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**The ecology and reproductive cycle of a population of
Marenzelleria viridis (Annelida: Polychaeta: Spionidae) in the Tay
Estuary**

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Synopsis

The occurrence of a population of the spionid polychaete *Marenzelleria viridis* (Verrill 1873) in the middle reaches of the Tay Estuary is reported. This is a new British and European record of a North American species, and its principal characteristics are described and compared with earlier accounts. Size frequency analysis of the population showed it to be dominated by large animals from July 1984 to May 1986. The population matured coelomic gametes during winter 1985-86 and spawned in March 1986 to produce a heavy settlement in May, which subsequently grew rapidly. The distribution of *M. viridis* in relation to other species, sediment and other ecological parameters is described from a single survey of the Invergowrie Bay mudflats. *Marenzelleria* population densities of up to 1500 m^{-2} were negatively correlated with all other species of a low diversity macrofaunal community dominated by predatory polychaetes and filter feeding bivalves. *Marenzelleria* was abundant down to sediment depths of 20-30 cm. The significance and origin of this population is discussed.

Introduction

The biological characteristics of the Tay Estuary have been described by Khayrallah & Jones (1975). During a survey of the intertidal sand and mudflats of Invergowrie Bay in 1984, the typical estuarine communities were found to contain a population of a large spionid polychaete not previously recorded from Britain. The species *Marenzelleria viridis* (Verrill 1873) has been recorded only from the northeastern coasts of America (Maciolek 1984) and this paper describes the morphology, life cycle and ecology of this isolated population. A very similar animal from the Forth Estuary was provisionally identified as *M. wireni* Augener 1913 (Elliot 1983).

Materials and methods

The ecological survey was based upon six transects sampled in July 1984 radiating out from a central point (the discharge point of a major sewage outfall) as shown in Figure 1. Stations were established at 25 m intervals on each transect and at each station a single core with a surface area of 0.05 m^2 was taken to a depth of 30 cm. The cores were sieved in seawater on site using a 1 mm mesh diameter sieve and the

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$\frac{\text{cm}^3}{\text{sec}}$

992 P_L (m^3/year)

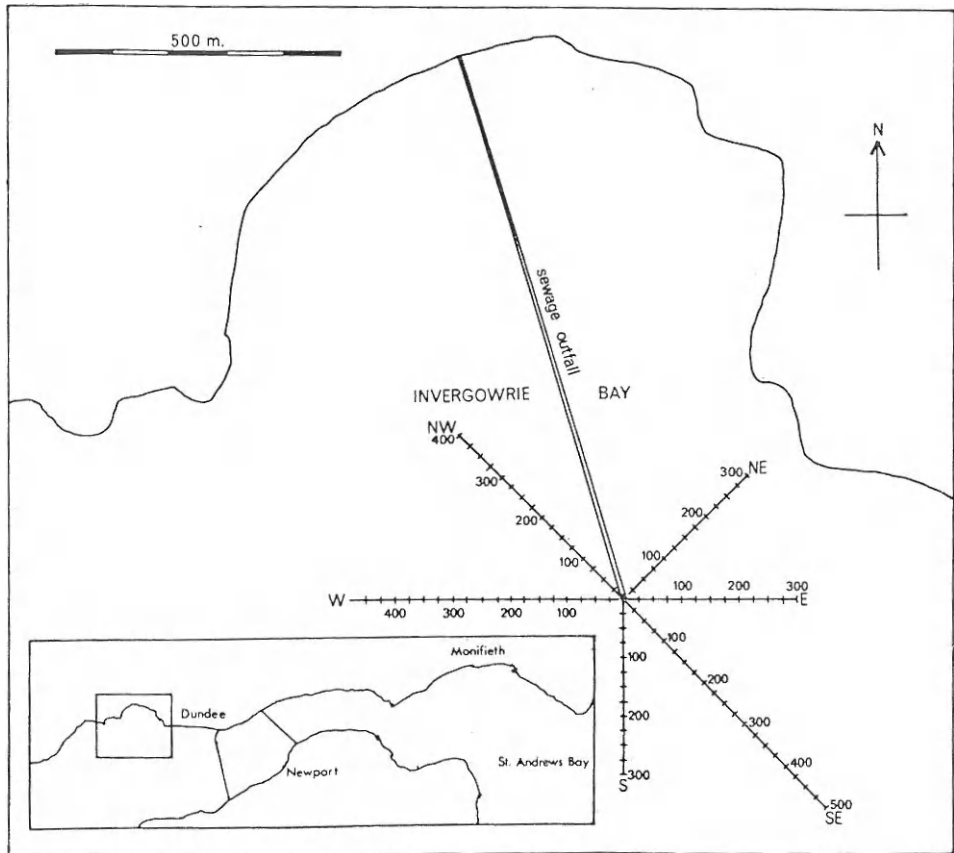


Figure 1. Map of Invergowrie Bay in the Tay Estuary, showing the sewage outfall, transects and sampling stations.

