

Relationship of non-specific commensalism in the colonization of the deep layers of sediment

Daniela Prevedelli*, Roberto Simonini and Ivano Ansaloni

Università degli studi di Modena e Reggio Emilia, Dipartimento di Biologia Animale, Via Campi 213/d,
41100 Modena, Italy. *Corresponding author, e-mail: prevedelli.daniela@unimo.it

The macrofauna of samples collected with a box-corer from northern Adriatic Sea muddy bottoms in five survey campaigns from 1985 to 1993 has been analysed separately in sediment strata of varying depth. Samples were collected before, during and after the dumping of large amounts of inert particulate material that covered the seabed and caused an almost total defaunation. After this disturbance the seabed was recolonized by a new community. This new community differed from the original one mainly on account of the abundance of *Mysella bidentata*, a small bivalve filter or surface deposit-feeder. In the original community *M. bidentata* was confined to the more superficial sediment layers (0–5 cm) at low population density. In the new community it was very abundant and evenly distributed even in the deep layers (5–20 cm). Analysis of species association performed on data from each of the 54 corer samples collected in the last sampling period, points to a marked association between *M. bidentata* and *Nephtys incisa* in deeper sediment layers. Deep layer colonization by *Mysella* in association with the burrowing polychaete *N. incisa* suggests a case of commensalism between these two species.

INTRODUCTION

The study of the biology of benthos carried out using traditional sampling methods has made important contributions to knowledge of species composition, bionomy and structure. A more functional approach involves studying the sediment in vertical section and analysing the way in which successive layers are colonized by the various species, depending on their morphological characteristics and trophic–ecological requirements (Johnson, 1967; Clavier, 1984; Hayashi, 1986).

In the course of a research project carried out over eight years on the soft-bottom communities of the northern Adriatic Sea, a large number of samples were analysed using this technique. In particular, the evolution of the community was monitored prior to, during and after drilling operations that discharged large amounts of cuttings and drilling muds into the sea and brought about the almost total elimination of the fauna. This was followed by a phase of bottom re-colonization during which large variations in the abundance of some species were observed.

This study is based on the community data of the initial (June 1985) and final periods (September 1993). The distribution of species and of trophic–ecological groups in the different sediment layers were analysed with the aim of establishing whether the capacity to colonize a particular sediment layer is solely due to intrinsic species characteristics or whether biotic interactions between different species might also play an important role.

MATERIALS AND METHODS

The samples were taken in the upper Adriatic Sea off the coast of Ravenna at the mouth of the Fiumi Uniti river at a depth of about 10 m (Figure 1). Samples were

taken at nine stations forming part of a wide grid at the centre of which boring operations had been conducted. The selected stations extended in a north-west to south-east direction following the prevailing flow of the current. In five programmes from 1985 to 1993, samples were taken after the release of particle materials. Samples were collected before (June 1985), during (February 1986, September 1986) and after short term (June 1987) and long term (September 1993) the dumping of large amounts of inert particulate material that covered the seabed and caused an almost total defaunation. Each sample consisted of six replicates collected using a box-corer with a surface of 10×20 cm. Each replicate was then subdivided into four layers representing depths of 0–2, 2–5, 5–10, and 10–20 cm, respectively, and passed through a sieve (mesh size 0.5 mm). The retained material was preserved in 4% neutral formalin in seawater. The animals were extracted from the residual sediment and polychaete and mollusc fraction identified to species level.

The main structural parameters of the community were calculated for each station as follows: number of species, number of individuals, Shannon–Wiener specific diversity index (Shannon & Weaver, 1949), evenness index (Pielou, 1975) and dominance index (Simpson, 1949). The data were arranged in a species/station-layer matrix and processed using factorial analysis of correspondence (FAC) (Benzecrì, 1982). The significance of the axes extracted in this analysis was evaluated using Lebart's tables (1975).

