A model on the distribution and abundance of the tube-building polychaete *Lanice conchilega* (Pallas, 1766) in the intertidal of the Wadden Sea

Jens Heuers, Sandra Jaklin, Ruth Zühlke, Sabine Dittmann, Carmen-Pia Günther, Hanno Hildenbrandt and Volker Grimm

Synopsis

In the intertidal of the Wadden Sea, assemblages of the tube-building polychaete *Lanice conchilega* show – on the scale of tens to hundreds of meters – marked differences in density, ranging from 10 to 10.000 tubes/m². These different densities emerge within three to four years after severe winters where all individuals of *L. conchilega* are killed in the intertidal. In some areas the distribution of *L. conchilega* is characterized by a small-scale mosaic of mounds with dense aggregations of *L. conchilega* tubes and depressions with almost no tubes. The typical scale of this mosaic pattern is one to three meters. The causes of both the regional and the local patterns were unknown up to now. Therefore we performed field experiments which showed that larvae of *L. conchilega* mainly settled at the tubes of adult worms and build their tube attached to the tubes of the adults. The success of initial larval settlement, that is the number of recruits per adult tube, increased with the density of adult tubes. We present a simple simulation model which tries to answer the question if the findings of our experiments are sufficient to explain the distribution patterns of *L. conchilega*. A first model based on a linear relationship between the density of tubes and the settlement of larvae does not reproduce the wide range of observed densities within four years after defaunation during a severe winter. Only a model where the near-bottom flow regime is taken into account phenomenologically is capable to reproduce the full range and dynamic of the observed densities. As a result of the model, we formulate testable hypothesis about the causes of the regional distribution pattern of *L. conchilega*. Finally, we use the model to present a graphical model which explains the emergence of the small-scale mosaic pattern.

Intertidal, tube-building polychaete, Lanice conchilega, larval settlement, flow regime, spatial pattern, model

1 Introduction

Patchy distributions of benthic organisms are a common feature in the marine world (e.g. ROSENBERG 1974; ANDREW & MAPSTONE 1987). Depending on the observed scale of space and time the explanations for the patterns of abundance and distribution differ. The duration of emersion and submersion, sediment type, the mode of feeding as well as movement are main factors determining large-scale distribution patterns in marine coastal systems (BEUKEMA 1976; WARWICK & DAVIES 1977). Within these patterns, other physical, chemical and biological (e.g. promotion, predation and competition) processes affect the distribution on a smaller scale (REISE 1985).

In her review BUTMAN (1987) emphasises the importance of larval settlement for structuring benthic communities. Planktonic larvae drift with the ocean currents for variable periods of time before settling on the sea floor. The settlement phase of the larvae is either passive, entirely determined by the hydrographic regime (ARMONIES & HELLWIG-ARMONIES 1992), or active, in which case the larvae are able to select their habitat (e.g. PAWLIK 1986; BUTMAN & GRASSLE 1992). Both passive deposition and active habitat selection are influenced by small-scale hydrodynamic processes in the bottom boundary layer. Here, protruding biogenic structures such as seagrass, macroalgae and worm tubes are known to divert the normal laminar near-bottom flow. ECKMAN (1985) shows that flow effects around tubes can enhance microbial colonisation. Similarly, modifications of the near-bottom hydrodynamic environment might influence larval settlement.

The tube-building polychaete *Lanice conchilega* is one of the prominent species in the Wadden Sea (REISE 1985). It constructs tubes of up to 40 cm length out of agglutinated sand grains. The tubes protrude 2–3 cm out of the sediment surface. The density varies between one and 10.000 tubes/m² (ZIEGELMEIER 1952). Areas with low or high density are tens to hundreds meters wide (HERTWECK 1995). Inbetween are often areas without *L. conchilega*, although the sediment does not differ from the populated areas.

In some parts of the intertidal, mosaic distribution patterns are formed in which patches of low and high density alternate on a scale of meters. In many cases the more dense patches are on mounds of sediment while the patches of low density are located in depressions. The mosaic pattern persisted for several years until a severe winter in 1995/96 extinguished the intertidal population in the study area. HERTWECK (1995) reports that after an earlier severe winter the distribution pattern of *L. conchilega* reestablished rather quickly, that is within three to four years.

