

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 interannual 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-week intervals, for flushing purposes (Rouillois, 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) interannual 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 interannual 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)
No. 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 no. of series	8	12	12	25	16
Fauna sorted	Total macrofauna	four top rank species	four top rank species	Total macrofauna	300 µm < Meiofauna < 1mm

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 (C. 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 m² 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 m², which samples more than 80% of species (Clavier, 1983).

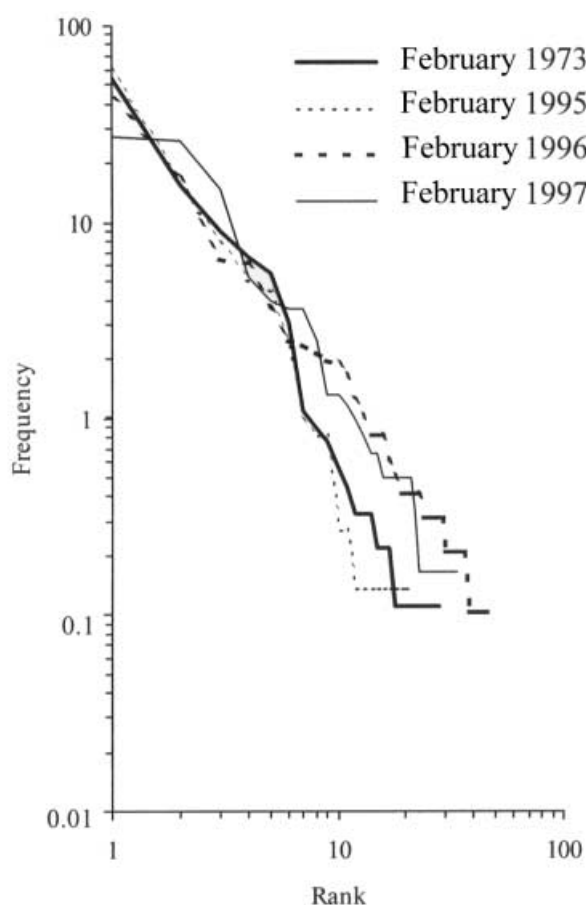
The meiobenthos was sampled every 10 d from the end of May 1996 to the end of October 1996 with a small 1/470 m² hand corer. The sampling grid consisted of a 10×10 m topographically and edaphically homogeneous area, divided into 25 unit squares of 2×2 m. Organisms were sampled by SCUBA divers who positioned the corer trap randomly inside each square. Ten samples were systematically performed on each date. The number of subsamples 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 interannual 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, nemerteans, 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 rank–frequency diagrams of the *Abra alba*–*Corbula gibba* community.

To emphasize the range of interannual 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 $F1 \times F2$ plane has been shown separately from the projection of species. Analyses were done only for species with a frequency $\geq 12.5\%$. 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 auto-correlated, 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 interannual 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

