Population variation in *Ficopomatus enigmaticus* (Fauvel) (Polychaeta, Serpulidae) in a brackish water millpond at Emsworth, West Sussex, U.K.

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ABSTRACT

Since 1982 a population of *Ficopomatus enigmaticus* has been monitored with respect to larval settlement and tube accumulation on settlement panels. Prodigious settlements (1.3 x 10^7.m^{-2} max.) were recorded over the period 1982–85 and globular, reef–like aggregations increased in number on the muddy floor of the pond but, prior to the onset of breeding in 1986, the population `crashed' dramatically. While live adults were not observed in the years 1986–88 larval settlements continued, but with greatly reduced and decreasing maxima (1.6x10^3.m^{-2}, 1986; 1.1x10^3. m^{-2}, 1987 and 9.7 x 10^2. m^{-2}, 1988). Since 1989 the adult population has recovered, being observed on the tide–gates and adjacent walls in particular (1989–90) and as small aggregates on the pond bottom (1991). The increase in the adult population has been reflected in in"reasing settlement densities (2.8 x 10^5. m^{-2}, 1989 to 2.5 x 10^6. m^{-2}, 1991). Evidence is offered to explain the population "crash" of 1986 and it is suggested that it resulted from the age of the adult population and a lack of both overwintering reserves and recruitment. It is also suggested that serpulid polychaetes which exhibit population "explosions", such as *F. enigmaticus*, are equally likely to suffer population "crashes" and, further, that population numbers may well fluctuate in a cyclical manner.

RÉSUMÉ

Variation de la population de *Ficopomatus enigmaticus* (Fauvel) (Polychaeta, Serpulidae) dans une retenue d'eau saumâtre à Emsworth, West Sussex, RU.

Depuis 1982, une étude, concernant l'établissement de larves et l'accumulation de tubes sur les panneaux expérimentaux, a été menée sur une population de *Ficopomatus enigmaticus*. De 1982 à 1985, des fixations considérables ont été enregistrées et des agrégats de forme sphérique semblables à des récifs augmentèrent en nombre sur le fond vaseux du bassin de retenue. Cependant, la population s'effondra de façon drastique et ceci avant le début de la période de développement de 1986. Alors qu'aucun adulte vivant ne fut observé de 1986 à 1988, la fixation de larves continuait mais leur abondance était extrêmement réduite et continuait à decroître (1.6 x 10^3.m^{-2} en 1986; 1.1 x 10^3. m^{-2} en 1987 et 9.7 x 10^2. m^{-2} en 1988). Depuis 1989, la population adulte s'est rétablie et elle fut observée sur les portes des marées et sur les parois adjacentes, tout particulièrement en 1989 et 1990. En 1991, de petites agrégats s'établirent au fond du bassin de retenue. L'augmentation de la population adulte est le reflet de cette densité d'établissement larvaire (2.8 x 10^5. m^{-2} en 1989 à 2.5 x 10^6. m^{-2} en 1991). Quelques hypothèses sont

THORP, C.H., 1994. — Population variation in *Ficopomatus enigmaticus* (Fauvel) (Polychaeta-Serpulidae), in a brackish water millpond at Emworth, West Sussex, U.K. *In*: J.-C. DAUVIN, L. LAUBIER & D.J. REISH (Eds), Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. natn. Hist. nat.*, **162** : 585-591. Paris ISBN 2-85653-214-4

avancées afin d'expliquer l'effondrement de la population de 1986. Il est suggéré qu'elle fut causée par l'âge de la population adulte, et par l'absence de réserves hivernales ainsi que par l'absence de recrutement. Il est aussi suggéré que les serpules qui, comme les *F. enigmaticus*, connaissent des explosions de leurs populations, pourraient de la même façon, subir un effondrement drastique de celles-ci. De surcroît, il se pourrait que ces populations fluctuent de façon cyclique.

