Distribution and Mobility of Juvenile Polychaeta in a Sedimentary Tidal Environment

Verbreitung und Mobilität juveniler Polychaeten in sandigen Watten

---

Norma Angélica Hernández-Guevara

Ber. Polarforsch. Meeresforsch. 502 (2005)
ISSN 1618 - 3193

Norma Angélica Hernández-Guevara
Wattenmeerstation Sylt
Alfred-Wegener-Institut für Polar- und Meeresforschung
Hafenstr. 43
25992 List/Sylt
Germany

Die vorliegende Arbeit ist die inhaltlich unveränderte Fassung einer Dissertation, die 2004 im Fachbereich Zoologie der Universität Kiel vorgelegt wurde.

Contents

ZUSAMMENFASSUNG

Es wird traditionell angenommen, dass die räumliche Verteilung benthischer Populationen hauptsächlich von *pre-settlement* (vor der Ansiedlung) Prozessen bestimmt wird. Doch häufen sich die Indizien, dass auch viele *post-settlement* (nach der Ansiedlung) Prozesse eine wichtige Rolle spielen können. In dieser Studie wurde die Ausbreitung juveniler Stadien nach der Ansiedlung als ein mögliches Schlüsselereignis für Verteilungsmuster von Adultpopulationen untersucht. Da Borstenwürmer (Polychaeten) eine der vielfältigsten und zahlreichsten Tiergruppen in marinen Weichböden sind, wurden sie als Beispiel herangezogen. Zuerst wurden Verteilungsmuster von juvenilen und adulten Polychaeten im Sylter Wattenmeer verglichen. Eine Beprobung erfolgte in fünf Habitaten: Sandwatten, Seegraswiesen, Schlickgrasbulten, Muschelschillfeldern und Miesmuschelbänken. Insgesamt wurden 43 Polychaetenarten bestimmt. Acht Arten trugen mit mehr als 90% zu der Gesamtabundanz bei (*Scoloplos armiger*, *Pygospio elegans*, *Nereis virens*, *Capitella capitata*, *Microphthalmus* sp., *Exogone naidina*, *Spio martinensis* und *Phyllodoce mucosa*). Der Anteil der übrigen Arten an der Geamtabundanz betrug jeweils weniger als 1%. Juvenile waren signifikant zahlreicher in strukturierten Habitaten (Seegraswiesen und Muschelschillfeldern) als in nicht-strukturierten Habitaten (Sandwatten). Strukturierte Habitate könnten also als Kinderstube dienen. Eine räumliche Trennung von juvenilen und adulten Würmern durch verschiedene Habitate wurde für *Ophelia rathkei*, *Microphthalmus* sp. und *Phyllodoce mucosa* festgestellt. Das lässt vermuten, dass in diesen Populationen Wanderungen nach der Ansiedlung stattfinden könnten. Ein weiteres Anzeichen für eine räumliche Verbreitung durch frühe benthische Entwicklungsstadien fand sich bei nahezu täglicher Beprobung von Verteilungsmustern juveniler Würmer auf kleinräumiger Skala (4 m^2) über einen Zeitraum von zwei Monaten. In diesen zeitlich und räumlich hoch aufgelösten Verteilungsmustern zeigten *Spio martinensis*, *Typosyllis hyalina*, *Ophelia rathkei* und *Capitella minima* eine hohe Variabilität, die größtenteils auf fortlaufende Ein- und Auswanderungen zurückzuführen sind. Sowohl aktive Wanderung als auch

passive Drift können dabei eine Rolle spielen. Anders als bei driftenden juvenilen Muscheln, wurden nur wenige juvenile Würmer in Wasserproben und bodennahen Driftnetzen gefunden. Um zu untersuchen, ob juvenile Polychaeten entweder im Boden bzw. im Übergangsbereich Wasser-Sediment kriechen oder in der bodennahen Wassersäule schwimmen, wurde ein *in situ*-Experiment durchgeführt. Hierfür wurde eine Kombination von Driftnetzen und in den Boden eingesenkten, nach oben abgedeckten Rinnen verwendet. Die Rinnen wurden mit von Polychaeten befreitem Sediment gefüllt, und über drei aufeinander folgende Gezeiten exponiert. In den Driftnetzen wurden keine juvenilen Würmer gefunden. In den Rinnen hingegen wurden *Ophelia rathkei*, *Pygospio elegans* und *Typosyllis hyalina* registriert, die eine Strecke von wenigstens einem Meter pro Tag aktiv innerhalb der Rinnen kriechen konnten. *Capitella capitata* erwies sich als weniger mobil. Es wird angenommen, dass eine benthische Ausbreitung der Juvenilen nach der Erstansiedlung (*post-settlement*-Verbreitung) für die Populationsökologie einiger Polychaeten eine wichtige Rolle spielt. Junge Würmer siedeln sich dort an, wo für sie günstigste Bedingungen herrschen, unabhängig von den Habitaten, die von Adulten bevorzugt werden. Aktive, benthische Wanderungen bringen die jungen Würmer zur richtigen Zeit zu geeigneten Orten, wo sie ihren Lebenszyklus vollenden können.

SUMMARY

It has been assumed that the distribution of marine benthic populations depends mainly on pre-settlement processes. However, evidence for many post-settlement processes has been provided recently. Juvenile dispersal after settlement is here investigated whether it attains a key role in determining spatial patterns of adult populations. Since polychaetes are one of the most diverse and abundant taxonomic groups in soft-sediment environments, they are chosen to explore the importance of this process. The first step in this study was to compare the distribution patterns of juvenile and adult polychaetes in a sedimentary tidal area of the Wadden Sea near the Island Sylt. Sampling included sandy flats, seagrass beds, cordgrass patches, mussel beds and fragmented shell patches. A total of 43 polychaete species is recorded. Eight species together comprised more than 90% of total abundance (*Scoloplos armiger*, *Pygospio elegans*, *Nereis virens*, *Capitella capitata*, *Microphthalmus* sp., *Exogone naidina*, *Spio martinensis* and *Phyllodoce mucosa*). All other species contributed less than 1%. Juvenile abundance was significantly higher in structured habitats (Seagrass beds and fragmented shell patches) than in non-structured ones (sandy flats). Structured habitats could serve as nurseries. Spatial separation of juveniles from adults across habitats was found in *Ophelia rathkei*, *Microphthalmus* sp. and *Phyllodoce mucosa*. This may indicate juvenile migration as a mandatory process in such populations. A second indication of dispersal by juvenile benthic stages was found, when small-scale distribution patterns (4 m^2) were analyzed almost daily over a two months period. At high spatio-temporal resolution, distribution patterns for *Spio martinensis, Typosyllis hyalina, Ophelia rathkei* and *Capitella minima* exhibited a high variability explained mostly by ongoing immigration and emigration. Both processes, active migration and passive transport may play a role. In contrast to extensive drifting in juvenile bivalves, only few juvenile polychaetes were found in water samples or in nets above the bottom. With the hypothesis that juveniles crawl at or below the sediment-water interface, an *in situ* experiment was set up. A combination of drift

nets and covered grooves placed level with the sediment surface were used in order to trace crawling performance in juveniles. Grooves were filled with sediment free of polychaetes and placed on intertidal flats for three tidal cycles. No juvenile worms were found in the drift nets, while in the grooves *Ophelia rathkei*, *Pygospio elegans*, and *Typosyllis hyalina* were able to crawl actively at least one meter per day, while *Capitella capitata* was less mobile. It is assumed that post-settlement dispersal plays an important role in the population ecology of some polychaetes. Juveniles are able to settle in habitats favorable specifically for juveniles irrespective of habitats preferred by adults. Active migrations at the bottom may bring juveniles in due time to sites suitable for the completion of their life cycle.

1. GENERAL INTRODUCTION

An understanding of the patterns of distribution and abundance in organisms is often the basis for ecological evaluations and management decisions (Andrew and Mapstone 1987). An important task for marine ecologists concerns the knowledge of processes that regulate these patterns in benthic communities (Valiela 1984). Patterns are generated by a combination of physical forces and biological interactions. Sediment type, waves action, erosive currents and light intensity are examples of physical factors which limit benthic populations; biological ones include dispersal potential, intra- and interspecific competition, predation and parasitism.

In general benthic marine invertebrates release propagules that either remain near their parents or disperse as planktonic larvae. The latter may reach distant destinations more or less favorable for settlement and metamorphosis (Fraschetti *et al.* 2003). The structures of marine benthic populations with a pelago-benthic life cycle arise from pre- and post-settlement processes (Fig. 1; Possingham and Roughgarden 1990).

The relative importance of pre- and post-settlement processes differs between localities, hard and soft-bottoms as well as species (Stoner 1990, Ólafsson *et al.* 1994, Hunt und Scheibling 1997, Todd 1998, Fraschetti *et al.* 2003). Usually planktonic larvae are considered to serve as the dispersal phase of the population (Strathmann 1974, Scheltema 1986). Planktonic larvae are also considered the most vulnerable stage in the life cycle in marine invertebrates, since larval mortality exceeds 90% (Thorson 1950). Nevertheless, it is discussed whether benthic distribution patterns are predictably based on the fate of larvae (Bhaud 1982, 1998 and 2000, Todd 1998).

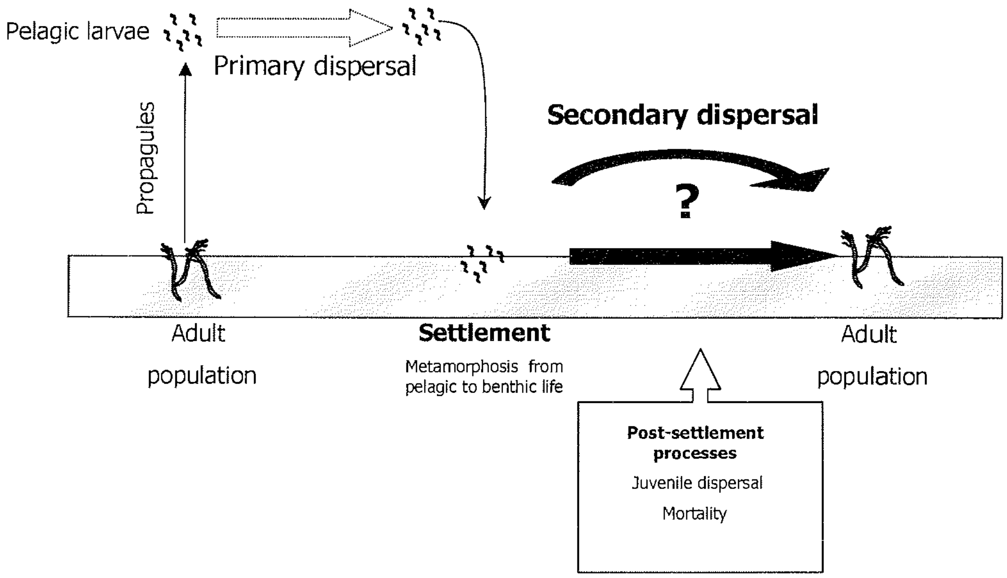


Figure 1. Scheme of pre- and post-settlement with primary and secondary dispersal in benthic invertebrates with pelago-benthic development. By means of secondary dispersal juveniles may either return to the parent population or found an adult population at a new site. The modes and importance of secondary dispersal in juvenile polychaetes is the subject of this study (bold signs).

Settlement is a critical process (see Woodin 1986, and Butman 1987 for reviews). However, a clear definition is still pending. Butman (1987) considers settlement as the moment when the organism adopts a behavior which is indicative of the benthic life history stage. The site of settlement is critical for the success of recruitment. While settlement is a biological phenomenon, recruitment is operationally defined as the entry into the benthic population of individuals that have survived up to a specific size after settlement (Fraschetti *et al.* 2003). Recruitment has five major components: input of propagules into the water column, their transport, planktonic mortality, settlement and post-settlement growth and survival (Jenkins *et al.* 1999).

Post-settlement events include a wide spectrum of processes, from adult-juvenile interactions (chemical cues, bioturbation, competition for space, etc.) to predation, interspecific competition and performance in the vagaries of the physical environment (Ólafsson *et al.* 1994, Todd 1998, Fraschetti *et al.* 2003). Early juvenile mortality may rival the loss of larvae as the most important factor influencing benthic populations, since in some cases mortality is higher than 90% of the larvae that have settled. Factors involved in juvenile mortality after settlement were reviewed in Gosselin and Qian (1997) and Hunt and Scheibling (1997). Particularly studies on colonization or recolonization of disturbed areas emphasized the importance of post-settlement stages (juveniles and adults) to disperse into a vacated area (Bonsdorff 1983, Levin and DiBacco 1995, Whitlatch *et al.* 1998). For bivalves a secondary dispersal phase (also called bysso-pelagic migration phase, Bayne 1964) is well documented (Armonies 1992, Armonies and Hellwig-Armonies 1992, Lasiak and Barnard 1995, Dunn *et al.* 1999, Norkko *et al.* 2001). Secondary dispersal may be passive (resuspension, drift), active (swim, crawl), or a combination of both, and takes place in the sediment-water interface or the water column (Günther 1992). Post-settlement events generally operate at smaller spatial scales than pre-settlement ones (Fraschetti *et al.* 2003).

The objective of this study is to explore post-settlement dispersal in polychaete worms. Polychaetes are often the most abundant or second most abundant after bivalves in the marine macrobenthic fauna in the Wadden Sea (Beukema 1989, Lackschewitz and Reise 1998). They are also one of the groups with the highest diversity of reproductive traits among marine invertebrates (Giangrande 1997). This is probably due to the relative simplicity of their reproductive systems combined with a high plasticity and adaptability to different habitats (Wilson 1991).

A study of Rodríguez-Valencia (2003) has dealt with the planktonic part of the polychaete community in the List tidal basin between the islands of Sylt and Rømø in the northern Wadden Sea. He describes larval distribution patterns and factors that could affect larval ecology. This companion study deals with the benthic component. Three main questions are treated:

- How are early post-settled polychaetes distributed in space and time in relation to the adult distribution? (Chapter II *Abundance and distribution of juvenile and adult polychaetes: are tidal flats nursery habitats?*)
- What evidence exists that polychaete post-settlers have the ability of secondary dispersal? (Chapter III *Small-scale dispersion of juvenile polychaetes: indirect evidence of benthic mobility*)
- Can this secondary dispersal be traced either in the water column or in the sediment? (Chapter IV *Mobility of marine benthic invertebrates: an experimental approach with juvenile polychaetes on a sandy tidal flat*)

Finally chapter V (*Final discussions*) gives an overview on the ecological implications of the results found during this study. The importance of some post-settlement events for benthic-pelagic coupling is briefly discussed.

2. ABUNDANCE AND DISTRIBUTION OF JUVENILE AND ADULT POLYCHAETES: ARE TIDAL FLATS NURSERY HABITATS?

Abstract

In marine benthic populations, juvenile benthic stages may be found outside the area of their adults. Since pelagic larvae may disperse over wide distances, it is possible that settlement occurs far away from their source population and in different habitats. Are juveniles after settlement capable to return to source areas, or the habitat types of the adults, or do they remain at the sites of settlement? In a tidal basin of the northern Wadden Sea (North Sea) where sandy tidal flats dominate, distribution patterns of juvenile and adult polychaetes were compared. Since structured habitats may provide protection against wave disturbance or predators, high abundance of juveniles was expected in such habitats. Samples were taken in seagrass beds, cordgrass patches, mussel beds, and fragmented shell patches as well as in the more extensive sandy flats (as non-structured habitat) at intertidal and subtidal sites. Juvenile stages were found in 10 out of 43 polychaete species. For *Eulalia viridis* juveniles were recorded only. Both, juveniles and adults showed a preference for the structured seagrass beds and fragmented shell patches. Cordgrass patches and mussel beds were not suitable habitats for polychaetes. High densities of juvenile polychaetes in seagrass beds and fragmented shell patches stress the role of these structured habitats as potential nurseries. This implies that juveniles may undertake migrations to reach the unstructured area where the bulk of their adults reside.

1. Introduction

The description of patterns is of fundamental importance in ecology and the information on the distribution and abundance of organisms is often the sole basis for management decisions (Andrew and Mapstone 1987). There is still only a modest understanding on how patterns in marine benthic invertebrates are maintained (Snelgrove and Butman 1994, Snelgrove *et al.* 2001).

Spatial patterns in soft sediment assemblages from temperate regions have primarily been correlated with changes in water depth and sediment characteristics (Gray 1974, 1981; Whitlatch 1981). Early post-settled organisms were often ignored in these studies. In invertebrates with a bentho-pelagic life cycle these post-settlers represent only a temporary part of the population. Also, methods were often size-selective and the small juveniles were overlooked. Most studies on post-settled organisms focused on recruitment rather than initial colonization, and where experimental sediments were spatially separated from the natural habitat (non *in-situ* approaches) migration potential was disregarded (Snelgrove *et al.* 2001).

The "specific-area", a term introduced by Bhaud (2000), is defined as that area where larvae can settle, juveniles can grow, and adults can reach maturity and reproduce. Thus, records of species occurrence not including the whole life cycle are insufficient (Bhaud 2000). Some habitats like seagrass beds may play a very important role in the distribution of some benthic species, because they could act as nursery habitats (Boström and Bonsdorff 2000). In the selected study area, List tidal basin, an overview on macrobenthic abundances is given by Reise and Lackschewitz (1998). Studies on specific habitats and their associated biota are available for seagrass beds (Schanz 2003), mussel beds (Buschbaum 2002, Saier 2002), fragmented shell patches (Wolf 2002), cordgrass patches (Löbl 2002). Specific studies of polychaete distribution patterns are scarce (Reise 1983a and b, 1984; Reise *et al.* 1994, Zühlke and Reise 1994). The main questions to be answered in this study are: How are benthic polychaete stages distributed in the List tidal basin? Have early post-settled worms different distributions than adults? Do juveniles prefer structured over non-structured habitats?

It could be expected that juveniles have higher abundances in structured habitats because these offer protection against wave disturbance, predation, or provide specific food (Beck *et al.* 2003).

2. Methodology

2.1 Study Area

This study was carried out at the northernmost part of the German Wadden Sea (North Sea) in the List tidal basin (Fig 1). This basin was formed about 5,500 years ago and became confined by causeways constructed at the first half of the 20th century (Bayerl and Köstner 1998). This bight comprises about 400 km^2; with one third being intertidal flats. Sandy sediments predominate, and 3% of the tidal area consists of muddy flats and 2% of salt marshes (Bayerl *et al.* 1998). Mean tidal range is 2 m. Tides are semidiurnal, and the high tide water volume is twice the low tide volume (Backhaus *et al.* 1998). Salinity remains close to 30 PSU and water temperature in summer rarely exceeds 22°C (Asmus 1982). The tidal inlet "Lister deep" (2.5 km wide) is the only connection with the North Sea and it transports about 7×10^8 m^3 of water during each tide.

Diverse habitats are represented in the List tidal basin: sand flats, mud flats, mussel beds, seagrass beds (*Zostera noltii* and *Z. marina*), fragmented shell patches, and cordgrass patches (*Spartina anglica*). Gätje and Reise (1998) provide a detailed description of the hydrodynamic and biotic characteristics of the List tidal basin.

2.2 Materials and Methods

2.2.1 Sampling Methods

Samples were taken at several sites of the List tidal basin and one site is located south of Hindenburgdamm (See Fig 1, Table 1). A detailed description of sampling methods and design is given below.

Table 1. Sample sites with dates and habitats. Numbers in ( ) indicate depth (m) above (+) and below (-) mean tide level. For locations see Fig. 1.

I= Intertidal zone, S= Subtidal zone

Site (location in study area map)		Date of sampling	Habitats
Ostfeuerwatt (A)	I	2000: Apr 28, May 12, Jun 9 2001: Mar 11 and 31, Apr 16, Aug 1 and 15 2002: Aug 1	Sandy flats (+0.5)
Möwenbergwatt (B)	I	2000: Apr 20, May 8 and 15, Jun 2, Aug 16 2001: Mar 10 and 30, Apr 15, Jul 24, Aug 22 2002: Aug 12	Sandy flats (+0.5) Mussel beds (-0.5)
Oddewatt (C)	I	2001: Jul 24, Aug 14 2002: Aug 14	Sandy flats (-1.0) Fragmented shell (-1.5) Mussel beds (-1.5)
Lister Ley (D)	S	2001: Jul 13 and 27, Aug 10 2002: Aug 20	Sandy flats (-3.5)
Uthörn (E)	I	2001: Mar 10 and 30, Apr 15	Sandy flats (+0.5)
Blidsel (F)	I	2001: Aug 3	Sandy flats (+0.5) Cordgrass patches (+0.75) Seagrass beds (-1.0)
Hunningen Sände (G)	S	2000: May 15, Jul 17, Aug 22 2001: Mar 5, May 14, Jun 18	Sandy flats (-4.0) Fragmented shell (-4.0)
Rantum (H)	I	2001: Aug 7 and 20	Sandy flats (+0.5) Cordgrass patches (+0.75) Seagrass beds (-0.5)

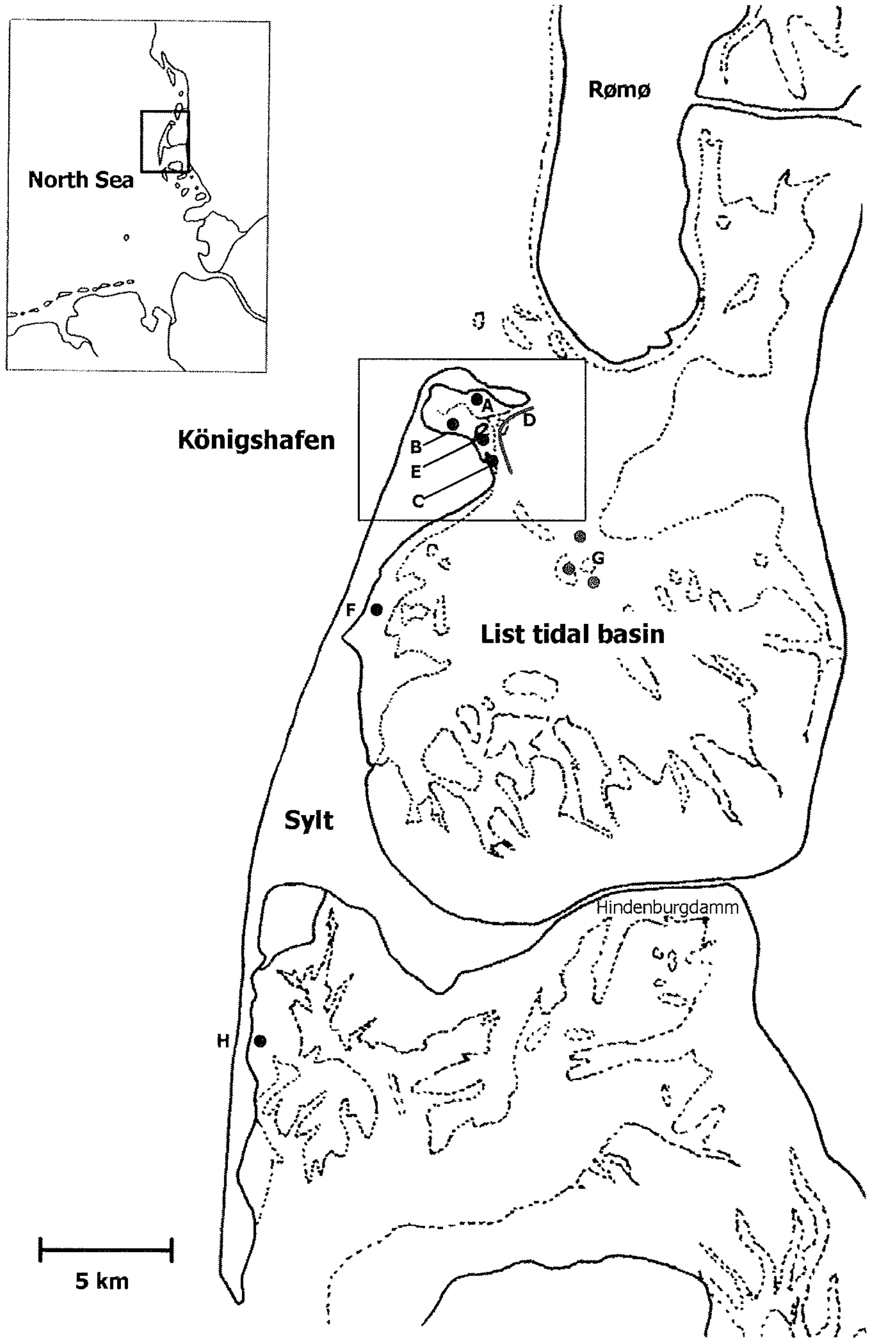


Figure 1. Study area in the northern Wadden Sea. Spring low tide is stippled. For sampling locations A-H see Table 1.

In order to determine abundance of juvenile and adult Polychaeta in different habitats, samples from sandy flats, seagrass beds, cordgrass patches, mussel beds, and fragmented shell patches were collected.

Each sample consisted of a sediment box corer 15 x 15 cm (0.0225 m^2) down to a sediment depth of ca. 20 cm. From each core, three sub-samples (10 cm^2 x 5 cm depth) were obtained. After that, the core was sectioned as follows: the first 5 cm were sieved through 500 µm mesh and the rest (aprox. 15 cm) was sieved through a 1000 µm mesh while the retained material was taken to the laboratory for analysis. Sub-samples were sieved through a 250 µm mesh in the laboratory (Fig. 2).

Sampling design

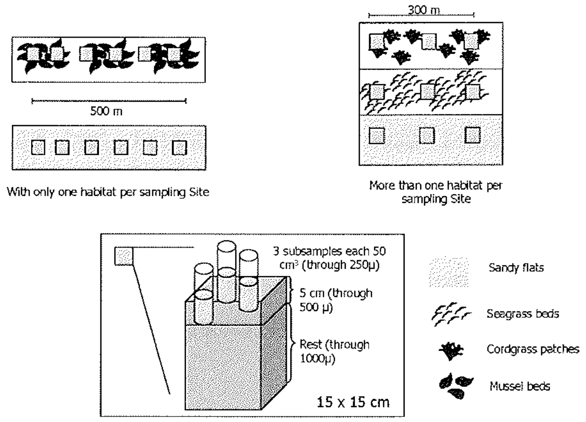
Intertidal sites:

At the intertidal sites if only one habitat type was present (e.g. Ostfeuerwatt with only sandy flats), 6 samples (box corer 15 x 15 cm) were collected along a transect (ca. 500 m) parallel the mean water line with a 100 m interval between samples. Where more than one habitat was present (e.g. Blidsel with seagrass beds, *Spartina anglica* patches and sandy flats), one transect (ca. 300 m) was defined along each habitat and 4 to 6 samples were taken (Fig. 2).

