LABORATORY EXPERIMENTS ON GROWTH OF JUVENILE LUGWORMS, ARENICOLA MARINA

by

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CONTENTS

I. INTRODUCTION

The common lugworm, *Arenicola marina* L., represents one of the main macrobenthos species of the tidal mud flat areas of northwestern Europe. According to BEUKEMA *et al.* (1978) its biomass ranks third after that of *Cerastoderma* and *Mytilus* in the Dutch Wadden Sea. The lugworm is an important link in a number of food chains, to which also valuable commercial fishes belong. According to KUIPERS (1977) and DE VLAS (1979) plaice predates heavily on this source of food. The same holds for a number of wader birds (HULSCHER, 1975). Notwithstanding its importance there is relatively little information on growth of the lugworm. The main reason will be the absence of reliable methods for age determination of the individual worm, as no solid parts with growth structures are present. Indirect methods based on population structure, by studying length- and weight frequency distributions (Peterson method), are unreliable as growth is irregular and hence sizes in the various age groups overlap. Moreover, migration and dispersal patterns are insufficiently understood. The present paper of BEUKEMA & DE VLAS (1979) gives valuable information on the population structure, production and migrations found in a natural population in the western Wadden Sea. However, only the O-group could,

by their pink colour and transparency, easily be identified, and an estimate of growth was only possible in the small worms. According to LONGBOTTOM (1970), BEUKEMA (1974) and own observations the biomass value of *Arenicola* populations may show large variations throughout the year. SMIDT (1951) and WOLFF & DE WOLF (1977) mention growth to take place only during the summer whereas in winter growth is absent or weight reduction occurs. CAZAUX (1967) distinguished 3 different classes from weight frequency distributions, possibly representing age groups. DE VOOYS (1975) made similar observations in a population near Texel. However, calculations of growth from such data give disputable results. The present laboratory study describes growth and mortality of juvenile lugworms under the influence of the environmental factors temperature and food.

II. MATERIAL AND METHODS

Sediment cores with a diameter of 18 cm and a height of 10 cm were taken from places where dense populations of O-group lugworms occurred on a typical nursery flat (the Mok) near the south point of the island of Texel, the Netherlands. The cores were transferred to rectangular plastic boxes with an upper surface of 200 cm² and a height of 12 cm. The boxes were brought undisturbed to the laboratory and placed in shallow basins which were circulated with running sea water of a constant quality and a salinity of $25 \pm 1\%_0$ S at a rate of 25 l·h⁻¹. The animals were kept permanently submersed. Four cool white fluorescent tubes, 30 cm over each basin, served a 12 h light 12 h dark rhythm.

The animals were reared at 5 different temperatures (5, 10, 15, 20 and 25° C) by means of heat exchangers in the circulatory system (temperatures were $\pm 1°$ C, except that during a fortnight in July and August the two coldest series rose to 8.0° and 12.5° C respectively).

The number of specimens present in each box at the start and during the course of the experiments was tentatively estimated from the number of newly produced casts. To this end the boxes were cleared of existing casts and the sediment surface was carefully graded and smoothened. After a time interval of 2 to 3 h, which was found to give the best results, the casts present were counted. By application of some correction, the number of animals was calculated. At the start of the experiment in June 1975 average body length of the lugworms (tail-end not included) was 11.14 mm, mean ash-free dry weight 3.59 mg and the average density per box 45 animals.

In 30 boxes, 6 of each of the 5 temperatures, the original sediment was maintained without any addition during the course of the experi-

ments. Though there was a small, not measured, primary production by microphytobenthos on the sediment surface, the organic food was rapidly depleted in these boxes, further referred to as "non-fed".

A second series of 35 boxes, 7 of each temperature, was supplied with food and will be referred to as "fed". Natural "food" was collected weekly at the original sampling site in the Mok. The upper 1 mm sediment layer was scraped from places rich in benthic algae or deposited organic matter. In the laboratory the material was spread in shallow trays and incubated in moist condition during 2 days at room temperature (18 to 20° C). Once a week the upper 1 cm layer of the sediment in the boxes with *Arenicola* was carefully removed and replaced by the incubated sediment. In the course of the 120 days experiment the amount of replaced sediment was increased by doubling the feeding frequency and by augmenting the thickness of the replaced sediment layer.

