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ANNUAL VARIATIONS IN VERTICAL DISTRIBUTION AND DENSITY OF *BATHYPOREIA PILOSA* LINDSTRÖM AND *BATHYPOREIA SARSI* WATKIN AT JULEBÆK (NORTH-SEALAND, DENMARK)

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ABSTRACT

The annual variations in vertical distribution and density of *Bathyporeia pilosa* and *B. sarsi* were investigated on a locality in the near tideless inner Danish waters. The main trends in distribution could be explained by variations in water movement, temperature, desiccation and oxygen content of the interstitial water. Other factors, including permanent water cover and rather low and changing salinities seemed to be of minor importance.

Predation was probably the major source of mortality. Mortality mainly took place in the reproductive period.

INTRODUCTION

Several investigations have shown that *Bathyporeia pilosa* and *Bathyporeia sarsi* and, frequently, other members of the genus commonly occur singly or together in the intertidal zone of exposed sandy beaches of western Europe (Salvat 1967, Ladle 1975, Khayrallah & Jones 1980a, and other papers quoted therein). It is further known that the rise and fall of the tide exerts a great direct and indirect influence on their zonation on the shore (Salvat 1967).

B. pilosa and *B. sarsi* are often found in shallow sandy beaches in inner Danish waters, and *B. pilosa* even extends into the Baltic proper (Persson 1982). Due to the essentially tideless nature of these waters, the two species are forced to live in sediments which nearly always are covered by water; hence living conditions differ very much from those of an intertidal zone.

Despite the common occurrence of the two species in inner Danish waters there are no previous accounts of their vertical zonation and the factors that control it. The present paper reports on the annual variations in vertical zonation and density of *B. pilosa* and *B. sarsi* in the Julebæk beach on the coast of North-Sealand and the controlling factors.

MATERIALS AND METHODS

On the north-facing Julebæk beach, situated about 4 km west of Helsingør, a transect was established and sampled at close intervals for more than a year. The transect was nearly at right angles to the shore line. Depending on weather conditions, between 16 and 20 stations were measured out at 5 m intervals from a given fixpoint on the shore and marked with tonkin rods (Fig. 2). The water level relative to the fixpoint was then measured and the water depth at each station recorded. From these data the beach profile relative to the fixpoint was determined.

At each station five bottom samples were taken at distances less than a metre from the tonkin rod. The bottom sampler was a hand-operated core sampler covering an area of 80 cm^2 (see Kanneworff & Nicolaisen 1983). The animals were transported alive to the laboratory and killed by formaldehyde immediately before examination.

Primarily, identification was based on Watkin (1939a). We found, however, that the two species more easily could be distinguished by the colour of the contents of the hepatopancreatic caecae which was clearly visible through the cuticle of both living and newly killed animals. In *B. pilosa* the colour was brownish whereas it was bright green in *B. sarsi*. In addition, *B. pilosa* has a red pigmentation on the abdomen which is not present in *B. sarsi*.

On each sampling occasion the water temperature was measured at the inner and outer parts of the profile.

At one occasion grain size analyses were carried out by means of standard dry sieving techniques.

PHYSICAL AND CHEMICAL FACTORS

Salinity

The surface salinity of the Øresund is a function of the water interchange between the North Sea and the Baltic. As a result of the freshwater run-off to the Baltic the surface current is normally out-going in the straits of Denmark. In the Øresund, the depth of the out-going surface layer is normally between 6 and 10 m and the salinity is in the range 8-12‰. Below the homogeneous surface layer the water normally moves in the opposite direction. The salinity increases regularly with depth to reach a maximum of more than 30‰ below 20 m depth. However, the direction of the surface current is often reversed mainly due to the action of westerly winds. Incomming saline water from the Kattegat then increases the surface salinity, often to more than 20‰.

The surface salinity of the Øresund was recorded daily from the Lappegrund light vessel at a position 2 km off the Julebæk locality. The lowest salinity recorded was about 8 ‰ which occur during short periods throughout the year. This is the salinity of the Baltic water when it enters the Øresund. Generally, each low salinity period lasted a few days but it occasionally lasted a couple of weeks. These periods alternated with periods with higher and more varying salinities. In the winter the surface salinity frequently was above 20 ‰ (max. about 25 ‰). In the months May-October it was seldom more than 15 ‰.