In this paper, we test the hypothesis that the distribution patterns of *L. conchilega* result from the mutual relationship between larval settlement, the tubes of adult worms, and the near-bottom flow regime. In addition to two years of field study on abundance, distribution, larval supply and settlement of *L. conchilega*, we performed experiments with artificial tubes. Results of field study, experiments, and current knowledge from literature about *L. conchilega* in the intertidal, are integrated in a simple simulation model which demonstrates the consequences of different assumptions about the relationship between settlement, tube density, and flow regime.

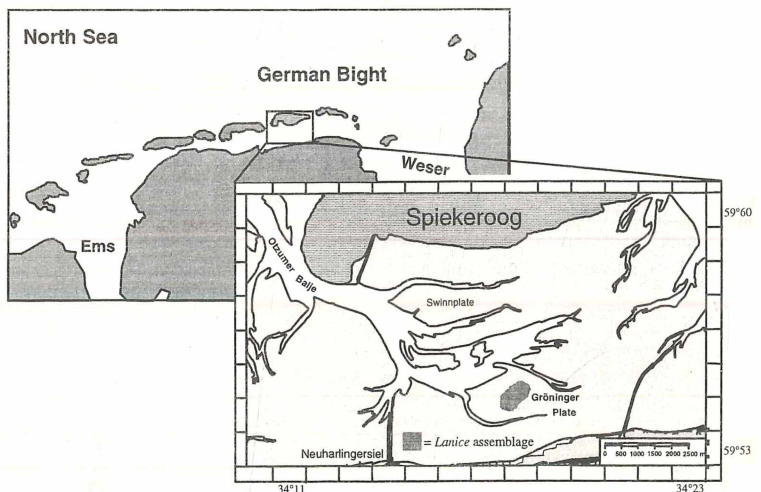## 3 Empirical background

3.1 Sampling design

The study area was an intertidal sandflat (Gröninger Plate) between the island of Spiekeroog and the East Frisian mainland (Fig. 1). To investigate where, when, and in which densities *L. conchilega* settles, field work and experiments were carried out in 1994 and 1995 at different sites of the Gröninger Plate.

Sampling was carried out in intervals of a week or a fortnight from March to October each year by taking seven replicate sediment samples with a corer at each site (33 cm^2 surface area, 20 cm sediment depth) from areas of 100 m^2. Samples were analysed in the laboratory using a sieve column of 500, 250 and 125 µm mesh size. Living *L. conchilega* and all tubes were counted and separated into juvenile and adult under the stereo microscope. In order to estimate the number of larvae drifting above the bottom as potential settlers, driftnet samples were taken at each sampling date parallel to the sediment samples. The driftnet (55 cm long; 20 cm diameter opening; 0.5 mm mesh size) was attached to a vertical pipe 15 cm above the sediment surface and could adjust itself to the current (detailed description of the net construction see ARMONIES 1992). The net was set up during low tide and sampled after a complete tidal cycle. The larvae of *L. conchilega* were counted under the stereo microscope.

3.2 Distribution of adult and juvenile *L. conchilega*

In both years initial settlement of larvae took place mainly in the assemblage of adult worms (see Fig. 1: *L. conchilega* assemblages). Only a few individuals settled in other areas of the Gröninger Plate. The larvae built their new tubes directly attached to the adult tube. Juvenile *L. conchilega* were not found in samples without adult tubes (Fig. 2). No significant correlation between the number of larvae in the driftnet and the number of newly settled *L. conchilega* could be recorded over the years. Since only two postlarvae of *L. conchilega* were found in the driftnet, secondary dispersal, which is also known to in-

