Helgol Mar Res (2001) 55:161–165
DOI 10.1007/s101520100076

ORIGINAL ARTICLE

K. Reise · M. Simon · E. Herre

Density-dependent recruitment after winter disturbance on tidal flats by the lugworm *Arenicola marina*

Received: 24 May 2000 / Received in revised form: 7 May 2001 / Accepted: 8 May 2001 / Published online: 20 July 2001

Abstract The polychaete *Arenicola marina* is abundant and widespread on intertidal sand flats in Königshafen (island of Sylt, North Sea). Juveniles overwinter in subtidal channels and then colonize the upper tidal zone above the range of the adults. In the summers of 1995 and 1997, after a mild and a moderate winter, a distinct nursery belt fringing the shoreline was apparent. The severe winter of 1995/96 changed this pattern. Population size of the adults was halved, and in summer 1996 the juveniles were no longer restricted to an upper intertidal belt and settled over a wide range of tidal flats where adults were diminished. This spatial expansion of recruits is assumed to be a density-dependent response. An overcompensation by one-third of the previous population size did not carry over into the next year. Compared to some other species of the tidal-flat fauna, the disturbance effect by the severe winter on the lugworm population was small and brief.

Keywords *Arenicola marina* · Winter · Recruitment · Adult–juvenile interaction · Wadden Sea

Introduction

The lugworm *Arenicola marina* (L.) has a predominantly northern distribution along Atlantic coasts including the arctic (Wells 1964; Hartmann-Schröder 1996). On sandy tidal flats of the cold-temperate zone *A. marina* is a dominant component of the zoobenthos. Its share in zoomass ranges between 15 and 30% in the Wadden Sea (Beukema 1989; Reise et al. 1994). *A. marina* is a deposit-feeder dwelling in J- or U-shaped burrows down to a sediment depth of up to 0.4 m. Surface sediment slides through a feeding funnel down to this depth, where the sediment is consumed (Riisgård and Banta 1998). Meiofauna and some macrofaunal species find an extended habitat in and alongside these burrows (Reise 1985; Lackschewitz and Reise 1998), while other species of the macrofauna become displaced by the burrowing activity of *A. marina* (Cadée 1976; Flach 1992). Through its capacity for facultative anaerobiosis the lugworm is well adapted to intertidal conditions (Schöttler 1980). At temperatures below 5°C, North Sea lugworms turn to anaerobic metabolism (Sommer et al. 1997).

The population of *A. marina* is distinguished from most others of the tidal-flat benthos by a relatively constant density in space and time (Reise 1985; Beukema et al. 1993; Flach and Beukema 1994). After hibernating in mussel beds (Reise 1985) and in shell gravel of deep tidal channels (M. Simon, unpublished), the juveniles settle from May to October in conspicuous nursery beds at the upper margin of the adult range (Wohlenberg 1937; Farke et al. 1979; Reise 1985). From there the juveniles migrate downshore before or during the next winter (Werner 1956; Flach and Beukema 1994), leaving an empty upper tidal zone for the next generation arriving the following spring. The largest, and presumably oldest, individuals of the population are to be found in seaward, low-lying sand flats and possibly also in some subtidal sands (Beukema and de Vlas 1979; Lackschewitz and Reise 1998).

A. marina is known to be a winter hardy species with a relatively stable abundance and biomass even after exceptionally cold winters (Beukema 1979, 1990). Two mechanisms may be involved when coping with extreme winter conditions. On the one hand, *A. marina* may endure freezing in winter to some extent (Sommer and Pörtner 1999). On the other, strong frost may be avoided by downshore migration. Postlarvae drift with the tidal currents, and some mobility – including swimming – may occur throughout the entire lifetime (Farke and Berghuis 1979a, b). The emptied intertidal space may then be available for the recruits and allow the lugworm population to readily compensate for winter losses on the tidal flats. We used the severe winter of 1995/96, which

