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Influence of spatial scales of observation on temporal change in diversity and trophic structure of fine-sand communities from the English Channel and the southern North Sea

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Along the coast of France in the English Channel, muddy fine-sand communities are restricted to bays and estuaries, but in the southern North Sea they stretch out to larger areas (mesoscale continuum). We studied three regions containing these communities, each subject to different hydrological conditions and contrasting trophic structures of the water column. The Bay of Morlaix was strongly affected by the "Amoco Cadiz" oil spill of 1978 and recovered slowly. The Bay of Seine is influenced by high levels of nutrient input from the River Seine. A retention structure exists in the eastern part ensuring recruitment stability. The Gravelines area in the southern North Sea was invaded by the American jackknife clam (*Ensis directus*), which became a key species several years after its accidental introduction. These areas are important nursery grounds for demersal fish species. The distribution and evolution in trophic structure and diversity of macrofauna were analysed in each region, permitting the identification of the roles of disturbance and natural factors in the organization and long-term evolution (including recovery after an event) of the communities. The effects of different spatial scales of observation on the resulting image of macrobenthic community evolution are discussed.

Key words: *Abra alba* community, English Channel, macrobenthos, North Sea, spatial scales of observation, temporal change.

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Introduction

Spatio–temporal fluctuations in diversity and trophic group status often reflect the state of the benthic ecosystem and its response to different forms of disturbance. These indices have certain limitations, but their use remains common. We compare three isolated regions of the same muddy fine-sand *Abra alba* community in the English Channel and the southern part of the North Sea: the Pierre Noire, Gravelines, and Bay of Seine sampling sites. The data for the first two regions consist of long-term series (20 years) collected at one sampling site and for the third region, a cluster of 31 sites over four non-consecutive years. Thus, the first two sites display the benefits of a temporal approach and the third site those of adopting a spatial approach. Several studies have been conducted for each region separately (Dauvin, 1998; Carpentier *et al.*, 1997; Thiébaut *et al.*, 1997), and others have compared the long-term series (Fromentin *et al.*, 1997a, 1997b), but variations in diversity (Shannon H′) and trophic group status as a result of the different forms of disturbance operating in each respective region have not been compared.

Our aims are twofold: (i) to observe benthic community evolution in different regions subject to different types of disturbance in terms of diversity and trophic structure; and (ii) to identify the importance of spatial scales of observation and their relative efficiencies in detecting spatial scales of ecological organization.

Material and methods

Sampling sites and disturbances

The Pierre Noire site in the Bay of Morlaix, in the *Abra alba-Hyalinoecia bilineata* fine-sand community, is

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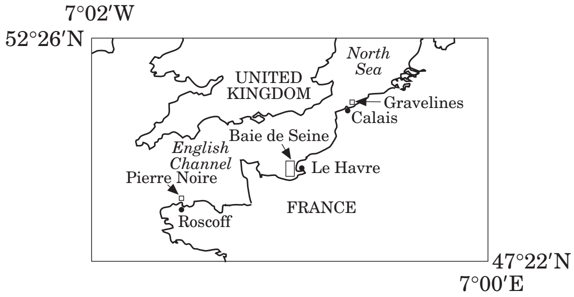

Figure 1. Map with location of the sampling sites: Pierre Noire (1 site; 1977–1996), Gravelines (1 site; 1978–1997), and Bay of Seine (31 sites; 1986, 1987, 1988, and 1991).

situated in the western part of the English Channel (Fig. 1) and influenced by temperate Atlantic waters. In 1977, a survey of temporal changes in this community was initiated. One year later, in spring 1978, the site was polluted by hydrocarbons from the "Amoco Cadiz" accident, resulting in the disappearance of the dominant *Ampelisca* populations (Amphipoda), Of the 220 000 t of oil spilled into the sea from the wreck, between 10 000 and 92 000 t became trapped in subtidal sediments (Dauvin, 1984). Hydrocarbon concentrations in the sediments at Pierre Noire reached 200 ppm (mg kg^{-1} dry sediment) in the summers of 1978 and 1979, but did not exceed 50 ppm after the winter of 1981 (Dauvin, 1984, 1998). A single species of *Ampelisca* was found in very low numbers after the event. Amphipods, characteristic representatives of these communities, lack pelagic larvae, and therefore form distinct populations (Dauvin, 1987). However, the amphipods gradually recolonized the area, forming an assemblage similar to that of the past. The region is dominated by suspension feeders, reflecting strong bentho-pelagic coupling. Dauvin (1998) presents a substantial account of the effects of the oil spill.