INTRODUCTION

The serpulid *Ficopomatus enigmaticus* (Fauvel), first reported in Britain from the London Docks in 1921 (MONRO, 1924), has been recorded from a number of brackish water sites, mostly confined to southern coasts (ZIBROWIUS & THORP, 1989). Although transitory populations have been recorded from Danish waters, (WESENBURG–LUND, 1941; HARTMANN–SCHRÖDER, 1971), and a population sustained by heated power station effluent (RASMUSSEN, 1958), *F. enigmaticus* is considered to reach its northern limit of reproduction on British coasts, several records again being associated with warm water effluents (NAYLOR, 1959; MARKOWSKI, 1962). *F. enigmaticus* was first recorded from Chichester Harbour, West Sussex, in 1974 (THORP, 1980) and since 1980/81 has flourished in the brackish water millpond of the now defunct Slipper tidemill at Emsworth, West Sussex (50°50.5'N, 0°56'W). The millpond has a surface area of 2.7 ha and, apart from a meandering deeper water channel, has a maximum depth < 1.5 m (THORP, 1987). Seawater enters from the adjacent Chichester Harbour through tide–gates at the south end during spring tides > 4.3 m while fresh water enters from the north as part of the River Ems. A relatively constant water level is maintained within the pond during low tide periods by the tide–gates (THORP, 1987). Within the pond limited hard substrata are readily "colonised" by *F. enigmaticus*, from the tide–gates and adjacent brick walls to the stems of fringing reeds, but the most characteristic growths are globular mini–reefs (aggregates). The aggregates, apparently resting on the soft mud substratum in depths of 0.75–1.0 m (cf. RULLIER, 1943), have resulted from larval settlement on small solid objects such as pebbles, stones, cans, bottles, etc.

Since May 1982 water temperature, salinity and *F. enigmaticus* settlement have been monitored weekly. Temperature and salinity are very variable and, despite the shallowness of the ponds, exhibit frequent and marked discontinuities between the surface and the pond bottom at 0.75–1.0 m (THORP, 1987). The overall salinity regime (0.3–34.1 P.S.U.) of the bottom waters, where greatest growth of the aggregates occurs, is both lower and more variable in winter/spring than in summer/autumn (THORP, 1987). The overall pattern of salinity variation is of high salinity over spring tide and low salinity over neap tide periods. Apart from when the River Ems is in spate, spring tide salinities are gradually reduced over the neap tide period with an abrupt return to high salinity at the next springs. The temperature range of the bottom waters also varies, from 5.5–30 °C in the warmer months of the year (May–October) to –1–20 °C (November–April). Larval settlement is confined to the period May to October/November, when the minimum bottom water temperature is > 10°C, and exhibits a marked lunar periodicity with settlement occurring over the neap tides (THORP, 1987 and unpublished data). Maximum settlements have exceeded 10×10^6. m^{-2} (THORP, 1987). In water temperatures > 10 °C spawning is apparently initiated (triggered) by an influx of higher salinity water (spring tides). The minimum salinity required has not been determined and spawning can be delayed in the absence of adequate phytoplankton levels (THORP, 1987).

Although there are many records of the incidence of *Ficopomatus* spp., several giving data for a few years (TEBBLE, 1953; HILL, 1967; STRAUGHAN, 1972) and/or detailed seasonal data (HILL, 1967; STRAUGHAN, 1972; DIXON, 1981), continuous observations of a single population over a long period are lacking. The present paper, therefore, presents some results from monitoring a population of *F. enigmaticus* over the period 1982–92 and suggests reasons to explain the pattern of variation.

MATERIALS AND METHODS

Panel studies employed 25 x 25x 0.6 cm 'Tufnol" panels attached horizontally to a frame, constructed from 1.8 cm "Durapipe". The panels were held 15cm above the pond bottom at 0.75–1.0 m depth. Settlement was assessed using weekly (6–8 days) panels while seasonal panels were used to assess tube accumulation (weight). Settlement density was determined using a 10 x 10 cm grid within a 2 cm wooden frame. Light settlements were scored by placing the grid in each of the four corners of the panel and counting the total number of worms within the10 x 10 cm grid area under a binocular microscope. Progressively heavier settlements were scored using random numbers to select 10 1 x 1 cm squares within each grid and/or using a squared eyepiece grid within the

1 x 1 cm squares. Mean values were expressed as numbers/m2. Seasonal panels were weighed weekly on a spring balance after standard drainage and removal of silt, attached algae and crabs.