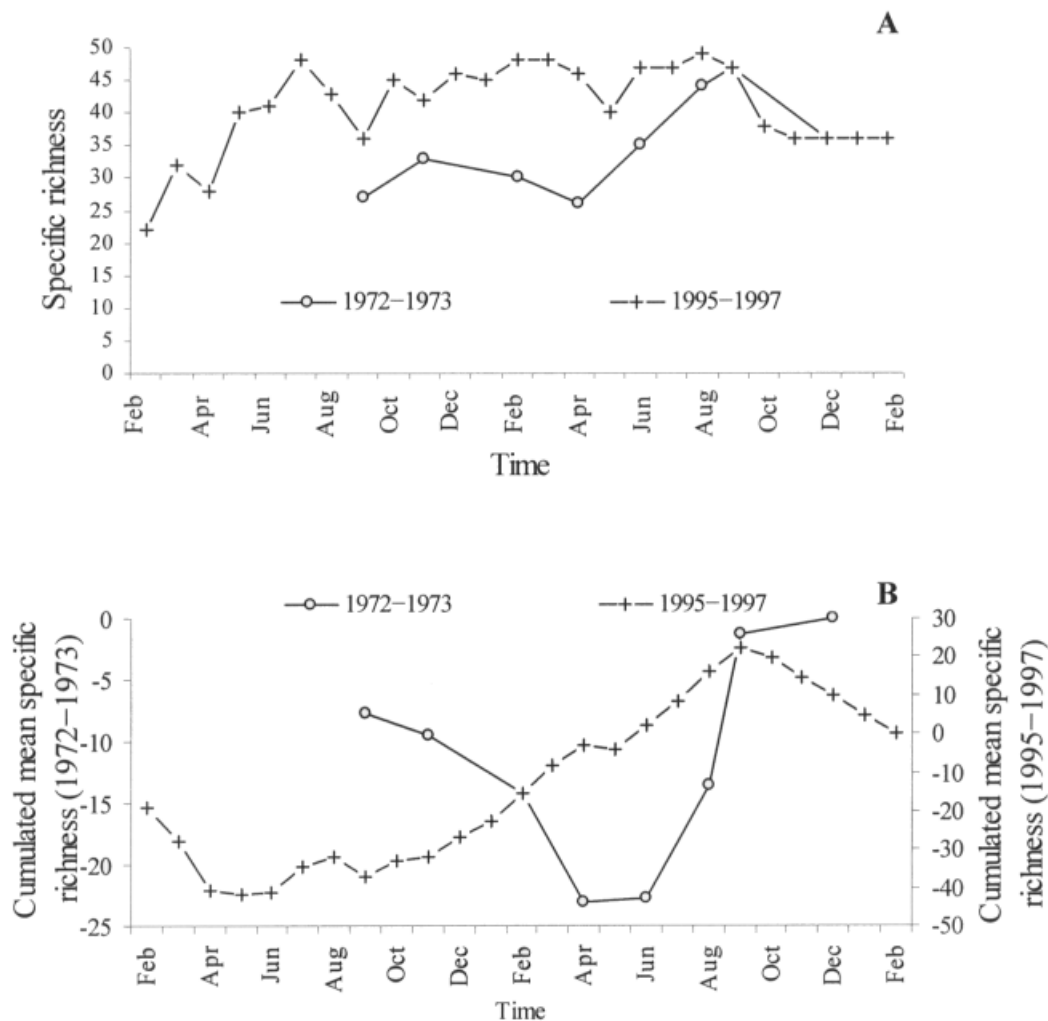


Figure 2. (A) Change of the specific richness in 1972–1973 and 1995–1997; (B) summed cumulated function of the mean specific richness for the two periods.

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 ~ 800 ind 0.1 m^{-2} and ~ 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 the 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 ($2.5 < \text{diversity index} < 3.5$). Regularity index remained constant, fluctuating from 0.5 to 0.6.

Factorial correspondence analysis (FCA)

A FCA 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 \times 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

