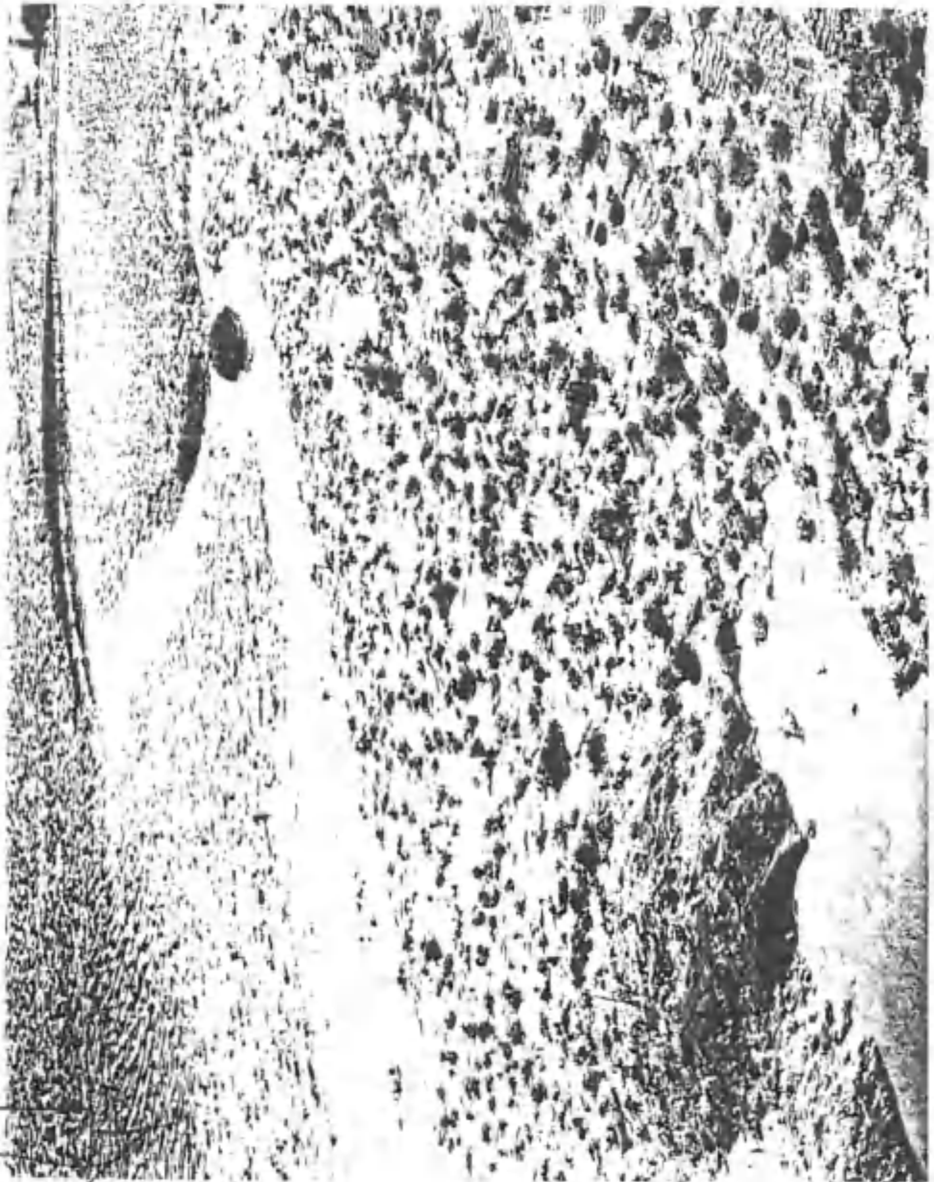

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POPULATION PARAMETERS OF THE LUGWORM, ARENICOLA MARINA, LIVING ON TIDAL FLATS IN THE DUTCH WADDEN SEA

by

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CONTENTS

I. INTRODUCTION

The lugworm, *Arenicola marina* (L.), is by far the most important worm inhabiting the tidal flats of the Dutch Wadden Sea. Its biomass is higher than that of all other worm species together and accounts for no less than about 20% of the total macrozoobenthic biomass (BEUKEMA, 1976). Within the ecosystem of the Wadden Sea, lugworms play a significant role as a source of food for flatfishes (KUIPERS, 1977; DE VLAS, 1979) and as reworkers of sediment (CADÉE, 1976), causing a layer rich in coarse material at a depth of 20 to 30 cm below the surface of the tidal flats (VAN STRAATEN, 1952).

Studies on the population dynamics of *Arenicola* have been hampered undoubtedly by problems connected with sampling (because the individuals change place at least some times during their life and the adults live deeply burrowed) and aging (because no permanent structures with year marks have been found and fitting lugworms with a long lasting mark is difficult). Moreover, part of the life history of lugworms has been poorly known for a long time. Only some scattered population data, derived from short term studies in restricted areas are available, *e.g.* NEWELL (1948), CHAPMAN & NEWELL (1949), CAZAUX (1967) and POLLACK (1979).

This paper will provide some data on lugworms collected mainly during a 10 year study of the macrozoobenthos living on Balgzand, a tidal flat area in the westernmost part of the Dutch Wadden Sea. Series of observations on numerical densities and sizes were made on a number of sampling stations, and allow conclusions on distribution patterns, migration, growth rates, annual recruitment, mortality, biomass and production.

II. SAMPLING AREA AND METHODS

The Dutch part of the Wadden Sea contains about 1300 km² of intertidal flats which are exposed at mean low tide. The mean tidal range gradually increases from west to east (136 cm near Den Helder to 280 cm near Delfzijl). By far the largest part of the tidal flats is situated below MTL. Higher intertidal flats are almost restricted to strips of variable width (up to 1 or 2 km) along the coasts. Balgzand is a 50 km² area of intertidal flats and shallow channels in the westernmost part of the Wadden Sea.

Silt (plus clay) percentage (*i.e.* the weight fraction of grain sizes smaller than about 60 μm) and median particle diameter of the top 5 cm of the substratum were determined by methods described earlier (BEUKEMA, 1976). The surface of the tidal flats mainly consists of fine sands. Silty areas are usually found on higher tidal flats along the mainland coasts, whereas tidal flats far off shore are generally low and sandy. Consequently, the correlation between silt percentage of the sediment and intertidal height is positive ($r = +0.46$, $P < 0.001$ for 86 transects scattered all over the Wadden Sea), whereas median particle size and height show an inverse relationship ($r = -0.40$, $P < 0.001$, 86 transects).

Sampling stations were selected to represent all parts of the Wadden Sea with the various sediment types and intertidal levels roughly in accordance with their area coverage. The locations of the 99 transects that were sampled during summer or autumn of 1971 or 1972 were shown already (BEUKEMA, 1976: fig. 1). The western half of these transects were sampled again during 1977 (BEUKEMA, DE BRUIN & JANSEN, 1978). The 12 transects on Balgzand (numbered 1 to 12 in Fig. 1) were sampled annually in late winter (late February to early April) during the 1970 to 1979 (inclusive) period, but in 1969 and 1970 twice a year (again in August and September). The 1 km long transects were sampled by taking equally spaced cores of 0.018 m² each, thus collecting 50 samples at 20 m distances at Balgzand and 25 samples at 40 m in all other areas. In addition, 3 sampling squares of 900 m² each on Balgzand (A, B and C in Fig. 1) were sampled 4 or

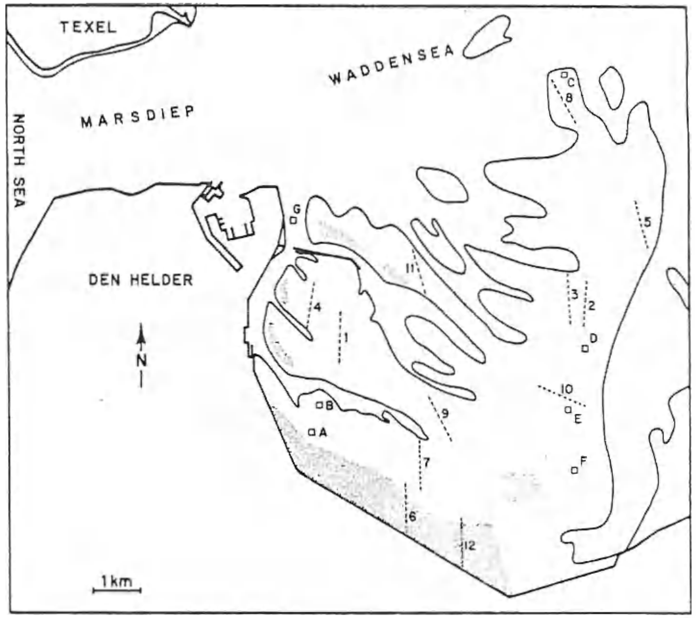


Fig. 1. Map of Balgzand, showing the location of sampling stations (A to F on tidal flats, G in channel) and transects (1 to 12). The approximate borders of the tidal flats at LLWS are shown; shaded is the area above MTL.

more times annually by collecting 9 or 16 cores of 0.1 m² each. The locations of these cores within the squares were determined by a random number method. Starting from the summer of 1969 all samples have been taken to a depth of 30 to 40 cm which is sufficiently deep to contain all lugworms present.