Fig. 1

The study area (Gröninger Plate) between the island of Spiekeroog and the mainland and the location of the main assemblages of *Lanice conchilega* at the Gröninger Plate.
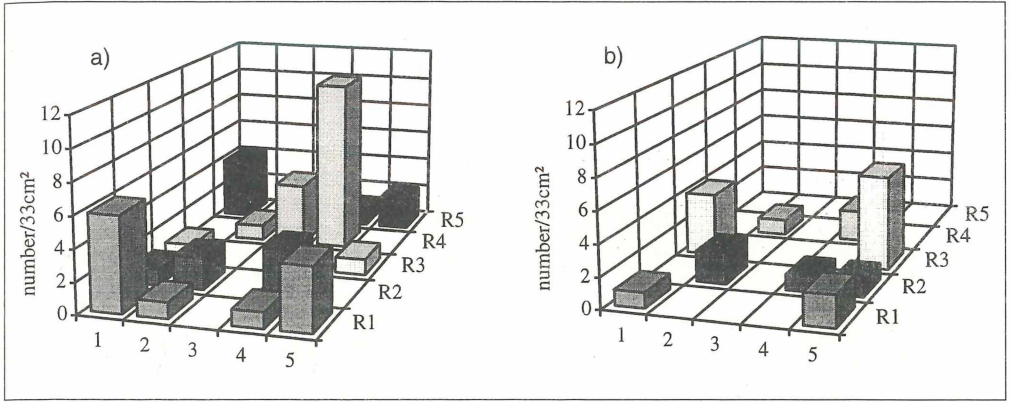
Fig. 2
Abundance and distribution of adult (a) and juvenile (b) *Lanice*-tubes within 1 m² (separated in 25 squares) in July 1994 at the Gröninger Plate.

fluence distribution patterns of other macrobenthic species, (GÜNTHER 1992), seems negligible.

3.3 Experiments with artificial tubes

The annual investigations documented a clear dependence of larval settlement on tubes of adult *L. conchilega*. Therefore the importance of protruding structures, such as tubes, for settling larvae was tested in two parallel experiments set ups in 1995. In the first experiment artificial tubes were offered for settlement in May 1995. The artificial tubes consisted of dried sediment glued to wooden sticks, 4 mm in diameter. All natural worm tubes were removed from sites of 2 x 2 m² size within the *L. conchilega* assemblage and the artificial tubes were inserted into the sediment, simulating patches of high and low densities. After three months the artificial tubes were removed and scanned for juvenile *L. conchilega* and their tubes.

In a second experiment the effect of tubes on sediment properties and macrofaunal colonisation was tested. Within the *L. conchilega* assemblage, experimental plots of 1 m² were arranged and two treatments carried out. In the first treatment 1000 metal sticks were placed on a square meter, each 4 mm in diameter and protruding 3 cm above the sediment surface. As a control, 1000 metal sticks were inserted into the sediment so that they ended plane to the surface.

3.4 Results of the experiments

In the first experiment, artificial tubes were accepted by *L. conchilega* larvae with the same frequency as

natural tubes. No difference was visible in the mode of attachment of juvenile *L. conchilega* between natural and artificial tubes. Patches of higher tube-density increased larval settlement per adult tube (Fig. 3) and therefore the number of juvenile tubes found in the samples.

A rather quick formation of mounds, comparable to those observed in the natural *L. conchilega* assemblage, was observed as an effect of the protruding artificial tubes in the second experiment. No mounds developed in the control.
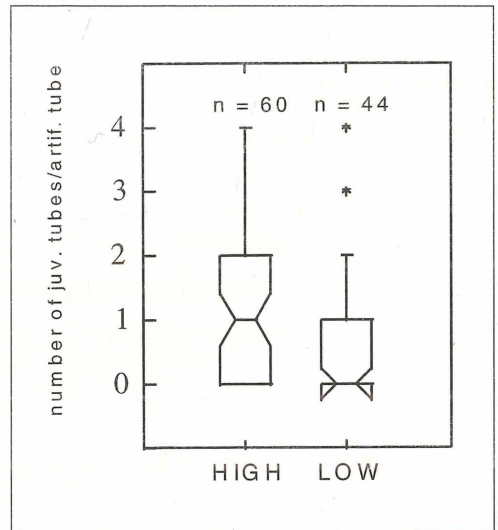

Fig. 3
Settlement of larvae of *Lanice conchilega* on artificial tubes. Number of juvenile tubes found on artificial tubes of higher (high) and lower (low) density; n = number of observed tubes.

