Michael L. ZETTLER

Universität Rostock, Fachbereich Biologie/ Allgemeine und Spezielle Zoologie

Larval settlement behaviour and habitat selection of a new established spionid polychaete *Marenzelleria viridis* (VERRILL, 1873): field and laboratory experiments

Herrn Prof. Dr. rer. nat. habil. Ernst-Albert Arndt zum 70. Geburtstag gewidmet

Abstract

Field and laboratory experiments were performed in autumn and winter 1994 to study the settlement behaviour of larval *Marenzellaria viridis*. They showed that the larvae prefer muddy (median grain size 0.149 mm, organic content 2.01 %, water content 38.62 %, silt 4.74 %) rather than sandy sediments (median grain size 0.345 mm, organic content 0.03 %, water content 17.02 %, silt 0.32 %). Their settlement behaviour is thus the opposite to that of older juveniles and adult *M. viridis*. The effects of adult *M. viridis*, adult *Hediste diversicolor* and adult *Corophium volutator* on their settlement behaviour was studied at the same time. Adult *M. viridis* and *H. diversicolor* had no significant effect, whereas sediments colonized by *C. volutator* appeared to attract larval *M. viridis* significantly (p<0,01). Possible causes of the preference for and/or avoidance of certain biotope conditions are discussed. In addition, a possible interpretation is given of the successful spreading and establishment of this immigrant spionid in European coastal waters since the mid-eighties.

Introduction

The dynamics exhibited by benthic communities are an expression of the constant interaction of the organisms with their environment. In aquatic biotopes, the presence, abundance and life cycles of species are influenced by abiotic factors such as sediment quality, salinity, water chemistry, exposure (wind, wave action, light) and oxygen content (ALLER 1980; ARNDT 1989; DANKERS & BEUKEMA 1981). However, biotic factors (predation, parasitism, competition, food availability) also have a major impact on plant and animal distribution patterns (GRAY 1974; KREBS 1994). The influence of these factors can be primary, i.e. acting during larval settlement (initial settlement), or secondary in the form of migration, predation and drifting (MEADOWS & CAMPBELL 1972; BUTMAN 1987).

Since first observed in brackish North Sea and Baltic Sea ecosystems in the early eighties, the North American spionid polychaete *Marenzelleria viridis* (VERRILL 1873) has spread rapidly in these waters and is now a dominant element of the fauna in some areas (ESSINK & KLEEF 1993; DEKKER 1991; ZETTLER 1994). The first specimens were discovered in the Darss-Zingst bodden chain, an estuary on the South Baltic coast (BICK & BURCKHARDT 1989) in 1985, and the species is now established and the most abundant macrozoobenthos species in this area (ZETTLER et al. 1995). Investigations into distribution patterns of *M. viridis* have shown that the density of settlement varies considerably (ZETTLER & BICK 1996). In particular, significant variations in the abundances of juveniles that have just settled (ZETTLER et al. 1995) suggest that the distribution and abundances of the species are governed by factors influencing larval settlement behaviour. The purpose of the work described here was to study the influence of sediment quality and the presence of a few abundant species (adult *M. viridis*, adult *Hediste* (=*Nereis*) *diversicolor* (MÜLLER, 1776) and adult *Corophium volutator* (PALLAS, 1766) on distribution patterns of juvenile *M. viridis*.

Material and methods

The field and laboratory studies into the settlement behaviour of *M. viridis* larvae were performed in autumn/winter 1994.

Field studies

The field studies were undertaken in the Darss-Zingst bodden chain, a shallow estuary on the South Baltic coast (north-east Germany) with a mean salinity of 5 ‰. The position of the station is shown in Fig. 1. Details of the investigation area are given in ZETTLER et al. (1995). In an experiment to study the influence of three sediment qualities on the settlement of *M. viridis* larvae, 36 boxes (283 cm² each) were placed in the water in late October, 1994, 18 at a water depth of 1.2 m (station KB1) and 18 at a water depth of 0.6 m (station KB3) (Fig. 2).
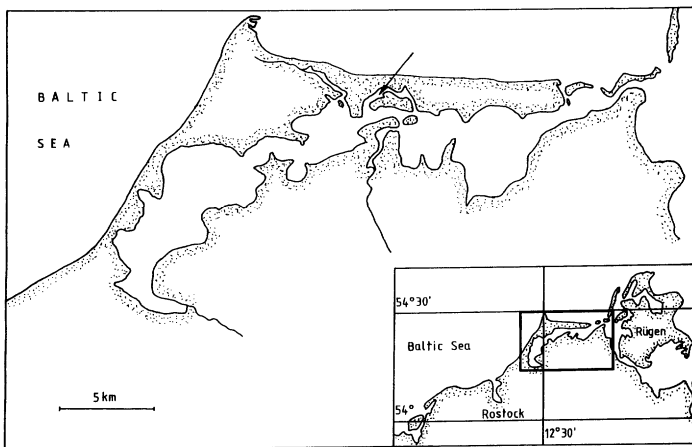
Fig. 1 Investigation area (Darss-Zingst bodden chain) showing the station used for field experiments.
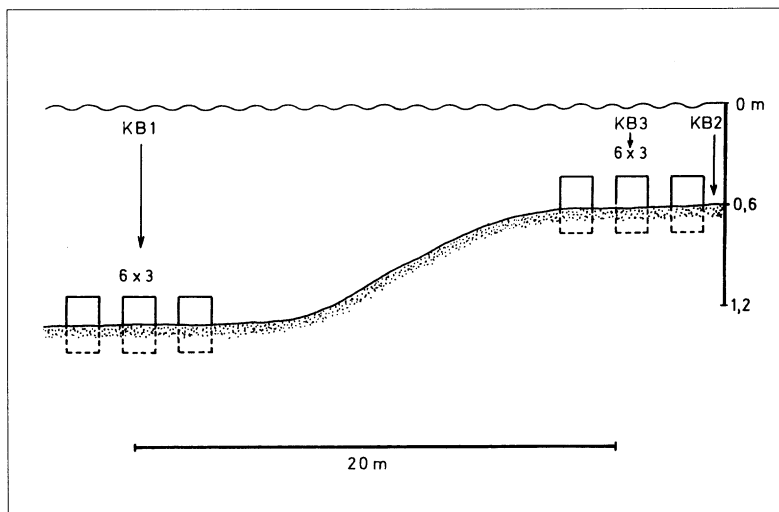