With intervals of about 2 weeks one box of each series was liquidated, the content inspected, sieved over 2.0 mm and 0.8 mm nylon gauzes and the number of worms counted. The results were compared with those from the cast-counting method. Before measuring and weighing the worms they were kept for one day in water of 25‰ S, in which time 95% of the gut content is lost. The trunk part of the living worm was gently stretched under water and its length read on a mm grid. The tail end was excluded from measurement as this part of the worm is subject to large variations (KUIPERS, 1977; DE VLAS, 1979). The worms were subdivided in 0.5 cm classes. The living wet weight of the animal, superficially dried on blotting paper, was measured in 0.1 mg classes. Ash-free dry weights were obtained from the difference of the weight after 2 days drying at 60° until constant weight and the weight after heating in an oven during 2 h at 650°.

As a consequence of the method adopted to use animals in undisturbed sediment cores from outside, also other macrofauna elements were introduced in the boxes. Generally their numbers were negligible, *viz.* *Cerastoderma* (2 ×), *Macoma* (4 ×), *Nephtys* (3 ×) and *Lanice* (6 ×). *Hydrobia ulvae* and *Nereis diversicolor*, however, occurred in large numbers. *Hydrobia*, a browser, was considered to be harmless, and it was easily removed from the sediment. *Nereis*, which in the 3 upper temperature series rapidly developed from almost invisible juveniles to 2 to 4 cm long worms, were suspected to interfere seriously with the experiment (*cf.* WITTE & DE WILDE, 1979). Because of their alertness and their hidden way of life removal was difficult.

Three times, in July, September and October, lugworm samples were collected from the nursery area in the Mok to determine the average weight of the original juvenile population.

III. RESULTS AND INTERPRETATION

1. ANIMAL NUMBERS; SURVIVAL RATES

Survival is calculated as the numbers present in the boxes at the moments of their liquidation expressed as a percentage of the initial number (Fig. 1). It will be evident that the survival observed is strongly related to feeding condition, the "non-fed" group showing a far higher
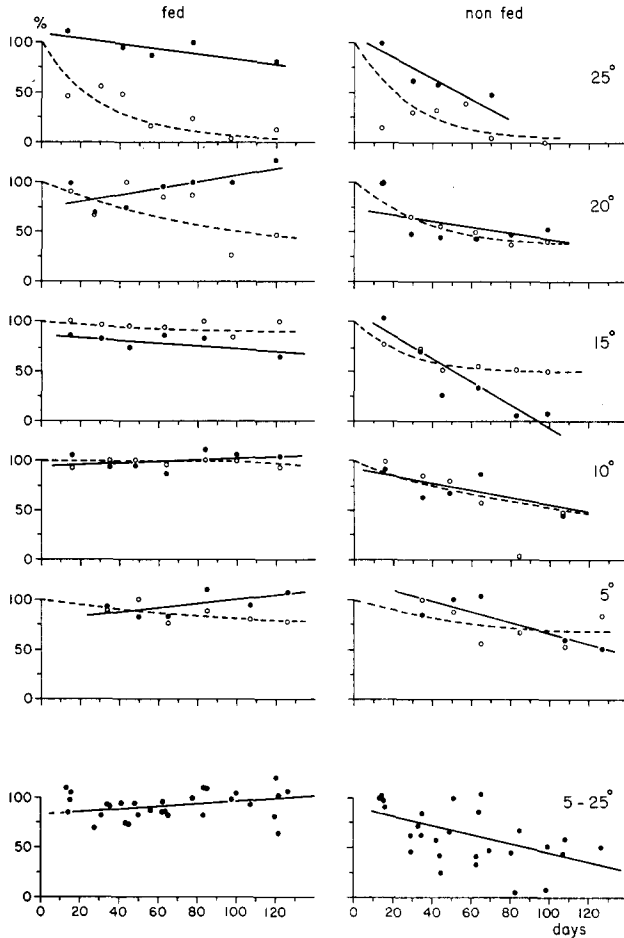

Fig. 1. Percentages of survival, obtained from liquidated boxes (○, broken lines), and defecation activity, as observed in all the remaining boxes, expressed as a percentage of the actual number found in the liquidated boxes (●, solid lines) in fed and non-fed *Arenicola marina* during the period June to October 1975, shown for 5 experimental temperatures; defecation percentages also for all temperatures taken together (lowermost graphs).

decline in numbers than the "fed" group. In addition a positive relationship between mortality and temperature is demonstrated in the fed group. With moderate and low temperatures, mortalities are low, being almost negligible at 10° and 15° C, and about 20% in 130 days at 5° C. In the higher temperature range mortalities are higher, being 50% at 20° and even 90% at 25° C within a period of 4 months. In the non-fed animals at 5°, 10°, 15° and 20° C mortalities range from 40 to 60%, and at 25° the mortality observed is nearly 100%.