Temperature

Our temperature measurements on the inside and the outside of the sand bar are shown in Fig. 1, together with the surface temperatures measured at the Lappegrund light vessel.

From April to September, the temperature on the inside of the sand bar was always above the temperature at the Lappegrund, often by as much as 10°C (average about 5 °C). From September through October it was fairly close to the Lappegrund temperature whereas it often was below by as much as 3-4°C (close to freezing) in the winter months.

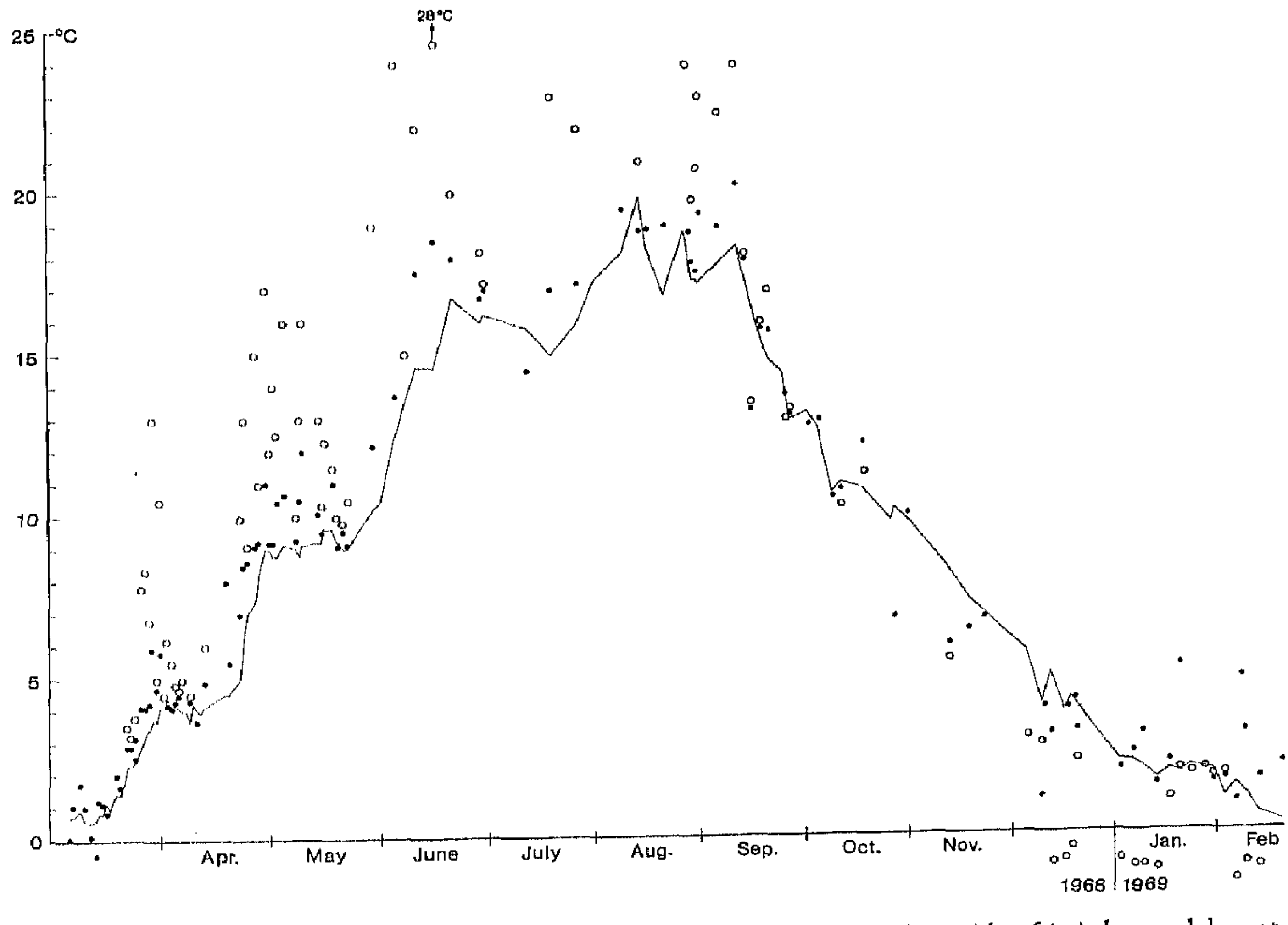


FIG. 1. Annual variations in temperature measured inside of (○) and outside of (●) the sand-bar at Julebæk. The fully drawn curve shows the surface temperatures at the Lappegrund light-vessel.