4   The model

Within the wide areas with low or high densities of *L. conchilega*, the distribution of *L. conchilega* is more or less homogeneous (except the areas with the mosaic pattern). Since the model does not primarily address the mosaic pattern, it seems sufficient to consider only a small transect of 1–3 meter length and 10 cm depth. This transect is divided into distinct »cells« of 1 cm width. Each cell may be empty or may contain one to *maxT* (= 10) tubes of adult worms. With all cells having 10 tubes, the overall density would be 10.000 tubes/m² , which is the highest density observed in the field.

Time is not described continously, but proceeds in discrete steps representing one year. Within one year, the distribution of tubes is updated twice according to the two processes »settlement« and »mortality«.

With settlement, it is assumed that each year there is a larval supply of *maxL* larvae which may settle in each cell. *MaxL* represents the average abundance of larvae which is available in the water column during the time of settlement. For each cell and for all of the *maxL* larvae it is decided individually if the larva settles. This is done by drawing a uniformly distributed random number from the computer, i.e. a number which is between 0 and 1. If this number is smaller then the probability of settlement, *Ps*, than the larva settles, otherwise it does not. *Ps* is the sum of a small, spontaneous settlement probability *Psp* which describes settlement on the bare sediment, and the probability *Pd* which depends on the local density of tubes within the cell. The local density N_i of the i-th cell is calculated as the average of the density of the i-th cell and its four neighbour cells in both directions. This is based on the following consideration: Larval settlement takes place directly at adult tubes. Sooner or later the juvenile worm will build its new tube close to the tube of the adult animal (the point of its initial settlement). Since there is no clear information about the distance between the point of initial settlement and the point where the juvenile worm establishes its final tube, 5 cm was assumed to be a reasonable value. N_i thus represents the influence of all tubes within the i-th cell and its neighbourhood on the probability of settlement or, to be more precise, on the probability that a juvenile worm will establish a new tube in the i-th cell. What the calculation of N_i essentially does is to smooth the real distribution of tubes. In this way, larvae do not detect small-scale heterogeneities of the tube distribution. Technically speaking, N_i is calculated from the real distribution of tubes by applying a moving average or low pass filter.

Under the assumption that each tube makes the same contribution to the density-dependent probability *Pd*, the probability of settlement of a larva in the i-th cell, Ps_i, calculated as

$$Ps_i = Psp + Pd_i = Psp + \frac{N_i}{scale}$$

where *scale* is a constant which scales the local density to the probability *Pd*. Because of the linear relationship between local density and Ps_i in this model, we will in the following refer to this model as the »linear« model. Applying the linear model to a parameter set in which *Psp* is zero, *scale* is 20, and N_i is set to the maximum value of *maxT* = 10 ind./cell, the probability of settlement Ps_i would be 0.5. For a larval supply of *maxL* = 10 larvae there would be a mean of 5 larvae per year settling in this cell. It is important to notice that both the parameters *maxL* and *scale* determine the maximum settlement success of the larvae. After settlement, the newly established tube is counted as an »adult« tube. If there are more than *maxT* tubes within a cell, the number of tubes is set equal to *maxT*. In this way exponential growth of the population is prevented.

After the process »settlement« has been applied to all cells, the process »mortality« is applied, that is for each individual worm or tube, respectively, it is decided according to the probability *Pmort* if it dies.

As an alternative to the linear model we also tested a »nonlinear« model. The empirical background of the nonlinear model are studies (e.g., CAREY 1983, ECKMAN 1983, BUTMAN 1986, PAWLIK & BUTMAN 1993) which show a modification of the near-bottom flow caused by protruding structures. Protruding structures may reduce shear stress and flow velocity near the bed as indicated by enhanced sediment deposition in the second field experiment (see above). But how does the effect of protruding structures depend on the density of the structures and on the velocity of the near-bottom flow? MORRIS (1955; cf. ECKMAN 1983) calls the flow through assemblages of protruding structures, where shear stress and velocity are reduced, »skimming flow«. Here, the flow velocity is reduced and the flow is no longer laminar but more or less turbulent, i.e. characterized by small eddies (CAREY 1983). These eddies could enhance the chance that larvae become attached to the protruding structures.

