Cyclical changes in the fauna associated with tube aggregates of *Ficopomatus enigmaticus* (Fauvel)

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ABSTRACT

Studies were undertaken on the fauna associated with the tube aggregations of *Ficopomatus enigmaticus* in a brackish water lagoon, in southern England, from 1982–1992. During this time a population crash and partial recovery was observed. Aggregates, consisting of living animals, were occupied in abundance by the amphipods *Leptocheirus pilosus*, *Corophium insidiosum* and *Melita palmata*, with numbers declining in dead colonies. Initially moribund aggregates were invaded in large numbers by the isopod *Lekanesphaera hookeri*. At the same time the polychaete *Hediste (Nereis) diversicolor* showed an increase in numbers. *Leptocheirus pilosus* returned in abundance by 1989. The fluctuations in associated species were related to the ability of *F. enigmaticus* to prevent deposition and accumulation of sediment and organic material. Parallel sampling of the adjoining muddy sediments revealed catastrophic disappearance and re–appearance of species, similar to that shown by *F. enigmaticus*. These included the rare lagoonal polychaete, *Alkmaria romijni*. Both living and dead aggregates of *F. enigmaticus* provide an extensive benthic sub–habitat. The living aggregates may also regulate invertebrate food resources. The ecology of the benthos was controlled by the interaction of this factor with variables such as saline intrusion.

RÉSUMÉ

Changements cycliques de la faune associée aux agrégats de tubes de *Ficopomatus enigmaticus* (Fauvel)

Des études ont été entreprises sur la faune associée aux agrégats de tubes de *Ficopomatus enigmaticus* dans une lagune d'eau saumâtre au sud de l'Angleterre de 1982 à 1992. Au cours de cette période, on a observé la disparition puis la reconstitution partielle de la population de *F. enigmaticus*. Les agrégats constitués par des animaux vivants étaient colonisés en abondance par les amphipodes *Leptocheirus pilosus*, *Corophium insidiosum* et *Melita palmata*, dont le nombre décroissait dans les agrégats morts. Les agrégats de moribonds ont été initialement, envahis, en grand nombre, par l'isopode *Lekanesphaera hookeri*. Simultanément, les polychètes *Hediste (Nereis) diversicolor* ont montré une très forte augmentation numérique. *Leptocheirus pilosus* à retrouvé une grande abondance en 1989. Les fluctuations des espèces associées sont liées à la capacité de *F. enigmaticus* d'empêcher le dépôt et l'accumulation de sédiments et de matière organique. Des échantillons, prélevés simultanément sur les sédiments vaseux voisins, ont révélé une disparition catastrophique puis une réapparition d'une faune similaire à celle déja rencontrée dans les agrégats de *F. enigmaticus*. L'espèce lagunaire, *Alkmaria romijni*, espèce rare, a été récoltée dans ces échantillons. Les deux types d'agrégats vivants et morts de *F. enigmaticus* fournissent un large sous–habitat

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benthique. Les agrégats vivants peuvent réguler les ressources en nourriture des invertébrés. L'écologie du benthos était contrôlée par l'interaction de ce facteur avec des variables telles que les intrusions salines.

INTRODUCTION

FAUVEL (1933), in describing the distribution of the serpulid *(Mercierella) Ficopomatus enigmaticus*, frequently mentioned the varied fauna associated with the aggregated tubes. Observations by FISCHER–PIETTE (1925, 1928), BERTRAND (1938), RULLIER (1943), EUZET & PUJOL (1963) and VUILLEMIN (1965) showed that this associated fauna was similar in species composition. The sessile species were generally limited to a few species of bryozoa, *Balanus* and ascidians. In contrast the mobile fauna were quite diverse, consisting mainly of amphipods, isopods and polychaetes. There was a high degree of uniformity in the family groups observed, although the species frequently vary. Principal amongst these were species of *Corophium*, *Gammarus* and *Lekanesphaera (Sphaeroma)*. The amphipod *Leptocheirus pilosus* Zaddach, 1844 appeared to be almost universally found. Spatial and temporal variation in species composition has been observed by RULLIER (1943) and EUZET & PUJOL (1963), and related to fluctuations in local conditions and the health of the aggregates.