From early spring through the summer the temperatures measured on the outside of the sand bar were generally also above the Lappegrund temperatures, but the deviations were much smaller (average about 1 °C). In the autumn they were close to the Lappegrund temperatures whereas they were close to or above the Lappegrund temperatures in winter (by as much as 2-3 °C).

Hence, from early spring through the summer the temperature on the inside of the sand bar was above the temperature on the outside of the bar, the average difference being about 4 °C. In winter this trend was reversed, as the temperature on the inside of the bar was below the temperature on the outside of the bar by 3-4 °C on the average.

Wave exposure

As the Julebæk locality faces north it is sheltered from the often strong westerly winds which prevails in the area. Especially during autumn and winter strong winds from the north-west and north, however, can cause pronounced alterations of the beach profile.

Water level

In the inner Danish water the tidal amplitude, which is only about 15 cm, is superimposed on larger irregular variations due to winds, air pressure variations and variable run-off from the Baltic.

The water level off Hornbæk (10 km north of Julebæk) was monitored from 1891 to 1925 by the Danish Meteorological Institute. From these observations the following information is obtained.

The mean monthly water level is lowest in March-May (about 10 cm below the mean annual level). From then on, the mean monthly water level increases steadily, and the highest level is reached in July-September (about 10 cm above mean annual level). The mean monthly water level then decreases until March the following year.

The short-term variations in water level may, as mentioned above, be much larger. The highest and lowest water levels recorded were about +175 cm and −125 cm, respectively. They occur in winter time and are of short duration (less than 2 hr). The short-term variations are much lower and of shorter duration in the months June-September than in the rest of the year. This is especially true for the low water levels. In the summer period low waters of 40 cm seldom last more than an hour or less and never more than a few hours. Outside the summer period low waters of 40 cm often last a day and may occasionally last a week. High waters generally last longer than low waters, but they are of less consequence to sediment-living animals.

Annual variations in beach profile and sediment factors

According to Ingle (1966) there is a lack of a standardized terminology associated with the beach environment. Our use of terms is broadly similar to that of Ingle, but topographic differences necessitate some modifications. The concavity immediately seaward of the shoreline we term the trough or the runnel if the width is only a few metres. The bar is the remainder of the profile seaward of the trough. The breaker zone is situated on the seaward face of the bar. The area between the breaker zone and the bar top we term the swash zone.

Fig. 2 shows the changes of the profile throughout the period of study.

Between 7 and 30 October 1967, the changes of the profile were relatively minor; consisting mainly of a smoothening-out of the bar. On 13 December the shape of the profile had changed considerably, the accretion being caused by a strong wind from the north (7-8 Beaufort), associated with high water (90 cm above normal). From December through February the following year great changes continued to take place shoreward of station XIV and especially on the bar. Seaward of station XIV, however, changes were insignificant. Through the spring, summer and autumn the changes in relief were small compared to the winter. Due to the slow shoreward movement of the bar the trough gradually became narrower until it was reduced to a runnel in the autumn. On most sampling days after December 1967 the highest part of the bar was above the water level. This was because we chose calm days when possible. However, the bar top must have been frequently covered by water as living animals nearly always were present. Throughout most of 1968, the air-exposed top was situated immediately seaward of the trough. The height of this part of the bar diminished gradually through 1968 until it was nearly leveled out in late autumn. Generally, the breaker zone was located around station XIV. The exact position varied with the weather conditions.

The transects from 1969, 1970 and 1973 show that the profile changed much after 1968.

From April through October, the sediment of the trough was oxygen-deficient as shown by the presence of black sulphide layers a few mm below the surface. Judged from the absence of black sulphide layers the sediment of the higher parts of the bar was oxidized to several cm depth. At the deep end of the profile the redox conditions were intermediate between those of the trough and those of the higher parts of the bar.

On one occasion we determined the grain size distribution at all stations sampled. In the trough the median grain size was about 170 μm. On the top of the bar the median grain size was about 185 μm. Seaward of the bar top the median grain size decreased regularly with water depth and was about 125 μm at station XVI. The sediment was well sorted, especially on the bar top.