2. NUMBERS OF FAECAL CASTINGS IN RELATION TO ANIMAL NUMBERS AND CONDITION

During the course of the experiment numbers could be estimated only indirectly from the faecal castings produced. By plotting the number of castings of each box, an eye-fitted curve was obtained. A selection of such curves is given in Fig. 2. The curves include the actual number, found with the liquidation of the box. The number at the start of the experiment was obtained by extrapolating the curve to the day of sampling, but in some cases which showed a violent decrease in numbers during the first days, the first faecal count was considered to present the initial value. When the actual number counted at the end was larger than the estimate obtained by extrapolation (4 cases) the actual end number was also used as initial number. The mean of calculated initial numbers in all boxes was 44.13 (standard deviation 11) which means that locally the population density of juvenile *Arenicola* at the nursery amounted to some 2000 *Arenicola* · m^{-2}.

In natural populations of *Arenicola* it was found that faeces production depends on the season (CADÉE, 1976). In the laboratory the various experimental conditions also resulted in considerable differences between actual numbers and number of casts observed, indicating part of the animals to be inactive. In most of the experiments the numbers present were counted at various occasions throughout the experiment. This offers an opportunity to test the reliability of estimating numbers present by counting faecal casts under different temperature conditions with and without food supply (Fig. 1). In the non-fed worms an increasing deviation from the 100% line is observed, indicating that the worms show a smaller and far less frequent faeces production. A distinct temperature effect is not present. In the well-fed worms only small deviations from the actual number occur. At higher temperatures (15° and 25° C) a small temperature effect occurs, but here an interference with the presence of *Nereis* might have plaid a part. Pooling the data of all temperatures for the fed and non-fed series, shows that faeces production is related to the feeding regime (Fig. 1).

In sediment rich in food a high percentage of *Arenicola* can be expected to have a regular food uptake and faeces production. In such sediments, application of the "cast method" provides a reliable estimate of the population, although underestimates of up to 20% appear to occur. In sediments very poor in food the method gives a substantial bias, and underestimates of 60% and even higher are to be expected.
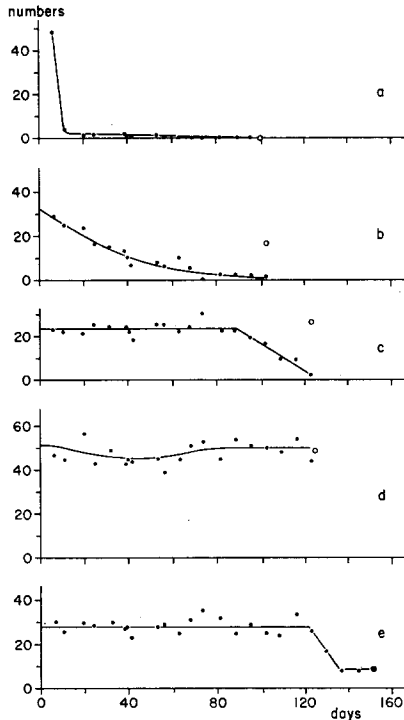

Fig. 2. Examples of defecation activity found in laboratory reared *Arenicola* populations at different environmental conditions. Animal numbers (●) as judged from the casts counted; also the actual number of animals in the box present at the moment of liquidation is indicated (○). a. A sudden drop in defecation activity caused by high initial mortality (non-fed, 25° C). b. A gradual decrease in activity caused by undernutrition suggesting a much lower population than actually present (non-fed, 15° C). c. Presence of *Nereis diversicolor* has a negative influence on cast production and causes an underestimate of actual numbers (fed, 15° C). d. With sufficient food and the right temperature, the cast numbers give a correct impression of the animals present (fed, 10° C). e. An actual loss of animals caused by migration is reflected by a sudden fall in the cast numbers (fed, 5° C, the migrated worms were recovered in the circulatory water system).