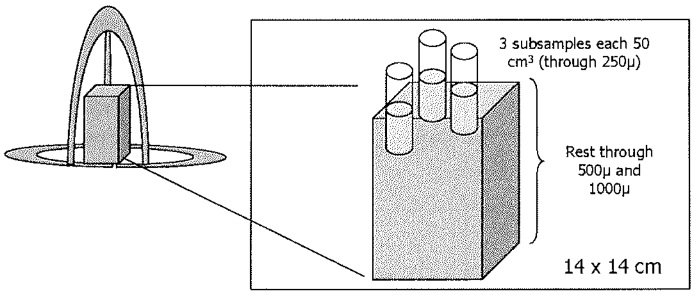
Subtidal sites:

In the subtidal zone near of Lister Ley, samples were taken at 8 sites along a transect. At each sample site three box cores (0.02 m^2) were collected.

At Hunningen Sände, samples were taken at three sites, and also at each site three box cores were collected (Fig. 2).



Intertidal



Subtidal

Figure 2. Schematic description of sampling methods applied at intertidal and subtidal zones.

Adult polychaete stages were identified with Hartmann-Schröder (1996), larval stages with Bhaud and Cazaux (1992). For juvenile stages no identification keys are available. They were identified with adult and larval identification keys, since a combination of morphological characteristics of both developmental stages were present in juveniles. A reliable determination was only possible with both identification keys and additional literature on specific taxa. Dr. Angel de León-González (University on Nuevo León, Mexico) confirmed the identifications.

The number of organisms found as well as their developmental stage was recorded. Here, larvae were considered as organisms having characteristics for planktonic life (pigments, yolk reserves, swimming organ, cilia, etc.; Bhaud and Cazaux 1992) but found alive in the sediment and without traces of metamorphosis. Juvenile stages were defined as organisms that have already metamorphosed but lacking size and morphology known from reproductive individuals. Adults were sexually mature organisms and which show conspicuous adult characteristics. Criteria used in specific cases are presented in Table 2.

Table 2. Distinguishing characteristics for juvenile and adult polychaetes of the most frequent species found in the study area.

Species	**Juveniles**	**Adults**
Scoloplos armiger	Size: 0.2 mm- 15 mm	Size: > 15 mm
Pygospio elegans *Spio martinensis* *Polydora ciliata* *Polydora cornuta*	Presence of melanophores, swim cilia and setae	Without larval pigments (melanophores)
Capitella capitata	Size: 0.2 mm-10 mm Transparent	Size:>10 mm
Capitella minima	Size: 0.2 mm- 10 mm	Size: >10 mm
Phyllodoce mucosa	Size: 0.2 mm- 30 mm Transparent coelome	Size: >30 mm
Lanice conchilega	Size: 0.2 mm- 30 mm	Size: >30 mm
Microphthalmus sp.	Size: 0.2 mm- 5 mm Transparent	Size: >5 mm
Nereis virens *Nereis diversicolor*	Size: 1- 30 mm	Size: >30 mm
Typosyllis hyalina	Size: 0.2 mm-10 mm	Size:>10 mm

2.2.2 Habitat preferences

Comparisons of habitat preferences were done with samples taken in August 2001. For this section all species are considered.

To test if structured habitats were preferred over a non-structured habitat, seagrass beds, cordgrass patches and sandy flats were compared at the same locality. Also mussel beds, fragmented shell patches and sandy flats were compared at a single locality.

In order to test for differences in abundance or species composition within intertidal sandy flats, comparisons between sites in Königshafen (Fig. 1: A, B, C) were made.

Comparison between sub- and intertidal habitats was done for intertidal sandy flats Königshafen (Fig. 1: A, B, C) and a subtidal site in Lister Ley.

All comparisons were made with One-way ANOVA-tests using STATISTICA for Windows Version 6 [Stat Soft, Inc. (2003)]. In case of significant differences, post-hoc tests (Tukey HSD test) were made.

Comparison of species composition in sandy flats was made by means of Cluster analyses using PRIMER 5 for Windows Version 5.2.9.

2.2.3 Species-specific patterns

For the most abundant species tests on habitat preferences were made as described above.

In order to test whether adult and juveniles are distributed in the same way, analyses of abundances over time were made for 2001 due to a high temporary resolution of sampling in that year. Mean abundances of juveniles and adults per sampling month were obtained lumping all subtidal sites and all intertidal sites near Königshafen (Fig. 1: A-D) together.

3. Results

3.1 Species spectrum

Eighteen polychaete families were found in benthic stages, 29 genera and 43 species. 42 were found as adult stages, 31 as juveniles and 4 also as larvae (Table 3). Spionidae were the most diverse with 11 species, followed by Nephtyidae (6 species) and Phyllodocidae (4 species). *Eulalia viridis* was only found in juvenile stages. For *Magelona mirabilis*, *Nephtys hombergii*, *N. longosetosa*, *N. caeca*, *Phyllodoce maculata*, *Protodrilus adhaerens*, *Sphaerodoropsis baltica*, *Scolelepis foliosa*, *Spio filicornis*, and *Spiophanes bombyx* no juvenile stages were found.

Table 3. List of identified polychaete species in the benthos near the island of Sylt (northern Wadden Sea) from 2000 to 2002. For locations see Figure 1 and Table 1. Letters in [] indicate the development stages found. L=larvae, J=juvenile, A=adult.

Family	Species	Location
Phyllodocidae	*Phyllodoce (Anaitides) maculata* (Linne, 1767) **[A]**	D
Oersted, 1843	*Phyllodoce (A.) mucosa* Oersted, 1843 **[A, J]**	ABCDEFGH
	Eteone (Eteone) longa (Fabricius, 1780) **[A, J]**	ABCDEFGH
	Eulalia viridis (Linné, 1767) **[J]**	D
Hesionidae	*Microphthalmus* sp. (Webster & Benedict, 1887) **[A, J]**	ABCDEFGH
Malmgren, 1867		
Syllidae	*Typosyllis (Typosyllis) hyalina* (Grube, 1863) **[A, J]**	ABCDEG
Grube, 1850	*Exogone (Exogone) naidina* Oersted, 1845 **[A, J]**	ABCDEG
Nereididae	*Nereis (Hediste) diversicolor* O.F. Müller, 1776 **[A, J]**	ABCFH
Johnston, 1865	*Nereis (Neanthes) virens* Sars, 1835 **[A, J]**	ABCDEFGH
Nephtyidae	*Nephtys caeca* (Fabricius, 1780) **[A]**	DG
Grube, 1850	*Nephtys cirrosa* Ehlers, 1868 **[A, J]**	DG
	Nephtys hombergii Savigny, 1818 **[A]**	ABCDG
	Nephtys incisa Malmgren, 1865 **[A]**	G
	Nephtys longosetosa Oersted, 1842 **[A]**	CDG
	Nephtys pulchra Rainer, 1991 **[A, J]**	D

Table 3. Continued.

Family	Species	Location
Sphaerodoridae Malmgren, 1867	*Sphaerodoropsis baltica* (Reimers, 1933) **[A]**	G
Orbiniidae Hartman, 1942	*Scoloplos (Scoloplos) armiger* (O.F. Müller, 1776) **[A, J]**	ABCDEFGH
Spionidae Grube, 1850	*Malacoceros fuliginosus* (Claparède, 1868) **[A, J]**	ABCDFG
	Polydora (Polydora) ciliata (Johnston, 1838) **[A, J, L]**	BCDG
	Polydora (Polydora) cornuta Bosc, 1802 **[A, J]**	ABCD
	Polydora sp.	ABFH
	Pseudopolydora sp.	B
	Pygospio elegans Claparède, 1863 **[A, J, L]**	ABCDEFGH
	Scolelepis (Scolelepis) foliosa (Audouin & Milne-Edwards, 1833) **[A]**	BD
	Scolelepis (S.) squamata (O.M. Müller, 1806) **[A, J]**	ADG
	Spio filicornis (O.F. Müller, 1766) **[A]**	BDG
	Spio martinensis Mesnil, 1896 **[A, J, L]**	ABCDEGH
	Spiophanes bombyx (Claparède, 1870) **[A]**	BCDGH
Magelonidae Cunningham & Ramage, 1888	*Magelona alleni* Wilson, 1958 **[A, J]**	G
	Magellona mirabilis (Johnston, 1865) **[A]**	BDG
Protrodrilidae Czerniavsky, 1881	*Protodrilus adhaerens* Jägersten, 1952 **[A]**	DG
Paraonidae Cerruti, 1909	*Aricidea (Aricidea) minuta* Southward, 1956 **[A, J]**	ABCDEG
Cirratulidae Carus, 1863	*Aphelochaeta marioni* (Saint-Joseph, 1894) **[A, J]**	CDF
	Tharyx killariensis (Southern, 1914) **[A, J]**	A
Opheliidae Malmgren, 1867	*Ophelia limacina* (Rathke, 1843) **[A, J]**	G
	Ophelia rathkei McIntosh, 1908 **[A, J]**	ABCDEGH
Capitellidae Grube; 1862	*Capitella capitata* (Fabricius, 1780) **[A, J]**	ABCDEFGH
	Capitella minima Langerhans, 1880 **[A, J]**	AC
	Heteromastus filiformis (Claparede, 1864) **[A, J]**	ABCDEFH
Arenicolidae Johnston, 1846	*Arenicola marina* (Linné, 1758) **[A, J]**	ABCDEFH

Table 3. Continued.

Pectinariidae QUATREFAGES, 1865	*Pectinaria (Lagis) koreni* MALMGREN, 1865 **[A, J]**	BDH
Terebellidae MALMGREN, 1865	*Lanice conchilega* (PALLAS, 1766) **[A, J, L]**	BCDEGH
Sabellidae MALMGREN, 1876	*Fabricia stellaris stellaris* (MÜLLER, 1774) **[A, J]**	ABEH

3.2 Dominance

Few species together hold more than 90% of the total abundance: *Scoloplos armiger* (33%), *Pygospio elegans* (15%), *Nereis virens* (15%), *Capitella capitata* (12%), *Microphthalmus* sp. (7%), *Exogone naidina* (3%), *Spio martinensis* (3%) and *Phyllodoce mucosa* (2%). 35 species were present with less than 1% of the total abundance.

S. armiger was the most abundant species throughout the study period (Table 4). The less abundant species changed ranks between years.

Table 4. Relative abundance of top ranking species in all samples taken in three consecutive years. For Dates see Table 1.

2000	%	2001	%	2002	%
S. armiger	40	*S. armiger*	26	*S. armiger*	47
N. virens	30	*C. capitata*	18	*Microphthalmus* sp.	18
P. elegans	18	*P. elegans*	13	*P. elegans*	7
C. capitata	6	*Microphthalmus* sp.	12	*A. minuta*	6
S. martinensis	3	*E. naidina*	6	*S. martinensis*	4
		P. mucosa	4	*P. mucosa*	4

3. 3 Habitat preferences

Comparisons were made first between seagrass beds, cordgrass patches (both as structured habitats) and sandy flats (non-structured habitat).

Juveniles were more abundant in seagrass beds than in sandy flats or cordgrass patches ($F_{(2)}$=7.1151, $p<0.05$) (Fig. 3, Table 5). Of juveniles, 11 species were present in seagrass beds, 5 in cordgrass patches and 8 in sandy flats. *Fabricia stellaris, S. armiger, P. elegans* and *C. capitata* were the dominant species in seagrass beds. *S. armiger, C. capitata* and *N. virens* had more than 80% of the abundance in cordgrass patches. *S. armiger, C. capitata* and *F. stellaris* were in sandy flats the most abundant species.

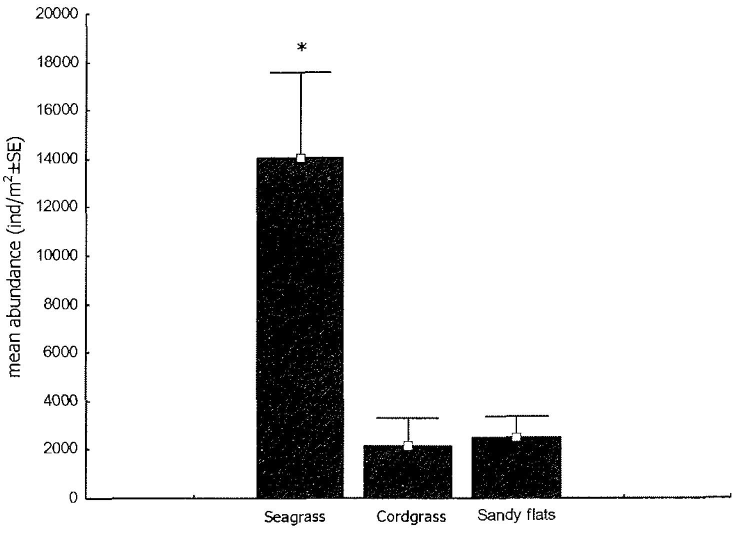


Figure 3. Mean juvenile abundance in three habitats (August, 2001. Sites F, H in Fig. 1). * indicates significantly higher abundances differences (seagrass n= 10, cordgrass patches n=9, sandy flats n=9).

Table 5. Habitat preferences of juveniles. One-way ANOVA test results and Tukey HSD post-hoc values.

One- way ANOVA

	SS	dF	MS	*F*	P
Habitat	8.480261E+08	2	424013040	7.11517	0.003931
Error	1.370634E+09	23	59592800		

Tukey HSD post-hoc test

	seagrass	cordgrass patches	sand
seagrass		0.007528	0.015941
cordgrass patches	0.007528		0.994867
Sand	0.015941	0.994867	

Also adults were more abundant in seagrass beds than in cordgrass patches and sandy flats ($F_{(2)}$=21.42, p<0.01) (Fig. 4 and Table 6). 13 species were found in seagrass beds, while in cordgrass patches only 6 species were recorded, and 8 in sandy flats. Different species were dominant in each habitat. In seagrass beds *Aphelochaeta marioni*, *S. armiger*, *Microphthalmus* sp., *P. elegans* and *C. capitata* comprised 80% of total abundance. In cordgrass patches *C. capitata*, *Microphthalmus* sp. and *H. filiformis* had together more than 80% of total abundance and in sandy flats *C. capitata*, *S. armiger* and *Microphthalmus* sp. were the most abundant species.

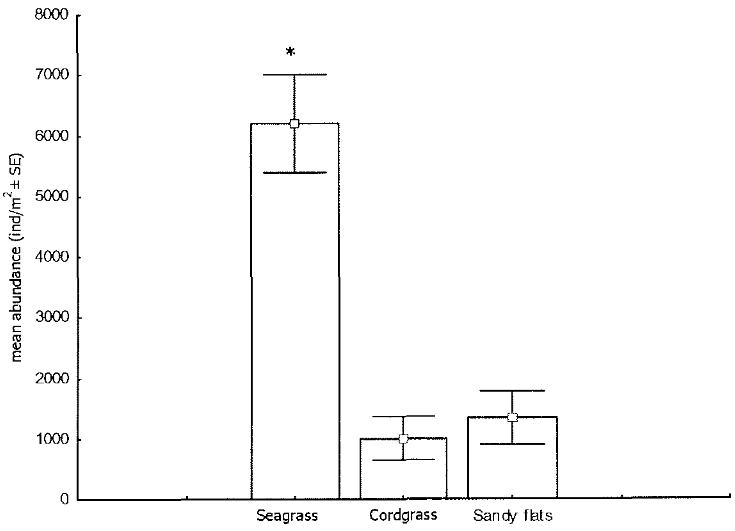


Figure 4. Mean adult abundance in three habitats (August, 2001. Sites F, H in Fig. 1). * indicates significantly higher abundance (seagrass n= 10, cordgrass patches n=9, sandy flats n=9).

Table 6. Habitat preferences of adults. One-way ANOVA test results and Tukey HSD post-hoc values.

One-way ANOVA

	SS	dF	MS	*F*	P
Habitat	157068803	2	78534401	21.41675	0.000006
Error	84340102	23	3666961		

Tukey HSD post-hoc test

	Seagrass	cordgrass patches	sand
seagrass		0.000143	0.000213
cordgrass patches	0.000143		0.935205
Sand	0.000213	0.935205	

A second comparison was made between mussel beds, fragmented shell patches (both as structured habitats) and sandy flats (as non-structured habitat). In both, juveniles ($F_{(2)}$=7.8143, $p<0.01$) and adults ($F_{(2)}$=10.8745, $p<0.01$) a significant preference for fragmented shell patches was found (Fig. 5 Tables 7 and 8).

Juvenile mean abundance in mussel beds was significantly lower than in sandy flats and fragmented shells patches (after Tukey HSD-test, $p<0.05$). 13 species were found as juveniles in sandy flats, where *P. elegans*, *S. martinenis*, *C. capitata*, *Microphthalmus* sp. and *S. armiger* had more than 80% of the total abundance. In fragmented shells patches 12 species were found. Juveniles of *S. armiger*, *C. capitata*, *P. elegans* and *Microphthalmus* sp. comprised 80% of the total abundance in this habitat. In mussel beds only 4 species were found as juveniles and only *N. virens* and *S. armiger* were here dominant.

Adult mean abundance was higher in fragmented shell patches than in sandy flats and mussel beds (after Tukey HSD-test, $p<0.01$). 17 species were found in sandy flats as well as in fragmented shell patches, and only 7 in mussel beds. In sandy flats, *Malacoceros fuliginosus* together with *Exogone naidina*, *P. elegans*. *Phyllodoce mucosa* and *Microphthalmus* sp. were the dominant species. In patches of fragmented shell more than 80% of the total abundance was recorded with *E. naidina*, *Microphthalmus* sp. and *P.mucosa*. In mussel beds the dominant species were *P. elegans*, *C. capitata* and *Polydora ciliata*.

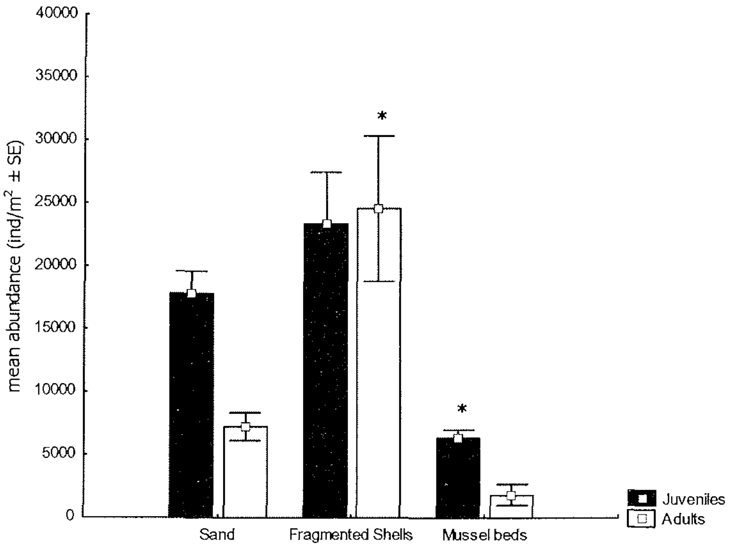


Figure 5. Mean adult abundance of juveniles and adults in three habitats (June and August, 2001. Sites B, C in Fig. 1). * indicates significantly different abundance compared to the other habitats within juveniles and adults (sand n= 6, fragmented shell patches n=6, mussel beds n=6)

Table 7. Habitat preferences of juveniles. One-way ANOVA test results and Tukey HSD post-hoc values.

One-way ANOVA

	SS	dF	MS	*F*	P
habitat	5.049768E+08	2	2.524884E+08	7.81435	0.009044
Error	3.231086E+08	10	3.231086E+07		

Tukey HSD post-hoc test

	sand	fragmented shell	mussel beds
Sand		0.332741	0.041352
fragmented shell	0.332741		0.007571
mussel beds	0.041352	0.007571	

Table 8. Habitat preferences of adults. One-way ANOVA test results and Tukey HSD post-hoc values.

One-way ANOVA

	SS	dF	MS	*F*	P
Habitat	1.067135E+09	2	5.335675E+08	10.87456	0.003100
Error		10	4.906565E+07		

Tukey HSD post-hoc test

	sand	fragmented shells	mussel beds
Sand		0.008669	0.543763
fragmented shells	0.008669		0.004583
mussel beds	0.543763	0.004583	

As sandy flats are the most extensive habitat in Königshafen, a comparison of three intertidal sandy sites inside the bay was made.

No significant differences in adult densities were found ($F_{(2)}$=0.379512, p>0.05), while those in juveniles were different ($F_{(2)}$=5.1221, p<0.01) (Fig. 6 Table 9 and 10). In Ostfeuerwatt highest mean densities were recorded (after Tukey HSD-test, p<0.05).

Table 9. Mean abundance of juveniles at three sandy intertidal sites in Königshafen. One-way ANOVA test results and Tukey HSD post-hoc values.

One-way ANOVA

	SS	dF	MS	*F*	p
locality	52061886	2	26030943	5.12210	0.019085
Error	81313399	16	5082087		

Tukey HSD posc-hoc test

	Odewatt	Ostfeuerwatt	Möwenbergwatt
Oddewatt		0.047530	0.890558
Ostfeuerwatt	0.047530		0.030125
Möwenbergwatt	0.890558	0.030125	

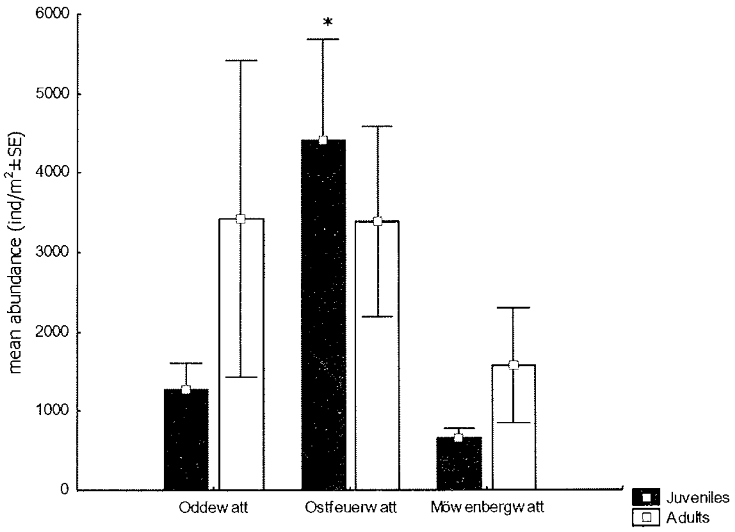


Figure 6. Mean density ± SE of juveniles and adults in sandy flats at three localities in Königshafen (August, 2002. Sites A, B, C in Fig. 1). * indicates significant differences within juveniles (all sites n=7).

Table 10. Mean abundance of adults at three sandy intertidal sites in Königshafen. One-way ANOVA test results.

	SS	dF	MS	*F*	p
locality	12442151	2	6221076	0.379512	0.690192
Error	262276647	16	16392290		

A cluster analyzes of the juvenile species composition between sandy flats for August 2002 shows a high similarity between all sites (Fig 7). Sampling sites do not fall into distinct groups.

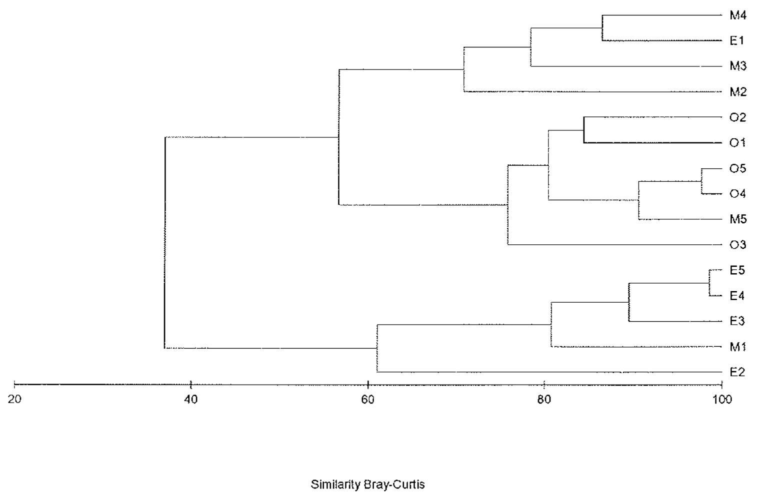


Figure 7. Cluster diagram of species composition analysis for sandy tidal flats in Königshafen, August 2002. (O=Oddewatt, M=Möwenbergwatt, E=Ostfeuerwatt) Index of similarity used: Bray-Curtis.

Comparisons between sub- and intertidal sandy flats for both juvenile and adult polychaetes revealed for juveniles no significant differences ($F_{(1,52)}=3.8084$, $p>0.05$), while abundances of adults in sub- and intertidal flats were different ($F_{(1,52)}=28.7259$, $p<0.01$) (Fig. 8). 13 species were recorded as juveniles in the intertidal sandy flats of Königshafen, while in the adjacent subtidal flats 17 species were found. In both, inter- and subtidal flats, *S. armiger*, *P. elegans*, *C. capitata* and *S. martinensis* were the most abundant species. Adults were most abundant in the subtidal flats near Königshafen, where also more species were recorded (31 species). In intertidal flats 25 species were found. *P. elegans, S. armiger,* *Microphthalmus* sp., *C. capitata* and *M. fuliginosus* comprised in both, inter- and subtidal sandy substrata, more than 80% of total abundance.