RESULTS

SEASONAL SETTLEMENT. — Figure 1 presents weekly settlement data for the years 1982–1992. Settlement begins in mid to late May and ends in late October/November. The overall pattern demonstrates a series of peaks and troughs which result from settlement occurring over neap tides (THORP, 1987 and unpublished data). The lack of precision in figure.1 reflects that weekly sampling was dictated by teaching commitments rather than a precise relation to the tidal phases. Thus, panel changing in the course of a set of neap tides could result in consecutive panels attracting heavy settlements. The 10–year period can be split into three phases. Firstly 1982–85, which saw a prolonged period of high settlements, several > 1x 10^6. m^{-2} and some > 10 x 10^6. m^{-2}. This prolific phase was followed by greatly reduced settlements from 1986–88. In early March 1986 the population suffered a catastrophic

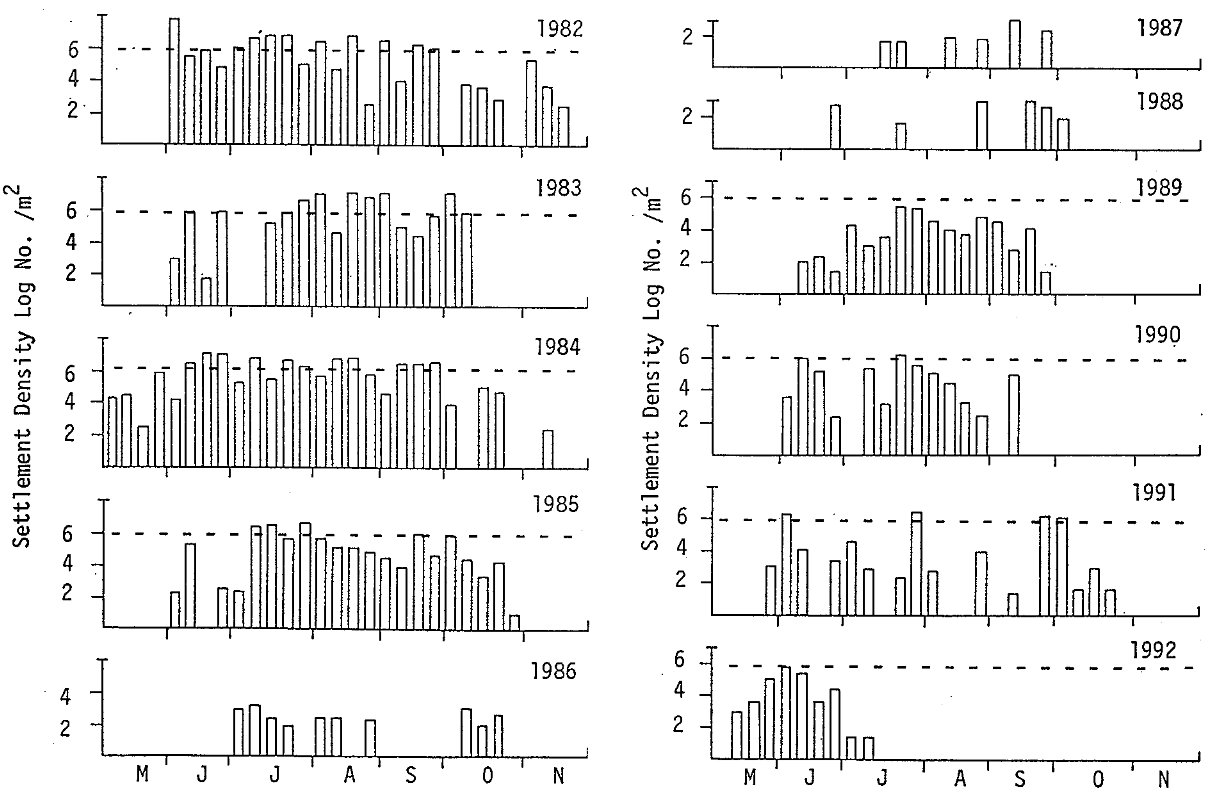

FIG. 1. — Settlement density of *F. enigmaticus* on weekly settlement panels, 1982–92.