3. GROWTH IN LENGTH

The length increase of the worms during the 4 month period of the experiment is shown in Fig. 3. All plots have the same starting point, the average length derived from the animals in 3 boxes ($n = 111$). The plots suggest a linear growth. This is confirmed by a least square computation, indicating that the growth in length is described most satisfactory by a linear function (an extremely high value found at day 97 in the 20° "fed" series is omitted, as there were only 13 worms
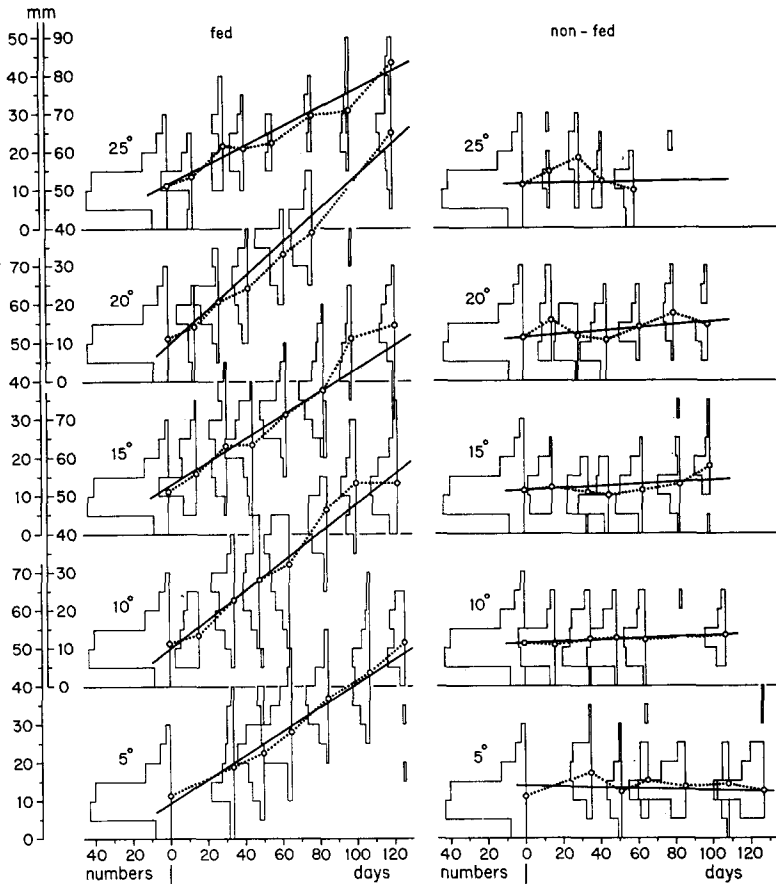

Fig. 3. Length growth in mm at 5 different temperatures in fed and non-fed *Arenicola marina* during a 4 months period in 1975. Represented are length frequency distributions and average body lengths ($\bigcirc$, broken lines) of worm populations in successively liquidated boxes. Linear regressions (solid lines) are calculated; in the fed animals these are: at 5° C, $y = 7.79 + 0.33x$; at 10 °C, $y = 8.93 + 0.39x$; at 15° C, $y = 9.61 + 0.37x$; at 20° C, $y = 7.50 + 0.44x$; at 25°C, $y = 10.48 + 0.26x$.

present). In the boxes constantly supplied with new sediment, presumably rich in digestable food, rapid growth occurred. In the boxes without additional food supply signs of food exhaustion occurred soon, and growth was low or even absent (Fig. 3, right side).

The slopes of the regression lines of the fed animals differ with temperature in a slight but significant way ($P < 0.001$). This effect of temperature on length growth indicates an optimum around 20° C, a small influence between 5° and 20° C, and a strong influence between 20° and 25° C as at 25° C the growth rate is considerably lower than at 5° C.

4. GROWTH IN WEIGHT

With additional feeding also a remarkable rapid growth in weight is observed (Fig. 4a) whereas in the non-fed animals growth in weight is again nearly absent or tends to be negative. Negative growth can be explained by emaciation and by an increased mortality in the largest animals.

