. Furthermore, it is possible that other benthic species, such as rays, could also be affected.

Acknowledgements

This study was supported by the French National Program on Coastal Environments (NOCES). We would like to thank P. Le Mao and the crew of the *R*/*V* Louis Fage for their help during sample collection. We are also very grateful to Y. Désaunay and P. Beillois who provided fish data from the end of the 1970's. The authors are also grateful to the two anonymous reviewers for their helpful advices.

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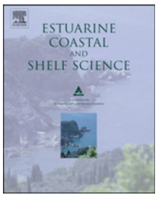
Estuarine, Coastal and Shelf Science 94 (2011) 1–15

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss



Changes in North Sea macrofauna communities and species distribution between 1986 and 2000

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ARTICLE INFO

Article history:
Received 31 August 2010
Accepted 14 April 2011
Available online 5 May 2011

Keywords:
long-term variability
distribution shift
NAOI
regime shift
non-native species
benthic communities

ABSTRACT

The North Sea Benthos Project 2000 was initiated as a follow-up to the 1986 ICES North Sea Benthos Survey with the major aim to identify changes in the macrofauna species distribution and community structure in the North Sea and their likely causes.

The results showed that the large-scale spatial distribution of macrofauna communities in the North Sea hardly changed between 1986 and 2000, with the main divisions at the 50 m and 100 m depth contours. Water temperature and salinity as well as wave exposure, tidal stress and primary production were influential environmental factors on a large (North Sea-wide) spatial scale.

The increase in abundance and regional changes in distribution of various species with a southern distribution in the North Sea in 2000 were largely associated with an increase in sea surface temperature, primary production and, thus, food supply. This can be most likely related to the North Sea hydro-climate change in the late 1980s influenced by the variability in the North Atlantic Oscillation (NAO). Only one cold-temperate species decreased in abundance in 2000 at most of the stations. Indications for newly established populations of offshore non-native species were not found.

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doi:10.1016/j.ecss.2011.04.008

Differences in macrofauna community structure on localised spatial scales were predominantly found north of the 50 m depth contour off the British coast along the Flamborough Head Front towards the Dogger Bank, off the coast of Jutland and at the Frisian Front. These changes were most likely attributed to stronger frontal systems in 2000 caused by the increased inflow of Atlantic water masses in relation to the hydro-climate change in the late 1980s.

1. Introduction

The North Sea macrofauna has been studied regularly on local or on national (EEZ) scales since the beginning of the last century. A summary of the various regional and long-term datasets is given in Kröncke and Bergfeld (2003).

Datasets covering the whole North Sea are very limited. For the macrofauna, one data set is available from the North Sea Benthos Survey (NSBS) in 1986 initiated by the ICES Benthos Ecology Working Group (Künitzer et al., 1992; Heip and Craeymeersch, 1995; Craeymeersch et al., 1997). The data from surveys from 1980 to 1985 in the northern North Sea by Basford and Eleftheriou (1988), Eleftheriou and Basford (1989) and Basford et al. (1990, 1993) were added to the NSBS. The detailed analyses by Künitzer et al. (1992) and Craeymeersch et al. (1997) identified eight macrofauna communities, which reflected the three étages of Glémarec (1973) defined by the <50 m, >50 m and >100 m depth contours. Most species occurred either south of the 50 m depth contour or north of it. Species with a southern distribution occurred in the central North Sea but never north of the 100 m contour and species with a northern distribution were not found south of the 50 m depth contour. The distribution of other species was mainly related to certain sediment types.

Changes in sublittoral North Sea benthic communities in the last decades have been found in different areas (Ibanez and Dauvin, 1988; Rachor, 1990; Frid et al., 1996, 1999; Kröncke et al., 1998, 2001; Wieking and Kröncke, 2001; Dippner and Kröncke, 2003; Franke and Gutow, 2004; Schröder, 2005; van Hoey et al., 2005; Rees et al., 2006; Reiss et al., 2006; van Hoey et al., 2007; Neumann et al., 2008, 2009a, b; Schückel et al., 2010; Lindley et al., 2010). Most shifts in the community structure were directly or indirectly correlated to the variability of the North Atlantic Oscillation Index (NAOI) in winter, especially to the increase in NAOI since the late 1980s, and resulted in the increase in warm-temperate species, a decrease in cold-temperate species or the invasion of non-native species. Since similar changes were found in the North Sea plankton (e.g. Beaugrand, 2004; Bonnet and Frid, 2004; Wiltshire and Manly, 2004; Kirby et al., 2007; McQuatters-Gollop et al., 2007) and in North Sea fish stocks in the same period (Ehrich and Stransky, 2001; Reid et al., 2001a; Kirby et al., 2006; Ehrich et al., 2007), Reid and Edwards (2001) and Beaugrand (2004) concluded that a “regime shift” had occurred at the end of the 1980s, which was directly related to a significant increase in the NAOI (Hurrell, 1995). The time series of the first principal component of the Sea Surface Temperature (SST) anomalies in the North Sea during this period was highly correlated to the NAOI (Dippner, 1997). Consequently, during positive NAOI winters, the moderating influence of the ocean results in unusually warm winter temperatures, as has been found in many years since 1988 (Hurrell, 1995). The winters of 1978/79, 1981/82, 1984/85, 1985/86, 1995/96 and 1996/97 were cold and related to a negative NAOI. The mean annual SST has increased in the last decades by 1.1 °C (Beare et al., 2002).

The North Sea Benthos Project (NSBP) 2000 (Reiss et al., 2007) was initiated by the members of the ICES Benthos Ecology Working Group as a follow-up to the earlier 1986 ICES North Sea Benthos Survey (NSBS). The major aim of the NSBP 2000 was to compare the spatial distribution of macrofauna communities and species with that of the 1986 NSBS, in order to identify any changes and their likely causes. The 1986 NSBS reflects the spatial distribution of species and communities after three cold winters, while the communities studied during the NSBP 2000 were influenced by the hydro-climate change at the end of the 1980s as well as by the cold winters of 1995/96 and 1996/97.

The aims of this study were therefore 1) to compare the spatial distribution of macrofauna species, 2) to identify any decrease in cold-temperate or increase in warm-temperate species, 3) to compare the spatial distribution of communities in order to examine the influence of changes in the hydro-climate and primary production at the end of the 1980s.

2. Material and methods

2.1. Macrofauna data 1986 – North Sea Benthos Survey (NSBS)

The North Sea Benthos Survey (NSBS) was carried out during April 1986. At each station the macrofauna was sampled either by 0.1 m^2 van Veen grab or by 0.068 m^2 box corer (Künitzer et al., 1992). Generally, three replicates were taken per station, and the macrofauna samples retained on a 1 mm mesh sieve were fixed in 4% buffered formalin.

The area north of 58°N was not sampled during the NSBS in 1986. Therefore, data from this area, sampled by Eleftheriou and Basford (1989) between 1980 and 1985, were included in the analysis. The same sampling gear was used, but samples were sieved over a 0.5 mm mesh. A detailed description of methods used is given in Künitzer et al. (1992) and Heip et al. (1992).

2.2. Macrofauna data 2000 – North Sea Benthos Project (NSBP)

Although quasi-synoptic sampling was intended for late spring to summer in 2000, several regions of the North Sea could only be covered by including material from adjacent years (mainly 2001). Most of the infauna sampling for NSBP 2000 was conducted with a 0.1 m^2 van Veen grab; Dutch and Scottish samples were obtained with box corers (0.068 m^2; and 0.25 m^2, respectively), English samples mostly with a 0.1 m^2 Day or Hamon grab, depending on the sediment type. Samples were sieved over a 1 mm mesh and fixed in 4–5% formalin. Sieving was done before fixing, except for some of the samples from Belgian waters, where they were fixed before sieving. Generally, two to three replicates per station were taken. In total 1349 stations were sampled, but only 156 stations were used in this study (see below). A more detailed description of methods used for sampling and processing the infauna is given by Vanden Berghe et al. (2007).

Information on species feeding modes and zoogeographical distribution was obtained from available literature (e.g. Fauchald and Jumars, 1979; Lincoln, 1979; Hartmann-Schröder, 1996; Wieking and Kröncke, 2001).

2.3. Environmental variables

The environmental variables included in this study were depth, sediment characteristics (including % mud and median grain size), average water temperature and salinity (winter and summer), stratification of the water column, chlorophyll content of the surface water column, tidal stress and peak wave stress (see Vanden Berghe et al., 2007).

Most 1986 NSBS and NSBP 2000 data contributors collected information on the sediment granulometry during the individual infauna surveys, but procedures were not standardized. Therefore, all sediment datasets were collated into a uniform database and reprocessed (see Hillewaert, 2007).

Data on temperature and salinity were derived from the hydrodynamic Hamburg Shelf Ocean Model (HAMSOM), which is a three-dimensional, baroclinic primitive equation model for simulations of oceanic and coastal and shelf sea dynamics (Backhaus, 1985). It has a horizontal resolution of 12 min in latitude and 20 min in longitude and a vertical resolution up to a maximum of nineteen layers. For details of the specific HAMSOM application see Pohlmann (1996).

The ECOlogical North Sea Model HAMburg (ECOHAM1) was used to estimate the primary production of the water column. ECOHAM1 is a model that can be used to calculate annual and long-term phytoplankton dynamics, nutrient transport, and primary productivity for shelf seas in a three-dimensional physical environment (Skogen and Moll, 2000). It is based on a simple phosphorus/nitrogen cycle and takes four state variables into account, namely three pelagic variables: phytoplankton, phosphate (DIP), nitrogen (DIN), and one for benthic detritus. The horizontal grid size of the numerical model is 20 × 20 km, the vertical resolution is 5 m for the upper 50 m and increasing layer thickness below 50 m up to a maximum of 19 layers. The ECOHAM1 model was validated using observed chlorophyll (Moll, 1998), phosphate concentrations (Moll, 2000), and primary production values (Skogen and Moll, 2000).

Tidal parameters were generated using a three-dimensional hydrodynamic model (Davies and Aldridge, 1993), run in depth-integrated form on a grid of approximately 3.5-km resolution covering the European continental shelf. Average and peak wave stress were calculated from a one-year model run covering the period September 1999 to September 2000, on a grid of approximately 12-km resolution, using the WAM spectral wave model run at the Proudman Oceanographic Laboratory (Osuna and Wolf, 2005). The stratification parameter 'S' was derived from the formulation presented in Pingree and Griffiths (1978), using modelled M2 tidal velocities and measured depths at the benthic stations.

Sea surface temperature (SST) anomalies were obtained from ICES Annual reports (ICES, 2006).

2.4. Data analysis

Instead of using the published results of the 1986 NSBS data (Künitzer et al., 1992), data were re-analysed since both datasets (1986 and 2000) had to be taxonomically adjusted to allow comparisons. All abundance data were standardized to a 1 m^2 sampling area. The two datasets (1986 and 2000) were reduced to stations with matching positions or at least those relatively close to each other (Fig. 1). The nearest stations were determined using GIS software (ArcView 3.1) and a dataset was created including stations with a maximum distance of 21 NM. In total, 85 stations had identical positions and 71 stations had a mean difference in the position of 7.5 ± 5.1 NM, of which most were situated in the northern North Sea.

We used the PRIMER v6 program package to perform cluster analyses and multidimensional scaling of abundance data from 1986 and 2000 to reveal similarities between stations in each year (Clarke and Warwick, 1994). Similarities were calculated using the Bray–Curtis coefficient. Fourth-root transformation was used prior to computation. Similarity percentage analysis (SIMPER) was used to identify species which were mainly responsible for differences in community structure. The similarity among the community structures was tested using the RELATE routine in PRIMER v6. The main clusters were classified based on a range of similarity levels of about 25–35% and 20–30% for the cluster analyses results of 1986 and 2000 data, respectively.

The comparison between the community structure (clusters) of 1986 and 2000 was based on the 1986 clusters. Thus, communities revealed with the 1986 data were compared with the corresponding stations in 2000, irrespective of community classification of the 2000 stations in the separate analysis. The significance of any differences in community structure at stations sampled in 1986 and 2000 was tested with the Analysis of Similarities (ANOSIM) routine.

In addition, the data of 1986 and 2000 were combined in one dataset and a cluster analysis was carried out to estimate differences in the cluster classification. A high similarity between stations was assumed, when both corresponding stations were grouped in the same sub-cluster, a medium similarity when grouped in the same main cluster but different sub-clusters, and a low similarity when grouped in different main clusters.

Since different gears were used for sampling, the Hurlbert Index (ES*n*), a less sample-size dependent diversity index, was used, which is based on the rarefaction technique of Sanders (1968), modified by Hurlbert (1971). In this index the expected number of species (ES) is calculated for a specified number of randomly-sampled individuals, e.g. 100 individuals (ES100) as used in the present study.

We analysed the relationship between macrofauna community structure and environmental variables via canonical correspondence analysis (CCA) using CANOCO 4.5 (ter Braak and Smilauer, 1998).

3. Results

3.1. Differences in species distribution and abundance

On a North Sea wide scale neither a clear latitudinal distribution shift of species (based on the reduced station grid), nor a range expansion of species into the North Sea or newly established non-native species were found, although 43 taxa of the overall 455 taxa were detected in 2000 but not in 1986. The majority of these taxa were rare with 88% found at less than five stations in 2000 (40% only at one station).

However, significant changes in the abundance of species with a core distribution in the southern North Sea were found, hereinafter referred to as 'southern' species (Fig. 2). In 2000, the abundance of small 'southern' bivalve species such as the surface-deposit feeding *Abra alba*, the suspension-feeding *Corbula gibba* and the subsurface-deposit feeding *Nucula nitidosa* increased at the Oyster Ground (e.g. 4–30 or 104 m^{-2}). A higher abundance of the warm-temperate interface-feeding brittle star *Acrocnida brachiata* in 2000 was found in the German Bight as well as at the Dogger Bank "Tail End", where it was associated with an increase in abundance of the 'southern' interface-feeding polychaete *Lanice conchilega* (2–128 m^{-2}) and the 'southern' sand-licking sea urchin *Echinocyamus pusillus* (10–49 m^{-2}). The 'southern' and interface-feeding bivalve *Tellina* spp. also increased at the Tail End but decreased in other areas of the Dogger Bank. *Tellina* spp., *L. conchilega* and the 'southern' sand-licking amphipod *Urothoe poseidonis* also occurred in higher numbers in 2000 along the southern coastal 30 m depth contour. The abundance of the interface-feeding polychaetes *Spiophanes bombyx* (eurytherm) (97–367 m^{-2}) and *Myriochele* spp. (cold-temperate) (3–232 m^{-2})

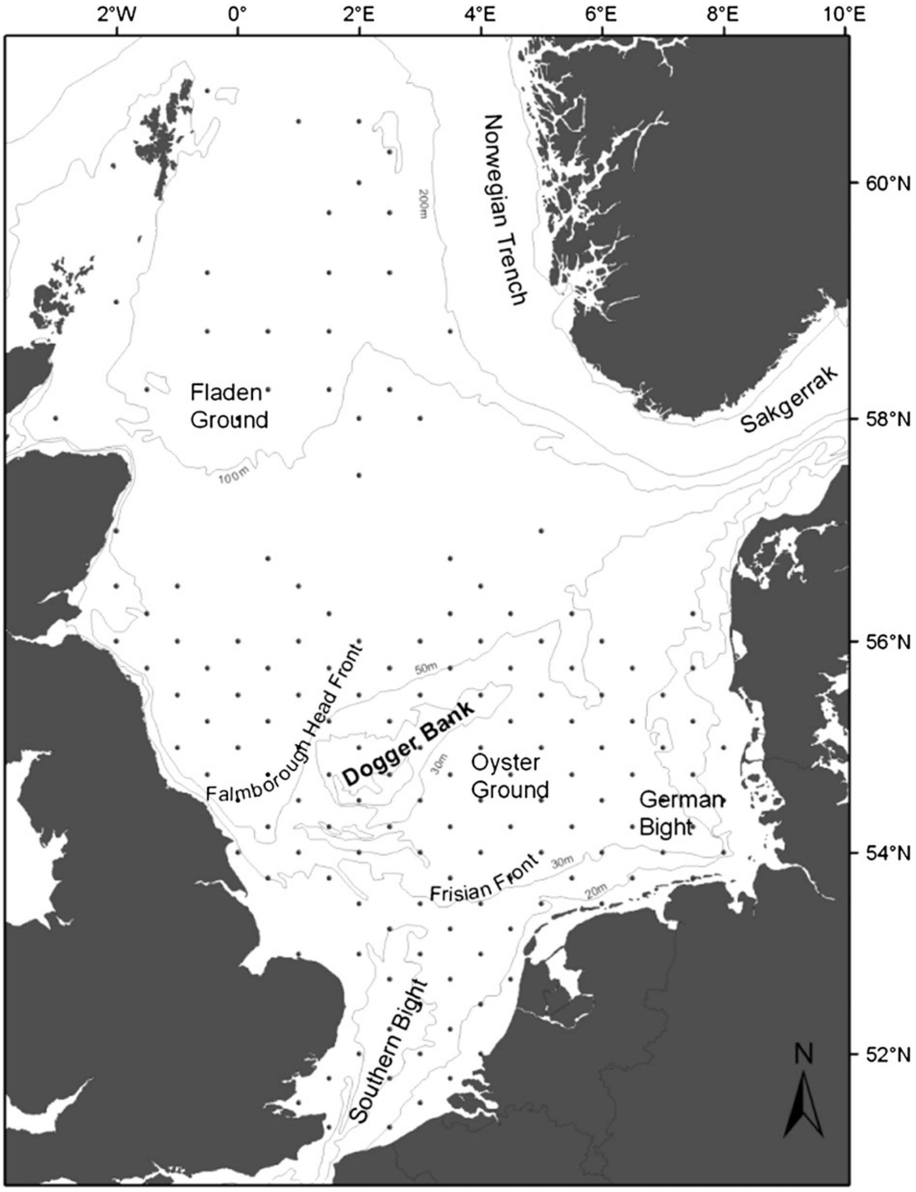


Fig. 1. Location of sampling stations in the North Sea.

as well as the cold-temperate omnivorous *Paramphinome jeffreysii* (8–128 m^{-2}) increased especially north of the 50 m depth contour.

Species such as the eurytherm sand-licking amphipod *Bathyporeia* spp. and the eurytherm interface-feeding polychaete *Magelona* spp. and eurytherm suspension-feeding *Phoronida* increased in abundance in 2000 in some areas e.g. in the eastern North Sea, but in others they decreased. The cold-temperate subsurface-deposit feeding polychaete *Ophelia borealis* is the only species which decreased in abundance in 2000 at most of the stations.

3.2. *Differences in total abundance and diversity (ES100)*

Fig. 3a shows that the mean total abundance decreased in 2000 compared to 1986 mainly at stations in the northern North Sea (>100 m) and at the central Oyster Ground, but increased at and north of the 50 m depth contour at the Dogger Bank, off the British coast and at several coastal stations. The mean expected species number ES(100) (Fig. 3b), was generally lower in 2000 at stations north of the 50 m depth contour, at the eastern Oyster Ground and northern Southern Bight. ES(100) increased only at stations >100 m and at a few stations >50 m as well as in the western Southern Bight.

3.3. *Large-scale (i.e. North Sea-wide) differences in community structure*

Although a higher spatial heterogeneity of communities was found in 1986 according to the higher number of clusters calculated for the 1986 data than for the 2000 data, Fig. 4 reveals that the large-scale distribution of the macrofauna communities in 2000 was broadly similar to that in 1986 (Künitzer et al., 1992). In 2000, the major divisions in the communities of the North Sea still occurred at the 50 and 100 m depth contours and greater heterogeneity of communities in the southern North Sea (<50 m) compared to the north is also still evident as also found by Rachor et al. (2007). The dominant species for the individual communities are given in Tables 2 and 3. The comparison of the similarity matrices for the 1986 and 2000 abundance data also revealed

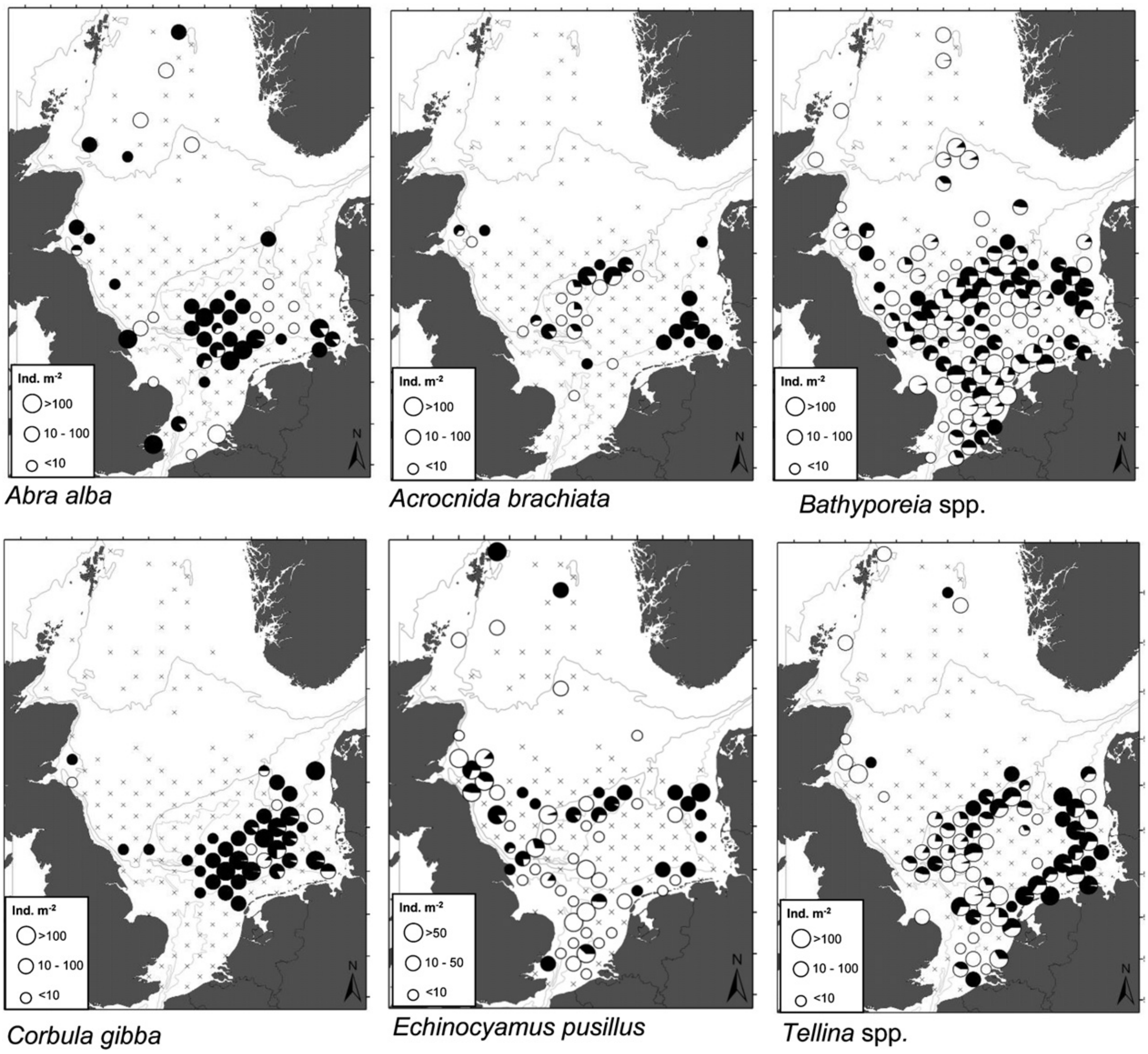


Fig. 2. Species distribution maps with mean total abundance (m^{-2}) classes superimposed given as the sum for both years (19986 and 2000), where black represents presence in 2000 and white represents presence in 1986. Where a species was present at a station in both years, the pies are proportionally divided accordingly. Species absences in both years are displayed as a cross.

a significant relationship between the two community patterns, even for different transformations of the data (Table 1).