The cores were washed through a 1 mm sieve in the field. In the laboratory, the lugworms were sorted from the mixture of dead shells and peat and grouped into 2 natural size classes which in almost all samples could easily be recognized. The numbers in each class were counted, reconstructing fragmented worms into approximately whole worms. The groups of worms were dried during 3 to 5 days at 60° C in a well-ventilated stove, weighed, placed in a furnace at 600° C for 2 hours, and weighed again. The weight loss at 600° C is considered to represent the ash-free dry weight (ADW) of the animals. "Small" or "juvenile" worms had an ADW of less (generally much less) than 100 mg each. All heavier lugworms are called "big" or "adult".

In addition, about 100 whole adult lugworms were collected by careful digging near each of the 3 stations D, E and F (Fig. 1), at approximately monthly intervals during 1976, to study weight changes in more detail. These worms were dried, ashed and weighed individually.

During the period July 1970 to May 1971, with intervals varying from a week to a month a coarse plankton net with a 1 m² aperture was lowered to mid-depth (about 5 m) from a vessel anchored in the middle of the main tidal stream of Balgzand (G in Fig. 1). Catches were inspected for fishes, molluscs and worms (DE VLAS, 1973).

III. RESULTS

a. SEASONAL PATTERNS OF DISTRIBUTION

On almost all of the 99 transects scattered over the tidal flats of the Dutch Wadden Sea and sampled during late summer and autumn, lugworms were found. Numerical densities varied from less than 1 to about 100 per m² in adults or to some hundreds in juveniles. The mean density amounted to 17 lugworms per m² (95% confidence limits 14 and 20, $n = 99$) of which $4\frac{1}{2}$ were classified as small. By grouping the transects, mean densities of large and small lugworms can be calculated at various distances from the shore. Numbers of small lugworms rapidly declined with increasing distance from shore (Fig. 2a). Adults showed their highest densities at 1 to 4 km from the shore and were significantly less abundant both at shorter distances (within 1 km) and at longer distances from the coasts (Fig. 2).

Big lugworms outnumbered small ones almost everywhere. Only within narrow strips near the shores small lugworms predominated. Such strips with high densities of small lugworms were especially distinct along most of the Wadden coasts of the barrier islands. Along the mainland coasts such strips were often less clearly defined or even absent.

This pattern of lugworms distribution resulted from a single sampling of 99 transects carried out during the summers and autumns of 1971 and 1972 (BEUKEMA, 1976). A second sampling of about half of these transects during the same season in 1977 (BEUKEMA, DE BRUIN & JANSEN, 1978), yielded the same general pattern though with somewhat lower numerical densities in areas more than 3 km from the shores.

Data bearing on other seasons are available from Balgzand where 12 transects and 3 stations have been sampled annually during 10 successive years in late winter and early spring. The observed patterns of distribution of big lugworms (Fig. 2b) is very similar to the pattern found in summer (Fig. 2a). The distribution of the small lugworms in

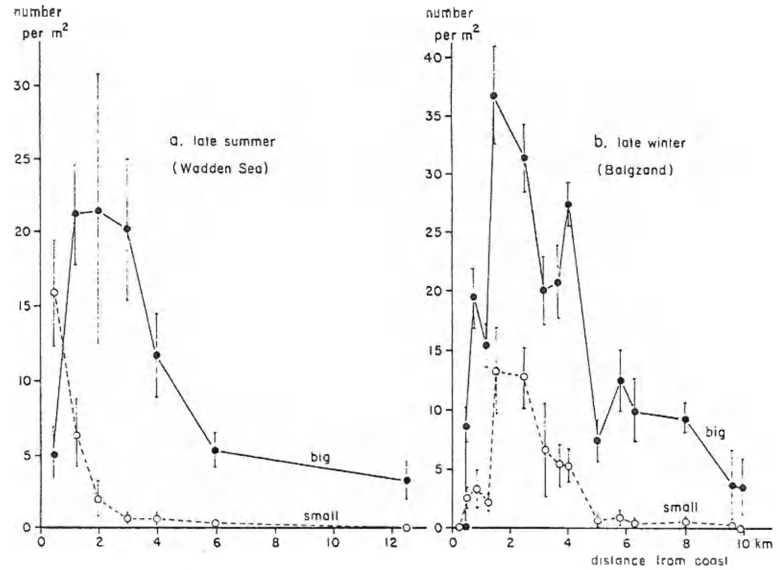


Fig. 2. Numerical densities (means ± 1 standard error) of small (○) and big (●) lugworms on tidal flats at various distances from the coast. a. During late summer (data from a single sampling of 99 transects scattered over the Dutch Wadden Sea, grouped according to distance from the coast, $n = 11$ to 19 per group). b. During late winter (data from 15 sampling places on Balgzand, means of 10 sampling years).

late winter, however, differs from the summer pattern. Highest densities then no longer occur close to the coasts, but at 1 to 4 km off the shores as in big lugworms. Apparently, between autumn and late winter the small lugworms adopt the distributional pattern of the adults.

b. RELATIONSHIPS WITH TIDAL HEIGHT AND SEDIMENT COMPOSITION

With increasing distance from the shores, some environmental conditions on the tidal flats change gradually. Generally, the tidal flats slope gently downwards so that the daily periods of exposure to the air become shorter, while also the silt percentage of the sediment decreases. As these two environmental factors tend to be mutually dependent, it makes little sense to relate lugworm densities to only one of them. Therefore, plots with both factors (position to mean tidal level and silt percentage) together are composed (Figs 3 and 4) to show their influence on the numerical density of lugworms. As lugworm distributions were found to differ in relation to size class (at least in summer)

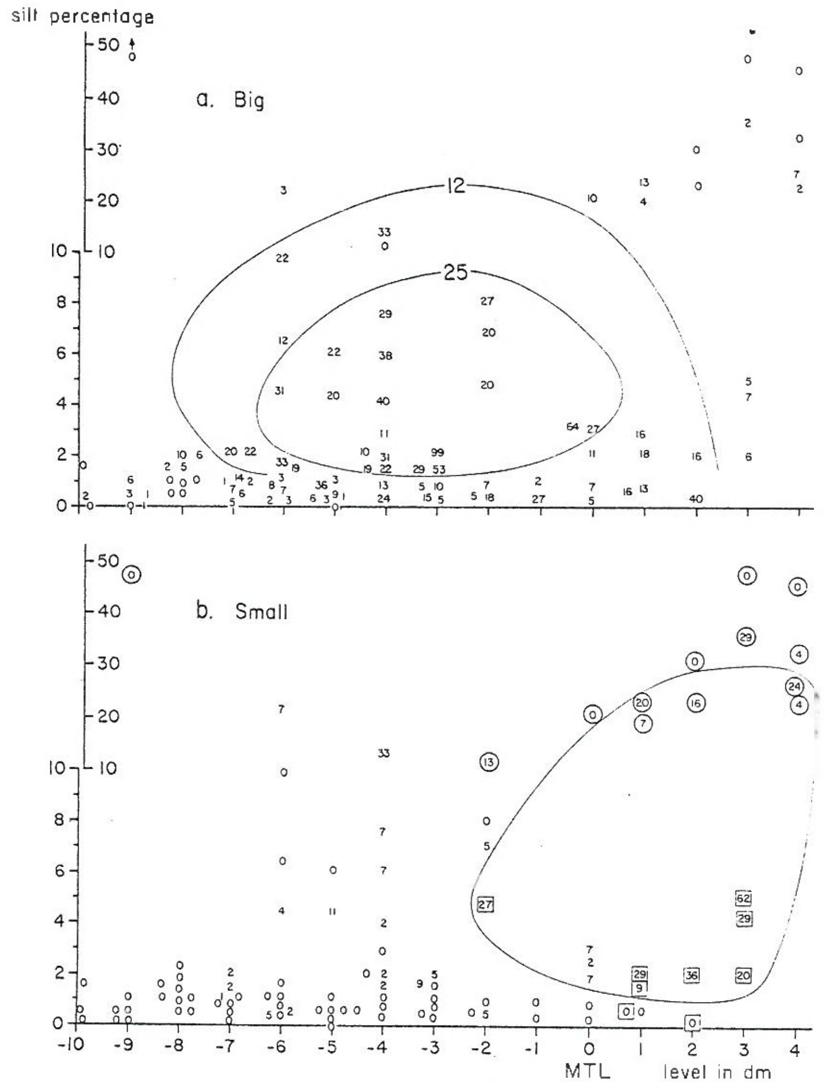


Fig. 3. Mean numbers per m² (a.) of big (>100 mg) and (b.) of small (<100 mg) lugworms at various combinations of tidal level and silt percentage of the sediment. Isopleths drawn by eye. Data from one sampling during late summer of 99 transects (sampled area 0.45 m² per transect) scattered over the Dutch Wadden Sea. Encircled and ensquared figures (in b.) denote sampling places near mainland and near island coasts, respectively.