The populations of *F.enigmaticus* in the brackish water of the Emsworth, Slipper and Peter, millpond complex (Fig. 1) have been investigated since 1982 by THORP (1987, 1994). These studies have revealed considerable population variations, with a "crash" occurring in 1986, consisting of the apparent death of the adult population and a massive reduction in larval settlement. This event was followed in 1989–91 by a recovery in larval settlement, with some aggregates demonstrating regeneration and others appearing as new aggregates on the mud surface. The population decline was attributed to the age of the adult population, lack of overwintering reserves and a failure of recruitment (THORP, 1992). The last two are regulated by phytoplankton levels during summer, which in turn are controlled by sunlight, temperature and salinity. Recruitment success was also thought to depend on availability of suitable substrata for settlement.

The millpond complex in Emsworth (Fig. 1) has a combined area of 2.7 hectares and, apart from a deeper water entrance and channel, a maximum depth of less than 1.5 m (THORP, 1987). Seawater enters on high spring tides from Chichester Harbour, through tide gates at the southern end. Fresh water enters from the River Ems in the north. Winter and spring bottom salinities vary from 0 to 30 and summer to autumn salinities are normally from 10 to 34. The substratum is composed of silty muds (median diameter 0.022 mm to 0.047 mm) and high levels of organic material (9 % to 16 %) (unpublished data), although stones and other hard substrata, such as broken bottles, are scattered over the surface. These hard objects are the surfaces upon which the aggregations of *F. enigmaticus* occur.

Concurrent with the study by THORP (1994) on fluctuations in the population of *F. enigmaticus*, the opportunity was taken to determine how the associated fauna varies with the health of the aggregates. The present paper describes and attempts to explain some of the changes observed, and relates these to the benthic faunal communities of the millpond complex.

MATERIALS AND METHODS

Samples of sediment and aggregates of *F. enigmaticus* were collected in the autumns of 1982, 1987, 1989 and 1991. On each occasion at least five small aggregates of *F. enigmaticus* were collected, with volumes between 0.5 and 1.5 litres. At the same time two cores (9 cm diameter x 15 cm deep) of mud were collected from each of five sites (Fig. 1). Additional cores were collected, in the latter three years, for the analysis of sediment particle size and organic material content. All the samples were taken to the laboratory where the aggregates were frozen and the sediment samples sieved through a 0.5 mm mesh.

Each frozen aggregate was measured by placing it into a plastic bag and then plunging it into a Eureka can to determine the volume. The plastic bag was then removed and the volume measured again. A final volume was taken once all the sediment had been washed from the aggregate. It was possible then to calculate the interstitial space and the percentage of that space occupied by sediment. The sediment removed from the aggregates was also washed through a 0.5 mm sieve and all animals sorted, preserved and identified to species where possible.

Particle size analysis was undertaken using an initial wet sieving technique followed by dry sieving of the > 0.063 mm fraction and wet suspension of the < 0.063 mm fraction; organic content was estimated by loss on ignition (HOLME & MCINTYRE, 1971).

RESULTS

The full species list for both aggregates and adjacent sediment is given in Table 1, showing the composition and abundance of the species, in both the aggregates and the sediment, over the four sampling periods. The changes in the species numbers are demonstrated in Figure 2. There is an apparent inverse relationship between the number of species in the aggregates and in the sediments. The number of species was greatest in theaggregates in the period 1987 to 1989. This period corresponds to the lowest species numbers in the sediment. The reverse was true in 1982 and 1991, although species numbers in the 1991 aggregates were relatively high.

The state of health of the aggregates can be seen to be related to the number of species and abundance of individuals (Fig. 3). Although lower species numbers occurred in the live aggregates, they supported a greater number of individuals. The physical condition of the aggregates can be related, to some extent, to the quantity of sediment they contain. Figure 3 demonstrates that greater quantities of sediment occupied the dead and regenerating aggregates with levels as high as 40% in the latter.