3.4. Small-scale differences in community structure

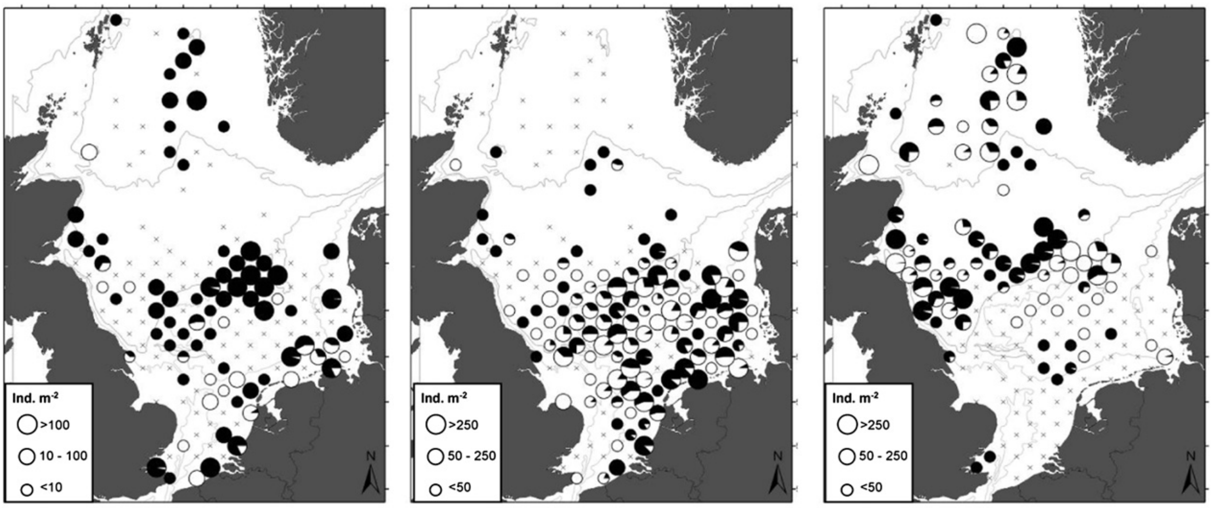
Temporal differences in community structure at localised spatial scales between 1986 and 2000 were compared on the basis of the clusters identified in 1986. Significant differences were found between all clusters, but most distinct ones occurred in the eastern North Sea, along the Flamborough Head Frontal System and the Frisian Front as well as north of the 100 m depth contour in the northern North Sea (Fig. 5, Table 4).

In 2000, the community structure in the northern North Sea (>100 m, 1986 clusters A and E1), was similar to the >50 m community in 1986 (Figs. 4 and 6). The differences in the communities between 1986 and 2000 were caused by the increase in abundance of the small polychaete *Paramphinome jeffreysii* and the decrease in abundance of the polychaete *Ophelia borealis* (Fig. 2, Table 5).

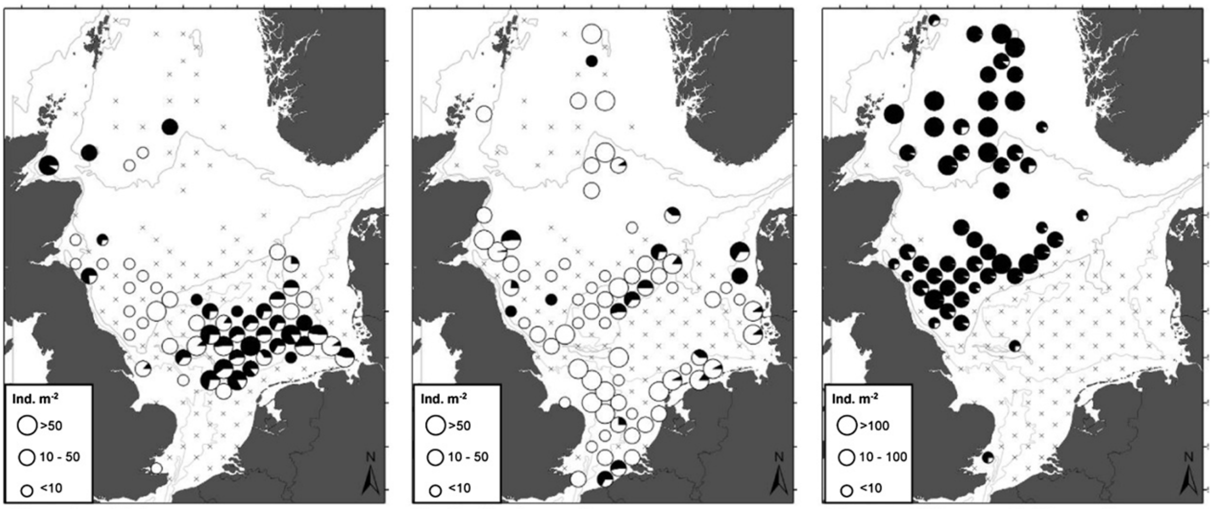
In 1986, the communities off the northern British coast (>50 m) along the Flamborough Frontal System were split into several clusters (B, C, E4), while in 2000 the area was separated mainly into the two clusters M1 and M2 (Figs. 4 and 6). Differences in communities were caused by the increase in abundance in 2000 of the polychaetes *Paramphinome jeffreysii*, *Myriochele* spp. and *Spiophanes bombyx*, but a decrease of the polychaete *O. borealis* at some stations (Fig. 2, Table 5).

In the eastern North Sea and in the central Southern Bight (1986 clusters D1 and F2), differences in communities between 1986 and 2000 (Figs. 4 and 6) were caused by an increase in the abundance of phoronids, the small sea urchin *Echinocyamus pusillus*, the polychaetes *Spiophanes bombyx*, *Lanice conchilega*, *Magelona* spp., and the amphipod *Urothoe poseidonis*, while the abundance of the amphipod *Bathyporeia* spp. and the polychaete *Ophelia borealis* decreased in 2000 (Table 5, Fig. 2). The abundance of the polychaetes *L. conchilega*, *S. bombyx* and *Pectinaria* spp. as well as of the bivalve *Spisula* spp. increased in coastal areas (1986 cluster F2) (Fig. 2).

The community structure in the Oyster Ground and at the Frisian Front (1986 cluster D2) remained rather stable between 1986 and 2000 (Figs. 4 and 6), although the abundance of the ophiurids *Amphiura filiformis* and *Ophiura albida* decreased and the



Lanice conchilega *Magelona* spp. *Myriochele* spp.



Nucula nitidosa *Ophelia borealis* *Paramphinome jeffreysii*

Fig. 2. (*continued*).

abundance of the bivalves *Corbula gibba* and *Abra alba* increased in 2000 (Fig. 2, Table 5).

The Dogger Bank community (1986 cluster D1) also remained rather stable (Figs. 4 and 6), despite the decrease in abundance of the polychaete *Ophelia borealis* (Fig. 2) and the bivalve *Abra prismatica*. In particular, at the Tail End abundances of *L. conchilega* and the amphipods *Urothoe poseidonis* and *Bathyporeia* spp. increased, while the abundance of the amphipods decreased at the shallow South West Patch (Fig. 2).

The abundance of the bivalves *Nucula nitidosa*, *Corbula gibba* and the brittle star *Acrocnida brachiata* increased in 2000 in the German Bight (1986 cluster D2) (Fig. 2, Table 5).

3.5. *Relationship between spatial distribution of communities and environmental factors*

The CCAs performed for the relationship between spatial distribution of communities and environmental factors in 1986 and 2000 show that the communities were associated with a depth gradient along the 1st axis in both years (Fig. 7). An increase in depth was related to the communities >50 m and >100 m as well as to the SST in February and salinity in February and June in both years (1986 clusters A, E1, E2, E4, F1, F2; 2000 clusters M1 and M2). The communities in shallow areas such as the Dogger Bank and the eastern North Sea were related to average wave exposure, tidal stress, primary production and SST in June. The main difference between the relationship in 1986 and 2000 is that in 1986 the communities <50 m were spatially separated in relation to single environmental factors (Fig. 7a), while in 2000 no such separation was visible (Fig. 7b).

4. Discussion

4.1. *Changes in species distribution and abundance: increase in SST and food availability?*

Indications of range extension and changes in abundance of species along a north-south gradient probably caused by warming of the sea have been recorded in the North Atlantic (e.g. Southward et al., 2004; Mieszkowska et al., 2006), but mainly for species of intertidal or coastal habitats and less so for species in off-shore waters.

For the reduced station grid used for this study, 455 macrofauna species were included in the analyses, while the entire NSBP 2000

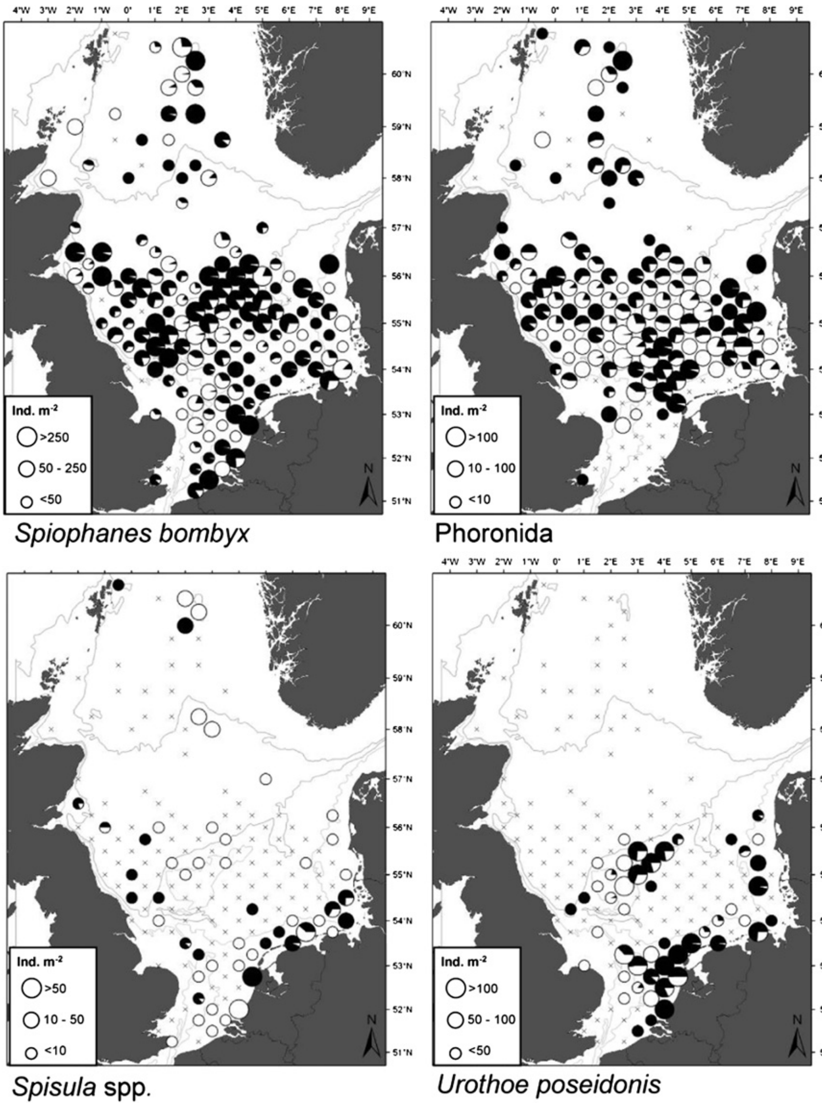


Fig. 2. (*continued*).

dataset contained more than 1500 taxa (Rees et al., 2007), of which many were rare species with one or a few records only. However, we haven't found clear indications for an immigration of non-native macrofauna species or neozoans in the subtidal North Sea as did Neumann et al. (2010) recently for the epifaunal non-native decapod species *Goneplax rhomboides*. Furthermore, we found no clear indication of a large-scale latitudinal shift in the distribution of macrofauna species in the North Sea, but the detection of these shifts might be hampered by the inconsistencies of the sampling schemes and, consequently, the relatively low number of comparable stations used in this study (see above).

In contrast to off-shore waters the environmental conditions along the coastal regions of the North Sea change more gradually, enabling a more continuous range expansion of species. Thus, distribution shifts of several intertidal species of up to 50 km per decade were observed (Helmuth et al., 2006). In the deeper waters of the North Sea, the large-scale bathymetrical and hydrographical conditions mainly trigger the spatial patterns of environmental gradients, which may act as barriers for further north-south range expansions in the North Sea (e.g. the differences in bottom temperature, stratification and currents north and south of the 50 m depth contour). This is supported by the finding of corresponding separation in benthic communities along the depth contours, which remained rather stable over the studied time period (see below).

Instead, we found an increase in abundance and a spatial extension within the core distribution areas of macrofauna species in the North Sea, which might be related to a SST mediated increase in pelagic or benthic primary production (McQuatters-Gollop et al., 2007).

The abundance of species with a core distribution in the southern North Sea, such as the small bivalves *Abra alba*, *Corbula gibba and Nucula nitidosa* increased in the entire Oyster Ground towards the southern flank of the Dogger Bank between 1986 and 2000. These deposit-feeding species are also common in the nutrient enriched inner German Bight and seem to benefit from the higher food supply (Rachor, 1980; Kröncke et al., 2004; McQuatters-Gollop et al., 2007; Holmes and Miller 2006).

Also the increase in abundance of 'southern' interface- and suspension-feeding species such as the bivalve *Tellina* spp., the polychaete *Lanice conchilega* and the warm-temperate ophiurid *Acrocnida brachiata* as well as the sand-licking sea urchin *Echinocyamus pusillus* at the Dogger Bank Tail End or off Jutland in 2000 gives evidence for an SST mediated increase in pelagic and benthic

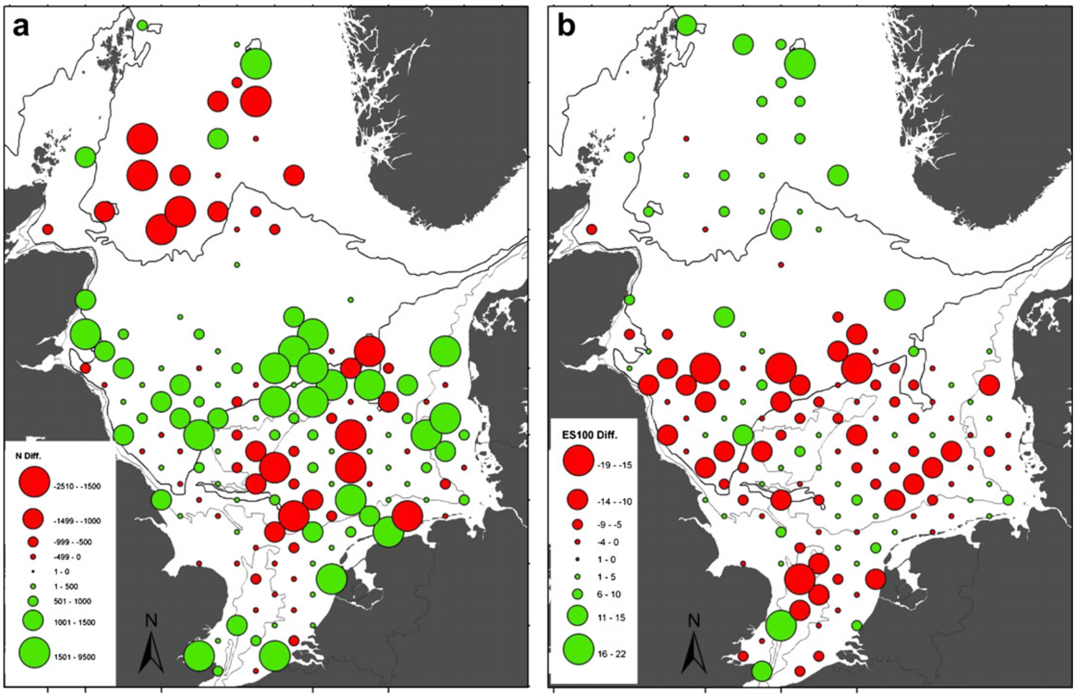


Fig. 3. Differences in a) mean abundance per m^2 and b) mean ES(100) between 1986 and 2000. Green dots indicate an increase and red dots a decrease in 2000 compared to 1986. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

primary production and food availability in these areas (Bauerfeind et al., 1990; Niermann, 1996; Kröncke et al., 2001, 2004, in press; Wieking and Kröncke, 2001).

The increase in abundance of the ophiurid *Acrocnida brachiata* in 2000 at the Dogger Bank and especially in the German Bight, where this species was hardly found in 1986, seems to be a response to higher water temperatures since the late 1980s and higher sediment mobility, since it is a warm-temperate species and buries deeper in the sediment than the eurytherm *Amphiura filiformis* (Ursin, 1960). *Acrocnida brachiata* was also previously found in increased numbers in shallow exposed parts of the Dogger Bank, compared with the late 1980s (Wieking and Kröncke, 2003). This finding was related to rising SST and hydrodynamic energy related to the changes in the NAO (Siegismund and Schrum, 2001; Beare et al., 2002.)

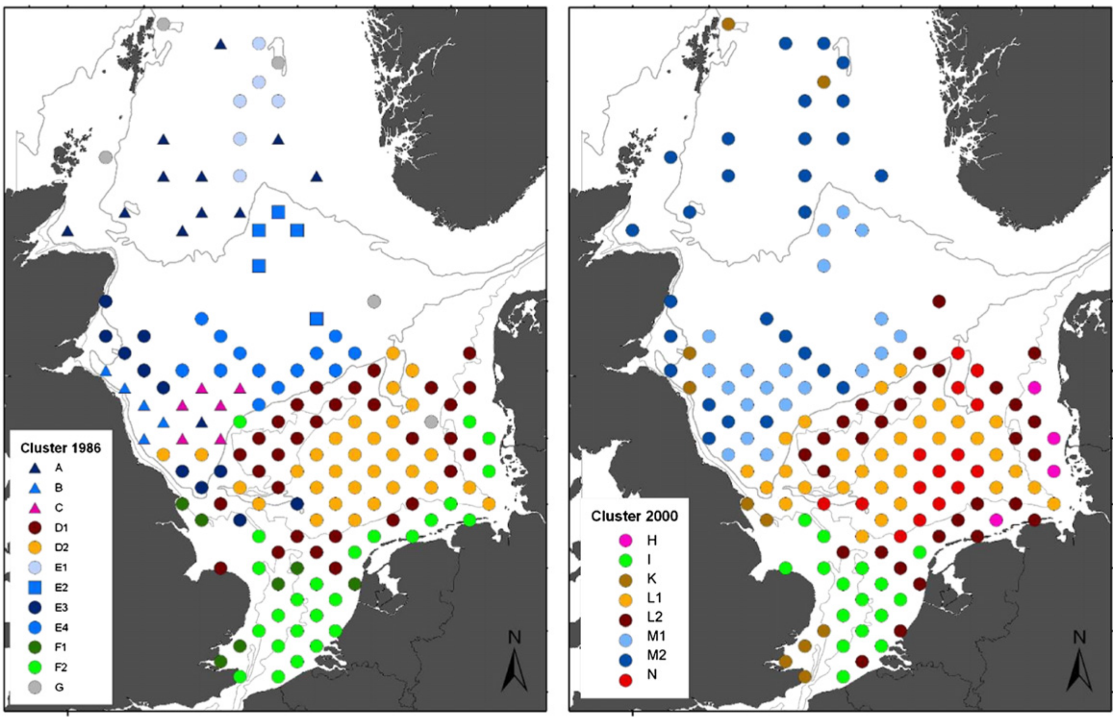


Fig. 4. Spatial distribution of macrofauna communities in 1986 (left) and 2000 (right) based on fourth-root transformed abundance data. Symbols denoting individual communities are not corresponding between 1986 and 2000.

Table 1
Correlation coefficients (Spearman rank) relating the similarity matrices of 1986 and 2000 data for different transformation types (RELATE).

	R	p
Fourth root	0.533	0.001
Square root	0.527	0.001
Presence-absence	0.511	0.001
No transformation	0.421	0.001

North of the 50 m depth contour, the substantial increase in abundance of *Paramphinome jeffreysii* and of the interface-feeding polychaetes *S. bombyx* and *Myriochele* spp. seemed also to be related to the increase in food availability (Pearson and Mannvik, 1998). Calmer conditions and better light penetration might have enhanced the subsurface primary production usual in these areas (Riegman et al., 1990; Nielsen et al., 1993; Richardson et al., 1998), which also feeds benthic foraminiferans, the favourite prey for *P. jeffreysii* (Pearson et al., 1996).

In contrast, the cold-temperate polychaete species *Ophelia borealis* had decreased in abundance in the entire North Sea from 1986 until 2000. Also Wieking and Kröncke (2001) found a decrease in abundance of this species at the Dogger Bank in the late 1990s, which they attributed to the increase in SST since 1988.

Since this study is based on the comparison of two time periods only, general conclusions about consistency of changes are difficult to draw, but other long-term studies on a more local scale showed similar trends of an increase in abundance of 'southern' or warm-temperate species and a decrease of northern or cold-temperate species in the southern North Sea (Kröncke et al., 2001; Wieking and Kröncke, 2003). These changes were also found for other ecosystem components of the North Sea such as plankton and fish (see introduction), which were also related to hydro-climate change since the late 1980s.

4.2. Changes in community structure on a North Sea wide spatial scale

The large-scale spatial distribution of the North Sea macrofauna communities in 2000 (NSBP) (see also Rachor et al., 2007) was rather similar to that in 1986 (NSBS) as described by Künitzer et al. (1992). The major divisions in community structure still occur at the 50 and 100 m depth contours, and correspond with the three étages described by Glémarec (1973). These divisions were also found for epifauna and fish by Zühlke et al. (2001), Callaway et al. (2002) and Reiss et al. (2009a). Künitzer et al. (1992) identified water temperature, different water masses, sediment structure and food availability as important influences on North Sea benthic communities.

Similarly, the CCAs of this study revealed that water depth and hydrographic variables such as bottom water temperature, bottom water salinity, tidal stress and stratification were the most important environmental factors structuring the macrofauna communities. This was also found for epifauna and fish communities (Callaway et al., 2002; Rees et al., 2007; Ehrich et al., 2009; Reiss et al., 2009a), suggesting similar underlying drivers for structuring large-scale community patterns of the majority of benthic ecosystem components in the North Sea.

4.3. Changes in community structure on localised spatial scales

On localised spatial scales differences between the 1986 and the 2000 macrofauna communities occurred mainly north of the 50 m and the 100 m depth contours as well as in the eastern North Sea, at the Frisian Front and in the coastal Southern Bight.

The differences in total abundance and in community structure found at >100 m depth were partly caused by the use of different mesh sizes in this region in 1986 (0.5 mm) and 2000 (1 mm). Nevertheless, the diversity (ES100) was slightly higher in 2000, which was not expected since the use of smaller mesh sizes in 1986 should have led to a higher diversity in 1986. Also the strong increase in abundance of the small polychaete *Paramphinome jeffreysii* in 2000, as also found by Schückel et al. (2010), cannot be attributed to the differences in the mesh size used, since this species should be more efficiently sampled with smaller meshes. Nevertheless, changes in community structure between 1986 and 2000 can be more reliably discussed for the areas <100 m, where the same mesh size was used in sample processing.

Table 2
Main macrofauna assemblages in the North Sea in 1986 with information dominant and characteristic species (based on SIMPER), mean abundance (m^{-2}), the average similarity (Av. sim.; %) of each cluster, and number of stations in the cluster (N).