retained material fixed in 10% buffered formaldehyde solution. The fauna was hand-sorted in the laboratory and species identified and counted using a binocular microscope.

The sediment data consisted of granulometric analysis, organic carbon content and levels of shell material computed according to Buller & McManus (1979). Granulometric analysis was determined for samples collected at 25 m intervals also, while organic carbon and shell contents were measured at alternate stations only (i.e. every second macrofaunal station) on each transect.

Subsequent sampling for studies of population structure and life cycle was carried out during 1985–86 using an identical sampling procedure at the 200 m station on the southeast transect (Fig. 1), a region of maximum abundance of *Marenzelleria*. At approximately two monthly intervals twelve replicate samples were taken for local assessment of density variations, two of which were divided into 3×10 cm sections for studies of the vertical distribution of the population. Sampling frequency was increased to fortnightly intervals during the spawning and settlement period when two meiofauna samples were also collected to obtain first indications of a new recruitment. The latter were collected using a 5 cm diameter coring tube to a depth of

15 cm, and meiofauna was extracted after staining with rose bengal by swirling and decanting through a 63 μm mesh (Gray & Reiger 1971). Population structure was determined for each sample by measuring the body width of the tenth setiger of each adult individual and the maximum body width of juveniles with less than fifty setigers, using an eyepiece graticule in an Olympus Zoom stereomicroscope. This parameter has been shown to be very highly correlated with ash-free dry weight for a range of polychaete species including spionids (Warwick *et al.* 1978; Rees 1983; Atkins 1985).

Shannon diversity (H) and the related evenness index (J) were calculated for each sample after log transformation of the data. Statistical analyses including Pearson's correlation coefficient (r) were calculated on a BBC microcomputer using the UNISTAT programme (University software).

Results

Site description

Invergowrie Bay is located in the inner reaches of the Tay Estuary (Fig. 1). The beach in this region consists of almost level sand and mud flats at about mean tide level (MTL); the sediment is composed of various mixtures of mud, sand and gravel, and sediment parameters are summarised in Table 1. All transects began in a localised area of muddy gravel surrounding the sewer outfall point, thereafter rapidly grading into more typical fine sands and muds with increasing distance from the outfall. The sediments of the west, northwest and northeast transects were muddy throughout their length, with increased proportions of fine grades towards high water mark. The south, southeast and east transects became progressively coarser and comprised well-sorted coarse sand towards the main channel. Despite the proximity to a major sewage outfall only moderate levels of organic matter were recorded (Table 1) and the sediment in the *Marenzelleria* population area was characterised by the absence of a true black layer. A uniform graying, only, of the sediment was present, indicating significant interstitial circulation.

Table 1. Grain size parameters of Invergowrie Bay sediments (data supplied by J. McManus)

	Mean	S.D.	Min	Max	n
Percent silt and clay (< 63 μm)	7.46	5.29	0.3	17.8	86
Median grain size	143.9	11.65	123	178	86
Percent organic matter	3.98	2.44	0.1	10.3	36
Percent shell material	5.27	5.22	1.04	34.3	44

Systematics and external morphology

A full review and diagnosis of the genus *Marenzelleria* was conducted by Maciolek (1984) in which *Scolecopides viridis* (Verrill) was transferred to the genus *Marenzelleria* on the basis of the absence of ventral acicular chaetae in anterior setigers which are present in the genus *Scolecopides*. Of the three species of *Marenzelleria* described by Maciolek (1984) the Invergowrie specimens most closely resemble *M. viridis*. The description below records the principal similarities and differences and is, therefore,

not a complete taxonomic treatment. Further taxonomic studies of the Scottish *Marenzelleria* specimens are currently being undertaken by one of the authors (PRG).