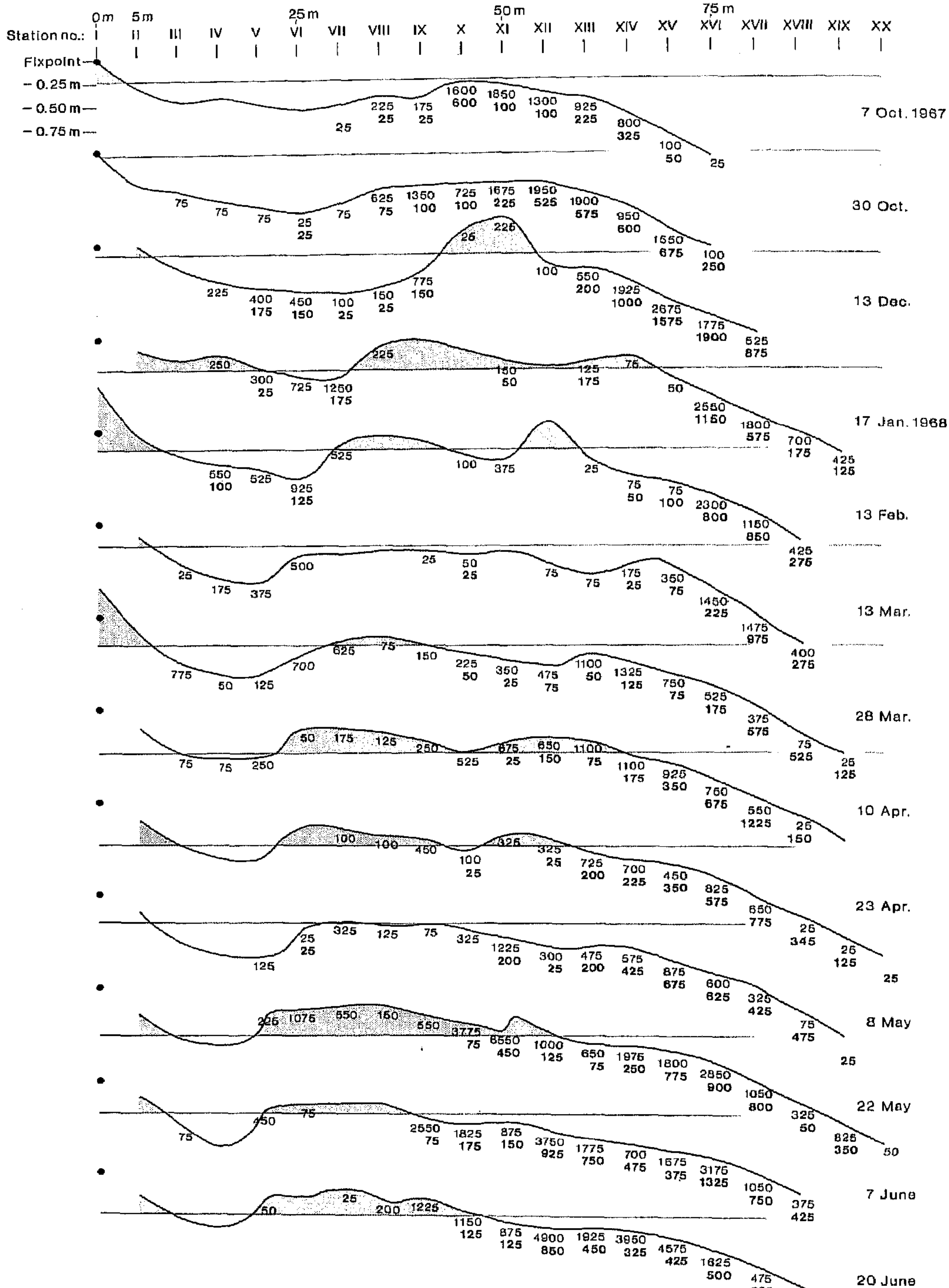