The transition from laminar to turbulent flow while passing protruding structures depends on the velocity of the overall flow regime. For individual protruding structures turbulence does not occur at velocities below a critical value (ANDERSON & CHARTERS 1982). Consequently, a settlement experiment (HARVEY & al. 1995) conducted with artificial benthic algae did not lead to the expected increase in larval settlement because the chosen current velocity was too low to develop the transition into a turbulent flow.

The nonlinear model takes these empirical findings into account by introducing phenomenologically three different flow velocities: low, intermediate, and high. For each velocity an exponential relationship between the local density N_i and the probability Pd_i is assumed:

$$Pd_i = \frac{e^{(vscale\ N_i)} - 1)}{scale}$$

The parameter *vscale* stands for the effect of the flow velocity on the exponential relationship between N_i and Pd_i, that is *vscale* has three different values for low, intermediate and high flow velocity. Fig. 4 shows the relationship between Pd and N_i for both the linear and the nonlinear model.

5   Results

Each simulation starts with five adult *L. conchilega* distributed randomly along the transect. Fig. 5 shows how the distribution and abundance of *L. conchilega* develops during a period of ten years (t = 10) for two different larval supplies *maxL*. Ten years were chosen because this is the mean time interval between severe winters where the entire population of *L. conchilega* is killed in the intertidal. A larval supply of 20 larvae/cell leads to very low densities even after 10 years, and a high supply of 40 larvae/cell leads to high densities after 10 years. In the latter case, however, after three years density is still rather low. This

does not match the real situation where high densities are established already after three or four years (HERTWECK 1995). There are two ways to increase the emergence of high-densities in the linear model: decreasing the mortality *Pmort* or increasing the spontaneous settlement probability *Psp*. Further simulations showed that both alternatives finally led to high densities even if larval supply was low. In summary it can be concluded that the linear model does not adequately reproduce the whole range of densities and the colonization dynamics observed in real *L. conchilega* populations.

Fig. 6 presents results from the nonlinear model. The development of the distribution and abundance is compared for the three different flow velocities. This model is able to reproduce *L. conchilega* assemblages of either low or high density within a short time (t = 4) by using the same larval input (*maxL* = 20). At least with low and high currents the densities remain more or less constant even after ten years.

5   Discussion

In the field studies and experiments, three factors affecting larval settlement of *L. conchilega* emerged. First, the larvae need epibenthic structures to establish their own first tube. Bare sediment seems to be unsuitable for settlement and shear stress imposed by near-bottom flow can prevent the establishment of
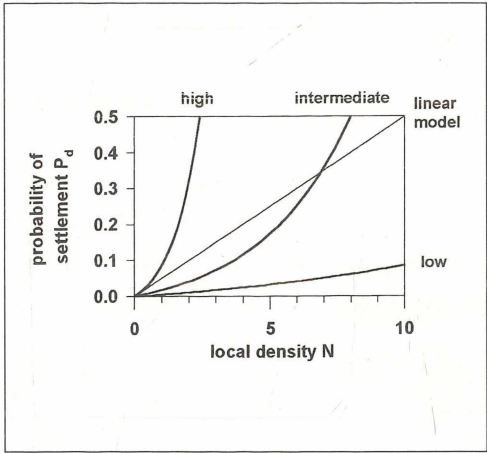