Communicated by H.-D. Franke

K. Reise (✉) · M. Simon · E. Herre
Alfred-Wegener-Institut, Wattenmeerstation Sylt,
25992 List, Germany
e-mail: kreise@awi-bremerhaven.de
Tel.: +49-4651-956110, Fax: +49-4651-956200

was the ninth most severe of the last century with respect to the duration of ice development on the German North Sea coast (Strübing 1998), to study (1) how a severe winter affected the distribution pattern of adult and juvenile lugworms and (2) how the summer recruits responded to spatial changes of adult abundance. To answer these questions we compared the lugworm population from the summer immediately after the severe winter with that of one summer before and one summer later.

Materials and methods

The basis of this study are mappings of the *Arenicola*-population in Königshafen, a bay at the northern end of the island of Sylt with 3.63 km^2 of tidal flats. This study area and its biota are described by Wohlenberg (1937), Reise (1985) and Reise et al. (1994). Mean tidal range is 1.8 m. The tidal area is predominantly sandy except for a muddy depression at its western part (Austen 1992). The topography of the bay was surveyed in 1991 and graphed with 0.1 m isoline intervals on a map of 1:10,000 (Amt für Land- und Wasserwirtschaft, Husum).

The procedure of mapping *Arenicola marina* followed Quinones (1984) and Simon (1991) to allow for long-term comparisons. We recorded the density of fecal castings and differentiated between those of juveniles (fecal string <2 mm in diameter) and adults (>2 mm). Transects perpendicular to the shoreline run at intervals of 250 m across the bay. Along these 16 transects the density was estimated by counting fecal castings every 150 m within a 10 m radius in ten random replicates of 0.25 m^2. Intervals were shortened to 50 m when changes in abundance were apparent on a smaller scale. This was the case in the region of the lugworm nursery belt. The total number of stations varied between 126 and 140.

The number of fecal castings varies with the feeding activity of the lugworms and can only be taken as an approximation for the abundance of *A. marina*. Some standardization was achieved by carrying out all surveys in the same month (August), and during the second half of tidal emergence when no more new castings appear at the surface. Surveys lasted about a week and were interrupted during rain and storm when fecal mounds became blurred.

Means of the counts of fecal castings from each of the 126–140 stations were corrected by a factor of 0.9 to estimate real abundance. This factor was determined by Quinones (1984) for the month of August. Abundances of juveniles and adults were categorized into three classes and these are depicted by isolines and shading in Fig. 1. The areal extent of each class of abundance was multiplied by its arithmetic mean to arrive at estimates for the total number of juvenile and adult *A. marina* in the bay.

Results

Patterns of abundance

Arenicola marina occurred throughout the entire intertidal area of Königshafen (Fig. 1). Juveniles were concen-