Fig. 2 Apparatus for field experiments. See text and Table 1 for further details.

Stations KB1 and KB3 were about 20 m apart. All boxes were pressed into the sediment until their sides protruded about 15 cm above the sediment surface. The sediment in the boxes at station KB1 was left in its natural state, whereas sand was added at station KB3. The substrate surrounding the boxes at station KB3 served as a control (station KB2). The three stations (KB1, KB2 and KB3) differed in respect of sediment quality (Table 1).

Table 1   Sediment properties at the three stations used for the field experiments and laboratory experiment 1

	KB1 mud	KB2 medium	KB3 sand
median grain size (mm)	0.149	0.257	0.345
organic content (%)	2.01	1.11	0.03
water content (%)	38.62	29.9	17.02
silt <0.063 mm (%)	4.74	2.14	0.32

Core samples with a cross section of 21.73 cm² were collected every 6 to 8 days from all three stations from November 3rd to December 8th 1994. Three cores (one from each of 3 boxes) were taken from all stations on each sampling date. Boxes that had already been sampled were excluded from later sampling. Earlier studies had shown that freshly settled *M. viridis* juveniles do not penetrate deeper than 3 to 5 cm (Zettler et al. 1994). Since quantitative data were required only for juveniles, the penetration depth was restricted to 6 cm and the cores were fixed as full samples in 4 % borax-buffered formalin. The samples were passed through a 0.3 mm sieve at the laboratory and the animals then sorted by hand at a 10-16X magnification.
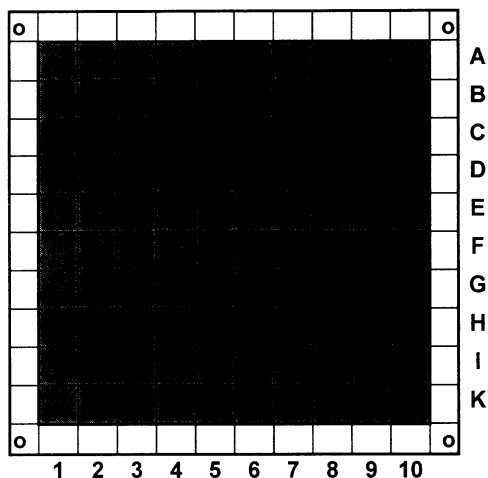
Laboratory studies

All laboratory experiments were conducted in aquariums at a salinity of 7 ‰ and a temperature of 10°C.

To study settlement behaviour under controlled conditions, a plastic grid with a height of 5 cm was placed in each aquarium (50 x 50 x 30 cm) (Fig. 3).
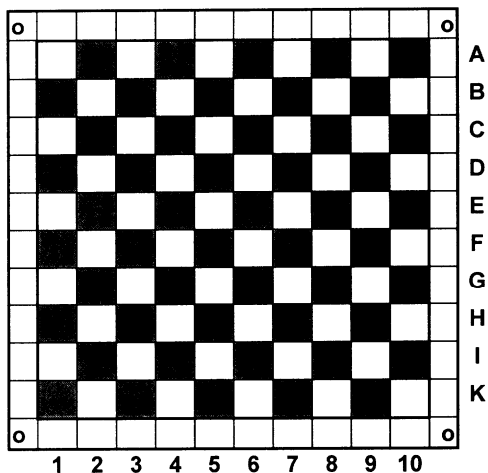
Fig. 3 Apparatus for laboratory experiments 1-4; a) abiotic parameters, b) biotic parameters; dark squares = mud, light squares = sand; aeration in corners; marginal areas excluded from the experiment.

The grid consisted of 10 x 10 spaces with an area of 16 cm² each (4 x 4 cm). To eliminate borderline effects, the boundary areas (each 3.5 cm wide) were excluded from the experiment. The aerators were in the corners of aquarium and adjusted to

avoid appreciable currents. Four experiments were conducted with this apparatus using animals taken from the Darss-Zingst bodden chain in each case. The experiments are summarized in Table 2.