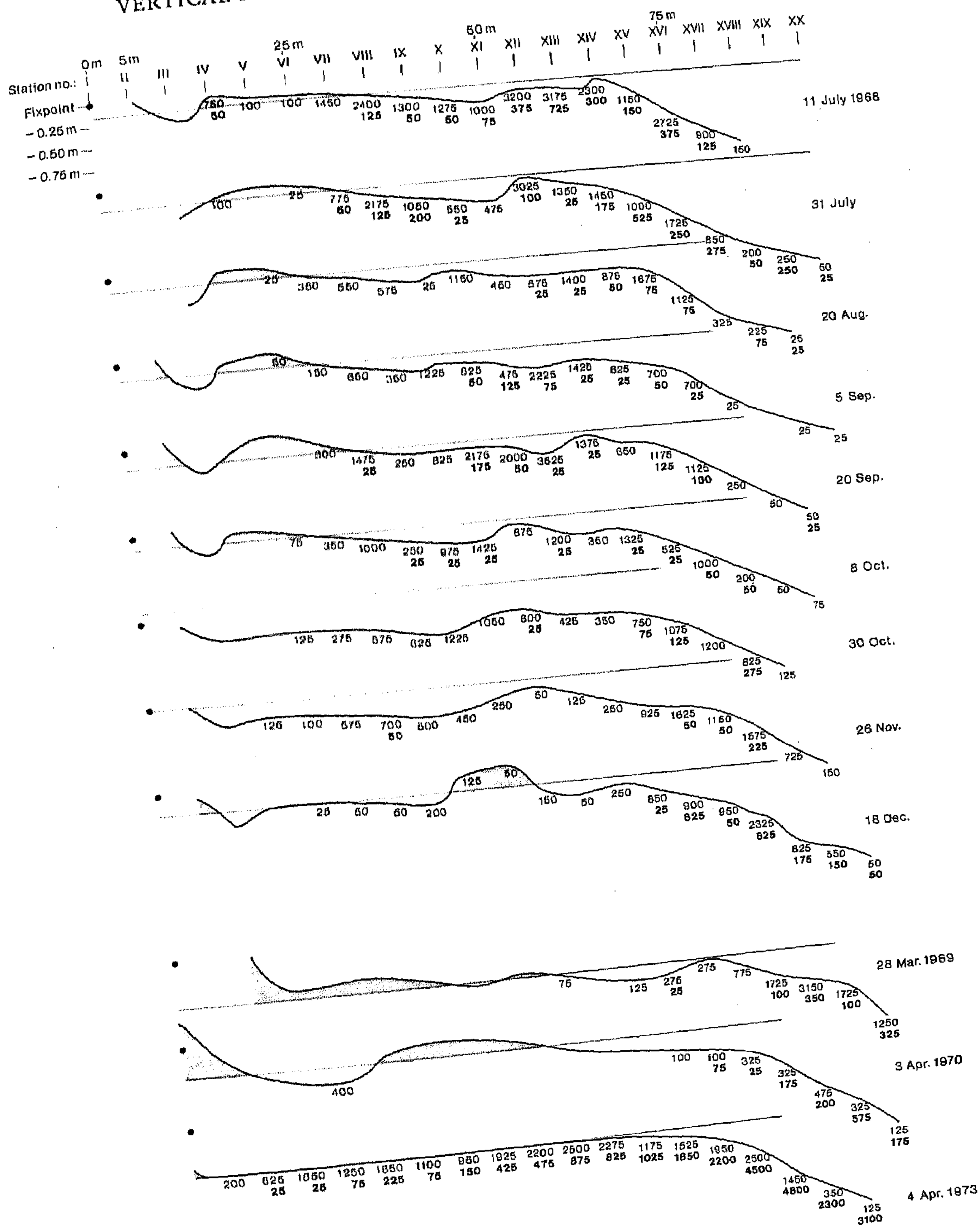