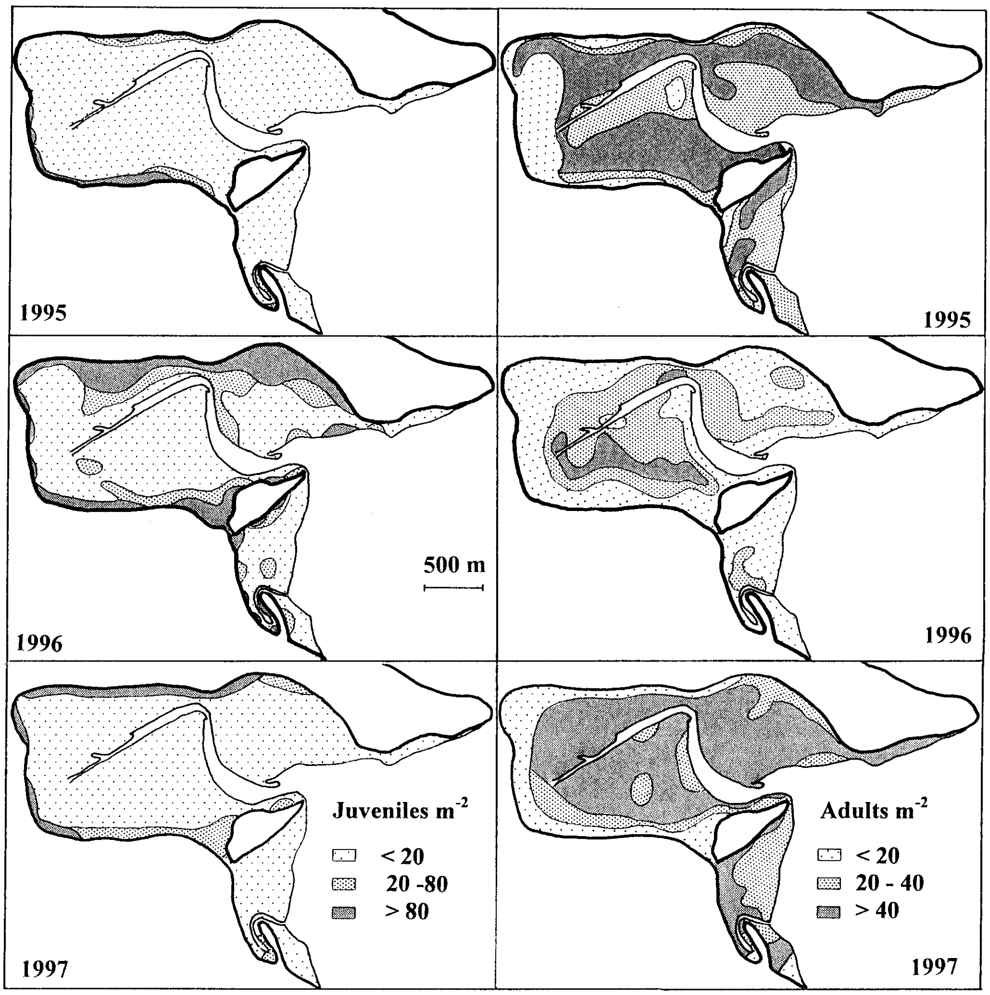

Fig. 1 Distribution and abundance of juvenile (fecal strings <2 mm diameter) and adult (>2 mm diameter) *Arenicola marina* on intertidal flats in Königshafen, island of Sylt, August 1995, 1996 and 1997

trated close to the shoreline, while adults attained their highest densities in the center of the bay. The patterns for 1995 and 1997 were similar. In 1996 the pattern differed, with juveniles spread over a wider area and with the area of adults contracted compared with the other summers.

Details in the distribution of abundance-classes bear relationships to the topography and sediment composition in Königshafen. Conspicuous nurseries were found close to the shoreline in the inner (western) part of the bay and at a sandy hook in the southeast. These are the only flat areas of >0.4 m above mean tide line, with a tidal submergence of 2–3 h. Adult lugworms were absent in this zone or remained <20 m^{-2}. The nearshore zone in the northeast and at the isle of Uthörn in the lower right of the bay is steep and lacks high tidal flats. In southeast Königshafen there is a dike, without high tidal flats in front. There no nurseries could be found. Adult *A. marina* occurred with a frequency of >20 m^{-2} in these nearshore but steep tidal zones in 1995 and 1997. A low abundance of adults in the westernmost part of Königshafen is correlated with muddy sediments. All other tidal flats are sandy and were densely (30–50 m^{-2}) populated by adults in August 1995 and 1997.

Juveniles extended their range from a belt of mostly <100 m in the high nearshore zone in 1995 and 1997 to some 300 m in 1996. In addition, the nearshore zone in the northeastern bay and at the isle of Uthörn were also colonized in 1996. Juveniles ranged down to mean tide level, with about 6 h of tidal submergence. In the northeast, there were even aggregations of juveniles along the low-water line. These were all areas where adults had occurred with a frequency of >20 m^{-2} and often >40 m^{-2} in the previous year but were scarce in 1996. In that year high abundances of adults were limited to an area below mean tide line in the center of an extensive tidal flat south of the tidal channel and a small area just north of it. In summer 1997 the pattern of adults switched back to the configuration of 1995, with a slightly larger share of the abundance-class >40 m^{-2} than in 1995. The nurseries in 1997 resembled the pattern of 1995 as well.