The Gravelines site in the southern North Sea (Fig. 1) is situated in a large fine-sand *Abra alba* community stretching along the coast from Calais to Germany. The site has a continental climate, characterized by relatively warm summers and cold winters with dominating NE winds in spring, ensuring an eastern flow of larvae from the Belgian coasts. This results in important faunal fluctuations induced by strong recruitment events in dominant species having bentho-pelagic life cycles (Dewarumez *et al.*, 1986). In 1991, the American jackknife clam (*Ensis directus*), imported from the USA *via* ballast water of ships, was introduced accidentally (Luczak *et al.*, 1993). Over time this species has established itself successfully in the area in contrast to neighbouring regions where it died out (Luczak, 1996).

The Bay of Seine sampling sites (Fig. 1) consisted of a common grid of 40 sites, but for our comparison only 31 sites were used. This area has continuous eutrophic conditions owing to considerable discharges from the River Seine. The hydrodynamics of the bay ensure larval retention (Thiébaut *et al.*, 1992), leading to a certain degree of stability (Gentil *et al.*, 1986; Thiébaut *et al.*, 1997). The dominant species have bentho-pelagic life cycles.

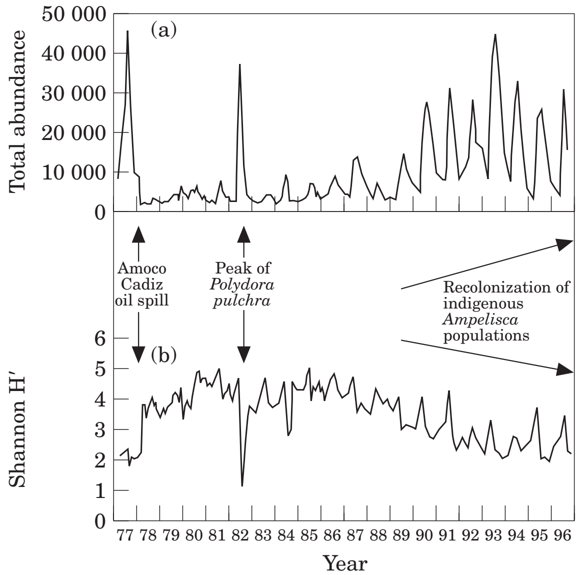

Figure 2. Long-term variations in (a) total abundance (ind. m^{-2}) and (b) diversity (Shannon H′) at Pierre Noire, 1977–1996.

Sampling

Ten replicate samples (Smith McIntyre grab, 0.1 m^2) were taken at the Pierre Noire and Gravelines sites five times per year (early March, June, August, October, and December) to estimate the abundance and biomass of macrofauna, and retained material was fixed with 4–5% neutralized formalin. In the Bay of Seine, two replicate samples were taken (Hamon grab, 0.25 m^2) at each site over four non-consecutive years (1986, 1987, 1988, and 1991) in winter just before recruitment. For further details, Dauvin (1998) may be consulted for Pierre Noire, Dewarumez *et al.* (1986) and Carpentier *et al.* (1997) for Gravelines, and Thiébaut *et al.*, (1997) for the Bay of Seine. Biomass was measured as decalcified dry weight. Diversity was calculated using the Shannon index (H′) in logarithm base 2.

Results

Pierre Noire

There was an increase in diversity following the pollution event (Fig. 2). The expected response according to classical hypothesis (Pearson and Rosenberg, 1978) is