FIG. 2. The beach profiles and water levels together with densities (number/m^2) of *Bathyporeia pilosa* (light numerals) and *B. sarsi* (bold numerals). The parts of the profiles which were above the water level are shaded.


0 m
5 m
25 m
50 m
75 m
Station no.:
II III IV V VI VII VIII IX X XI XII XIII XIV XV XVI XVII XVIII XIX XX
Fixpoint
– 0.25 m
– 0.50 m
– 0.75 m
11 July 1968
31 July
20 Aug.
5 Sep.
20 Sep.
8 Oct.
30 Oct.
26 Nov.
18 Dec.
28 Mar. 1969
3 Apr. 1970
4 Apr. 1973

ANNUAL CHANGES IN DISTRIBUTION AND ABUNDANCE OF ANIMALS

Bathyporeia pilosa (Fig.2)

In early October 1967, *B. pilosa* were found on the top and the seaward side of the bar, whereas none were found in the trough. In late October they appeared in the trough, but apart from that the distribution had remained nearly unchanged. In December, following a period of heavy accretion, the top of the bar was exposed to the air and here only a few animals were found. On the seaward face of the bar the highest densities now occurred in deeper water, viz. at stations XIV to XVI. In the trough the density had increased strongly. From January to 13 March, the pattern of distribution changed little. On the top of the bar only few animals were found. The highest densities were found at stations XVI to XVII. The densities in the trough were comparable to those found in December. On 28 March the pattern had changed considerably. The density had increased significantly on the top of the bar, and the highest densities occurred closer to the shore (stations XIII to XIV) than on the previous three sampling occasions. The density in the trough was comparable to that of a fortnight earlier. The distribution found on 10 April resembled that found on 28 March. On 23 April and 8 May no animals were found in the trough. The distributions on the top and seaward face of the bar resembled those found on 28 March and 10 April. On 22 May newly hatched juveniles had appeared. The distribution pattern resembled that found on 23 April and 8 May. The relatively high densities found on the exposed top of the bar are noteworthy. The distribution patterns from 7 June to 26 November remained much the same. However, on the exposed top of the bar few animals were found. No animals were found in the runnel. The large majority of animals were found from immediately seaward of the exposed top to the breaker zone. On 18 December the distribution had shifted seaward and the densities on the highest parts of the bar had decreased significantly. On 28 March 1969 it was found that the seaward move of the population had continued after 18 December.

When comparing the distribution patterns from around the beginning of April in 1968, 1969, and 1970 and 1973 it appears that the shoreward move began earlier in 1968 and 1973 than in 1969 and 1970.

The total number of individuals of *B. pilosa* collected on a given sampling day (shown in Fig. 3) is taken as a measure of the true population size.

The slowly decreasing trend in total numbers between October 1967 and early May 1968 was not apparant in the data from October 1968 to March 1969, but this may be due to the uncertainties in sampling. It is safe to conclude, however, that outside the period May to September, the mortality was very small. From May to September the mortality was high as, despite a large pro-

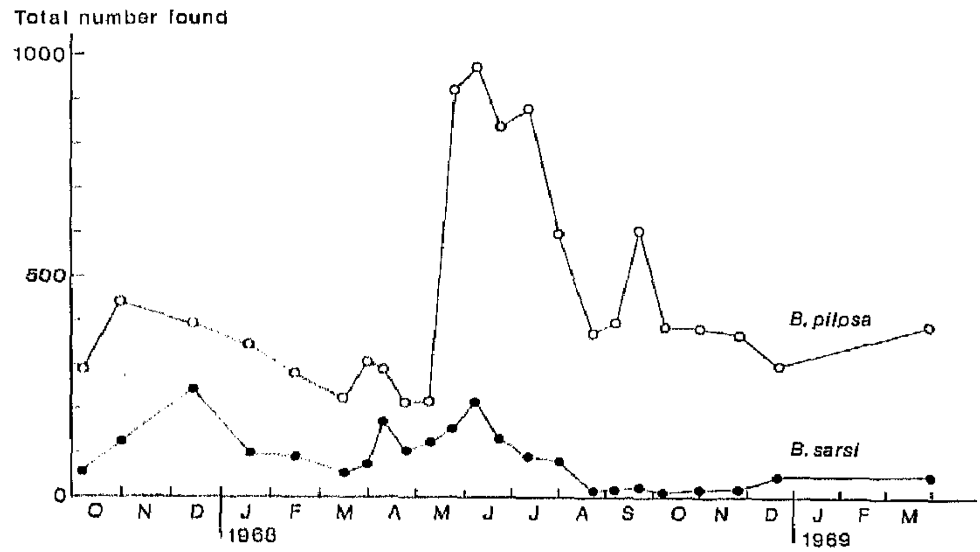


FIG. 3. The total numbers of *Bathyporeia pilosa* and *B. sarsi* collected on each sampling occasion.

duction of juveniles in that period, the total numbers found in October-November 1968 were comparable to those found in March-April 1968.

From the total numbers found around the beginning of April in 1968, 1969, 1970 and 1973, it appears that the population size may change from year to year. It seems to have been lowest in April 1970, intermediate in 1968 and 1969 and highest in 1973.