The worms are cream to dark green in colour and are typically darker anteriorly. They are large worms up to 68 mm long and 2 mm wide and with more than 200 setigers in the largest specimens. The prostomium has a slightly curved anterior edge, sometimes with a small median notch, and is expanded laterally to give a bell shape (Fig. 2A). The prostomium extends back to setiger 1 medially, bearing four eyes in a trapezoid arrangement and on each side a nuchal epaulette extends from the posterior margin of the prostomium to setiger 2. The nuchal organs are often well pigmented although in some fixed specimens they may be difficult to see. The peristomium is distinct and slightly expanded; the pair of short palps bear pigment spots and in fixed specimens reach back to setiger 5, as compared to setiger 8–10 in Maciolek's specimens. The branchiae begin on setiger 1 and, in anterior setigers, they are long and straplike and coloured red to dark brown. They are best developed in the first forty to fifty setigers, extending well beyond the midline for approximately ten setigers and are thus larger than described by Maciolek. They are basally fused to the notopodial post-setal lamella (Fig. 2C,D), decreasing in size from setigers 40–50 until they disappear at about setiger 100.

Notopodial post-setal lamellae are broadly oval, extending on to the dorsum; neuropodial post-setal lamellae are of a similar shape anteriorly. Both are reduced in posterior segments. Pre-setal lamellae are present as distinct ridges, at least anteriorly. Each segment is biannulate with two rows of distinct cells probably bearing cilia. The positions and types of capillary chaetae are broadly similar to Maciolek's description with minor differences. The first setiger bears chaetae of two types, an anterior row of relatively short limbate granular capillaries and a posterior row of longer thin capillaries. Dorsally on the notopodium is a group of five to six long capillaries which are anteriorly directed. On all setigers a group of capillaries is recognisable in this dorsal position. Strongly curved granular sabre chaetae are present from setiger 4, numbering two to four per parapodium. Bidentate hooded hooks (Fig. 2E) begin on the neuropodium from setigers 30–50 and on the notopodium from setigers 50–60 in adult animals. One to two hooks are present anteriorly, increasing to a maximum of eight dorsally and twelve ventrally. They are thus present more posteriorly and in greater numbers than in Maciolek's specimens. Both the setiger on which the hooded hooks first appear and the number of hooks in each parapodial ramus are dependent on the size of the specimen. The number of hooks decline in posterior setigers and are absent from the last six to eight, where only capillaries are found. The pygidium is bluntly rounded and bears about ten short cirri; the posterior end of the animal is extremely fragile and few intact specimens were collected.

Of the three described species of the genus *Marenzelleria* (Maciolek 1984) the Tay specimens most closely agree with *M. viridis*. The differences between *M. viridis* and *M. wireni* are, however, small and further work is planned to establish whether or not the two are synonymous.

A heavy recruitment of juveniles was observed in early May 1986 and the smallest animals were very recently settled (see below). They were typically ten to twenty setigers in length (2–3 mm) and closely resembled the adults in most important respects. The characteristic bell-shaped prostomium with median notch is conspi-