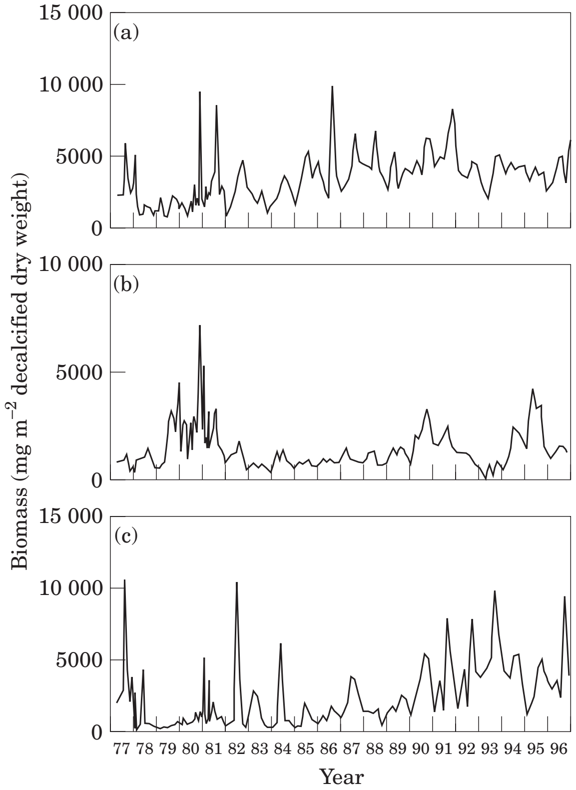

Figure 3. Long-term variations in biomass (mg m^{-2}; decalcified dry weight) of (a) carnivores and omnivores, (b) surface deposit and subsurface deposit feeders, and (c) suspension feeders at Pierre Noire, 1977–1996.

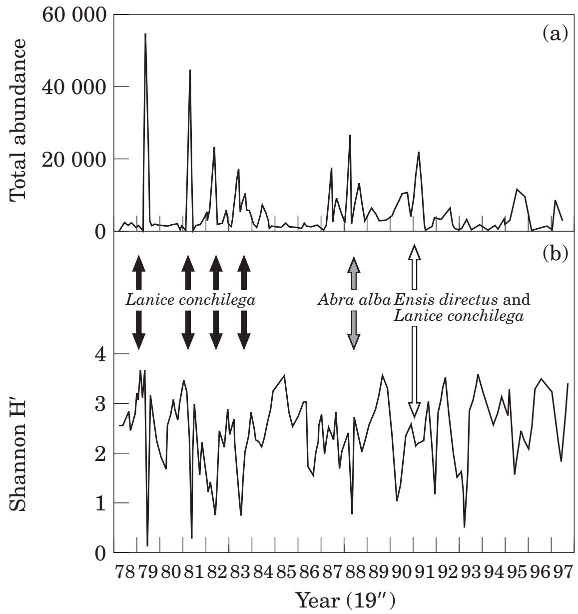

Figure 4. Long-term variations in (a) total abundance (ind. m^{-2}) and (b) diversity (Shannon H′) at Gravelines, 1978–1997.

for diversity to decrease immediately after a pollution event as a result of the proliferation of opportunistic species. In extreme situations the affected region may temporarily become azoic. Diversity is supposed to increase later during the "transition zone" (Pearson and Rosenberg, 1978), representing a mixture of opportunistic and other species. The increase in diversity observed directly after the pollution event was a result of the removal of the dominant populations of amphipods. In 1982 (Fig. 3) the polychaete *Polydora pulchra* temporarily colonized the site. Approximately 10 to 11 years were required for the site to return to original conditions with the original annual abundance fluctuations and low diversity levels (Dauvin, 1998).

Suspension feeders (Fig. 3) declined after the oil spill, corresponding to the removal of the dominant amphipod populations. A similar pattern can also be observed for carnivores and omnivores. In contrast, surface and subsurface deposit feeders increased in importance after the event, reflecting proliferation of opportunistic species, but they decreased after 1982, remaining at low values until 1989. The sharp peak in suspension feeders in 1982 corresponds to the peak in the opportunistic *P. pulchra*. Strong seasonal fluctuations are also evident. Again, a period of 10 to 11 years seems to be the time interval required for a return to original population levels: after 1989 suspension feeders returned to original fluctuations, marking the recolonization by previously dominant amphipods. Assuming an annual benthic carrying capacity of 10–11 g m^{-2} under pre-"Amoco Cadiz" conditions, a deficit of approximately 0.65 t wet weight of fish biomass over the area covered by the fine-sand community (2.5 km^2) was estimated by Dauvin (1998) over the 11-year disturbance period.