Table 2   Summary of data for laboratory experiments 1-4: a = mean abundance of larval *M. viridis* at outset; b = mean abundance of settled juvenile *M. viridis*; c = initial abundance of experimental animals (VT = adult *M. viridis* in exp. 2, adult *H. diversicolor* in exp. 3, adult *C. volutator* in exp. 4); d = final abundance of experimental animals

	larvae/m³ (a)	Ø juv./m² (b)	Ø VT/m² initial (c)	Ø VT/m² final (d)
Exp. 1	901,402	42,419	-	-
Exp. 2	253,728	10,025	1,000	640
Exp. 3	285,444	10,700	400	400
Exp. 4	253,248	9,825	4,000	4,000

Influence of sediment quality on settlement [lab exp. 1]:

This experiment took the results of the field experiments into account and used the same sediments (Table 1: sand, mud). Mud and sand respectively were placed in alternate grid squares in a chess board arrangement (Fig. 3a). In mid-November 1994, *M. viridis* larvae were collected by plankton net (0.1 mm) from the Darss-Zingst bodden chain and placed in the prepared aquariums. The mean size of the larvae was 10 setigers. When no more larvae could be seen in the open water in the aquarium (this was after about three weeks, which is roughly the time needed for development to the benthic stage with 17 to 20 setigers under natural conditions (BOCHERT 1993)), the contents of each square were taken as a complete sample and fixed in formalin. The samples were washed through a 0.3 mm sieve and sorted at 10-16X magnification.

Influence of adult *Marenzelleria viridis* (>200 setigers)
on settlement [lab exp. 2]:

All grid squares were filled with mud, the substrate preferred by the larvae (see above, Fig. 3b). Sand was used as a substrate only in the boundary squares.

250 adult *M. viridis* were placed in the aquarium, correspond to a mean abundance of 1,000 ind./m². The *M. viridis* larvae were added three days later to give the adults time to become established. The samples were taken and handled as for lab experiment 1.

Influence of adult *Hediste diversicolor* (>80 setigers) on settlement [lab exp.3]:

The experimental arrangement was as for lab experiment 2. 100 adult *H. diversicolor* corresponding to an abundance of 400 ind./m^2 were placed in the aquarium. This abundance was chosen because only the influence of adult *H. diversicolor* (>80 setigers) on the settlement of *M. viridis* larvae was being studied and field studies had shown that abundances of *H. diversicolor* in this size class vary between 100 and 600 ind./m^2. As in lab experiment 2, the nereids were given three days to become established before the *M. viridis* larvae were added.

Influence of adult *Corophium volutator* on settlement [lab experiment 4]

The same experimental arrangement was used as for lab experiments 2 and 3. The number of *C. volutator* specimens was 1,000, corresponding to an abundance of 4,000 ind./m^2. Mean abundances in the field vary between 2,000 and 6,000 ind./m^2. In this case, too, the *M. viridis* larvae were added three days later.

Differences were checked for significance by the rank sum test (Wilcoxon test) for paired comparisons.

Results

Abiotic parameters (sediment)

Field studies

The field experiments revealed that *M. viridis* larvae vary significantly in their choice of substrate for settlement, showing a marked preference for station KB1 (mud substrate) compared with the other stations (Fig. 4).
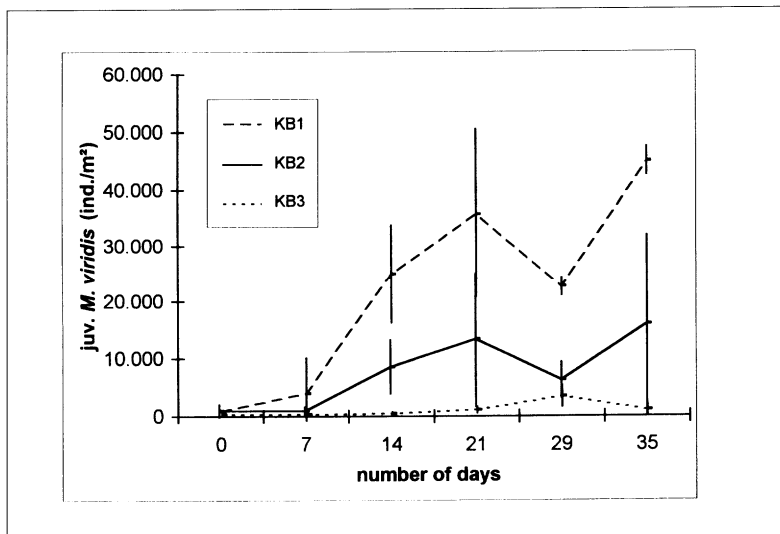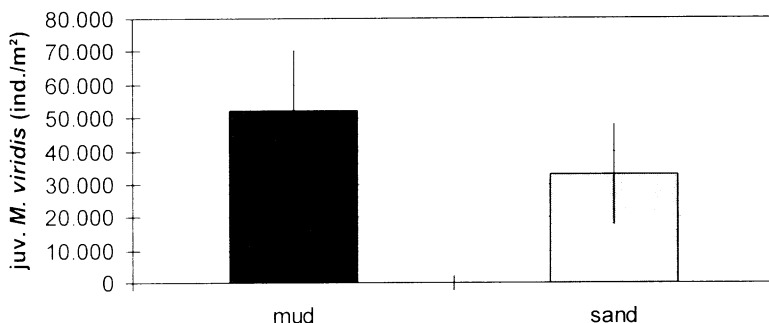
Fig. 4 Settlement behaviour of *M. viridis* larvae in the field experiment (abiotic parameters); see Table 1 for sediment parameters in the different regions (KB1, KB2, KB3).