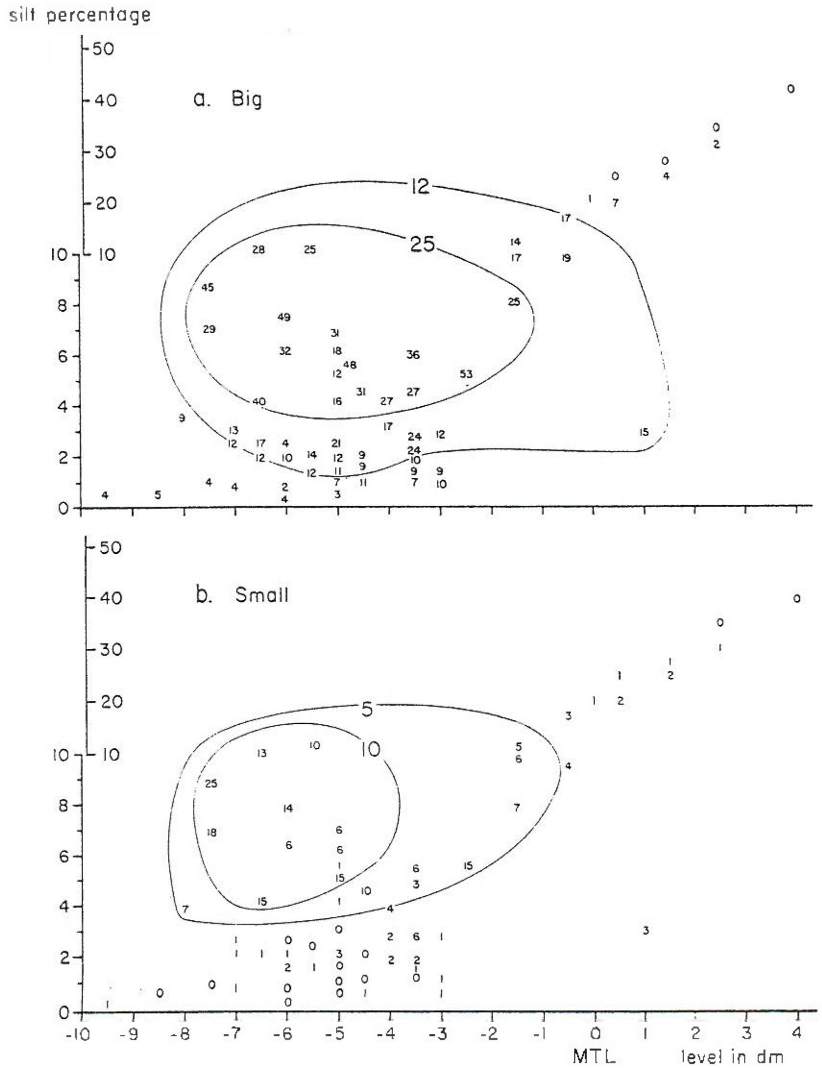


Fig. 4. Mean numbers per m² (a.) of big (>100 mg) and (b.) of small (<100 mg) lugworms at various combinations of tidal level and silt percentage of the sediment. Isopleths drawn by eye. Data are means from 10 annual samplings during late winter at 63 places on Balgzand (sampled area per place: 2 to 3 m² per year at the 3 stations and 0.18 m² per year at the 60 places along the 12 transects).

and season (at least in small worms) 4 plots are represented (2 size groups and 2 seasons).

Three out of the 4 plots show roughly similar patterns, with highest densities of lugworms at intermediate silt percentages and at levels below MTL. This distributional pattern of adult lugworms (Figs 3a and 4a) and of juveniles in late winter (Fig. 4b) has not yet been adopted by small lugworms in summer (Fig. 3b). During the first half year after settlement in the sediment of the tidal flats in spring, highest densities are found above MTL, but not in extremely silty areas (silt percentage exceeding 30 or 40%) nor in extremely clean sands (silt percentage below 1%). High tidal flats situated well above MTL are almost restricted to a strip within 1 or 1½ km from the shores. Along the mainland the sediments of these strips contain more silt (more than 10%) than along the coasts of the islands (less than 6%). The righthand part of the plot (Fig. 3b) shows 2 clusters of numbers, representing those two coastal areas. Densities of small lugworms near the islands (boxed; mean 24 per m²) are generally higher than those observed near the mainland (encircled; mean 10 per m²). Note that highest numbers were found at the lower silt contents near the mainland and at the higher contents near the islands. Apparently, the small lugworms avoided extreme sediment compositions in both areas. In practice, they thus avoided soft substrates near the mainland and clean sands near the islands, preferring in both areas intermediate silt contents, as did the adults (Figs 3a and 4a).

The different distribution of small and big lugworms in summer is determined mainly by the position as to MTL (compare Fig. 3a and b), and therefore directly to the distance from the coast (see Fig. 2a). However, also some effect of the silt percentage may be observed, as areas around and above MTL with silt percentages below 1% were populated by big lugworms (Fig. 3a) but not by small ones (Fig. 3b). This shift of the adults to more sandy sediments must be a secondary effect of the off-shore migration, as these sandy areas were nearly all located at long distances (3 km or more) from the coast.

C. DISPERSAL

The patterns of distribution of big and small lugworms indicate, that small worms migrate between late summer and late winter in an off-shore direction. Some direct evidence for this migration is available from Balgzand, where summer densities of big and small lugworms were estimated at 3 stations during 9 successive years and along 12 transects in 1969 and 1970. Comparison of these summer estimates with densities found at the same place during subsequent late winter

and early spring shows the expected decrease in small lugworms in coastal strips and an increase in off-shore areas (>2 km from the coast) (Fig. 5). In the period concerned, big lugworms decreased in both areas at about the same rate. The increased density in off-shore areas, limited to small lugworms, can be explained only by an off-shore migration, that must have taken place during the autumn-winter season.

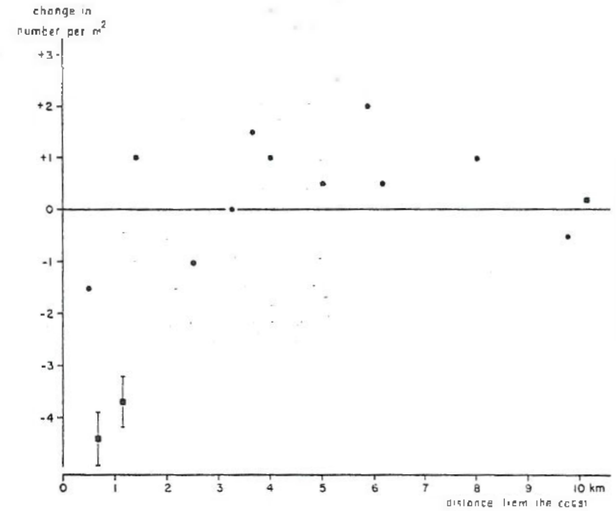


Fig. 5. Changes in numerical density of small lugworms from late summer to late winter at various distances from the coast southwest of Balgzand. Data from 12 transects (●) as means of 2 years (1969–1970 and 1970–1971) and from 3 stations (■) as means of 9 years (with 1 standard error).

The distances of some kilometers involved can be covered easily by passive tidal transport. During a study of such transport in juvenile *Macoma*, involving a year-round sampling of tidal currents by passive plankton nets (DE VLAS, 1973; BEUKEMA, 1973), dozens of lugworms were caught, but only during January, February and March (Fig. 6).