Gravelines

The community at Gravelines is completely different (Fig. 4): it is prone to large seasonal fluctuations as a result of mass recruitment of different species. This feature is partly related to the exposed nature of the region. When strong NE winds dominate for a prolonged period, the resulting currents carry large numbers of larvae from neighbouring regions situated on the Belgian coast opposite the Scheldt estuary (Dewarumez *et al*., 1993). Sporadic recruitment events of the polychaete *Lanice conchilega* in particular during the earlier years were replaced by *Abra alba* in 1988. These fluctuations have been partly linked to climatic factors by Fromentin and Ibanez (1994) and Carpentier *et al*. (1997). Since 1991, after the introduction of *E. directus*, *L. conchilega* has also appeared again in high numbers (Luczak, 1996).

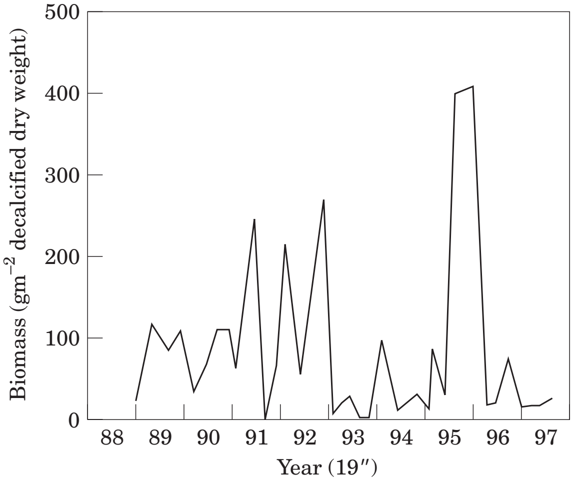

Figure 5. Seasonal trends in biomass (g m^{-2}; decalcified dry weight) for Gravelines, 1989–1997. The maximum in 1995 was caused by good recruitment of *Lanice conchilega* and *Sagartia troglodytes,* while *Ensis directus* was reaching maturity.

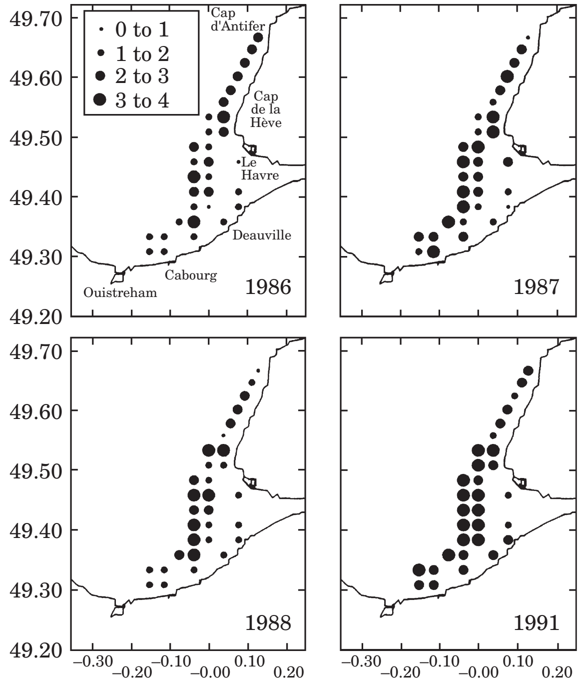

Figure 6. Spatio-temporal distribution of diversity (Shannon H′) in the Bay of Seine, 1986–1991.

Biomass values (Fig. 5; only available since 1989) show a major increase in 1995, resulting from the maturation of the American jackknife clams accidentally recruited in 1991 in conjunction with mass recruitments of *L. conchilega* and *Sagartia troglodytes* (Fig. 5).

Bay of Seine

The grid of 31 stations (Fig. 6) shows the heterogeneous distribution of diversity in the Bay of Seine region during the four years. High-diversity indices are observed in front of the estuary mouth, while diversity in the inner estuary remains relatively low. Although the region is known to be stable overall, local fluctuations are evident, especially at the north-south grid extremities.

Discussion

The prospective benefits from studying long-term subtidal benthic data series are clearly demonstrated. Some 10 to 11 years were necessary for the Pierre Noire site to return to pre-"Amoco Cadiz" conditions (Dauvin, 1998). Had the time scale of the study been shorter, the recovery might not have been observed. Initially, the Shannon diversity index increased after the pollution event when dominant *Ampelisca spp.* populations were eliminated, indicating that high diversity may not always be indicative of a good ecological state of a region. During the transition period (1978–1987), diversity was relatively high for Pierre Noire compared with the other sites. In Gravelines, the different nature of the environment leads to much more pronounced seasonal fluctuations, which evidently result from the sequence of good recruitments of different species. The study underlines the limitations of this particular diversity index, noted also by Warwick and Clarke (1995), who indicated that the index serves as a relative measure to be used for comparisons within a study area rather than as a standard index of ecological state.