Cluster	Dominant (d) and characteristic (c) taxa	Mean total abundance	Mean ES100	Av. sim.	N
A	*Thyasira* spp. (c,d), *Myriochele* (d), *Capitella* spp. (d), *Levinsenia gracilis* (d,c), *Notomastus* (c), *Lumbrineris latreilli* (c)	2507 ± 1124	28.0 ± 3.7	35.0	12
B	*Myriochele* spp. (c,d), *Ampelisca spinipes* (d), *Capitella* spp. (c,d), *Goniada* spp. (c), *Levinsenia gracilis* (c,d)	841 ± 293	34.4 ± 6.9	41.9	5
C	*Amphiura filiformis* (c,d), *Eudorellopsis deformis* (d) Phoronida (c,d), *Scoloplos armiger* (c,d)	529 ± 162	21.2 ± 5.7	42.0	6
D1	*Bathyporeia* spp. (c,d), *Magelona* spp. (c,d), *Spiophanes* spp. (c,d), *Tellina* spp. (c,d), *Polinices* spp. (c), Phoronida (c,d), *Harpinia antennaria* (c)	1265 ± 600	21.8 ± 5.7	46.9	31
D2	*A. filiformis* (c,d), *Mysella bidentata* (c,d), *Myriochele* spp. (d), *Pholoe baltica* (c,d)	1926 ± 1075	24.1 ± 4.8	49.6	30
E1	*Spiophanes* spp. (c,d), *Owenia fusiformis* (c,d), *Myriochele* spp. (c,d), *Prionospio* spp. (c,d), *P. baltica* (c)	1944 ± 545	29.8 ± 1.1	46.7	6
E2	*Bathyporeia* spp. (c,d), *Scoloplos armiger* (c,d), *E. deformis* (c,d), *Ophelia borealis* (c)	925 ± 431	27.2 ± 1.7	41.6	5
E3	*O. borealis* (c,d), *A. filiformis* (c,d), *Spiophanes* spp. (c,d)	603 ± 217	31.9 ± 3.3	46.2	11
E4	*Myriochele* spp. (d), *A. filiformis* (c,d), *Spiophanes* spp. (d), *S. armiger* (c,d), Nemertina (c)	694 ± 439	32.6 ± 6.6	48.6	13
F1	*Nicomache* spp. (d), *Urothoe poseidonis* (d), *M. bidentata* (c,d), P. baltica (c,d), Nemertina (c)	1200 ± 973	26.4 ± 5.3	36.0	7
F2	*Magelona* spp. (d), *Spisula* spp. (d), *Pisione remota* (d) Nemertina (c), *O. borealis* (c,d), *Bathyporeia* spp. (c,d)	693 ± 624	17.2 ± 3.5	38.0	25
G	*Exogone* spp. (c,d), *Glycera lapidum* (d), *Aonides paucibranchiata*(c,d), *Goniada* spp. (c,d)	879 ± 668	22.3 ± 1.6	25.0	5

Table 3
Main macrofauna assemblages in the North Sea in 2000 with information on dominant and characteristic species (based on SIMPER), mean abundance (m^{-2}), the average similarity (Av. sim.; %) of each cluster, and number of stations in the cluster (N).

Cluster	Dominant (d) and characteristic (c) species	Mean Total Abundance	Mean ES100	Av. sim.	N
H	*Spio* spp. (d), *Aoinides paucibranchiata* (c,d), *Goodallia triangularis* (d), *Branchiostoma lanceolata* (d), *Ophelia borealis* (c)	4850 ± 384	10.7 ± 2.2	29.9	4
I	*Gastrosaccus spinifer* (d), *Spiophanes* spp. (c,d), *Nephtys cirrosa* (c,d), *Urothoe poseidonis* (d), *Bathyporeia* spp. (c,d), *Spio* spp. (c)	317 ± 219	14.0 ± 6.8	27.3	16
K	*Lanice conchilega* (d), *Pectinaria* spp. (d), *Pisidia longicornis* (d), *Pomatocerus* spp. (c,d), Nemertina (c), *Cauleriella* spp. (c)	1788 ± 1599	29.4 ± 7.4	29.7	10
L1	*Spiophanes* spp. (c,d), *Amphiura filiformis* (c,d), *Mysella bidentata* (d), *Magelona* spp. (c,d), Phoronida (c), *Pholoe baltica* (c)	1441 ± 669	21.2 ± 3.6	41.4	30
L2	*Spiophanes* spp. (c,d), Phoronida (d), *Magelona* spp. (c,d), *Bathyporeia* spp. (c,d), *Spisula* spp. (d), *Tellina* spp. (c,d)	2606 ± 2431	17.7 ± 5.7	41.0	30
M1	*Myriochele* spp. (d), *Spiophanes* spp. (c,d), *A. filiformis* (c,d), *Scoloplos armiger* (c),*Paramphinome jeffreysii* (c)	1130 ± 687	22.7 ± 5.7	44.5	20
M2	*Myriochele* spp. (c,d), *P. jeffreysii* (c,d), *Spiophanes* spp. (c,d), *Goniada* spp. (c)	1387 ± 846	32.2 ± 5.1	44.5	27
N	*A. filiformis* (d), *Myriochele* spp. (d), *Corbula gibba* (d), *Abra alba* (d), *Harpinia antennaria* (c), *Nephtys hombergii* (c), *Notomastus* spp. (c)	1807 ± 1405	20.6 ± 4.9	40.4	15

Significant changes in community structure between 1986 and 2000 were found for all communities (Table 4), but the most distinct changes occurred north of the 50 m depth contour off the British coast along the Flamborough Head frontal system and its extension north of the Dogger Bank, along the Frisian Front and along the eastern North Sea frontal system (Fig. 4) (Otto et al., 1990; Hill et al., 1994). Some of these changes were caused by an increase in abundance of short lived polychaete species (Table 5). These opportunistic species are characterised by the ability to respond quickly to changes in food availability. Thus, by comparing two time periods only, our findings may rather reflect short-term responses of macrofauna than consistent long-term trends. However, this increase in abundance of opportunistic species was frequently found in different regions of the North Sea over the last decades, ranging from off-shore areas to the intertidal (e.g. Reise, 1982; Beukema, 1991; Kröncke, 1992; Kraan et al., 2011), indicating a consistent large-scale trend in North Sea macrofauna communities.

As mentioned above, most obvious changes in macrofauana communities were found in regions with frontal systems, which are areas of enhanced primary production. Frontal systems are influenced by changes in e.g. wind direction, currents, flow velocities and flushing times (Otto et al., 1990; Hill et al., 1994; Siegismund, 2001). The NAOI related hydro-climate change at the end of the 1980s coincided with an increased inflow of Atlantic water masses in particular through the Fair Isle current and from the North. This probably resulted in stronger frontal conditions, in particular along the Flamborough Frontal system and north of the Dogger Bank (Reid et al., 2001b; Siegismund, 2001; Siegismund and Schrum, 2001; Wieking and Kröncke, 2001), but also along the Frisian Front (Amaro et al., 2007; van Nes et al., 2007) due to changes in inflow of Atlantic water masses through the English Channel into the southern North Sea. Frontal systems are typically areas of enhanced primary production and food supply for the benthos. The increase in SST and the changes in the hydro-climate seem to have also enhanced the primary production in these areas, which may have caused increasing abundances of macrofauna species sensitive to organic enrichment.

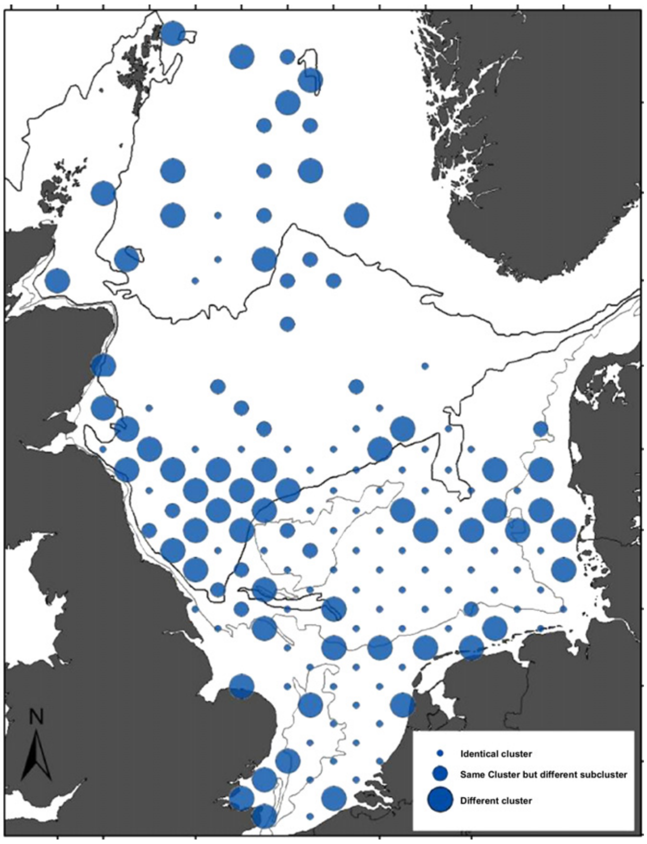


Fig. 5. Differences in the cluster classification between 1986 and 2000 based on combined data sets (1986 and 2000) with fourth-root transformed abundance data. Small-sized circles represent stations which were classified identically in 1986 and 2000. The largest circles represent stations classified in different main clusters.

Table 4
Differences between 1986 and 2000 data revealed with ANOSIM for the MDS-plots shown in Fig. 6. Comparison based on 1986 clusters (Fig. 4).

Cluster	R	*p*
A	0.511	0.001
B	0.426	0.016
C	0.648	0.002
D1	0.177	0.001
D2	0.181	0.001
E1	0.837	0.002
E2	0.588	0.008
E3	0.372	0.001
E4	0.377	0.001
F1	0.202	0.042
F2	0.131	0.001
G	0.404	0.032

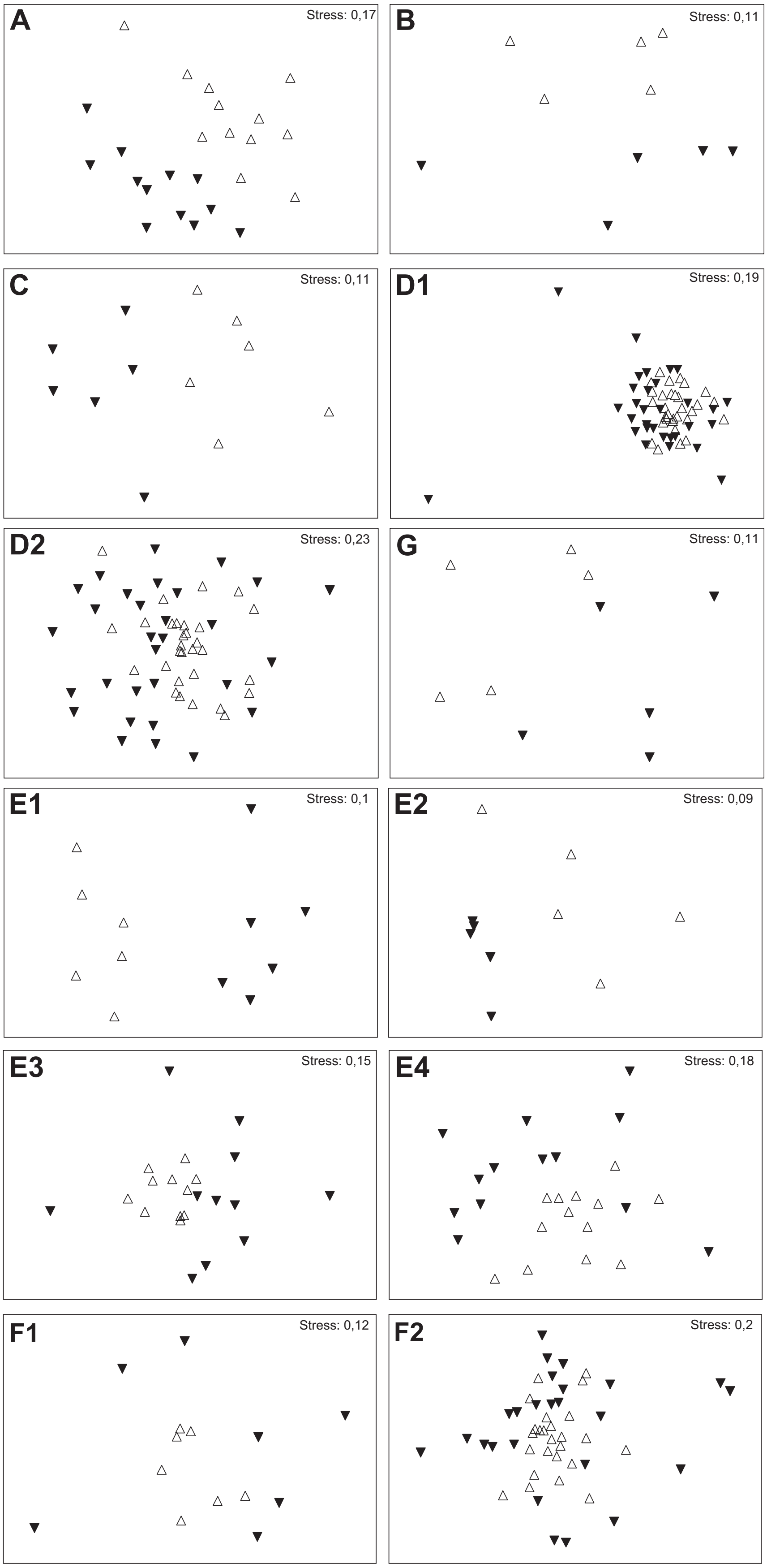


Fig. 6. MDS-plots revealing similarities between communities of single clusters for 4th root transformed abundance data of 1986 (△) and 2000 (▼), based on 1986 cluster separation.

Table 5
Temporal trends of mean abundance per m^2 of dominant and characteristic species in 1986 and 2000, and average dissimilarity (AvDis.%) between clusters in 1986 and 2000 revealed with SIMPER. Comparison based on 1986 clusters (Fig. 6).

	Taxon	Trend	1986	2000	Av Dis.
A	*Thyasira* spp.	(↓)	346	18	72.5
	Lumbrineris latreilli	(↓)	26	0	
	Myriochele spp.	(↓)	166	109	
	Paramphinome jeffreysii	(↑)	30	97	
	Capitella spp.	(↓)	125	2	
B	*Capitella* spp.	(↓)	42	0	66.4
	Ampharete lindstroemi	(↑)	0	81	
	Praxillella spp.	(↓)	6	0	
	Paramphinome jeffreysii	(↑)	1	25	
	Ampelisca spinipes	(↓)	43	1	
C	*Spiophanes bombyx*	(↑)	37	348	66.3
	Paramphinome jeffreysii	(↑)	4	24	
	Myriochele spp.	(↑)	13	61	
D1	Phoronida	(↑)	77	327	62.1
	Spiophanes bombyx	(↑)	97	367	
	Bathyporeia spp.	(↓)	205	155	
	Lanice conchilega	(↑)	2	128	
D2	*Amphiura filiformis*	(↓)	539	411	59.7
	Mysella bidentata	(↓)	216	107	
	Corbula gibba	(↑)	4	103	
	Ophiura albida	(↓)	44	7	
	Abra alba	(↑)	2	30	
E1	*Paramphinome jeffreysii*	(↑)	8	128	65.5
	Echinocardium flavescens	(↓)	113	1	
	Eudorelopsis deformis	(↓)	105	3	
	Amphiura chiajei	(↑)	0	40	
	Laonice sarsi	(↑)	5	22	
E2	*Amphiura filiformis*	(↑)	38	113	62.0
	Myriochele spp.	(↑)	3	232	
	Ophelia borealis	(↓)	34	1	
	Paramphinome jeffreysii	(↑)	8	25	
	Phoronida	(↑)	3	20	
E3	*Ophelia borealis*	(↓)	55	4	68.4
	Amphiura filiformis	(↑)	49	66	
	Spiophanes bombyx	(↑)	34	357	
	Myriochele spp.	(↑)	7	116	
E4	*Paramphinome jeffreysii*	(↑)	2	61	62.0
	Myriochele spp.	(↑)	132	357	
	Nephtys longosetosa	(↓)	14	1	
	Spiophanes bombyx	(↑)	46	243	
F1	*Pholoe baltica*	(↓)	53	17	78.6
	Lanice conchilega	(↑)	31	532	
	Capitella spp.	(↓)	31	0	
	Lumbrineris latreilli	(↓)	27	0	
F2	*Spiophanes bombyx*	(↑)	23	396	72.9
	Ophelia borealis	(↓)	45	4	
	Magelona spp.	(↑)	73	119	
	Urothoe poseidonis	(↑)	16	58	
G	*Spiophanes bombyx*	(↑)	14	53	80.1
	Paramphinome jeffreysii	(↑)	0	247	
	Aonides paucibranchiata	(↓)	64	19	
	Magelona spp.	(↑)	0	87	
	Amphiura filiformis	(↑)	3	64	

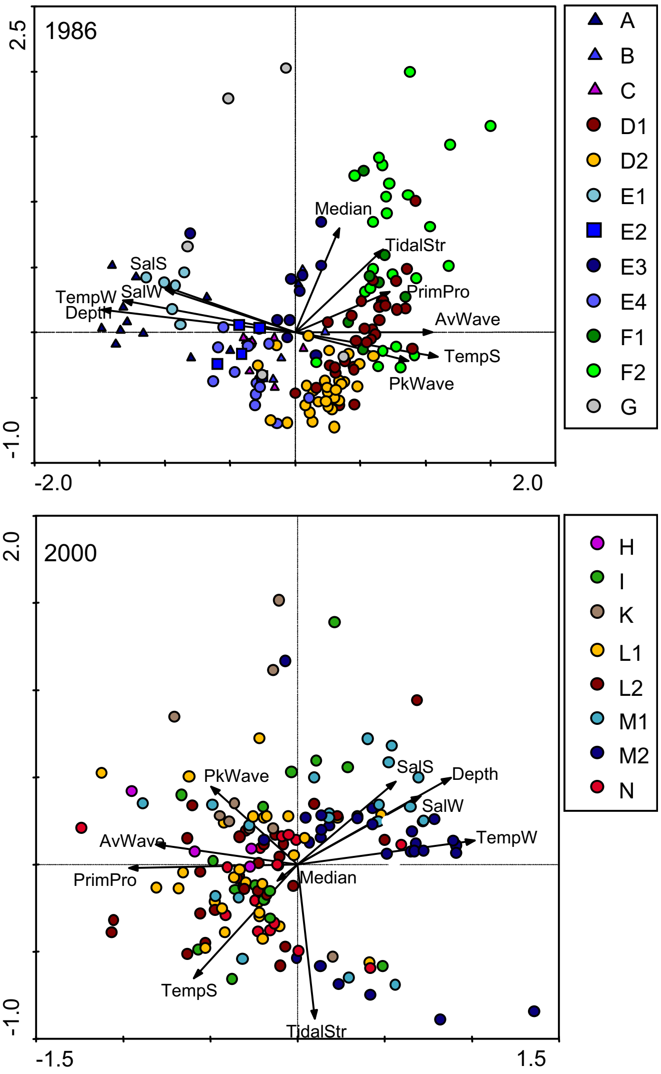


Fig. 7. Triplots of the CCA ordination for macrofauna communities and environmental parameters in 1986 and 2000. The vector lines represent the relationship of environmental variables to the ordination axes and their length is proportional to their relative significance. (Wave = peak wave stress; AvWave = average wave stress; TempS = summer bottom temperature; TempW = winter bottom temperature; SalS = summer bottom salinity; SalW = winter bottom salinity; PrimPro = primary production; TidalStr = tidal stress; Median = median grain size).

4.4. Other stressors

Beside the climate related changes in the benthic communities discussed above, several other anthropogenic impacts such as commercial fishing, oil and gas exploitation, dredging and eutrophication are known to influence the North Sea benthos to varying degrees, of which fishing might be considered the most important one, at least in terms of the large spatial scale of potential impacts (e.g. OSPAR, 2000). Thus, it is possible that trawling disturbance may be responsible for the changes in the macrofauna communities and species distribution in the North Sea observed in this study. The southern North Sea is characterised by intensive beam trawling activity, which can affect diversity, secondary production and species composition of benthic communities on various spatial scales (Kaiser et al., 2000; Rumohr and Kujawski, 2000; Jennings et al., 2001; Hiddink et al., 2006; Callaway et al., 2007; Reiss et al., 2009b). Furthermore, Callaway et al. (2002) hypothesised that the high diversity of sessile epibenthic species in the northern North Sea might be caused by the less severe impact of otter trawling in this area compared to intensive beam trawling in the southern North Sea.

Unfortunately, detailed information about the changes of total fishing effort between 1986 and 2000 in the North Sea is relatively sparse. The effort of the UK fleet landing in Scotland, which mainly comprises fishing activities with otter trawls in the central and northern North Sea, did not change markedly within this time period (Greenstreet et al., 2009). In contrast, Jennings et al. (1999) described an increase in beam trawling and a decrease in otter trawling effort in the southern North Sea from 1985 to 1995, but the beam trawling effort seemed to have decreased again during the last decade (Neumann et al., 2009a). However, the changes in fishing effort summarized for such large areas of the North Sea can hardly be related to the changes in the different benthic communities, because fishing effort is known to be very patchily distributed (Rijnsdorp et al., 1998; Jennings et al., 1999) and responses of macrofauna to fishing disturbance can vary significantly on small spatial scales (Reiss et al., 2009b).

Nevertheless, demersal fishing has been carried out across the entire North Sea and undoubtedly affected benthic communities. Without detailed information on the distribution of fishing effort and temporal trends, it cannot be ruled out as a possible causal factor for the changes in macrofauna communities observed in this study. But the observed large-scale changes in macrofauna communities seem to rather reflect the variation in hydroclamatic conditions than to follow trends expected from variations in fishing (see also Craeymeersch et al., 2007).

Acknowledgements

We thank the captains and crews of all research vessels involved in the NSBP 2000 for their help with sampling, as well as all research scientists, technicians and students of all institutes involved for their help with sorting the samples and identifying the organisms. This publication is initiated and facilitated by the Study Group on the North Sea Benthos Project 2000 (NSBP) and the Benthos Ecology Working Group (BEWG), which are expert groups of the International Council for the Exploration of the Sea (ICES). We thank the anonymous referees for their valuable comments. The work of I. Kröncke and H. Reiss is a contribution to the Research Centre "Biodiversity and Climate (BiK-F)" funded by LOEWE.

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Vol. 449: 221–232, 2012
doi: 10.3354/meps09563

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published March 8

Trophic ecology of juvenile flatfish in a coastal nursery ground: contributions of intertidal primary production and freshwater particulate organic matter

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ABSTRACT: Coastal and estuarine nurseries are essential habitats for juvenile flatfish. These small but productive areas provide food supply and sustain adult fish populations. The Mont-Saint-Michel Bay (MSMB) supports an important flatfish nursery ground but differs from many other nursery habitats due to limited freshwater inputs. The objectives of the present study in the MSMB were to (1) use gut content analysis to identify prey of the 2 most abundant flatfish species (common sole *Solea solea* and plaice *Pleuronectes platessa*) for different juvenile age-classes (0-group and 1-group for sole, 0-group for plaice), (2) use C and N stable isotope analysis to model the production sources sustaining juvenile flatfish production, and (3) compare these results with previous knowledge of estuarine nursery grounds located in western Europe. Items found in gut contents differed between species and size classes, with juvenile plaice having a larger prey spectrum. Despite accounting for sensitivity to large uncertainties in source signatures and trophic enrichment factors, stable isotope mixing models led to robust outputs. In contrast to previous studies in estuarine nurseries, we found that microphytobenthos was the major carbon source contribution to juvenile flatfish. The contribution of freshwater particulate organic matter was nonetheless significant, in spite of the very limited river inputs to MSMB.

KEY WORDS: Microphytobenthos · Organic matter origin · Benthic food web · Coastal nursery ground · Juvenile flatfish

INTRODUCTION

Coastal and estuarine ecosystems are the most productive environments in the world and represent half of oceanic secondary production (Costanza et al. 1997). They are essential fish habitats as they play the key role of nursery grounds for many marine species widely distributed on the continental shelf (Beck et al. 2001, Peterson 2003), such as flatfish (van der Veer et al. 2000). The capacity and quality of these habitats have considerable influence on the renewal of marine populations (Rijnsdorp et al. 1992, Gibson 1994, Johnson et al. 1998, Peterson et al. 2000). Better understanding of the functioning of coastal and estuarine nursery grounds is crucial for the development of proper management policies (Beck et al. 2001).

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In many estuaries (Vilaine, Rhône, Thames, Gironde, Tagus, and Danube), the influence of river flow on nursery-ground carrying capacity has been established and incorporation of continental organic matter into juvenile-flatfish food webs has been documented (Le Pape et al. 2003, Darnaude et al. 2004, Leakey et al. 2008, Pasquaud et al. 2008, Vinagre et al. 2008, Banaru & Harmelin-Vivien 2009, Kostecki et al. 2010). However, the origin of food sources incorporated into juvenile-flatfish food webs is still not understood in the case of non-estuarine nursery areas.