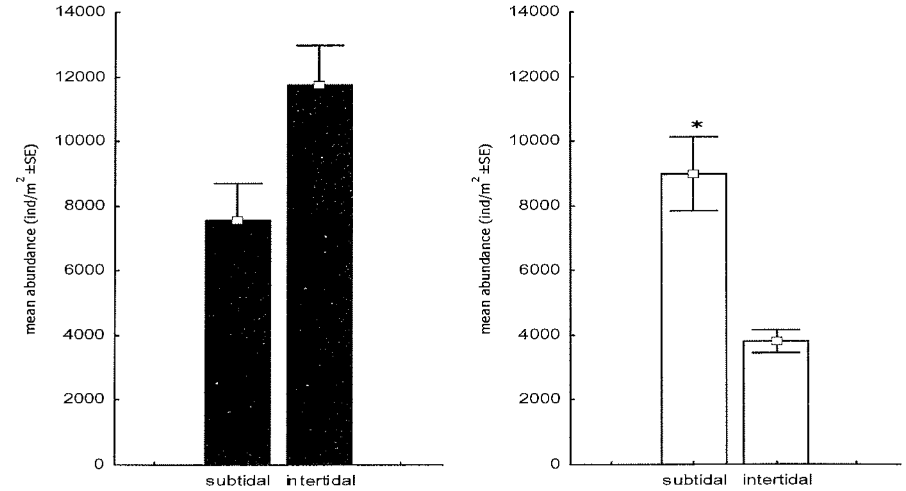


Figure 8. Mean abundance ± SE of juvenile and adult polychaetes in both sub- and intertidal flats in Königshafen (August, 2001. Sites A, B, C, and D in Fig. 1). Black bars=juveniles, white bars= adults (subtidal n=16, intertidal=32).

Only three species were found as larvae at high densities on mussel beds at two times (Table 11). This habitat seems to be an adequate settlement substrate. Larvae were not or only sporadically present in the benthic samples during this study.

Table 11. Larval densities on mussel beds.

Species	**Density**	**Date and site**
P. elegans	1,777±777 ind/m^2	May 8, 2000. Möwenbergwatt
S. martinensis	111±10 ind/m^2	May 8, 2000. Möwenbergwatt
L. conchilega	583±95 ind/m^2	March 3, 2001 Möwenbergwatt

3.4 Species-specific patterns

Patterns of spatial distribution for abundant species were investigated to detect a possible spatial segregation between juveniles and adults with respect to habitat types as well as the intertidal and subtidal zone.

Scoloplos armiger

Highest juvenile density was 12,760 ± 4,624 ind/m^2 and for adults it was 2,719 ± 734 ind/m^2. Juveniles were absent in cordgrass patches, while in fragmented shell patches abundances were significantly higher than in sandy flats and seagrass beds ($F_{(2)}$= 27.98677, p<0.01).

Juveniles showed similar dynamics at inter- and subtidal zones. Density increased continuously from March to August in both environments (Fig. 9). Adults showed an even temporal pattern over the same period. *S. armiger* juvenile and adults share the same habitat through time.

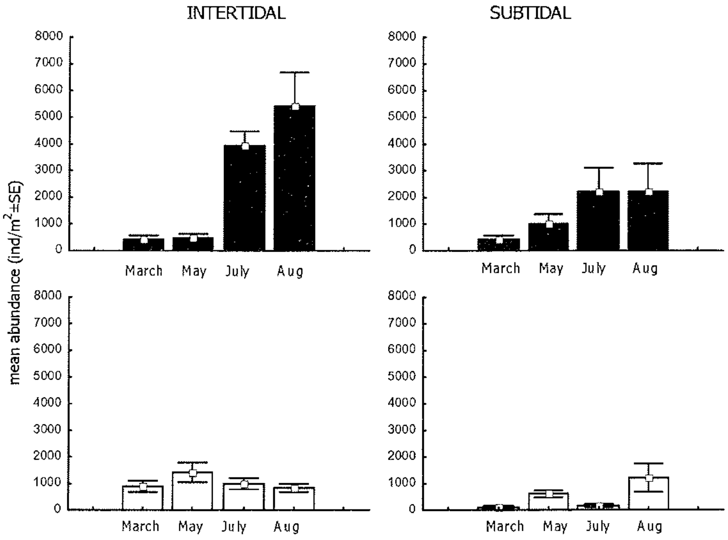


Figure 9. Temporal variability of juvenile and adult *Scoloplos armiger* in 2001 in Königshafen (sites A, B, C, E and D in Fig. 1 respectively) (black bars=juvenile, white bars= adults).

Nereis virens

Juvenile densities up to 12,796 ± 4,875 ind/m^2 were observed. Juveniles of *N. virens* were absent in seagrass beds but no significant differences in mean densities occurred between habitats in the intertidal zone ($F_{(2)}=2.3668$ $p>0.5$).

Juveniles of *N. virens* were most abundant in the intertidal zone but were present also in the subtidal. Adult densities were similar between intertidal and subtidal ($F_{(2)}=2.4723$, $p>0.05$). No segregation patterns between juvenile and adult worms were found, but it may be possible that intertidal juveniles migrate to the subtidal in order to maintain this adult population at the same density as in the intertidal (Fig. 10)

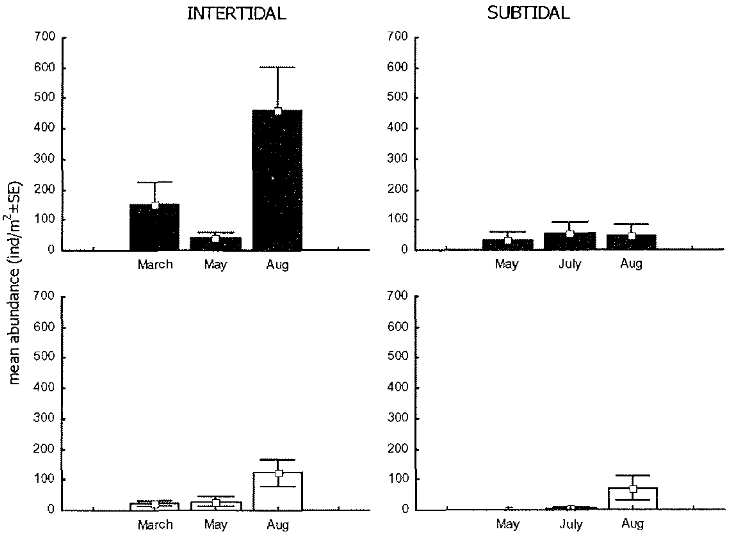


Figure 10. Temporal abundance variability in 2001 of *N. virens* at inter- and subtidal flats in Königshafen (sites A, B, C, E and D in Fig. 1 respectively) (black bars=juveniles, white bars=adults).

Pygospio elegans

The highest density of juvenile *P. elegans* was 7,419 ± 983 ind/m^2, and up to 3,809 ± 1,574 ind/m^2 adults were recorded. Post-settled larvae were found only in the subtidal zone (475 ± 23 ind/m^2).

Fragmented shell patches were the most suitable habitat for juvenile *P. elegans* ($F_{(3)}=149.9072$, $p<0.01$). And for adults sandy flats were the most adequate substrata ($F_{(3)}=3.4073$, $p<0.05$). This may indicate a juvenile migration to the surrounding sandy habitats.

The temporal variability of juvenile and adult abundances showed no differential patterns between tidal zones (Fig. 11).

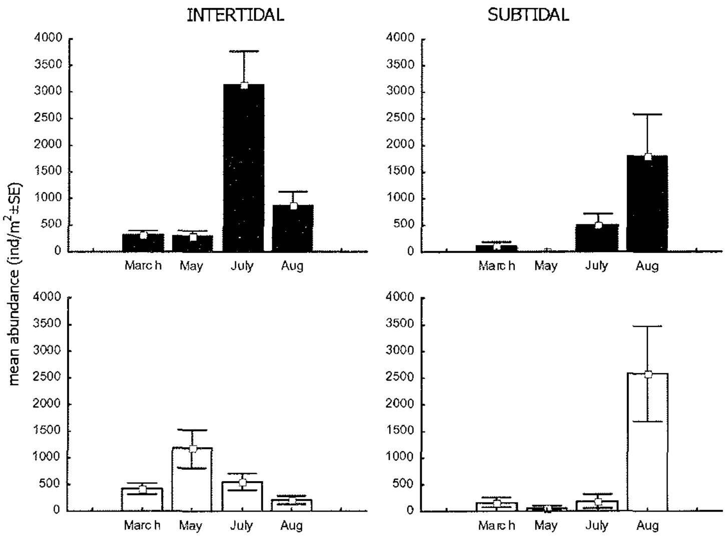


Figure 11. Temporal variability in 2001 of juvenile and adult *P. elegans* in Königshafen (sites A, B, C, E and D in Fig. 1 respectively) (black bars=juvenile, white bars= adults).

Ophelia rathkei

Juveniles were present in sandy flats and fragmented shell patches, with no significant differences in abundance ($F_{(2)}=0.0033$, $p>0.5$). Juveniles were present only at the intertidal zone with densities up to 125±71 ind/m^2. This represents a spatial segregation between adults and juveniles (Fig. 12).

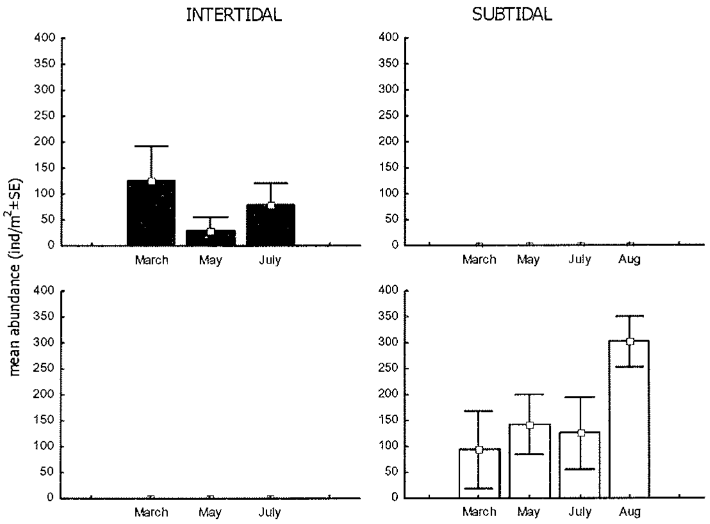


Figure 12. Temporal abundance variation of juvenile and adult *O. rathkei* in inter and subtidal regions around Königshafen (sites A, B, C, E and D in Fig. 1 respectively) (black bars=juveniles, white bars=adults).

Microphthalmus sp.

Maximal abundance of juveniles was 2,987 ± 984 ind/m^2, of adults 16,171 ± 7,273 ind/m^2. Juveniles of *Microphthalmus* sp. were only found in sandy substrata and among fragmented shells but no significant differences were found ($F_{(1)}=1.1147$, $p>0.05$).

The temporal abundance variation showed that juveniles were mainly at the intertidal, while adults occurred in both zones. The adult peak in August (Fig. 13) may stem from intertidal juveniles which migrated to the subtidal.

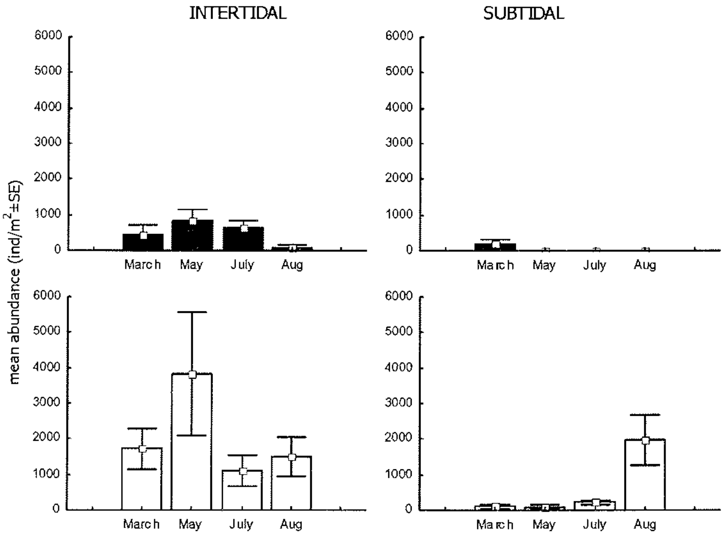


Figure 13. Temporal abundance variation in 2001 of juveniles and adults of *Microphthalmus* sp. in Königshafen (sites A, B, C, E and D in Fig. 1 respectively) (black bars=juveniles, white bars=adults).

Phyllodoce mucosa

As in *Microphthalmus* sp. and *O. rathkei* juvenile *P. mucosa* were only found in sandy flats and among fragmented shell patches but no significant differences occurred ($F_{(1)}=0.65930$, $p>0.05$). Juveniles were often found in *L. conchilega* tube-mats in the subtidal zone (per. Observ.). Adults were present in the intertidal zone as well as in the subtidal. Juveniles had highest abundances in the subtidal from July to August. In the intertidal, only in July an abundance peak was observed (167±27 ind/m^2). Juveniles from the subtidal may supply the intertidal part of the adult population (Fig. 14).

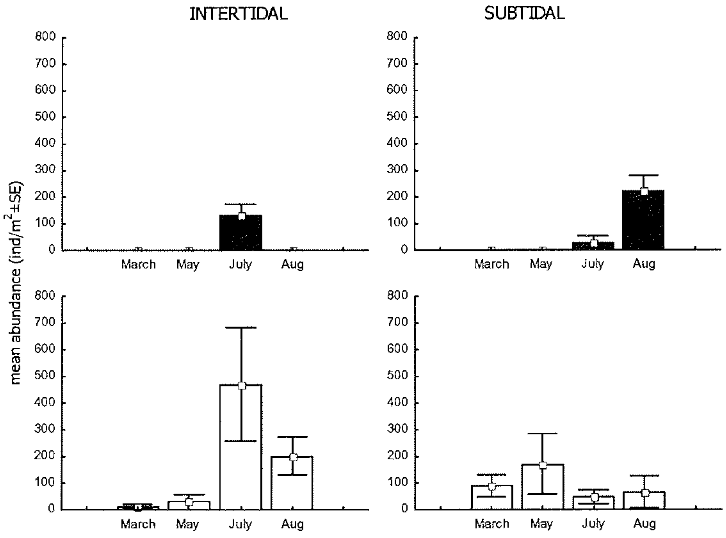


Figure 14. Temporal abundance variability in 2001 of juvenile and adult *P. mucosa* at the intertidal and subtidal around Königshafen (sites A, B, C, E and D in Fig. 1 respectively) (black bars=juvenile, white bars=adults).

Discussion

Species spectrum and dominance

Hundred-thirteen polychaete species have been registered for the Northern Wadden Sea, in larval, adult and juvenile stages (reviewed in Rodriguez-Valencia 2003). The present study detected 41. The absence of some species may be explained by a limited sampling effort over habitat types and seasons. Species which are present only as larvae were not taken into account. The identification of juveniles based on identification keys for larvae and adults may cause errors in identification. Another factor generated this low number of species here found, could be the high fluctuation in benthic composition due to climatic factors (Strasser *et al.* 2001 a and b, Strasser and Pieloth 2001). Westheide (1966) record 45 polychaete species for the study area, most of them mainly present in sandy beaches, this habitat was not sampled in this study. The dominance of *S. armiger*, *P. elegans*, and *C. capitata* over various habitat types in the study area is well known (Reise 1983, Reise *et al.* 1994). Nevertheless, the lack of samples from muddy substrates in this study, let to a low degree of dominance in some other species that are also important components of the Wadden Sea fauna (e.g. *Heteromastus filiformis* and *Tharyx* sp.).

Habitat preferences

Sandy sediments cover about 72% of the intertidal and predominate also the subtidal zone in the List tidal basin (Bayerl *et al.* 1998). Polychaete biomass in these areas is dominated by *Arenicola marina* (Reise and Lackschewitz 1998). Adult and juvenile polychaete densities were lower in sand in contrast to in seagrass beds. This may be explained with sandy flats being a less structured habitat, and sediment instability and high exposure to predators. Some differences in juvenile abundance between sandy areas inside Königshafen were found, although the sediment composition seems to be similar. The northern most part (Ostfeuerwatt) was characterized as an erosion area (Higelke 1998), and here juveniles were most abundant. This may be due the common occurrence of fragmented shells at eroding flats.

The intertidal zone of the List tidal basin is covered up to 12% with seagrass. Meadows are located in areas protected from westerly storms and are more or less stable (Reise and Lackschewitz 1998, Schanz 2003). Abundances of juvenile worms were higher in seagrass beds than in other habitats. They may offer a more structured habitat than the sandy flats (Bell *et al.* 1992, Valentine and Heck 1990, Mantilla *et al.* 1999, Boström and Bonsdorff 1997 and 2000). Results of this study show that seagrass beds were a preferred habitat for juvenile and adult polychaete worms.

Cordgrass patches were poorly colonized by juveniles and adults. Cordgrass patches are a relatively new habitat. The species was introduced in the 1920s in the German Wadden Sea as a land reclamation measure and its distribution is still expanding (Löbl 2002). Löbl (2002) found that only juvenile *Arenicola marina* were present between stems of *S. anglica*. Despite the highly structured habitat, patches of *S. anglica* offer no nursery function for other polychaete species probably due to the position in the upper intertidal with a short immersion time.

Intertidal mussel beds represent about 1% of the basin's surface (Saier 2000). Only *P. ciliata* as adult seems to be representative for mussel beds, while its juveniles are also present in other habitats (pers. obser.). Since larvae of *P. elegans, S. martinensis* and *L. conchilega* were found only in mussel beds, it is possible that these beds act as larval traps or settlement substrata but are unsuitable for adults. Adults of all three species are common in sandy substrata (Hartmann-Schröder 1996). Active or passive secondary dispersal may have occurred in this case.

Fragmented shell patches are considered as a temporary dynamic habitat but the area covered is not known (Wolf 2002). Here both adults and juveniles had a higher density than in mussel beds or sandy flats. Wolf (2002) could not find a significant difference between densities of infauna in both fragmented shell patches and sandy sediments, but found a higher abundance of adults from *M. fuliginosus*, *P. mucosa* and *Polydora* spp. compared to ambient sand flat areas.

From the above it may be concluded that structured habitats like seagrass beds and fragmented shell patches are habitats preferred by juvenile and adult polychaetes over unstructured sandy bottoms. Other structured habitats were not favorable. Cordgrass patches may be to high in the intertidal zone and in mussel beds the sediments may be too anoxic to attract polychaetes. With respect to tidal zones juvenile polychaetes dominate the intertidal and adults dominate subtidally.

Species-specific patterns

For many benthic marine invertebrates extensive dispersal is assumed to occur primarily during the planktonic larval stage over large distances (Strathmann 1974, Scheltema 1986), whereas dispersal during the post-settlement juvenile and adult stages is thought to be less important (Norkko *et al.* 2001). Nevertheless, the spatial segregation between juvenile and adults of some species reported here, suggest that polychaetes are able to undertake some migrations. In mussels the so-called bysso-pelagic migration phase (Bayne, 1964) was observed. Armonies (1992, 1994 and 1999) describes the drifting of meio- and macrobenthic invertebrates on tidal flats in the study area. He concludes that active initiation of drifting may occur: a) by individuals in order to escape from an unexpected threat, b) by group evasion as a reaction to factors accumulating over the time or c) as a habitat change in the course of development.

In polychaetes the best studied case of juvenile segregation and their subsequent migration is for *Arenicola marina* (Farke and Berghuis 1979, Farke *et al.* 1979). But also *Armandia amakusaensis* (Tamaki 1985) presents this phenomenon. In this study *A. marina* was not considered. The clearest case found was *O. rathkei*. It has shown juveniles spatially separated from the adults, but this may be due an inadequate sampling of coarse sand in the intertidal. Reise (1982) found adult *O. rathkei* in the beach while juveniles occurred on the tidal flat.

Post-settlement movements by intertidal benthic macroinvertebrates seem to be a common event (Cummings *et al.* 1995) that enable organism to respond to habitat patches of different quality (Hastings 1990, Possingham and Roughgarden 1990). For the maintenance of populations in estuarine habitats, dispersal of young benthic stages seems to be important (Daunys *et al.* 2000, Essink and Dekker 2002).

N. virens is commonly present from the upper intertidal to 150 m depth in the subtidal zone (Hartmann-Schröder 1996). In the study area it was found to be mainly restricted to the subtidal and the lower intertidal (Reise pers. comm.). During this study it was observed that the distribution reaches the high tide line. For *S. armiger* no segregation between adults and juveniles was recorded, but it was considered as only one species with two different reproductive modes (pelagic larvae and direct development). Now two different species for the genus *Scoloplos* in the study area are proposed (Kruse *et al.* 2003, Albrecht 2004). Juvenile *Scoloplos* spp. are capable to migrate in the water column (Armonies 1999), but it is unknown if these movements may take a specific direction. Reise (1987) reports the lower, seaward flats as the preferential habitat of juvenile *S. armiger*.

The question to answer is: are tidal flats in the List tidal basin a nursery habitat for polychaetes? According to this study, seagrass beds as well as fragmented shells patches retain a large number of juvenile polychaeta (e.g. *Scoloplos armiger* and *Pygospio elegans*). In *Phyllodoce mucosa* the subtidal beds of *Lanice conchilega* may qualify as a nursery.

The importance of some habitats as nurseries has been widely discussed (Boesch and Turner 1984, Robertson and Blaber 1992, Primavera 1998). In the Wadden Sea mussel beds were described as nurseries for the periwinkle *Littorina littorea* (Saier 2000), and the intertidal flats for juveniles of *Crangon crangon* (Cattrijsse *et al.* 1997) and for *Macoma baltica* due the low predation pressure in this habitat (Hiddink *et al.* 2002).

Beck *et al.* (2003) proposed that a near-shore habitat serves as nursery for juveniles of a particular fish or invertebrate species, if it contributes disproportionately to the size and numbers of adults relative to other juvenile habitats. The disproportionate contribution to the production of adults can come from any combination of four factors: density, growth, and survival of juvenile animals, and their movement to adult habitats.

3. SMALL-SCALE DISPERSION OF JUVENILE POLYCHAETES: INDIRECT EVIDENCE OF BENTHIC MOBILITY.

Abstract

Spatial and temporal patterns of juvenile polychaete abundances were investigated on a sandy tidal flat near the Island of Sylt in the North Sea on a small spatial scale. From a plot of 4 m^2 25 samples in a grid arrangement were taken almost daily during two months. A turnover rate of lost/won organisms was calculated from differences between subsequent days. Also an index of dispersion was calculated. Temporal and spatial distributions revealed that *Scoloplos armiger, Microphthalmus* sp. and *Capitella capitata* have several small-scale patches of high density. From the spatio-temporal dynamics, passive immigration events are inferred for *Capitella minima* and *Ophelia rathkei*, while *Spio martinensis* and *Typosyllis hyalina* may have immigrated actively. For three other species, *S. armiger*, *Microphthalmus* sp. and *C. capitata*, several small-scale patches of high density occurred intermittently, but these were inconclusive with respect to post-settlement juvenile mobility.

1. Introduction

Spatial patterns defined as areal variation of species densities in their environment, are an important component of community structure in ecosystems (Sandulli and Pinckney 1999). In marine benthic invertebrates sediment type and microhabitat characteristics play a major role in faunal distributions (e.g. Schneider *et al.* 1987, Auster *et al.* 1989, Malatesta 1992, Snelgrove *et al.* 2001). Also factors like larval supply and various physical and biotic pre- and post-settlement processes influence species distribution patterns (see Ólafsson *et al.* 1994 and Fraschetti *et al.* 2003 for reviews). These patterns are scale-dependent with different processes operating at different scales (Levin 1992, Bergström *et al.* 2002). Particularly in habitats affected by waves and currents, the transport of sediment and the passive transport of organisms could alter the distribution of macrofauna species (Mukai *et al.* 1986, Tamaki 1987, Günther 1992, Gibson 2003). In addition, active dispersal (winter migrations, crawling and burrowing in search for food) may occur (Günther 1992). In some bivalve species active juvenile dispersal is common (Bayne 1964, Armonies 1992, Norkko *et al.* 2001). A list of polychaete species with benthic dispersal is given by Günther (1992). In this study further evidence is sought for juvenile mobility in polychaetes. This is done by comparing small-scale dispersion over time. If patterns are random throughout, no evidence for mobility can be obtained. However, if aggregations occur and these show short-term changes in position, it is likely that mobility of individuals caused such positional shifts.

Truly randomly distributed populations are unlikely to occur in nature and patchy distributions prevail on small scales (Reise 1979, Taylor 1984). The patchy structure of most environments coupled with the behavior of species determines the spatial arrangement of individuals (Thrush *et al.* 1989). Reise (1979) investigated the dispersion of motile polychaetes and found that deposit-feeders like *Scoloplos armiger* and *Capitella capitata,* were spatially aggregated as well as the carrion feeding *Phyllodoce mucosa*, while the predator *Eteone longa* showed no gregarious pattern.

Since most of the studies made on spatial patterns are snapshots in time, no information is available on the dynamics of these patterns. I studied small-scale spatial dynamics in juvenile polychaetes on a sedimentary tidal flat over a period of 60 days to test whether there is evidence for mobility. The aim is to show that benthic patterns in polychaetes of soft-sediments are not merely the outcome of settlement patterns but to some extent are affected by juvenile dispersal above, on or in the sediment.

2. Methods

2.1 Study area

This study was carried out on an intertidal sandy flat in Königshafen, a small embayment at the northernmost end of the Island of Sylt (Fig. 1). Oddewatt is located at the outermost part of the bay.

Average salinity is 30 PSU and mean temperature is 15° in summer and 4° in winter. Tides are semidiurnal with amplitude of 1.8 m. Oddewatt is located close to List tidal inlet which is the only connection with the North Sea. Sediments consist mainly of medium to fine sand where the study was conducted (Armonies 1992). Austen (1992) described sediments of the study area as relatively stable. Gätje and Reise (1998) provide a detailed description of the biota, sedimentology and hydrography of the List tidal basin.

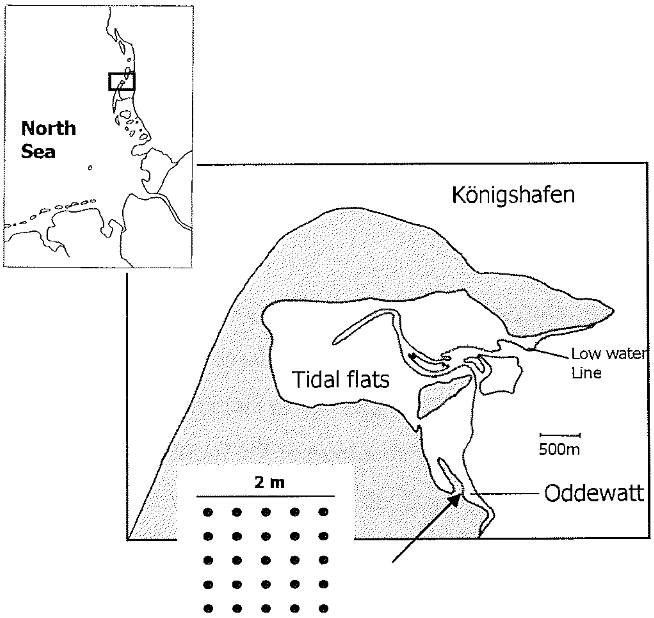


Figure 1. Oddewatt with location of sampling grid of 2 x 2 m.