"crash"; all aggregates died and live adults were not observed within the pond. Despite the apparent lack of live adults, small settlements (max. 1600 m^{-2}) occurred during shortened settlement seasons. The third phase, 1989–91, witnessed an increase in both the length of the settlement season and settlement density, settlements > 1 x 10^6. m^{-2} being recorded in both 1990 and 1991. Live adults again became abundant on the tide–gates and adjacent brick walls and, in 1991, small irregular aggregates were observed on the muddy pond bottom. The 1992 season began well, with promising settlements in May and June. Late June, however, witnessed very extensive and dense (80–90 % cover) growth of the green alga *Ulva lactuca* on the pond bottom and July saw a dramatic reduction in settlement. Throughout August and September the pond was allowed to flush tidally to give low–tide access for repairs to a road bridge which crosses the pond and no further settlements were recorded. The 10–year period, therefore, exhibits a cyclical pattern of initial abundance followed by a dramatic decline and subsequent recovery.

TUBE ACCUMULATION. — Table 1 demonstrates considerable variation in the weight of worms (+ tubes) accumulating on weekly panels which does not appear to be related to settlement density. Increase in weight of

TABLE 1. — Tube accumulation (g dry weight) of *F. enigmaticus* on weekly panels.

Immersion Date	Settlemennt ($x10^6 . m^{-2}$)	Dry weight of tubes	Weight Increase (/day)
13-21.06.84	12.1	3.24	0.40
21-27.06.84	10.6	2.57	0.43
04-12.07.84	8.5	8.76	1.09
20-27.07.84	5.5	1.11	0.16
10-16.08.84	6.3	1.58	0.26
16-23.08.84	8.7	6.84	0.98

seasonal panels also fails to reveal any trend (Table 2). There is again no apparent relationship between weight increase and initial settlement density in the long term although, in 1983, the later panel (12.8.83) initially increased in weight more rapidly which may reflect the greater settlement density. This, however, is not supported by the different initial settlements in 1984. In both 1983 and 1984 the initial low settlements were probably augmented by much greater settlements within three weeks (Table 2).

The explosive increase of *F. enigmaticus* in 1982/83 encouraged a considerable increase in the number of shore crabs (*Carcinus maenas L.*) within the pond which resulted in predatory damage to both the naturally–occurring aggregates and those on the panels, seriously affecting the late season accumulation.

DISCUSSION

SEASONAL SETTLEMENT. — Settlement is confined to summer/autumn when the minimum bottom temperature is > 10 °C (THORP, 1987) which contrasts with a minimum of 18 °C in the Thames Estuary (DIXON, 1981). In the first four years (1982–85) prodigious settlements occurred but it is possible to observe the onset of the 1986–88 decline during 1985. In that year only three weekly panels attracted more than $1 \times 10^6 . m^{-2}$ in contrast to 9, 6 and 11 panels in the previous three years respectively. The cause of the reduced settlements can be deduced from the physical conditions prevailing throughout summer/autumn 1985. Through April, and particularly May, 1985 little or no sunshine prevented any phytoplankton increase. Strong sunshine in the last week of May, however, resulted in a rapid increase in visible phytoplankton levels which probably triggered spawning, with small settlements in the first two weeks of June. This was followed by settlements > $2 \times 10^6 . m^{-2}$ in July and a subsequent decline until late September. The sunny period of late May/early June was followed by a long period of poor summer weather during which pond water clarity suggested very low phytoplankton levels. In mid–September 2–3 weeks of better weather promoted a small plankton increase. As the bottom water temperature was > 10 °C throughout this period it is probable that the decline in settlement can be attributed to low phytoplankton levels. The "events" of the 1985 summer most probably led, at least in part, to the catastrophic decline of the adult population in March 1986. Overwintering adults withdraw to the lowermost levels of their tubes during cold winters and assume a state of torpor (ZIBROWIUS & THORP, 1989). Consequently, organic and inorganic debris settling from the water column accumulate within upward–facing tubes and must be cleared before normal activity can be resumed. That this does not always happen is inferred from aggregates where the central area, containing the upward–facing tubes, dies out leaving the more oblique and lateral–facing tubes to form atoll–like structures. It is probable that, with winter inactivity and zero phytoplankton levels, *F. enigmaticus* has to overwinter on reserves built up over the previous summer/autumn. The low phytoplankton levels through 1985 could have resulted in reduced somatic reserves for overwintering, causing weakened animals, unable to clear their tubes, to perish. KNIGHT–JONES & MOYSE (1961) reported that gregarious animals can assume a growth form to maximise their feeding potential, and it is this strategy which results in *F. enigmaticus* tubes being evenly spaced and their feeding apparatus (branchial crown) deployed to its best advantage. In practice the branchial crowns of adjacent animals are contiguous, largely preventing the settlement of larvae or sediment within the aggregates. While the longevity of *F. enigmaticus* remains unclear it is possible that by 1986 the aggregates comprised animals which were 4–5 years old. This is based on the likelihood that there is little or no secondary settlement as long as the aggregates maintain their integrity and also, that the limited hard substrata within the pond complex were rapidly occupied. Thus "old age" and a lack of overwintering reserves could have resulted in debility which led to the massive mortality.