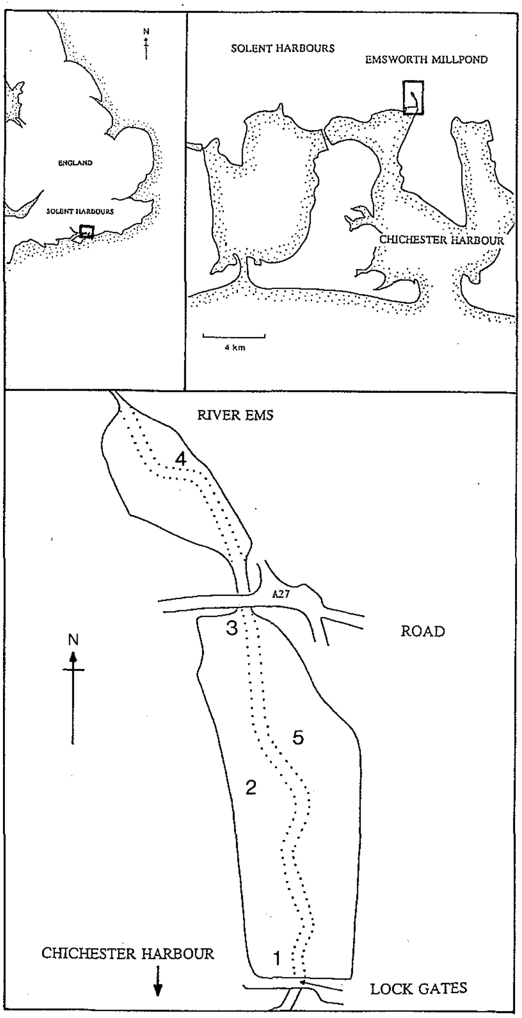

FIG. 1. — Sampling sites in the Emsworth millpond complex, with its location indicated in the Solent Harbours system, on the south coast of England.

TABLE 1. — List of fauna associated with live, dead and regenerating *Ficopomatus* aggregates (Agg) and in the mud of the Emsworth millpond complex. *: low abundance, **: medium abundance, ***: high abundance.

Species	1982	Live	1987	Dead	1989	Dead	1991	Regen.
	Agg	Mud	Agg	Mud	Agg	Mud	Agg	Mud
Anthozoa								
Actiniria								
Nematostella vectensis	-	***	-	-	-	-	-	-
Annelida								
Oligochaeta								
Tubificoides benedeni	-	**	*	-	-	-	-	-
Oligochaete indet.	-	-	-	-	-	-	-	*
Polychaeta								
Eteone longa	-	***	-	-	-	-	-	*
Nereis diversicolor	*	**	***	***	**	***	**	***
Alkmaria romijni	-	**	*	**	-	-	-	***
Streblospio shrubsoli	-	*	*	-	**	***	-	***
Polydora ciliata	-	*	-	-	**	**	*	*
Spionid indet.	-	-	*	*	**	**	-	*
Capitella sp.	-	*	*	-	-	-	-	-
Tharyx marioni	-	*	-	-	-	-	-	-
Manayunkia aestuarina	-	*	-	-	-	-	-	-
Crustacea								
Cirripedia								
Balanus improvisus	-	-	-	-	*	-	-	-
Amphipoda								
Leptocheirus pilosus	***	*	*	-	***	-	***	**
Melita palmata	***	**	*	-	***	-	*	*
Gammarus zaddachi	-	-	**	-	-	-	-	-
Gammarus salinus	-	-	**	-	-	-	-	-
Gammarus locusta	-	-	-	-	*	-	-	-
Gammarus duebeni	-	-	-	-	-	-	*	-
Corophium insidiosum	***	-	-	-	-	-	-	-
Corophium volutator	-	**	-	-	*	-	-	*
Jassa falcata	-	*	-	-	-	-	-	*
Isopoda								
Lekanesphaera hookeri	-	-	***	**	*	-	***	*
Cyathura carinata	-	**	*	**	**	***	***	***
Tanaidacea								
Heterotanais oerstedi	-	-	-	-	***	-	*	-
Decapoda								
Carcinus maenas	*	-	*	-	*	-	*	-
Mollusca								
Gastropoda								
Hydrobia ulvae	-	-	-	-	-	-	*	*
Pelecypoda								
Cerastoderma edule	-	*	-	-	*	-	**	**
Ostrea edulis	-	-	-	-	-	-	*	-
Mya arenaria	-	-	-	-	-	*	-	*
Ascidiacea								
Ascidiella aspersa	-	-	-	-	*	-	-	-
Ciona intestinalis	-	-	-	-	*	-	-	-
Total N°. Species	5	16	13	5	16	6	12	16

The principal species found in the aggregates show clear differences in abundance between aggregate types (Fig. 4). The live aggregates were co–dominated by the amphipods *Leptocheirus pilosus*, *Corophium insidiosum*