2.2 Sampling methods

In order to obtain small-scale spatial patterns of juvenile polychaetes, samples were taken with a benthic core-sampler (10 cm^2 surface down to a sediment depth of 5 cm). A plot (2 x 2 m) located at mean water level was sampled from June 20 to August 20, 2002 at 36 days within an interval of 60 days (see Table 1 for dates). A total of 25 samples uniformly distributed (25 cm distance between samples) were obtained each date. Samples were sieved (250 mμ mesh) and the juvenile and larval polychaetes were counted under a dissection microscope.

Table 1. Sampling dates of this study.

June 2002	**July 2002**		**August 2002**	
20	1	16	4	13
21	3	19	5	15
22	5	23	7	16
24	7	27	8	17
27	8	28	9	18
28	9	29	10	20
	11	30	11	
	12	31		
	15			

2.3 Data analysis

Abundances of juveniles on 250 cm^2 are plotted for 36 day together with the estimated turnover of individuals. This is expressed as the rate of lost/won organisms, calculated as the difference in abundance between subsequent sampling dates. Positive differences are taked as arrivals (immigrants) to the plot, while negative differences are considered to be departures (emigrants) from the plot. From each date and for each species a contour map of abundances was created by means of Surfer software (vers. 6.1, Golden Software Inc.) calculated from 25 sampling points. To test whether dispersion patterns of species at each date were significantly different from randomness, the variance-to-mean ratio (Index of Dispersion= ID) was calculated. Significance of departures from unity was tested against the χ^2 distribution with (n-1) degrees of freedom. The ratio can depart in two directions, so α is set to 0.025 for clumped and 0.975 for regular dispersion (Ludwig and Reynolds 1988).

3. Results

A total of sixteen species present with juveniles and seven species present with larvae were recorded on the 4 m^2 plot. Most abundant were juveniles of *Spio martinensis* with 40% of the total, followed by *Ophelia rathkei* (16%), *Scoloplos armiger* (9%), *Microphthalmus* sp. (9%), *Capitella capitata* (8%), *Typosyllis hyalina* (7%), and *C. minima* (5%). Nine other species (*Pygospio elegans, Nereis virens, Exogone naidina, Phyllodoce mucosa, Polydora ciliata, Lanice conchilega, Malacoceros fuliginosus, Aricidea minuta* and *Eulalia viridis*) remained below 2% of total juvenile abundance. The most abundant larva was that of *Polydora cornuta* with the 46% of the total larval abundance. For the seven most abundant juveniles diagrams on abundance and contour maps are shown.

***Microphthalmus* sp.**

This small worm was present throughout the period of sampling, with an abundance peak of 80 individuals per 250 cm^2 (Fig. 2). The rate of lost/won individuals shows small oscillations except for a single event with a short-term immigration followed by emigration of about the same number of individuals within 4 days. Juveniles of *Microphthalmus* sp. showed at eighteen of 36 dates a clumped dispersion (See Appendix I for ID's and χ^2 significance tests).

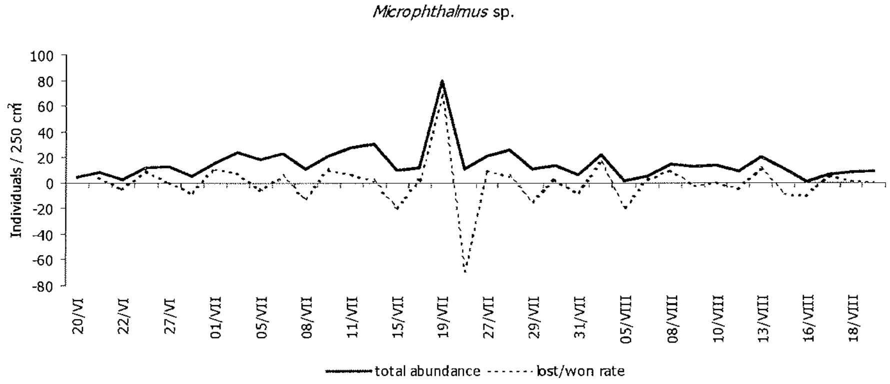


Figure 2. Temporal variability of abundance in juvenile *Microphthalmus* sp. on a 4 m^2 plot sampled at 25 evenly distributed points. Rate of lost/won individuals is shown as dotted line.

Patterns between consecutive days tend to be very different. Positions of high-density patches are never persistent. No one quadrant has a higher chance of high density than any of the others (Fig. 3). This pattern may either suggest that aggregations are much smaller in patch size than an individual quadrants in the grid or that individuals are continuously on the move and assemble in ephemeral aggregations.

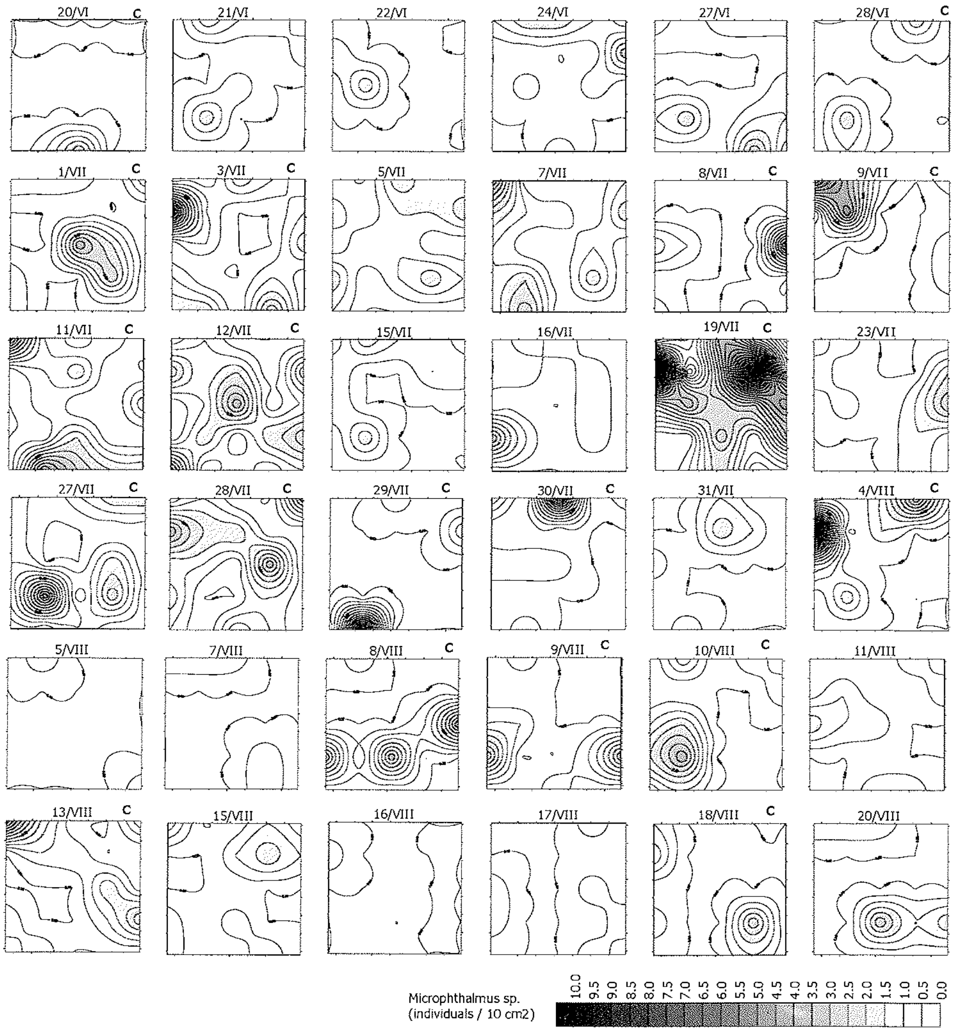


Figure 3. Dispersion of juvenile *Microphthalmus* sp. on 4 m^2 of a sand flat. Maps marked with C indicate a clumped pattern.

Scoloplos armiger

Juveniles of *S. armiger* were more abundant in the first half of sampling period (Fig. 4). A remarkable peak (145 individuals/250 cm^2) showed up at July 19 but did not persist. This peak coincided with that of *Microphthalmus* sp. In the second half of the period abundances decreased to 1-5 organisms per 250 cm^2. Rates of lost/won organisms remained close to zero (Fig. 4). At 4 dates a significant clumped dispersion occurred (Fig. 5) (See Appendix I for ID's and χ^2 significance tests).

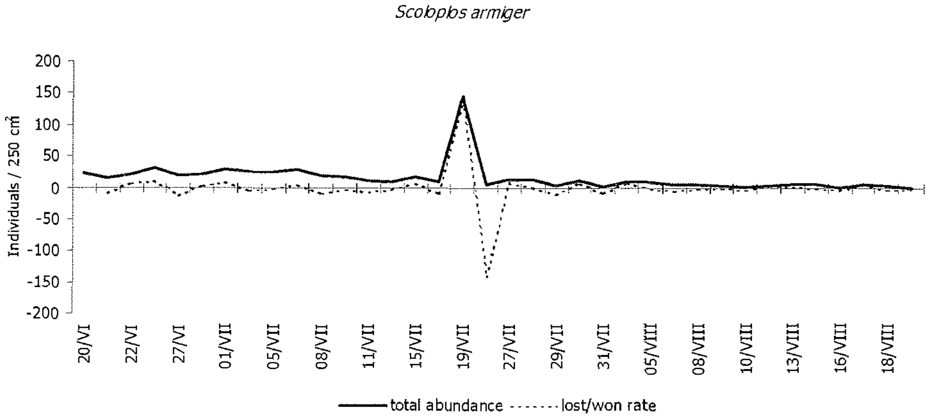


Figure 4. Temporal variability of abundance in juvenile *Scoloplos armiger* on a 4 m^2 plot sampled at 25 evenly distributed points. Rate of lost/won individuals is shown as dotted line.

Conspicuous high-density patches occurred end of June and early July, occasionally in adjacent plots. The upper row of plots tended to have a higher probability of aggregation than the other plots. However, positions of aggregations vary between consecutive dates. Compared to the previous species, average patch size tends to be larger and patterns of consecutive dates are less different, pointing to a lower small-scale mobility.

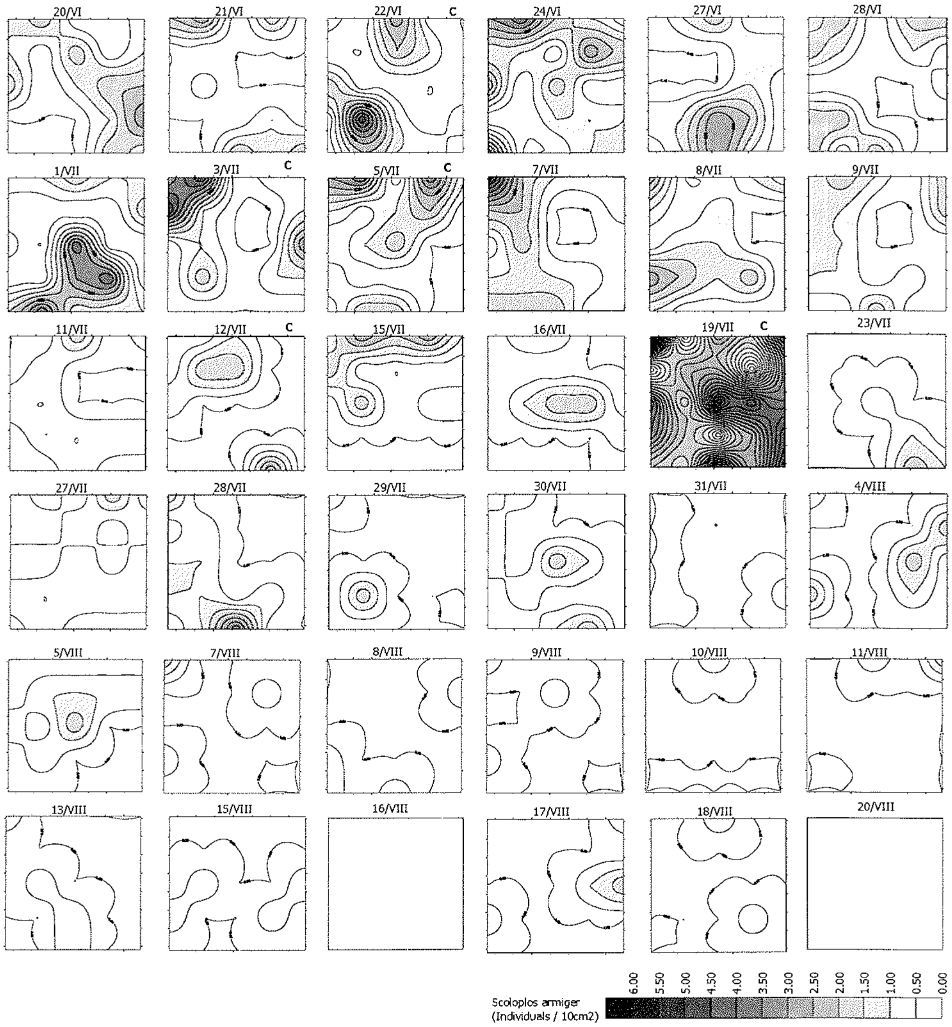


Figure 5. Dispersion of juvenile *Scoloplos armiger* on 4 m^2 of a sand flat. Maps marked with C indicate a clumped pattern.

Capitella minima

Abundances of juvenile *C. minima* were low, except for an intermittent period from July 11 to 15 with high density (Fig. 6). The Index of dispersion indicates a clumped pattern for 2 dates only (Fig. 7) (See Appendix I for ID's and χ^2 significance tests).

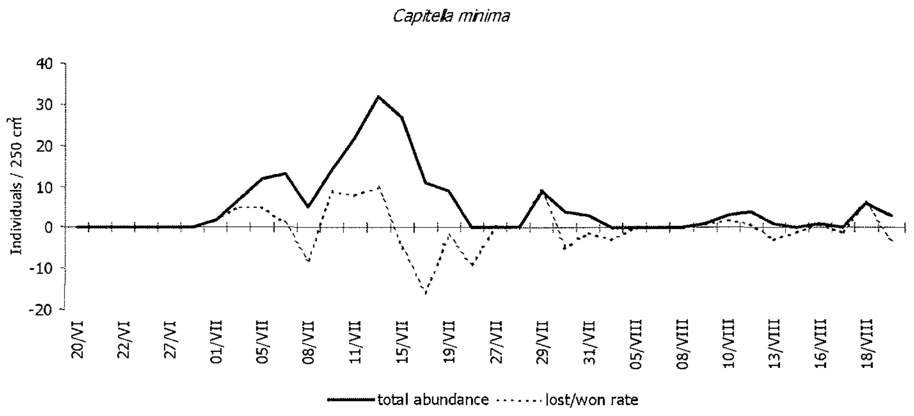


Figure 6. Temporal variability of abundance in juvenile *Capitella minima* on a 4 m^2 plot sampled at 25 evenly distributed points. Rate of lost/won individuals is shown as dotted line.

Positional consistency of high-density patches is low. There are no sub areas within the plot which have a higher possibility for aggregations. With respect to mobility one may only infer a transient immigration event in July of a few days in duration, probably followed by disaggregation due to emigration from the plot or mortality.

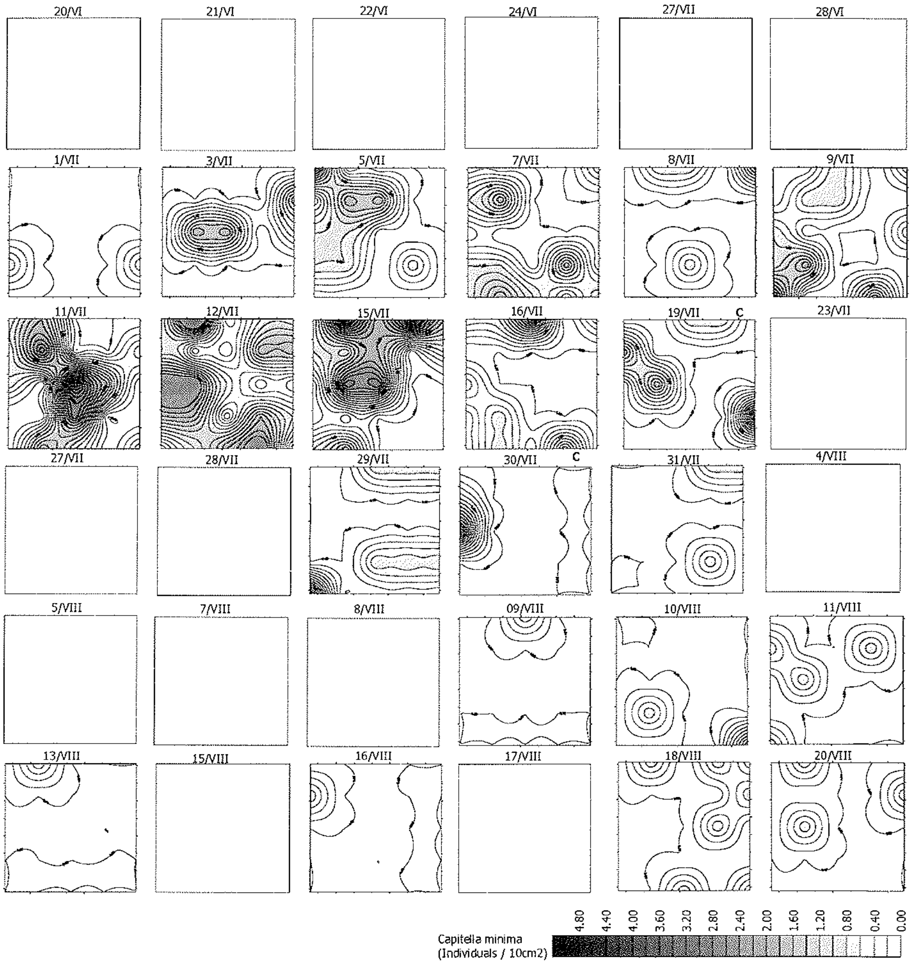


Figure 7. Dispersion of juvenile *Capitella minima* on 4 m^2 of a sand flat. Maps marked with C indicate a clumped pattern.

Spio martinensis

The temporal pattern of juvenile *S. martinensis* shows two abundance peaks. A minor one occurred early in July and a major one from the end of July to early August (112 individuals per 250 cm^2 and 247 individuals per 250 cm^2 respectively) (Fig. 8). Fluctuations in the lost/won rate indicate that juveniles were transported to and from the plot. For a period of two weeks (from 23 July until 9 August) a clumped distribution was found (Fig. 9) (See Appendix I for ID's and χ^2 significance tests).

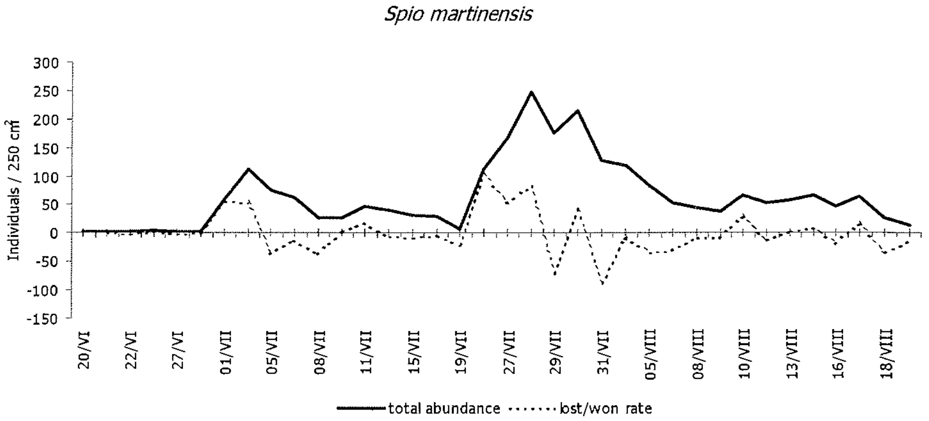


Figure 8. Temporal variability of abundance in juvenile *Spio martinensis* on a 4 m^2 plot sampled at 25 evenly distributed points. Rate of lost/won individuals is shown as dotted line.

Apart from the two immigration events with subsequent emigration or mortality, the patch dynamics show some consistency between consecutive dates, most apparent from July 10 to July 17. This suggests an intermittent residency within sub-areas of the plot.

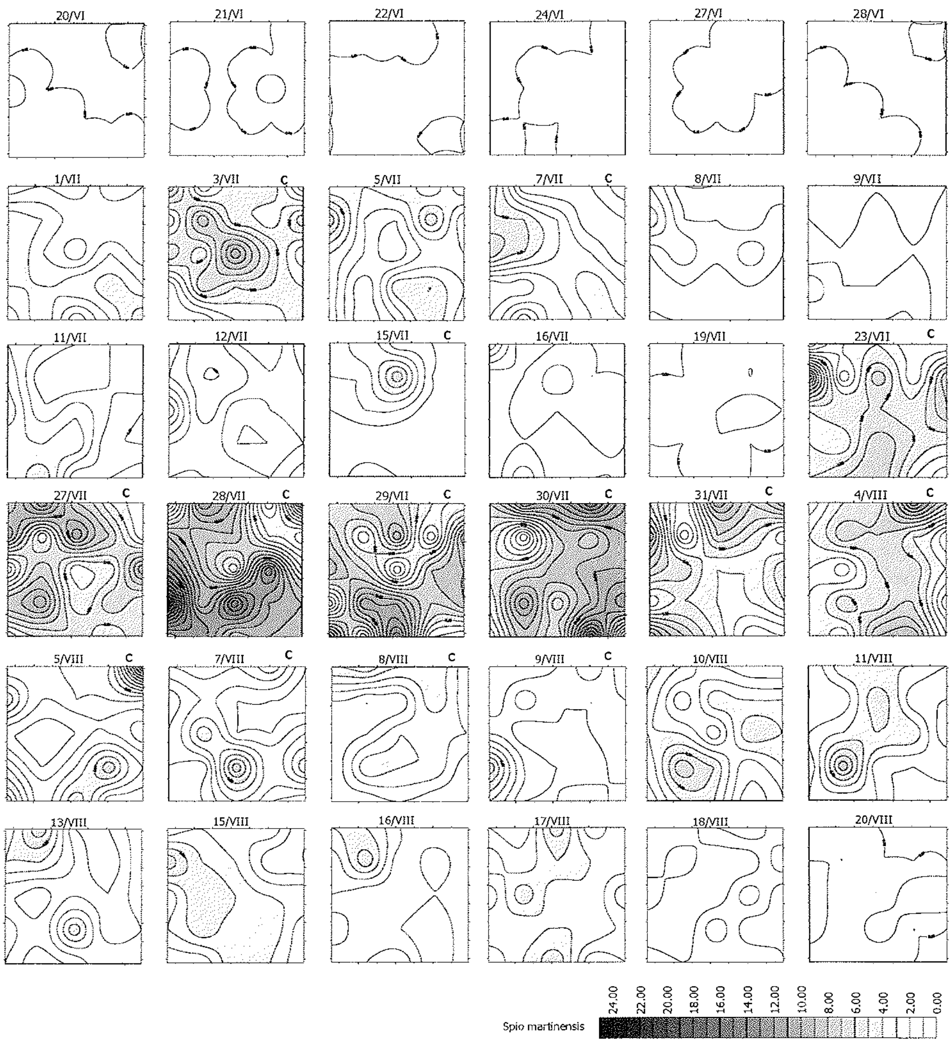


Figure 9. Dispersion of juvenile *Spio martinensis* on 4 m^2 of a sand flat. Maps marked with C indicate a clumped pattern.

Capitella capitata

Abundances of *C. capitata* remained low (0-1 individuals per 250 cm^2) until July 23, when a period of high abundance commenced and lasted until August 17 (Fig. 10). The rate of lost/won individuals is highly fluctuating. Random dispersion prevailed except for three dates in August (Fig. 11) (See Appendix I for ID's and χ^2 significance tests).

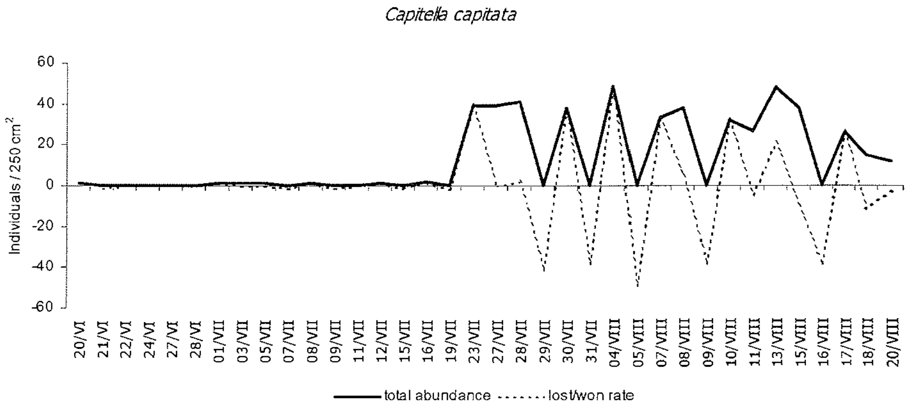


Figure 10. Temporal variability of abundance in juvenile *Capitella capitata* on a 4 m^2 plot sampled at 25 evenly distributed points. Rate of lost/won individuals is shown as dotted line.

The high fluctuations during the period with high abundances may originate from two different processes. Either aggregations are much smaller than quadrants and by chance were missed when sampling took place, or *C. capitata* exhibits a high turnover of individuals by immigrations and emigrations from the plot several times.