Settlement density reached its maximum of 45,000 ind./m² on the 35th day (08/12/94) at this station. Settlement at station KB1 differed significantly (p<0.05) from KB3 (sandy substrate) on all sampling dates and the larvae also showed a significant preference for KB1 over KB2 on several occasions (Table 3). Station KB3, where the abundance never exceeded 4,000 ind./m², was most sparsely settled.

Table 3 Comparison between abundances (ind./m²) of just settled *M. viridis* larvae at stations KB1, KB2 and KB3 in the field experiment (03/11 to 08/12/94); significant differences (p<0.05) between stations during the investigation period marked with a *

days	KB1/KB2	KB1/KB3	KB2/KB3
0	920 / 614	920 / 0*	614 / 0
7	3,988 / 614	3,988 / 0*	614 / 0
14	25,004 / 8,130*	25,004 / 153*	8,130 / 153*
21	35,742 / 12,885	35,742 /7 67*	12,885 / 767*
29	22,703 / 5,829*	22,703 / 3,068*	5,829 / 3,068
35	45,099 / 15,493*	45,099 / 767*	15,493 / 767*

a)

■ 50.000-100.000
☐ 0-50.000
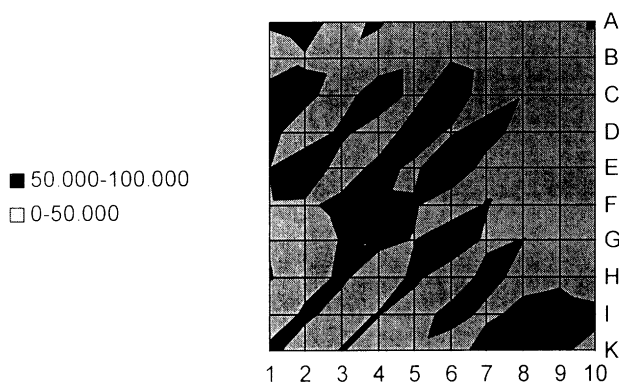
b)

Fig. 5   Settlement behaviour of *M. viridis* larvae in the laboratory experiment (abiotic parameters)
          [lab experiment 1]
          a)   significant preference for muddy squares (p<0.01)
          b)   uniform small scale horizontal distribution of the juvenile *M. viridis* shortly after
                settlement

Laboratory experiments
[Lab experiment 1]

    This experiment also showed that larval *M. viridis* prefer to settle in certain
substrate types (Fig. 5a). The means for the two substrate types differed significantly
(p<0.01). The mean abundance was 52,000 ind./m² in the mud grid squares compa-
red with 32,000 ind./m² in the sand-filled squares. The two-dimensional settlement

147

pattern of the *M. viridis* larvae (Fig. 5b) (high abundance = dark areas) was regular and identical to the arrangement of the mud squares in the grid.

Biotic parameters

Influence of adult *Marenzelleria viridis* (>200 setigers) on settlement [lab exp. 2]:

Adult *M. viridis* appeared to have no effect on the settlement of the larvae at the abundance used in the experiment. The mean abundance of *M. viridis* larvae varied between 8,000 and 11,000 ind./m² (Fig. 6).
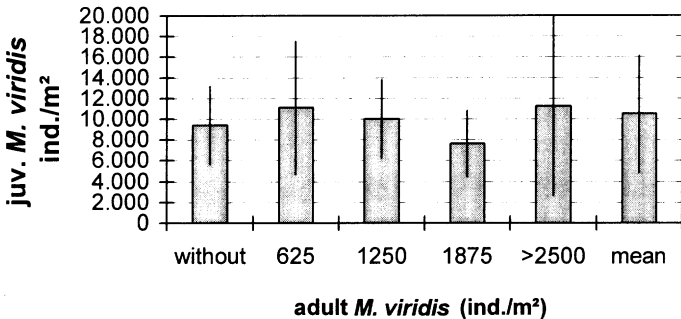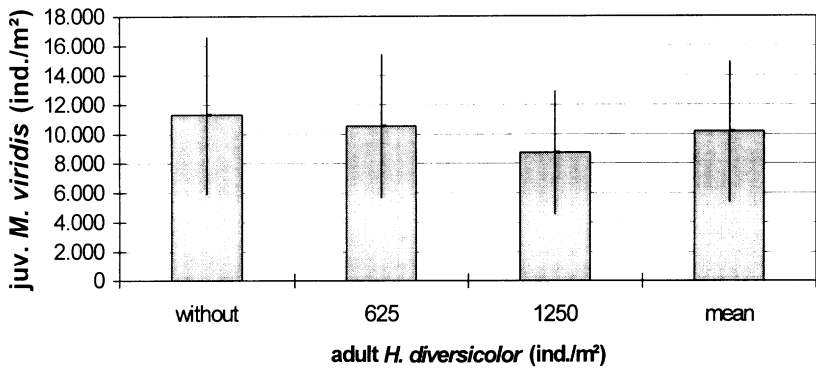

Fig. 6 Dependence of settlement behaviour of *M. viridis* larvae on the abundance of adult *M. viridis* (>200 setigers) [lab. experiment 2]

Influence of adult *Hediste diversicolor* (>80 setigers) on settlement [lab exp. 3]:

Like adult *M. viridis*, adult *H. diversicolor* had no influence on the settlement beha-viours of larval *M. viridis* (Fig. 7). The mean abundance of the *M. viridis* larvae varied between 9,000 and 11,000 ind./m². The apparent negative correlation suggested by comparison of the distribution patterns was not confirmed by the significance test.