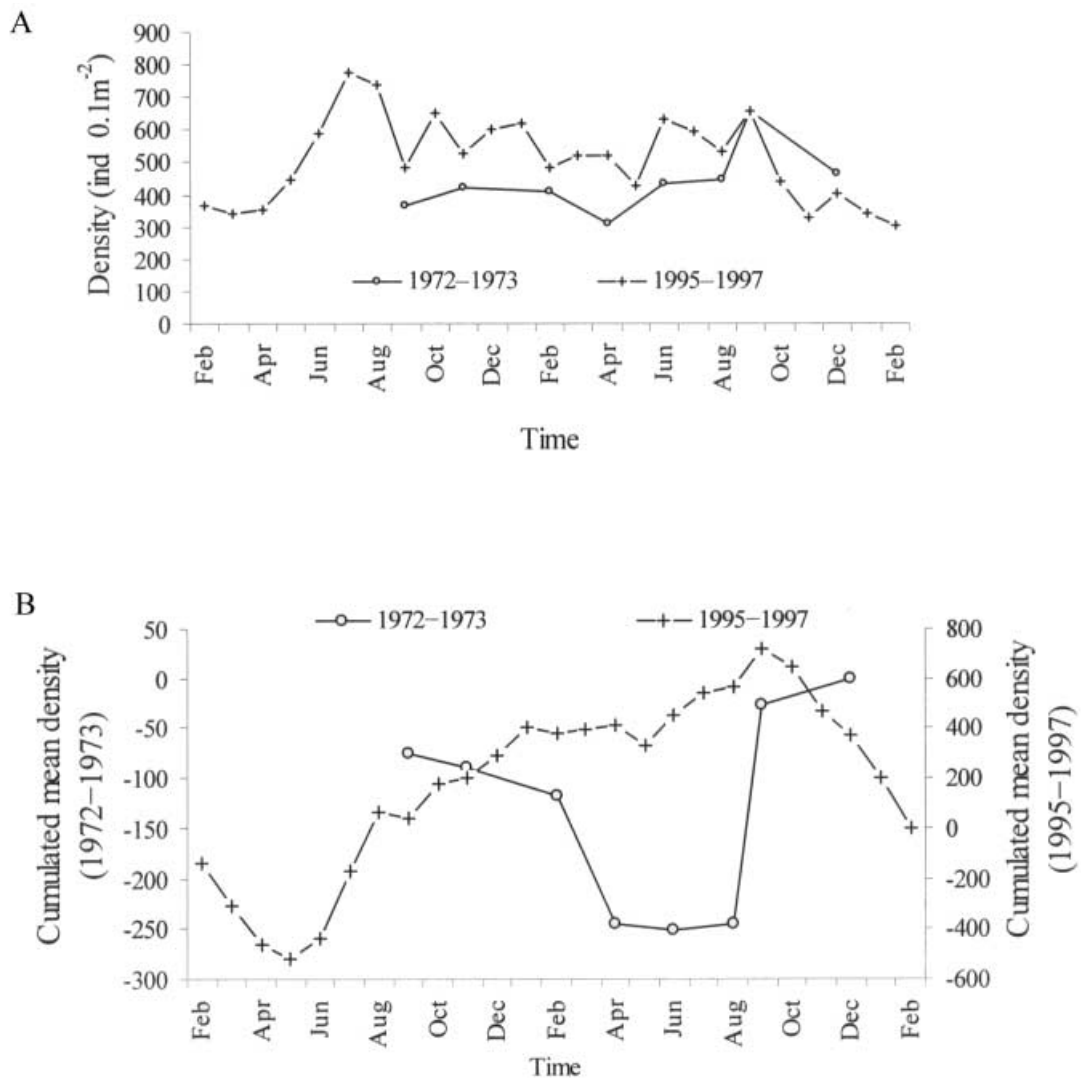


Figure 3. (A) Change of total density (Ampeliscidae excluded) in 1972–1973 and 1995–1997; (B) summed cumulated function of the mean density for the two periods.

contribution of 65.8%) to others (Figure 4A). This axis was determined by *Erichthonius punctatus*, *Amphithoe ramondi* 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. punctatus* (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	
<i>Melinna palmata</i>	255.0	<i>Melinna palmata</i>	186.2
<i>Chaetozone setosa</i>	49.3	<i>Euclymene oerstedii</i>	112.0
<i>Nephtys hombergii</i>	44.7	<i>Aponuphis bilineata</i>	37.4
<i>Euclymene oerstedii</i>	43.5	<i>Nephtys hombergii</i>	25.8
<i>Nucula nitidosa</i>	21.8	<i>Chaetozone setosa</i>	17.2
<i>Eudorella truncatula</i>	9.7	<i>Phoronis psammophila</i>	15.8
<i>Thyasira flexuosa</i>	5.7	<i>Thyasira flexuosa</i>	12.0