The association between different species was measured for the data relative to each of the 54 box-corer samples collected in the last programme using Yule's absolute association coefficient between pairs of defined species (1912) according to the following formula:

$$v = (ad - bc)/(mnrs)^{1/2} \quad (1)$$

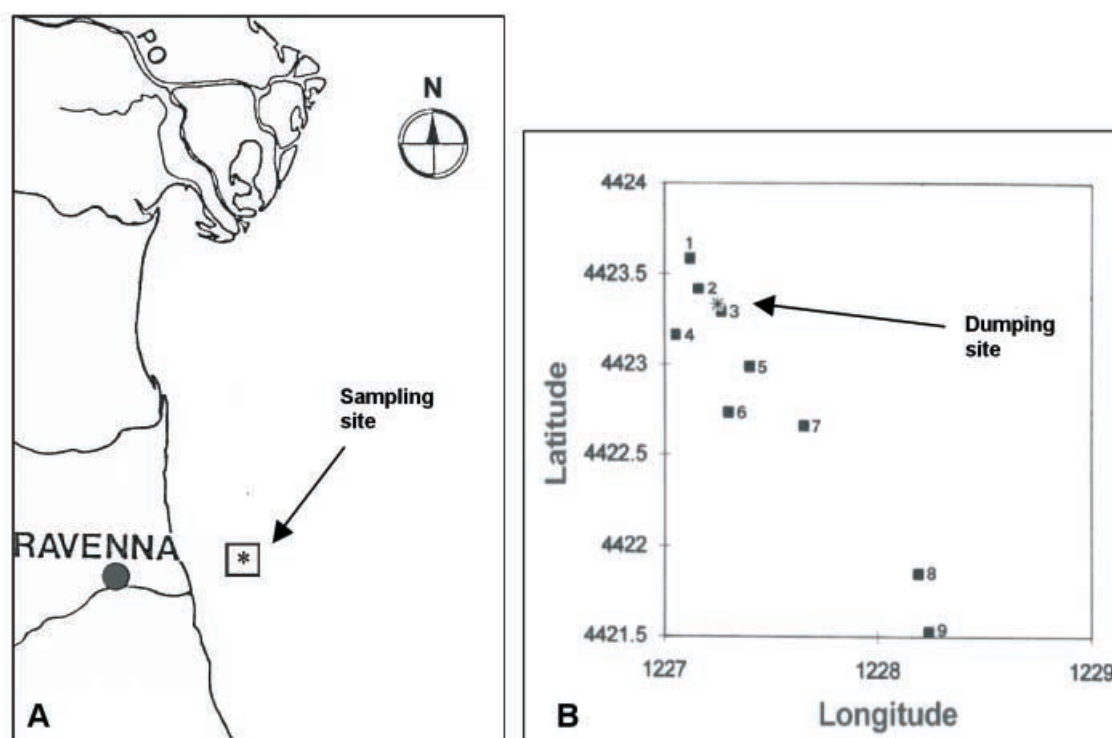


Figure 1. Location of sampling site and sampling points: the site of dumping of particulate material is indicated by the asterisk.

where a = number of double occurrences; b = number of occurrences of only species 1; c = number of occurrences of only species 2; d = number of double absences; $m = a+b$; $n = c+d$; $r = a+c$; and $s = b+d$.

The statistics analysis on Yule's index was carried out using the resampling methods (Caswell, 1989). The percentile method was used to generate 95% confidence intervals based on 2000 bootstrap estimates. The permutation tests were used to find out if the differences in Yule's index were significantly affected by strata and species (Levin, 1996).

RESULTS

In all samples, the sediment consisted of highly-hydrated clay-silt mud on the surface gradually changing to less hydrated and more compact mud lower down. The discharge of drilling muds and cuttings onto the seabed caused a drastic reduction in benthic fauna that sometimes resulted in an almost complete defaunation. A sharp

reduction of the fine sediment fraction and low energy bottom species occurred in the last period. Community parameters detected during the surveys performed from 1985 to 1993 are reported in Table 1. Comparison of the values of the different periods reveals an almost complete return to the original values in the final period with the sole exception of dominance that remains higher than that of the original community.

Originally, the macro-fauna was largely dominated by the polychaete-mollusc fraction with a notable occurrence of the bivalve *Corbula gibba*. Other common molluscs were the gastropod *Hyala vitrea* and the bivalves *Nucula nucleus* and *Tellina distorta*. The polychaetes were represented by the typical species of infra-littoral muddy bottoms such as: *Aricidea claudiae*, *Aricidea assimilis*, *Prionospio malmgreni*, *Polydora flava*, and *Spiochaetopterus costarum*. After recolonization, the community was very similar to the original one, with the dominance of *C. gibba*, the presence of many polychaetes and molluscs already present in the original community and the very

Table 1. Community parameters detected in the different periods: H' , Shannon-Wiener diversity index; J , Pielou's evenness index; dom , Simpson's dominance index.