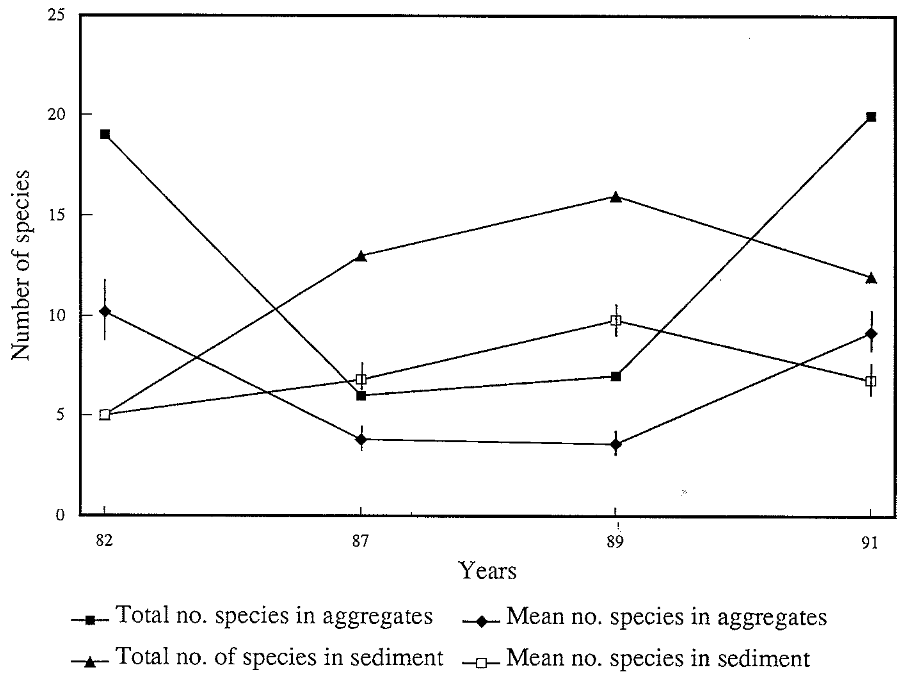

FIG. 2. — Mean and total number of species in the aggregates and in the sediment, 1982–91. (mean number of species ± s.e.).

Crawford, 1937 and *Melita palmata* (Montagu, 1804). The former species dominated in all aggregate types, whereas *C. insidiosum* occurred only in live aggregates. Several other species, but most noticably *Lekanesphaera hookeri* (Leach, 1814), *Cyathura carinata* (Kröyer, 1847) and *Hediste diversicolor* (O.F. Müller, 1776) were found in the greatest numbers in dead or regenerating aggregates, although all were found in the live aggregates on at least one occasion. *L. hookeri* and *H. diversicolor* in particular dominated the dead aggregates during 1987.

By further examining the changes in abundance that have occurred over the 10 year period and comparing these with Figure 4, it is possible to determine whether the state of health of the aggregates is the most important influencing factor. Figure 5 confirms that *L. pilosus* and probably *M. palmata* have responded to factors in addition to the collapse in the health of the aggregates, with low values occurring in 1987 followed by high values in 1989, both periods when dead aggregates were prevalent. *C. insidiosum* in contrast disappeared by 1987 and failed to re–appear, indicating that it may have been specific to live aggregates.

Of the secondary dominants, the three species *L. hookeri, C. carinata* and *H. diversicolor* all showed increases in abundance after the disappearance of the live aggregates (Fig. 6). This has been most pronounced for *L. hookeri* which was the dominant aggregate species in 1987. The changes in *C. carinata* and *H. diversicolor* have been less dramatic but were greatest in the period 1982 to 1987. Both of these species have stayed at relatively uniform levels in the adjacent mud (Fig. 7) suggesting that the death of the aggregates could be the most important factor influencing the changes observed.

The stability of *H. diversicolor* and *C. carinata* in the mud contrasts with several other species that were abundant in the sediments (Fig. 8). The polychaete species *Streblospio shrubsoli* (Buchanan, 1890) and *Alkmaria romijni* Horst, 1919 have undergone considerable variations. An equally large change has also been shown by the anthozoan *Nematostella vectensis* Stephenson, 1935 which disappeared by 1987 and was not found subsequently.