The Mont-Saint-Michel Bay (MSMB) in France is located in the English Channel in western Europe (see Fig. 1). It is a vast, productive bay supporting nursery areas for several marine species (Kostecki et al. 2011), particularly the common sole *Solea solea* (L., 1758) and plaice *Pleuronectes platessa* (L., 1758). In this bay, freshwater influence is limited by low river discharge and high hydrodynamic circulation linked to the megatidal regime (Cugier et al. 2010). Primary production in the MSMB is largely based on salt marshes and benthic diatoms, and secondary production is enhanced by large mudflats (Lefeuvre et al. 2000, Arbach Leloup et al. 2008). We analyzed the origin of food sources incorporated into juvenile-flatfish food webs in this non-estuarine but productive nursery area.

First, we aimed to document resource-use overlap by juvenile flatfish species. Since gut examination has some limitations (e.g. under-estimation of prey diversity; Hyslop 1980), this method was coupled with C and N stable isotope analysis to determine energy sources for flatfish in the bay (Peterson & Fry 1987). Six different sources were traced into the flatfish food web using the R software package 'stable isotope analysis in R' (SIAR), a mixing model based on Bayesian methods (Parnell et al. 2010). A sensitivity analysis to different trophic enrichment factors (TEFs) was performed (Bond & Diamond 2011). Finally, we compared our results with those of common juvenile sole in estuarine nursery grounds elsewhere in western Europe.

MATERIALS AND METHODS

Mont-Saint-Michel Bay

The MSMB is located in northwest France, in the western part of the English Channel (48° 40′ N, 1° 35′ W; Fig. 1). The bay is a semi-diurnal macrotidal system with a high tidal range, reaching 15.50 m during the highest spring tides (Larsonneur 1994) and with limited freshwater inputs (average annual discharge: 7.1, 5.1, and 10.0 $m^3 s^{-1}$ for the rivers Coues-

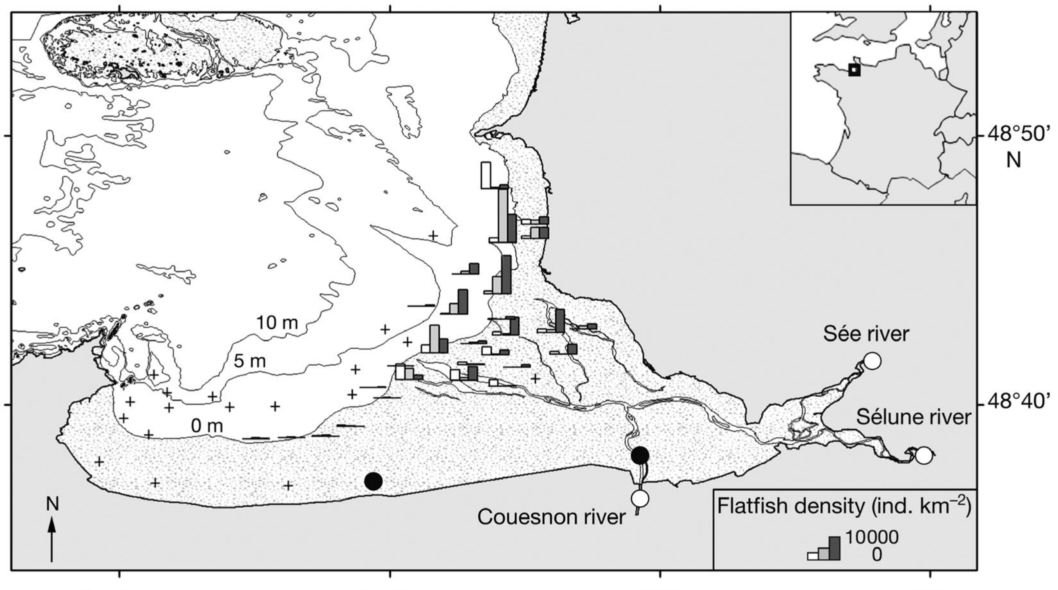

Fig. 1. Sampling stations in Mont-Saint-Michel Bay in August 2008: histograms show density of trawled age 0 (young-of-the-year) *Pleuronectes platessa* (0G-plaice) (white bar), age 0 (young-of-the-year) *Solea solea* (0G-sole) (light grey bar), and 1-group *S. solea* (1G-sole) (dark grey bar); +: no catch; circles: sampling sites for microphytobenthos (●) and freshwater particulate organic matter from rivers (○). Bathymetry lines are shown (0, 5, and 10 m). Inset (upper right) indicates general location of the study area

non, Sée, and Sélune, respectively). About half of this wide, shallow bay (500 km², depth <20 m) consists of mudflats (210 km²) and intertidal salt marshes (40 km²), which make the MSMB the largest salt marsh in Europe. The primary production of these large intertidal areas is central to ecosystem functioning (Lefeuvre et al. 2000), and estuarine influence is limited in the MSMB (Cugier et al. 2010). The MSMB is one of the most important nurseries in the English Channel for several fish species of commercial interest such as sea bass *Dicentrarchus labrax*, whiting *Merlangius merlangus*, elasmobranchs *Raja* spp., and flatfishes, mainly common sole and plaice, but also brill *Scophthalmus rhombus* (Legendre 1984, Laffaille et al. 1998, Kostecki et al. 2011).

Sample collection and preparation

Benthic macrofauna and flatfish were sampled during daytime with a beam trawl (2.9 m wide, 0.5 m high opening, and 10 mm stretched mesh net cod end) in August 2008. Forty-six hauls were carried out (Fig. 1) at 2.5 knots for 15 min, on average covering 3400 m² each haul. For each haul, benthic macrofauna and flatfish were sorted and identified to the lowest possible taxonomic level, generally to the species level. Due to proliferation of the invasive mollusk *Crepidula fornicata* in the western part of the MSMB, flatfish are restricted to the eastern part (Kostecki et al. 2011) (Fig. 1). Common sole and plaice were the 2 flatfish species for which catches were large enough to allow a quantitative study of both diet and stable isotope signatures. Fish were collected under the standardized conditions of mid- to high tide, sea bottom temperature ranging from 18.2 to 18.6°C, and bottom salinity ranging from 34.1 to 34.9. Individuals were measured and size-frequency histograms were used to discriminate cohorts. Two cohorts, age 0 (young-of-the-year) (0G-sole, total length <11 cm) and 1-group (1G-sole, total length <22 cm), were sampled for common sole, and only age 0 (young-of-the-year) (0G-plaice, total length <13 cm) were sampled for plaice (Table 1). Samples collected for flatfish gut content analysis were stored in 7% formaldehyde, and samples for stable isotope analysis (juvenile sole, plaice, and benthic invertebrates considered to be potential prey) were refrigerated on the boat and then stored at −20°C in the laboratory.

During the same survey, 3 samples of freshwater were collected in the Couesnon, Sée, and Sélune rivers (measured salinity: 0.0; Fig. 1). The water was first sieved (200 µm mesh) to extract detritus and large zooplankton. Particulate organic matter (POM) was obtained by filtering 1 l of this water over precombusted Whatman GF/F filters. Filters were acidified (10% HCl) to remove carbonates, rinsed with Milli-Q water, and oven-dried (50 to 60°C for 48 h).

Table 1. Total length (TL) ranges and sample sizes (n) of flatfish analyzed for gut content and stable isotope analyses

Species	Gut content analysis TL range (mm)	n	Stable isotope analysis TL range (mm)	n
0G-plaice	42–125	120	47–114	68
0G-sole	53–106	178	56–100	49
1G-sole	118–212	51	116–206	47

Four samples (2 samples at each of 2 sites) of microphytobenthos (MPB; mainly benthic diatoms; Riera 2007) were collected at low tide on the intertidal section of the bay (Fig. 1) in August 2008. Benthic diatoms were extracted at the laboratory using the method suggested by Riera & Richard (1996) and described in Kostecki et al. (2010).

Gut content analysis

Because plaice and sole have a small stomach and a long alimentary tract (Beyst et al. 1999, Amara et al. 2001), the entire digestive tract (stomach and intestine) of each fish was removed from the body and stored in 70% alcohol. The number of empty digestive tracts was counted and the vacuity index (proportion of empty digestive tracts) was calculated. Prey items found in digestive tracts were sorted and counted under a binocular microscope. All prey items were identified to the lowest possible taxonomic level, generally the species. Indices of relative abundance (%*N*, the number of a particular prey item as a proportion of the total number of all prey items in the entire digestive tract) and percentage occurrence (%*O*, the percentage of gut in which a prey item occurred) of each prey were calculated for each group (species, age) of flatfish. To compare dietary overlap between 2 species or cohorts, the Schoener diet overlap index, α, was used (Schoener 1971):

$$\alpha = 1 - 0.5\left(\sum_{i=1}^{n} \left|P_{xi} - P_{yi}\right|\right) \quad (1)$$

where α is the dietary overlap between species or cohorts x and y, P_{xi} and P_{yi} are proportions of food category i used by species or cohorts x and y respectively, and n is the total number of food categories. This index, varying between 0.1 (no overlap) and 1 (perfect overlap), is generally considered biologically significant when values exceed 0.6 (Banaru & Harmelin-Vivien 2009).

Stable isotope analysis

Sample preparation

The benthic invertebrate species chosen for isotopic analysis were (1) dominant in terms of abundance and biomass, (2) potential prey for sole and plaice juveniles, and (3) found in the fish gut contents, i.e. *Abra alba*, *Arenicola marina*, *Cerastoderma edule*, and *Nephtys* sp. (see 'Results—Gut content analysis' and Table 2). In order to minimize the effects of lipids on $\delta^{13}C$ (Bodin et al. 2007), muscle tissues (except for polychaetes) were used for stable isotope analysis. White muscle samples were taken from sole and plaice dorsal musculature (Table 1), as recommended for fish (Pinnegar & Polunin 1999, Sweeting et al. 2007), and from the siphon of bivalves. Viscera, setae, and the jaw were removed from large specimens of polychaetes by dissection, and stable isotope analysis was carried out on the remaining whole body (Le Loc'h & Hily 2005). After dissection, the tissue samples were washed with distilled water to prevent contamination by sediment carbonates (Kharlamenko et al. 2001, O'Reilly et al. 2002). Samples were individually frozen (–20°C) before freeze-drying. Dried samples were ground to obtain a homogeneous powder. All the samples (benthic invertebrates, juvenile flatfish, POM, and MPB) were weighed and encapsulated in tin foil.

Stable isotope analysis

Ratios of ^{13}C:^{12}C and ^{15}N:^{14}N were obtained from continuous-flow isotope-ratio mass spectrometry. Samples were analyzed using a Finnigan Delta Plus XP isotope-ratio mass spectrometer interfaced with a Carlo Erba NC2500 elemental analyzer. Isotope ratios were reported in conventional delta (δ) notation as parts per mil (‰) relative to the international standard for Peedee Belemnite Carbonate and atmospheric nitrogen. Repeat analyses of the International Atomic Energy Agency and laboratory standards (N1, N2, CH6, CH7, acetanilide, and peach leaf) showed that maximum standard deviations (SD) for $\delta^{13}C$ and $\delta^{15}N$ values were 0.14 and 0.18, respectively. SD for duplicate samples from the present data set averaged 0.13 for C and 0.22 for N. Single measurements were carried out on all remaining samples. Because the C:N ratio used as a proxy for lipid content in samples was low and steady (<3.5), lipid normalization was not necessary (Post et al. 2007).

Additional stable isotope data

Stable isotope values from samples of marine POM and dead leaves of *Halimione portulacoides* and *Elymus athericus* collected in May 2002 in the MSMB (Riera 2007) were used to complete our organic matter sources. Since organic matter derived from marsh halophytes is known to contribute to the diet of all the tidal flat invertebrates (Lefeuvre et al. 2000), dead plant tissues were chosen instead of live plants, as their isotopic signatures are different (Riera 2007).

Only a fraction of the sedimentary pool can be assimilated by consumers (Zetsche et al. 2011). Accordingly, even if the flatfish are benthivorous, sediment samples were not collected for the present analysis.

Data analysis

Mean comparisons

ANOVAs coupled with Tukey's multiple comparison test were performed using the software program R to test whether $\delta^{13}C$ and $\delta^{15}N$ of flatfish differed between species and age. A significance p-value level of 0.05 was used in all test procedures.

Stable isotope mixing model

Sources incorporated into food webs were identified using a mixing model that provides a combination of feasible solutions accounting for multiple possible sources that could explain a consumer's stable isotope values (Phillips & Greg 2003). In the present study, we used a Bayesian model developed by Parnell et al. (2010) and implemented this in the package SIAR with the software program R. This Bayesian model takes into account uncertainty and variability (SD) concerning sources and TEFs.

Freshwater POM data from the Sée and Sélune rivers were pooled in the mixing model since values were very close (Sée: $\delta^{13}C$, –25.51 and $\delta^{15}N$, 5.70; Sélune: $\delta^{13}C$, –24.80 and $\delta^{15}N$, 6.11; see Fig. 2). However, freshwater POM signatures from Couesnon River were different, i.e. ^{13}C-depleted ($\delta^{13}C$, –30.45) and ^{15}N-enriched (δ^{15}N, 8.55), so they were kept separate. Dead leaves of *Elymus athericus* were ^{13}C-depleted and ^{15}N-enriched compared to leaves of *Halimione portulacoides*, so these data were not pooled. Therefore, 6 sources were included in the model: 3 from the present survey (MPB, freshwater POM from Couesnon River, and freshwater POM from Sée and Sélune rivers) and 3 (marine POM, dead leaves of *E. athericus*, and dead leaves of *H. portulacoides*) from Riera (2007).

Pooling stable isotope data for consumers and sources collected at different dates in the same analysis could be considered problematic because stable isotope signature of sources can change over space and time, leading to errors in estimates of source contributions. The interest of the SIAR model is to integrate such uncertainty. In the present study, the variation rates for marine POM data were especially high (see Table 3 & Fig. 2). We compared this variability with POM data collected over a 2 yr time period (2009 to 2010) from an adjacent sector of the western English Channel (Roscoff sampling point, data from SOMLIT, i.e. French national coastal observation system; http://somlit.epoc.u-bordeaux1.fr). The SD for marine POM data collected by Riera (2007) and used in the models (C: 1.01 and N: 1.17) was higher than the interannual variation in the time series from Roscoff (C: 0.94 and N: 1.09). Stable isotope signatures are less variable in dead leaves of marsh halophytes (Riera 2007), and lower SDs were associated with *Halimione portulacoides* and *Elymus athericus* (see Table 3). Overall, the uncertainty associated with sources from previous data was considered high enough to overcome, at least partly, the interannual variability in their stable isotope signatures.

The trophic level for common sole and plaice is 3.13 (SE: 0.32) and 3.26 (SE: 0.39), respectively (Froese & Pauly 2010), and closer to 3 for young post-settled juveniles (Darnaude et al. 2001). Thus, to trace organic matter in juvenile flatfish, 2 TEFs have to be considered: one from primary producer or organic matter to primary consumer (i.e. juvenile flatfish prey), and the second from primary consumer to secondary consumer (i.e. flatfish juveniles). Because TEFs have an impact on model outputs and estimates of source contributions (Bond & Diamond 2011), different TEFs were compared. From primary producer or organic matter to juvenile flatfish prey, one TEF value was used: 1.00 for C and 2.20 for N (DeNiro & Epstein 1978, 1981, Post 2002, Fry 2006). Then, from prey to flatfish juveniles, the following TEF values were used (see Table 4):

(a) a local TEF was calculated for each flatfish species or cohort as the difference between the mean C and N stable isotope signatures of the 4 benthic invertebrate species analyzed and each flatfish cohort or species (see Tables 3 & 4);

(b) a TEF from an experiment performed by F. Le Loc'h et al. (pers. comm.) concerning juvenile common sole reared with food sources of known δ^{15}N and δ^{13}C values in natural conditions (temperature and salinity) in the Thau lagoon (France);

(c) a TEF meta-analysis from the scientific literature (DeNiro & Epstein 1978, 1981, Post 2002, Fry 2006).

A larger review of TEFs in the scientific literature demonstrated that other values are possible (Minagawa & Wada 1984). Nevertheless, the 3 TEFs tested in the present analysis covered the range of values found in the scientific literature and allowed us to estimate the sensitivity of sources' contributions to TEFs. Without standardized information about the variability in estimates of these 3 TEFs, their associated standard error was maintained in SIAR as the default 0.5 value.

For each flatfish group, a Chi-squared (χ^2) test was performed to compare mean source contributions resulting from estimates obtained with the different TEFs used in the sensitivity analysis.

RESULTS

Gut content analysis

The highest vacuity index was observed in 0G-sole; 67 % of stomachs and intestines were empty, compared with 20 % and 21 % for 1G-sole and 0G-plaice, respectively.

Juvenile flatfish prey differed among species and age groups in the MSMB (Table 2); plaice gut content analysis revealed the presence of 40 taxa, whereas diversity in 0G-sole (14 taxa) and 1G-sole (15 taxa) was lower. Cumacea (mainly *Pseudocuma longicorne* and *Cumopsis goodsir*) and Bivalvia (*Abra alba* and siphons of *Cerastoderma* sp.) were the most important items in 0G-plaice gut contents. Amphipoda (*Microprotopus maculatus*) and Cumacea (*P. longicorne*) were chiefly eaten by 0G-sole. In comparison, Polychaeta (*Arenicola marina* and *Nephtys* sp.) and Bivalvia (*Abra alba*) were the main components of 1G-sole diet. All flatfish groups ate Bivalvia, but siphons (sublethal cropping) were most frequently consumed by 0G fish.

Table 2. Relative abundance (%*N*) and percentage occurrence (%*O*) of taxa in juvenile flatfish diets from gut content analysis. n.i.: not identified

	0G-plaice		0G-sole		1G-sole	
	%*N*	%*O*	%*N*	%*O*	%*N*	%*O*
Arthropoda						
Crustacea n.i.	0.1	1.1	–	–	–	–
Amphipoda n.i.	0.3	3.2	4.7	5.2	–	–
Abludomelita obtusata	0.1	1.1	0	–		
Atylus falcatus	0.5	5.3	–	–	–	–
Corophium arenarium	–	–	0.7	5.2	–	–
Gammarus sp.	–	–	4.9	10.3	–	–
Microprotopus maculatus	0.3	3.2	39.9	34.5	–	–
Cumacea n.i.	17.7	35.8	0.7	1.7	–	–
Diastylis laevis	0.3	3.2	–	–	–	–
Diastylis sp.	0.2	2.1	–	–	–	–
Bodotriidae n.i.	0.1	1.1	–	–	–	–
Cumopsis goodsir	25	18.9	1.1	6.9	–	–
Eocuma dollfusi	1	6.3	5.7	13.8	1	2.5
Iphinoe sp.	0.1	1.1	–	–	–	–
Pseudocumatidae n.i.	0.1	1.1	–	–	1	2.5
Pseudocuma longicorne	21.1	27.4	21.1	24.1	–	–
Pseudocuma sp.	1.4	8.4	–	–	–	–
Harpacticoida n.i.	2.7	4.2	2.9	10.3	–	–
Decapoda n.i.	0.1	1.1	–	–	–	–
Crangon crangon	0.2	2.1	–	–	1	2.5
Diogenes pugilator	2	2.1	–	–	–	–
Paguridae n.i.	0.2	2.1	0.1	1.7	1	2.5
Pagurus bernhardus	0.1	1.1	–	–	–	–
Portumnus latipes	1.6	7.4	–	–	–	–
Mysida n.i.	0.2	1.1	–	–	–	–
Ostracoda n.i.	0.2	2.1	–	–	–	–
Mollusca						
Bivalvia n.i.	0.7	9.5	–	–	3.9	10
Bivalvia n.i. (siphon)	0.2	1.1	14.6	17.2	2.9	2.5
Abra alba	10.8	41.1	2.1	12.1	31.4	25
Cardiidae n.i.	0.1	1.1	–	–	–	–
Cerastoderma sp. (siphon)	6.5	13.7	–	–	–	–
Mactridae n.i.	0.1	1.1	–	–	1	2.5
Spisula elliptica	4	9.5	–	–	–	–
Nucula sp.	–	–	–	–	1	2.5
Veneridae n.i.	0.1	1.1	–	–	–	–
Gastropoda n.i.	0.2	3.2	–	–	–	–
Hydrobia ulvae	0.2	1.1	–	–	–	–
Echinodermata						
Amphiura sp.	0.4	5.3	–	–	–	–
Acrocnida brachiata	0.1	1.1	–	–	–	–
Annelida						
Polychaeta n.i.	0.6	8.4	0.5	6.9	13.7	35
Arenicola marina	–	–	–	–	20.6	50
Glycera convoluta	0.1	1.1	–	–	4.9	7.5
Nephtys sp.	0.9	11.6	–	–	10.8	27.5
Nephtys hombergii	0.1	1.1	0.9	10.3	–	–
Nereis sp.	–	–	–	–	1	2.5
Cirratulidae n.i.	–	–	–	–	4.9	5
No. of taxa	**40**		**14**		**15**	

The Schoener diet overlap index between 0G-sole and 0G-plaice was 0.30, while it was 0.07 between 0G-sole and 1G-sole, and 0.14 between 0G-plaice and 1G-sole.

Food sources and flatfish stable isotope signatures

POM from the Couesnon River was ^{13}C-depleted and ^{15}N-enriched compared to POM from the Sée and Sélune rivers and marine POM (Fig. 2, Table 3). Dead leaves of *Elymus athericus* were ^{13}C-depleted and ^{15}N-enriched compared to *Halimione portulacoides*. MPB was the most ^{13}C-enriched organic matter source. Thus, the different freshwater, estuarine, and marine food sources (freshwater and marine POM, plants, and MPB) had distinct δ^{13}C values that could be traced into the trophic network.

Benthic invertebrate species exhibited differences in stable isotope signatures: bivalves (*Abra alba* and *Cerastoderma edule*) were ^{15}N-depleted compared to polychaetes (*Arenicola marina* and *Nephtys* sp.). Differences in δ^{13}C were also apparent, with *C. edule* being the most ^{13}C-depleted invertebrate (Fig. 2, Table 3).

The 0G-plaice, 0G-sole, and 1G-sole were not significantly different in δ^{13}C (ANOVA; $F_{2,160}$ = 0.93,

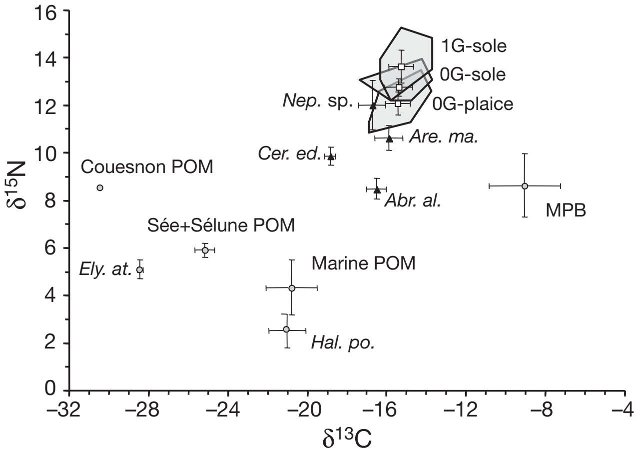

Fig. 2. Stable isotope signatures (mean ± SD) of organic matter sources to flatfish diets, benthic invertebrates, and juvenile flatfish. Organic matter sources (○): particulate organic matter (POM) from Couesnon River, POM from Sée and Sélune rivers, marine POM, microphytobenthos (MPB), and dead leaves of *Elymus athericus* (*Ely. at.*) and of *Halimione portulacoides* (*Hal. po.*). Benthic invertebrates (▲): *Nephtys* sp. (*Nep.* sp.), *Arenicola marina* (*Are. ma.*), *Cerastoderma edule* (*Cer. ed.*), and *Abra alba* (*Abr. al.*). □: Juvenile flatfish. The large grey shapes represent the smallest convex polygons containing all individuals of the same species and age-group

Table 3. Mean (±SD) $\delta^{13}C$ and $\delta^{15}N$ values and number of samples (n) of organic matter sources to flatfish diets, flatfish prey, and flatfish. POM: particulate organic matter

Sample	n	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Organic matter source			
Couesnon River POM	1	−30.45	8.54
Sée and Sélune rivers POM	2	−25.15±0.50	5.91±0.29
Marine POM[a]	4	−20.90±1.01	4.33±1.17
Elymus athericus[a]	3	−28.43±0.15	5.1±0.40
Halimione portulacoides[a]	3	−20.97±0.94	2.50±0.72
Microphytobenthos	4	−8.91±1.83	8.65±1.35
Prey			
Abra alba	10	−16.43±0.50	8.52±0.43
Cerastoderma edule	3	−18.79±0.26	9.90±0.37
Arenicola marina	20	−15.80±0.70	10.66±0.52
Nephtys sp.	13	−16.36±0.72	12.24±0.94
Flatfish			
0G-plaice	68	−15.35±0.62	12.13±0.49
0G-sole	49	−15.31±0.72	12.81±0.35
1G-sole	47	−15.18±0.61	13.70±0.70

[a] Additional data taken from Riera (2007)

Table 4. Trophic enrichment factors (TEFs) used for SIAR predictions with an SD of 0.5. The final column corresponds to the sum of TEFs from PP to C2: PP to C1 (taken from the literature[b]) then C1 to C2 (based on the present study, an experiment[a], or taken from the literature[b]). PP: primary producer or organic matter source, C1: primary consumer, C2: secondary consumer

Source	PP–C1	C1–C2	Σ(PP–C2)
TEF for carbon			
Present study			
0G-plaice		1.53	2.53
0G-sole		1.57	2.57
1G-sole		1.69	2.69
Experiment[a]		2.43	3.43
Literature[b]	1.00	1.00	2.00
TEF for nitrogen			
Present study			
0G-plaice		1.32	3.52
0G-sole		2.00	4.20
1G-sole		2.88	5.08
Experiment[a]		2.27	4.47
Literature[b]	2.20	3.40	5.60

[a] F. Le Loc'h et al. (pers. comm.)