Overall, diversity in Gravelines has not changed after the accidental recruitment event of a non-indigenous species. The timespan of three years that elapsed before the new species was integrated into the existing macrobenthic community was shorter than the observed recovery time of the benthic community in Pierre Noire after the oil spill. However, sampling only one site over time may enhance the possibility that local inferences were made in explaining a global event. The two forms of disturbance are of course different. The oil spill event affected a particular area where the return to original conditions depended partly on the degradation and dispersal of the pollutant and subsequent recolonization. The oil itself does not interact with the community to the same extent that a new species interacts with the original species. The introduction of *E. directus* may be considered as a form of biological perturbation that is more localized because its effects do not extend beyond the area where it has been able to establish itself. In fact, the new species did not survive in neighbouring areas. Moreover, the area occupied by the *Abra alba* community at Pierre Noire (6 km^2) is smaller than at Gravelines (>100 km^2), suggesting that one sampling site may offer

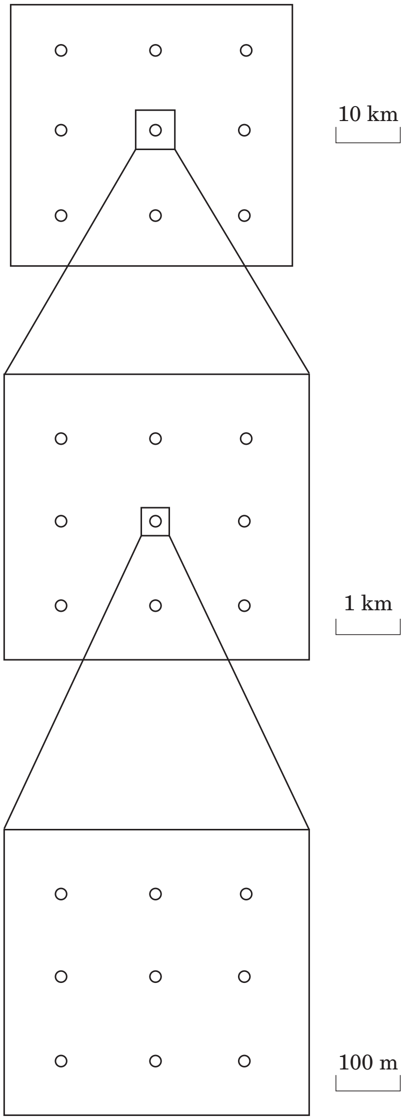

Figure 7. Nested sampling design for benthos studies encompassing a variety of spatial scales (modified from Morrisey *et al*., 1992, and Luczak, 1996).

more representative data at the former compared with the latter.

The Bay of Seine data set shows that, in the case of a locally heterogeneous environment, a long-term study of one site might lead to misleading generalizations because neighbouring sites may show opposing trends. In such cases incorporation of the spatial factor seems essential. The benthic community in this region has been described as being spatio-temporally persistent (Thiébaut *et al*., 1997), which is partly caused by the larval retention structure existing in the bay. Although the small-scale heterogeneity observed locally may seem in conflict with these conclusions, it may be argued that globally the area remains stable. The results for the Bay of Seine seem to corroborate the dynamical concept of stability proposed by Gray *et al*. (1985): species may vary in abundance but the overall structure is maintained.

The data collected at Pierre Noire and Gravelines refer to local populations and communities *sensu* Taylor and Woiwood (1980). Connell and Sousa (1983) pointed out that a community, when defined as the assemblage observed within a small area, is unlikely to be either stable or persistent because even small disturbances, or chance events, can cause local extinctions. The spatial scale of a study affects the judgement about the stability or persistence of a community, and different results might have been obtained, had additional sites been sampled in those areas. For example, the amphipod populations that recolonized the disturbed area in Pierre Noire must have moved in from unaffected areas as these species reproduce and recruit locally. Had more sites been sampled over a larger area, significant differences in recovery times after disturbance might have been observed for each site, depending on its relative proximity to surviving amphipod populations. In the case of Gravelines, the introduction of *E. directus* is known to have been short-lived at other sites within the same *Abra alba* community. The Bay of Seine presents a good example of how essential it is that larger areas be sampled by increasing the number of sites. However, the problem is often that routine sampling of many sites over long periods (more than 20 years) is neither economically nor physically feasible. Therefore, to provide potential answers to the questions raised, a different form of sampling strategy is proposed for future studies.