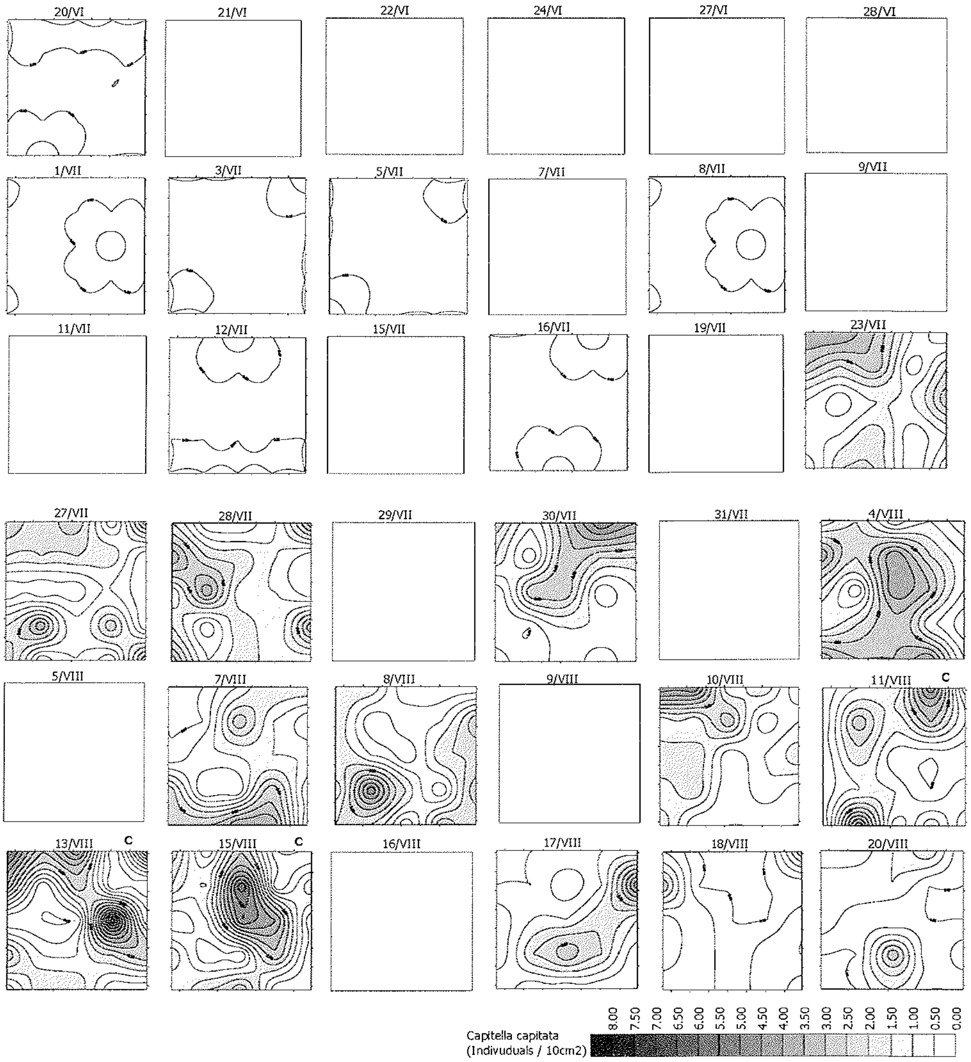


Figure 11. Dispersion of juvenile *Capitella capitata* on 4 m^2 of a sand flat. Maps marked with C indicate a clumped pattern.

Ophelia rathkei

Juveniles of this species show high fluctuations in abundance on the 4 m^2 plot throughout the sampling period. Short abundance peaks (61 individuals per 250 cm^2) followed by phases of low abundance prevailed (Fig. 12). The individual lost/won rate fluctuated accordingly.

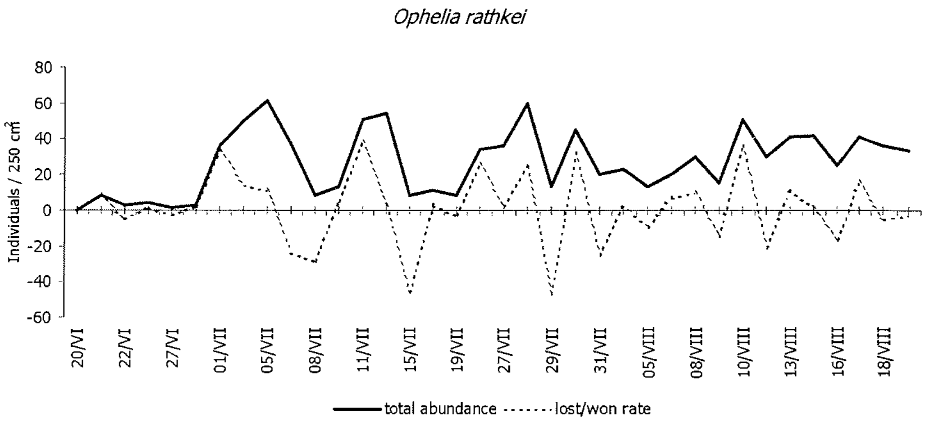


Figure 12. Temporal variability of abundance in juvenile *Ophelia rathkei* on a 4 m^2 plot sampled at 25 evenly distributed points. Rate of lost/won individuals is shown as dotted line.

The dynamic spatial pattern suggests at least several immigration events. Patches of high abundance lasted a few days (Fig. 13). At 11 dates a clumped dispersion was found, often very conspicuous (See Appendix I for ID's and χ^2 significance tests).

Positional consistency of aggregates between consecutive days is apparent. The pattern suggests that the plot was several times invaded and immigrants remained a few days where they arrived and then departed again or died.

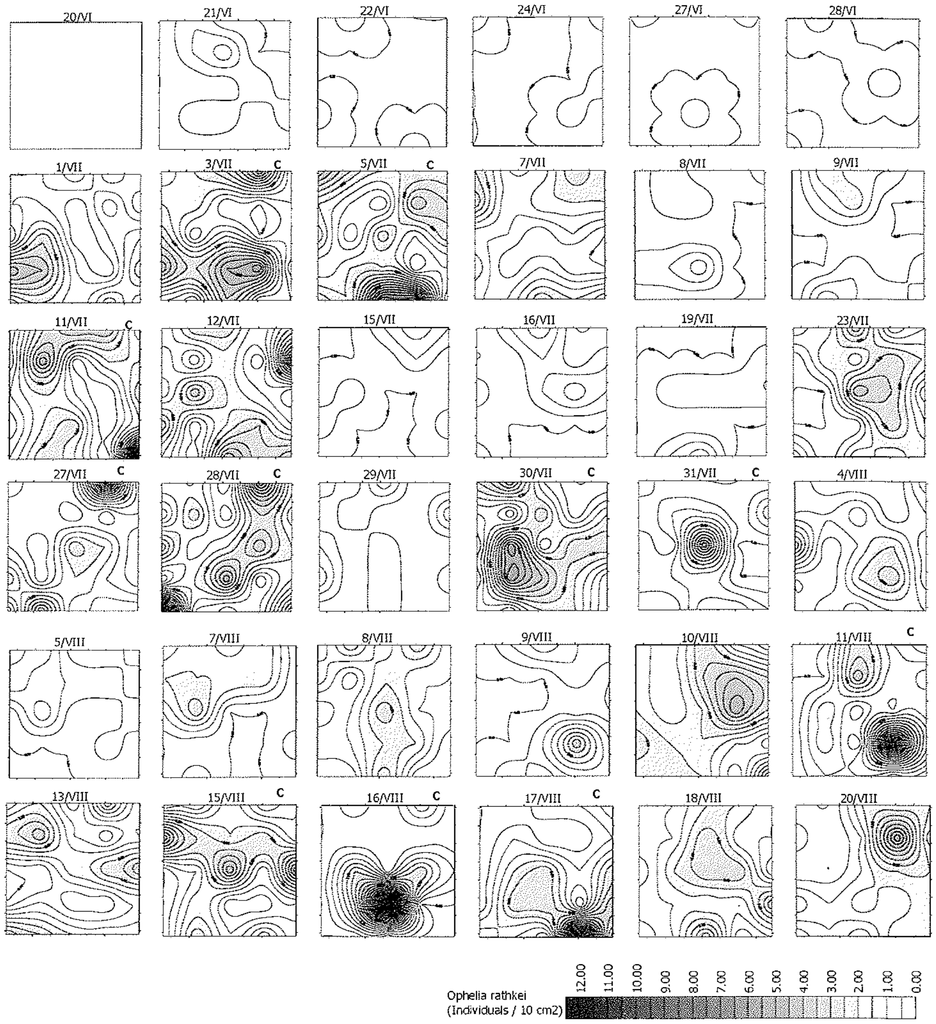


Figure 13. Dispersion of juvenile *Ophelia rathkei* on 4 m^2 of a sand flat. Maps marked with C indicate a clumped pattern.

Typosyllis hyalina

High fluctuations in abundance as well as in the rate of lost/won individuals indicated some degree of mobility in juvenile *Typosyllis hyalina* (abundance peaks up to 36 individuals per 250 cm^2 followed by low abundance periods with 4-5 individuals per 250 cm^2) (Fig. 14). A trend to higher abundances towards the end of the sampling period was observed. At 5 days clumped dispersion was significant (Fig 15) (See Appendix I for ID's and χ^2 significance tests).

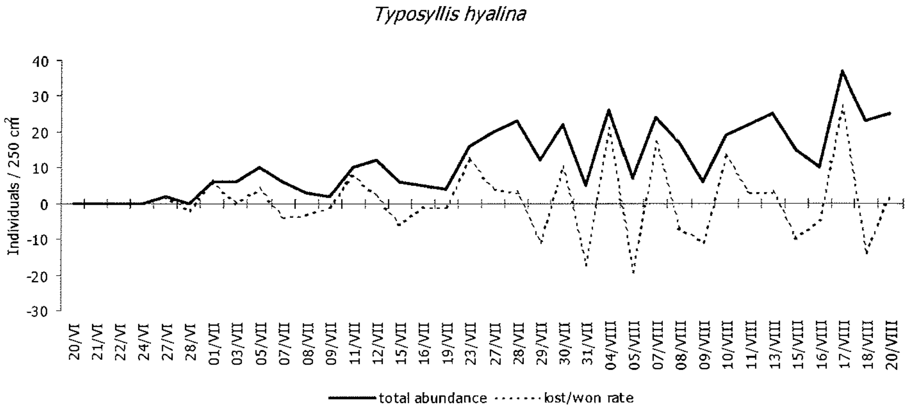


Figure 14. Temporal variability of abundance in juvenile *Typosyllis hyalina* on a 4 m^2 plot sampled at 25 evenly distributed points. Rate of lost/won individuals is shown as dotted line.

Positional consistency of aggregates was rather low. However, towards the end of the observation period the lowest row had a slightly higher chance to accommodate high-density patches than other subareas. Aggregates seem to be larger than single quadrants. The high patch-dynamics suggest several immigrations immediately followed by emigration or mortality.

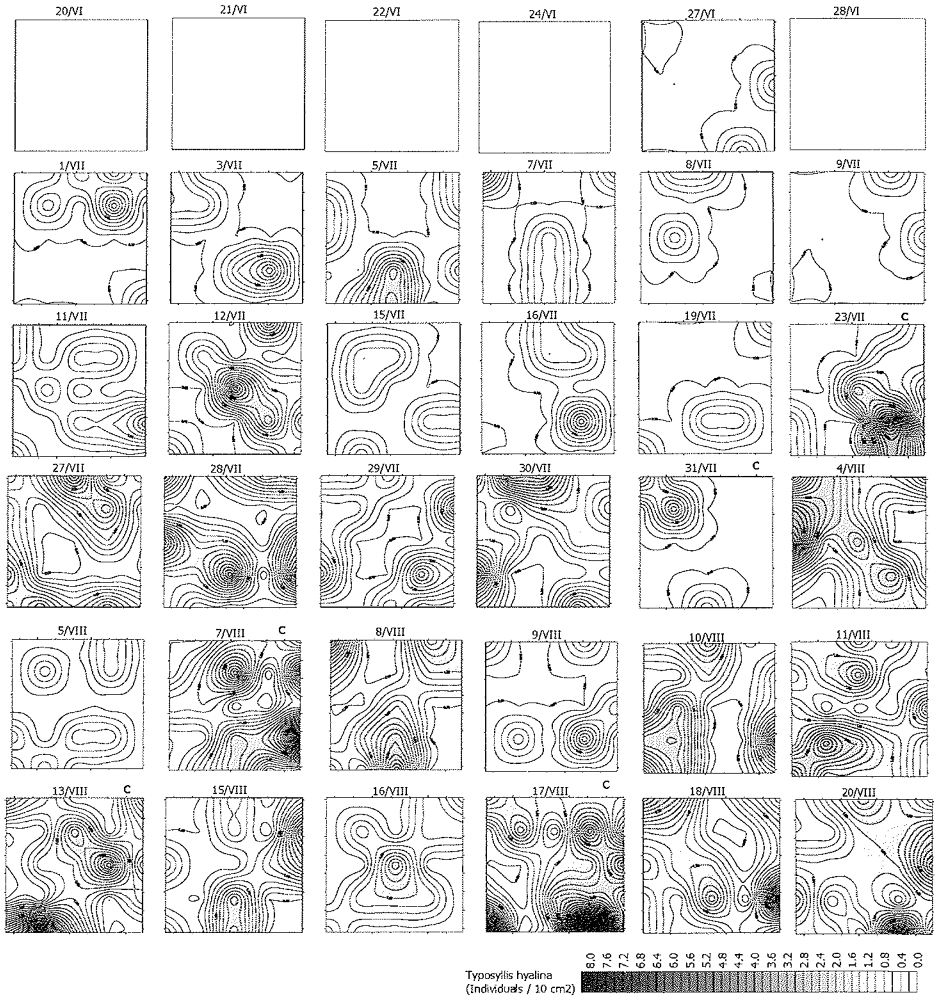


Figure 15. Dispersion of juvenile *Typosyllis hyalina* on 4 m^2 of a sand flat. Maps marked with C indicate a clumped pattern.

Polydora cornuta

The presence of larvae during the sampling period was restricted to those of *Polydora cornuta*. They appeared sporadically in low abundances (1 larvae per 250 cm^2) and three peaks are apparent (6, 17, and 9 larvae per 250 cm^2) (Fig. 16). Larval settlement with subsequent departure or death may explain this pattern. Abundance was too low for significance of clumped patterns to be detected (Fig. 17).

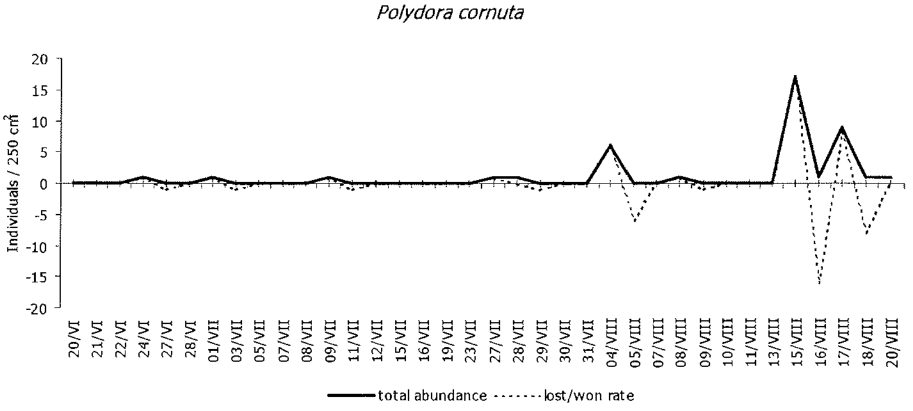


Figure 16. Temporal variability of abundance in *Polydora cornuta* larvae on a 4 m^2 plot sampled at 25 evenly distributed points. Rate of lost/won individuals is shown as dotted line.

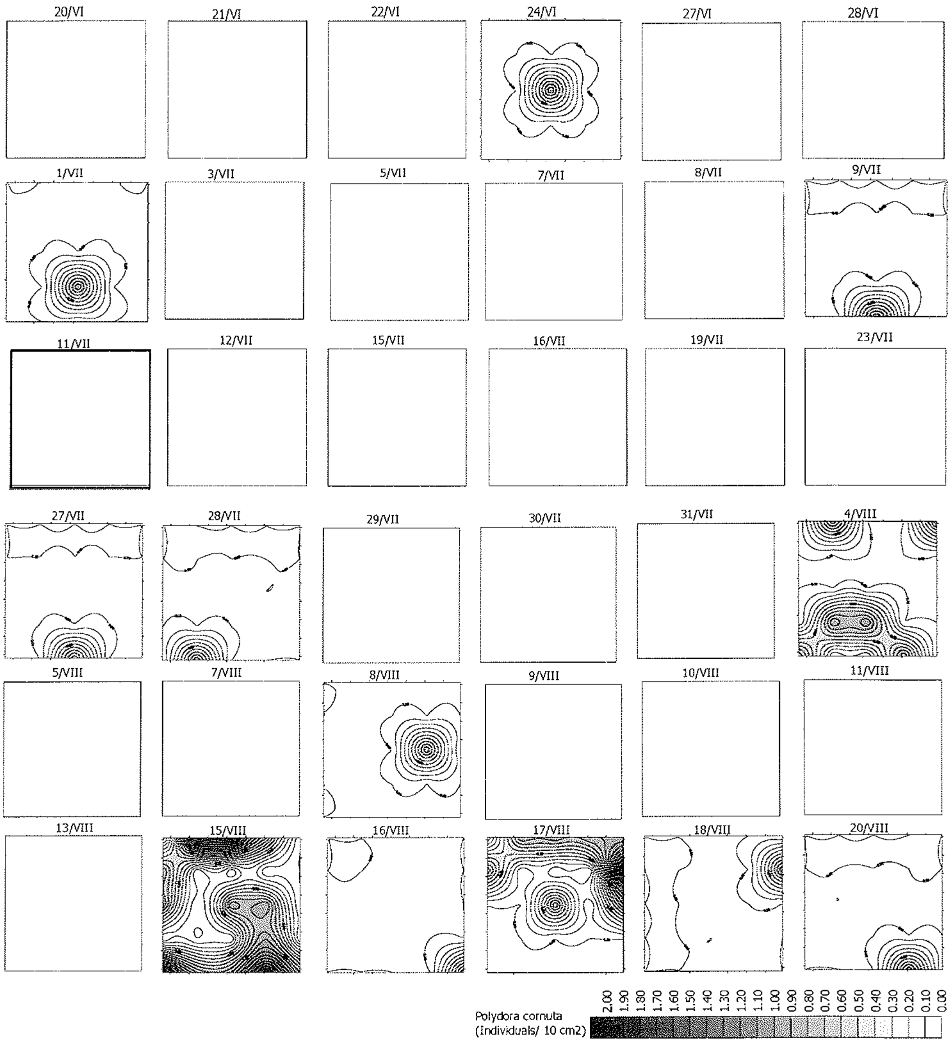


Figure 17. Dispersion of *Polydora cornuta* larvae on 4 m^2 of a sand flat.

4. Discussion

Processes cannot be directly inferred from patterns (Andrew and Mapstone 1987). Any attempt to obtain information on post-settlement mobility in juvenile polychaetes from spatial patterns is therefore subject to error and uncertainty. However, small polychaetes cannot easily be tagged and individual movements cannot be followed under natural conditions. Therefore we have to rely on indirect information, and the dynamic patterns described above do allow some conclusions on underlying processes.

With respect to juvenile polychaetes, the chosen sampling plot was fortunately rather homogeneous at the adopted sampling scale. There were only slight and non-significant tendencies for juvenile *Scoloplos armiger* and *Typosyllis hyalina* to prefer some subarea of the 4 m^2 plot for short time periods. Thus, the observed patterns are not considered to be biased by an environmental gradient or discontinuity within the plot.

Also, the areal size of the 4 m^2 is assumed to be sufficient to include the ambits of the animals in question. Individual body lengths were one or a few millimetres only. Active migration by crawling in or on the sediment might not bring an individual outside the plot from one day to another. This type of mobility may not be discovered at all or it may show up in positional shifts of aggregates.

On the other hand, juvenile polychaetes drifting or swimming in the water column with the tidal currents may swiftly pass through the entire plot (Günther 1992). When immigrations and emigrations are in balance, occur continuously and asynchronously among individuals, no change in pattern will be observed. However, when several individuals immigrate or emigrate synchronously and when these migrations are not balanced, conspicuous changes in abundance will be observed on the sampling plot. Further evidence on mobility may be revealed when dispersion is not random but clumped (Reise 1979). Then gradual shifts in clump position between consecutive days may indicate small-scale migrations, whereas discontinuous appearance of clumps at different positions between consecutive days may indicate independent immigration events from outside.

However, there is a pitfall. When clumps are much smaller than one of the 25 sampled quadrants of 1600 cm^2, sampling errors have to be considered. The patterns found in *Microphthalmus* sp., *Scoloplos armiger* and *Capitella capitata* suggest that such small clumps or aggregates may occur. In this case, one cannot separate variation in space from variation in time with the adopted sampling design. A small aggregate may have been missed or sampled by chance. Contiguous patterns analyzed by Reise (1979) confirm this observation. Consequently, for the juveniles of these three species no inferences are made on mobility.

With the exception of *Polydora cornuta*, no larval settlement was observed during the sampling period on the plot. This allows to ascribe the appearance of juveniles to post-settlement mobility. Such immigration events are evident in four species: *Capitella minima* showed one conspicuous event, *Spio martinensis* two events, *Ophelia rathkei* seven and *Typosyllis hyalina* several immigration events. When high abundances decline or aggregates disintegrate again, it is impossible to differentiate between emigration and mortality. Thus, only immigration events can be recognized.

In petri-dishes it was observed that *S. martinesis* and *T. hyalina* are capable of fast and directional swimming. In these two species active immigrations and emigrations are likely to have occurred. Juveniles of *C. minima* and *O. rathkei* were not observed to swim. Their immigrations and emigrations to and from the plots are therefore assumed to be passive drifting with waves or tidal currents. This was also assumed for *Armandia amakusaensis* which belongs to the same family as *O. rathkei* (Tamaki 1987, Saito *et al.* 2000).

In conclusion, out of seven polychaete species with abundant post-settlement juveniles, four show evidence of mobility at the scale of a 4 m^2 plot of a sandy intertidal flat. Two of these may have been active migrants, while the other two are assumed to have been drifted into the plot as juveniles. For three other species the spatial patch dynamics are inconclusive with respect to post-settlement mobility.

Appendix I.

A.

Dispersion patterns of *Microphthalmus* sp. and χ^2 significance tests. ID= index of dispersion, χ^2=Critical Chi squared values. (n= 25, d.F.= 24. With α 0.975, χ^2=12.40. With α 0.025, χ^2=39.364)

If critical values of χ^2 fall between 12.40 and 39.364, distribution patterns are random. If critical values of χ^2 are less than 12.40, regular distribution patterns are expected. If critical values of χ^2 are greater than 39.364, clumped patterns are expected (Ludwig and Reynolds 1988).

Date	**mean**	**variance**	**ID**	χ^2	**Distribution pattern**
20 Jun	0.16	0.39	2.437	58.5	Clumped
21	0.32	0.39	1.229	29.5	Random
22	0.12	0.19	1.611	38.66	Random
24	0.48	0.67	1.409	33.83	Random
27	0.52	0.59	1.141	27.38	Random
28	0.2	0.33	1.666	40	Clumped
1 Jul	0.64	1.15	1.807	43.37	Clumped
3	0.96	2.37	2.472	59.33	Clumped
5	0.72	0.54	0.754	18.11	Random
7	0.92	1.49	1.623	38.95	Random
8	0.44	1.59	3.613	86.72	Clumped
9	0.84	3.22	3.837	92.09	Clumped
11	1.12	2.61	2.330	55.92	Clumped
12	1.2	2.08	1.736	41.66	Clumped
15	0.4	0.41	1.041	25	Random
16	0.48	0.76	1.583	38	Random
19	3.2	13.25	4.140	99.37	Clumped
23	0.44	0.59	1.340	32.18	Random
27	0.84	1.89	2.25	54	Clumped
28	1.04	1.79	1.721	41.30	Clumped
29	0.44	2.67	6.075	145.81	Clumped
30	0.56	2.09	3.732	89.57	Clumped
31	0.24	0.27	1.138	27.33	Random
4 Aug	0.88	4.86	5.522	132.54	Clumped
5	0.08	0.07	0.9583	23	Random
7	0.2	0.16	0.833	20	Random
8	0.6	2.08	3.472	83.33	Clumped
9	0.52	1.26	2.423	58.15	Clumped
10	0.56	1.00	1.797	43.14	Clumped
11	0.36	0.32	0.898	21.55	Random
13	0.8	1.91	2.395	57.5	Clumped
15	0.44	0.42	0.962	23.09	Random
16	0.04	0.04	1	24	Random
17	0.24	0.19	0.791	19	Random
18	0.32	0.56	1.75	42	Clumped
20	0.36	0.57	1.59	38.22	Random

B.

Dispersion patterns of *Scoloplos armiger* and χ^2 significance tests. ID= index of dispersion, χ^2=Critical Chi squared values. (n= 25, d.F.= 24. With α 0.975, χ^2=12.40. With α 0.025, χ^2=39.364)

If critical values of χ^2 fall between 12.40 and 39.364, distribution patterns are random. If critical values of χ^2 are less than 12.40, regular distribution patterns are expected. If critical values of χ^2 are greater than 39.364, clumped patterns are expected (Ludwig and Reynolds 1988).

Date	**mean**	**variance**	**ID**	χ^2	**Distribution pattern**
20 Jun	0.88	0.85	0.977	23.45	Random
21	0.56	0.84	1.5	36	Random
22	0.8	1.5	1.875	45	Clumped
24	1.24	1.69	1.362	32.70	Random
27	0.72	0.87	1.217	29.22	Random
28	0.8	0.83	1.041	25	Random
1 Jul	1.16	1.80	1.557	37.37	Random
3	1	2.25	2.25	54	Clumped
5	0.96	1.62	1.690	40.58	Clumped
7	1.12	1.69	1.511	36.28	Random
8	0.76	0.94	1.236	29.68	Random
9	0.68	0.56	0.823	19.76	Random
11	0.44	0.34	0.772	18.54	Random
12	0.36	0.65	1.824	43.77	Clumped
15	0.64	0.99	1.546	37.12	Random
16	0.32	0.39	1.229	29.5	Random
19	5.8	10.91	1.882	45.17	Clumped
23	0.2	0.25	1.25	30	Random
27	0.48	0.34	0.715	17.16	Random
28	0.52	0.84	1.621	38.92	Random
29	0.12	0.19	1.611	38.66	Random
30	0.4	0.41	1.041	25	Random
31	0.04	0.04	1	24	Random
4 Aug	0.32	0.47	1.489	35.75	Random
5	0.32	0.31	0.968	23.25	Random
7	0.16	0.22	1.395	33.5	Random
8	0.16	0.14	0.875	21	Random
9	0.12	0.11	0.916	22	Random
10	0.04	0.04	1	24	Random
11	0.12	0.19	1.611	38.66	Random
13	0.16	0.14	0.875	21	Random
15	0.16	0.14	0.875	21	Random
17	0.2	0.25	1.25	30	Random
18	0.08	0.076	0.958	23	Random

C.