There is evidence that in some of the most densely populated boxes with feeding regime, competition for food occurred as higher weights were found in the boxes with relatively low animal numbers. Referring to weight, examples of density dependent growth are to be found in Fig. 4a on day 100 in the 10° and on day 97 in the 20° series; referring to length growth Fig. 3 gives examples at 10, 15 and 20° C. Therefore, notwithstanding the observed extremely rapid increase in both length and weight in fed animals, it is possible that growth in a considerable number of boxes was still sub-optimal by food limitation. In natural populations of juvenile lugworm always much lower growth rates were found than those observed in the experiments. Since the temperature effect on growth is small, this may be caused by an insufficient food supply on the tidal mud flats.

From a combination of the data on length and weight, a length-weight curve for *Arenicola marina* during its first growing season can be constructed (Fig. 5). As a rule such a relation is exponential (WINBERG, 1971). Plotting length and weight on a double logarithmic scale (Fig. 5, insert) shows that this is not the case with the present data; a distinct change in direction of the curve occurs at a length of about 25 mm.

5. BIOMASS DURING THE EXPERIMENT

As biomass is the product of numerical density and mean weight, the lugworm biomass in each box can be calculated. For reasons of comparison with field data the figures are expressed in grammes ash-free dry weight (ADW)·m^{-2} (Fig. 4b).

In the boxes with subsidial feeding, extremely high biomass values were reached in the relatively short period of 4 months. At the start of the experiment the biomass was approximately 10 g ADW·m^{-2}. At 5° C a weight increment of 140 g·m^{-2} was found, at 10° even 230 g·m^{-2}, whereas at 15° and 20° C somewhat lower values, around 190 g·m^{-2}, were measured. At 25° C biomass remained constant at 10 g·m^{-2}, partly resulting from a reduced growth rate (Fig. 4a), but mainly from a high mortality. This low survival is probably caused by a permanently low oxygen concentration and high sulphide concentration in the bottom because of the combination of the high amount of organic matter and high temperature.

In the boxes without additional food supply, invariably a low biomass was found, resulting from the low average weight of the worms.
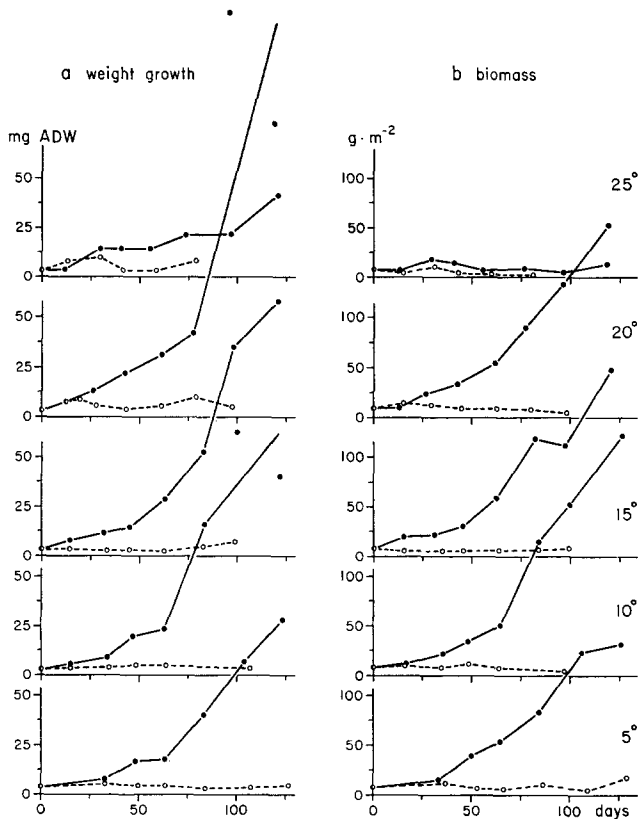

Fig. 4. a. Weight growth (average weight of worms in mg ADW) at different temperatures in fed (●) and non-fed animals (○). b. Increase in biomass (g·m^{-2}) obtained from "fed" (●) and "non-fed" boxes (○) at different temperatures.