Hierarchical structures exist both in space and time (Allen and Starr, 1982; O'Neill *et al*., 1989) and the spatial scale of observation is thus a determining factor. However, this is not a property of the community studied but rather a property of the investigative methods of the observer (Allen and Starr, 1982). Allen and Hoekstra (1991) introduce the notion of grain and extent in relation to scale. Grain is related to resolution and determines the smallest entities that can be observed. Extent is the span of all measurements and determines the largest entities that can be detected in the data. The scale of a study is an interaction of grain and extent. If the extent is large, the sampling protocol will be prohibitively expensive unless the grain is relatively coarse. Conversely, a study involving a fine grain necessarily has a narrow extent (Allen and Hoekstra, 1991). This hierarchical approach in ecosystem study requires a series of sampling sites organised on different spatial scales in order to analyse and understand how observed constraints on different hierarchical spatial scales may influence community structure and geographical distribution of individuals (O'Neill, 1989; Ricklefs, 1987). The resulting sampling strategy resembles the nested sampling design described by Morrisey *et al*. (1992) and used in other studies (Morrisey and Underwood, 1992; Lindegarth *et al*., 1995).

We recommend the design in Figure 7, adapted from the authors mentioned above, for use in future benthic sampling strategies. A similar strategy was adopted by Luczak (1996). The larger spatial scale sites (10 km) may be sampled less frequently than the sites on a smaller scale (100 m). Overall, the sampling strategy theoretically should be capable of detecting slower, larger-scale processes while simultaneously recording faster, smaller-scale processes, thereby reducing effort and costs (Luczak, 1996).

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References

Allen, T. F. H., and Hoekstra, T. W. 1991. Role of heterogeneity in scaling of ecological systems under analysis. *In* Ecological heterogeneity, pp. 47–67. Ed. by J. Kolasa, and S. T. A. Picket. Springer Verlag, N.Y.

Allen, T. F. H., and Starr, T. B. 1982. Hierarchy: perspectives for ecological complexity. University of Chicago Press, Chicago, Illinois, USA.

Carpentier, P., Dewarumez, J.-M., and Leprêtre, A. 1997. Long-term variability of the *Abra alba* community in the Southern Bight of the North Sea. Oceanologica Acta, 20: 240–283.

Connell, J. H., and Sousa, W. P. 1983. On the evidence needed to judge ecological stability or persistence. The American Naturalist, 121: 789–824.

Dauvin, J.-C. 1984. Dynamique d'écosystèmes macrobenthiques des fonds sédimentaires de la baie de Morlaix et leur perturbation par les hydrocarbures de l'Amoco Cadiz. Thèse de doctorat Etat, Université de Paris VI, 456 pp.+annexes, 192 pp.

Dauvin, J.-C. 1987. Evolution à long terme (1978–1986) des populations d'Amphipodes des sables fins de la Pierre Noire (Baie de Morlaix, Manche Occidentale) après la catastrophe de "l'Amoco Cadiz". Marine Environmental Research, 121: 247–273.

Dauvin, J.-C. 1998. The fine sand *Abra alba* community of the Bay of Morlaix twenty years after the Amoco Cadiz oil spill. Marine Pollution Bulletin, 36: 669–676.

Dewarumez, J.-M., Quisthoudt, C., and Richard, A. 1986. Suivi pluriannuel du peuplement à *Abra alba* dans la partie méridionale de la mer du Nord (région de Dunkerque-France). Hydrobiologia, 142: 187–197.

Dewarumez, J.-M., Belgrano, A., Craeymeersch, J., Duquesnes, S., Heip, C., Hilde, D., and Vincx, M. 1993. Influence de la circulation des masses d'eau dans la dynamique du peuplement à *Abra alba* de la Baie sud de la Mer du Nord. Journal de Recherche Océanographique, 18: 1–4.