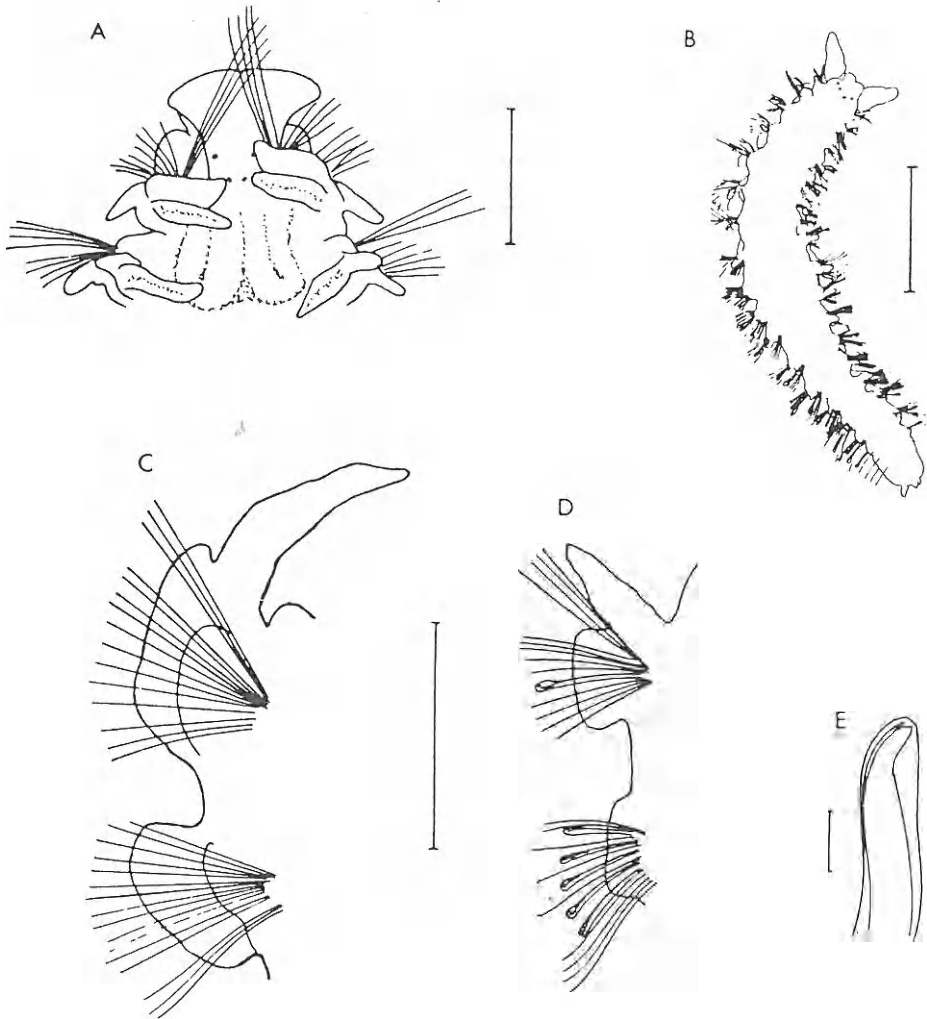
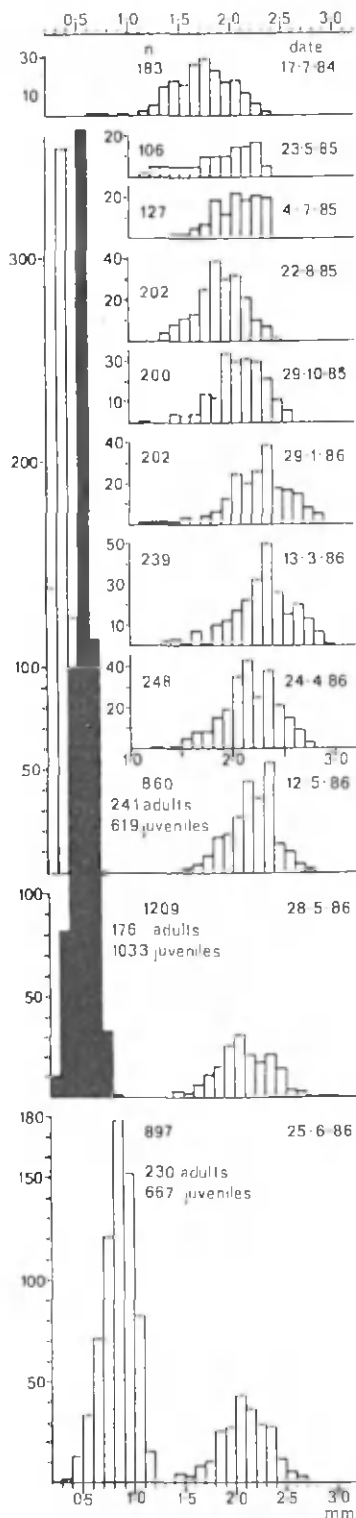


Figure 2. *M. viridis*
 (A) Prostomium and anterior setigers with epaulettes, anteriorly directed setae and large branchiae.
 (B) Seventeen setiger juvenile, drawn from slide showing hooded hooks.
 (C) Anterior view of the right parapodium at setiger 30 (note absence of hooded hooks).
 (D) Anterior view of right parapodium at setiger 60, showing small branchiae and hooded hooks.
 (E) Detail of hooded hook with bifurcate tip.
 (A, B, C and D, bar = 0.5 mm; E, bar = 0.015 mm).

cuous, as are the large branchiae declining in size posteriorly (Fig. 2B). Short curved sabre chaetae and long thin capillaries are present on anterior segments, while bidentate hooks commence in pairs in the neuropodium on setigers 8–10 and continued to the last well developed setiger. There are four to six cirri on the pygidium.