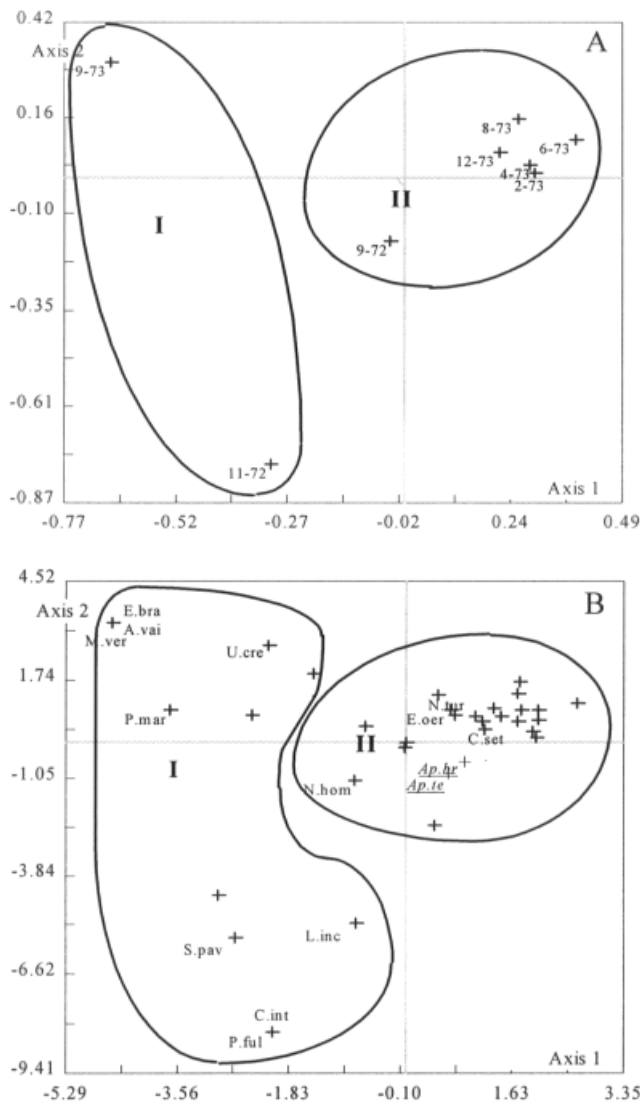


Figure 4. Stations (A) and species (B) on axes 1 and 2 of FCA performed with 1972–1973 data, with indication of the inertia groups. Ampeliscidae (underlined) were considered as supplementary elements. Ap.br, *Ampelisca brevicornis*; Ap.te, *Ampelisca tenuicornis*; A.vai, *Amphithoe ramondi*; C.set, *Chaetozone setosa*; C.int, *Cheirocratus intermedius*; E.oer, *Euclymene oerstedii*; E.bra, *Erichthonius punctatus*; 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*.

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:

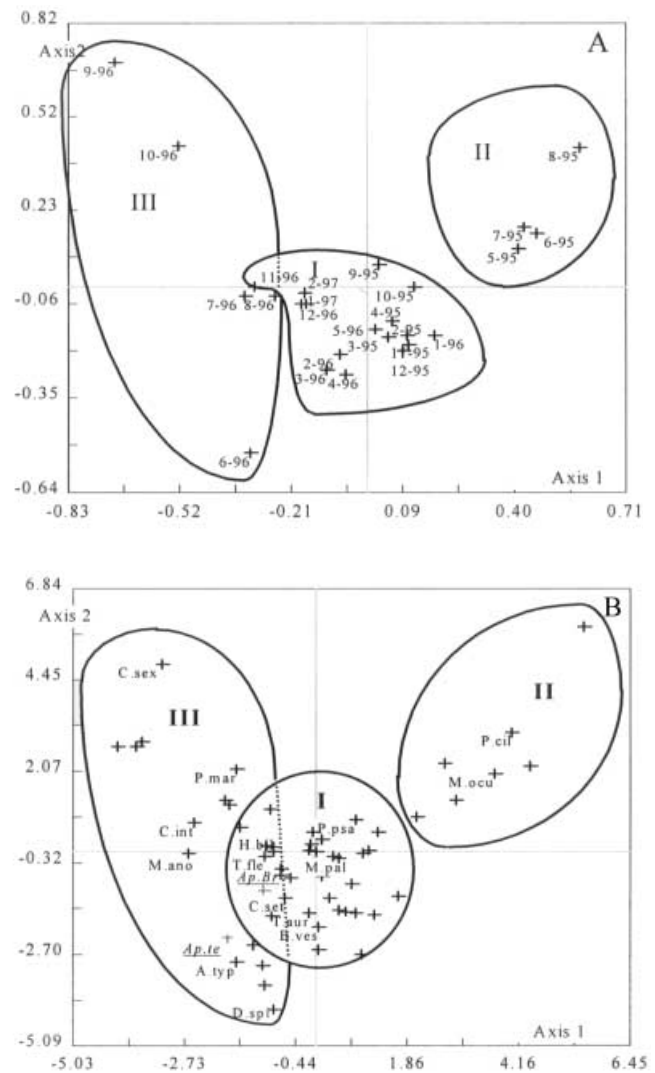


Figure 5. Stations (A) and species (B) on axes 1 and 2 of FCA performed with 1995–1997 data, with indication of the inertia groups. Ampeliscidae (underlined) were considered as supplementary elements. Ap.br, *Ampelisca brevicornis*; Ap.te, *Ampelisca tenuicornis*; A.typ, *Aora typica*; A.bil, *Aponuphis 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*.

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.