Of 21 lugworms caught in early January, all but one were classified as small. Their sizes ranged from 3 to 6 cm (in contracted condition) and their weights from 13 to 85 mg ADW (mean 35 mg).

The numbers of lugworms caught by plankton nets were two orders of magnitude lower than those of *Macoma*. A rough calculation indicates that only about 1% of the small lugworms, as compared to about 30% of the juvenile *Macoma*, present on Balgzand will have been swimming at any time in the water near station G (Fig. 1) at the mouth of the main tidal stream of Balgzand. The numbers caught during ebb tides did not differ significantly from those caught during flood tides (the former were even lower). Apparently, our station was not located within a main area of migration of small lugworms. Nevertheless, both the season of occurrence and the size range of the pelagic lugworms were as expected from the changing distribution of small lugworms between late summer and late winter.

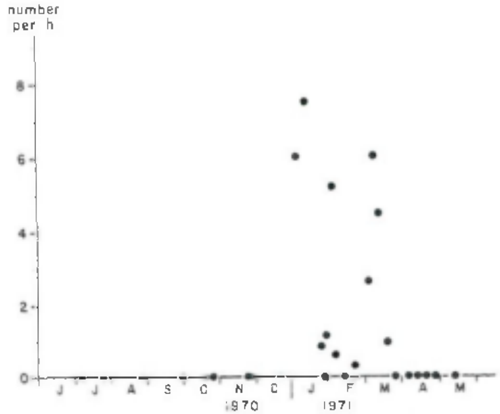


Fig. 6. Numbers of lugworms caught per 1 h fishing midwater in the main tidal stream of Balgzand at various times of the year.

d. INDIVIDUAL WEIGHTS

During spring, at the start of their life within burrows in the sediment of the coastal tidal flats, the O-group lugworms are only about 1 cm long and weigh less than 0.01 g each. They rapidly grow to attain a mean weight of about 0.05 g ADW at the end of the year (Fig. 7a). During the growing season of the following year, they soon reach the weight range of the big lugworms (>0.1 g).

Big lugworms show seasonal weight changes (Fig. 7b), growing rapidly during spring, becoming almost stationary during summer, and loosing weight during the rest of the year. Such "degrowth" during autumn and winter was also observed by NEWELL (1948). Weight losses in big lugworms were especially rapid (about 30% within a week, see right-hand part of Fig. 7b) during September or October, probably as a consequence of spawning.

Real growth rates during spring and summer will have been higher than the weight changes shown in Fig. 7b, because during this period young lugworms (1½ year old) with relatively low weights merge into the

size range of adults and become indistinguishable from them. Moreover, the cropping of tail ends by predators as plaice (DE VLAS, 1979) retards weight gain and is another reason why the weight changes shown in Fig. 7b are in fact an underestimate of real growth. Therefore it is thought impossible to obtain reliable estimates for lugworm production from such records of weight changes.

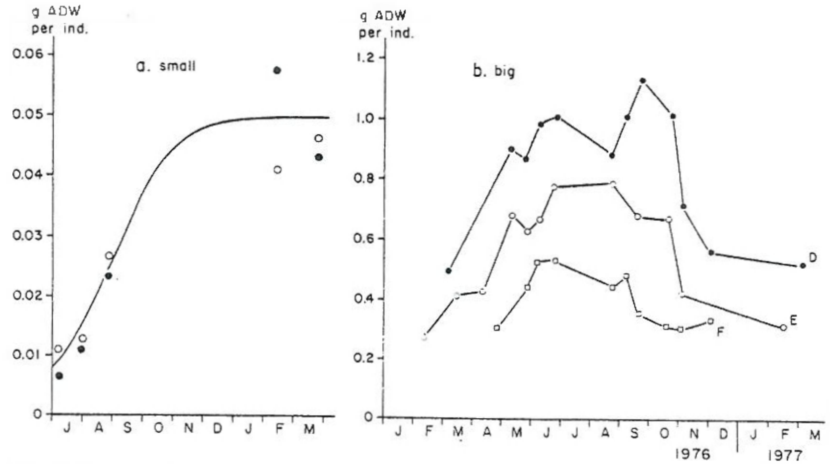


Fig. 7. Seasonal changes in mean individual weight (g ash-free dry weight). a. Small lugworms; 9-year averages from the two sampling stations A (●) and B (○) (cf. Fig. 1). b. Big lugworms from 3 stations (D, E and F; cf. Fig. 1) for 1 year (1976–1977).

Weight changes at various places (Fig. 7b) run roughly parallel, though at different levels. From the position of the sampling sites D, E and F (Fig. 1) it is clear that the mean weights of the big lugworms tend to decrease in the direction of the coast. Similar data for more years and more sampling sites on Balgzand (but limited to late winter) confirm that mean weights of big lugworms increase with the distance from the shore (Fig. 8b). Also for the whole Dutch Wadden Sea the big lugworms tend to be heavier on average at longer distances from the coasts (Fig. 8a).

Within the group of small (O-group) lugworms this relationship is less distinct (Fig. 8). As these O-group worms are very different from older ones by size and by appearance (being more pink and transparant), they can be easily recognised by eye. The I-group animals, however, cannot be separated easily from older ones. Therefore, it cannot be decided whether the increase of mean weight in adults with in-

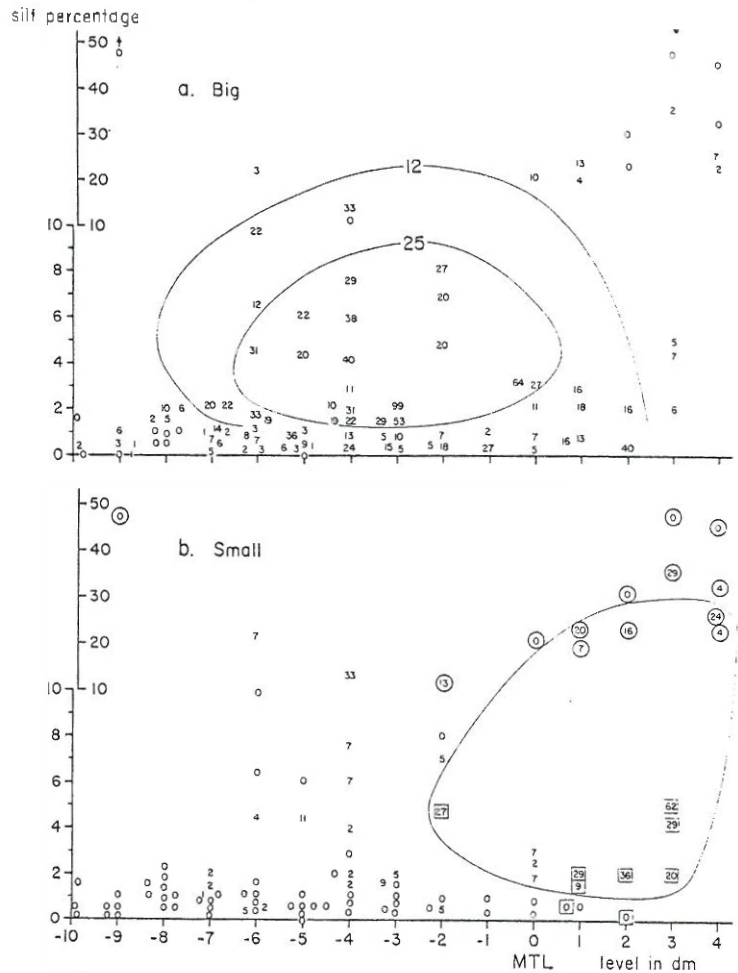
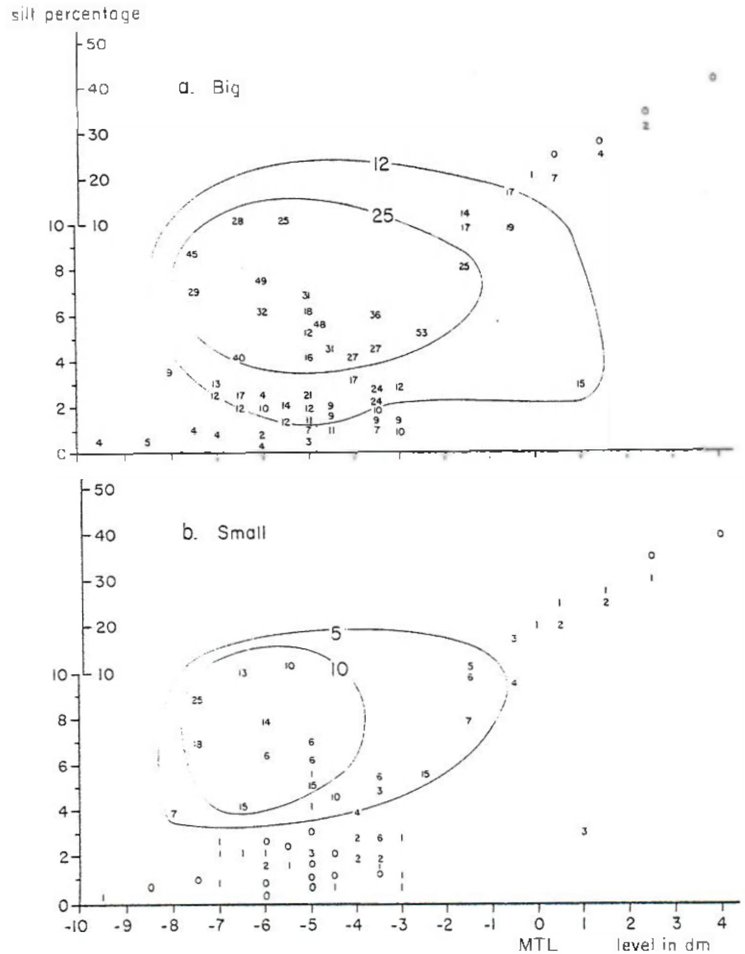