Population size in Königshafen

The distribution of abundances of juvenile and adult *A. marina* allows for a rough calculation of the population size in the intertidal Königshafen. Numbers vary between 159 and 265 million individuals on 3.63 km^2 of tidal flats. When distinguishing between juveniles and adults, distinct differences become apparent between the three years (Fig. 2). As with the distributional patterns, the years 1995 and 1997 resembled each other, while 1996 was clearly different in absolute numbers and in the juvenile–adult ratio. The number of juveniles was 6–8 times higher in 1996 and comprised three-quarters of the total population size, while in the other two years their share was less than a quarter. The severe winter of 1995/96 halved the adult stock of 1995 but also caused a conspicuous rejuvenation of the population. The total

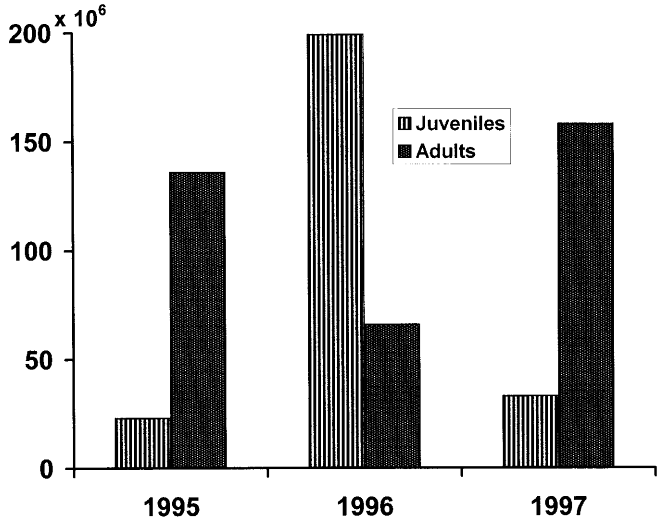

Fig. 2 Numbers of juvenile (fecal strings <2 mm diameter) and adult (>2 mm diameter) *Arenicola marina* on 3.63 km^2 of intertidal flats in Königshafen, island of Sylt, August 1995, 1996 and 1997

number of lugworms increased by one-third. However, by 1 year later, adults had almost returned to the level of 1995. In the years 1995 and 1997 we found an average of 37.5 and 43.5 adults m^{-2} in Königshafen while there were only 18.2 m^{-2} in 1996. The reverse was the case with the average density of the juveniles. This was 6.3 and 9.1 m^{-2} in 1995 and 1997 respectively, and 54.8 m^{-2} in 1996.

Discussion

We mapped the population density of *A. marina* in Königshafen near Sylt in the three consecutive years 1995–1997 to demonstrate the effects of the severe winter 1995/96, with 66 days of ice in Königshafen, on the lugworm population. The eight winters preceding the summer of 1995 were rather mild (with no or only short periods of ice on the tidal flats) and the one before the summer 1997 with 36 days of ice may be regarded as moderate relative to the centenary average for the entire German North Sea coast provided by Strübing (1998); for more details of the severe winter see Martens (2001). Dead lugworms were not found on the sediment surface nor in the sediment during or after the severe winter 1995/96. The decrease in abundance of adults may therefore be explained by downshore migration into subtidal sands triggered by the freezing conditions.