Period	Species number		H'		J		dom	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
June 1985	39.4	1.97	3.55	0.20	0.72	0.07	0.14	0.08
February 1986	12.0	1.95	2.21	0.42	0.60	0.08	0.21	0.12
September 1986	19.5	7.90	2.49	0.28	0.49	0.11	0.32	0.15
June 1987	33.0	6.53	2.57	0.16	0.58	0.06	0.25	0.18
September 1993	41.8	9.95	3.39	0.51	0.62	0.09	0.24	0.13

SD, standard deviation.

Table 2. Densities (spec m^{-2}) of the ten most abundant species collected in the first and in the last sampling periods.

June 1985			September 1993		
Species	Mean	SD	Species	Mean	SD
<i>Corbula gibba</i>	1001	733	<i>Corbula gibba</i>	1594	68
<i>Prionospio malmgreni</i>	218	289	<i>Mysella bidentata</i>	472	92
<i>Aricidea claudiae</i>	166	82	<i>Hyala vitrea</i>	329	12
<i>Hyala vitrea</i>	75	64	<i>Lumbrineris latreilli</i>	126	61
<i>Polydora flava</i>	74	61	<i>Owenia fusiformis</i>	127	10
<i>Lumbrineris latreilli</i>	66	32	<i>Aporrhais pespelecani</i>	109	10
<i>Aricidea assimilis</i>	57	51	<i>Pectinaria koreni</i>	101	70
<i>Prionospio cirrifera</i>	50	38	<i>Levinsenia gracilis</i>	79	69
<i>Euclymene oerstedii</i>	49	53	<i>Aricidea claudiae</i>	70	55
<i>Spiochaetopterus costarum</i>	47	21	<i>Nephtys incisa</i>	58	62

SD, standard deviation.

high abundance of *Mysella bidentata*. This bivalve, present in the original community at very low density ($17.22 \pm 14.21 \text{ ind m}^{-2}$) becomes co-dominant, second only to *C. gibba*, in the final period (Table 2). Successive layers of the sediment exhibit a progressive reduction in diversity and abundance, which is already obvious between the first and the second layer, and is even more marked in the subsequent layers. Different species are dominant in the different sediment layers depending on their ecological and trophic requirements. In the surface layer, the most common species were *C. gibba* and other small-sized, surface and sub-surface deposit-feeders such as *Prionospio cirrifera*, *P. malmgreni*, *A. claudiae* and *A. assimilis*. In the deeper layers, large-sized polychaetes predominate, most of them living inside tubes or burrows, such as *Spiochaetopterus costarum* which constructs a long translucent tube, and *Nephtys incisa* and *Ancistrosyllis groenlandica* which dig burrows in the sediment. The location of *M. bidentata* in the community of the final period is an exception to this general pattern. Its distribution extends down from the surface layers, where it is very abundant, to the deeper

layer where it is commonly found below 5 cm and, in many cases, even below 10 cm.

The communities of the individual layers (strata-coenoses) were analysed using FAC. The ordination models for the original and recolonized communities are shown in Figures 2 & 3, respectively. In the two cases the strata-coenoses are ordered in an essentially similar manner with a cloud of samples and species points distributed in a U-shape along the first axis. In a simple FAC analysis such a trend reflects the influence of a single parameter. The strata-coenoses are generally well differentiated along the first axis, albeit with, a lower resolution between the deep strata-coenoses in the final period. Species points (reported only partly in the figures) are generally located in conformity with their trophic and ecological characteristics. In fact, the small surface deposit-feeders become ordered near the surface strata-coenoses, while the large-sized tube dwellers or burrowers

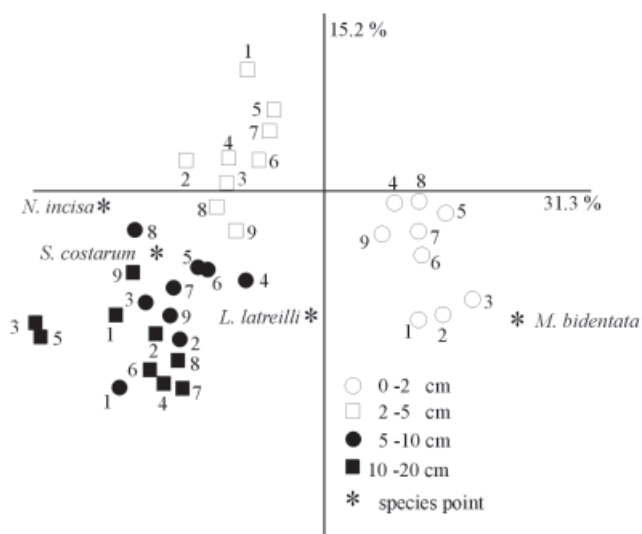


Figure 2. FAC ordination of strata-coenoses of the first survey (June, 1985). Only some species-points are evidenced.