Fig. 3. Mean numbers per m² (a.) of big (>100 mg) and (b.) of small (<100 mg) lugworms at various combinations of tidal level and silt percentage of the sediment. Isopleths drawn by eye. Data from one sampling during late summer of 99 transects (sampled area 0.45 m² per transect) scattered over the Dutch Wadden Sea. Encircled and ensquared figures (in b.) denote sampling places near mainland and near island coasts, respectively.



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creasing distances from the shore results from higher mean ages or from a more rapid growth in off-shore areas. Also the possibility that both factors play a part, cannot be excluded.

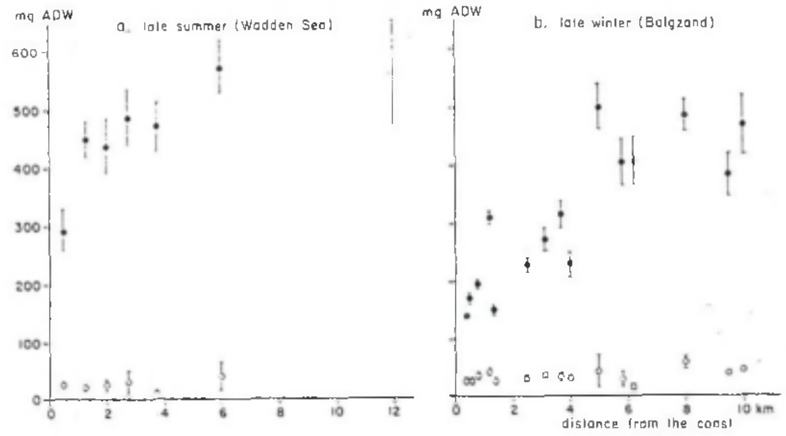

Fig. 8. Mean individual weights (mg ash-free dry weight) of small (○) and big (●) lugworms on tidal flats at various distances from the coast. a. During late summer (data from a single sampling of 99 transects scattered over the Dutch Wadden Sea, grouped according to distance from the coast, n = 11 to 19 per group). b. During late winter (data from 15 sampling places on Balgzand, means of 10 sampling years ± 1 standard error).

e. RECRUITMENT AND MORTALITY

The estimated mean density of lugworms in the Dutch Wadden Sea during the summers of 1971 and 1972, when 99 transects were sampled, amounted to 12½ big and 4½ small individuals, indicating a rate of recruitment of some 26% of the total stock. Now the problem is, whether this recruitment rate is sufficient to keep the population in a steady state.

Data on densities of small and big lugworms are available for Balgzand for 10 years, indicating a mean density of 15 big plus 4 small lugworms per m² in late winter (Fig. 9a). Proportions of small lugworms on Balgzand varied from 6 to 44% (mean 20%) of the total stock in late winter, *i.e.* when the small lugworms are almost 1½ year old and are on the verge of merging with the adult stock.

Annual mortality could be calculated by comparing the numbers of small plus big lugworms in year n with the numbers of big lugworms in year $n + 1$ (see arrows in Fig. 9a). The thus calculated annual rates of

mortality during 9 years ranged from 2 to 38% (mean 22%). These percentages are not significantly ($P > 0.1$) correlated with the numerical densities (Spearman's $r = +0.30$) nor with the proportions of small lugworms ($r = +0.35$).

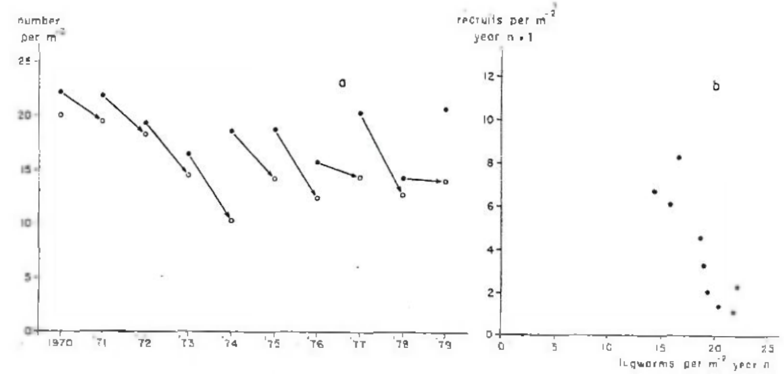

Fig. 9. a. Mean numerical densities on Balgzand of only big (○) and of all (●) lugworms during 10 years. b. Recruitment (mean numbers per m²) of 1½ year old lugworms on Balgzand related to the densities (mean numbers per m²) of older lugworms present 1 year before recruitment.

To keep lugworm density on Balgzand at a constant level, the mean share of recruits (*i.e.* number of small lugworms as a percentage of the total population in late winter), therefore should be 22%. On average, it has been 20% during the last 10 years, being almost sufficient. Expressed (more correctly) in absolute numbers, there were per m² 37 of worms disappearing and 35 recruiting during the 9 year period, indicating indeed a well-balanced situation on the long term. However, during the years 1970–1973 recruitment was only 12% or less, causing a gradual decline of the lugworm population on Balgzand (Fig. 9a). This decline was most conspicuous in the off-shore half of the area (BEUKEMA, DE BRUIN & JANSEN, 1978) where numbers of recruits have been extremely low (Fig. 2b).

The higher level of recruitment during almost all of the later years roughly equaled the mean rate of mortality, keeping the population density of adults almost constant during the 1975 to 1979 period (Fig. 9a).

Annual recruitment of about 1½ year old lugworms on Balgzand (Fig. 9b) was found to be inversely related to mean adult densities during the preceding year (Spearman's $r = -0.87$, $n = 9$, $P < 0.01$). Only a weak correlation was found between the numbers of recruits and the numbers of adults at the time of recruitment ($r = -0.44$, $n = 10$,

$P > 0.1$) which suggests no interference of adults with juveniles at the time of resettling (at age 1½ year). The significant correlation mentioned suggests that the older lugworms present at the start or during the early bottom life of young ones (growing up from an age of ½ to almost 1½ year) do exert a negative influence on their survival.

Unfortunately, the numbers of young lugworms at an age of ½ year were never measured and at an age of about 1 year only during 2 years. Therefore, the exact time at which this negative dependence of adult density on recruitment is generated remains unknown, but it is within ½ to 1 year after the start of the burrowed life.

f. BIOMASS AND PRODUCTION

With an average of 5.0 g·m^{-2} ADW, biomass of lugworms made up almost 20% of the total macrozoobenthic biomass present on the tidal flats of the Dutch Wadden Sea (BEUKEMA, 1976). On Balgzand, this percentage varied from 28 to 16% (mean 21%) during the period 1970–1979.

Biomass estimates for lugworms in summer were consistently higher than in winter. Winter values were on an average 75% and summer values 125% of the annual mean (means of values for the 3 frequently sampled stations A, B and C). These seasonal fluctuations result mainly from higher individual weights during summer (Fig. 7). Mean lugworm biomass, estimated on 15 stations in 10 years in late winter on Balgzand, amounted to 4.1 g·m^{-2} ADW. Annual mean and summer biomass on Balgzand were thus 5.5 and 6.8 g·m^{-2}, respectively.