Fig. 4
Relationship between the density-dependent probability of settlement, *Pd*, and the local density of tubes *N* for the linear model and for the nonlinear model with the three flow velocities low, intermediate, and high (*vscale* = 0.1, 0.3 and 1.0, respectively; *scale* = 20).
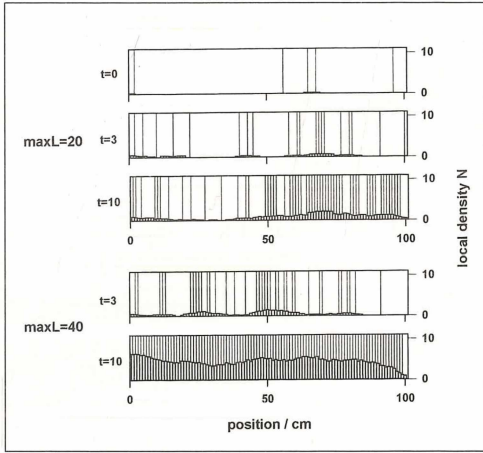

Fig.5
Distribution patterns of *Lanice conchilega* as produced by the linear model on a transect of 1 m length with two different larval supplies (*maxL* = 20 and *maxL* = 40). Parameters used are *Psp* = 0.005, *maxT* = 10, *scale* = 20, *Pmort* = 0.5. Bars indicate the local density of tubes, vertical lines indicate if at least one tube is present in the cell. The panels show the distribution pattern for the years *t* = 0, *t* = 3, and *t* = 10.
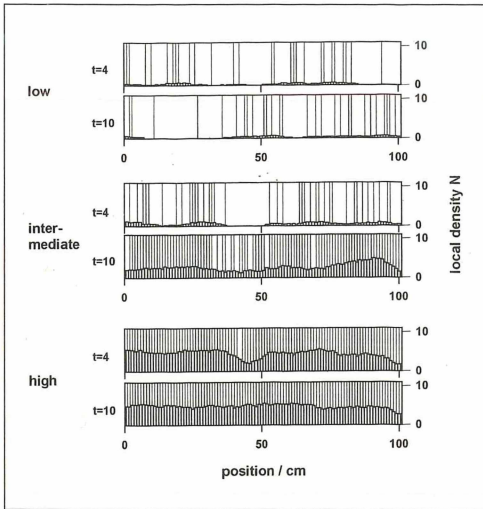
Fig. 6

Distribution patterns of *Lanice conchilega* as produced by the nonlinear model with the three flow velocities low, intermediate and high (*vscale* = 0.1, 0.3 and 1.0, respectively). Parameters used are: *maxL* = 20, *Psp* = 0.005, *maxT* = 10, *scale* = 20, *Pmort* = 0.5.

tubes which are not attached to structures anchored in the sediment. Epibenthic structures are rare on the intertidal so that tubes of adult *L. conchilega* provide the major substrate for attachment of larvae. Secondly, chemical attractors which are known to affect larval settlement of other tube-building polychaetes (PAWLIK 1986) play – at least on the scale of square meters – no role for the settlement of *L. conchilega*. The settlement experiment with artificial tubes showed that any protruding tube-like structure is accepted as substrate by *L. conchilega* larvae. And thirdly, the density of adult tubes affects larval settlement. Dense assemblages of artificial tubes caused sedimentation, leading to mounds just as in dense assemblages of living *L. conchilega*. This indicates that dense assemblages cause a »skimming flow« with reduced shear stress near the bottom. Flume experiments with artificial tubes show that within dense assemblages of tubes the velocity of the near-bottom flow is significantly reduced and normal, laminar near-bottom flow is deflected around and across the assemblages (FRIEDRICHS 1996, Diploma thesis, University of Kiel, Germany). A similar effect was measured and described for macrophytes in streams (SAND-JENSEN & MEBUS 1996).