Data on the sediment particle size and organic material levels have not been complete over the 10 year period but there has been no evidence of long term changes in either. Percentage sediment less than 0.063 mm in diameter has been recorded as between 60 to 80 % and organic material at an almost uniform 13 %.

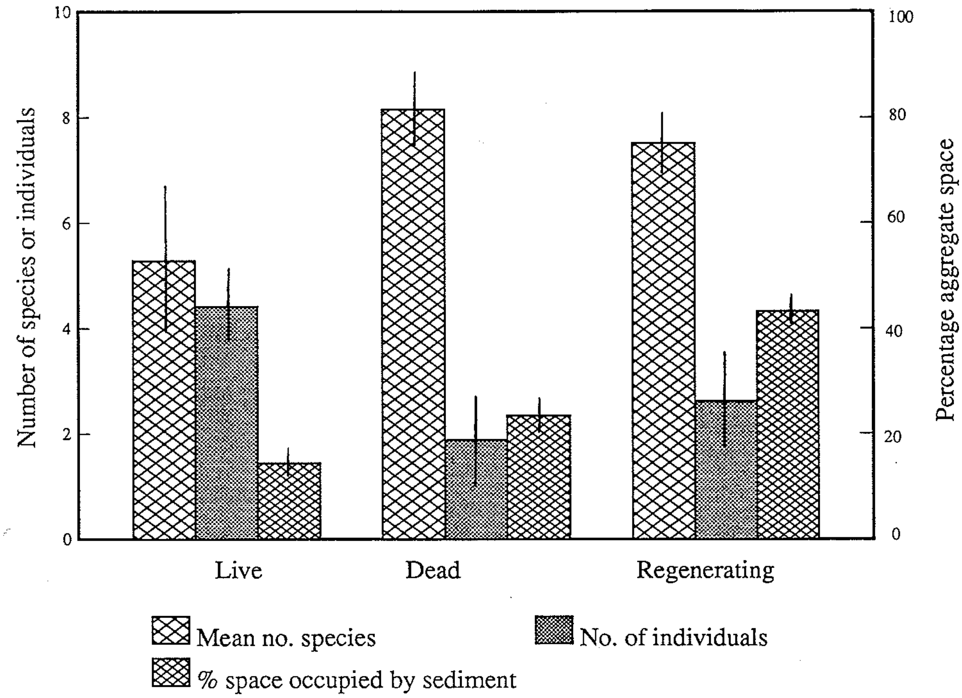

FIG. 3. — Species number, abundance and percentage interstitial sediment in live, dead and regenerating aggregates. (species numbers are means ± s.e.,abundances are mean numbers per cm^3 ± s.e. and percentage is mean ± s.e.).

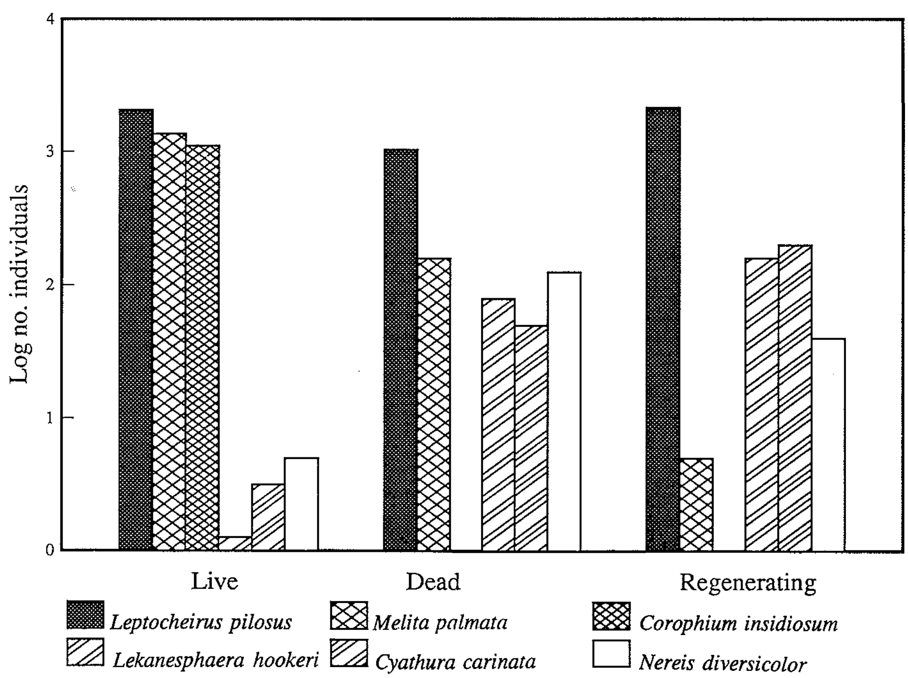

FIG. 4. — Abundance of dominant species in different aggregate types. (mean number of individuals per litre).