Size-frequency analysis of the *M. viridis* population in July 1984, and from May 1985 to April 1986, showed a stable unimodal population of large adult animals (Fig. 3). Mean body width in July 1984 was 1.78 mm and was 2.07 mm in July 1985. The size range (1.2 mm–3.0 mm) was similar throughout this period, although a few smaller animals were collected in July 1984. There was no evidence of a significant recruitment in any of these samples. Examination of the coelomic fluid revealed no evidence of gametogenesis in any specimens prior to September 1985, but development appeared to have begun in some specimens collected in late October 1985. By 29 January 1986, approximately 70% of both males and females were maturing coelomic gametes, and these percentages had increased to 78% and 85% respectively by 13 March. Most animals were gravid on this date and oocytes and spermatocytes appeared mature, most of the latter not clustered in sperm morulae but free swimming in the coelom. On 31 March, 80–90% of individuals had spawned all or part of their coelomic gametes, the majority appearing spent with the exception of a few males retaining small quantities of sperm. No juveniles were found in meiofauna or 0.5 mm mesh sieved samples on 31 March. Similar results were obtained from 24 April samples. The first juveniles of a new settlement were detected on 12 May at a density of approximately 1000 m⁻². Despite the small size of these individuals (2–3 mm length for ten setigers) they were collected in similar numbers by both the 1 mm and the 0.5 mm sieves, the smallest specimens being retained by the coarser mesh. The maximum recorded numerical density of the new cohort was on 28 May, indicating that settlement had continued beyond 12 May, although few individuals occupied the two smallest size classes by the later date (Fig. 3). The mean body width increased by 50% (0.40–0.59 mm) during the same period, demonstrating a high initial

Figure 3. Size frequency distributions of *M. viridis* obtained from body width measurements of all animals collected on each date from a sampling area of 0.6 m².

Table 2. Numbers of adult *M. viridis* at three sediment depths in paired cores on seven different occasions

Date	4-7-85		28-8-85		29-1-86		13-3-86		24-4-86		12-5-86		28-5-86		Total
Depth	1	2	1	2	1	2	1	2	1	2	1	2	1	2	%
0-100 mm	6	9	8	17	1	1	0	3	0	2	2	12	1	3	24.2
100-200 mm	5	15	6	13	9	2	8	4	8	12	9	7	5	6	40.5
200-300 mm	0	4	1	2	10	9	17	4	8	5	5	8	8	12	35.3

growth rate. The adult population remained stable numerically, despite the appearance of the juvenile cohort.

Results from the samples divided into vertical sections are shown in Table 2. This shows that 75% of the adult population was consistently found at depths greater than 10 cm and 35% were more than 20 cm deep. Small numbers of *Nereis diversicolor* (about 5% of the population) and occasional large *Mya arenaria* were also found down to 20 cm but, these excepted, no other macrofauna occurred below 10 cm. 80-90% of the juvenile cohort of *Marenzelleria* were consistently found in the upper 10 cm of sediment.

Ecology

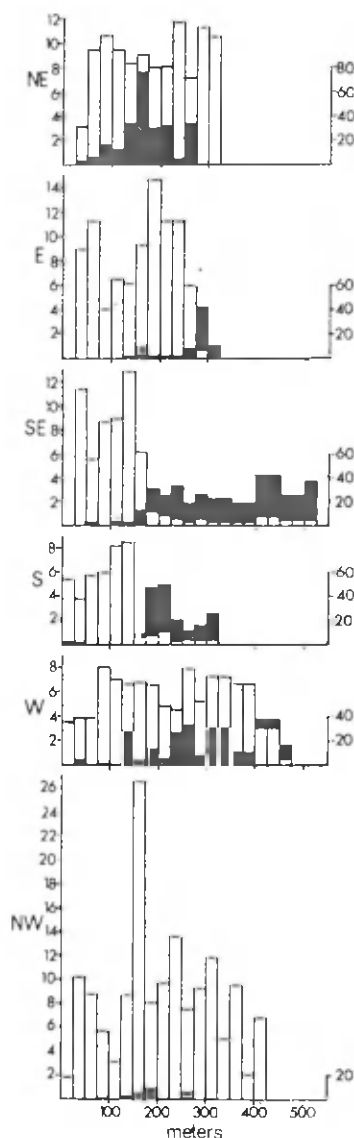
Table 3 gives the mean densities, standard deviations and value ranges of the eight common macrofaunal taxa found in this habitat during the 1984 survey. The community was dominated numerically by *Corophium volutator*, *N. diversicolor* and Oligochaetes, these groups being an order of magnitude more abundant than the others. Occasional or rare species also found are listed in Table 4. Numbers of all the polychaete species except *M. viridis*, of Oligochaetes and of *C. volutator* all tended to reach a peak a short distance (50-150 m) from the sewage outfall. This basic pattern was complicated or obscured for some species and on some transects, however, by the high levels of organic matter present along the entire transect lengths and/or by variations in the sediment character. The total numbers of individuals along each of