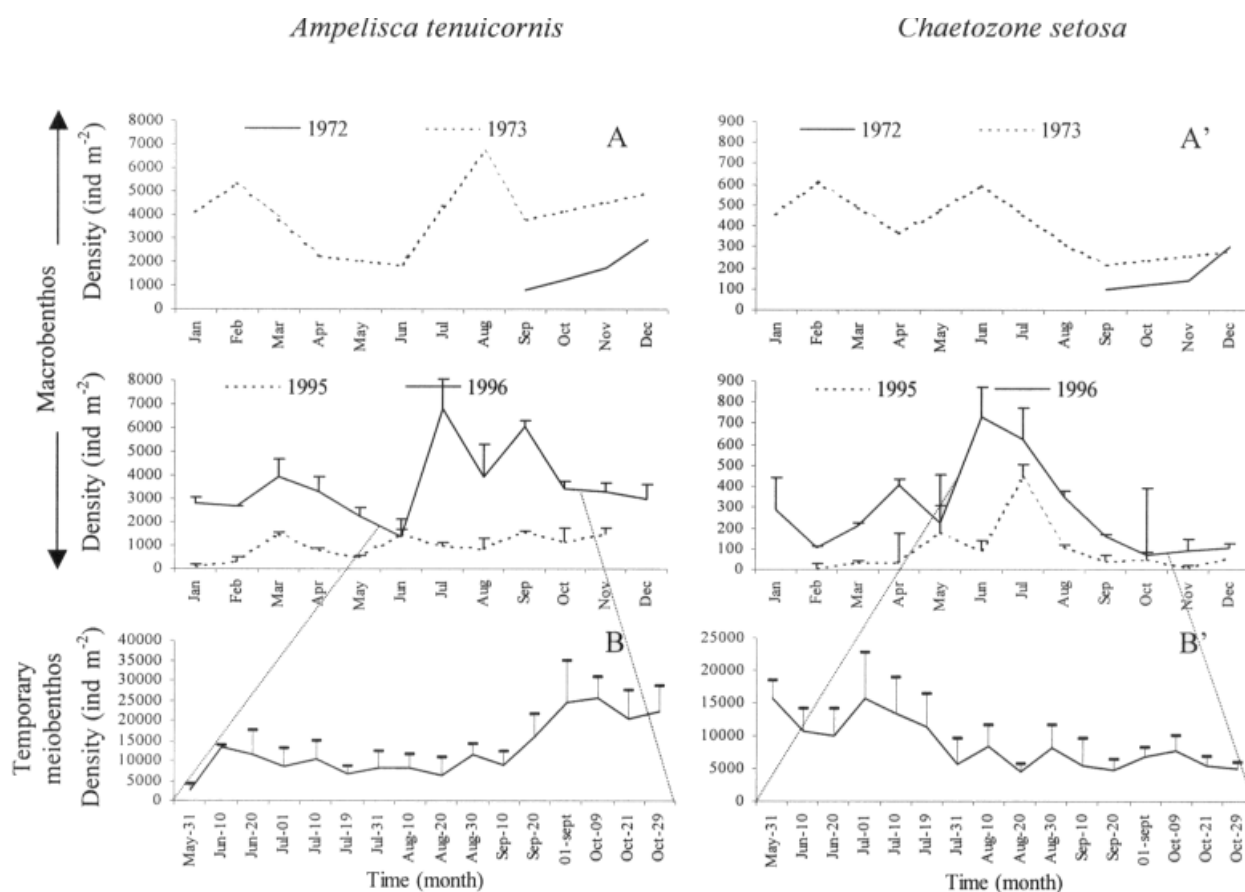


Figure 6. Changes in density (+SD) of macrozoobenthic (1972–1973 and 1995–1996) and meiobenthic (May–October 1996) populations of *Ampelisca tenuicornis* (A–B) and *Chaetozone setosa* (A'–B').

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 spring 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