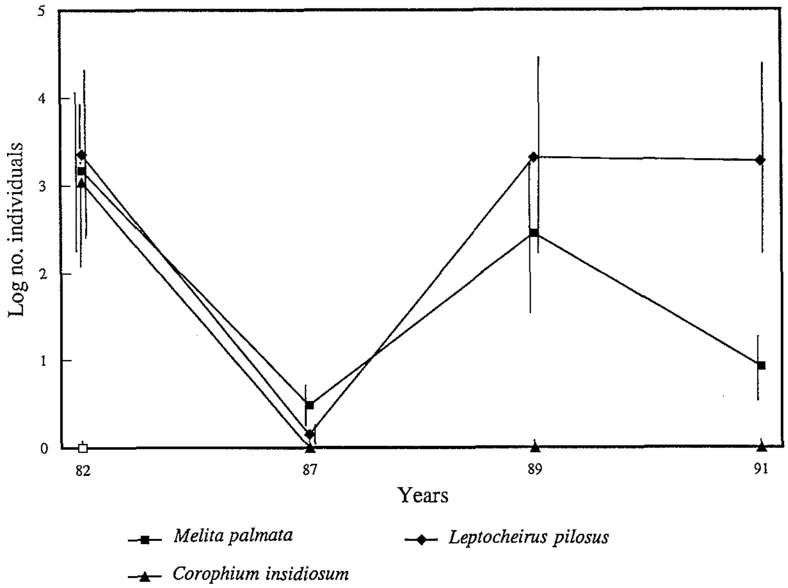

FIG. 5. — Changes in the abundance of dominants in aggregates. ($\log_{10}$, mean number of individuals per litre ± s.e.).

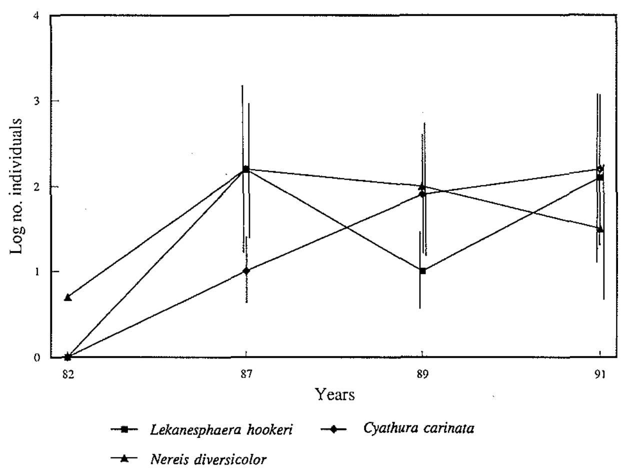

FIG. 6. — Changes in abundance of secondary dominants in aggregates. ($\log_{10}$, mean number of individuals per litre ± s.e.).

DISCUSSION

Two of the most commonly occurring species in the live aggregates of *F. enigmaticus*; *L. pilosus* and *C. insidiosum*, are tubicolous amphipods (LINCOLN, 1979) which exploit particulate material suspended in moving water, such as that found in the millponds complex. They are unable to tolerate the high silt and clay levels in the sediments, which are more suited to the burrowing polychaetes and crustaceans. Both species were found by GOODHART (1939), living in a brackish water sluice pond, similar to the millpond. There *L. pilosus* constructed its tubes on the thallus of *Chondrus crispus* thus remaining in moving water above the soft sediment floor. *C. insidiosum* has also been found by SHEADER (1978) in high turbidity waters associated with mats of *Rhodochorton* sp. *M. palmata* differs in that it is normally found amongst stones and gravel in silty environments (LINCOLN, 1979) and is probably occupying the silt filled areas at the base of the aggregations.