Table 3. Statistics of common species abundances and community parameters calculated using data from all eighty-six macrofaunal samples

	Mean	s	Min.	Max.	Patchiness
<i>Marenzelleria viridis</i> Verrill	11.93	15.26	0	76	19.51
<i>Pygospio elegans</i> Claparède	10.98	14.05	0	66	17.97
Oligochaeta	84.26	93.06	0	397	4.71
<i>Nereis diversicolor</i> O.F.Müller	111.56	87.95	0	356	69.34
<i>Eteone longa</i> Fabricius	6.97	7.01	0	35	7.24
<i>Corophium volutator</i> (Pallas)	183.5	297.7	0	824	4.49
<i>Mya arenaria</i> Linnaeus	7.41	6.41	0	24	3.24
<i>Macoma balthica</i> (Linnaeus)	6.36	4.15	0	17	2.67
Number of species	7.98	1.19	5	12	
Number of individuals	619	449	18	2655	
Diversity (H)	1.12	0.27	0.19	1.84	
Evenness (J)	0.55	0.13	0.28	0.86	

Table 4. Occasional species collected in Invergowrie samples

Crangon vulgaris (Linnaeus)
Gammarus sp.
Bathyporeia sp.
Cerastoderma edule (Linnaeus)
Hydrobia ulvae (Pennant)
Lepidochitona cinereus (L.)
Arenicola marina (Linnaeus)
Capitella capitata (Fabricius)
 Nematoda



the six transects (Fig. 4) reflect the distributions of the dominant species. The numbers of species per station were low and were fairly consistent along each transect, except where the overall community character changed as a result of sedimentary parameters changing; thus on the south and southeast transects (Fig. 1), a sharp drop in total numbers and number of species was recorded some 150 m from the outfall as a result of an abrupt decrease in the levels of silt and clay and organic matter in the sediment.

Both the species individually and the whole community tended to be well correlated with sediment parameters (Fig. 5 and Table 5). Six of the eight common taxa were highly significantly ($P < 0.01$) positively correlated with the percentage of silt and clay and four species were highly significantly ($P < 0.01$) negatively correlated with median grain size. Only *M. viridis* was negatively correlated with the percentage of silt and clay and only *M. viridis* and *Eteone longa* were positively correlated ($P < 0.01$) with median grain size. Correlations with organic content and with shell content of the sediments followed similar trends, although these correlations were not statistically significant ($P > 0.05$). Only *M. viridis* was negatively correlated with organic content, while most other species were negatively correlated with shell content. The species richness increased slightly with increasing silt and clay content, but declined with increases in other sediment parameters, while diversity and evenness were highly significantly ($P < 0.01$) negatively correlated with silt and clay content.

Figure 4. Numbers of animals at each station along each transect; left hand scale: total individuals (hundreds 0.05 m^{-2} —unshaded); right-hand: numbers of *M. viridis* (0.05 m^{-2} —shaded).