6. MATURATION

From the end of August onwards gonad development was observed in the largest animals. These were dissected and the coelomic fluid inspected with a microscope. On 26 August the first female with small developing oocytes (diameter >30 μm) was observed. During Sep-
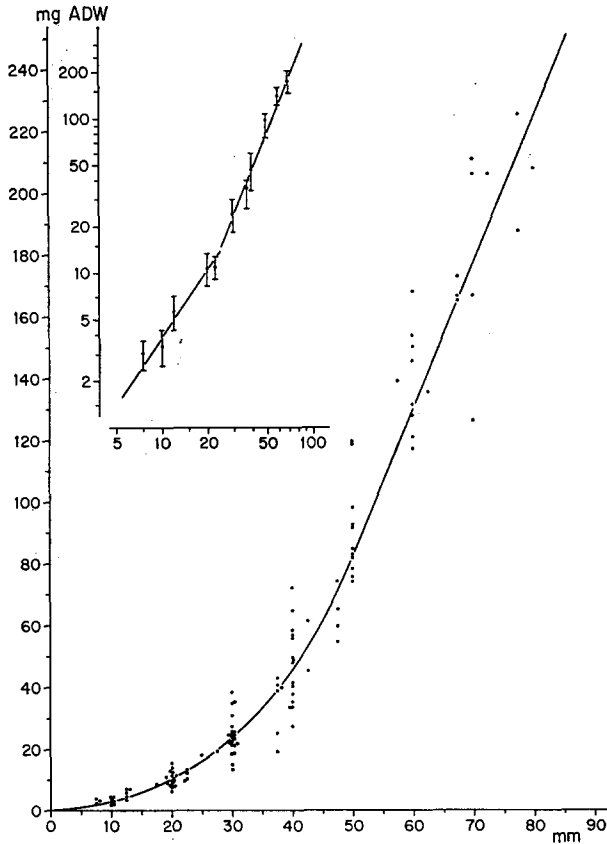

Fig. 5. Length-weight relation in laboratory reared juvenile *Arenicola marina* (body weight in mg ADW; body length in mm as trunk part only). Insert: the same, but plotted logarithmically; calculated regression lines indicate anisometric growth.

tember and October part of the fed animals at the temperatures of 15° and 20° showed oocytes and sperma disci in various stages of development. In the non-fed worms no sexual maturation occurred. In Fig. 6 maturation is shown in relation to body weight and ambient temperature. It appears that *Arenicola* under favourable con-

ditions will reach sexual maturity towards the end of its first year and that maturation depends on body size and temperature. The body weight of worms reaching maturity is negatively related to the experimental temperature, the smallest worm becoming mature at 15° C was much heavier (1.3 g) than at 20° C (1.0 g) and at 25° C (0.5 g). At the low temperatures (5° and 10° C) no gonad development had taken place at the end of the experiment.
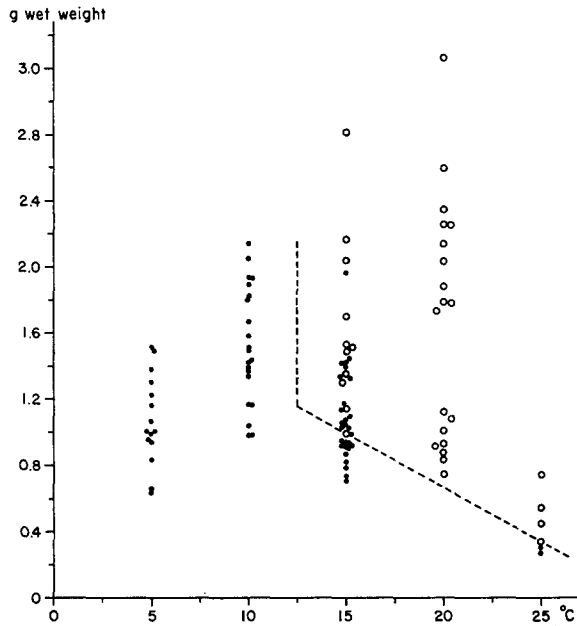

Fig. 6. Sexual maturation in O-group *Arenicola marina* in relation to body (wet) weight and ambient temperature; indicated are specimens in which no traces of sexual products were observed (●), males and females with developing gametes (○) and the limitation of the maturing worms (broken line).

According to literature (NEWELL, 1948; SMIDT, 1951; DUNCAN, 1960; CAZAUX, 1967), *Arenicola* matures at the end of its second year. This will partly be caused by low winter temperatures, and by the suboptimal growth under natural conditions.