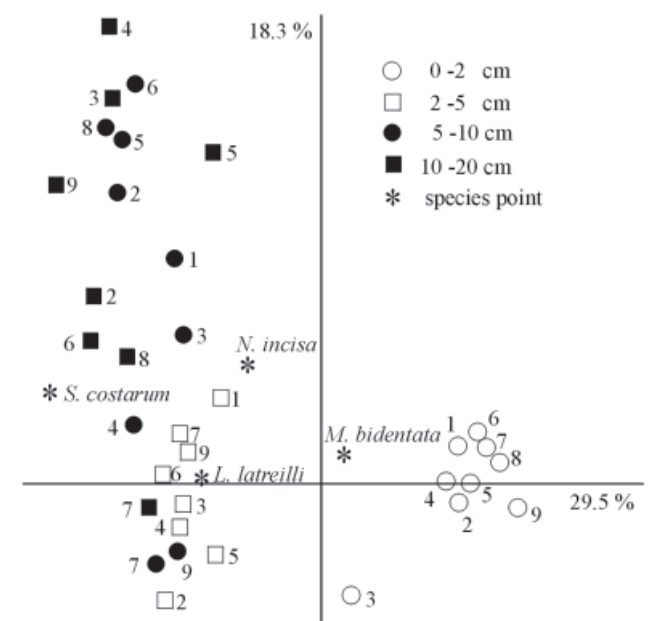


Figure 3. FAC ordination of strata-coenoses of the last survey (September, 1993). Only some species-points are evidenced.

Table 3. Values of Yule's absolute association coefficient between pairs of defined species with corresponding 95% confidence intervals in the superficial and deep layers.

Yule's coefficient	Superficial			Deep		
	<i>Mys–Spio</i>	<i>Mys–Neph</i>	<i>Mys–Lumb</i>	<i>Mys–Spio</i>	<i>Mys–Neph</i>	<i>Mys–Lumb</i>
Mean	0.235	0.214	0.172	0.149	0.573	0.094
Lower confidence interval	−0.058	−0.070	−0.116	−0.143	0.334	−0.171
Upper confidence interval	0.553	0.499	0.435	0.427	0.783	0.367

Mys, *Mysella bidentata*; *Spio*, *Spiochaetopterus costarum*; *Neph*, *Nephtys incisa*; *Lumb*, *Lumbrineris latreilli*.

Table 4. Significance of the Yule's coefficient difference between pairs in the superficial and deep levels (Permutation test).

	Superficial	Deep
<i>Mys–Spio</i> vs <i>Mys–Neph</i>	$P=0.8915$	$P=0.029$
<i>Mys–Spio</i> vs <i>Mys–Lumb</i>	$P=0.6925$	$P=0.757$
<i>Mys–Neph</i> vs <i>Mys–Lumb</i>	$P=0.809$	$P=0.0135$

Mys, *Mysella bidentata*; *Spio*, *Spiochaetopterus costarum*; *Neph*, *Nephtys incisa*; *Lumb*, *Lumbrineris latreilli*.

Table 5. Significance of the Yule's coefficient difference between superficial and deep levels (Permutation test).

	<i>Mys–Spio</i>	<i>Mys–Neph</i>	<i>Mys–Lumb</i>
Deep vs superficial	$P=0.641$	$P=0.049$	$P=0.7125$

Mys, *Mysella bidentata*; *Spio*, *Spiochaetopterus costarum*; *Neph*, *Nephtys incisa*; *Lumb*, *Lumbrineris latreilli*.

are associated with the deeper strata-coenoses. Figures 2 & 3 only show the species points for *M. bidentata* and those polychaete species that colonize the deep layers (below 5 cm) to a significant extent, namely: *N. incisa*, *Lumbrineris latreilli* and *S. costarum*. In the two periods, the localization of *Mysella* in the model is significantly different; whereas in the first period this species is ordered in a very polarized way, highlighting a specific association with the surface strata-coenoses, in the second period it is ordered close to the origin of the axes, showing a much lower layer specificity. In contrast, the tube-dwelling and burrowing polychaetes remain mainly associated with the deeper strata-coenoses in both cases.