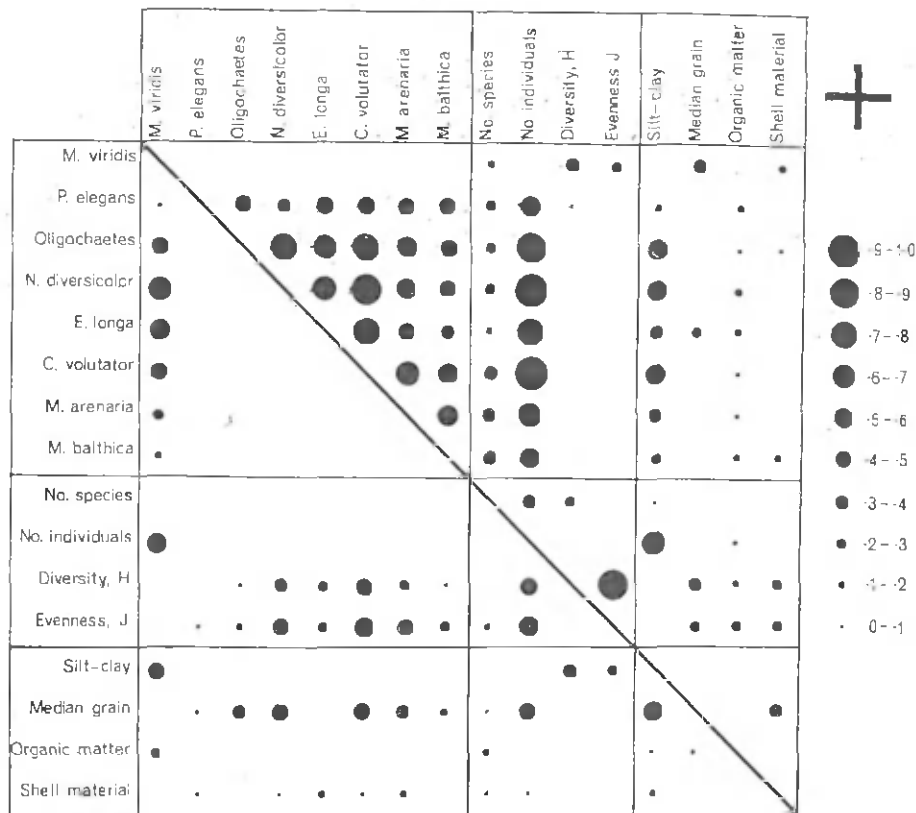


Figure 5. Pearson's correlations between dominant species, community and sediment parameters, showing relative size and sign of each coefficient and separation of *M. viridis* from other species (see text).

Shannon diversity values were low, reflecting the low species richness in the habitat, although evenness was high as a result of the low dominance in the community. The eight common species were all somewhat under dispersed and patchiness indices (s^2/\bar{x}) ranged from 2-70. The values for five of the species were less than ten and only *N. diversicolor* was relatively highly aggregated. Table 5 also shows Pearson's correlation coefficient calculated pairwise between species densities and sample community parameters. All correlations between species were highly significant ($P < 0.01$) except for that between *M. viridis* and *Pygospio elegans*. These correlations were all positive with the exception of those with *M. viridis* which was found to be negatively correlated with all other species. Correlations between the community parameters (numbers of species and individuals, diversity and evenness) and each species produced similar results with *M. viridis*, showing a very different correlation to that of all other species.

Table 5. Actual correlation coefficients from Figure 5, with significance levels: * = significant at $p=0.05$, ** = significant at $p=0.01$; $n=86$ for species and community parameters, $n=44$ for correlations with organic carbon levels and $n=36$ for correlations with shell content

	<i>M. viridis</i>	<i>P. elegans</i>	<i>Oligochaeta</i>	<i>N. diversicolor</i>	<i>E. longa</i>	<i>C. volutator</i>	<i>M. arenaria</i>	<i>M. balthica</i>	No. species	No. individuals	Diversity H	Evenness J	Silt-Clay	Median grain	Organic matter	Shell material
<i>M. viridis</i>									.14	.33	.27		.34			.16
<i>P. elegans</i>	.09		.49	.37	.47	.50	.43	.42	.28	.51	.01		.19		.10	
<i>Oligochaeta</i>	.44			.72	.63	.78	.56	.47	.27	.81			.59		.10	.06
<i>N. diversicolor</i>	.58				.69	.86	.59	.42	.23	.90			.58		.17	
<i>E. longa</i>	.53					.70	.45	.31	.17	.72			.34	.28	.13	
<i>C. volutator</i>	.49						.68	.59	.30	.96			.57		.07	
<i>M. arenaria</i>	.23							.51	.36	.68			.38		.09	
<i>M. balthica</i>	.18								.39	.56			.29		.11	.11
No. species										.34	.20		.06			
No. individuals									.53				.61		.03	
Diversity H			.07	.39	.21	.43	.27	.09		.44		.84	.33	.19	.22	
Evenness J		.07	.12	.46	.24	.53	.41	.21	.18	.56			.27	.24	.30	
Silt-Clay	.43										.32	.28				
Median grain		.09	.38	.45		.40	.34	.17	.05	.41			.58			.36
Organic matter		.01							.18				.04	.01		
Shell material		.01	.09	.12	.01	.12			.03	.15			.12			