148

Fig. 7 Dependence of settlement behaviour of *M. viridis* larvae on the abundance of adult *Hediste diversicolor* (>80 setigers) [lab. experiment 3]

Influence of adult *Corophium volutator* on settlement [lab exp. 4]:

This experiment revealed that substrate colonized by adult *C. volutator* seems to attract larval *M. viridis*. Comparison of the two-dimensional distribution pattern reveals that distribution is the same for both species (Fig. 8).
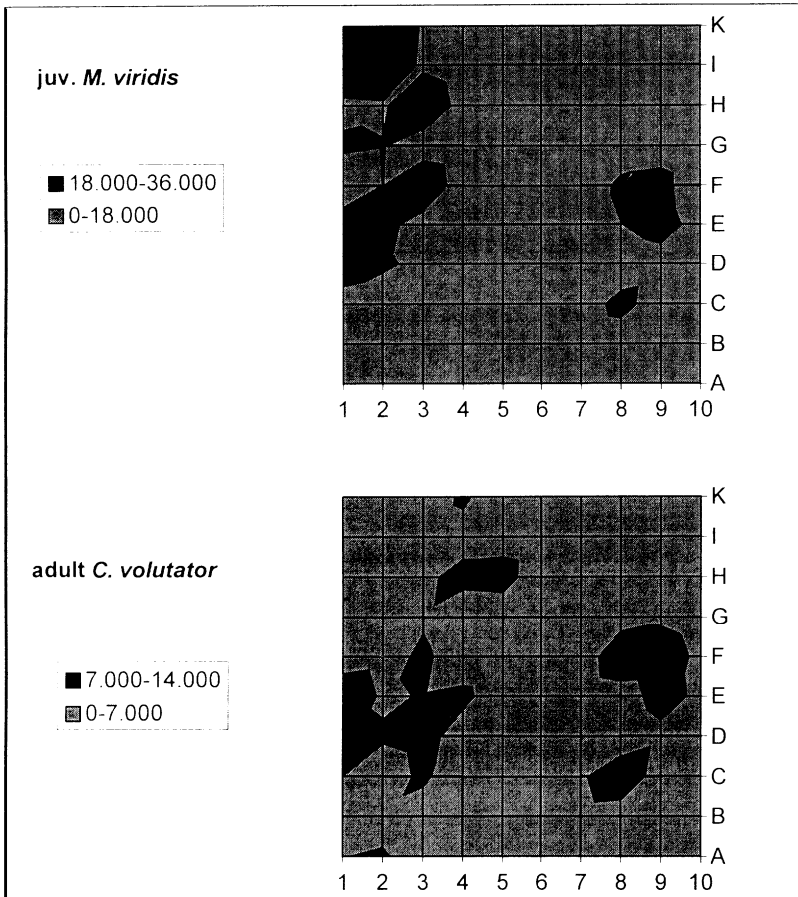
Fig. 8 Dependence of settlement behaviour of *M. viridis* larvae on the abundance of adult *C. vo-lutator*; patchy small scale horizontal distribution of juvenile *M. viridis* shortly after settlement; close correspondence between aggregations of *M. viridis* and *C. volutator*.

Discussion

Many authors have studied the stimulatory or inhibitory effects of abiotic and/or biotic factors on the settlement behaviour of the larvae of benthic organisms. Most of them have considered the effects of sediment properties (BUTMAN 1987; HSIEH 1994; SCHELTEMA 1974), currents (BUTMAN et al. 1988; GRASSLE & BUTMAN 1989; PAWLIK & BUTMAN 1993) and interspecific interactions (CROWE et al. 1987;

on settlement (WOODIN 1976) have also been considered, as have drifting and accumulations of larvae (SNELGROVE 1994). However, relatively little is known concerning the effects of primary larval settlement on the distribution patterns shown by adults of the same species (BUTMAN 1987, 1989). Active and passive habitat selection are often presented as alternatives, but they are not mutually exclusive. As BUTMAN (1987) observed: "The intention is to illustrate that habitat selection and passive deposition need not be competing, but are likely complementary, hypotheses by providing examples or proposed scenarios where both mechanisms would be operating, but separated in space and time."

Unlike variations in time, spatial colonization patterns are influenced by preferences for or the rejection of sediment characteristics, currents, mortality after settlement and interactions with adult benthic organisms (BUTMAN 1987; WOODIN 1986). Our *M. viridis* larvae showed a marked preference for muddy sediments. However, previous studies and experiments with the apparatus described here had shown that this changes a few weeks after settlement, when the juveniles exhibit a significant preference for sandy sediments. This later preference is identical to that shown by adult *M. viridis* (ZETTLER et al. 1995; ZETTLER unpubl.). It is known from the literature that the larvae of benthic organisms usually actively select a habitat that also satisfies the requirements of adults of the same species (PAULIK & BUTMAN 1993; SCHELTEMA 1974; WOODIN 1976). Exceptions are known, however, such as the polychaetes *Arenicola marina* and *Scoloplos armiger*, the juveniles of which "grow up" in so called nurseries and only migrate into areas colonized by adults when they have reached a certain stage in development (FARKE et al. 1979; REISE 1987, 1991).