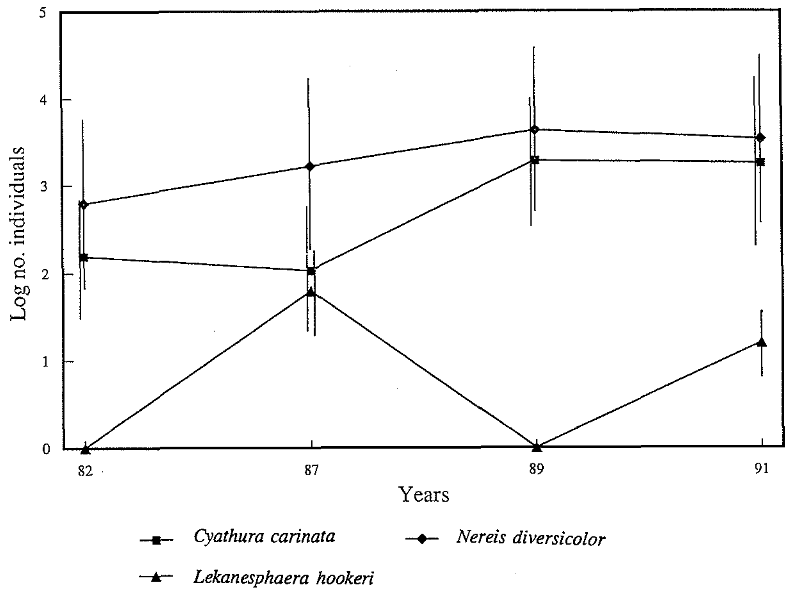

FIG. 7. — Changes in the abundance of dominants in sediments. ($\log_{10}$, mean number of individuals.m^2 ± s.e.).

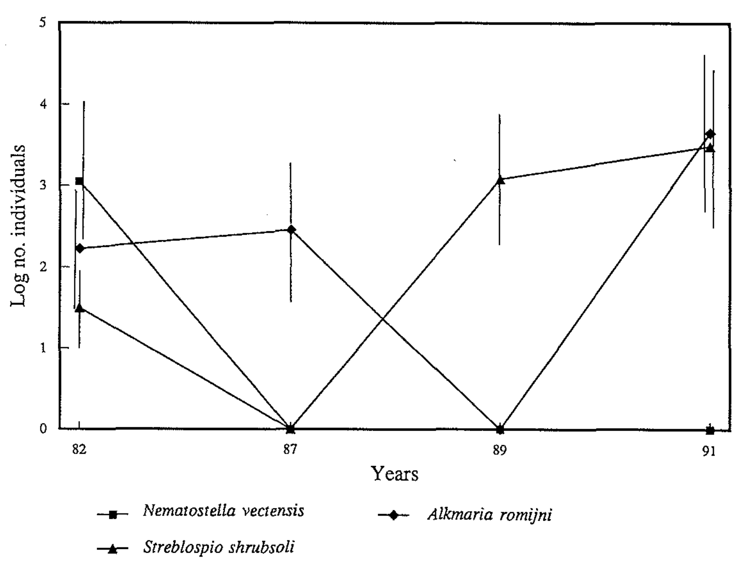

FIG. 8. — Changes in abundance of secondary species in sediments. ($\log_{10}$, mean number of individuals m^2 ± s.e.).

The death of the aggregates of *F. enigmaticus* in 1987 may have contributed to several of the changes observed in the associated fauna. Most important amongst these was the demise of *C. insidiosum*. The other two abundant species, although they almost disappeared in 1987, were able to return to dominance in 1989.

The burrowing and mobile scavenging fauna which developed in 1987 evidently responded to the increased area available for occupation, created by the greater quantitiesof particulate material within the aggregates. Similar changes were observed by RULLIER (1943), who found that *H. diversicolor* was present in abundance in recently dead aggregates. The accumulation of sediment may also have prevented some of the live aggregate species from occurring, such as *C. insidiosum*, although the quantity of sediment was never sufficient to eliminate all of the mobile amphipods. These species are still able to exploit the remaining space and utilise the high levels of suspended particulate material found in the water. As a consequence the dead aggregates are able to support a wider range of species than the live aggregates. Likewise the regenerating aggregates contain greater levels of sediment, principally in a central degenerated area, surrounded by an atoll of regenerating individuals. As a result the regenerating aggregates retain an equally diverse fauna.