[b] DeNiro & Epstein (1978, 1981), Post (2002), Fry (2006)

p = 0.40; Fig. 2) but differed significantly in $\delta^{15}N$ (ANOVA; $F_{2,160} = 122.42$, $p < 0.001$). Tukey's multiple comparison test indicated that 0G-plaice were significantly ^{15}N-depleted compared with 0G- and 1G-sole (Fig. 2). The highest $\delta^{15}N$ values were observed in 1G-sole.

Source contributions

Mixing model estimations of each organic matter source contribution to fish diet were quite similar for the 2 juvenile sole cohorts and the 0-group plaice (Fig. 3). The major sources contributing to flatfish isotope signatures were MPB and POM from the Couesnon River. Conversely, contributions of Sée River and Sélune River POM, marine POM, dead leaves of *Elymus athericus*, and dead leaves of *Halimione portulacoides* were marginal.

Differences in TEFs (Table 4) led to significant differences in source contributions ($\chi^2_{0G\text{-plaice}} = 34.56$, $\chi^2_{0G\text{-sole}} = 45.45$, $\chi^2_{1G\text{-sole}} = 29.79$; df = 8, $p < 0.001$). Nevertheless, accounting for this variability, MPB consistently made a major contribution to the flatfish food web in all models (Fig. 3). Models differed in their estimated contributions of freshwater POM from the Sée and Sélune rivers and the Couesnon River, but differences in the total contribution of freshwater POM were minor.

DISCUSSION

Moderate trophic niche overlap between juvenile flatfish species in MSMB

Both plaice and sole juveniles ate benthic invertebrates, but taxonomic comparison showed dissimilarities among species present in gut contents, and no dietary overlap was observed among age groups or species in MSMB. Juvenile plaice had a larger prey spectrum than both 0G- and 1G-sole, while 0G-sole ate smaller prey items (mainly Amphipoda and Cumacea) compared to 1G-sole (mainly Bivalvia and Polychaeta). This latter difference reflects the larger gape width of the 1G-sole, allowing them to capture a wider range of prey, including invertebrates of higher trophic levels (Jennings et al. 2001). The $\delta^{15}N$ results support these observations based on diet. Juvenile plaice had significantly lower $\delta^{15}N$ values compared with 0G- and 1G-sole, indicating that they were feeding at a slightly lower trophic level. The changes in diet observed between 0G- and 1G-sole were similarly supported by small differences in $\delta^{15}N$.

A similar lack of dietary overlap for juvenile flatfish has been observed in other nursery grounds in Europe (Beyst et al. 1999, Amara et al. 2001). Juvenile plaice have a larger prey spectrum compared with juvenile common sole (Amara et al. 2001). The ontogenetic shift in diet between 0G- and 1G-sole observed

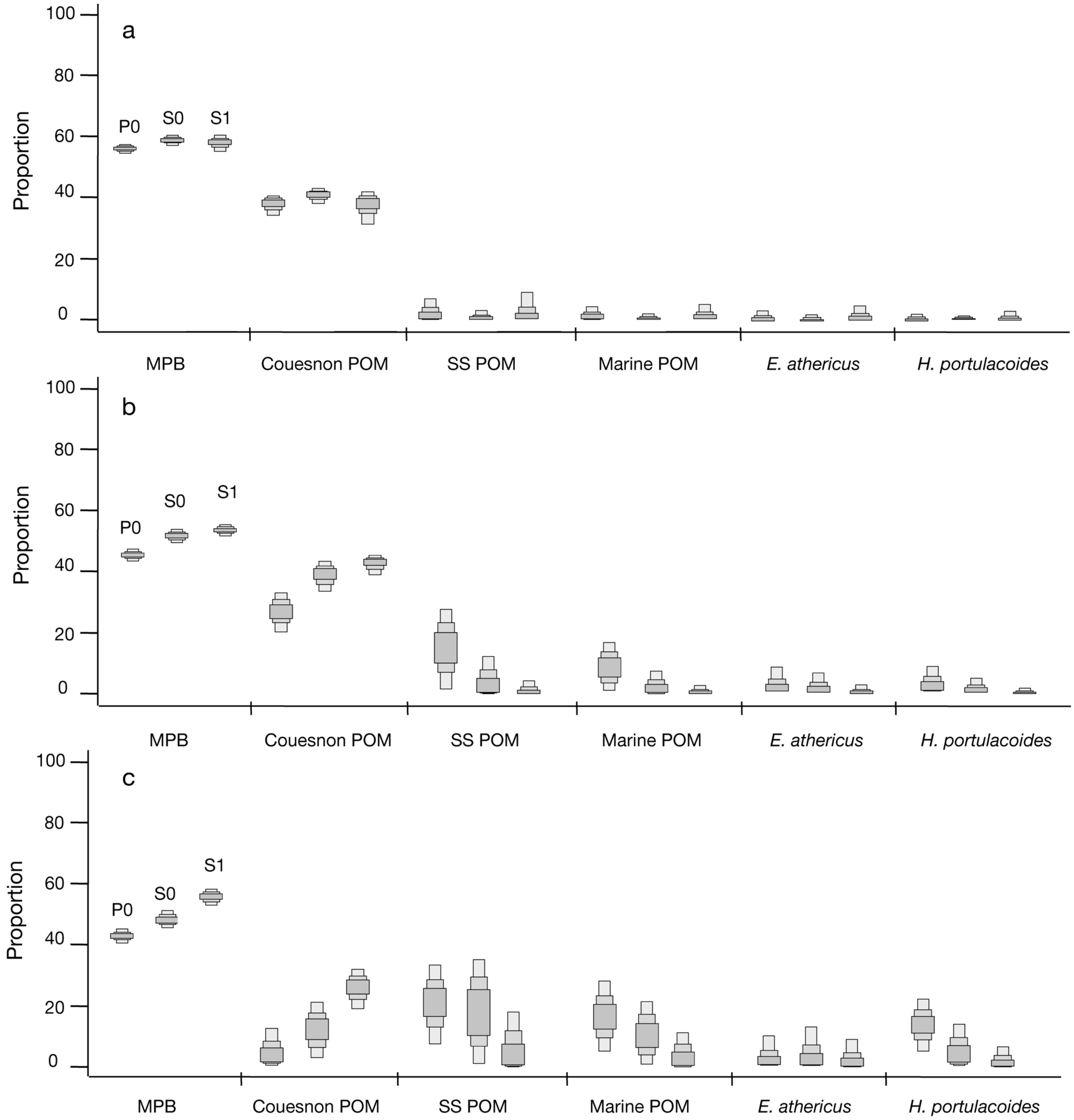

Fig. 3. Boxplots of 3 mixing-model estimates of contributions to flatfish diets from 6 organic matter sources: microphytobenthos (MPB), Couesnon River particulate organic matter (POM), POM from Sée and Sélune rivers (SS POM), marine POM, *Elymus athericus*, and *Halimione portulacoides*, using trophic enrichment factors: (a) calculated using data from the present study, (b) based on *in situ* experiments (F. Le Loc'h pers. comm.), and (c) taken from the literature (see Table 4). Bars represent 25th, 75th, and 95th Bayesian credibility intervals. P0: 0G-plaice, S0: 0G-sole, S1: 1G-sole

in the MSMB is similar to results obtained by Lagardère (1987), Molinero & Flos (1991), and Cabral (2000). While bivalve siphons were an important prey item for both 0G flatfish, only 0G-plaice were found to eat *Cerastoderma* sp. siphons in the present study and in the Seine estuary (Amara et al. 2001), another estuarine nursery system of the English Channel. By contrast, in the Rance estuary (France), close to the MSMB, competition for *Cerastoderma* sp. occurs between young sole and plaice (Le Mao 1986).

Both sole and plaice have a small mouth size, small esophagus and stomach, and a complicated intestinal loop, which are features appropriate for consumption of small-sized benthic prey (De Groot 1971, Braber & De Groot 1973). The dissimilarities observed in gut contents can be explained by differences in feeding strategy: plaice are visual feeders, specializing on slow-moving bottom-dwellers such as active crustaceans, while sole are night feeders, predating sessile or barely mobile organisms (Batty & Hoyt 1995, Harvey 1996, Beyst et al. 1999). Benthic invertebrates eaten by young plaice were mainly deposit- and suspension-feeders, while common sole's prey were deposit-feeders and carnivorous (with a higher trophic level).

Because of the differences in time of feeding, the stomachs of daytime-feeding plaice were more full compared to nighttime-feeding sole because sampling was undertaken during the daytime (De Groot 1971). While our daytime sampling was probably not optimal to encompass the variability in resource consumption by juvenile flatfish because we were obtaining single snapshots of a consumer's diet that may not correspond to relevant ecological timescales (Hyslop 1980), the differences in diet we observed were consistent with the stable isotope results. Stable isotope analysis of a consumer's tissues provide for time- and space-integrated representations of the trophic ecology of organisms and energy assimilated by the consumer (Peterson & Fry 1987), giving us confidence that the differences in feeding strategies among flatfish juveniles in the MSMB we observed were real.

Moderate sensitivity to uncertainty in production source data and TEFs

Trophic sources were well discriminated from their signatures in spite of large SDs. The δ^{13}C values for freshwater POM were lower than other organic matter sources, following a well-documented pattern of trophic sources in coastal and estuarine systems (Darnaude et al. 2004, Kostecki et al. 2010). An increasing δ^{13}C of POM from fresh to marine waters was observed, which is consistent with previous studies (Yokoyama & Ishihi 2007). Detrital salt-marsh species had distinct C and N stable isotope values, allowing discrimination, and MPB displayed the highest δ^{13}C signature of all sources in MSMB. These patterns fit with previous stable isotope analyses in this bay (Lefeuvre et al. 2000, Riera 2007) and elsewhere (Yokoyama & Ishihi 2007, Choy et al. 2008).

Stable isotope mixing models can be sensitive to variation in TEFs (Wilson et al. 2009, Bond & Diamond 2011). However, the present sensitivity analysis (Fig. 3) demonstrated that SIAR model outputs appeared relatively insensitive to changes in TEF values and found consistency in the most important source contributions, despite accounting for moderate differences in TEFs. Thus by accounting for variability in sources' data and TEFs, we were able to quantify food sources in the juvenile flatfish trophic chain from SIAR model outputs.

Significance of MPB for juvenile-flatfish food webs in MSMB

The origin of organic matter in food webs of flatfish was similar for juvenile plaice (0-group) and sole (0- and 1-group) in the MSMB, despite differences in prey preferences and, to a lesser extent, in trophic levels. The most important organic matter sources were MPB (i.e. mainly benthic diatoms; Riera 2007) and, to a lesser proportion, freshwater POM subsidies. The origin of organic matter for juvenile flatfishes contrasts with the diet of shellfish (cultivated mussels and oysters, and invasive slipper limpet), the dominant secondary producers in the MSMB, representing 40 % of all secondary production in the bay (Arbach Leloup et al. 2008, Cugier et al. 2010). The diet of these filter-feeding mollusks was primarily based on marine plankton, with no significant contribution from benthic diatoms (Riera 2007). An investigation of organic matter and nutrient fluxes between salt marshes and marine waters in the MSMB (Lefeuvre et al. 2000) using stable isotopes and fatty acids demonstrated the importance of organic matter produced by salt marshes in the diet of tidal-flat invertebrates and for transient fish species that colonize salt marshes to forage or graze. Conversely, the present study found that salt marshes, represented by 2 C_3 plants, did not seem to be an important source of organic carbon to flatfish nurseries. This could be related to their limited surface (40 km^2), 5 times lower than the intertidal mudflats (210 km^2), where MPB production is important (Arbach Leloup et al. 2008).

Our results in the MSMB system tend to underline the large influence of local primary production on coastal food chains when freshwater inputs of organic matter are limited. Many studies have shown the importance of benthic algae primary production in estuaries and lagoons. Quan et al. (2010) characterized the major pathways for energy flow in an artificial lagoon using 4 primary producers; >50% of organic carbon in the food chain was derived from epibenthic microalgae, suggesting that the lagoon food web was mostly based on this production source. Melville & Connolly (2003) used stable isotopes to determine the autotrophic sources supporting production of fish in a tropical estuary. They demonstrated the importance of seagrass, epiphytic algae, and local POM (including phytoplankton), in addition to organic matter from adjacent mangroves, for resident fish species. In the MSMB, different sources of primary production appear to be significant to the different components of the MSMB benthic food web; e.g. phytoplankton for cultivated and invasive shellfish (Riera 2007, Arbach Leloup et al. 2008) and MPB for juvenile flatfish in their nursery ground.

MSMB nursery ground: a contrasting function compared with estuarine nursery grounds?

In MSMB, production of MPB and continental organic matter present in freshwater POM entered the flatfish-juvenile food web. This combination of local primary production and freshwater organic matter has already been demonstrated to sustain juvenile flatfish in nursery sectors, especially in estuaries (Darnaude et al. 2004, Leakey et al. 2008, Pasquaud et al. 2008, Vinagre et al. 2008, Kostecki et al. 2010). The present study provides new insight about the importance of MPB, which is usually considered a subsidiary for juvenile flatfish in estuaries.

Continental subsidies can vary in space (Pasquaud et al. 2008, Kostecki et al. 2010) and time (dry years vs. wet years; Kostecki et al. 2010), but are frequently considered predominant in estuaries. In non-estuarine areas, and especially in bays, which are important nursery grounds (Riou et al. 2001, Le Pape et al. 2003), the importance of intertidal primary production, and especially MPB, may be predominant and sustain nursery function.

Nevertheless, the contribution of freshwater POM in the juvenile-flatfish food web is quite important (i.e. about one-third) in the MSMB. In this bay, juvenile flatfish are concentrated in a restricted area (Kostecki et al. 2011) in front of the 3 river mouths (Fig. 1), where the estuarine influence is moderated but higher than elsewhere in the bay (Cugier et al. 2010). Even if the common sole faced a reduction of its habitat in this bay, as a consequence of the proliferation of the invasive slipper limpet, the heart of its distribution has been located in the same place for 3 decades (Kostecki et al. 2011). This situation allows us to understand the significant contribution of freshwater POM in spite of the very limited river discharge at the MSMB scale. This has implications for the maintenance of freshwater flow to this coastal system: freshwater loadings provide both inorganic nutrients enhancing intertidal primary production from MPB (Underwood & Provot 2000) and organic matter, thus it is an important input to sustain the nursery function in the bay.

Acknowledgments. This project was supported by the French National Programme for Coastal Environment (PNEC, project NOCES). We are grateful to all of the colleagues on board the RV 'Louis Fage' (Museum National d'Histoire Naturelle, Dinard, France) for their help in fieldwork. We also thank P. Riera for his source data, F. Le Loc'h for his trophic enrichment factor data, and M. Perdriau and D. Huteau for their valued assistance in stable isotope sample preparation. This project also used data from the French Coastal Monitoring Network SOMLIT (Service d'Observation en Milieu LITtoral; http://somlit.epoc.u-bordeaux1.fr/fr/). We thank the SOMLIT team of Roscoff (PI: P. Morin) for providing data. We are grateful to the anonymous reviewers for their helpful advice and significant improvements of the manuscript.

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Editorial responsibility: Edward Durbin,
Narragansett, Rhode Island, USA

Submitted: February 24, 2011; Accepted: December 14, 2011
Proofs received from author(s): March 5, 2012

Vol. 479: 115–126, 2013
doi: 10.3354/meps10128

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published April 8

Distribution patterns in the benthic diversity of the eastern English Channel

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ABSTRACT: Understanding the distribution of specific diversity is currently an important focus in marine research, and the role of marine biodiversity has been fully recognised as essential for the proper functioning of the biosphere. The objective of this study was to explain the distribution of macrobenthic taxonomic richness (vagile epifauna, endofauna and sessile epifauna) in the eastern part of the English Channel using both classical methods and applying the mid-domain effect (MDE) model. High diversity was encountered in the eastern English Channel (875 taxa), with high-diversity areas often comprising gravelly or pebbly sediments. Sessile epifauna represented 25% of this inventory, revealing the importance of this group. Our results underline the existence of randomness in the observed species richness distribution due to large number of species with restricted ranges.

KEY WORDS: Benthic community distribution · Species richness gradient · Mid-domain effect · Chao index

INTRODUCTION

The role of marine biodiversity has only recently been fully recognised as essential for the proper functioning of the biosphere (Worm et al. 2006). In community ecology, understanding the spatial distribution of specific diversity has become an important research focus. *In situ*, the species taxonomic level is the most easily approachable study unit. Specific diversity is evaluated by estimators of the number of species (species richness) and other indices, such as Shannon's diversity or Pielou's equitability index, derived from information theory. However, these estimators more or less reduce biodiversity to the number of species, ignoring that certain functions provided by ecosystems, and often involved in their resilience, can result from interactions among species (Elmqvist et al. 2003).

Less is known about marine biodiversity than about terrestrial ecosystems (Hendriks et al. 2006), since the challenges faced in the marine environment in terms of size and inaccessibility make it considerably more difficult to conduct studies. However, it is essential that marine biodiversity should be documented to enhance our understanding of temporal and spatial ecosystem functions within specific regions of the world. This would ultimately lead to an integrated approach focusing on entire ecosystems rather than fragments of systems.

Since the work of Sanders (1968), biologists, ecologists and biogeographers have tried to understand how benthic species diversity is distributed with

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respect to large-scale gradients such as depth (Willig et al. 2003). Relationships between latitudinal changes and biodiversity do not necessarily need to follow linear or even monotonic functions to be useful (Rex et al. 1993, Thrush et al. 2006), and emergent patterns are often driven by the interaction of processes operating at different scales. To understand the role of broad-scale processes in biodiversity, it is necessary to integrate responses operating at different scales of space and time (Thrush et al. 2006). Following these ideas, Ellingsen (2001) and Ellingsen & Gray (2002) conducted studies along the Norwegian continental shelf and showed that patterns of diversity within a region may depend on the spatial scale over which they are measured, and that differences can occur among habitats considered uniform. In many of their analyses conducted over large areas (considered benthoscapes as defined by Zajac 2008), correlations among various measures of diversity and environmental variables were not strong. The unexplained part of variation may lie in how populations and communities and the diversity patterns generated are shaped by the benthoscape structure. The importance of habitat characteristics in structuring soft sediment diversity was reinforced by Hewitt et al. (2005), who showed that small-scale biogenic structures and habitat-forming deposits (such as shell debris) can significantly affect β-diversity. Another biogeographic theory, the mid-domain effect (MDE), was developed in the mid-1990s by Colwell & Hurtt (1994) and was based on (and sensitive to) the distribution range of a given species (extremes of a range boundary and midpoint within a bounded domain). The MDE is considered a null model, i.e. excluding all environmental, biological and historical processes. Under most conditions, this model, which runs random combinations of geographical ranges within a defined bounded domain, produces a unimodal curve with a mid-domain peak (Colwell 2008). This model has been confirmed in spatialised applications in 1 (Willig & Lyons 1998, Colwell & Lees 2000) and 2 dimensions (Bokma et al. 2001). Reviews and critiques of this model can be found in Zapata et al. (2005), Hawkins et al. (2005) and Colwell et al. (2004).

The objective of the present paper is to explain the distribution of macrobenthic taxonomic richness (vagile epifauna, endofauna and sessile epifauna) in the eastern part of the English Channel using both classical methods and the MDE. Data used were collected during surveys that aimed to update the knowledge on benthic fauna in the eastern part of the English Channel acquired 30 yr ago in historical surveys, and to provide a quantitative description of benthic communities and data usable in trophic food-web studies or ecosystem approaches.

MATERIALS AND METHODS

Study site

From 2004 to 2007, a total of 461 stations were sampled from the RV 'Côtes de la Manche', in the eastern basin of the English Channel and the South Bight of the North Sea, between 49° 30′ 00″ and 51° 18′ 00″ N latitude and 1° 00′ 00″ W and 2° 30′ 01″ E longitude.

In the eastern English Channel, tidal current strengths increase from 1.5 to 3 knots from the south to the northeast as the narrower part of the Dover Strait is approached. Flow velocity decreases in the southern North Sea where it does not exceed 2 knots (SHOM 1968). Variations in the speed of the tidal current create a sedimentary gradient (Larsonneur et al. 1982); pebbles and gravels dominate in the open sea, whereas coastal areas are dominated by large homogeneous sand banks and associated channel systems (Fig. 1).

The water quality of the sampling area is largely influenced by 2 main estuaries: the Seine estuary in the south-west and the Scheldt delta in the north-east. Depending on the direction, intensity and duration of the wind, the plumes of both rivers can reach the Dover Strait zone and modify water salinity up to 2 to 3 nautical miles off the French coast (Brylinski et al. 1988). Other smaller rivers (i.e. Somme, Authie, Canche, Liane, Aa and Yser, Fig. 1) and runoff from sea cliffs contribute to a decrease in the salinity of coastal waters. Although the outflows from these sources are relatively low, they may be locally significant at low tide.