Our experiments have shown that *M. viridis* prefers to start its benthic life in a muddy sediment, but develops are preference for sandy bottoms a few weeks later. This is consistent with ESSINK & KLEEF's (1993) observations in the Ems estuary (North Sea); juveniles were most abundant in muddy sediments, whereas adults dominated in sandy substrates. This change in preferences may be a result of the transition from deposit feeding during early benthic life to suspension feeding as fully developed juveniles and adult animals. For suspension feeders, the organic content of the sediment may be of secondary importance or even undesirable (oxygen deficiency, hydrogen sulphide formation). This would apply particularly in the eutrophic to hypertrophic regions of the North Sea and Baltic Sea where *M. viridis* is dominant and food is plentiful in the open water. However, the low Chl a content in the outer coastal waters of the Baltic Sea may necessitate a different feeding strategy. The ability of *M. viridis* juveniles and adults to migrate actively on account of their high motility and the presence of juveniles among the plankton in spring also suggest that sandy sediments are colonized secondarily (DAUER et al. 1982; ZETTLER et. al. 1995).

Inter and intraspecific interactions between macrozoobenthos organisms can take the form of adult-adult, adult-juvenile, adult-larva, juvenile-juvenile, juvenile-larva and larva-larva interactions. The interactions themselves can take the form of inhibition, tolerance and facilitation, the last two forms predominating among burrowing organisms (GALLAGHER et al. 1983). Naturally, the effect of adult animals on larvae depends on abundance and feeding type (TAGHON 1992; WOODIN 1976). HINES et al. (1989) showed that filter feeding and siphoning bivalves (*Arenomya arenaria*

and *Macoma balthica*) ingest larval *M. viridis* and therefore negatively affect their settlement.

Adult *Marenzelleria viridis* and adult *Hediste diversicolor* did not affect the settlement behaviour of *M. viridis* larvae at the abundances we used. DAUER et al. (1981) described how the respiratory current caused by *M. viridis* negatively affected recruitment of another spionid (*Streblospio benedicti*) by drawing its larvae into the burrows. LEVIN (1982) has reported interspecific aggression between the spionids *M. viridis*, *Polydora ligni* and *Spio setosa*. Several publications have described *H. diversicolor* as potential predators (e.g. JENSEN 1988; OLAFSSON & PERSSON 1986; RÖNN et al. 1988). Negative correlations between *M. viridis* and *H. diversicolor* in the Tay estuary (Scotland) have also been reported by ATKINS et al. (1987). Although these reports make a negative influence of the two polychaetes on the settlement of larval *M. viridis* credible, our experiments revealed no such effects. On the other hand, we were also unable to confirm that these burrowing organisms exercised an attraction on the larvae (in the sense described by GALLAGHER et al. 1983). Perhaps higher abundances lead to different effects. Higher temperatures would naturally also influence the feeding intensity of *H. diversicolor*, but do not occur during the reproduction of *M. viridis* in autumn and winter when temperatures vary between 0 and 10 °C.

In our experiments, *M. viridis* larvae were attracted to sediments colonized by *Corophium volutator*. The positive correlation was significant. However, ZETTLER (1995) reported a significant negative correlation between adult *M. viridis* and this amphipod in the boddens south of Darss-Zingst, and RÖHRIG (1995) reported similar observations during her field and experimental studies. It is difficult to say why *M. viridis* larvae prefer to settle near *C. volutator*. Conceivable reasons include the enlargement and roughening of the surface by the burrows and improved oxygenation owing to the respiratory current. NOJI & NOJI (1991) noted that aggregations of spionid burrows represent an improvement of uncolonized areas for subsequent recolonization. Possibly, the considerable bioturbation caused by the activity of *C. volutator* in the top centimetre of the substrate represents an ideal settlement substrate for the larvae.

The large and meso scale distribution of *M. viridis* is a result of interactions between the organism and its environment. Although passive drifting governs the large scale distribution of the larvae in the boddens (BOCHERT et al. 1994; WROGE-MANN 1994), settlement on a smaller scale involves active habitat selection (BUTMAN 1989; ZETTLER & BICK 1996). The distribution pattern of this spionid polychaete is governed by the active location of certain sediments and communities, increased mortality in unsuitable regions or due to predation, and the ability of the juveniles and adults to migrate and settle elsewhere (secondary settlement). The successful establishment of *M. viridis* in the bodden chain south of Darss-Zingst is certainly also due at least in part to the absence of potential "predators" (e.g. filter feeders such as *Macoma balthica* and *Arenomya arenaria*, cf. HINES et al. 1989) or the greatly reduced or changed feeding activity of predators such as *Hediste diversicolor* during reproduction and larval settlement of *M. viridis* in autumn and winter (GOERKE 1966, RIISGARD 1991).

Settlement of the substrate can be considered a kind of trial and error model, but one for which chemotactic receptors are needed. "Animals find, return to, or stay in their usual habitat by a process of choice in which they are continuously assessing and responding to information received from the environment. Habitat selection, therefore, is essentially the relationship between behaviour and environment, and we consider that it largely determines the local distribution of animal species." (MEADOWS & CAMPBELL 1972).

References

ALLER, R.C. (1980). Relationships of tube-dwelling benthos with sediment and overlying water chemistry. *In*: Marine benthic dynamics. K.R. Tenore & B.C. Coull (eds.), University of South Carolina Press: 285-308.