The above average of 5.0 g·m^{-2} for the tidal flats of the whole Dutch Wadden Sea has been corrected for the season (BEUKEMA, 1976) and applies to the 1971–1972 period. During those years mean lugworm biomass on Balgzand amounted to 5.9 g·m^{-2} ADW, indicating that the lugworm biomass on Balgzand is fairly representative for the tidal flats of the whole Dutch Wadden Sea.

Distribution of biomass (Fig. 10) is roughly similar to that of adult numbers (Fig. 2). As, however, individual weights of adults tend to increase with increasing distances from the coasts (Fig. 8), biomass values do not completely reflect adult numbers. Nevertheless, numerical densities of adult lugworms appear to be decisive for lugworm biomass values, and consequently, relationships of lugworm biomass to such environmental factors as percentage silt fraction or tidal height closely resemble those of adult numbers (Figs 3a and 4a).

Because of their small size (mean weights generally 10% or less of adult weights) and low numbers (Fig. 2), small lugworms hardly contribute to total biomass of lugworms. Only within a narrow strip

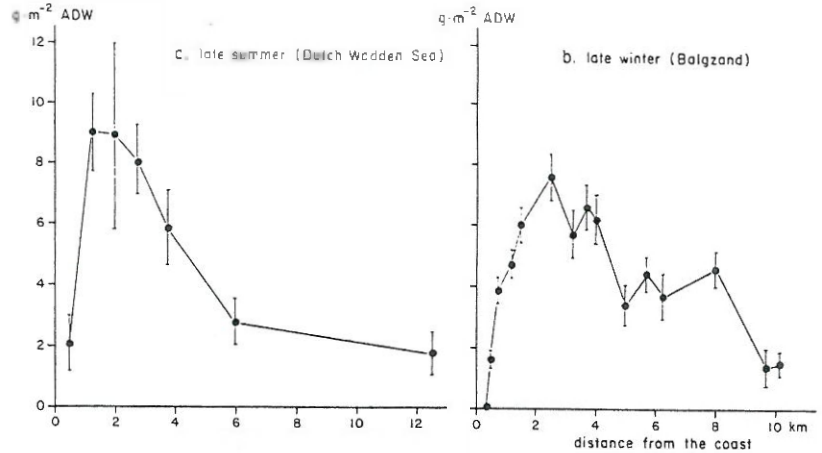

Fig. 10. Mean biomass (g·m^{-2} ash-free dry weight) of lugworms on tidal flats at various distances from the coast. a. During late summer (data from a single sampling of 99 transects, grouped according to distance from the coast, $n = 11$ to 19 per group). b. During late winter (data from 15 sampling places on Balgzand, means of 10 sampling years ± 1 standard error).

along the south coasts of the barrier islands, biomass of small lugworms may exceed that of big ones during summer and autumn.

Expressed as an instantaneous rate, a mean annual mortality of 22% would amount to 0.26. Mean annual elimination is thus 0.26 × 5.5 = 1.4 g·m^{-2} ADW in the form of whole lugworms. For this calculation the annual mean biomass of 5.5 g·m^{-2} is used because there is no evidence for differential mortality as to season, for instance by an enhanced mortality during spawning.

The second author estimated the consumption of tail ends of lugworms by flatfish (mainly plaice) along 5 transects on the eastern part of Balgzand during 1976. This consumption varied from 0.3 to 3.0 g·m^{-2} ADW (roughly proportional to lugworm biomass at the various sampling places), with an average of 1.32 g·m^{-2} (DE VLAS, 1979). Mean lugworm biomass on this part of Balgzand during 1976 amounted to 5.1 g·m^{-2}. Thus, elimination of lugworm biomass by predation on tail ends amounted to 26% of the mean annual biomass (24% by plaice plus 2% by flounder).

KUIPERS (1977) estimated, by a partly different method, the intake by plaice of lugworm tail ends on Balgzand during 1973 as 1.86 g·m^{-2} ADW. During that year mean lugworm biomass on the part of Balgzand where KUIPERS worked amounted to 5.2 g·m^{-2}. Thus during

1973 elimination of lugworm biomass by plaice predation alone amounted to 36% of the mean annual lugworm biomass. Therefore, 30%, or 0.39 as an instantaneous rate, will be a fair estimate of lugworm biomass elimination in the form of regenerating tail ends.

Taking together both the adult mortality rate and the removal of regenerating parts by flatfish predation, the total annual rate of biomass elimination would amount to $0.26 + 0.39 = 0.65$. Production from weight increments will have been similar because lugworm biomass was almost constant during the years round 1976. Thus in a stable situation and considering only somatic production, the P/B ratio for the adult lugworm population on Balgzand would amount to about 0.6 or 0.7. From weight increments of lugworms in 3 populations living on tidal flats in the southwestern part of the Netherlands, WOLFF & DE WOLF (1977) found P/B ratios varying from 0.7 to 1.1, the higher value belonging to the population with the highest percentage of juveniles. POLLACK (1979), also from weight changes, found P/B ratios varying for various sampling sites and 2 years, from 0.7 to 1.5 for lugworms living at tidal flats in Brittany. No relationship with mean age or tidal level is apparent from his data, but the annual average was 1.3 in the year with the higher growth rate as compared to 1.0 during the other year.

Weights of spawning products were not measured directly. From the sudden weight losses observed during the spawning season in autumn, elimination of biomass may be estimated roughly at about 30% of the summer biomass at maximum (Fig. 7). As there is also a gradual weight loss during this season that is probably somatic, the real weight loss by spawning products will have been some 25% of summer biomass (see also DE WILDE & BERGHUIS, 1979a), or about 30% of the annual mean biomass of lugworms, raising the P/B ratio to about 1.0.

As compared to values found for other worm species, P/B ratios for *Arenicola* are low (cf. HEIP & HERMAN, 1979: table 2). Lugworms, however, are relatively large and reach relatively high ages.

IV. DISCUSSION

In most areas young (age $\frac{1}{2}$ to $1\frac{1}{2}$ year) and old lugworms live more or less separated, the young ones on higher grounds and at shorter distances from the coast. CAZAUX (1967) found young, about $\frac{1}{2}$ year old, lugworms appearing during March at the level of the first *Spartina* plants near Arcachon, France; SMIDT (1951) observed such young lugworms from May onward near the high-water mark and at other high-lying parts of the Danish Wadden Sea; THAMDRUP (1935) found high numbers of young lugworms during summer and autumn at higher tidal levels than adults in the Danish Wadden Sea; WERNER (1956) observed in late autumn a "Junggutwatt" closer to the coast of the island Sylt, German Wadden Sea, than the tidal flats with high densities of adult lugworms. POLLACK (1979) also observed small lugworms in summer to be almost restricted to areas near the high-water mark at various places in Brittany, France. FARKE, DE WILDE & BERGHUIS (1979) describe a similar pattern on tidal flats near the Wadden island Texel.

In the Dutch Wadden Sea we observed young lugworms during summer in high numbers only on relatively high tidal flats, mostly well above MTL, but only in places where silt percentages were neither below 1% nor above 30 or 40% (Fig. 3b). Such conditions with a combination of high grounds and a moderate silt content are almost limited to strips along the Wadden coasts of the barrier islands, because along most of the mainland coasts the sediment is too silty. Around such small islands as Griend, Richel, Rottumerplaat and Rottumeroog and also at the east and west ends of the longer barrier islands, the sediments of the tidal flats are too sandy as a consequence of exposition to wave action.

Where densities of small lugworms were high, *viz.* at the typical nursery strips along the islands with tens to hundreds per m², adults occurred only in low numbers or were even absent (*cf.* FARKE, DE WILDE & BERGHUIS, 1979). The intensive reworking of the sediment by lugworms (CADÉE, 1976) would make areas with high adult densities unfavourable for juveniles which would hardly be able to maintain their burrows. However, in places where the highest tidal flats are extremely silty, as along most of the mainland coast, most juvenile lugworms have to grow up at lower tidal heights amidst adults. In such areas, as Balgzand, the observed negative dependence of recruitment on adult density can arise.