Field sampling design

Sampling was carried out during 6 surveys conducted between March 2004 and August 2007. The sampling grid was regular (resolution of 5′ in latitude and longitude, Fig. 2) with areas more intensely sampled in the framework of local scientific programmes (e.g. Flanders sandbanks, south Dover Strait sandbanks, Ridens of Boulogne; Fig. 1). Sampling was quantitative or qualitative, depending on the sediment encountered. On soft sediments, quantitative samples were collected with a Hamon grab. Three replicates

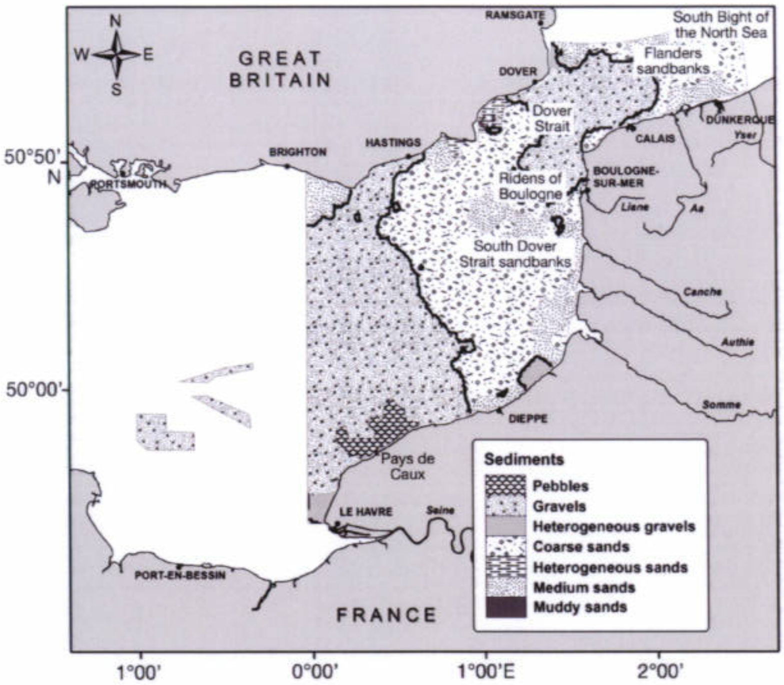

Fig. 1. Sediment categories in the eastern English Channel (adapted from Folk 1954 in Foveau 2009). Thick black lines show the boundaries between gravel/pebble and sand sediments

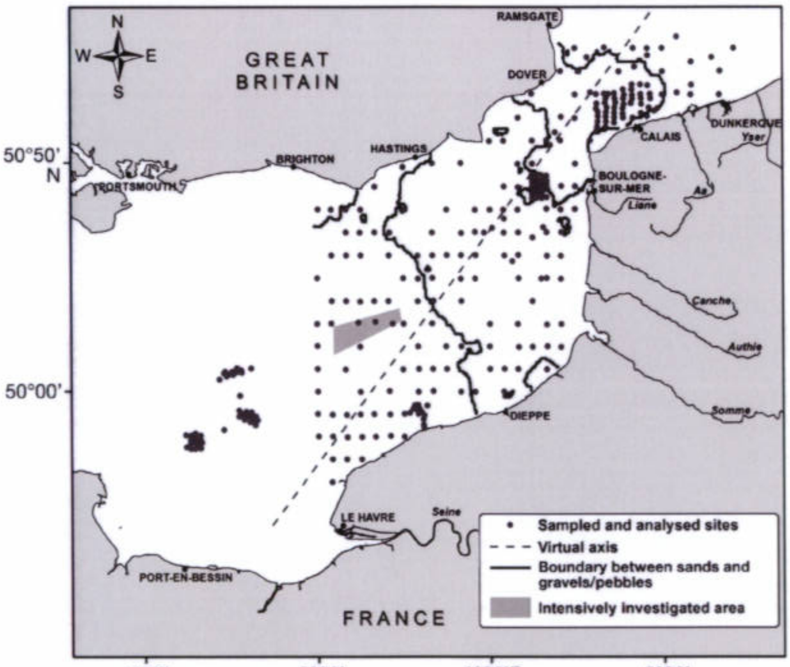

Fig. 2. Location of samples taken in the eastern English Channel (grey dots: sites of the principal grid sampled and analysed; grey area: intensively investigated site (high station density), exact positions of stations cannot be provided), dashed line: virtual axis; thick black lines: boundaries between gravel/pebble and sand sediments

($0.25\ m^2$) were taken at each station, the first for granulometric analysis, and the other 2 for benthic fauna analysis (species and biomass determinations). In the presence of hard substrates (gravels, pebbles and cobbles), a Rallier du Baty dredge was used (sampling standardised to 30 l). Sieving was performed onboard using 2 mesh sizes: a circular 2 mm mesh (which does not retain juveniles but collects more than 95% of the macrobenthic biomass, see Ghertsos 2002) and a circular 1 mm mesh. The retained material was preserved for analysis in 5% buffered formaldehyde. A visual description of the sediment type was recorded, along with the depth of the water column, and the location and times at which the sample was collected (replicates were collected from within a close range of each site, using the Differential Global Positioning System).

Sediment samples were analysed for grain size distribution (wet sieving). The macrofauna, including sessile epifauna (countable and non-countable taxa), were identified to the lowest possible taxon and enumerated when possible. The biomass of each taxon was determined based on g of ash-free dry weight per $0.5\ m^2$ (loss of weight of dry organisms after 6 h at 520°C) as recommended by the ICES Benthos Ecology Working Group (BEWG 1986). As far as possible, photographs of sediment and species were taken, and a specimen of each species was conserved to create a photo database and a reference collection.

Analysis of sedimentary and biological data

Of the 461 stations sampled, samples from 318 stations (sieved on 2 mm mesh) were retained for analysis (Fig. 2). In order to account for substrate heterogeneity, the number of stations studied was increased in heterogeneous areas and reduced in homogeneous ones.

Table 1. Sediment type equivalents among classifications: groups used in present study, modified Folk (1954) classification (in Foveau 2009) and Folk (1954) classification

Group in present study	Modified Folk classification	Folk classification
Gravel/pebbles	Pebbles	Gravels (G): >80 % is >2 mm and >50 % is >20 mm
	Gravels	Other gravels (G): >80 % is >2 mm and <50 % is >20 mm Sandy gravels (sG): 30–80 % is >2 mm and sand:mud ratio is >9:1
	Heterogeneous gravels	Muddy sandy gravels (msG) Gravelly muddy sands (gmS)
Sand	Coarse sands	Gravelly sands (gS) Slightly gravelly sands ((g)S)
	Medium sands	Sands (S)
	Muddy sands	Muddy sands (mS)
	Heterogeneous sands	Slightly gravelly muddy sands ((g)mS) Slightly gravelly sandy muds ((g)sM)

A modified Folk classification (Folk 1954, Foveau 2009), based on 7 categories of sediment types (Table 1), was used to determine the sedimentary type for each station. Sediments were categorised in this study into coarse sediments (gravels/pebbles) and fine particles (sand; see Fig. 1 for locations of these sediments in the studied area).

Although an evaluation of several diversity indices was undertaken (Foveau 2009), only results for total taxa are presented here. The taxonomic richness for all taxa (countable and non-countable) was mapped, using the kriging interpolation method and Genstat software (© VSN International), and represented via ArcGIS software (© ESRI).

PRIMER software was also used to realise the species accumulation curve. Because it is the most pertinent for analysing presence/absence data including epifauna, we used the Chao2 (Chao 1984) estimator and compared it to the accumulation curve of the number of taxa observed. The non-parametric Chao2 method is based on species occurrence. It rests on the hypothesis that non-observed taxa are rare species, and considers that a species is rare when the taxon occurs at only 2 stations.

Changes in the taxonomic richness were studied along a virtual south-west/north-east axis (Fig. 2). All stations were represented according to their geographic coordinates expressed in a Lambert II geodesic system, and a regression line (with the best R^2) was drawn between these points ($y = 0.7288x + 2252$). All stations were projected on this axis, and new coordinates (in Lambert II, which allows translation in km) were assigned to stations and associated to values of taxonomic richness. To visualise how taxonomic richness changes along the eastern English Channel, the virtual axis was divided either by fixing the number of sampled stations (constant sampling effort, 32 stations) or by defining a number of equidistant sections (for example, sections of 22.43 km if the virtual axis of 224.3 km was divided into 10 sections). For each configuration, the number of species was counted per division and represented as histograms. Along this transect, numbers of taxa were also reported for each sampling station, and an accumulation curve was built from these projections (for all stations, but also for the 2 categories of sediment i.e. sand and gravel/pebbles). The observed taxonomic richness distribution was compared to the MDE null model, created using the RangeModel 5.0 software (Colwell 2006), which produces a randomisation disposition of the observed range sizes within the defined studied area (continuous model, Box 5 in Colwell & Lees 2000). The generation of observed species distribution and predicted mean pattern of richness across the domain was used to represent the 95 % confidence intervals, for 100 randomisations of range placement, as suggested by Colwell (2008). The mean displacement (*D*) between the simulated and the average random curves was calculated with the program developed by Veech (2000).

RESULTS

General characteristics of taxonomic richness and links to superficial sediment cover

In total, we identified 875 taxa. Fauna consisted of 251 annelid taxa (28.7 % of the fauna), 234 arthropod taxa (26.7 %), 159 mollusc taxa (18.2 %), 72 bryozoan taxa (8.2 %) and 55 cnidarian taxa (6.3 %) for the main phyla (Table 2). Unique taxa (present at only 1 site) and taxa present at 2 sites represented 21.6 and 10.4 %, respectively. About 13.8 % of the taxa were recorded at ≥50 sites, but no taxon was present throughout the entire study area (the most frequently represented taxon occurred at 223 stations).

Table 2. Total number of taxa found in this study compared to results of previous studies; percentage values in parentheses. Sources — 1: Rees et al. (1999) for the English part of the North Sea, English Channel and Celtic Sea; 2: Rees et al. (2007) for the North Sea; 3: Kröncke et al. (2011) for the central and southern North Sea; 4: Hily et al. (2008) for the Bay of Biscay; 5: Dauvin & Dewarumez (2002) for Roscoff; 6: Dauvin & Dewarumez (2002) for Wimereux; 7: European Register of Marine Species (W. Appeltans pers. comm.). Gaps indicate that data were not analyzed. RT: taxonomic richness

	Present study	Previous studies						
		1	2	3	4	5	6	7
Total RT	875	430	1500	455	163	1856	769	20 927
Annelida	253 (28.9)	186 (43.3)			76 (47.0)	429 (23.1)	160 (20.8)	2271 (10.9)
Arthropoda	237 (27.1)	112 (26.0)			37 (23.0)	251 (13.5)	148 (19.2)	6703 (32.0)
Mollusca	159 (18.2)	76 (17.7)			29 (18.0)	421 (22.7)	161 (20.9)	3861 (18.4)
Bryozoa	72 (8.2)					142 (7.7)	64 (8.3)	802 (3.8)
Cnidaria	55 (6.3)					213 (11.5)	91 (11.8)	1266 (6.0)
Porifera	31 (3.5)					200 (10.8)	52 (6.8)	1472 (7.0)
Echinodermata	23 (2.6)	19 (4.4)			14 (9.0)	45 (2.4)	20 (2.6)	659 (3.1)
Chordata	15 (1.7)					62 (3.3)	31 (4.0)	402 (1.9)
Others	30 (3.5)	37 (8.6)				93 (5.0)	42 (5.5)	3491 (16.7)

Most of the stations associated with sand (muddy to coarse sands, heterogeneous or not) had a taxonomic richness less than 80 (Fig. 3, grey bars). On gravel/pebbles (heterogeneous or not), taxonomic richness per station was higher, ranging from 60 to 150 (Fig. 3, black line). Some exceptions were observed in boundary areas, where the assignment of sediment type was problematic (especially for the gravel/coarse sand proportions).

The absolute value estimated by the Chao2 index (1071.1 ± 37.6 taxa) was higher than the observed value (Fig. 4). The absence of an asymptote on the estimated taxonomic richness curve suggested that the value was underestimated.

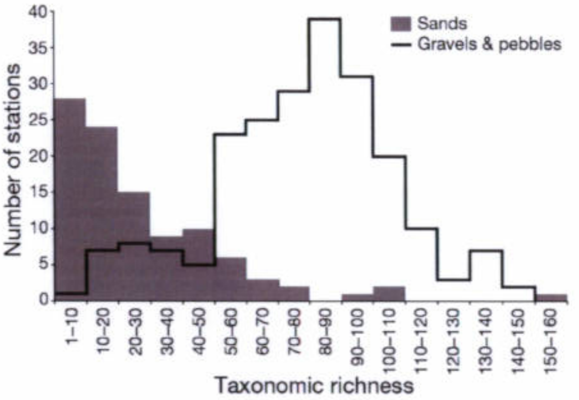

Fig. 3. Number of sampled stations plotted against observed taxonomic richness, divided into the 2 sediment groups, sands and gravels/pebbles

Spatial distribution of taxonomic richness in the eastern English Channel

Total taxonomic richness reached a maximum in the central part of the Channel, off the 'Pays de Caux' and in the Dover Strait (Fig. 5). The lowest values were observed on the sandbanks located south of the Dover Strait and in the South Bight of the North Sea (Fig. 5). Uncountable taxa, belonging to the sessile epifauna, were logically mainly associated with pebbled areas, located in the 'Pays de Caux' and the Dover Strait (Fig. 6). The location of diversity hotspots (total or sessile epifauna only) coincided with the distribution of gravel and pebbles (Figs. 5 & 6).

Regardless of the partition type considered (fixed number of stations or equidistant sections), taxonomic richness varied along the virtual axis following a bimodal distribution (Fig. 7). The highest values of taxonomic richness (>400 taxa) were observed in the first

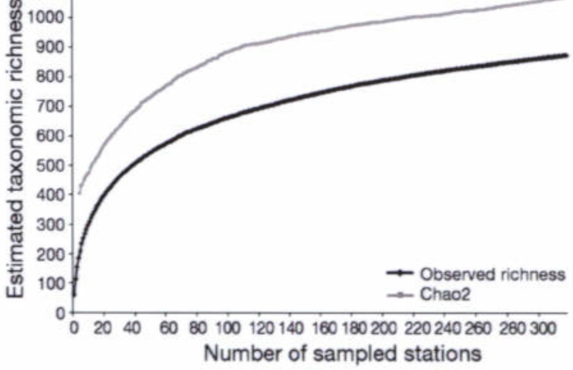

Fig. 4. Species accumulation curve obtained from the Chao2 estimator and for the observed taxonomic richness

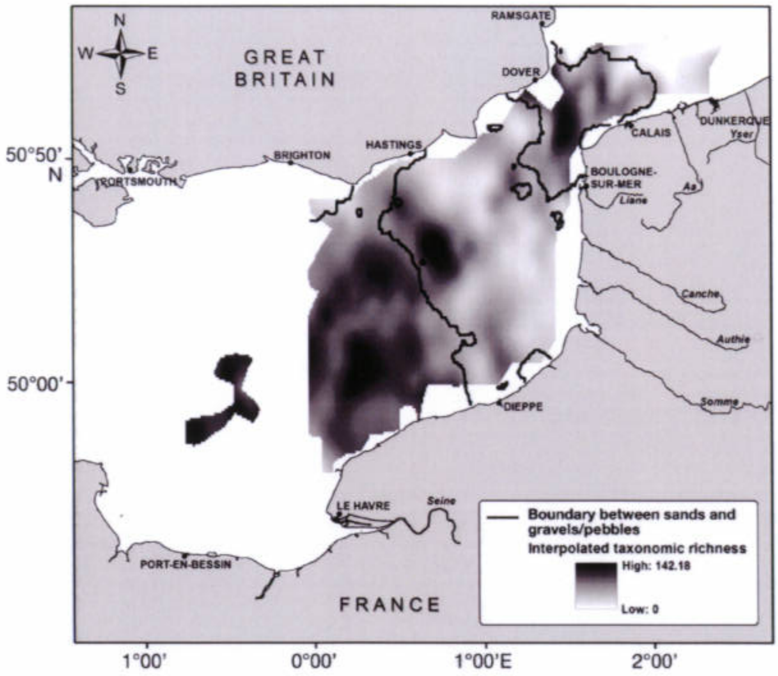

Fig. 5. Distribution of the total taxonomic richness in the eastern part of the English Channel

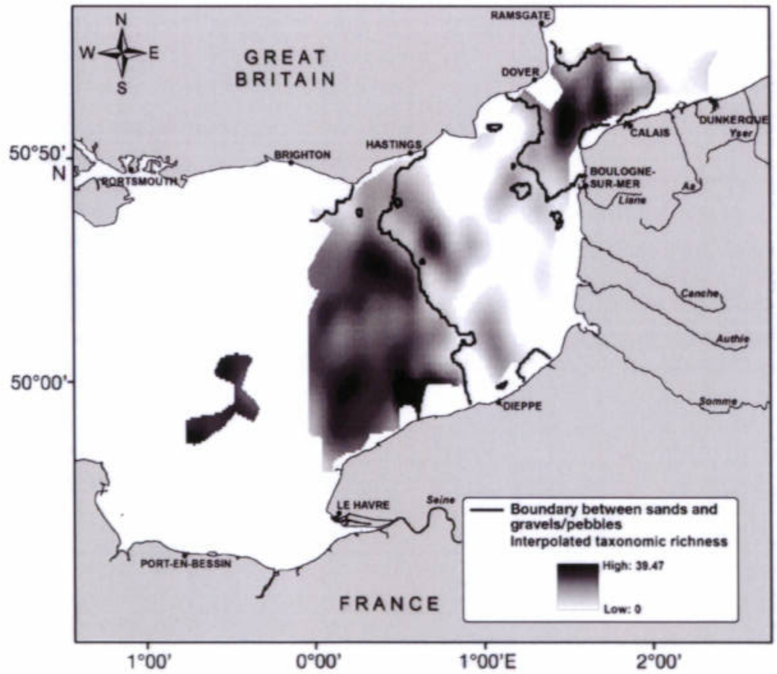

Fig. 6. Distribution of the taxonomic richness of sessile epifauna in the eastern part of the English Channel

and third sections, i.e. in the gravel/pebbles area, and in the Dover Strait area respectively (>300 taxa). The lowest values were observed in the area where sand dominated. The same approach, when carried out on the sand and gravel/pebble categories separately, confirmed the stronger contribution of gravel/pebbles to taxonomic richness. For sand, 2 peaks were observed, corresponding to the large sandbank areas (south Dover Strait sandbanks and Flanders sandbanks), and raising the overall level of taxonomic richness (grey areas in Fig. 7).

When the virtual axis was divided into sections of 1 km length, the sum of the number of species recorded followed a bell-shaped curve (Fig. 8A) with a maximum of 502 taxa in the middle of the area studied. The absence of an inflexion point in the cumulative curve could mean that the turnover of taxa (i.e. replacement of one taxon by another) in this area was constant. The same methodology was applied for each sediment type (Fig. 8B,C). While a nearly centred bell-shaped curve is observed for gravel/pebble sediments, the curve characterising sand sediments is asymmetrical. However, these 3 cumulative curves follow a similar pattern.

Compared to the curve computed with RangeModel, our observed taxonomic richness curve exhibits higher values in the western and central parts of the gradient (Fig. 9). Results from Veech's displacement test give an observed value, D_{obs}, at 256.29 with a range of predicted values, D_{pred}, between 2.17 and 22.06 and a probability of <0.0001 that $D_{obs} \leq \max D_{pred}$ (based on 1000 trials). The taxonomic richness curve is highly significant: D_{obs} is high (256.29), and no null iterations (out of 1000) had a higher D value or a higher p-value than the observed value. According to Veech (2000), our results suggest that the observed species richness distribution is partly random (the influence of the axis pattern on the data responses was not evaluated here).

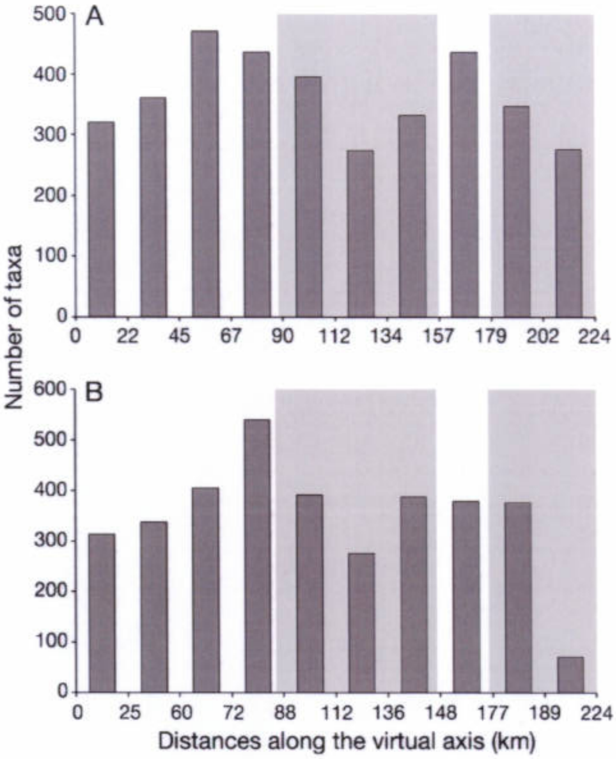

Fig. 7. Number of taxa for (A) fixed number of stations (i.e. constant sampling effort) and (B) equidistant sections along the virtual axis for all data (countable and non-countable taxa; see 'Materials and methods'). Grey areas correspond to the extent of sand sediments

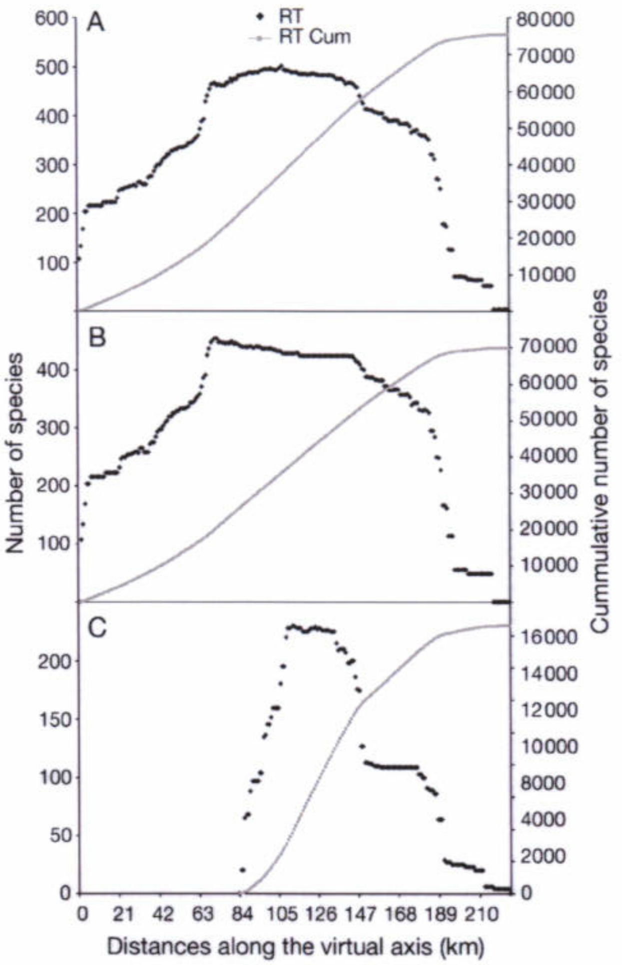

Fig. 8. Evolution of the taxonomic richness along the virtual axis (black) and cumulative number of taxa along the virtual axis (grey) for (A) all stations, (B) gravel/pebble sediments, and (C) sand sediments. RT: taxonomic richness; RT Cum: cumulative taxonomic richness

DISCUSSION

Characterising biological diversity as well as analysing the identity and the role of species in a given ecosystem are important current focuses in ecology. Since the role of a given species in an ecosystem can be variable, certain species may be redundant, thereby ensuring a faster recovery of this ecosystem in the case of disturbance (resilience principle). To better understand these interactions, it is necessary to analyse a stable and diversified ecosystem (Ives & Carpenter 2007). In the eastern English Channel, a high taxonomic diversity was recorded, with over 860 taxa collected at the 318 stations analysed. Converted to Shannon's index, they correspond to exceptional values (maxima are close to 6 bits) at the scale of the Channel. The taxonomic richness observed in the present study is among the highest in the studies compared here (Table 2). Nevertheless, a quantitative comparison remains difficult because of differences in e.g. scales (local, regional, biogeographical), methodologies (gears, mesh type, sorting) or heterogeneity of habitat. For example, we observed a total taxonomic richness of 875 taxa, which was half that of the Roscoff inventory (1856 taxa; Dauvin & Dewarumez 2002) representing the diversity of the complex mosaic of habitats of the western English Channel, but was nearly twice as high as the more homogeneous central and southern North Sea (455 taxa). In terms of the relative proportions of phyla in the overall diversity of the area, some phyla were of the same order of magnitude as reported in other studies, such as Mollusca and Echinodermata, with proportions of ~18 and ~2.5%, respectively. In contrast, phyla such as Annelida, Porifera and the catch-all group 'Others' were completely different depending on the study analysed. Compared to the

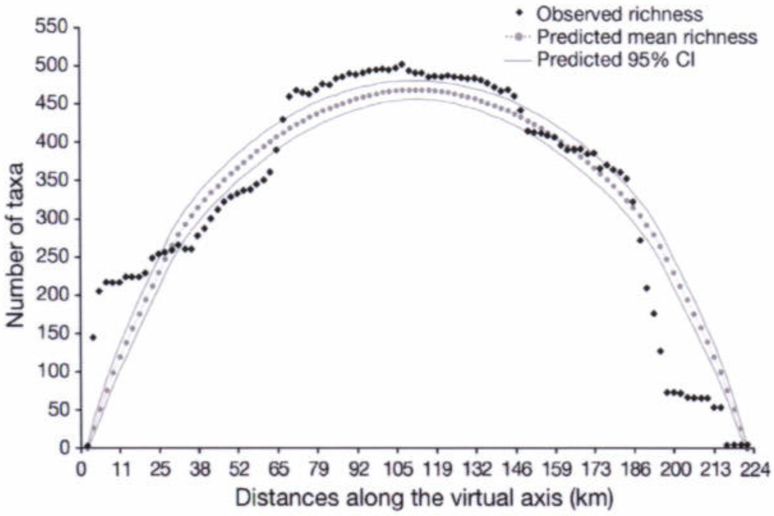

Fig. 9. Observed and predicted taxonomic richness curves for the benthic taxa along the virtual axis in the eastern English Channel. These curves were obtained using RangeModel 5

European dataset (W. Appeltans at European Register of Marine Species pers. comm.), our measures of phyla diversity were similar for Arthropoda, Mollusca, Cnidaria, Echinodermata and Chordata but differed for Annelida (28.9 versus 10.9%), Bryozoa (8.2 versus 3.8%), Porifera (3.5 versus 7.0%) and Others (3.5 versus 16.7%) in our study and in the European dataset, respectively.