Dispersion patterns of *Capitella minima* and χ^2 significance tests. ID= index of dispersion, χ^2=Critical Chi squared values. (n= 25, d.F.= 24. With α 0.975, χ^2=12.40. With α 0.025, χ^2=39.364)

If critical values of χ^2 fall between 12.40 and 39.364, distribution patterns are random. If critical values of χ^2 are less than 12.40, regular distribution patterns are expected. If critical values of χ^2 are greater than 39.364, clumped patterns are expected (Ludwig and Reynolds 1988).

Date	**x**	**S^2**	**ID**	**χ^2**	**Distribution pattern**
1 Jul	0.08	0.07	0.958	23	Random
3	0.28	0.46	1.642	39.42	Random
5	0.48	0.67	1.409	33.83	Random
7	0.52	0.51	0.980	23.53	Random
8	0.2	0.25	1.25	30	Random
9	0.56	0.67	1.202	28.85	Random
11	0.88	1.36	1.545	37.09	Random
12	1.28	1.37	1.075	25.81	Random
15	1.08	1.74	1.614	38.74	Random
16	0.44	0.59	1.340	32.18	Random
19	0.36	0.65	1.824	43.77	Clumped
29	0.36	0.49	1.361	32.66	Random
30	0.16	0.39	2.437	58.5	Clumped
31	0.12	0.11	0.916	22	Random
9 Aug	0.04	0.04	1	24	Random
10	0.12	0.19	1.61	38.66	Random
11	0.16	0.14	0.875	21	Random
13	0.04	0.04	1	24	Random
16	0.04	0.04	1	24	Random
18	0.24	0.19	0.791	19	Random
20	0.12	0.11	0.916	22	Random

D.

Dispersion patterns of *Spio martinensis* and χ^2 significance tests. ID= index of dispersion, χ^2=Critical Chi squared values. (n= 25, d.F.= 24. With α 0.975, χ^2=12.40. With α 0.025, χ^2=39.364)

If critical values of χ^2 fall between 12.40 and 39.364, distribution patterns are random. If critical values of χ^2 are less than 12.40, regular distribution patterns are expected. If critical values of χ^2 are greater than 39.364, clumped patterns are expected (Ludwig and Reynolds 1988).

Date	**mean**	**variance**	**ID**	χ^2	**Distribution pattern**
20 Jun	0.16	0.2233	1.3958	33.5	Random
21	0.16	0.2233	1.3958	33.5	Random
22	0.08	0.007	0.9583	23	Random
24	0.2	0.166	0.8333	20	Random
27	0.12	0.11	0.9166	22	Random
28	0.12	0.11	0.9166	22	Random
1 Jul	2.36	2.74	1.161	27.86	Random
3	4.48	7.67	1.713	41.12	Clumped
5	3	4	1.33	32	Random
7	2.48	4.51	1.818	43.64	Clumped
8	1.04	1.62	1.560	37.46	Random
9	1.12	0.777	0.693	16.64	Random
11	1.88	2.52	1.343	32.25	Random
12	1.64	1.99	1.213	29.12	Random
15	1.28	2.37	1.856	44.56	Clumped
16	1.16	1.39	1.198	28.75	Random
19	0.32	0.31	0.968	23.25	Random
23	4.48	7.67	1.713	41.12	Clumped
27	6.64	11.57	1.742	41.83	Clumped
28	9.88	25.52	2.58	62.008	Clumped
29	7.04	15.87	2.25	54.11	Clumped
30	8.60	16.16	1.879	45.11	Clumped
31	5.08	11.07	2.180	52.33	Clumped
4 Aug	4.72	8.29	1.75	42.16	Clumped
5	3.36	10.24	3.04	73.14	Clumped
7	2.16	4.30	1.993	47.85	Clumped
8	1.8	3.5	1.944	46.66	Clumped
9	1.48	3.01	2.033	48.81	Clumped
10	2.68	3.72	1.390	33.37	Random
11	2.16	3.30	1.530	36.74	Random
13	2.28	3.04	1.33	32.03	Random
15	2.68	2.97	1.110	22.65	Random
16	1.88	1.86	0.989	23.74	Random
17	2.52	2.34	0.929	22.31	Random
18	1.12	1.27	1.139	27.35	Random
20	0.52	0.677	1.301	31.23	Random

E.

Dispersion patterns of *Capitella capitata* and χ^2 significance tests. ID= index of dispersion, χ^2=Critical Chi squared values. (n= 25, d.F.= 24. With α 0.975, χ^2=12.40. With α 0.025, χ^2=39.364)

If critical values of χ^2 fall between 12.40 and 39.364, distribution patterns are random. If critical values of χ^2 are less than 12.40, regular distribution patterns are expected. If critical values of χ^2 are greater than 39.364, clumped patterns are expected (Ludwig and Reynolds 1988).

Date	**Mean**	**variance**	**ID**	χ^2	**Distribution pattern**
20 Jun	0.04	0.04	1	24	Random
1 Jul	0.04	0.04	1	24	Random
3	0.04	0.04	1	24	Random
5	0.04	0.04	1	24	Random
8	0.04	0.04	1	24	Random
12	0.04	0.04	1	24	Random
16	0.08	0.07	0.958	23	Random
23	1.56	1.59	1.019	24.46	Random
27	1.56	2.09	1.339	32.15	Random
28	1.64	1.90	1.162	27.90	Random
30	1.52	2.01	1.322	31.73	Random
4 Aug	1.96	1.95	0.998	23.95	Random
7	1.32	1.97	1.497	35.93	Random
8	1.52	1.59	1.048	25.15	Random
10	1.28	2.04	1.596	38.31	Random
11	1.08	2.24	2.077	49.85	Clumped
13	1.92	4.57	2.38	57.20	Clumped
15	1.52	3.09	2.035	48.84	Clumped
17	1	1	1	24	Random
18	0.6	0.75	1.25	30	Random
20	0.48	0.59	1.236	29.66	Random

F.

Dispersion patterns of *Ophelia rathkei* and χ^2 significance tests. ID= index of dispersion, χ^2=Critical Chi squared values. (n= 25, d.F.= 24. With α 0.975, χ^2=12.40. With α 0.025, χ^2=39.364)

If critical values of χ^2 fall between 12.40 and 39.364, distribution patterns are random. If critical values of χ^2 are less than 12.40, regular distribution patterns are expected. If critical values of χ^2 are greater than 39.364, clumped patterns are expected (Ludwig and Reynolds 1988).

Date	**mean**	**variance**	**ID**	χ^2	**Distribution pattern**
21 Jun	0.32	0.31	0.968	23.25	Random
22	0.12	0.11	0.916	22	Random
24	0.16	0.14	0.875	21	Random
27	0.04	0.04	1	24	Random
28	0.12	0.11	0.916	22	Random
1 Jul	1.44	1.756	1.219	29.27	Random
3	2	3.666	1.833	44	Clumped
5	2.44	4.42	1.812	43.50	Clumped
7	1.48	1.26	0.851	20.43	Random
8	0.32	0.31	0.968	23.25	Random
9	0.52	0.51	0.980	23.53	Random
11	2.04	4.87	2.388	57.33	Clumped
12	2.16	3.14	1.453	34.88	Random
15	0.32	0.31	0.968	23.25	Random
16	0.44	0.42	0.962	23.09	Random
19	0.32	0.31	0.968	23.25	Random
23	1.36	1.74	1.279	30.70	Random
27	1.44	3.34	2.319	55.66	Clumped
28	2.4	6.58	2.743	65.83	Clumped
29	0.52	0.51	0.980	23.53	Random
30	1.8	3.66	2.037	48.88	Clumped
31	0.8	1.66	2.083	50	Clumped
4 Aug	0.92	1.16	1.260	30.26	Random
5	0.52	0.51	0.980	23.53	Random
7	0.8	0.91	1.145	27.5	Random
8	1.2	1.08	0.902	21.66	Random
9	0.6	0.83	1.388	33.33	Random
10	2.04	1.62	0.795	19.09	Random
11	1.2	3.8	3.194	76.66	Clumped
13	1.64	2.07	1.264	30.34	Random
15	1.68	3.39	2.019	48.47	Clumped
16	1	6.33	6.33	152	Clumped
17	1.64	5.32	3.24	77.90	Clumped
18	1.44	1.34	0.930	22.33	Random
20	1.32	1.64	1.244	29.87	Random

G.

Dispersion patterns of *Typosyllis hyalina* and χ^2 significance tests. ID= index of dispersion, χ^2=Critical Chi squared values. (n= 25, d.F.= 24. With α 0.975, χ^2=12.40. With α 0.025, χ^2=39.364)

If critical values of χ^2 fall between 12.40 and 39.364, distribution patterns are random. If critical values of χ^2 are less than 12.40, regular distribution patterns are expected. If critical values of χ^2 are greater than 39.364, clumped patterns are expected (Ludwig and Reynolds 1988).

Date	*Mean*	**variance**	**ID**	χ^2	**Distribution pattern**
27 Jun	0.08	0.07	0.958	23	Random
1 Jul	0.24	0.27	1.138	27.33	Random
3	0.24	0.27	1.138	27.33	Random
5	0.4	0.41	1.041	25	Random
7	0.24	0.27	1.138	27.33	Random
8	0.12	0.11	0.916	22	Random
9	0.08	0.07	0.958	23	Random
11	0.4	0.33	0.833	20	Random
12	0.48	0.67	1.409	33.83	Random
15	0.24	0.19	0.791	19	Random
16	0.2	0.25	1.25	30	Random
19	0.16	0.14	0.875	21	Random
23	0.64	1.07	1.677	40.25	Clumped
27	0.8	0.75	0.937	22.5	Random
28	0.92	1.16	1.260	30.26	Random
29	0.48	0.51	1.062	25.5	Random
30	0.88	0.94	1.071	25.72	Random
31	0.2	0.33	1.666	40	Clumped
4 Aug	1.04	1.12	1.080	25.92	Random
5	0.28	0.21	0.75	18	Random
7	0.96	1.62	1.690	40.58	Clumped
8	0.68	0.89	1.313	31.52	Random
9	0.24	0.27	1.138	27.33	Random
10	0.76	0.85	1.127	27.05	Random
11	0.88	0.85	0.977	23.45	Random
13	1	1.666	1.666	40	Clumped
15	0.6	0.75	1.25	30	Random
16	0.4	0.33	0.833	20	Random
17	1.48	3.26	2.202	52.86	Clumped
18	0.92	1.07	1.170	28.08	Random
20	1	1	1	24	Random

4. MOBILITY OF MARINE BENTHIC INVERTEBRATES: AN EXPERIMENTAL APPROACH WITH JUVENILE POLYCHAETES ON A SANDY TIDAL FLAT

Abstract

Planktonic larvae of marine invertebrates populations have been considered as the main dispersal stage. However, this does not imply that dispersal after settlement is without any importance. In some polychaete species juvenile stages are spatially separated from adults, which implies that at the end of juvenile life migrations are mandatory. However, the incidence of juveniles in water samples and in nets placed near to the bottom is very low. Since the oxic layer of the sediment comprises often only a few mm, the route of migrations is likely to be confined to a thin surface layer of sediment or to the water-sediment boundary layer. An experiment was set-up to detect whether juveniles either move through the water column or in the sediment. Linear grooves (1 m long and 0.1 m wide) were used to estimate crawling performance of juveniles with the incoming and outgoing tidal flow. Grooves were filled with polychaete-free sediment but contained all other organisms. They were placed level with the sediment surface for one, two, and three tidal cycles on a sandy tidal flat. Small polychaete species (e.g. *Pygospio elegans, Ophelia rathkei*) were highly active species that could move > 0.5 m in one tidal cycle. Also larvae move through the sediment but slower than juveniles. The latter could not be detected in the water column above the sediment.

1. Introduction

Dispersal is probably the most important life history trait in both, species persistence and species evolution (Colbert *et al.* 2001). Planktonic larvae are considered as a major dispersal route in marine benthic invertebrate populations (Thorson 1961, Strathmann 1974, Scheltema 1986, Bhaud 2000). However, also post-settled individuals may be important for dispersal. Armonies (1992, 1994, 1996, 1999); Armonies and Hellwig-Armonies (1992); Cummings *et al.* (1995);

Whitlatch *et al.* (1998); Norkko *et al.* (2001) dealt with drifting of post-settled organisms in the water column.

Colonization and re-colonization of the sea floor may occur by 1) settlement of planktonic larvae, 2) active lateral or upward migrations of juveniles and adults, 3) passive re-suspension, transport, and deposition of all life stages (Levin and DiBacco 1995). Processes 1 and 3 should be traceable using water samples, but active lateral migrations of juveniles and adults can be only assessed on and in the sediment.

Studies on the active lateral dispersal of juveniles and adults *in situ* are scarce, and have focused mainly on colonization/re-colonization processes in defaunated or disturbed sediments (Simon and Dauer 1997, Hall 1994, Grassle and Grassle 1994, Levin and DiBacco 1995, Shull 1997, Snelgrove *et al.* 2001, Whitlatch *et al.* 1998 and 2001). Sedimentary tidal flats in the study area are very dynamic environments where infauna could be eroded from the sediment (Armonies 1994). Waves and tidal currents could be an important vector of transporting juveniles.

As described in chapter II juveniles and adults of some polychaete species are spatially segregated. It is supposed that juvenile worms migrate to areas where adults are able to live and reproduce. In chapter III of this study, indirect evidence of juvenile dispersal was inferred from spatially dynamic populations. This chapter describes, how mobility on or in the sediment surface can be experimentally measured *in situ*. Both modes of benthic dispersal, active migration and passive re-suspension are taken into account for early benthic developmental stages in polychaetes.

The hypothesis tested is that juvenile worms which rarely swim or drift in the water column, are capable to crawl over considerable distances active in the sediment-water boundary layer or just below the sediment surface. To compare this to swimming or drifting worms, water samples were taken concurrently above the sediment. A new device for tracking worms crawling on or in the sediment surface was developed and employed on sandy flats in Königshafen, Island of Sylt in the northern Wadden Sea.

2. Methods

2.1 Study Area

Experiments were conducted in Oddewatt, a sandy tidal flat in the outermost part of Königshafen. Königshafen is a shallow intertidal bay at the north of the Island Sylt, northern Wadden Sea (Fig. 1). Average salinity is 30 PSU and mean temperature is 15° in summer and 4° in winter. Tides are semidiurnal with amplitude of 1.8 m. Oddewatt is located next to a tidal inlet. Sediments in the experimental area consist mainly of medium to fine sand (Armonies 1992). Gätje and Reise (1998) provide a detailed description of the biota, sedimentology and hydrography of the List tidal basin and Königshafen which is part of it.

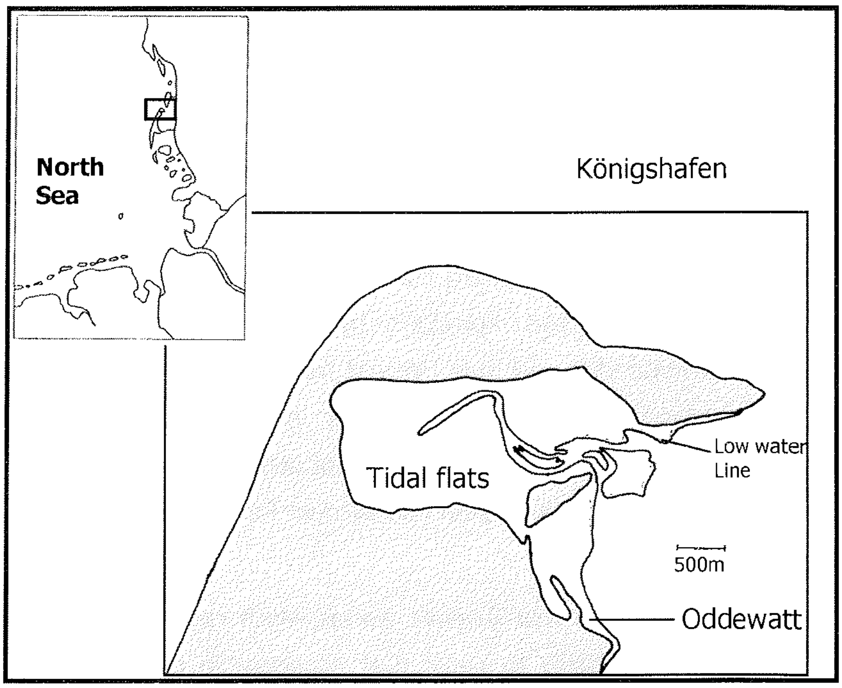


Figure 1. Study site in an intertidal embayment at the northern end of the island of Sylt in the eastern North Sea. The experiment was conducted in Oddewatt.

2.1. Experimental design

2.1.1 Devices: In order to trace *in situ* juvenile polychaete worms that crawl on or in the sediment surface half-open pipes (grooves) were designed and placed on tidal flats. For juveniles which drift or swim in the water column, drift nets were used (Armonies 1992).

Grooves: PVC pipes (1 m long, 10 cm diameter) were cut in half in longitudinal direction to obtain 2 grooves. In each one, a partition wall was insert in the middle. The grooves were covered with a mesh (250 µm) in order to avoid entrance from the water column (Fig. 2a and b). The only possible access to the grooves was at both ends. Three perforations on the bottom covered with 250 µm mesh were to prevent anoxic conditions in the grooves.

Nets: Horizontal plankton nets were used for collect drifting polychaetes (Fig. 2c). Nets were 55 cm long and 21 cm diameter. Nets were placed with the lower most margin of the net ca. 10 cm above the sediment surface. All nets in this experiment had a 250 µm mesh. For a detailed description see Armonies (1992).

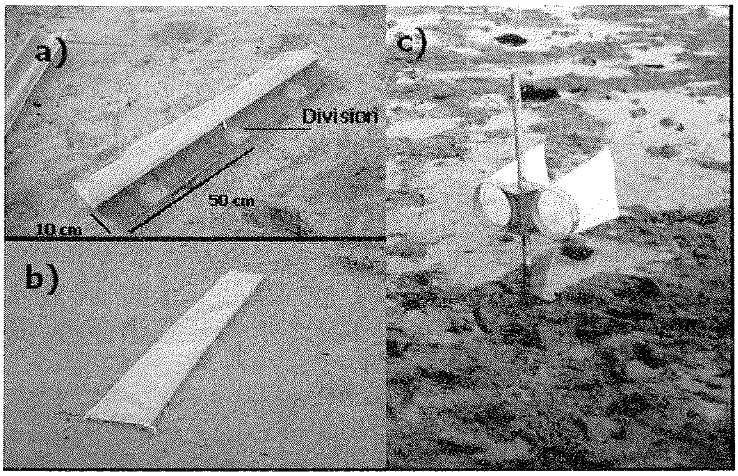


Figure. 2. Devices used: a) PVC grooves with middle division, b) position of a filled groove level with ambient sediment surface, c) plankton net to catch drifting organisms near the bottom in the tidal flow.

2.1.2 Design

Sediment from the study area was taken to the laboratory and only polychaete worms were picked out using a dissection microscope. All other organisms, as well as fragmented shells and pebbles were left in order to keep conditions as natural and undisturbed as possible.

A total of 12 grooves filled with polychaete-free sediment and 5 plankton nets were placed on the tidal flat. Six grooves were parallel to and six perpendicular to the main tidal current. Grooves were positioned in a way that between sediment surface and the cover-mesh a free space of 5 mm remained (Fig. 3).

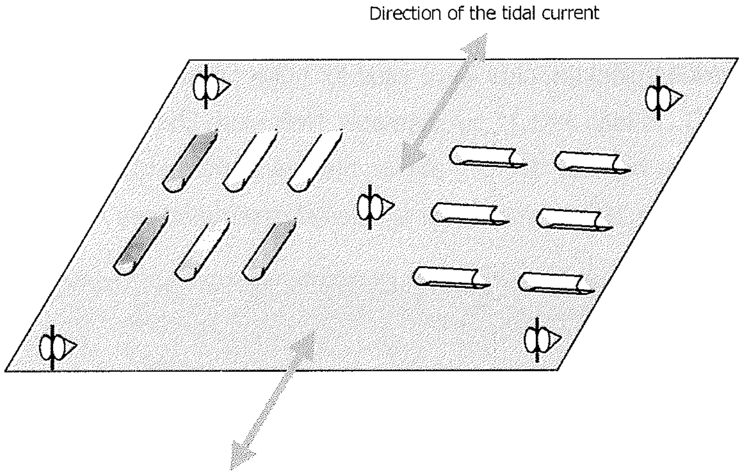


Figure 3. Experimental design. One set includes 12 grooves, 6 parallel and 6 perpendiculars to the tidal current, and five plankton nets which direct themselves into the current.

Each run started (T0) at low tide. 10 control samples (ambient sediment) were taken next to each groove with a 4 cm diameter (10 cm^2) core. Altogether 120 control samples were obtained.

At T1 (next low tide, approximately 12 hrs after T0) four grooves (two of each direction) were removed and sectioned into 6 parts (three in each half: outer, intermediate and inner sections (Fig. 4). In the laboratory, sediment was sieved trough a 250µ mesh and all polychaetes were counted. Drift nets were cleaned and the sediment as well as net contents were fixed with buffered formalin solution (7%). Water samples from the nets were analyzed with a dissection microscope and all polychaetes were counted.

At T2 (ca. 24 hrs after T0) and T3 (ca. 36 hrs after T0) the same procedure as at T1 was followed.

Three runs were made at the following dates: A full run at September 30 to October 2, 2001 (S/O-2001); a full run in July 27-29, 2002 (J-2002) and at September 15-18, 2002 (S-2002) a run with only 6 grooves disposed perpendicular to the tidal current.

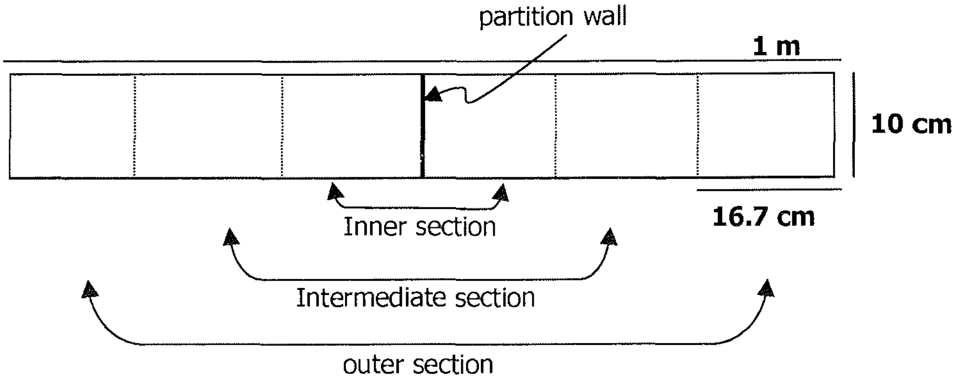


Figure 4. Grooves with partition wall in the middle and the six sections analyzed separately. Each section consists of 656 cm^3 of sediment.

2.2 Parameters measured

2.2.1 Drifting Organisms

Organisms found in the plankton nets were recorded and polychaetes were counted for each submersion period.

2.2.2 Effect of grooves

In order to detect if grooves attract or repel juveniles or larvae, comparisons of mean abundance between T3 and control (T0) were conducted using One-Way ANOVA. Similarity (Bray-Curtis index) of species composition in the grooves and in ambient sediment was also calculated. The hypothesis tested was whether grooves provide the same conditions as the ambient sediment sampled at T0 and whether tidal cycles were sufficient to complete recolonization.

2.2.3 Activity

Activity is defined here as the mean time interval after which a species showed up first in the grooves.

Species are classified into three degrees of activity:

- **High activity**: Species that entered grooves at T1
- **Intermediate activity**: Species that entered grooves at T2
- **Low activity**: Species that entered grooves at T3
- **No activity**: Species that have not entered grooves until T3

2.2.4 Crawling speed

Crawling speed of a species is expressed in $cm \cdot d^{-1}$.

Four degrees of crawling speeds are defined:

- **Slow species**: At least 60% of individuals occurred in the outer section after one tide (species crawl 8 cm in 12 h or 16 $cm \cdot d^{-1}$).
- **Species with intermediate speed**: At least 60% of individuals occurred in the intermedial section after one tide (species crawl 25 cm in 12 h or 50 $cm \cdot d^{-1}$).
- **Fast species**: at least 60% individuals occurred in the inner section after one tide (species crawl 42 cm in 12 h or 84 $cm \cdot d^{-1}$).

- **Very fast species**: abundance evenly distributed over all sectors. (A period of 12 h is already too long to estimate crawling speed with device of 50 cm length. Species crawl > 50 cm in 12 h or > $1 m \cdot d^{-1}$).

2.2.4 Effect of Tides

To test whether tidal flow has an effect on crawling performance, abundance of polychaete species in grooves parallel and perpendicular to current direction are compared with One-way ANOVA. It was further tested in grooves which were arranged parallel to tidal flow whether there occurred differences between those parts of the grooves which were open to flood direction and to ebb direction of tidal flow respectively (Fig. 5).

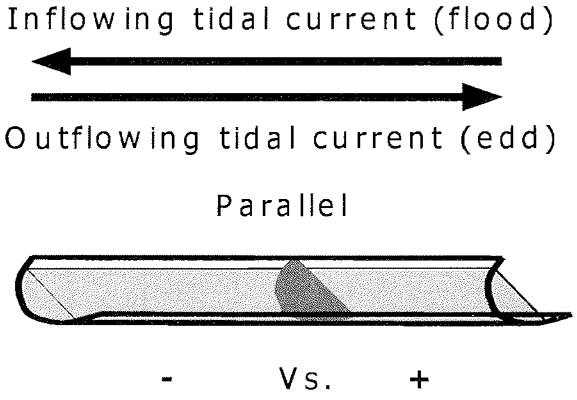


Figure 5. Schematic presentation of the comparisons made to define tidal effects.

3. Results

A total of twenty five polychaete species were found at the experimental site from September 2001 to September 2002 (Table 1). Five of them were found only as larvae, twelve only as juveniles. *Aphelochaeta marioni* was found only in the control samples.