IV. DISCUSSION

Growth in *Arenicola* under field conditions was only observed during spring and summer (NEWELL, 1948; SMIDT, 1951; POLLACK, 1979; BEUKEMA & DE VLAS, 1979). During autumn and winter the weight of adults tends to decrease (NEWELL, 1948; BEUKEMA & DE VLAS, 1979)

whereas in juveniles sometimes a slight gain in weight was found also in that season (THAMDRUP, 1935; CAZAUX, 1967; LONGBOTTOM, 1970; DE VOOYS, 1975; GRIFFITHS, 1978). NEWELL's (1948) data on the growth in a juvenile population at the Whitstable Flats, S.E. England, show a length increase from 9 to 44 mm from April to the middle of September, followed by a small decrease in October and November. Growth over the first 120 days amounted to 27 mm which is low compared to the results of our experiments with additional feeding where the average length increase in 120 days varied from 31 mm at 25° to 53 mm at 20° C. NEWELL's data suggest a nearly linear length growth as in the present experimental results. The growth in weight in the present experiments can be compared with the data obtained in the field on the sampling station (de Mok) during the same period with temperatures ranging from 15° to 20° C (Fig. 7). It appears that at this
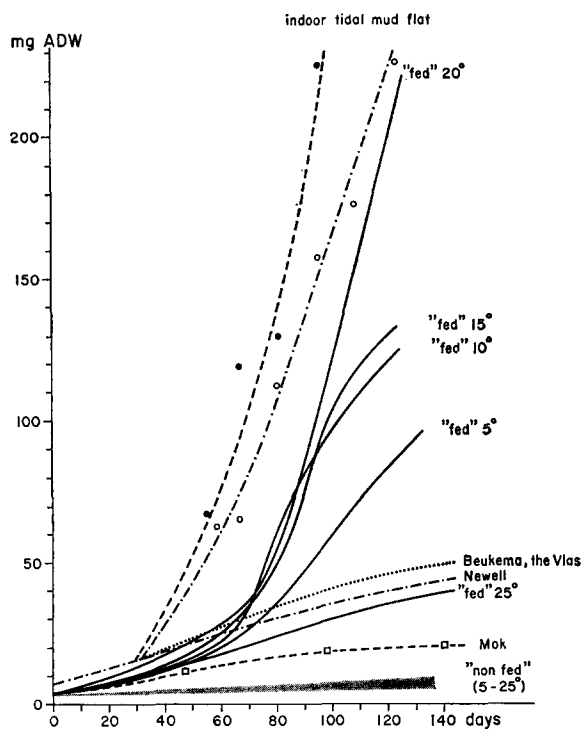

Fig. 7. Growth curves obtained from the present experiments for fed *Arenicola marina* at different temperatures and for non-fed animals (shaded bar), in comparison to growth of juvenile *Arenicola* in the field situation at the nusery area at the Mok, Texel (□), at the Balgzand area as reported by BEUKEMA & DE VLAS (1979) (dotted line), and at Whitstable, flats, England as reported by NEWELL (1948), and in two different indoor tidal mud flats, (○ and ●).

station growing conditions were unfavourable for juveniles, although possible effects of a size selective migration or predation cannot be excluded. NEWELL's data (1948) refer to length only but can be compared after conversion into weight with the length-weight relationship presented in Fig. 5. Again a low weight growth of young *Arenicola* at Whitstable is evident (Fig. 7). Also the data of BEUKEMA & DE VLAS (1979) who describe the seasonal changes in weight of small lugworms in the Balgzand area during a summer with nearly normal temperatures (10° to 20° C) demonstrate a relatively slow growth (Fig. 7).

Finally some unpublished data on weight growth in juvenile lugworms kept in 2 large indoor tidal mud flats (DE WILDE & KUIPERS, 1977) at about 20° C are added to Fig. 7. The extraordinary weight increment in 3 months apparently is caused by the surplus of nutritious sediment present in these systems.

In conclusion growth in juvenile *Arenicola marina*, kept at optimal temperatures, moderate animal densities, and favourable feeding conditions, may exceed 4 to 10 times that found in the field, both in the nurseries and on the extensive mud flats. Certainly, the reduced activity of the animals during low tide will limit the food uptake of the worms on intertidal flats. But also in the subtidal parts of the Wadden Sea a similar slow growth pattern was observed. In the experiment indications were obtained for a density dependent growth (page 494). It may be assumed that the main limiting factor for the growth of *Arenicola*—one of the dominant macrobenthos species in the Wadden Sea—is food limitation. This tentative conclusion seems to be contradictory to the fact, that recent estimates indicate the imput of some 1000 g ADW of organic matter annually into the western Wadden Sea, suggesting a "surplus" of food for the benthos in the area (DE JONGE & POSTMA, 1974; CADÉE & HEGEMAN, 1977). The low growth rates found for *Arenicola* in this study demonstrate a food shortage caused either by food competition with other small mud flat inhabiting organisms, feeding directly at the sediment surface, or by a poor quality of the organic matter available (*cf.* BOON & HAVERKAMP, 1979).