Interannual 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 April to

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

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

***P* < 0.01.

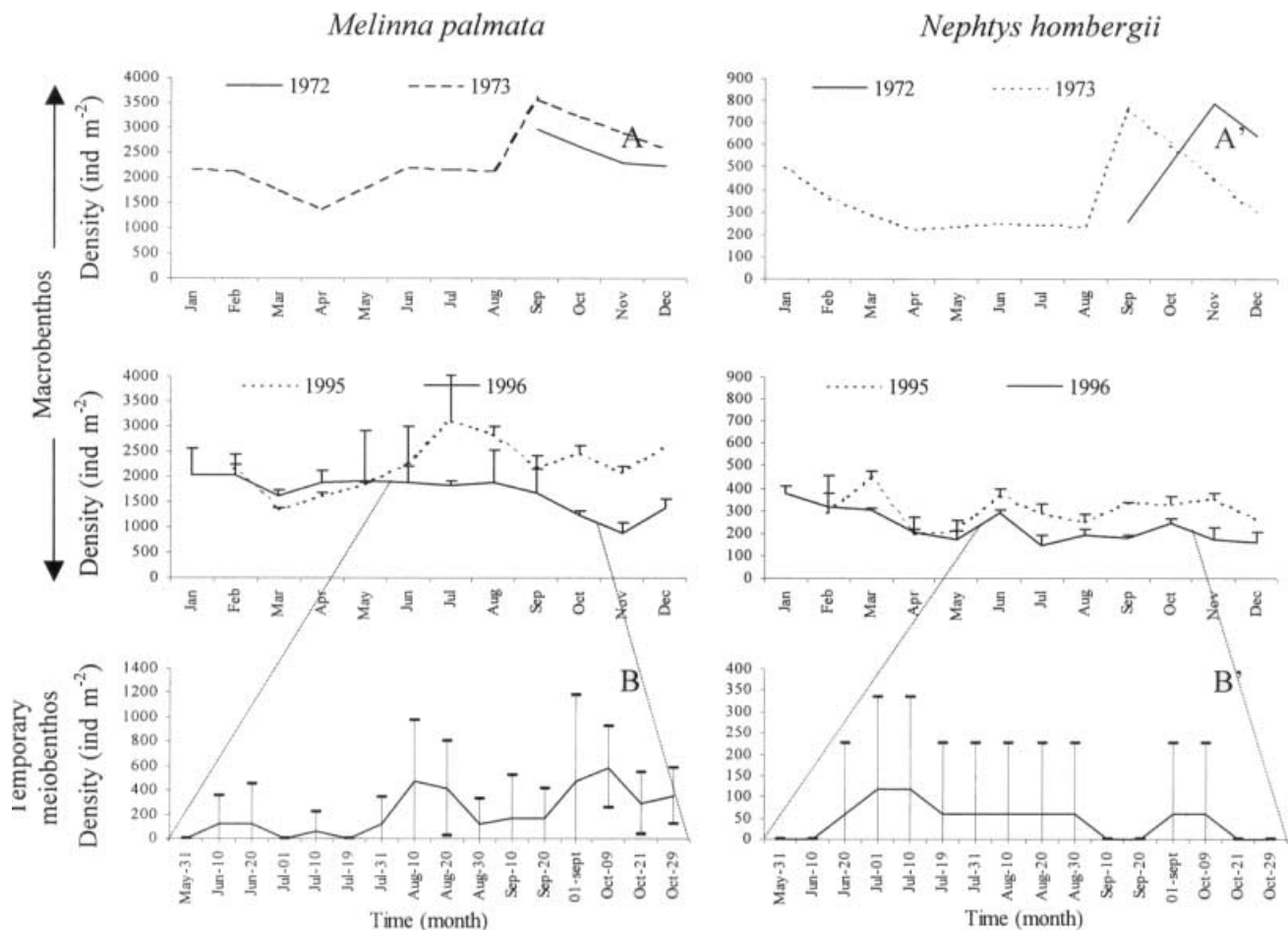


Figure 7. Changes in density (+SD) of macrozoobenthic (1972–1973 and 1995–1996) and meiobenthic (May–October 1996) populations of *Melinna palmata* (A–B) and *Nephtys hombergii* (A'–B').

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 interannually 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, 300 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 recolonize 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