Such winter migrations are not well documented. However, singular observations by Werner (1956) in Königshafen and by Flach and Beukema (1994) in the southern Wadden Sea suggest that these occur with the ebbing tide. If this was the case in winter 1995/96, then it can be assumed that many individuals have left the Königshafen altogether. Lackschewitz and Reise (1998) found *A. marina* of distinctly larger size than those in

Königshafen at low-lying sandy shoals in the flood tide delta of the Sylt-Rømø tidal basin of which Königshafen is a part (see Reise et al. 1994). Since juvenile or small lugworms were never found on these outer shoals, the big ones must have immigrated from elsewhere. Thus, it is likely that winter emigrants from Königshafen arrived at these shoals or settled in subtidal sands of the tidal basin.

The few areas with >40 adults m^{-2} in August 1996 were adjacent to the nurseries of the year before. This implies that the 1-year-old lugworms left the nurseries and moved to the mid-tide zone and may not have left the bay. Recruitment in summer 1996 originated from spawning in late summer and autumn 1995. Only a small proportion of the postlarvae seem to stay over winter in the tidal zone (Simon 1991, unpublished). Most of them hibernate in mollusc shell gravel of the deep tidal channels. From there they drift back to the tidal zone in April/May and settle primarily in the uppermost tidal zone above the densely populated range of the adults (Reise 1985). These juveniles have fecal strings of <2 mm in diameter when recorded in August. An enhanced recruitment in summer 1996 implies that the postlarvae suffered no increased mortality during the severe winter 1995/96. Their subtidal hibernation sites did not experience frost or ice cover.

Since no causal mechanism is known for how a severe winter could increase the survival rate of hibernating postlarval *A. marina*, we assume that the cause of high recruitment in summer 1996 has to be found at the intertidal sites of settlement. The adult population being diminished by winter emigration to about half its former size is the most likely cause. This is corroborated by the spatial pattern. In 1996 nurseries expanded into those tidal zones where adult density had decreased to <20 m^{-2}.

Intraspecific competition in populations of *A. marina* has been suggested by Flach and Beukema (1994) based on (1) field experiments with overcrowded patches which caused high emigration, (2) observations that juveniles preferentially settled where adults were scarce, and (3) high recruitment in years with low adult abundance. The latter two points can be supported by this study when comparing the summer situation after the severe winter with those of the years before and after. The distribution pattern as well as the population size indicate that juvenile lugworms need empty space at the margins of the adult range. Only at low densities of adults (<20 m^{-2}) may juveniles also settle in between the adults.

Flach and Beukema (1994) assume high bioturbation activity or food limitation as possible mechanisms that keep juveniles away from adults. This would be a case in an asymmetric adult–juvenile-interaction (see Woodin 1976). A strong adult population cuts down the recruitment success. The result of such a density-dependent regulation is a relatively constant population size in spite of the highly variable living conditions in the intertidal Wadden Sea. This is here documented by the response to a severe winter. The emigration of adults from the intertidal zone of Königshafen is compensated for by an increased recruitment in the subsequent summer. In the next year the population size and the distributional pattern had already returned to the same state as before the severe winter.

An overcompensation by one-third of the former population size occurred in summer 1996. Juveniles comprised 75% of the population. However, this did not result in a conspicuous increase of the adult population in the following year. Population size returned to about the same level as in 1995. This indicates high mortality or emigration rate in the 1- to 2-year old lugworm generation which had settled in summer 1996. In the other two years, juveniles comprised only 14% and 17%, respectively. This small share of recruits suggests low mortality in normal years and, as a corollary, considerable longevity of adult lugworms. As the high recruitment rate in 1996 was sufficient to explain the recovery of the adult stock 1 year later, there is no need to assume that winter emigrants might have returned from offshore shoals or subtidal sands into the Königshafen tidal zone.