Using the non-aggregated data for each of the 54 box-corer samples of the final period the Yule's index of absolute association was calculated between *M. bidentata* and the polychaetes *N. incisa*, *L. latreilli* and *S. costarum*. Results are shown in Table 3. The association between the pairs in the upper layers is fairly low with little differentiation, and the differences between the associations in the surface layers are never significant (Table 4). In the deep layers, however, the indices are significantly differentiated and highlight a strong association exclusively between *M. bidentata* and *N. incisa* (Table 4). In fact it is only between *Mysella* and *Nephtys* that the values of surface and deep-level Yule's indices are statistically (but only just) different (Table 5).

DISCUSSION

The most obvious difference between the original community and that found after the long-term recolonization, regards the density of *Mysella bidentata*, which increases enormously in the second period. The FAC showed that the abundance of *M. bidentata* varies in accordance with the sediment profile; in the first, low-density period, *M. bidentata* is more abundant in the upper layers, while in the second high-density period, it appears more uniformly distributed throughout the sediment layers.

After recolonization, there is only a weak association between *M. bidentata* and the tube-dwelling and burrowing polychaetes at the surface, but a strong association with *Nephtys incisa*, in the deeper layers. It could indicate that the location of *Mysella* in these layers might be favoured by the use of the galleries constructed by *N. incisa* to colonize the deep sediments. The association was found only between *M. bidentata* and *N. incisa* and is attributable to the different habitats of the three polychaete species considered. Only *N. incisa* digs burrows in which it moves actively causing the circulation of oxygen-rich water. The galleries can therefore be a suitable habitat for *Mysella*. By contrast, the other two species considered are tube dwellers: *Spiochaetopterus costarum* lives in rigid tubes of transparent material, while *Lumbrineris latreilli* lives in tubes made from mucus and sediment. In both cases, the tube adheres to the body of the animal and does not leave sufficient space for the intrusion of commensal animals. Furthermore, the sediment outside the tube is not modified by the presence or activity of these organisms. The comparison of the association of *Mysella* and *Nephtys* between surface and deep-level was significant but only just ($P=0.049$). This is probably due to the greater variation in species composition within lower strata in the sediment profile during the final survey. Furthermore, large deep-burrowing polychaetes such as *N. incisa* are patchily distributed compared to small species inhabiting superficial layers.

According to Franz (1973), *M. bidentata* is free living. However, it thrives in rigorously defined habitats which allows it to achieve high density despite the small dimensions of the adult and its very slow growth. Many observations (Boss, 1965; Gage, 1966, 1968; Morton, 1962) have shown that *M. bidentata* and other small bivalves can benefit enormously from commensal interactions, living in contact with a host without adhering to it. The best-known and most extensively studied association is that between *M. bidentata* and *Amphiura filiformis* (Ockelmann & Muus, 1978; Kunitzer, 1989). It has been demonstrated

that this association leads to improved use of food resources and significant reduction in the mortality of *M. bidentata*. However, the association between *M. bidentata* and *A. filiformis* is not so close and specific as has sometimes been hypothesized. Ockelmann & Muus (1978) observed that *Mysella* only spends a part of its time, varying according to age, in association with the host, while for the remaining time it is free living, behaving as a filter-feeder and detritivore near to the surface of the substrate. The variety of commensal organisms for *M. bidentata* is exceptionally large, ranging from polychaetes to sipunculids, other bivalves, and holoturoides (Hayward, 1990; Josefson & Conley, 1997; Olivier & Retière, 1998). In addition, *M. bidentata* has recently been indicated as a symbiotic organism established in the channels excavated by the echiuroid *Maxumelleria lankesleri* (Nickell et al., 1995). Moodley et al. (1998) have also found a large number of *Mysella* sp. deeper than 5 cm in the sediment in bioturbated areas.

Our finding of an association between *M. bidentata* and *N. incisa* confirms the tendency in this species towards non-specific commensalism with other benthic species that are particularly active in the bioturbation of the sediment. In the deep layers, however, the indices are significantly differentiated and highlight a strong association exclusively between *M. bidentata* and *N. incisa*.

In our case, the association between *M. bidentata* and *N. incisa* was found only: (i) in conditions of high density of *M. bidentata*; and (ii) in the deep layers of sediment. Both observations could indicate that it may be competition that induces *M. bidentata* to colonize the deeper layers through commensalism. In fact, only in conditions of high density does part of the population move habitat towards the lower sediment layers. In this way, the commensal population could be partially separated from that at the surface, lowering the effective density and therefore the overall level of competition.

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