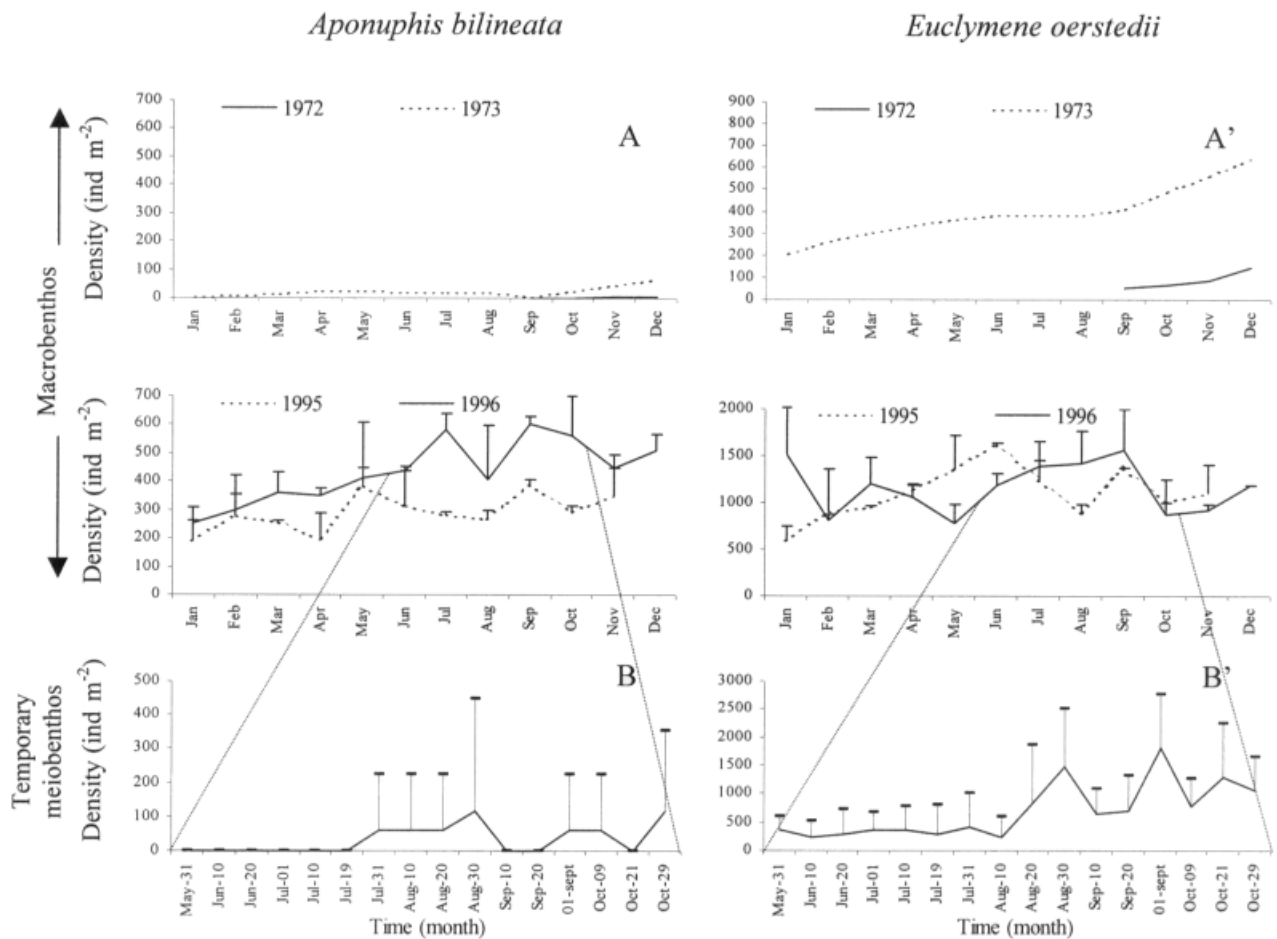


Figure 8. Changes in density (+SD) of macrozoobenthic (1972–1973 and 1995–1997) and meiobenthic (May–October 1996) populations of *Aponuphis bilineata* (A–B) and *Euclymene oerstedii* (A'–B').

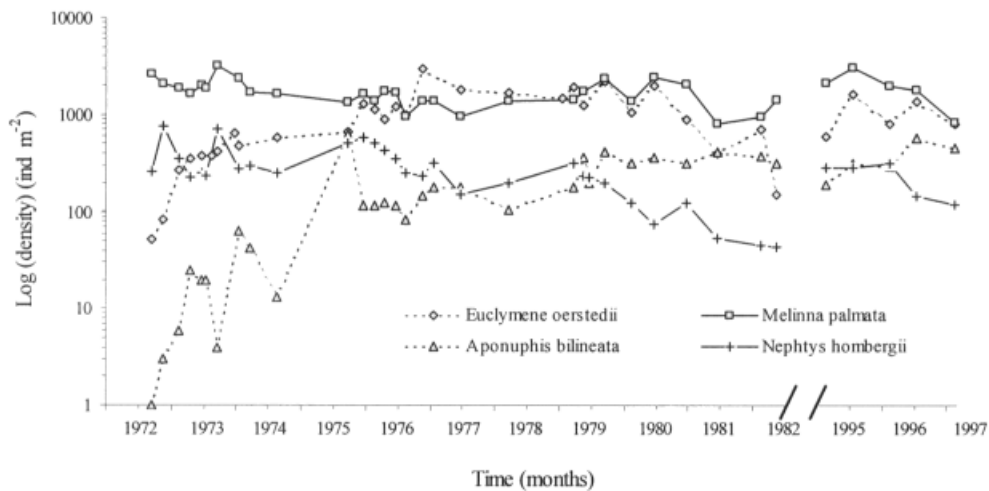


Figure 9. Long-term changes in density of *Aponuphis bilineata*, *Euclymene oerstedii*, *Melinna palmata* and *Nephtys hombergii* from 1972 to 1982 and 1995 to 1997.

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 reorganization 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 precise enough to take account of the functioning rhythm of the power station would be necessary to test this hypothesis. This could assess: (i) the relative interannual 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- ($\text{m}^2 \text{ week}^{-1}$) and meso-scale ($100\text{--}1000 \text{ m}^2 \text{ month}^{-1}$) 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 $\text{km}^2 \text{ y}^{-1}$) 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.

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