Difficulties involved in estimations of species richness

Despite the fact that it may slightly overestimate the richness value, Foggo et al. (2003) considered the Chao1 index to be the best estimator of diversity, and ignored Chao2 and incidence-based coverage estimator indices. In contrast, Walther & Morand (1998) considered the Chao2 index to be the best, emphasising that almost all of the species richness estimators yielded over-estimations (which is inherent to the sampling methodology). In our case, Chao2 index computation highlighted that, despite a large sampling effort, taxonomic richness remained underestimated. All aforementioned authors agreed that both sampling strategy and scale were the factors that had the greatest influence on the richness estimators. Some studies (Ellingsen 2001, Ellingsen & Gray 2002) have effectively demonstrated that sampling effort in a determined area must be well thought out. However, in the marine environment, effective sampling is undermined by difficulties in determining boundaries and extents of habitats/assemblages, which often leads to blind sampling (Gray 2000).

The representativeness of the sampling strategy is often a major problem in studies (Gentil & Dauvin 1988, Ellingsen 2001). An accurate collection of rare species (those known to have low occurrences, i.e. are present at <5% of sites, with low probability of collection and variation in pattern distribution) requires a well planned sampling effort. When rare species are 'spot' species (i.e. abundant at 1 site), their distribution patterns are restricted in spatial extent (Colwell & Coddington 1994, Gray 2000), and a poor sampling strategy would partly miss them, even though they are locally abundant (Ellingsen & Gray 2002). In our study, the fact that most of the taxa are rare (>500 taxa or 65% of the total number of taxa) tended to indicate that the sampling strategy was either exhaustive or that these taxa were widely dispersed and thus difficult to collect. Rarity and frequency of collection of a species could also influence the reliability of a species richness estimator. Most of the estimators are sensitive to the number of single species, but also to the spatial structure of a community, which results from the aggregation pattern of each individual species (Foggo et al. 2003).

Sessile epifauna: the main compartment

Following the recommendation of Colwell & Coddington (1994), we chose the Chao2 index as our species richness estimator, primarily to integrate the sessile epifauna (which could be considered as aggregated species) in the inventory (25% of the taxonomic richness in the Channel area). Often neglected because of sampling and identification difficulties, this benthic compartment is an important indicator for some marine typologies, such as the EUNIS classification (Connor et al. 2004). This compartment is all the more important because sessile species often provide various microhabitats (see Tsuchiya & Nishihira 1985 and Kostylev et al. 2005) for other invertebrates, such as the isopod crustacean *Anthura gracilis*, which is always found in tubes of the polychaete *Spirobranchus* spp., Terebellidae (polychaete), whose numbers increase with the complexity of the 3D structure, or the amphipod *Ericthonius punctatus*, whose numbers increase with the size of hydroids (A. Foveau pers. obs.). The increase in topographical complexity may increase species richness by creating micro-climate areas, making food resources available and generating refuges and new ecological niches (McCormick 1994, Kostylev et al. 2005). Interstices between heterogeneous/coarse elements also offer enclaves for deposits of fine sediments and the settlement of species that rely on muddy sediments. These microhabitat opportunities could partly explain the differences in specific richness observed between the sand and gravel/pebble sediment categories, as shown by the repartition of the number of species per sediment type in Fig. 3.

Centres of diversity in the English Channel

Añorve-Sanvicente et al. (1996), who studied the diversity in the eastern English Channel from data collected in the 1970s by Cabioch et al. (1977), highlighted that biological diversity was globally low at the scale of the whole Dover Strait. They did, however, note a diversity hot-spot in the centre of the Dover Strait, which was unusual for the English Channel. This patch, crossing several sediment and community types, was characterised by high species richness with a marked dominance of a few species. The authors thought that this particular pattern of diversity was linked to a large-scale hydrodynamic process, notably the residual transport from the English Channel to the south of the North Sea (Grochowski et al. 1993), which determines larval dispersion, as shown by Dewarumez et al. (1993).

In our study, no clear dominant pattern could be identified (Shannon's diversity index and Pielou's equitability index having high values; see Foveau 2009 for details), and the taxonomic diversity seems highly linked to sediment and benthic community types. High values of species richness were observed on gravel/pebble substrates, located in the western part of the studied area and the Dover Strait. Such differences between historical and recent patterns are difficult to explain since the English Channel is a biogeographical crossing. The longitudinal climatic gradient is a factor determining the distribution of numerous species in the benthic communities (Holme 1966, Cabioch et al. 1977). Depending on their ecological preferences, 2 groups of species may be present (Gentil & Cabioch 1997): the western species, regrouping (1) oceanic species with a large northward distribution but which also occur in the southern English Channel, and (2) species of warmer climates; the eastern species, also called boreal species, which prefer cold waters and are deterred by the warmer western waters.

Climatic change (e.g. sea temperature increase), inducing species to adapt their distribution patterns (see Mieszkowska et al. 2006), may cause variations in species richness. Areas of high species richness might, then, represent recent increases in the number of species overlaps (ter Hofstede et al. 2010). Climate change may also facilitate the settlement of exotic species or the explosion of some formerly cryptic ones (Burgiel & Muir 2010, Dewarumez et al. 2011).

Can MDE explain the high diversity in the eastern English Channel?

Many authors (e.g. Colwell & Hurtt 1994, Gaston et al. 1998) agreed that in addition to ecological phenomena, geological and evolutionary processes may also influence the distribution of taxonomic richness. In the eastern English Channel, physical and biological parameters contribute to maintaining high biodiversity.

Hydrodynamics are among the most important parameters involved in structuring the species composition in the study region. Indeed, in our study area, strong hydrodynamics associated with low bathymetry causes a mixing of water masses over the whole water column (Agoumi et al. 1983), and coastal and offshore waters have different characteristics (Salomon & Breton 1991). The central water mass, originating from the Atlantic Ocean, is characterised by low thermal variation, stable marine salinity and low variation of biological and hydrological parameters such as turbidity, nutrient concentrations, phytoplankton composition and abundance (Visser et al. 1996). Conversely, the coastal water mass is characterised by high variation of nearly all physical and biological parameters, essentially in response to the existence of a 'fleuve côtier' (a coastal water flow, directed northward, fed by rivers, in particular the Seine, and characterised by low salinities and high organic matter content), inducing a strong hydrological front whose distance to the coast may shift rapidly according to hydrodynamic and wind regimes (Brylinski et al. 1988). If some communities can withstand such temporal variation of the environment, they may support more species, as suggested by Palmer (1994). Moreover, hydrodynamics have structured the superficial sediment cover. Thus, the eastern English Channel is a mosaic of different sediment types (Vaslet et al. 1979). Superficial sediment cover consists of a gradient ranging from coarse sediments (pebbles and gravels) in areas of high tidal energy to fine sediments (sands and muds) in areas of lower energy, such as bays. Finally, the hydrodynamics allow exchanges of larvae coming from the west (western English Channel or Atlantic water masses) or from the North Sea, depending on tidal and wind regimes. The existence of a distribution gradient of species from west to east, as mentioned in some studies (Holme 1966, Cabioch et al. 1977), confirms the openness of the Channel and the possible existence of many species.

The second important element is the heterogeneity of the habitats, particularly in heterogeneous sediments. The fact that elsewhere a variety of micro-habitats may be observed in heterogeneous sediments led us to use a fine enough sampling grid to detect, as far as possible, the entire range of taxa. The existence of all of these micro-habitats increased the availability of niches, increasing the possibility of a large number of species, including rarer species, occurring. In this case, competition could be a factor regulating population. However, niche overlap does not necessarily assume competition as long as the conditions of the environment are favourable (Pianka 1974), as might be the case in the eastern English Channel, an area not considered limited in food availability. Moreover, the more species in a community can share resources or use different resources, the richer the community becomes (Pianka 1974, Palmer 1994). However, this particular point cannot be resolved without a serious review of biological species traits and interspecific competition, which is beyond the scope of the present study.

The last important point is the evolution of the communities supported by these habitats. Despite all the niches or food availabilities, communities suffer from natural fluctuations, that are not easily quantifiable. Community evolution could be explained by 'compensatory mechanisms' (Connell et al. 1984), presupposing that, given time, rarer species will tend to increase and commoner ones will decrease, maintaining a sort of equilibrium in the ecosystem. In the eastern English Channel, there is a mix between mature and 'immature' (i.e. non-equilibrium status) communities (rank-frequency diagrams, Foveau 2009, unpublished results), which can explain high values of diversity. These mature and immature communities are created by hydrodynamic factors; life history strategies and resilience of the communities then maintain the equilibrium. May & MacArthur 1972, Pianka 1974 and Palmer 1994 have shown that in a community, the non-equilibrium status increases species richness because of the existence of high species overlap ('niche overlap hypothesis').

In his review on variation in species richness, Palmer (1994) highlighted the question that has been raised by many ecologists: 'Why do so many species coexist?' He developed the 'competitive exclusion principle' (also known as Gause's law), with 7 associated conditions. For a given 'suite of species, interspecific competition will result in the exclusion of all but one species' (Palmer 1994, p. 519), and the more the conditions associated with this principle are violated, the more species are encountered. In the eastern English Channel, most of the conditions are violated, which can explain the high diversity encountered.

Even though some ecological or biological phenomena may be inferred (Colwell & Hurtt 1994), random distribution might also explain the observed patterns of species diversity. Random distribution is based on the assumption that for all taxa, all range sizes and placements tend to follow the same distributions between the limits of the studied domain. Random distribution may be related to theories of extinction and minimum viable population size (Lande & Barrowclough 1987), which state that a large number of individuals is required in a population to ensure its genetic viability, by allowing long-term survival through genetic plasticity and therefore adaptability to environmental changes. The model used in our study emphasises that the spatial variation in range size is linked, in many communities, to the existence of many species restricted to relatively small areas and some species associated with larger areas, the species' geographic range being the fundamental unit. The distribution of taxa with large ranges may affect the geometric constraints of the null model (Colwell & Hurtt 1994, Colwell et al. 2004). Taxa with small ranges can occur virtually anywhere in a considered domain, in contrast to those with large ranges that are necessarily centred and contained within the domain (since this is a condition of the model). As a consequence, the MDE model seems to be a better predictor of species with large ranges (whose distributions often largely overlap the domain boundary) than of those with small ranges.

The logical continuation of this study, currently underway, concerns the trophic interactions between biological compartments, to better understand the structure of the trophic network (Garcia et al. 2011). Coupling this extraordinary dataset to life-history traits or the role of engineer species should allow us to determine the respective importance of various compartments to ecosystem functional diversity and estimate the impact of decreasing marine biodiversity (Gray 2000). This means continuing to collect data *in situ* and ensuring the highest possible precision in the identification of collected taxa as well as taking into account innovative methods such as habitat modelling. Integrated into management plans of marine ecosystems, such crucial knowledge is strategic for the designation of marine protected areas and associated conservation plans.

Acknowledgements. We thank C. Garcia and everyone involved in the sorting and identification of the species; the officers and crew of the RV 'Côtes de la Manche' for their help at sea; S. Vaz for comments and corrections in English syntax and grammar; and the referees for their helpful suggestions and comments. We also thank R. Colwell for valuable advice with RangeModel and J. Veech for advice about his program script. This work was carried out with various financial contributions, particularly industrial funding (ENERTRAG France, Lafarge Granulats and GIE-GMO), and the European Union's Interreg IIIa and IVa France (Channel) – England cross-border European cooperation programmes (European Regional Development Funds) CHARM 2 and 3 projects coordinated by A. Carpentier, Ifremer, Boulogne-sur-Mer.

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Editorial responsibility: Romuald Lipcius,
Gloucester Point, Virginia, USA

Submitted: March 21, 2012; Accepted: October 22, 2012
Proofs received from author(s): March 12, 2013

Journal of Sea Research xxx (2012) xxx–xxx

Contents lists available at SciVerse ScienceDirect

Journal of Sea Research

journal homepage: www.elsevier.com/locate/seares

The role of structuring benthos for juvenile flatfish

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ARTICLE INFO

Article history:
Received 10 November 2011
Received in revised form 17 July 2012
Accepted 19 July 2012
Available online xxxx

Keywords:
Juvenile flatfish
Shelter
Feeding ground
Lanice conchilega
Ecosystem engineer
Pleuronectes platessa

ABSTRACT

Within coastal nurseries, the distribution of juvenile flatfish may depend on small-scale habitat variability. The presence of ecosystem engineers is known to have important impacts in coastal sediments. *Lanice conchilega* is a well-known marine ecosystem engineer of shallow soft bottom ecosystems, shaping the macrobenthic community and attracting flatfish. The present study examines the relation between juvenile flatfish and *L. conchilega* reefs through two experiments. In a field experiment in the Dutch part of the North Sea, the benthic habitat is evaluated by comparing relative differences in numbers of juvenile flatfish between ecosystem engineered habitats and adjacent bare sand (*i.e.* non-ecosystem engineered) habitats. The hypothetical shelter seeking behaviour was further examined using stomach content analyses. Results show that juvenile plaice *Pleuronectes platessa* was the dominant species within the tube worm habitat and the species selects specifically for this biogenic habitat. This selection was explained as feeding behaviour. In a complementary laboratory study, food was excluded and the shelter function of the ecosystem engineered habitat was investigated. This experiment quantifies the selection for this habitat by juveniles of the common sole *Solea solea*. Results from the flume experiment, manipulating the number of tube worms, show that distribution of sole was not random when current velocities are high. The selected habitat is the one with low density tube worm aggregations. Overall, we conclude that structuring benthos plays an important role for juvenile flatfish, both as refuge and as feeding ground.

1. Introduction

Structurally complex benthic habitats may play an important role in the ecology and population dynamics of juvenile flatfish species (Pappal, 2006). These systems are heavily used by a variety of taxa, as a consequence of food availability, shelter or simply changing hydrodynamics.

Habitat complexity is the result of different processes. Ecosystem engineers can exert a strong influence on ecosystem properties because of their functional characteristics and this influence exceeds normal expected levels with respect to their mere relative abundance (Hooper et al., 2005). The ecosystem engineers build biogenic structures that add complexity to the habitat. Through these structures, ecosystem engineers modify the hydrodynamic flow regime near the sea floor (Eckman et al., 1981) with significant effects on processes like sedimentation and erosion, food availability driven by hydrodynamic forces and the recruitment, and growth and survival of larvae and/or juveniles (Koenig et al., 2000; Turner et al., 1999).

Animal tubes can cause sediment stabilization as a consequence of several factors (Eckman et al., 1981). By decreasing the water velocity and deflecting the earlier laminar flow around the assemblages, tube worms change the hydrodynamic flow near the sea floor. Flow alterations may have important ecological consequence on sedimentation, food availability, larval and juvenile recruitment, growth and survival. Increased abundances of associated fauna cannot only be attributed to enhanced food availability but also to the provision of shelter from larger predators.

The tube building polychaete *Lanice conchilega* is a dominant ecosystem engineer in coastal marine areas (Rabaut et al., 2007; Van Hoey et al., 2008). The species tends to aggregate in high density patches, with specific biological, physical and temporal features (Rabaut et al., 2009). For the macrobenthic community, the habitat modifying capacity of *L. conchilega* has been suggested to lie in the creation and regulation of safe havens for species, in influencing the interactions between local species and in changing the physical environment (Rabaut et al., 2007; Van Hoey et al., 2008). Patches of high abundance of the species not only attract the aulophora larvae but also hydrodynamically trap sediment (Dittmann, 1999; Eckman,

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1385-1101/$ – see front matter © 2012 Published by Elsevier B.V.
http://dx.doi.org/10.1016/j.seares.2012.07.008

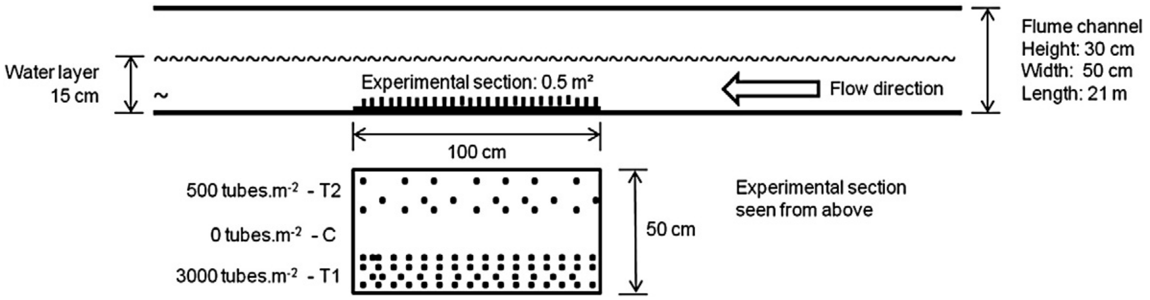

Fig. 1. Experimental set up. Above: cross section of flume tank (total flume tank length: 21 m, width 50 cm). Below: experimental section seen from above. 200 *S. solea* individuals are left for 20 h in the total flume tank after which densities in the experimental section are counted. Three different tube densities were applied next to each other: 3000 tubes.m^{-2} (treatment 1, T1), 500 tubes.m^{-2} (treatment 2, T2) and 0 tubes.m^{-2} (control, C). The tubes were spaced randomly as to mimic the irregular spatial arrangement *in situ*. All treatments had an inert sand (125 μm) as substratum layer of 10 cm. Responses were tested for two different water flow velocities: 3 and 15 m.s^{-1}. Tests were replicated three times for each water current velocity with the relative position of the treatment compartments changed for each replicate run to avoid position bias in the flume.

1983; Heuers et al., 1998). It results in the occurrence of gentle mounds and shallow depressions (Carey, 1987; Féral, 1989; Hartmann-Schröder, 1996; Hertweck, 1995; Zühlke, 2001). Modelling studies suggest that high flow velocities lead to a continuous growth of patches while a mosaic of patches originates at intermediate flow velocities (Heuers et al., 1998). Therefore, the species has been described as an important ecosystem engineer. Its effect on benthic biodiversity has been extensively described (Callaway, 2006; Carey, 1987; Dittmann, 1999; Féral, 1989; Rabaut et al., 2007; Van Hoey, 2006; Zühlke et al., 1998). It was already shown that post-larval *Pleuronectes platessa* selects for this habitat in intertidal areas, (Rabaut et al., 2010) however, it is not clear whether this habitat plays a role in the distribution and ecology of juvenile flatfish in subtidal areas.

Effects on habitat selection of flatfish are thought to be mainly related to food availability (Beyst et al., 1999; Phelan et al., 2001; Wouters and Cabral, 2009) and therefore the attractiveness of the habitat lies mainly in the increased availability of high quality food items (i.e. larger preys). The shelter function the *L. conchilega* habitat is providing is of potential importance for juvenile flatfish as predation is a major cause of mortality during the early live stages of fishes (Lemke and Ryer, 2006). The demonstrated influence of *in situ* reefs on juvenile flatfish does, however, not elucidate the extent to which the attraction is due to increased feeding possibilities or to the reefs functioning as a refuge.

In the present study the selection by flatfish of small scale subtidal habitats formed by tube worm aggregations is tested. Two different flatfish species are used: Plaice (*P. platessa*) and Sole (*Solea solea*). *P. platessa* is a visual feeder, which mostly takes slow-moving food living on the bottom, but they also feed on active crustaceans. *S. solea*, on the other hand, is a nocturnal and olfactrorial feeder with a poorly developed vision which feeds on sessile or barely mobile organisms (Beyst et al., 1999; De Groot, 1971). The size of the mouth, oesophagus and stomach determines the size of the animals that can be ingested. *P. platessa* and *S. solea* have a relatively small mouth and are restricted to the consumption of small-sized prey (Beyst et al., 1999). The diet of both species is therefore quite similar: mostly dominated by polychaetes and, depending on the area, possibly complemented by siphons of the bivalve *Spisula* spp. (Rijnsdorp and Vingerhoed, 2001).

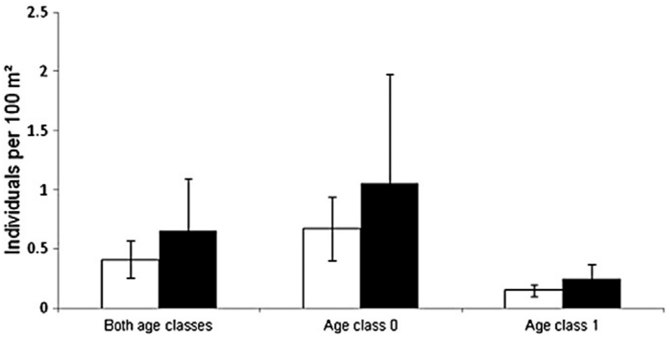

Fig. 2. Flatfish densities. White bars represent flatfish densities in non-ecosystem engineered habitat; black bars represent flatfish densities in ecosystem engineered habitat (standard error bars are indicated).

Present study tests the selection by flatfish of small scale subtidal habitats formed by tube worm aggregations. A first hypothesis is that prey availability determines juvenile flatfish densities: field observations test the feeding behaviour of *P. platessa* inside and outside the structured habitat through gut content analyses (i.e. focus on prey availability as an explanatory factor). The second hypothesis is that structural habitat components are important in determining fish density: laboratory flume tank experiments expose juvenile *S. solea* to different densities of artificial worm tubes at two different current velocities to test the shelter function (excluding food effects).

2. Methodology

2.1. Field sampling and treatment

The research area was located in the Dutch part of the North Sea in sub-littoral areas (54°00′N, 7°50′E, just outside the Wadden Sea). Two habitats were identified based on differences in density of *L. conchilega* in 50 Van Veen grab samples. Only high density samples were qualified as an ecosystem engineered habitat (Rabaut et al., 2007, 2009). The densities of the ecosystem engineer in the different habitats (ecosystem engineered habitat versus non-ecosystem engineered habitat) were investigated for each area and prior to further analysis; more that 150 ind.m^{-2} were considered as high density presence while less than 20 ind.m^{-2} as low density. Differences between habitats were tested in generalized linear models with habitat as a fixed factor and the ecosystem engineer densities as the response variable. The habitats coincided with the areas adjacent to Ameland Island (ecosystem engineered habitat) and Schiermonnikoog island (non-ecosystem engineered habitat). The sampling design of two very similar adjacent areas is important to

Table 1
Differences in flatfish densities between age, habitat and interaction effect (p-values). Statistical test: generalized linear model to compare densities (Poisson distribution; proc genmod procedure in SAS software). Asterisks indicate significant differences. Differences between ‘Habitats’ refer to the differences between ecosystem engineered and non-ecosystem engineered habitats.