In order to test if these three factors looked at on a small spatial scale are sufficient to explain the distribution pattern on the regional scale of an entire sandflat, we constructed a simple individual-based, spatially explicit simulation model. The modelling ap-

proach we used has been successfully used in terrestrial ecology (e.g., WENNERGREN & al. 1995, JELTSCH & al. 1997), but is rather new to marine ecology. The model is a tool to explain patterns which are observed in nature (»pattern-oriented modelling«, GRIMM 1994, GRIMM & al. 1996). The model cannot be tested itself, but only the hypotheses formulated with the help of the model. Based on the model results we formulate three hypotheses:

(1) *The distribution pattern of* L. conchilega *is no result of local differences in larval supply.* – For some benthic organisms, e.g. barnacles, larval supply is determined by the flow regime on the regional scale (e.g., GAINES & ROUGHGARDEN 1985). For *L. conchilega*, no empirical evidence exists on differences in larval supply on different parts of a tidal flat. Our hypothesis could be tested by locating driftnets in areas with low or high density of *L. conchilega* tubes.

(2) *The density of* L. conchilega *is related to the flow regime: assemblages of low density occur in areas with prevailing low flow velocities, assemblages of high densities in areas with high flow velocities.* – This hypothesis can be tested directly by measuring the flow regime in areas with different tube densities. Current measurements carried out in June 1994 on the Gröninger Plate gave flow velocities of about 10 cm/s at the *L. conchilega* assemblage with low densities and velocities of about 20 cm/s close to another site with higher *L. conchilega* densities (BRANDT & al. 1995, VAN BERNEM et al., unpubl.).

A survey of macrobenthos assemblages in the backbarrier tidal flat of Spiekeroog island (HERTWECK 1995) shows highest densities of *L. conchilega* on the central, elevated sandflats and lower densities on lower lying areas. A similar pattern was observed on another sandflat (Dornumer Nacken) in a nearby backbarrier tidal flat: low densities at lower areas, intermediate densities with a mosaic pattern of mounds and depressions at intermediate elevations, and high densities near the top of the sandflat (J. REICHERT, pers. com.). However, these findings cannot be interpreted unambiguously since there is no simple relationship between elevation and the mean velocity of the tidal currents, given the complex morphology of the sandflats, varying distances to tidal channels and different directions of the tidal currents.

Thus, the existing empirical evidence on the relationship between flow regime and the distribution pattern of *L. conchilega* is incomplete. Only a detailed empirical comparison of the flow regime and the distribution pattern of *L. conchilega* would allow a test of our second hypothesis. So far, we do not know which aspect of the flow regime is really relevant for larval settlement. We used »flow velocity« in a wide sense, comprising several parameters characterizing tidal currents (mean velocity of near-bottom

flow, maximum velocities, submersion time, wave impact, near-bottom turbulence).

Other than flow regime, sediment characteristics, e.g. grain size, could determine the distribution of *L. conchilega*. But the Gröninger Plate has a homogeneous grain size distribution (fine sand; FLEMMING 1993). Similarly, BUHR (1979) found no correlation between sediment type and distribution patterns of *L. conchilega* and assumed that the flow regime is more important.

The main focus of our model is to explain the regional distribution patterns of *L. conchilega*. But we can also discuss the implications of the model results with respect to the small-scale mosaic pattern. In the panels of Fig. 7, the development of a simulated distribution of *L. conchilega* is shown. Initially, there are three sparse assemblages of tubes evenly spaced along a transect of three meters length (Fig. 7, upper panel). After four years, three main assemblages emerged. Due to the way the local density is calculated (see above), the assemblages grow laterally. Two simulation years later, there is only a small gap with almost no tubes between the middle and the right assemblage.

The emergence of dense assemblages has consequences for the near-bottom flow. As indicated by the arrows below the panels of Fig. 7, the near-bottom flow is deflected around the assemblages, leading to higher flow velocities at the edges of the assemblages. Note that the arrows are not produced by the

simulation model, but represent an additional verbal model on the relationship between dense assemblages of tubes and the near-bottom flow. In the lower panel of Fig. 7, the flow deflected around the middle and the right assemblage superimpose, leading to a very high velocity of the near-bottom flow. This in turn leads to a stronger shear stress which might prevent the establishment of new tubes outside the assemblages. Thus, the lateral expansion of the assemblages would stop. If we additionally assume that sediment accumulates within the assemblages and erodes within the gaps, then the process described in Fig. 7 leads to the emergence of a mosaic pattern of mounds and depressions which we also observe in nature. Based on this interpretation of the simulation model, our third hypothesis is:

(3) *A mosaic pattern of mounds with high tube densities and depressions with almost no tubes emerges at intermediate flow velocities, that is between those velocities that lead to low or high tube densities, respectively.* – Low flow velocities only lead to low tube densities which cause no deflection. For high flow velocities, lateral expansion of the assemblages is very fast, as is the growth in abundance and size of new assemblages which establish within the gaps. Therefore, there is no time for the mosaic pattern to emerge.