The population response of *A. marina* distinctly differs from that of other benthic macrofauna of the Wadden Sea which has been studied with respect to the severe winter 1995/96. In the cockle, *Cerastoderma edule*, this winter wiped out almost the entire intertidal population and recruits must have been supplied by survivors in the subtidal channels or coastal waters of the North Sea (Strasser 2000; Strasser et al. 2001a, b). Due to a reduced standing stock, larval supply after a severe winter may be rather low despite higher egg production by the surviving adults (Honkoop and van der Meer 1998). However, retarded predation on recruits at the bottom allows for a high survival rate and this seems to be the key factor in the population dynamics of this species in the Wadden Sea. In the long term, population size of *C. edule* is highly variable, with peaks subsequent to the irregular occurrence of severe winters (Reise 1985). By contrast, half of the adult lugworms survived the cold winter on the tidal flats, spawning already occurs before the winter, and juveniles survive their first winter in subtidal habitats where freezing temperatures are damped. Success of recruitment is inversely related to the adult stock, which seems to be the key factor in the rather stable long-term dynamics of this species. The polychaete *Lanice conchilega* is most sensitive to cold winters and recruitment in the tidal zone is a function of larval supply from surviving subpopulations in the offshore North Sea (Armonies et al. 2001; Strasser 2000; Strasser and Pieloth 2001). Population size in the intertidal zone gradually builds up subsequent to a severe winter and crashes at freezing events, resulting in a highly variable population size. Compared to *C. edule* and *L. conchilega*, the lugworm *A. marina* is best adapted to cope with harsh winter conditions in the Wadden Sea, showing only minor and brief fluctuations in population size and composition in response to the severe winter 1995/96.

Acknowledgements We thank Markus Quack for help in mapping the fecal castings of the lugworm population. Werner Armonies and Matthias Strasser kindly improved the manuscript. The study was supported by the German Federal Ministry of Research (BEO 03f0179 A).

References

Armonies W, Herre E, Sturm M (2001) Effects of the severe winter 1995/96 on the benthic macrofauna of the Wadden Sea and the coastal North Sea near the island of Sylt. Helgol Mar Res 55: DOI 10.1007/s101520100077

Austen I (1992) Geologisch-sedimentologische Kartierung des Königshafens (List/Sylt). Meyniana 44:45–52

Beukema JJ (1979) Biomass and species richness of the macrobenthic animals living on a tidal flat area in the Dutch Wadden Sea: effects of a severe winter. Neth J Sea Res 13:203–223

Beukema JJ (1989) Long-term changes in macrozoobenthic abundance on the tidal flats of the western part of the Dutch Wadden Sea. Helgol Meeresunters 43:405–415

Beukema JJ (1990) Expected effects of changes in winter temperatures on benthic animals living in soft sediments in coastal North Sea areas. In: Beukema JJ, Wolff WJ, Brouns JJWM (eds) Expected effects of climatic change on marine coastal ecosystems. (Developments in hydrobiology 57) Kluwer, Dordrecht, pp 83–92

Beukema JJ, Vlas J de (1979) Population parameters of the lugworm, *Arenicola marina* living on tidal flats in the Dutch Wadden Sea. Neth J Sea Res 13:331–353

Beukema JJ, Essink K, Michaelis H, Zwarts L (1993) Year-to-year variability in the biomass of macrozoobenthic animals on tidal flats of the Wadden Sea: how predictable is this food source for birds? Neth J Sea Res 31:319–330

Cadée GC (1976) Sediment reworking by *Arenicola marina* on tidal flats in the Dutch Wadden Sea. Neth J Sea Res 10:440–460

Farke H, Berghuis EM (1979a) Spawning, larval development and migration behaviour of *Arenicola marina* in the laboratory. Neth J Sea Res 13:512–528

Farke H, Berghuis EM (1979b) Spawning, larval development and migration of *Arenicola marina* under field conditions in the Western Dutch Wadden Sea. Neth J Sea Res 13:529–535

Farke H, Wilde PAWJ de, Berghuis EM (1979) Distribution of juvenile and adult *Arenicola marina* on a tidal mud flat and the importance of nearshore areas for recruitment. Neth J Sea Res 13:354–361

Flach EC (1992) Disturbance of benthic infauna by sediment-reworking activities of the lugworm *Arenicola marina*. Neth J Sea Res 30:81–89