The lack of sediment makes live aggregates unsuitable for burrowing species, but an additional factor reducing the diversity of the associated fauna could be competitive exclusion. KNIGHT–JONES & MOYSE (1961) have indicated that the growth form of *Filograna* aggregations optimises food utilisation, and *Ficopomatus* has somewhat similar spacing of individuals within the aggregates. The limited species numbers but large numbers of individuals found in live aggregates indicate that *L. pilosus, M. palmata* and *C. insidiosum* may have specific feeding requirements that do not conflict with that of *F.enigmaticus*. Between these species full exploitation of the available food resources may well occur, thus excluding other species. While conditions are stable the amphipod populations are likely to remain in balance with *F.enigmaticus,* maintaining themselves by larval brooding and direct settlement (LINCOLN, 1979).

The filter–feeding activity of *F. enigmaticus* is also likely to have an effect on the total energetics of the millpond. DAVIES *et al.* (1989) in a study of the Marina de Gama, near Cape Town, calculated that *F. enigmaticus* had the potential to reduce the particulate load of the water within the lagoon by 50 % each day. This ability to change the water quality has the potential to affect the fauna profoundly, within both the aggregates and the adjacent mudflats. The disappearance of live *F. enigmaticus* aggregates in 1987 corresponded with changes in the mudflat fauna, particularly a reduction in diversity. The remaining species, such as *H. diversicolor* and *L. hookeri,* mostly exhibited non–specialised feeding habits. These species were probably able to exploit the increased levels of suspended food that were not previously available to the sediment fauna. A further feature, related to the loss of the aggregates, was the substantial reduction in the numbers of *F. enigmaticus* larvae (THORP, 1994) which may have formed an important food source for some of the species with more specialised feeding habits. A good example of this is the polychaete *Eteone longa* (Fabricius, 1780), which FAUCHALD & JUMARS (1979) have indicated feeds specifically on other annelid larvae. With the reappearance of the live aggregates, and hence reduction in suspended food and an increase in larval numbers, it could be expected that the benthic species numbers in the sediment would increase. To some extent this situation has occurred, species numbers falling in the aggregates and increasing substantially in the sediment.

Considerable variation in the benthic fauna is evident, however, which cannot be explained wholly by the death of *F. enigmaticus*. Clearly other factors operate in the millpond which affect the benthic fauna and may have contributed to the demise of *F. enigmaticus*. Of principal importance amongst these is the intrusion of high salinity water. In 1982 the benthic fauna was composed of a range of species, that included several marine species, commonly occurring in Chichester Harbour; for example, *E. longa, Tharyx marioni* (de Saint–Joseph, 1894), *Manayunkia aestuarina* (Bourne, 1883) and *Cerastoderma edule* (L., 1758) (THOMAS, 1987). The disappearance of this group in 1987 and the appearance of several low salinity species, for example *Gammarus zaddachi* Sexton, 1912 and *Gammarus salinus* Spooner, 1947 suggests that a period of low salinity may have eliminated most of the marine species. THORP (1987) has indicated that protracted periods of low salinity occurred during the winter and spring of 1983–1987. The species most successful during this period were the typically euryhaline species, *H. diversicolor* and *Cyathura carinata*. The appearance of marine species in 1989 *Ascidiella aspersa* (O.F. Müller, 1771) and *Ciona intestinalis* (L., 1767) was localised in the vicinity of the tide gates where maximum salinities occur. This was followed in 1991 by the re–appearance of several species which clearly entered from Chichester Harbour; specifically *Ostrea edulis* L., 1758, *Eteone longa, Jassa falcata* (Montagu, 1880) and *Hydrobia ulvae* (Pennant, 1777). All of these species occurred in the year which followed a winter of almost constant high salinities, with zero salinity recorded only 15 % of the time.

These fluctuations in salinity, in combination with the biological effects due to the changes in health of the aggregates, have created a dynamic and unstable environment in the millpond. This is demonstrated by fluctuations in abundance of several of the benthic species, particularly *N. vectensis* and *A. romijni*, both of which are protected species in the U.K. These species, in keeping with many others that occupy extreme environments, can exploit to the maximum suitable conditions when they occur. Extreme conditions have also been cited by TEN HOVE (1979) as a factor in the development of mass occurrences of serpulids. These may be followed by dramatic declines, with, in the case of the serpulids, only the dead tubes to provide evidence of previous existence.

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