The only empirical evidence that we have to confirm the third hypothesis is the observation along the slope of a sandflat where the mosaic pattern is lo-
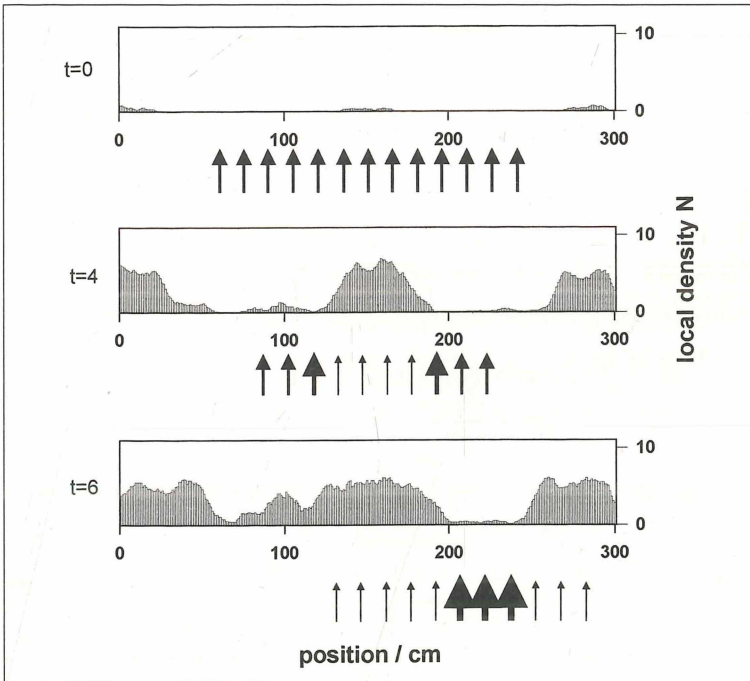

Fig. 7
Graphical model of the emergence of the small-scale mosaic pattern on a transect of 3 m length. Parameters used are: *maxL* = 20, *Psp* = 0.005, *maxT* = 10, *scale* = 20, *Pmort* = 0.5, *vscale* = 1.0. **Arrows are explained in the text.**

cated between areas with low and high densities (J. REICHERT, pers.com.; see above). Empirical tests of the third hypothesis would involve small-scale hydrodynamic measurements within the mosaic pattern, and experimental modifications of the local flow regime by constructing flow channels.

The model and the results presented in this paper are only a first step in trying to understand the causes of the distribution patterns of *L. conchilega*. The next step must be field and laboratory studies. Our three hypotheses might help to focus future empirical work on those aspects which are essential for the distribution and abundance of tube worms and their effects in the intertidal of the Wadden Sea.

Acknowledgements

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Addresses

Dr. Jens Heuers
Diplom-Biologin Sandra Jaklin
Alfred-Wegener-Institut für
Polar- und Meeresforschung
Columbusstraße
D-27568 Bremerhaven, Germany

Diplom-Biologin Ruth Zühlke
University of Wales, Swansea
School of Biological Science
Singleton Park
Swansea SA2 8PP
Great Britain

Dr. Sabine Dittmann
Dr. Carmen-Pia Günther
Forschungszentrum Terramare
Schleusenstraße 1
D-26382 Wilhelmshaven
Germany

Diplom-Physiker Hanno Hildenbrandt
Cappeler Str. 40
D-35037 Marburg
Germany

Dr. Volker Grimm
UFZ Umweltforschungszentrum Leipzig-Halle
Sektion Ökosystemanalyse
PF 2, D-04301 Leipzig
Germany