TABLE 2. — Tube accumulation (Kg wet weight) of *F. enigmaticus* on nseasonal panels. Is: Initial settlement density. Is+3: Additional settlements withing 3 Is. c : Crab predation of tubes.

Immersion Date	Weeks Immersion						Max. Wt	Is (10^6. m^{-2})	Is+3 (10^6. m^{-2})
	2	4	9	10	12	15			
14.07.83		1.2	4.8	6.3	7.5	9.3c	9.4	0.81	2.1/9.6
12.08.83		2.2	5.0	5.1	5.1c		5.2	11.97	7.1/13.4
17.05.84			2.4	3.2	4.5c	5.4	5.4	0.94	3.3
27.06.84		1.2	3.3	3.4c	3.5	3.6	3.7	0.21	8.5/13.5
27.07.84	0.5	1.0	1.8		1.5c		1.8	2.12	6.3/8.2
05.06.85		0.5		1.2	1.9	2.3c	2.6	0.15	-
07.06.90		0.5	2.5	3.0	3.4c	3.2	3.4	0.18	0.2
09.07.91			1.2	1.4	1.5c	1.5	1.5	2.54	-
08.05.92		0.5	0.6					0.11	0.59

Through 1986–88 a few adults must have survived to provide the small settlements observed, but these years were also notable for low phytoplankton levels. The years 1989–91 not only witnessed very hot and prolonged summers, particularly 1989, but also increased and extended phytoplankton "blooms". Consequently, not only did the breeding season of *F. enigmaticus* increase in length, but maximum settlements increased, with four weekly counts > 1 x 10^6. m^{-2} in 1991.

It was expected that 1992 might witness a population explosion. Thick and prolonged ice–cover in February 1991, while it may have caused considerable mortality in the adult population, crushed the remaining "dead" aggregates freeing additional hard substrata. After good settlements in mid–May, which accompanied high phytoplankton levels, settlement declined markedly in July. While this failure can be associated with a 'crash' in the phytoplankton level it can not be related to reduced sunshine levels. It does, however, appear to be associated with the very heavy growth of *Ulva lactuca* which developed on the bottom of the pond from early June. HIMMELMANN (1980) reported the significance of phytoplankton levels in the synchronisation of spawning in marine invertebrates and, while the *Ulva* undoubtably `blanketed' the existing aggregates its true effect probably was to greatly reduce the nutrients available to sustain the phytoplankton and consequently remove an essential spawning trigger. While *Ulva* featured in the millpond as shortlived, dense growths in previous years, notably 1991 (THORP, unpublished data), it was the density and prolonged nature of the 1992 growth that was significant. With 1992 being the fourth 'dry' year in succession in Britain the fresh water flow from the River Ems has been greatly reduced bothnaturally and through increased abstraction by the local water authority. Consequently the weekly bottom water salinity only fell below 20 twice in 1992 (Jan/July). Seawater entering the millpond is probably high in dissolved nutrients, as a result of the high sewage effluent loading of the adjacent and connected Langstone Harbour (Portsmouth Polytechnic, 1976). THOMAS (1987) also referred to localised increases in organic pollution in Chichester Harbour arising from both small sewage discharges and land drainage from the surrounding agricultural land. Not only do point discharges occur in the area of the harbour adjacent to the millpond but the River Ems also drains a considerable area of farmland. Thus *Ulva*, which grows prolifically in Langstone Harbour, has been able to flourish in relatively high salinity, warm, nutrient–rich water at the expense of possibly brackish water phytoplankton species.