Table 1. Species relative abundance (in percent) and developmental stages encountered during the experiment in drift nets, in grooves and in ambient sediment (control samples) respectively. L=larvae, J=juveniles, indet. = not identified.

	Nets		Grooves		Controls	
	L	J	L	J	L	J
Aphelochaeta marioni						<1
Arenicola marina				<1		<1
Aricidea minuta				2		2
Capitella capitata				10		5
Eteone longa	0.5			<1		
Exogone naidina				<1		<1
Eulalia viridis				4		<1
Lanice conchilega	63.1		9		2	
Microphthalmus sp.				8		26
Nereis virens				<1		<1
Nereis sp.	2.1		2		3	
Nephtyidae indet.			6		20	<1
Ophelia rathkei				13		8
Polydora ciliata			26	<1	2	<1
Pygospio elegans			<1	12	17	7
Polydora cornuta	4.3		42		27	
Polydora sp.	1.6					
Phyllodoce mucosa	0.5			<1		<1
Phyllodocidae indet.			6		12	
Scoloplos armiger	1.1			2		5
Spiophanes bombyx				<1		<1
Scolelepis bonnieri	2.7					
Scolelepis sp.	2.7					
Spio martinensis	21.4		8	38	17	35
Scolelepis squamata				<1		<1
Typosyllis hyalina				8		10

3.1 Drifting polychaetes

In drift nets only larvae were collected (Table 2), while juveniles and adults were not retained. Species diversity as well as the number of individuals of larvae were highest in July 2002, and runs in September/October 2001 and September 2002 differed considerably.

Table 2. Polychaete larvae encountered in nets in all runs. Values given are numbers of individuals found in all nets during 3 tidal cycles. S/O-2001= first run September -October 2001; J-2002= second run July 2002; S-2002= third run September 2002.

Species	**S/O-2001**	**J-2002**	**S-2002**
Eteone longa	0	1	0
Lanice conchilega	0	70	48
Nereis sp.	0	4	0
Phyllodoce mucosa	1	0	0
Polydora cornuta	0	8	0
Polydora sp.	0	3	0
Scolelepis spp.	0	8	2
Scoloplos armiger	0	0	2
Spio martinensis	0	32	8
TOTAL	**1**	**126**	**60**

3.2 Effects of grooves

Abundance of juveniles and larvae in the ambient sediment was in all runs significantly higher than in the grooves (Tab. 3). At run September-October 2001, juveniles of *Polydora ciliata* and *Scolelepis squamata* were only found in ambient sediment, while in July 2002 only *Aphelochaeta marioni* had not entered the grooves, and in September 2002 *Exogone naidina* and *Scoloplos armiger* were only found in ambient sediment. This indicates that 3 tidal cycles were not sufficient to recolonize the sediment of the grooves completely.

Table 3. Comparison between mean abundance and species composition inside and outside the grooves. Section B shows ANOVA values.

	T3 vs T0 (Control) mean abundance (ind/m^2±SD)	Similarity of Species Composition (Bray-Curtis measure)
S/O-2001	T3= 443 ± 318 T0= 3,528 ± 2,529 **F**$_{(1,28)}$=17.4672, p<0.01	67
J-2002	T3= 531 ± 250 T0= 7,347 ± 4,812 **F**$_{(1,46)}$=23.7128, p<0.01	75
S-2002	T3=1,776 ± 1,971 T0 (Control)=14,055 ± 5,741 **F**$_{(1,22)}$=29.9242, p<0.01	77

B)

ANOVA values	SS	dF	MS	***F***	P
S/O-2001 T3 vs T0	68527105	1	68527105	17.4672	0.0002
J-2002 T3 vs T0	418117296	1	418117296	23.7128	0.0000
S-2002 T3 vs T0	7.627360E +8	1	7.627360E+8	29.9242	0.0000

3.3 Activity

Most species fall into the category of high activity, entering the grooves already during the first tidal cycle (Tab. 4). *Capitella capitata*, *Ophelia rathkei*, *Pygospio elegans* and *Spio martinensis* were in all 3 runs among the highly active species. A few species (e.g. *Phyllodoce mucosa*) displayed an inconsistent pattern between experimental runs.

Larval stages of 8 species were found in runs from July 2002 and September 2002 (Tab. 5). Larvae of *S. martinensis* were highly active. Almost all show high to intermediate activity in entering the grooves.

Table 4. Activity of juvenile polychaetes in entering experimental grooves at T1. S/O-2001= first run September 30 to October 2, 2001; J-2002= second run July 27-29, 2002; S-2002= third run September 15-18, 2002.

S/O-2001	J-2002	S-2002
High activity	**High activity**	**High activity**
Arenicola marina	*Aricidea minuta*	*C. capitata*
Capitella capitata	*C. capitata*	*O. rathkei*
Eulalia viridis	*E. longa*	*P. elegans*
Microphthalmus sp.	*Exogone naidina*	*Spiophanes bombyx*
Nereis virens	*Microphthalmus* sp.	*S. martinensis*
Ophelia rathkei	*O. rathkei*	*T. hyalina*
Pygospio elegans	*P. elegans*	
P. mucosa	*S. armiger*	
S. armiger	*S. martinensis*	
S. martinensis	*T. hyalina*	
Scolelepis squamata		
Intermediate activity	**Intermediate activity**	**Intermediate activity**
P. ciliata	*S. squamata*	*E. naidina*
Typosyllis hyalina		*S. squamata*
Low activity	**Low activity**	**Low activity**
	P. mucosa	*Microphthalmus sp.*
		P. mucosa
No activity	**No activity**	**No activity**
	A. marioni	*S. armiger*
		N. virens
		Nephtyidae indet.

Table 5. Activity of polychaete larvae found in experimental runs. None were recorded in grooves in 2001. J-2002= second run July 2002, S-2002= third run September 2002.

J-2002	S-2002
High activity	**High activity**
Nephtyidae indet.	*Nereis* sp.
S. martinensis	*P. ciliata*
Phyllodocidae indet.	*P. cornuta*
	S. martinensis
	Phyllodocidae indet.
Intermediate activity	**Intermediate activity**
L. conchilega	
P. elegans	
P. cornuta	
Nereis sp.	
Low activity	**Low activity**
P. ciliata	

3.4 Crawling speed

For most species a twelve-hour tidal cycle was too long to differentiate crawling speeds at a scale of 50 cm. They were evenly distributed over all sectors and were classified as very fast species (Tab. 6). For *O. rathkei* and *P. elegans* this was consistent over all experimental runs, while *C. capitata* always remained below this category.

Table 6. Mean crawling speeds of juveniles found in all experimental runs. S/O-2001= first run September - October 2001; J-2002= second run July 2002; S-2002= third run September 2002.

S/O-2001	J-2002	S-2002
Slow species (8 cm·12 h)	**Slow species (8 cm·12 h)**	**Slow species (8 cm·12 h)**
A. marina *E. viridis*	*C. capitata*	*S. bombyx*
Intermediate speed (25 cm·12 h)	**Intermediate speed (25 cm·12 h)**	**Intermediate speed (25 cm·12 h)**
C. capitata *Microphthalmus* sp. *S. armiger*	*E. longa*	*T. hyalina*
Fast species (42 cm·12 h)	**Fast species (42 cm·12 h)**	**Fast species (42 cm· 12 h)**
	A. minuta *E. naidina* *Microphthalmus* sp.	*C. capitata*
Very fast species (> 50 cm·12 h)	**Very fast species (> 50 cm·12 h)**	**Very fast species (> 50 cm·12 h)**
N. virens *O. rathkei* *P. ciliata* *P. elegans* *P. mucosa* *S. martinensis* *S. squamata*	*O. rathkei* *P. elegans* *S. armiger* *S. martinensis* *T. hyalina*	*O. rathkei* *P. elegans* *Microphthalmus* sp.

Larval stages of five species could be classified according to crawling speed. Only *P. cornuta* larvae belong to the very fast species. The others (*S. martinensis*, *Nereis* sp., *P. ciliata* and Nephtyidae indet.) were categorized as slow to intermediate with respect to crawling speed.

3.6 Effect of tidal flow

In comparisons between grooves being arranged parallel and perpendicular to the tidal current direction in both cases S/O-2001 ($F_{(1,34)}$=32.0630, p<0.01) and J-2002 ($F_{(1,34)}$=16.2273, p<0.01) a significant difference was found (Tab. 7). Perpendicular grooves had higher abundance than parallel ones.

Mean abundances between the flood- and ebb-flow direction sides of the grooves parallel to the tidal flow were not significantly different (Tab. 7). Inflowing and outflowing currents had the same effect on crawling in juvenile/larval worm movements.

Table 7. Comparison of mean abundance (ind/167 cm^2±SD) between groove directions with respect to the tidal current flow and in grooves parallel to the tidal flow between flood (+) and ebb (-) flow direction (ns= no significant differences).

	Parallel vs. Perpendicular			Parallel (+ vs -)		
	parallel	perpendicular		Flood +	Ebb -	
S/O-2001	5.30±4.76	13.61±4.00	$F_{(1,34)}$=32.0630, p<0.01	5.30±3.67	5.33±5.89	Ns
J-2002	4.75±3.18	9.44±3.78	$F_{(1,34)}$=16.2273, p<0.01	4.50±3.91	5.00±2.46	Ns

ANOVA Values	SS	dF	MS	***F***	p
S/O-2001					
Parallel (+ vs -)	4.594	1	4.594	0.0479	0.8287
J-2002					
Parallel (+ vs -)	1.388	1	1.388	0.1290	0.7241
S/O-2001					
Parallel vs. Perpendicular	620.84	1	620.84	32.063	0.0000
J-2002					
Parallel vs. Perpendicular	198.34	1	198.34	16.227	0.0002

4. Discussion

Drifting juveniles.

No evidence was found that juvenile polychaete worms drift in the water column during July to October. The presence of polychaete larvae and other organisms in the drift nets indicated that the sampling device was working properly. It cannot be excluded that in other seasons or when the sea is rough juvenile polychaetes enter the water column and drift over wide distances with the tidal current. Armonies (1999) reported juvenile *A. marina* and *S. armiger* in the water column as resuspended organisms due wind effects. In another study on polychaete larvae in Königshafen between 2000 and 2002 (Rodriguez-Valencia 2003) the incidence of juveniles in water samples was low (Table 8). Considering the high number of juvenile polychaetes in the sediment it is supposed that worms primarily stay and move in the sediment and avoid the water column. This is in contrast to other taxa of the soft bottom macrofauna (Armonies 1994, Günther 1992). Particularly infaunal bivalves, hydrobiid snails and amphipods enter the water column for dispersal.

Table 8. Mean abundance of juvenile polychaetes in the water column from May to August 2000 (ind / 10 l). Wind data for each sampling date are given (Rodriguez-Valencia, unpublished data).

	Pygospio elegans	*Scoloplos armiger*	*Nereis diversicolor*	*Scolelepis squamata*	*Ophelia rathkei*	*Polydora cornuta*	*Magelona mirabilis*	*Phyllodoce mucosa*	*Typosyllis hyalina*	Wind ($m \cdot s^{-1}$)
May 8	0	0.013	0.120	0.003	0.023	0	0	0	0	E 7
May 15	0	0.008	0	0	0	0	0	0	0	S 4.4
May 25	0	0.003	0	0	0	0	0	0	0	E 8.7
May 28	0.003	0.004	0	0	0	0	0	0	0	E 8.3
May 31	0	0.003	0.005	0	0	0	0	0	0	W 7.4
June13	0	0	0	0	0.003	0.003	0.003	0.003	0	W 10.7
Aug 7	0	0	0	0	0	0	0	0	0	NW 9.9
Aug 22	0	0	0	0	0	0	0	0	0.05	NW 5.8

Crawling on or in the sediment surface seems to be the preferred mode of juvenile dispersal in polychaetes. The presence of juveniles in the experimental grooves clearly demonstrates that lateral movement through the sediment is a common mode of dispersal.

Larval settlement inside the grooves was not possible and it is surprising that even larvae have the ability to crawl into the experimental devices, albeit at as lower speed than juveniles do.

Little information is available on how far a single polychaete worm can actively move in the sediment. Günther (1992) argued that transport of postlarvae and juvenile could be regarded as meso scale dispersal, ranging from meters to kilometers, and in time scales from hours to seasons (Armonies 1994). Passive tidal transport of juvenile *A. marina* can reach up to some kilometers during the autumn-winter season (Beukema and de Vlas 1979), and *Armandia amakusaensis* swims only short distances (Tamaki 1985). Post-settled larvae of *P. koreni* are also able to migrate, but movement rates are unknown (Thiébaut *et al.* 1996). So, no information on active transport or migration rates on or in the sediment is available. Therefore activity and mobility rates given in this study provide a new insight.

Highly active as well as the very fast species were the smallest ones (*P. elegans*, *O. rathkei*, *S. martinensis*, *T. hyalina*). Shull (1997) found that colonization rate of the small polychaete *Streptosyllis arenae* was a function of sediment transport. Observations of colored sand of different grain sizes conducted parallel to this study, showed that small particles were passively transported only 1-2 cm inside the grooves. Juveniles and larvae moved wider than this distance. Therefore, they must have undertaken active movements on or in the sediment. In most species crawling distances may exceed 0.5 m per tidal cycle which is more than 100 times of the body length of the juvenile polychaetes in question. This result has implications for small-scale experiments conducted in marine soft-sediments. On the other hand it should be noted that not all individuals and species move that much. For example, juvenile *Capitella capitata* were less active crawlers. Also the experimental grooves after three tidal cycles still showed significantly lower abundances than the ambient sediment. This indicates that it takes time until barriers are bypassed.

Inflowing and outflowing tidal currents had no effect on abundance in the grooves, since no significant differences between either half of the grooves were found when parallel to the flow. Movements seaward and landward have the same preference. Movements mainly in an offshore direction have been observed for *Armandia* sp. (Tamaki 1985) and in both directions for *Arenicola marina* (Beukema and de Vlas 1979).

Tidal currents seem to have a negative effect on the movement of juveniles and larvae because in those grooves positioned in current direction the abundance was lower than in grooves perpendicular to the tidal current. Apparently, at the experiment site a stabilization of the sediment, as inadvertently accomplished by perpendicular grooves, is attractive for juvenile polychaetes. This is confirmed by high abundances of juveniles in seagrass beds and fragmented shell patches (see chapter II)

Advantages and disadvantages of the experiment

Many *in situ* experiments or sample devices were developed to study larval settlement (Butman 1987, Whitlatch *et al.* 1998) or colonization (Smith 1985, Snelgrove *et al.* 1999, Levin and DiBacco 1995). This is a first attempt to evaluate the active movement and crawling speeds of post-settled polychaetes near the sediment surface in non-disturbed sediments.

Due to the high effort in time to obtain sediment free of polychaetes, this experiment was conducted at a small spatial scale and a few times only. Evidently, results are hampered since abundances of juveniles and larvae vary seasonally. Nevertheless, the consistency of results in both years suggests for juvenile polychaetes that crawling on or in the sediment may be in the order of one meter per day, and that dispersal though the water column is less important.

The developed device could serve as a basis for future experiments with a better effort-cost balance. With respect to crawling speed, longer grooves than the ones used are recommended.

5. FINAL DISCUSSION

Dispersal

Results of this study show that juvenile and adult polychaetes could have different habitat preferences. The juveniles of some species preferred structured habitat as nurseries, while adults were also abundant in non-structured ones. Juvenile migrations to adult habitat may be a mandatory process. Indirect evidence of benthic migrations were found for species like *Spio martinensis* and *Capitella capitata*, when small-scale distribution patterns were analyzed. Direct measurements of the crawling performance of some juvenile polychaetes indicate that some juveniles are capable to crawl at least one meter per day. While secondary dispersal brings juvenile mollusks and some amphipods over wide distances (Günther 1992), the scale of such dispersal seems to be smaller in polychaetes. Nevertheless it is enough in order to accomplish a habitat change, that is, a few hundred of meters from a structured (e.g. seagrass or shell beds) to a non-structured habitat (e.g. sandy flats) within the tidal zone and to adjacent subtidal bottoms.

The fact that post-settlers could serve dispersal has been particularly recognized for bivalves (Günther 1992, Armonies 1994, 1999). In polychaetes the presence of spatially separate juveniles and adults in some species (e.g. *Ophelia rathkei*) indicates that movement of juveniles to reproductive areas may be mandatory. For juvenile worms passive transport in the water column as drifting organisms seems to be related with resuspension by waves (Armonies 1999). The indirect evidence of organism transport found in this study (Chapter III), revealed that juveniles are capable to move near to the sediment surface or by actively crawling on or in the sediment. This also seems to be a common mode in the re-colonization of defaunated sediments (Levin and DiBacco 1995).

Direct evidence was provided for juveniles crawling about one meter per day through the surface layer of the sediment (Chapter IV). Synchronous to the crawling experiment, nets set up above the sediment to catch drifting or swimming juveniles failed in summer/autumn to catch any. However, the nets filtered the water not directly above the sediment surface but 10 to 40 cm above. The grooves to measure crawling were covered with a mesh to prevent larval settlement and lateral access to the grooves. This device may have hampered polychaetes swimming and drifting in close contact to the sediment surface since the space between sediment and cover-mesh was only a few mm. Thus, there may be a gap no covered in this study which is between the upper sediment layer and the water column: the sediment-water interface. Future studies on polychaete dispersal should focus this boundary layer.

The fact that also polychaetes with holobenthic development (e.g. *Capitella capitata*) show benthic dispersal, emphasizes the importance of the secondary dispersal by benthic stages for the maintenance of the population. In this study area, at least 10% of the 117 polychaete species recorded, show direct development.

Suggestions for further research

Distribution patterns: A systematic sampling design with transects from the high tidal level to the subtidal and throughout all seasons, is necessary in order to obtain a more complete picture of juvenile and adult distribution patterns in polychaetes of the Wadden Sea. This is important to ascertain in how many species post-settlement drift or migration is mandatory.

Small-scale dispersion patterns: A combination of dispersion analyzes and cohort tracking may allow to separate the effect of mortality and immigration and emigration on the dispersion patterns. If size (e.g. total length or peristomium diameter, depending on species) is taken as a proxy for age, it is possible to obtain more accurate measurement of dispersing groups of juveniles.

Benthic dispersal: As discussed above, the grooves used in the experimental design were for some species too short. Longer grooves could improve the estimates of distances potentially covered by dispersal. Since in the grooves can only trace organisms which crawl in or on sediments, and drift nets were placed

10 cm above the sediment surface, it is necessary to concentrate the effort in this 10 cm gap, where no samples were taken. For some polychaete species with a good swimming capability, this space could be important in order to move over wide distances.

Observations on juveniles stained with vital color and the recapture of these organisms may provide further insight on their mobility.

Planktonic and benthic polychaete stages in the List tidal basin

Parallel to this study, another one was done on planktonic stages of polychaete worms in the List tidal basin (Rodriguez-Valencia 2003). He compiled a list on previous records on polychaetes found in the study area. Together with the species recorded in this study, a list of 117 species is obtained (See appendix 1). For each species, the developmental stages found (adults, juveniles and larvae) are also indicated. Remarkable is the fact that not for all species all developmental stages were found. A synopsis of possible causes is presented in Figure 1. For 14% (16 species) all development stages were recorded.

Adults	Juveniles	Larvae		
✓	✓	✓	⇨	Common, established, and abundant species (*Pygospio elegans, Lanice conchilega*)
✓	o	✓	⇨	Spatial segregation, differential habitat preferences, low sampling frequency (*Aonides paucibranchiata, Nephtys hombergii* and *N. caeca*)
✓	✓	o	⇨	Direct development, long distance planktonic dispersal, larval export (*Tharyx killariensis, Arenicola marina, Nereis virens*)
✓	o	o	⇨	Loss of species since recorded as adult in the benthos, taxonomic confusion, species with low abundance (*Scolelepis foliosa, Harmothoe sarsi, Amphitrite johnstoni*)
o	o	✓	⇨	Taxonomic confusion, long distance vagrants, low settlement success (*Polydora* Typ I, II, *Scolelepis bonnieri, Harmothoe ljungmani*)

Figure 1. Summary of causes for the lack of developmental stages. ✓=present, o=absent.

For 6% of all species no juveniles were found. An explanation could be the low sampling frequency, although juvenile life of some polychaete species could be up to one year (age of first reproduction) (Gosselin and Qian 1997). Also a possible differential habitat requirement of juveniles and adults (e.g. nursery habitat, winter refuge) or a spatial segregation as reported in chapter II, and the lack of sampling in a specific habitat could have contributed to the missing of juveniles. For 12% of all species no pelagic larval stage was found. Many of these species (*Arenicola marina*, *Capitella minima*, *Tharyx killariensis*) have direct development (Hartmann-Schröder 1996). However for other species (e.g. *Magelona alleni*, *Aricidea (A.) minuta*, *Nepthys cirrosa*) where the presence of planktonic larvae is assumed, these were not found.

For a large number of species (47%) only adult stages are reported. This is primarily due to a sampling effort biased towards the larger benthic stages. For 21% of species only the larval stage is known until now. Rodriguez-Valencia (2003) argued that long distance vagrants imported from the North Sea with low settlement success may account for this phenomenon. Of course, taxonomic ambiguities probably underlay several cases where either only adults or only larvae have been recorded.

Concluding remarks

Although polychaete worms represent often the most abundant and diverse macrobenthic taxon in marine sediments, their ecology and taxonomy is less well known than in the other major taxa. This study has focused on the benthic or semi-benthic dispersal of juvenile stages. Indirect evidence has been presented that this dispersal phase in the polychaete life cycle deserves more attention. To close this gap in knowledge emphasis should be given to innovative sampling devices and to improvements in taxonomy.

Appendix I. List of polychaete species recorded at the List tidal basin (Modified from Rodriguez-Valencia 2003). Developmental stages known for each species are given. A= adult, J= juvenile, L=larva.

SPECIES	**A**	**J**	**L**
1. *Scoloplos (S.) armiger*	X	X	X
2. *Tharyx killariensis= T. marioni*	X	X	
3. *Aricidea minuta*	X	X	
4. *A. (Allia) suecica= A. jefreysii*	X		
5. *Paraonis fulgens*	X		
6. *Aonides paucibranchiata*	X		X
7. *Laonice cirrata*			X
8. *Malacoceros fuliginosus*	X	X	X
9. *Marenzelleria viridis*	X		
10. *Polydora (P.) ciliata*	X	X	X
11. *P.(P.)cornuta=P. ligni*	X	X	X
12. *P.(P.) hermaphroditica*			X
13. *P. quadrilobata*	X		
14. *P. pulchra*			X
15. *Polydora* Type I			X
16. *Polydora* Type II			X
17. *Pygospio elegans*	X	X	X
18. *Scolelepis (S.) bonnieri*			X
19. *S. (S.) squamata*	X	X	X
20. *S. (S.) girardi*			X
21. *S. (S.) foliosa*	X		
22. *S. ciliata = Colobranchus ciliatus = M. tetracerus*	X		
23. *Scolelepis* Type I			X
24. *Spio martinensis*	X	X	X
25. *S. theelli*			X
26. *S. filicornis*	X		
27. *S. mecznikowianus*	X		
28. *Spiophanes bombyx*	X	X	X
29. *Streblospio benedicti=S. shrubsolii*	X		
30. *Microspio wireni*	X		
31. *Magelona alleni*	X	X	
32. *Magelona mirabilis=M. papillicornis*	X		X
33. *Poecilochaetus serpens*			X
34. *Chaetozone setosa*	X		
35. *Cirratulus cirratulus*	X		
36. *Capitella capitata*	X	X	X
37. *Capitella minima*	X	X	
38. *Capitella* Type I			X
39. *Capitella* Type II			X
40. *Capitomastus minimus*	X		

Appendix I. List of polychaete species recorded at the List tidal basin (Modified from Rodriguez-Valencia 2003). Developmental stages known for each species are given. A= adult, J= juvenile, L=larva. (Continued).

SPECIES	**A**	**J**	**L**
41. *Arenicola marina*	X	X	
42. *Heteromastus filiformis*	X	X	
43. *Ophelia limacina*	X	X	
44. *O.rathkei=O.cluthensis*	X	X	
45. *Scalibregma inflatum*	X		
46. *Phyllodoce (A.) mucosa*	X	X	X
47. *P. (A.) rosea*			X
48. *P. (A.) maculata*	X		X
49. *Eteone (E.) longa*	X	X	X
50. *E. (E.) spetsbergensis*	X		
51. *E. (M.) barbata*			X
52. *Eulalia viridis*	X	X	X
53. *E. bilineata*	X		
54. *Pseudomystides limbata*			X
55. *Eumida sanguinea*	X		
56. *E. punctifera*	X		
57. *Harmothoe (H.) antilopes*			X
58. *H. (H.) glabra*			X
59. *H. (H.) impar*	X		X
60. *H. (H.) ljungmani*			X
61. *H. (H.) imbricata*	X		
62. *H. (Antionella) sarsi*	X		
63. *H. lunulata*	X		
64. *Harmothoe* Type I			X
65. *Lepidonotus squamatus*	X		
66. *Gattyana cirrosa*	X		
67. *Pholoe minuta*	X		
68. *Neolanira c.f. tetragona*			X
69. *Keferesteinia cirrata*	X		
70. *Microphthalmus aberrans*	X	X	X
71. *M. sczelkowii*	X		
72. *M. similis*	X		
73. *M. listensis*	X		
74. *Hesionides arenaria*	X		
75. *H. maxima*	X		
76. *Exogone naidina*	X	X	
77. *Typosyllis hyalina*	X	X	
78. *Streptosyllis websteri*	X		
79. *Nereis (Nereis) pelagica*	X		
80. *N. (Neanthes) succinea*	X		
81. *N. (Neanthes) virens*	X	X	

Appendix I. List of polychaete species recorded at the List tidal basin (Modified from Rodriguez-Valencia 2003). Developmental stages known for each species are given. A= adult, J= juvenile, L=larva. (Continued).