Maximum numerical densities of adult lugworms were observed at intermediate tidal heights and at moderate silt percentages (Figs 3a and 4a). As in Brittany (POLLACK, 1979), the mean size of these adult lugworms was largest at long distances from the coasts (Fig. 8), *i.e.* at low tidal levels and in sandy sediments. Larger lugworms were even found incidentally in subtidal areas. POLLACK (1979) observed more rapid growth the lower the lugworms were living in the intertidal. From the data available from the Wadden Sea, it cannot be concluded whether in this area growth rate or mean age of the lugworms was the main cause of this trend in the mean size of adults. The gradual increase of mean individual weights observed in off-shore areas of the Wadden Sea during the last years (BEUKEMA, DE BRUIN & JANSEN, 1978: fig. 5b) was caused by a failing recruitment and, therefore, will have resulted in an increase of mean age. The accompanying low densities will have deminished competition for food and long immersion times prevailing in the off-shore areas also will have fostered growth rates (POLLACK, 1979). Therefore, both a higher mean age and a more rapid growth will have contributed to the greater size of the lugworms at the off-shore low tidal flats.

Biomass is a function of both numerical density and individual weight. Consequently, lugworm biomass was highest at slightly longer distances from the coasts than maximum abundance (compare Fig. 10 with Fig. 2 and also see Fig. 11). Also the biomass maximum was found at slightly lower tidal levels (about 5 or 6 dm below MTL) and in somewhat coarser and cleaner sediments (at median particle sizes of about 120 to 140 μm and at about 3 to 6% silt). LONGBOTTOM (1970) found the highest biomass values of lugworms at the north Kent coast at lower median particle diameters (*viz.* 80 to 120 μm), and explained this distribution by the higher concentrations of organic matter in the finer sediments and hence a higher nutritive value as compared with coarser sands. However, it is doubtful whether in the Dutch Wadden Sea food resources for lugworms are inadequate in the coarser sediments. One could hardly imagine a situation with the largest individuals occurring invariably in areas with inadequate food densities. As in the Kent area, food density (measured both as chlorophyll and as organic carbon content) is higher on high and silty tidal flats of the Wadden Sea than at lower and sandier places (CADÉE & HEGEMAN, 1977). Therefore, other environmental factors appear to limit lugworm size and biomass in such silty and high areas with high food densities. Too long emersion times, limiting the duration of the daily feeding periods, may be such a factor, as suggested for *Macoma* in the same area (BEUKEMA, CADÉE & JANSEN, 1977) and for *Arenicola* at tidal flats in Brittany (POLLACK, 1979). DE WILDE & BERGHUIS (1979b), however, are of the opinion that food supply is the main limiting factor for growth rates of infaunal species living on the tidal flats of the Wadden Sea, because supplementary feeding of lugworms in the laboratory greatly accelerated growth rates.

Lugworms appear to be almost stationary during summer and autumn and move frequently during winter and early spring (CHAPMAN & NEWELL, 1949). In accordance with observations at Sylt by WERNER (1956) and in an estuarine area in the southwest Netherlands by WOLFF (1973), we observed lugworms swimming in the water of tidal channels only in winter (Fig. 6). WERNER (1956) counted and measured lugworms washed ashore, and found high percentages of adults. Our pelagic catches in a tidal channel contained mainly small (about 1 year old) worms. Possibly, size distribution of lugworms

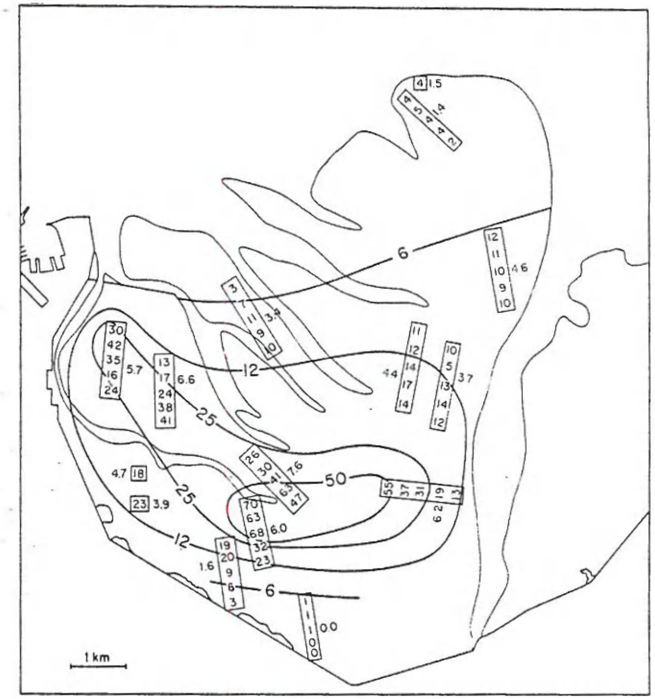

Fig. 11. Mean numerical densities (63 boxed figures along transects and at stations) of lugworms (big and small) on Balgzand, the isopleths indicating equal numbers per m² (drawn by eye) and mean biomass values (15 figures placed beside the boxes). Means of 9 annual samplings during late winter.

washed ashore is not representative of those migrating successfully. Because on Balgzand (and in other parts of the Dutch Wadden Sea) big lugworms outnumber small ones, displacement will be relatively more frequent in small ones than in adults. This is confirmed by the change in distribution pattern resulting from the winter dispersal which concerns especially young lugworms. In accordance with our observations (Fig. 5), WERNER (1956), WOLFF & DE WOLF (1977) and POLLACK (1979) also observed a significant decline in the density of young lugworms during winter on high coastal tidal flats and at the same time an increase of densities of young lugworms at lower and more off-shore stations. SMIDT (1944, 1951) after severe winters found increased densities of lugworms in off-shore areas and lowered densities in coastal areas. Unfortunately, he gives no separate data for big and small lugworms, but it is tempting to explain his results by similar off-shore migration.

In general the mass dispersal of juveniles in winter will be in an off-shore direction. In addition and also during winter, there may be some dispersal of adults that is less well directed (WERNER, 1956). Winter dispersal will be stimulated by low temperatures (WERNER, 1956). During a period with mild winters, recruitment by dispersal to areas far off shore was inadequate to maintain those populations at their original level (BEUKEMA, DE BRUIN & JANSEN, 1978).

Although densities of juvenile lugworms may be locally high at the typical nursery wadden, for the whole Wadden Sea total numbers of young lugworms appear to be low relative to the numbers of adults. During the 1971–1972 survey of the whole Dutch Wadden Sea, the share of small lugworms was 26% and during 1977 only 7% in the western half of the area. These percentages are within the range observed in the 10 years study on Balgzand (Fig. 9a), giving an average recruitment of 20%. SMIDT (1951), from many years of observation in the Danish Wadden Sea, also found adults to be more numerous than juveniles. His conclusion that the annual death rate must be low, is in agreement with our observations, indicating a mean annual rate of mortality of about 22%. This would mean that lugworms become old, some 5 or 6 years at the least. In aquaria, THAMDRUP (1935) observed a life-span of at least 6 years. By contrast CAZAUX (1967) inferred from weight frequency distributions that only 3 year classes were present near Arcachon, the oldest animals dying after spawning. His figures, however, are not convincing, as the members of the oldest yearclasses could not be separated properly, and more than one yearclass may have been present within one broad peak of his frequency diagrams. Also, the disappearance of the heaviest lugworms during the spawning season may have been caused by weight losses (*cf.* Fig. 7b), moving them back into the preceding peak of the frequency distribution. We never observed mass mortality of lugworms during or after spawning in the Wadden Sea, nor could we find convincing evidence for such mortality in the literature. The sudden disappearance of about 40% of the lugworms, observed by NEWELL (1948) during the spawning season at Whitstable Flats, England, may have been an effect of his method of counting the faeces mounds, and caused by the temporary inactivity of the females after spawning (FARKE & BERGHUIS, 1979). In fact, NEWELL (1948) found only few dead lugworms during that period.

During the last 10 years, the population of over one year old lugworms on Balgzand fluctuated within the relatively narrow range of 14 to 22 individuals per m^2 (Fig. 9). Only in the far off-shore areas a consistent decline was observed, caused by inadequate dispersal of

juveniles, probably as a consequence of relatively high temperatures during almost all of the winters in the period of observation (BEUKEMA, DE BRUIN & JANSEN, 1978). Apart from this local decline, the population as a whole has been remarkably stable.

Two factors will have contributed to this stability. The low rate of mortality (22% per year) means a relatively long life-span and hence a population consisting of many yearclasses. Therefore, the effect of fluctuations in recruitment on total density will be restricted. Moreover, the observed inverse relationship between adult density and subsequent recruitment (Fig. 9b), implying an increased chance for a strong new yearclass when adult density is low, will also tend to stabilize the population.