Flach EC, Beukema JJ (1994) Density-governing mechanisms in populations of the lugworm *Arenicola marina* on tidal flats. Mar Ecol Prog Ser 115:139–149

Hartmann-Schröder G (1996) Polychaeta. (Die Tierwelt Deutschlands 58, 2nd edn) Fischer, Jena, pp 446–448

Honkoop PJC, Meer J van der (1998) Experimentally induced effects of water temperature and immersion time on reproductive output of bivalves in the Wadden Sea. J Exp Mar Biol Ecol 220:227–246

Lackschewitz D, Reise K (1998) Macrofauna on flood delta shoals in the Wadden Sea with an underground association between the lugworm *Arenicola marina* and the amphipod *Urothoe poseidonis*. Helgol Meeresunters 52:147–158

Martens P (2001) Effects of the severe winter 1995/96 on the biological oceanography of the Sylt-Rømø tidal basin. Helgol Mar Res 55: DOI 10.1007/s101520100078

Quinones R (1984) Die Population von *Arenicola marina* (Polychaeta) und ihre Besiedlungsgrenzen im Wattenmeer bei Sylt (Nordsee). Master's thesis, University of Bochum

Reise K (1985) Tidal flat ecology. (Ecological studies 54) Springer, Berlin Heidelberg New York

Reise K, Herre E, Sturm M (1994) Biomass and abundance of macrofauna in intertidal sediments of Königshafen in the northern Wadden Sea. Helgol Meeresunters 48:201–215

Riisgård HU, Banta GT (1998) Irrigation and deposit feeding by the lugworm *Arenicola marina*, characteristics and secondary effects on the environment: a review of current knowledge. Vie Milieu 48:243–257

Schöttler U (1980) Der Energiestoffwechsel bei biotop-bedingter Anaerobiose: Untersuchungen an Anneliden. Verh Dtsch Zool Ges 1980:228–240

Simon M (1991) Populationsökologie von *Arenicola marina*. Masters thesis, University of Marburg

Sommer A, Pörtner HO (1999) Exposure of *Arenicola marina* to extreme temperatures: adaptive flexibility of a boreal and subpolar population. Mar Ecol Prog Ser 181:215–226

Sommer A, Klein B, Pörtner HO (1997) Temperature induced anaerobiosis in two populations of the polychaete worm *Arenicola marina* (L.). J Comp Physiol B 167:25–35

Strasser M (2000) Rekrutierungsmuster ausgewählter Wattfauna nach unterschiedlich strengen Wintern. Ber Polarforsch Meeresforsch 377:1–127

Strasser M, Pieloth U (2001) Recolonization pattern of the polychaete *Lanice conchilega* on an intertidal sand flat following the severe winter of 1995/96. Helgol Mar Res 55: DOI 10.1007/s101520100081

Strasser M, Hertlein A, Reise K (2001a) Differential recruitment of bivalve species in the northern Wadden Sea after the severe winter of 1995/96 and of subsequent milder winters. Helgol Mar Res 55: DOI 10.1007/s101520100080

Strasser M, Reinwald T, Reise K (2001b) 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 Mar Res 55: DOI 10.1007/s101520100079

Strübing K (1998) The ice winter of 1996/97 on the German coasts between Ems and Oder, with a survey of the entire Baltic Sea. Dtsch Hydrogr Z 50:1–9

Wells GP (1964) Temperature, taxonomic technique and the zoogeography of lugworms (Arenicolidae, Polychaeta). Helgol Wiss Meeresunters 10:404–410

Werner B (1956) Über die Überwinterung von *Arenicola marina* L. (*Polychaeta sedentaria*). Helgol Wiss Meeresunters 5:353–378

Wohlenberg E (1937) Die Wattenmeer-Lebensgemeinschaften im Königshafen von Sylt. Helgol Wiss Meeresunters 1:1–92

Woodin SA (1976) Adult–larval interactions in dense infaunal assemblages: patterns of abundance. J Mar Res 34:25–41