TUBE ACCUMULATION. — Mass formation of serpulids has been variously attributed to a complex of environmental factors including competition for space and food; reduced predation; gregarious behaviour; larval retention; primary productivity and hydrographic factors such as temperature and salinity (SCHROEDER &

HERMANS, 1975; BOSENCE, 1979; HOVE, 1979). Significantly HOVE (1979) also stated that decreased competition with other animals, mainly for space, may lead to massive numbers in species at the periphery of their ranges. In optimum conditions the millpond embraces all these factors, acting as a brackish lagoon and experiencing elevated temperatures, limited substrate availability and high primary productivity. The tide–gate control of water level will encourage larval retention and there are no major competitors for space or food. It is rather the success of *F. enigmaticus* which creates the problems.

While the length of settlement season is governed by temperature, tube accumulation within seasons may be affected by both food availability and initial settlement density. Tube accumulation in both 1983 and 1984 can be related to the length of the immersion period (Table 2) and there appears to be some support for the idea that initial settlement density is involved within years, cf. 14/7 and 12/8 in 1983 particularly at 9 weeks. Similar data for 1984 (15/5 and 27/6), however, more likely reflects the high subsequent settlements on the 27/6 panel. In the absence of phytoplankton data it is difficult to comment on the effect of food level, although the 1985 panel (5/6) suggests a strong connection. While the low rate of accumulation in 1985 may reflect the small initial settlement ($1.5 \times 10^5 . m^{-2}$) when compared to the 1990 panel (7/6), it may well result from the low phytoplankton levels observed in 1985. Heavy metal levels in Chichester Harbour will be very low (THOMAS, 1987) and unlikely to have any deleterious effect. Although there are >8,000 small boats (98.7% < 12 m in length) moored or berthed in marinas in the harbour, as 74 % (2,115 ha) of the total harbour area (2,849 ha) is intertidal (Chichester Harbour Conservancy, pers.comm), it is probable that tidal flushing greatly reduced any effects of organo–tins prior to the ban on their general use in antifouling paints in 1987.

The overall pattern, of population proliferation followed in turn by a catastrophic decline and subsequent recovery, possibly represents the normal pattern in a species with great fecundity, relative longevity and occupying a habitat with limited available substrata. Indeed BOSENCE (1979) stressed the importance of limited substrata in the rapid build–up of tube aggregates in *Serpula vermicularis*. Massive settlement of *F. enigmaticus* would quickly occupy all available hard substrata within perhaps one or two seasons and the close packing and disposition of the tubes would prevent significant recruitment and lead to an ageing population prone to disaster. It is suggested that disaster struck due to a lack of overwintering reserves resulting from the poor summer of 1985. Thus, gregarious species with an epidemic spawning capacity could be expected to exhibit an alternating pattern of success and decline. In this respect it is interesting to note that the invasive serpulid, *Hydroides ezoensis* Okuda, exhibited a similar, if partial, population decline in Southampton Docks in 1987/88. *H. ezoensis*, first recorded as a single specimen from the intake channel of Fawley Power Station, Southampton Water, in 1977, formed massive encrustations (30cm thick) in the intertidal region of most dock structures (THORP *et al.*, 1987). The population on the Town Quay, however, died and sloughed off in 1988/89, this event preceding demolition and reconstruction of the quay (THORP, unpublished data).

KEENE (1980) and DAVIES *et al.* (1989) both reported an apparent beneficial interrelationship between populations of *F. enigmaticus* and sediment and nutrient levels within semi–enclosed waters. Circumstantial evidence from the present study suggests a similar relationship within the Slipper pond where high phytoplankton levels complement high settlement densities. While it is truly a "chicken and egg" situation as to which comes first, elsewhere it has been shown that the overall economy of the pond can be related to the success of *F. enigmaticus* (THOMAS & THORP, 1994).

ACKNOWLEDGEMENTS

I am happy to acknowledge the kindness that the trustees and members of the Slipper Millpond Preservation Association have extended towards me in allowing me to work in the pond. I am also indebted to Havant Borough Council, and particularly Alistair MARTIN, for making the Hayling Island, Beachlands, meteorological records available to me. I also acknowledge the assistance of James HEPBURN in making this a more complete record by covering some of my absences.

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