ARNDT, E.A. (1989). Ecological, physiological and historical aspects of brackish water fauna distribution. *In*: Reproduction, genetics and distribution of marine organisms, J.S. Ryland & P.A. Tyler (eds.), Olsen & Olsen, Fredensborg: 327-338.

ATKINS, S.M.; JONES, A.M. & GARWOOD, P.R. (1987). The ecology and reproductive cycle of a population of *Marenzelleria viridis* (Annelida: Polychaeta: Spionidae) in the Tay Estuary. Proc. Roy. Soc. Edinburgh 92B: 311-322.

BICK, A. & BURCKHARDT, R. (1989). Erstnachweis von *Marenzelleria viridis* (Polychaeta, Spionidae) fur den Ostseeraum, mit einem Bestimmungsschlüssel der Spioniden der Ostsee. *Mitt. Zool. Mus. Berlin* 65: 237-247.

BOCHERT, R. (1993). Reproduktion und Larvalentwicklung von *Marenzelleria viridis* (Verrill, 1873) (Polychaeta; Spionidae) in der Darß-Zingster Boddenkette. Dipl. Univ. Rostock: 47pp.

BOCHERT, R.; ZETTLER, M.L. & BICK, A. (1994). Untersuchung zur räumlichen Verteilung der Larven von *Marenzelleria viridis* (Polychaeta: Spionidae) in einem flachen Küstengewässer der Ostsee. Rost. Meeresbiol. Beitr. 2: 227-240.

BUTMAN, C.A. (1987). Larval settlement of soft-sediment invertebrates: The spatial scales of pattern explained by active habitat selection and the emerging role of hydrodynamical processes. Oceanogr. Mar. Biol. Ann. Rev. 25: 113-165.

BUTMAN, C.A. (1989). Sediment-trap experiments on the importance of hydrodynamical processes in distributing settling invertebrate larvae in near-bottom waters. J. Exp. Mar. Biol. Ecol. 134: 37-88.

BUTMAN, C.A.; GRASSLE, J.P. & WEBB, C.M. (1988). Substrate choice made by marine larvae settling in still water and in a flume flow. Nature 3: 771-773.

CROWE, W.A.; JOSEFSON, A.B. & SVANE, I. (1987). Influence of adult density on recruitment into soft sediment: a short-term *in situ* sublittoral experiment. Mar. Ecol. Prog. Ser. 41: 61-69.

DANKERS, N. & BEUKEMA, J.J. (1981). Distributional patterns of macrobenthic species in relation to some environmental factors. Rep. Wadden Sea Working Group 4: 69-103.

DAUER, D.M.; MAYBURY, C.A. & EWING, R.M. (1981). Feeding behaviour and general ecology of several spionid polychaetes from the Chesapeake Bay. J. Exp. Mar. Biol. Ecol. 54: 21-38.

DAUER, D.M.; EWING, R.M.; SOURBEER, J.W.; HARLAN, W.T. & STOKES, T.L. (1982). Nocturnal movement of the macrozoobenthos of the Lafayette River, Virginia. Int. Rev. ges. Hydrobiol. 67: 761-775.

DEKKER, R. (1991). *Marenzelleria viridis* (Polychaeta: Spionidae): Uitbreiding van het areaal in Nederland Mededeling. Zeepaard 51: 101-104.

ESSINK, K. & H.L. KLEEF, 1993. Distribution and life cycle of the North American spionid polychaete *Marenzelleria viridis* (Verrill, 1873) in the Ems Estuary. Neth. J. Aqu. Ecol. 27: 237-246.

FARKE, H., P.A.W.J. DE WILDE & E.M. BERGHUIS, 1979. Distribution of juvenile and adult *Arenicola marina* on a tidal mud flat and the importance of nearshore areas for recruitment. Neth. J. Sea Res. 13: 354-361.

GOERKE, H. (1966). Nahrungsfiltration von *Nereis diversicolor* O.F. Müller (Nereidae, Polychaeta). Veröff. Inst. Meeresforsch. Bremerh. 10: 49-58.

GRASSLE, J.P. & BUTMAN, C.A. (1989). Active habitat selection by larvae of the polychaetes, *Capitella* spp. I and II, in a laboratory flume. *In*: Reproduction, genetics and distribution of marine organisms J.S. Ryland & P.A. Tyler (eds.), Olsen & Olsen, Fredensborg: 107-114.

GRAY, J.S. (1974). Animal-sediment relationships. Oceanogr. Mar. Biol. Ann. Rev. 12: 223-261.

HINES, A.H.; POSEY, M.H. & HADDON, P.J. (1989). Effects of adult suspension- and deposit feeding bivalves on recruitment of estuarine infauna. Veliger 32: 109-119.

HSIEH, H.L. (1994). Larval development and substrate preference at settlement in *Pseudopolydora diopatra* (Polychaeta: Spionidae). Invert. Repr. Dev. 25: 205-214.

JENSEN, K.T. (1988). Recruitment and survival of *Nereis diversicolor* O.F. Müller and *Corophium volutatur* (Pallas) in an artifical saltwater lagoon in the Danish wadden sea. Kieler Meeresforsch. Suppl. 6: 366-374.

KREBS, C.J. (1994). Ecology. The Experimental Analysis of Distribution and Abundance. Harper Collins College Publishers, New York, fourth edition, 801pp.