Millions of lugworms are dug annually to be used as bait for the sport fishery. The estimated total annual yield from the tidal flats in the western part of the Wadden Sea is about $3 \cdot 10^7$ (DIJKSTERHUIS, 1977). As more than half of this activity is usually concentrated on Balgzand, about $2 \cdot 10^7$ adult lugworms will be removed annually from this area. Most of them are dug by a few digging machines, working in the restricted area with highest lugworm densities, generally exceeding 40 or 50 worms per m^2 (Fig. 11). The total population present on the tidal flats of Balgzand (an area of about $5 \cdot 10^7$ m^2) can be estimated at 50 to $100 \cdot 10^7$ adult lugworms. Hence, annual elimination by digging was only about 3% of the adult stock, and only about one seventh of total mortality. The lugworm population appears to be able to carry this additional mortality, as it was nearly stable during the last 10 years, to which the compensatory recruitment mechanism might have contributed. Therefore, as far as the lugworms are concerned, no serious harm seems to be inflicted by the present intensity of harvesting. Most individuals of some other benthic species may be killed at the digging sites, as observed in the worm *Heteromastus filiformis* by CADÉE (1977). Such effects will be limited, however, as the total area ploughed up annually covers less than 2% of the tidal flats.

V. SUMMARY

Lugworms, *Arenicola marina* (L.), were found almost everywhere on the tidal flats of the Dutch Wadden Sea. Mean biomass amounted to about 5 g·m^{-2} ash-free dry weight, mean numerical density to 17 per m^2 with only about one quarter of the animals being juveniles (about $1\frac{1}{2}$ year old).

Numbers of adults and total lugworm biomass showed a maximum in a zone at 1 to 4 km from the coasts, about halfway between high- and low-water mark and at intermediate silt content of the sediment.

Numerical densities as well as biomass values showed a bell-shaped relationship to both silt percentages and heights in the tidal zone. Numbers of adults were high at lower tidal levels and at a wider range of silt percentages than juveniles. Individual weights of adults increased in an off-shore direction, and were highest at low intertidal levels and in sandy sediments, where food availability was below average.

During their first period of burrowed life (April or May to winter) lugworms were most numerous on high grounds near the coast. They dispersed during winter at an age of 1 to 1½ year (at a mean weight of about 40 mg ADW), transported by tidal currents.

During a 10 year study on Balgzand, a 50 km² tidal flat area in the westernmost part of the Wadden Sea, lugworm numbers were found to decline at a mean annual rate of 22%. Annual recruitment of 1 to 1½ year old juveniles to the adult stock was irregular but on average (20%) almost equal to annual mortality. After an initial decline during some years of low recruitment, total population of adults was found to be stable. Population stability will have been enhanced by a long life-span and an inverse relationship between adult density and rate of recruitment.

From data on annual elimination by mortality plus predation on regenerating tail ends, a P/B ratio of almost 0.7 could be estimated for somatic production by a stable lugworm population; to include gametic production this figure will have to be raised to about 1.0.

VI. REFERENCES

BEUKEMA, J. J., 1973. Migration and secondary spatfall of *Macoma balthica* (L.) in the western part of the Wadden Sea.—Neth. J. Zool. **23**: 356–357.

——, 1976. Biomass and species richness of the macro-benthic animals living on the tidal flats of the Dutch Wadden Sea.—Neth. J. Sea Res. **10** (2): 236–261.

BEUKEMA, J. J., W. DE BRUIN & J. J. M. JANSEN, 1978. Biomass and species richness of the macrobenthic animals living on the tidal flats of the Dutch Wadden Sea: long-term changes during a period with mild winters.—Neth. J. Sea Res. **12** (1): 58–77.

BEUKEMA, J. J., G. C. CADÉE & J. J. M. JANSEN, 1977. Variability of growth rate of *Macoma balthica* (L.) in the Wadden Sea in relation to availability of food. In: B. F. KEEGAN, P. O. CEIDIGH & P. J. S. BOADEN. Biology of benthic organisms. Pergamon Press, Oxford: 69–77.

CADÉE, G. C., 1976. Sediment reworking by *Arenicola marina* on tidal flats in the Dutch Wadden Sea.—Neth. J. Sea Res. **10** (4): 440–460.

——, 1977. Het effect van pierenspitten op de worm *Heteromastus*.—Waddenbull. **12**: 312–313.

CADÉE, G. C. & J. HEGEMAN, 1977. Distribution of primary production of the benthic microflora and accumulation of organic matter on a tidal flat area, Balgzand, Dutch Wadden Sea.—Neth. J. Sea Res. **11** (1): 24–41.

CAZAUX, C., 1967. Évolution d'une population d'*Arenicola marina* (L.) à Arcachon. Cycle annuel—Période de réproduction.—Act. Soc. linn. Bordeaux, Serie A, **103** (15): 3–18.

CHAPMAN, G. & G. E. NEWELL, 1949. The distribution of lugworms (*Arenicola marina* L.) over the flats at Whitstable.—J. mar. biol. Ass. U.K. **28**: 627–634.

DIJKSTERHUIS, J., 1977. Revolutie in de wadpierspitterij en de mogelijke gevolgen. Intern verslag Rijksinstituut voor Natuurbeheer. Texel: 1–10.

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

FARKE, H., P. A. W. J. DE WILDE & E. M. BERGHUIS, 1979. Distribution of juvenile and adult *Arenicola marina* on a tidal mud flat and the importance of nearshore areas for recruitment.—Neth. J. Sea Res. **13** (3/4): 354–361.

HEIP, C. & R. HERMAN, 1979. Production of *Nereis diversicolor* O. F. Müller (Polychaeta) in a shallow brackish-water pond.—Estuar. coast. mar. Sci. **8**: 297–305.

KUIPERS, B. R., 1977. On the ecology of juvenile plaice on a tidal flat in the Wadden Sea.—Neth. J. Sea Res. **11** (1): 56–91.

LONGBOTTOM, M. R., 1970. The distribution of *Arenicola marina* (L.) with particular reference to the effects of particle size and organic matter of the sediments.—J. exp. mar. Biol. Ecol. **5**: 138–157.

NEWELL, G. E., 1948. A contribution to our knowledge of the life history of *Arenicola marina* L.—J. mar. biol. Ass. U.K. **27**: 554–580.

POLLACK, H., 1979. Populationsdynamik, Produktivität und Energiehaushalt des Wattwurms *Arenicola marina* (Annelida, Polychaeta).—Helgoländer wiss. Meeresunters. **32** (3): 313–358.

SMIDT, E. L. B., 1944. Das Wattenmeer bei Skallingen, 3: The effects of icewinters on marine littoral faunas.—Folia geogr. dan. **2** (3): 1–36.

——, 1951. Animal production in the Danish Waddensea.—Meddr Kommn Danm. Fisk.-og Havunders, Serie Fiskeri, **11** (6): 1–151.

STRAATEN, L. M. J. U. VAN, 1952. Biogenic textures and formation of shell beds in the Dutch Wadden Sea.—Proc. K. ned. Akad. Wet. (B) **55** (5): 500–516.

THAMDRUP, H. M., 1935. Beiträge zur Ökologie der Wattenfauna auf experimenteller Grundlage.—Meddr Kommn Danm. Fisk.-og Havunders., Serie Fiskeri, **10** (2): 1–125.

VLAS, J. DE, 1973. Migratie via getijstromen van jonge nonnetjes, *Macoma balthica* L., op en rond het Balgzand. Intern verslag Nederlands Instituut voor Onderzoek der Zee, Texel 1973-14: 1–30.

——, 1979. Annual food intake by plaice and flounder in a tidal flat area in the Dutch Wadden Sea, with special reference to consumption of regenerating parts of macrobenthic prey.—Neth. J. of Sea Res. **13** (1): 117–153.

WERNER, B., 1956. Über die Winterwanderung von *Arenicola marina* L. (Polychaeta sedentaria).—Helgoländer wiss. Meeresunters. **5**: 353–378.

WILDE, P. A. W. J. DE & E. M. BERGHUIS, 1979a. Spawning and gamete production in *Arenicola marina* in the Netherlands, Wadden Sea.—Neth. J. Sea Res. **13** (3/4): 503–511.

——, 1979b. Laboratory experiments on growth of juvenile lugworms, *Arenicola marina*.—Neth. J. Sea Res. **13** (3/4): 487–502.

WOLFF, W. J., 1973. The estuary as a habitat.—Zool. Verh., Leiden **126**: 1–242.

WOLFF, W. J. & L. DE WOLF, 1977. Biomass and production of zoobenthos in the Grevelingen estuary, the Netherlands.—Estuar. coast. mar. Sci. **5**: 1–24.