SPECIES	**A**	**J**	**L**
82. *N.(Hediste) diversicolor*	X	X	X
83. *Nereis* Type I			X
84. *Nereis* Type II			X
85. *Goniada maculata*	X		
86. *Goniadella bobretzkii*	X		
87. *Nephtys caeca*	X		X
88. *N. hombergii*	X		X
89. *N. ciliata*	X		
90. *N. longosetosa*	X		
91. *N. cirrosa*	X	X	
92. *N. pulchra*	X	X	
93. *Sphaerodorum balticum= Sphaerodoropsis baltica*	X		
94. *S. minimum*	X		
95. Sphaerodoridae Type I			X
96. *Ophryotrocha gracilis*	X		
97. *Parapodrilus psammophilus*	X		
98. Flabelligeridae Type I			X
99. *Sabellaria spinulosa*	X		X
100. *Pectinaria (L.) koreni*	X	X	X
101. *Lanice conchilega*	X	X	X
102. *Ampharete acutifrons = A. grubei*	X		
103. *A. baltica*	X		
104. *A. finmarchica*	X		
105. *Amphitrite johnstoni*	X		
106. *Neoamphitrite figulus*	X		
107. *Fabricia sabella*	X	X	X
108. *Chone* Type I			X
109. *Pomatoceros triqueter*	X		
110. *Manayunkia aestuarina*	X		
111. *Dinophilus gyrociliatus*	X		
112. *Psammodrilus balanoglossoides*	X		
113. *Stygocapitella subterranea*	X		
114. *Trilobodrilus axi*	X		
115. *Protodrilus symbioticus*	X		
116. *P. adhaerens*	X		
117. *P. chaetifer*	X		

REFERENCES

ALBRECHT, S. 2004. Vergleichende Morphologie eu- und sublitoraler Polychaeten der Gattung *Scoloplos* in der Nordsee. Master Thesis. Phillips-University of Marburg. 53 p.

ANDREW, N.L. & B.D. MAPSTONE. 1987. Sampling and the description of spatial pattern in marine ecology. Ocean. Mar. Biol. Ann. Rev. 25:39-90.

ARMONIES, W. 1992. Migratory rhythms of drifting juvenile mollusks in tidal waters of the Wadden Sea. Mar. Ecol. Prog. Ser. 83:197-206.

__________. 1994. Drifting meio- and macrobenthic invertebrates on tidal flats in Königshafen: a review. Helgol. Meeresunters.48:299-320.

__________. 1996. Changes in distribution patterns of 0-group bivalves in the Wadden Sea: Byssus-drifting releases juveniles from the constraints of hydrography. J. Sea Res. 3:323-334.

__________. 1999. Drifting benthos and long-term research: Why community monitoring must cover a wide spatial scale. Senckenbergiana maritima (Suppl.) 29:3-18.

__________, & M. HELLWIG-ARMONIES. 1992. Passive settlement of *Macoma balthica* spat on tidal flats of the Wadden Sea and subsequent migration of juveniles. Neth. J. Sea Res. 29(4):371-378.

ASMUS, R. 1982. Field measurements on seasonal variation of the activity of primary producers on a sandy tidal flat in the northern Wadden Sea. Neth. J. Sea Res. 16:389-402.

AUSTEN, I. 1992. Geologisch-sedimentologische Kartierung des Königshafen (List/Sylt). Meyniana 44:45-52.

AUSTER, P.J.; L.L. STEWART, & H. SPRUNK. 1989. Scientific imaging with ROV's: tools and techniques. Mar. Technol. Soc. J. 23(3):16-20.

BACKHAUS, J.; D. HARTKE, U. HÜBNER, H. LOHSE, & A. MÜLLER. 1998. Hydrography and climate of the List tidal basin. In: The Wadden Sea Ecosystem. Exchange, Transport, and Transformation Processes (C. Gätje and K. Reise Eds.) Springer Verlag Berlin. 39-54.

BAYERL, K.A.; R. KÖSTER, & D. MURPHY. 1998. Distribution and composition of sediments in the List Tidal Basin. In: The Wadden Sea Ecosystem. Exchange, Transport, and Transformation Processes (C. Gätje and K. Reise Eds.) Springer Verlag Berlin. 31-38.

__________, & R. KÖSTER. 1998. Morphogenesis of the List Tidal Basin. In: The Wadden Sea Ecosystem. Exchange, Transport, and

Transformation Processes (C. Gätje and K. Reise Eds.) Springer Verlag Berlin. 25-30.

BAYNE, B.L. 1964. Primary and secondary settlement in *Mytilus edulis* L. (Mollusca). J. Anim. Ecol. 33:513-523.

BECK, M.V.; K.L. JR. HECK, K.W. ABLE, D.L. CHILDERS, D.B. EGGLESTON, B.M. GILLANDERS, B.S. HALPERN, C.G. HAYS, K. HOSHINO, T.J. MINELLO, R.J. ORTH, P.F. SHERIDAN, & M.P. WEINSTEIN. 2003. The role of nearshore ecosystems as fish and shellfish nurseries. Issues in Ecology. No. 11. Ecological Society of America.

BELL, J.D.; D.J. FERRELL, S.E. MCNEILL, & D.G. WORTHINGTON. 1992. Variation in assemblages of fish associated with deep and shallow margins of the seagrass *Posidonia australis*. Mar. Biol. 114:667-676.

BERGSTRÖM, U.; G. ENGLUND, & E. BONSDORFF. 2002. Small-scale structure of Baltic Sea zoobenthos-- inferring processes from patterns. J. Exp. Mar. Biol and Ecol. 281:123-136.

BEUKEMA, J.J. 1989. Long-term changes in macrozoobenthic abundance on tidal flats of the western part of the Dutch Wadden Sea. Helgoländer Meeresunters. 43:405-415.

BEUKEMA, J.J. & J. DE VLAS. 1979. Population parameters of the lugworm *Arenicola marina*, living on tidal flats in the Dutch Wadden Sea. Neth. J. Sea Res. 13:331-353.

BHAUD, M. 1982. Relations entre stratégies de reproduction et aire de répartition chez les annélides polychètes. Oceanol. Acta 5(4):465-472.

__________. 1998. The spreading potential of polychaete larvae does not predict adult distributions; consequences for conditions of recruitment. Hydrobiologia 375/376:35-47.

__________. 2000. Two contradictory elements determine invertebrate recruitment: dispersion of larvae and spatial restrictions on adults. Oceanol. Acta. 23(4):409-422.

__________, & C. CAZAUX. 1982. Polychate larvae from French coasts. Oceanis 8(2):57-160.

BOESCH, D.F. & R.E. TURNER. 1984. Dependence of fishery species on salt marshes: the role of food and refuge. Estuaries 7(4A):460-468.

BOSTRÖM, C. & E. BONSDORFF. 1997. Community Structure and spatial variation of benthic invertebrates associated with *Zostera marina* (L.) beds in the northern Baltic Sea. J. Sea Res. 37:153-166.

__________. 2002. Zoobenthic community establishment and habitat complexity - the importance of seagrass shoot density, morphology and physical disturbance for faunal recruitment. Mar. Ecol. Progr. Ser. 205:123-138.

BUSCHBAUM, C. 2002. Siedlungsmuster und Wechselbeziehungen von Seepocken (Cirripedia) auf Muschelbänken (*Mytilus edulis* L.) im Wattenmeer. Dissertation. University of Hamburg. 146 p.

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

CATTRIJSSE, A.; H.R. DANKWA, & J. MESS. 1997. Nursery function of an estuarine tidal marsh for the brown shrimp *Crangon crangon*. J. Sea Res. 38:109-121.

CLOBERT, J.; E. DANCHIN, A.A. DHONDT, & J.D. NICHOLS (Eds). 2001. Dispersal. Oxford University Press. U.K. 443 pp.

CUMMINGS, V. J.; R. D. PRIDMORE, S.F. THRUSH, & J.E. HEWITT. 1995. Post-settlement movement by intertidal benthic macroinvertebrates: Do common New Zealand species drift in the water column? New Zealand Journal of Marine and Freshwater Research 29:59-67.

DAUNYS, D.; D. SCHIEDEK, & S. OLENIN. 2000. Species strategy near its boundary: the *Marenzelleria* cf. *viridis* (Polychaeta, Spionidae) case in the south-eastern Baltic Sea. Int. Rev. Hydrobiol. 85(5-6):639-651.

DUNN, R.; L.S. MULLINEAUX, & S.W. MILLS. 1999. Resuspension of postlarval soft-shell clams *Mya arenaria* through disturbance by the mud snail *Ilyanassa obsoleta*. Mar. Ecol. Prog. Ser. 180:223-232.

ESSINK, K. & R. DEKKER. 2002 General patterns in invasion ecology tested in the Dutch Wadden Sea: the case of a brackish-marine polychaetus worm. Biological Invasions 4:359-368.

FARKE, H. & E.M. BERGHUIS. 1979. Spawning, larval development and migration behavior of *Arenicola marina* in the laboratory. Neth. J. Sea Res. 13(3-4):512-528.

FARKE, H.; P. A. W.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(3-4):354-361.

FRASCHETTI, S.; A. GIANGRANDE, A. TERLIZZI, & F. BOERO. 2003. Pre- and post-settlement events in benthic community dynamics. Ocean. Acta 25:285-295.

GÄTJE, CH. & K. REISE. (Eds). 1998. The Wadden Sea Ecosystem. Exchange, Transport, and Transformation Processes. Springer Verlag Berlin. 571 p.

GIANGRANDE, A. 1997. Polychaete reproductive patterns, life cycles and life histories: an overview. Oceangr. Mar. Biol. Ann. Rev. 35:323-386.

GIBSON, R.N. 2003. Go with the flow: tidal migration in marine animals. Hydrobiologia 503:153-161.

GOSSELIN, L. A. & P.Y. QIAN. 1997. Juvenile mortality in benthic marine invertebrates. Mar. Ecol. Progr. Ser. 146:265-282.

GRASSLE, J.F. & J.P. GRASSLE. 1994. Notes from the abyss: the effect of a patchy supply of organic material and larvae in soft-sediment benthic communities. In: Giller, P.S.; A.G. Andrew, & D.G. Rafaelli (Eds). Aquatic ecology: scale, patterns and process. Blackwell Scientific Publications, Oxford. 499-516.

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

__________. 1981. The ecology of marine sediments. Cambridge University Press, Cambridge. 185.

GÜNTHER, C. P. 1992. Dispersal of intertidal invertebrates: a strategy to react to disturbances of different scales? Neth. J. Sea Res. 30:45-56.

HALL, S.F. 1994. Physical disturbance and marine benthic communities: life in unconsolidated sediments. Oceanogr. mar. Ann. Rev. 32:179-239.

HARTMANN-SCHRÖDER, G. 1996. Die Tierwelt Deutschlands. 58. Teil. Polychaeta. Gustav Fischer Verlag. 648 p.

HASTINGS, A. 1990. Spatial heterogeneity and ecological models. Ecology 71:426-428.

HIDDINK, J.G.; S.A.E. MARIJNISSEN, K. TROOST, & W.J. WOLFF. 2002. Predation on 0-group and older year classes of the bivalve *Macoma balthica*: interaction of size selection and intertidal distribution of epibenthic predators. J. exp. mar. Biol. Ecol. 269:223-248.

HIGELKE, B. 1998. Morphodynamics of the List tidal basin. In: The Wadden Sea Ecosystem. Exchange, Transport, and Transformation Processes (C. Gätje and K. Reise Eds.) Springer Verlag Berlin. 103-126.

HUNT, H.L. & R.E. SCHEIBLING. 1997. Role of early post-settlement mortality in recruitment of benthic marine invertebrates. Mar. Ecol. Progr. Ser. 155:269-301.

JENKINS, G.P.; K.P. BLACK, & M.J. KEOUGH. 1999. The role of passive transport and the influence of vertical migration on the pre-settlement distribution of a temperate, demersal fish: numerical model predictions compared with field sampling. Mar. Ecol. Progr. Ser. 184:259-271.

KRUSE, I.; T.B.H. REUSCH, & M.V. SCHNEIDER. 2003. Sibiling species or poecilogony in the polychaete *Scoloplos armiger*? Mar. Biol. 142:937-947.

LACKSCHEWITZ, D. & K. REISE. 1998. Macrofauna on flood delta shoals in the Wadden Sea with an underground association between the lugworm *Arenicola marina* and the amphipod *Urothoe poseidonis*. Helgoländer Meeresunters. 52:14-158.

LEVIN, L.A. 1992. The problem of pattern and scale in ecology. Ecology 73:1943-1967.

LEVIN, L.A. & C. DIBACCO. 1995. Influence of sediment transport on short-term recolonization by seamount infauna. Mar. Ecol. Prog. Ser. 123:163-175.

LÖBL, M. 2002. Das Schlickgras *Spartina anglica* C.E. Hubbard Ausbreitung und Habitatveränderungen im Sylter Wattenmeer. Master Thesis. Philipps University of Marburg. 67 p.

LUDWIG, J.A. & J.F. REYNOLDS. 1988. Statistical ecology. A primer on methods and computing. John Wiley & Sons Ed. 337 pp.

MALATESTA, R. J.; P.J. AUSTER, P. BRADLEY, & P.B. CARLIN. 1992. Analysis of transect data for microhabitat correlations and faunal patchiness. Mar. Ecol. Progr. Ser. 87:189-195.

MANTILLA, J.; G. CHAPLIN, M.R. EILERS, K.L. JR. HECK, & J.P. O'NEAL. 1999. Spatial and diurnal distribution of invertebrate and fish fauna of a *Zostera marina* bed and nearby unvegetated sediments in Damariscotta River, Maine (USA). J. Sea Res. 41:321-332.

MUKAI, H.; M. NISHIHIRA, H. KAMISATO, & Y. FUJIMOTO. 1986. Distribution and abundance of the sea-star Archaster typicus in Kabira Cove, Ishigaki Island. Okinawa. Bull. Mar. Sci. 38(2):366-383.

NORKKO, A.; V. J. CUMMINGS, S.F. THRUSH, J.E. HEWITT, & T. HUME. 2001. Local dispersal of juvenile bivalves: implications for sand flat ecology. Mar. Ecol. Prog. Ser. 212:131-144.

ÓLAFSSON, E.B.; C.H. PETERSON, & W.G. JR. AMBROSE. 1994. Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft-sediments: the relative significance of pre- and post-settlement processes. Oceanogr. Mar. Biol. An. Rev. 32:65-109.

POSSINGHAM, H.P. & J. ROUGHGARDEN. 1990. Spatial population dynamics of a marine organism with a complex life cycle. Ecology 71:973-985.

PRIMAVERA, J.H. 1998. Mangroves as Nurseries: Shrimp Populations in Mangrove and Non-mangrove Habitats. Estuarine, Coastal and Shelf Research 46:457-464.

REISE, K. 1979. Spatial configurations generated by motile benthic polychaetes. Helgoländer wiss. Meeresunters. 32:55-72.

__________. 1982. Long-term changes in the macrobenthic invertebrate fauna of the Wadden Sea: Are polychaetes about to take over? Neth. J. Sea Res. 16:29-36.

__________. 1983a. Sewage, green algal mats anchored by lugworms, and the effects on Tubellaria and small Polychaeta. Helgol. Meeresunters. 36:151-162.

__________. 1983b. Biotic enrichment of intertidal sediments by experimental aggregates of the deposit-feeding bivalve *Macoma balthica*. Mar. Ecol. Prog. Ser. 12:229-236.

__________. 1984. Experimental sediment disturbances on a tidal flat: Responses of free-living Platyhelminthes and small Polychaeta. Hydrobiologia 118:73-81.

__________. 1987. Distribution and abundance of small and juvenile macrofauna on the tidal flats in the Frisian Wadden Sea. In: Tougaard, S. (Ed.) Proc. of the 5th. International Wadden Sea Symposium. 7-25.

__________; E. HERRE & M. STURM. 1994. Biomass and abundance of macrofauna in the intertidal sediments of Königshafen in the northern Wadden Sea. Helgol. Meeresunters. 48:201-215.

__________, & D. LACKSCHEWITZ. 1998. Benthos of the Wadden Sea between the islands of Sylt and Römö. In: The Wadden Sea Ecosystem. Exchange, Transport, and Transformation Processes (C. Gätje and K. Reise Eds.) Springer Verlag Berlin. 55-64.

ROBERTSON, A.I. & S.J.M. BLABER. 1992. Plankton, epibenthos and fish communities. In: Tropical Mangrove Ecosystems (Robertson, A.I. & D.M. Alongi, Eds.) American Geophysical Union, Washington, D.C. 173-224.

RODRIGUEZ-VALENCIA, J.A. 2003. Composition and dynamics in space and time of polychaete larvae in coastal waters of the North Sea. Dissertation. Christian-Albrechts-University of Kiel. 121 p.

SAIER, B. 2000. Age-dependent zonation of the periwinkle *Littorina littorea* (L.) in the Wadden Sea. Helgol Mar. Res. 54:224-229.

SAIER, B. 2002. Ecological comparison of intertidal and subtidal mussel beds (Mytilus edulis L.) in the Wadden Sea. Dissertation. University of Hamburg. 164 pp.

SAITO, H.; A. TAMAKI, & M. IMAJIMA. 2000. Description of new species of *Armandia* (Polychaeta: Opheliidae) from western Kyushu, Japan, with character variations. J. Nat. Hist. 34:2029-2043.

SANDULLI, R. & J. PINCKNEY. 1999. Patch sizes and spatial patterns of meiobenthic copepods and benthic microalgae in sandy sediments: a microscale approach. J. Sea Res. 41:179-187.

SCHANZ, A. 2003. Impact of hydrodynamics on intertidal seagrass beds in the northern Wadden Sea. Dissertation. University of Bremen. 142 pp.

SCHELTEMA, R.S. 1986. On dispersal and planktonic larvae of benthic invertebrates: an eclectic overview and summary of problems. Bull. Mar. Sci. 39:290-322.

SCHNEIDER, D.C.; J.M. GAGNON, & K.D. GILKINSON. 1987. Patchiness of epibenthic megafauna on the outer Grand Banks of Newfoundland. Mar. Ecol. Prog. Ser. 39:1-13.

SHULL, D. H. 1997. Mechanisms of infaunal polychaete dispersal and colonization in an intertidal sandflat. J. Mar. Res. 55:153-179.

SIMON, J.L. & D.M. DAUER. 1997. Reestablishment of a Benthic Community Following Natural Defaunation. In: Coull, B.C. (Ed). Ecology of Marine Benthos. Univerity of South Carolina Press. Columbia. 139-154.

SMITH, C.R. 1985. Colonization studies in the deep sea: are results biased by experimental designs? In: Gibbs P.E. (Ed) Proceedings of the Nineteenth European Marine Biology Symposium. Cambridge University Press, Cambridge, 183-190.

SNELGROVE, P. V. R. & C. A. BUTMAN. 1994. Animal-sediment relationships revisited: cause versus effect. Ocean. Mar. Biol. Ann. Rev. 32:111-177.

SNELGROVE, P. V. R.; J. F. GRASSLE, J. P. GRASSLE, R. F. PETRECCA, & H. MA. 1999. In situ habitat selection by settling larvae of marine soft-sediment invertebrates. Limnol. Oceanogr. 44:1341-1347.

SNELGROVE, P. V. R.; J. F. GRASSLE, J. P. GRASSLE, R. F. PETRECCA, & K. I. STOCKS. 2001. The role of colonization in establishing patterns of community composition and diversity in shallow-water sedimentary communities. J. Mar. Res. 59:813-831.

STONER, D.S. 1990. Recruitment of a tropical colonial ascidian: relative importance of pre-settlement vs. post-settlement processes. Ecology 71(5):1682-1690.

STRASSER, M. & U. PIELOTH. 2001. Recolonization pattern of the polychaete *Lanice conchilega* on an intertidal sand flat following the severe winter of 1995/96. Helgol. Marine Research 55:176-181.

__________; T. REINWALD & K. REISE. 2001 a. Differential effects of the severe winter of 1995/96 on the intertidal bivalves *Mytilus edulis, Cerastoderma edule* and *Mya arenaria* in the northern Wadden Sea. Helgol. Marine Research 55:190-197.

__________; A. HERTLEIN & K. REISE. 2001 b. Differential recruitment of bivalve species in the northern Wadden Sea after the severe winter 1995/96 and of subsequent milder winters. Helgol. Marine Research. 55:182-189.

STRATHMANN, R.R. 1974. The spread of sibling larvae of sedentary marine invertebrates. Am. Nat. 108:29-44.

TAYLOR, L.R. 1984. Assessing and interpreting the spatial distributions of insect populations. A. Rev. Ent. 29:321-357.

TAMAKI, A. 1985. Zonation by size in the *Armandia* sp (Polychaeta:Opheliidae) population on an intertidal sand flat. Mar. Ecol. Prog. Ser. 27:123-133.

__________. 1987. Comparison of resistivity to transport by wave action in several polychaete species on an intertidal flat. Mar. Ecol. Progr. Ser. 37:181-189.

THIÉBAUT, E.; J.C. DAUVIN & Z. WANG. 1996. Tidal transport of *Pectinaria koreni* postlarvae (Annelida: Polychaeta) in the Bay of Seine (eastern English Channel). Mar. Ecol. Prog. Ser. 138:63-70.

THORSON, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. Biological Reviews. 25:1-45.

THORSON, G. 1961. Length of pelagic larval life in marine bottom invertebrates as related to larval transport by ocean currents. In: Sears, M. (Ed.), Oceanography. AAAS. No. 67:455-474.

THRUSH, S.F.; J.E. HEWITT, & R.D. PRIDMORE. 1989. Patterns in the spatial arrangements of polychaetes and bivalves in intertidal sandflats. Mar. Biol. 102:529-535.

TODD, C.D. 1998. Larval supply and recruitment of benthic invertebrates: do larvae always disperse as much as we believe? Hydrobiologia 375/376: 1-12.

VALENTINE, J.F. & K.L. HECK. 1999. Mussels in seagrass meadows: their influence on macroinvertebrate abundance and secondary production in the northern Gulf of Mexico. Mar. Ecol. Prog. Ser. 96:63-74.

VALIELA, I. 1984. Marine Ecological Processes. Springer Verlag. Ney York.

WESTHEIDE, W. 1966. Zur Polychaetenfauna des Eulitorals der Nordseeinsel Sylt. Helgoländer wiss. Meeresunters. 13:203-209.

WHITLATCH, R.B. 1981. Animal-Sediment relationship in intertidal marine benthic habitats: some determinants of deposit-feeding species diversity. J. exp. mar.Biol. Ecol. 53:31-45.

__________, A.M. LOHER, S.F. THRUSH, R.D. PRIDMORE, J.E. HEWITT, V.J. CUMMINGS, & R.N. ZAJAC. 1998. Scale-dependent benthic recolonization dynamics: life stage-based dispersal and demographic consequences. Hydrobiologia 375/376:217-226.

__________, A.M. LOHER, & S.F. THRUSH. 2001. Scale-dependent recovery of benthos: effects of larval and post-larval life stages. In: Aller, J.Y.; S.A. Woodin, & R.C. Aller (Eds). Organism-Sediment Interactions. University of South Carolina Press. Columbia. 181-198.

WILSON JR, W.H. 1991. Sexual reproductive modes in polychaetes: classification and diversity. Bull. Mar. Sci. 48(2):500-516.

WOLF, S. 2002. Die Besiedlung von Schillfeldern durch benthische Makrofauna im Sylter Wattenmeer. Philipps University of Marburg. 58 p.

WOODIN, S.A. 1986. Settlement of infauna: Larval choice? Bull. Mar. Sci. 39(2):401-407.

ZÜHLKE, R. & K. REISE. 1994. Response of macrofauna to drifting tidal sediments. Helgol. Meeresunters. 48:277-289.

ACKNOWLEDGEMENTS

This study has cost me blood, sweat and tears but it would not exist without the golden opportunity given to me by Karsten Reise, and the "pushing-work" of Alejandro Rodriguez. Many people helped me along over the time, to some I am especially grateful.

Thanks to Prof. Dr. Karsten Reise for academic advice, support and facilities during my research. His help was really invaluable.

Dr. Matthias Strasser, Dr. Alejandro Rodríguez and David Thieltges provided substantial criticism and endless discussions about the sense and non-sense of my work. They improved this thesis with worthy suggestions and corrections.

For logistic support and friendship I thank Lilo Herre and Hanne Halliger. Gurdy Bardt, Kristin Kessenich and Christiane Antrick provided help with administrative troubles. Dr. Ragnhild Asmus helped to attain some institutional support. Everyone at the Wadden Sea Station Sylt made my stay on the island a nice time.

Tons of sand and mud were sieved, thousands of worms were picked-up and counted. This incredible amount of work was only possible to manage, thanks to the eager help in the field and in the lab by Stefan Görlitz and Alejandro Rodriguez. For last minute corrections of typing errors, I thank Stefanie Hedtkamp.

Dr. Angel de León corroborated the taxonomy of my worms. Dr. Peter Martens provided his help when computers surrendered. Thanks also to the "Mya" crew: Niels Kruse, Peter Elvert and Timo Wieck for subtidal sampling, sometimes under difficult conditions. Reimer Magens helped with the construction of some "curious artifacts".

Funding for research and living was provided by DAAD (Deutscher Akademischer Austauschdienst, Germany), CONACYT (Consejo Nacional de Ciencia y Tecnología, México) and AWI (Alfred-Wegener-Institute for Polar and Marine Research, Germany).

The native species: David, Steff, Nils, Dörte and Inken granted a suitable habitat for this Mexican introduced species. We shared not only the same habitat in the same time, we developed also a positive symbiosis (I think so). Dago contributed to this work with a nice laboratory atmosphere and lots of HARIBO-Cuddly Bears. It was a great time. I will miss you all.

I thank my friends from here: Anja, Anke, Betti, Bine, Carsten, Christian, David, Dörte, Georgia, Inken, Kristin, Matthias, Matthias, Nils, Patrick, Steff, Susie, Tina and my friends from oversea: Alberto, Ana, Anacelia, Eleazar, Hermila, Maricarmen, Marina, Myrna, Ruben, and Vero for still being my friends through wind and storm. Thanks to Cool Snape for his patience and endless philosophical discussions. The Victoria city troop (especially Chely and Yuriko) has also contributed with good wishes. Thanks also to familiy Hernández-Ordaz. Many other persons helped me before, during and after this study, to all: Thank you.

My gratefulness to Eleazar, Steff, David, and Betti for having caught me when I fell, for having heard me when I cried, for being there when I needed them. I find not enough words to express my gratitude. I know: it was not easy.

Georgi: Alles wird gut, irgendwann...

My family -mama, papa and titi- gave me the reasons, the courage and the will to continue, when I did not see why.

Alejandro me llevó por la gloria y el infierno. Por las pequeñas y las grandes cosas que hizo por mi: gracias. Sin él no lo hubiera logrado, y a pesar de él, lo logré. Mi eterna gratitud y amor por su ayuda y apoyo durante el tiempo que conté con él.

That's all folks!