LEVIN, L.A. (1982). Interference interactions among tube-dwelling polychaetes in a dense infaunal assemblage. J. Exp. Mar. Biol. Ecol. 65: 107-119.

MCCANN, L.D. & LEVIN, L.A. (1989). Oligochaete influence on settlement, growth and reproduction in a surface-deposit-feeding polychaete. J. Exp. Mar. Biol. Ecol. 131: 233-253.

MEADOWS, P.S. & CAMBELL, J.I. (1972). Habitat selection by aquatic invertebrates. Adv. Mar. Biol. 10: 271-382.

NOJI, C.I.-M. & NOJI, T.T. (1991). Tube lawns of spionid polychaetes and their significance for recolonization of disturbed benthic substrates. A review. Meeresforsch. 33: 235-246.

OLAFSSON, E.B. & PERSSON, L.-E. (1986). The interaction between *Nereis diversicolor* O.F. Müller and *Corophium volutator* Pallas as a structering force in a shallow brackish sediment. J. Exp. Mar. Biol. Ecol. 103: 103-117.

PAWLIK, J.R. & BUTMAN, C.A. (1993). Settlement of a marine tube worm as a function of current velocity: interactiong effects of hydrodynamics and behavior. Limnol. Oceanogr. 38: 1730-1740.

REISE, K. (1987). Distribution and abundance of small and juvenile macrofauna on the tidal flats in the Frisian Wadden Sea. Biologiske Meddelser 31: 7-25.

REISE, K. (1991). Mosaic cycles in the marine benthos. *In*: Ecological Studies, Vol. 85, H. Remmert (ed.), Springer-Verlag, Berlin, Heidelberg: 61-82.

RIISGÅRD, H.U. (1991). Suspension feeding in the polychaete *Nereis diversicolor*. Mar. Ecol. Prog. Ser. 70: 20-37.

RÖHRIG, A. (1995). Aspekte zur Sedimentpräferenz von *Marenzelleria viridis* (Verrill 1873) (Polychaeta; Spionidae) sowie Interaktionen zwischen *M. viridis* und der autochthonen Fauna eines inneren Küstengewässers der südlichen Ostsee. Dipl. Univ. Hannover: 70pp.

RÖNN, C.; BONSDORFF, E. & NELSON, W.G. (1988). Predation as a mechanism of interference within infauna in shallow brackish water soft bottoms, experiments with an infauna predator, *Nereis diversicolor*. J. Exp. Mar. Biol. Ecol. 116: 143-157.

SCHELTEMA, R.S. (1974). Biological interactions determining larval settlement of marine invertebrates. Thal. Jugosl. 10: 263-296.

SNELGROVE, P.V.R. (1994). Hydrodynamic enhancement of invertebrate larval settlement in microdepositional environments: colonization tray experiments in amuddy habitat. J. Exp. Mar. Biol. Ecol. 176: 149-166.

TAGHON, G.L. (1992). Effects of animal density and supply of deposited and suspended food particles on feeding, growth and small-scale distribution of two spionid polychaetes. J. Exp. Mar. Biol. Ecol. 162: 77-95.

WOODIN, S.A. (1976). Adult-larval interactions in dense infaunal assemblages: patterns of abundance. J. Mar. Res. 34: 25-41.

WOODIN, S.A. (1986). Settlement of infauna: Larval choice? Bull. Mar. Sci. 39: 401-407.

WROGEMANN, H. (1994). Verbreitung und Populationsentwicklung von *Marenzelleria viridis* Verrill 1873 (Polychaeta; Spionidae) in einem inneren Küstengewässer der südlichen Ostsee. Staatsex. Tierärztl. Hochschule Hannover: 95pp.

ZETTLER, M.L. (1994). Immigration und Ausbreitung eines nordamerikanischen Polychaeten in ein inneres Küstengewässer der südlichen Ostsee und Auswirkungen auf das autochthone Makrozoobenthos. Erw. Zusammenf. Jahrestag. D.G.L., Hamburg 2: 695-699.

ZETTLER, M.L. (1995). Successful estabishment of the spionid polychaete *Marenzelleria viridis* (Verrill 1873), in the Darss-Zingst estuary (southern Baltic) and its influence on the indigenous macrozoobenthos. Arch. Fish. Mar. Res. 43: 273-284.

ZETTLER, M.L. & BICK, A. (1996). The analysis of small- and mesoscale dispersion patterns of *Marenzelleria viridis* (Polychaeta: Spionidae) in a coastal water of the southern Baltic. Helgol. Meeresunters. 50: 265-286.

ZETTLER, M.L.; BICK, A. & BOCHERT, R. (1995). Distribution and population dynamic of *Marenzelleria viridis* (Polychaeta: Spionidae) in a coastal water of the southern Baltic. Arch. Fish. Mar. Res. 42: 209-224.

ZETTLER, M.L.; BOCHERT, R. & BICK, A. (1994). Röhrenbau und Vertikalverteilung von *Marenzelleria viridis* (Polychaeta: Spionidae) in einem inneren Küstengewässer der südlichen Ostsee. Rost. Meeresbiol. Beitr. 2: 215-225.

Author

Dr. Michael L. Zettler
Universität Rostock
FB Biologie / Allg. & Spez. Zoologie
Universitätsplatz 5
18051 Rostock