Fromentin, J.-M., and Ibanez, F. 1994. Year to year changes in meteorological features of the French coast area during the last half-century. Examples of two biological responses. Oceanologica Acta, 17: 285–296.

Fromentin, J.-M., Dauvin, J.-C., Ibanez, F., Dewarumez, J.-M., and Elkaim, B. 1997a. Long-term variations of four macrobenthic community structures. Oceanologica Acta, 20: 43–53.

Fromentin, J.-M., Ibanez, F., Dauvin, J.-C., Dewarumez, J.-M., and Elkaim, B. 1997b. Long-term variability of macrobenthic communities of the North-West French coast. Journal of the Marine Biological Association, UK, 77: 287–310.

Gentil, F., Irlinger, J. P., Elkaim, R., and Proniewski, F. 1986. Premières données sur la dynamique du peuplement macrobenthique des sables fins envasés à *Abra alba* de la Baie de Seine Orientale. Actes de colloques IFREMER, 4: 409–420.

Gray, J. S., Valderhaug, V., and Ugland, K. I. 1985. The stability of a benthic community of soft sediment. *In* Proceedings of the 19th European Marine Biology Symposium, Plymouth, 16–21 September 1984, pp. 245–254. Ed. by P. E. Gibbs. Cambridge University Press, Cambridge, England, UK.

Lindegarth, M., André, C., and Jonsson, P. R. 1995. Analysis of the spatial variability in abundance and age structure of two infaunal bivalves, *Cerastoderme edule* and *C. lamarcki*, using hierarchical sampling programmes. Marine Ecology Progress Series, 116: 85–97.

Luczak, C. 1996. Dynamique du recrutement au sein du peuplement *Abra alba* dans la baie sud de la Mer du Nord: approche systémique. Thèse de doctorat. Université des Sciences et Technologies de Lille 1. 265 pp.

Luczak, C., Dewarumez, J.-M., and Essink, K. 1993. First record of the American jack-knife clam *Ensis directus* on the French coast of the North Sea. Short communication. Journal of the Marine Biological Association, UK, 73: 233–235.

Morrisey, D. J., and Underwood, A. J. 1992. Sampling for spatial variation in the distribution of fauna in sediments. *In* Proceedings of a Bioaccumulation Workshop: Assessment of the distribution, impacts and bioaccumulation of contaminants in aquatic environments, pp. 115–121. Ed. by A. G. Miskiewicz. Water Board and Australian Marine Sciences Association Inc., Sydney, Australia.

Morrisey, D. J., Howitt, L., Underwood, A. J., and Stark, J. S. 1992. Spatial variation in soft sediment benthos. Marine Ecology Progress Series, 81: 197–204.

O'Neill, R. V. 1989. Perspectives in hierarchy and scale. *In* Perspectives in Ecological Theory, pp. 140–156. Ed. by J. Roughgarden, R. M. May, and S. A. Levin. Princeton University Press, Princeton, New Jersey, USA.

O'Neill, R. V., DeAngelis, D. L., Waide, J. B., and Allen, T. F. H. 1989. A hierarchical concept of ecosystems. Princeton University Press, Princeton, New Jersey, USA. 253 pp.

Pearson, T. H., and Rosenberg, R. 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanography and Marine Biology Annual Review, 16: 229–311.

Ricklefs, R. E. 1987. Community diversity: relative roles of local and regional processes. Science, 235: 167–171.

Taylor, L. R., and Woiwood, I. P. 1980. Temporal stability as a density-dependent species characteristic. Journal of Animal Ecology, 49: 209–224.

Thiébaut, E., Dauvin, J.-C., and Lagadeuc, Y. 1992. Transport of *Owenia fusiformis* larvae (Annelida: polychaeta) in the Bay of Seine. I. Vertical distribution in relation to water column stratification and ontogenic vertical migration. Marine Ecology Progress Series, 80: 29–39.

Thiébaut, E., Cabioch, L., Dauvin, J.-C., Retière, C., and Gentil, F. 1997. Spatio-temporal persistence of the *Abra alba–Pectinaria koreni* muddy fine sand community of the eastern Bay of Seine. Journal of the Marine Biological Association, UK, 77: 1165–1185.

Warwick, R. M., and Clarke, K. R. 1995. New ''biodiversity'' measures reveal a decrease in taxonomic distinctness with increasing stress. Marine Ecology Progress Series, 129: 301–305.