Both high animal numbers and rapid individual growth will rise lugworm biomass. Biomass values of over 150 g (ADW)·m⁻² were found in the experiments with a maximum value of 240 g·m⁻² occurring at 10° C and not at 15° or 20° C, the temperatures showing better growth. This lower growth at 15° and 20° C is attributed to increased activity of the *Nereis* present in the containers. The presence of *Nereis* interferes with the numbers of *Arenicola* present as found by WITTE & DE WILDE (1979). *Nereis* may also show its carnivorous character, by actually predating on *Arenicola*. The biomass of *Nereis*, however, was small.

Compared to the biomass of the macrobenthos on the tidal flats of the Wadden Sea, the biomass of *Arenicola* in the laboratory containers was extremely high as BEUKEMA (1976) and BEUKEMA, DE BRUIN & JANSEN (1978) estimate mean biomass of the macrobenthos in the Dutch Wadden Sea to amount to about 27 g·m^{-2}, with only occasionally values above 100 g·m^{-2}. Mean biomass values for *Arenicola* only, were estimated between 6 and 4 g·m^{-2} in the coastal area and between 5 and 1 g·m^{-2} in the offshore area.

There is little information on the mortality occurring in natural populations of *Arenicola*. BEUKEMA & DE VLAS (1979) calculate an average annual mortality rate of 22% (a range from 2 to 38% during a period of 9 years) for the combined population of adults and subadults in the western Wadden Sea. Although mass mortalities in adults have been observed occasionally (MICHAELIS, 1980), generally mortality seems to occur gradually with a slight maximum following the spawning period (NEWELL, 1948). In juvenile populations a gradual decline as well as sudden dramatic drops in numerical densities have been observed. Migration of juveniles from the nurseries towards the open mud flats is thought to be a gradual redistribution process extending over long periods of the year (FARKE & BERGHUIS, 1979). On the other hand, juvenile populations will suffer high mortalities by unfavourable environmental conditions and predation. Poor feeding conditions, and a too high ambient temperature may cause heavy losses. WITTE (unpublished data) found in 1976 a nearly complete elimination of a population in a nursery area near Texel, resulting from high summer temperatures and subsequent low oxygen concentrations in the overlying water film during low tide.

WITTE & DE WILDE (1979) found predation of *Nereis* on juvenile lugworm in experiments. Also other predators, including various polychaetes, *Crangon*, *Carcinus*, *Gobius*, juvenile plaice and waderbirds may reduce the populations on the nursery flats. DE WILDE (unpublished) observed numerous small pools in a nursery flat, resulting from grundling by mallard ducks, foraging on juvenile *Arenicola*.

V. SUMMARY

During a 4 month period in 1975, faeces production, growth, biomass, maturation and mortality were studied in juvenile lugworms, *Arenicola marina*, reared in the laboratory at 5 experimental temperatures under restricted and subsidized feeding conditions.

Faeces production and hence food uptake is dependent on the food content of the sediment. In poor sediments a smaller and less frequent faeces production was measured. Therefore, the estimate of the size of

lugworm populations by counting cast numbers is subject to a considerable bias.

With favourable food conditions even in dense worm populations a rapid and almost linear length growth from 11 to about 80 mm and an increase in weight from 3.5 to about 200 mg (ash-free dry weight) was measured. The growth resulted in biomass values as high as 200 g (ADW)·m^{-2} or more, values never found in the Wadden Sea. Restricted feeding conditions caused stagnancy of growth and increased mortality. Retarded growth, as observed in natural populations of O-group worms on the extensive mud flats as well as on special "nursery" flats is attributed to an insufficient food supply on these flats, though these are characterized by a high input of primary organic matter, locally produced as well as imported from the adjacent North Sea. Over a wide range (5° to 20° C), the influence of temperature on growth was found to be relatively small. At 25° C, however, growth was retarded.

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