Discussion

M. viridis has only previously been recorded from a range of sites on the North American eastern seaboard but not in large numbers (Maciolek 1984). Results for the Invergowrie population present the first quantitative data on density of this species, and suggest that the densities in the Tay Estuary may be among the highest known. The morphological differences recorded between the three species of the genus are small and the specimens from the Tay Estuary also show subtle differences from the

published descriptions of *Marenzelleria* species. The significance of these differences is not yet established, but the authors do not regard them as indicating the Tay specimens belong to a new species; indeed, the separation of *M. viridis* and *M. wireni* is questioned.

The present data indicate a breeding cycle for this species in 1985–86 in the Tay Estuary commencing with gametogenesis in late October which was completed by late February. Spawning took place during March and settlement commenced in early May. Thus the planktonic stage was a minimum of four weeks but may have extended to approximately eight weeks (March and April), and metamorphosis took place at approximately the ten setiger stage. Reproduction and early development of *M. viridis* (as *Scolecopelides viridis*) from Nova Scotia was described by George (1966), who included adult and juvenile morphology with which the present observations and Maciolek's (1984) description are in close agreement. Spawning and settlement may have occurred rather earlier in the Nova Scotia population, although this could be due to annual or geographical variability. The overall reproductive cycle was very similar. George's conclusion that since all worms were gravid at the same time, the species must reach maturity in less than one year was also supported by the high growth rate in the Tay population, but the population structure (Fig. 4) indicates that successful recruitment has occurred only once in the three years 1984–86.

George further reported that early development was not affected by low salinities (10–30‰) and the persistence of this isolated population at Invergowrie where the salinity range of the overlying water is 6–21‰ and that of the interstitial water is 8–11‰ (R. Herbert, pers. comm.) requires this euryhaline reproductive capability. The persistence of this population in an estuary with a very short residence time and a very large mixing rate (Williams & West 1973, 1975) suggests that the life cycle should have a reduced or absent planktonic phase: a geographically isolated, estuarine population of a short lived species would not be expected to persist if larvae were dispersed in the plankton of an estuary such as the Tay. However, *Marenzelleria* does possess an extended planktonic phase of four to eight weeks during which the majority of larvae must leave the inner and middle estuary. The mechanism by which animals are retained in or return to the habitat is not understood.

The presence of this local and isolated population suggests that it has been introduced. Evidence of this is provided by the correlation data which clearly show that *Marenzelleria* is unique in this macrofaunal community in that it is negatively correlated with all other common species which were all otherwise positively correlated with each other. This suggests that *Marenzelleria* does not play an active role in this otherwise typical estuarine community. The sediment binding effect of its tubes evidently had no positive effect on other sediment stabilisers such as *P. elegans* or *C. volutator* as described for other spionid communities (Atkins 1985) and it was apparently not exploited preferentially by any predator. It also showed an opposite correlation to all other species with respect to sediment parameters and was found at substantially greater depths. Thus *M. viridis* is separated from the rest of the community by either or both its ecological requirements and its interspecific interactions.

The methods by which this species could have been introduced into the Tay Estuary are intriguing but must remain speculative. If the North American temperate, estuarine *M. viridis* is indeed distinct from *M. wireni*, an Arctic form known from

Europe and North America, then the Tay population must have originated from eastern North America. It seems most unlikely that any natural process could have transported it across the Atlantic Ocean, yet it is not possible for this infaunal species to have been carried by attachment to the exterior of modern shipping. It is conceivable that it could be transported in the ballast water taken on board a vessel in a North American estuary and subsequently discharged into the Tay Estuary; support for this hypothesis may be found in the record of five specimens having been collected in a plankton tow in a North American estuary (Maciolek 1984). If, however, the two forms are synonymous, then an origin in the European Arctic is possible and natural processes may be sufficient to account for the presence of the Tay population.

Acknowledgments

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