	Habitat	Habitat x age	Age
Both age classes	0.0001*	0.9699	0.1949
Age class 0	0.0024*	–	–
Age class 1	0.0076*	–	–

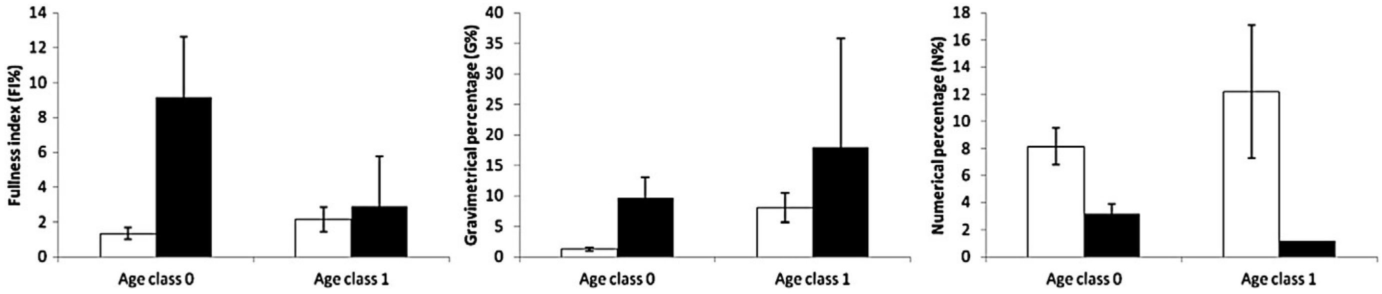

Fig. 3. Overall stomach analysis per age class of *P. platessa* representing fullness index (FI%) (left), proportional gravimetric differences (G%) (middle) and proportional numerical differences (N%). Non-ecosystem engineered habitat is represented with white bars; ecosystem engineered habitat is visualized as black bars.

be able to test the correlation with flatfish densities. This approach will provide insight on this appropriate level and extrapolation to larger scales may be difficult (as to avoid using the samples as pseudoreplicates). Flatfish sampling was done at a depth of ca. 6 m with a 2 m beam trawl deployed from the *RV* 'WR76 Herman Simon'. Three tracks were taken in each habitat. Length of each track was approximately 500 m, track lengths were measured *in situ* and fish densities were recalculated to individuals per 100 m². Fish were identified, counted and measured on board. Flatfish densities were compared between habitats. Differences were calculated using a generalized linear model in which the fixed factors habitat, age and their interaction effect were related to the flatfish densities (SAS software, proc genmod procedure). The response variables are count data (integers), so the residual error structure follows a Poisson distribution with the variance multiplied by an overdispersion parameter. Because the predictor and the mean response are not linearly related to each other, the relationship was specified by a log link function. The fixed effects structure was reduced in a backward stepwise manner (McCulloch, 2001).

In the field, flatfish was anaesthetized in a benzocaïne (ethyl amino-4-benzoate) solution to prevent regurgitation of the stomach contents and preserved in an 8% buffered formalin solution. Flatfishes were divided in two age classes: age class 0, containing individuals between 5 and 9 cm and age class 1 containing individuals between 9.1 and 13 cm (Amara et al., 2001; Beyst et al., 1999). For age class 0, no individuals smaller than 5 cm were subjected to analysis as these small individuals mainly fed on meiobenthos, while larger individuals shift to macrobenthos (Aarnio et al., 1996). *P. platessa* was the most abundant species for which enough individuals were available to do the analyses. Other flatfish species such as *Limanda limanda* and *S. solea* were caught in low densities. In the laboratory, ten *P. platessa* individuals, per age class and in each habitat were selected for further stomach analyses. All prey items in the stomachs were counted and identified to the lowest possible taxonomic level (further referred to as species). The biomass (mg AFDW) of each prey item present in the stomach as well as the flatfish biomass was measured.

The relative importance of prey in the diet (*i.e.* stomach content) was expressed as percent of numerical abundance (N%), weight (G%), and fullness (FI%). These percentages express the overall numerical and gravimetric importance of a stomach in a group of samples. N% and G% were calculated on nonempty stomachs (Frid et al., 1999), while FI% was calculated on all stomachs (including empty). Feeding activity was evaluated by the vacuity index (V%). These percentages were calculated for groups of samples as follows:

N% (Number of food items in a stomach/total number of food items in a group) × 100
G% (Total biomass in a stomach)/(total biomass in a group) × 100
FI% (AFDW of stomach content)/(AFDW of fish) × 100
V% (Number of empty stomachs in a group/total number of analysed stomachs in a group) × 100

To analyse more in detail, diet composition, numerical, gravimetric percentages and the frequency of occurrence (FO%) were further calculated per species within each sampling group. These percentages express the numerical and gravimetric importance on one species within one stomach. Calculations are as follows:

Ni% (Number of prey type i)/(total number of prey items in the stomach) × 100
Fi% (AFDW of prey type i)/(total AFDW of ingested food) × 100
FOi% (Number of stomachs containing prey item i)/(all stomachs) × 100

As the response variables for the stomach analyses are expressed as relative percentages, the residual error structure was assumed to follow a binomial distribution. Hence, a generalized linear model was used to evaluate the significance of the fixed effect habitat, age and their interaction effect. The relationship was specified by a logit link function. Differences between habitats were analysed for each age separately (generalized linear model with habitat as a fixed effect). Furthermore, a detailed analysis on species composition was performed. Differences in prey species composition were analysed using multivariate ANOSIM and SIMPER analysis (Clarke and Warwick, 2001). When two factors (habitat and age) were analysed together, two way crossed ANOSIM and SIMPER routines were run (Primer v6).

Prey species composition was analysed on the basis of the frequency of occurrence (FO%) and the relative contribution of individual prey species to the dissimilarity between groups (SIMPER analysis; two way crossed when two factors involved). These analyses were performed both on numerical and gravimetric indices. Differences in diversity of prey species were based on differences in Shannon Wiener index (Hampel et al., 2005), which was tested with a general linear model if there was homogeneity of variances (Levene's test) and if the residual error structure followed a normal distribution (Shapiro–Wilk's test). If assumptions were not met, non parametric tests on Shannon Wiener index were performed (Wilcoxon).

2.2. Laboratory set up

In the laboratory experiments, the ecosystem engineered habitat was artificially mimicked using false tubes made of a 3 mm diameter rubber band of 5 cm in length, coated by inert coarse sand, in order to resemble the flexibility and texture of real *L. conchilega* tubes. Artificial aggregations of tubes were applied in the experimental zone of a flume

Table 2
Differences (p-values) in stomach contents between ecosystem engineered and non-ecosystem engineered habitats expressed as FI% (fullness index), G% (proportional gravimetric values) and N% (proportional numerical values). Statistical test: generalized linear model to compare densities (binomial distribution; proc genmod procedure in SAS software).

	FI%	G%	N%
Age class 0	0.0002*	0.0005*	0.0030*
Age class 1	0.0089*	0.2806	0.1419

Please cite this article as: Rabaut, M., et al., The role of structuring benthos for juvenile flatfish, Journal of Sea Research (2012), http://dx.doi.org/10.1016/j.seares.2012.07.008

Table 3
Prey species community analysis. ANOSIM (R-values) and SIMPER dissimilarities between prey communities of flatfish caught inside ecosystem engineered habitats and those outside and between age classes (two way crossed analysis). ANOSIM R and correspondent p-values are given for numerical (N%) and for gravimetric (G%) percentages. SIMPER dissimilarities indicate differences in prey composition. Significant differences are indicated with an asterisk.

	N%			G%		
	R	p	Dissimilarity	R	p	Dissimilarity
Age	0.351	0.005*	71.46	0.311	0.001*	73.76
Habitat	0.581	0.001*	90.57	0.507	0.001*	94.12

tank system of 10.5 m². The experimental area had dimensions of 1 m length, 0.5 m width and 15 cm water height. Three different tube densities were applied next to each other: 3000 tubes.m^{-2} (treatment 1, T1), 500 tubes.m^{-2} (treatment 2, T2) and 0 tubes.m^{-2} (control, C) (Fig. 1). These tube densities were based on the biological and physical features of the structures formed (Rabaut et al, 2009). The tubes were spaced randomly as to mimic the irregular spatial arrangement *in situ*. All treatments had inert sand (125 μm) as substratum layer of 10 cm. Responses were tested for two different water flow velocities: 3 and 15 m.s^{-1}. For this experiment the flatfish species used is *S. solea* as these were commercially available and aged.

A total of 668 *S. solea* individuals (9 weeks old; 4–6 cm) were obtained from the hatchery *Solea BV* in IJmuiden, the Netherlands. Flow-through tanks were used to maintain the juvenile *S. solea* (temperature 14.5 +/− 1°C; salinity 34 +/− 0.1 psu).

During each experimental run, 200 *S. solea* individuals were added to the flume. The *S. solea* individuals were left in the flume tank for 20 h after which the amount of individuals in each tube density habitat of the experimental section (0.5 m²) was counted (see Fig. 1 for experimental set up). This was replicated three times for each water current velocity with the relative position of the treatment compartments changed for each replicate run to avoid position bias in the flume. Replicated G-tests for goodness of fit to chi-square distribution (Sokal and Rohlf, 1995) (also called the log-likelihood ratio test), *i.e.* 33.33% of individuals inside each of the three experimental areas, were conducted to determine significant deviations from the expected 1/1/1 (i.e., even) distribution. The general computational formula used was:

$$G = 2\Sigma^{a} f_{i} \ln(f_{i}/F_{i})$$

Where f_i represented the observed frequencies and F_i the expected frequencies.

Pair wise comparisons were performed at a critical probability of $\alpha = \alpha/k$, with k equal to the number of intended tests [Bonferroni approach, Sokal and Rohlf (1995)].

3. Results

3.1. Field study results

The results from the Van Veen grab analyses, to test differences between habitats with a generalized linear model with habitat as a fixed factor and the ecosystem engineer densities as the response variable, confirm that the densities of *L. conchilega* were significantly higher ($p < 0.0001$) within the ecosystem engineered habitat (242 +/− 90 SE ind m^{-1}) as compared to the very low densities outside (12 +/− 1 SE ind m^{-1}). Results from the beam trawl tracks showed that densities of *P. platessa* are significantly higher within the *L. conchilega* ecosystem engineered habitats as compared to the densities outside (Fig. 2, Table 1). No age effects or interactions were found (Table 1). *S. solea* was only found in low densities: 17 individuals in the *L. conchilega* ecosystem engineered area (all in the same beam trawl sample) and 1 individual outside.

Turning to stomach contents, both age classes had a higher fullness index and gravimetrical stomachs contained more food within the ecosystem engineered habitat (Fig. 3; Table 2). Nonetheless, stomachs seemed to have more prey items and less empty stomachs in the non-ecosystem engineered area: 27% of the stomachs were empty for individuals caught in the ecosystem engineered habitat against only 10% outside.

Analyzing the prey item composition, the two way crossed SIMPER results show a large dissimilarity between prey item assemblage caught in areas with and without ecosystem engineer (Table 3). Moreover, two way crossed ANOSIM results show that there was a significant habitat and age effect, both numerically and gravimetrically (Table 3). Based on the frequency of occurrence (FO%) and on multivariate analyses on G% and N% data, the four most important preys were *Spio* spec., *L. conchilega*, *Pontocrates altamarinus* and *Nephtys hombergii* (Table 4).

Spio spec. was an important prey for *P. platessa* in the non-ecosystem engineered habitat (both numerically and gravimetrically), while *L. conchilega* seemed to be an important prey in the ecosystem engineered habitat. No significant effects were found for *P. altamarinus* and *N. hombergii* (Fig. 4, Table 4). Differences because of age classes were found for *Spio spec.*, which occurred in significantly higher densities in age class 0 (N%, $p = 0.0266$; G%, $p = 0.002$) and for *L. conchilega*, which was more frequently eaten by *P. platessa* of age class 1 (only gravimetrically, $p = 0.0221$). In terms of diversity of species, no significant differences were found between habitats ($p = 0.2633$) or ages ($p = 0.5094$).

3.2. Laboratory results

Flume experiments showed that *S. solea* was found in higher densities in the lower tube density habitat of 500 tubes.m^{-2} as compared to the non-engineered habitat (C) and to the high tube density habitat of 1000 tubes.m^{-2} (Fig. 5; Table 5). There was no significant difference in selection found between the control area and the high tube density

Table 4
Most dominant prey items in ecosystem engineered and non-ecosystem engineered habitat. Importance of prey items is based on frequency of occurrence (FO%), species contribution to the dissimilarity of community composition between habitats (two way crossed SIMPER). Numerical and gravimetric differences of prey species between habitats is indicated with significance level (asterisks indicate significant differences).

Species	FO%		SIMPER		p level	
	Without ecosystem engineer	With ecosystem engineer	% contribution (N%)	% contribution (G%)	N%	G%
Spio sp.	68.75	25	39.51	39.56	<0.0001*	<0.0001*
L. conchilega	6.25	16.67	33.43	24.75	<0.0001*	<0.0001*
P. altamarinus	10	11.11	11.21	0.05	0.069	0.9828
N. hombergii	21.25	0	3.27	2.8	0.2926	0.0501

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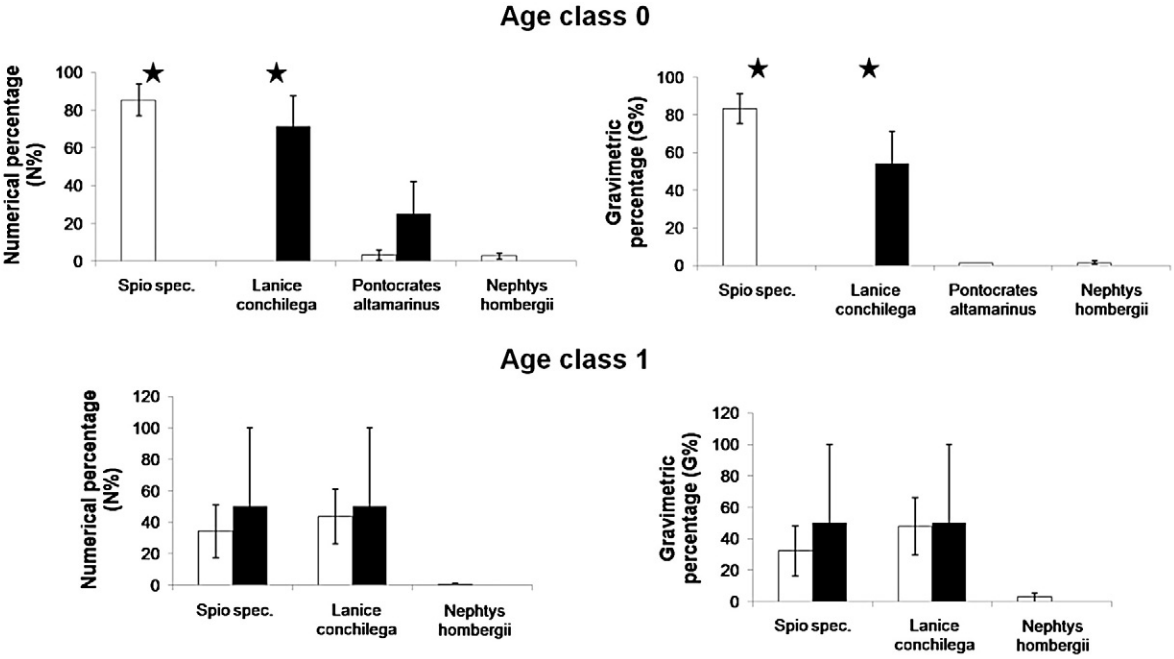

Fig. 4. Stomach content: prey species analysis. Numerical (N%) and gravimetric (G%) differences for the most important prey species are represented. Non-ecosystem engineered habitat is represented with white bars; ecosystem engineered habitat is visualized as black bars. Significant differences between habitats are indicated with a star.

habitat ($p > 0.05$). The differences in flatfish densities were only significant when current velocity is high (15 m s^{-1}), no statistical significant selection could be found with low water current velocities (3 m s^{-1}) (Fig. 5; Table 5).

4. Discussion

Results show that flatfish species occur in higher densities when the habitat is shaped by *L. conchilega* than in non-engineered habitats. The selection for these habitats by flatfish has been confirmed in several studies (Amara et al., 2001; Rabaut et al., 2010). Shucksmith et al. (2006) indicate that adult *P. platessa* densities correlate specifically with *L. conchilega* and *Chaetopterus* spec. *P. platessa* has been described earlier as being tightly associated with assemblages containing structuring epifauna such as hydroids, *Alcyonium digitum*, *A. diaphanum* and *Flustra foliacea* (Kaiser et al., 1999). On the contrary, some structured habitats such as vegetated habitats can have a negative effect on feeding and growth as indicated for juvenile European flounder (*Platichthys flesus*) in eelgrass environments (Gronkjaer et al., 2007). Our analyses suggest that there is no unique reason why juvenile flatfish is found in higher densities in the structured habitats but increased food availability and shelter may trigger juvenile flatfish to reside between *L. conchilega* tubes. However, the use of different species and both laboratory and *in situ* experiments has limitations (see below). Juveniles of *P. platessa* showed a clear feeding advantage when they were found within the ecosystem engineered habitat. Plaice has a higher fullness index within the ecosystem engineered areas. A higher fullness is thought to be a good predictor of growth (Tarpgaard et al., 2005). The higher gut fullness is also reflected in the gravimetric percentage. The numerical percentage, however, shows a totally opposite trend. The higher number of prey items in areas without the ecosystem engineer was fully attributed to *Spio* spec. It seems that in the absence of the ecosystem engineer *L. conchilega*, *P. platessa* turns to *Spio* spec. as main prey item. However, *Spio* spec. are described as positively associated with *L. conchilega* (Rabaut et al., 2007), but it appears that *P. platessa* feeds less on it when *L. conchilega* is available as prey. Although *P. altamarinus* is known to be negatively associated with *L. conchilega* (Rabaut et al., 2007), it occurs more frequently as prey in flatfish caught in *L. conchilega* aggregations. The main advantage seems to be that juvenile flatfish fill their stomach with larger items, i.e. the tube worm *L. conchilega* itself. On the contrary, the vacuity index is higher in the ecosystem engineered habitat and the number of prey items is lower implying that the feeding behaviour changes as a function of the presence of the bio-engineered habitat. Without the structured habitat, juvenile flatfish seems to feed on what can be found, which means constant foraging on smaller prey items. In the *L. conchilega* habitat, the flatfish becomes more selective for larger food items, leading to a lower feeding activity, a lower number of prey items but a higher fullness index and more biomass found in non-empty stomachs. This can potentially explain to some extent the higher flatfish densities within the ecosystem engineered habitat. Differences in growth rate are related to differences in food composition and availability as well (Gronkjaer et al., 2007; van der Veer and Witte, 1993). *P. platessa* generally prefers to consume common species (Lockwood, 1984; Wyche and Shackley, 1986). Therefore, we hypothesize that the selectivity of juvenile flatfish to feed within biogenically created habitats is a result of their feeding behaviour which is generally opportunistic (Beyst et al., 1999; Dolbeth et al., 2008; Holmes and Gibson, 1983). Increasing abundances of relatively easy-to-catch prey attract these opportunistic feeders. Besides

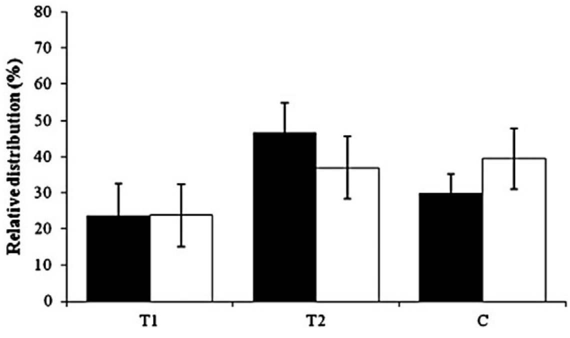

Fig. 5. Relative distribution over different habitats (T1 = 3000 tubes m^{-2}; T2 = 500 tubes m^{-2}; C = no tubes). Differences between habitats shown for high water current velocity (15 m s^{-1}; black) and low water current velocity (3 m s^{-1}; white). Habitat selection is more pronounced when water current velocities are high.

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Table 5
Significance levels for differences in flatfish densities between habitats. No significant differences are found with low current velocity while with high water current velocity, the juvenile *S. solea* selects clearly the intermediate tube density (T2 = 500 tubes m^{-2}) over both bare sand (C = no tubes) and very high tube density (T1 = 3000 tubes m^{-2}).

3 cm/s	T2 > T1: *Gp* = 2.06, P = 0.151
	C > T2: *Gp* = 0.63, P = 0.425
	C > T1: *Gp* = 4.971, P = 0.026
15 cm/s	T2 > T1: *Gp* = 8.6, P = 0.003*
	T2 > C: *Gp* = 7.1, P = 0.007*
	C > T1: *Gp* = 0.071, P = 0.789

the feeding advantage, our experiment shows that juvenile flatfish such as *S. solea* seems to select for the engineered habitat, even if food is absent. The selected habitat turns out to be the low density aggregations (500 ind.m^{-2}). It is important to mention here that the laboratory experiment and the field observations are aimed at different flatfish species. In the field observation, larger individuals in lower density tube worm habitats use the habitat to feed, while the laboratory experiment shows specific behaviour of very young *S. solea* individuals in higher tube worm reefs. Hence, the results are complementary as we can conclude that both food and other aspects can attract juvenile flatfish. However, we have no information on whether juvenile *S. solea* do feed in the ecosystem engineered habitat and it is uncertain whether juvenile *P. platessa* would use the tube worm reefs as shelter.

Further, in our experiment the highest tube densities of 3000 ind m ^{1} to which the species are exposed to in this experiment are too high to be selected by *S. solea*. The length of the 9-week old *S.solea* (4–6 cm) is small enough to occupy the space between the tubes as several individuals were found there during the experiment. Nevertheless, the higher flatfish densities in the lower density reef suggest that when tube densities are very high, the space between tubes might become the limiting factor and make this high density habitat less attractive. The lower tube density habitat harboured more *S. solea* than the control area, showing that *S. solea* is able to use the low density reefs.

The low tube density habitat was most likely characterized by more favourable hydrodynamic conditions. The lower density reefs become more selected than the control zones only when current velocity increases, suggesting that *S. solea* uses the ecosystem engineered habitat only when high water current velocities exist. It is known that biota can affect local sediment transportation and can stabilize or destabilize the environment. It is widely thought that animal tubes stabilize sediments by altering the character of near-bed flow. In some cases, the region of maximum turbulent kinetic energy and shear stress production occurs away from the bed (this is the so-called “skimming flow”) (Morris, 1950). In a study by Friedrichs et al. (2000), it was described that a skimming flow was created. This ecosystem engineering effect is considered as an important factor for the habitat selection of *S. Solea* and *P. platessa*. The inclusion of the abundance of benthic fauna in habitat suitability models has been proven as important in distribution predictions (Le Pape et al., 2007; Nicolas et al., 2007) and Ryer et al. (2004) suggest incorporating considerations of emergent structures of low-relief benthic habitats that impart structural complexity into models for flatfish habitat-suitability.

In conclusion, structured biogenic habitats within nursery areas seem to be attractive for juvenile flatfish and play an important role in juvenile flatfish distribution. Effects on habitat selection by flatfish seem to be partially related to food availability and the attractiveness of the habitat mainly lies in the increased availability of high quality food items (i.e. larger preys). The shelter provided by the biogenic structure, however, seems not unimportant. Interestingly, *S. solea* selects lower density reefs over very high density reefs, which is analogous to what has been described for the macrobenthic community. Both shelter function and food availability seems to be of more importance for smaller (age class 0) flatfish. The results of our study are complementary and highlight the importance of biogenic habitats within flatfish nursery areas in general and show that *L. conchilega* tube worm aggregations can function both as refuge and as feeding area.

Acknowledgments

This research was carried out within the WESTBANKS project (understanding benthic, pelagic and air-borne ecosystem interactions in shallow coastal seas; http://www.vliz.be/projects/westbanks) which is supported by the Belgian Science Policy (BELSPO; contract no. SD/BN/01). We further would like to thank the master and crew of the *RV* ‘Herman Simon’ for their patient and skilful help during sampling. We thank also the UMR CRESCO for the use of and logistic support for the flume tank facilities. We are indebted to Jezabel Lamoureux for technical support. We are very grateful for the assistance during AFDW measurements by Danielle Schram. We are indebted to Liesbeth Hiele for the valuable linguistic comments. The authors acknowledge the two anonymous reviewers and the editors for the valuable comments. The first author is particularly grateful for the fruitful discussions and useful comments provided during the 8th International Flatfish Symposium (IJmuiden, The Netherlands) by several researchers.

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