There were no clear trends for animals belonging to different size groups, development stages or sex to be differently distributed along the sampling profile.

The variations in density of *B. pilosa* did not in any obvious way correlate with the minor variations in topography of the bar.

Bathyporeia sarsi (Fig. 2)

In general, the annual changes in distribution pattern and population size followed the same trends as for *B. pilosa*. There were, however, some important differences.

As for *B. pilosa*, the *B. sarsi* population shifted seawards from January to early March. *B. sarsi* disappeared completely from the though in the course of the winter. The shoreward move of *B. sarsi* apparently began some weeks later than that of *B. pilosa*. The main difference in distribution pattern between the two species throughout the remainder of 1968 was that *B. sarsi* was comparatively rarer than *B. pilosa* on the higher parts of the bar, being almost totally absent on the air-exposed top.

A comparison of the distribution patterns from around the beginning of April in 1968, 1969, 1970 and 1973 shows, as for *B. pilosa*, that the shoreward move in spring of *B. sarsi* seems to have begun earlier in 1968 and 1973 than in 1969 and 1970.

Due to the lower numbers present the relative variations in total numbers of *B. sarsi* due to the sampling uncertainties are much larger than for *B. pilosa*, and tend to obscure the annual trends in population size changes (Fig. 3). It seems, however, that as a consequence of a partly unsuccessful breeding season, the total numbers of *B. sarsi* after September 1968 were lower than those preceding May 1968. It is also evident that throughout the main period of investigation the population size of *B. sarsi* was lower than that of *B. pilosa*.

Around the beginning of April the population size of *B. sarsi* was at about the same level in 1968, 1969 and 1970, whereas it was considerably higher in 1973.

As was found for *B. pilosa*, there were no clear trends for animals belonging to different size groups, development stages or sex to be differently distributed along the sampling profile.

As with *B. pilosa*, the density variations of *B. sarsi* did not correlate with the minor variations in topography of the bar.

Summary of the main trends in distribution and abundance of Bathyporeia pilosa and B. sarsi

In general, the distribution of the two species overlapped throughout the period of investigation.

From early spring to autumn (1967 and 1968) both species were mainly found on the highest parts of the bar, i.e. between the top and the breaker zone, and they were absent from the trough (runnel). On the exposed parts of the bar, only *B. pilosa* was found in significant numbers.

B. pilosa was commonly found in the trough from late October to mid April. *B. sarsi* was found in the trough from December to February. In the winter both species were present in low numbers on the top of the bar. The main part of the populations of both species had been displaced towards the deep end of the transect in the early part of the winter and remained there until the shoreward move started around 1st April (*B. sarsi* some weeks later than *B. pilosa*).

Following the appearance of newly hatched juveniles in the middle of May 1968, the population sizes started to increase, with that of *B. pilosa* being much more pronounced than that of *B. sarsi*. In 1968 the population size of *B. pilosa* was about the same in early spring and late autumn. Due to a less successful breeding season the population size of *B. sarsi* was lower in late autumn than in early spring. The mortality of both species was high in the breeding period and low outside this period.

In 1967 and 1968 the population size of *B. pilosa* was constantly higher than that of *B. sarsi*.

The sampling results from 1969, 1970 and 1973 indicate that there was some year-to-year variation in the absolute and relative population sizes of the two species.

Size, reproductive stage or sex did not significantly influence the distribution of the two species along the profile.

The distribution of the two species on the bar did not correlate with the minor varaiations in topography of the bar.

DISCUSSION

The main trends in distribution of *B. pilosa* and *B. sarsi* along the Julebæk transect can be explained by the interplay of the following factors: Water movement, temperature, desiccation and oxygen content of the interstitial water.

The water input to the interstices of sediments has been shown to be propelled by swash energy and the velocity fields associated with waves (Riedl 1971, Riedl, Huang & Machan 1972). The effect of the wave pump increases with wave hight, porosity of sediment and decreasing water depth. The effect is strongest under breaking waves. The depth of the redox discontinuity layer, and hence the thickness of the oxidized surface sediment, correlates with the water movement at the sediment surface. Relocation of the sediment increases with degree of water movement while the deposition of light organic particles from the water column decreases. Microbial activity in sediments increases with temperature (Fenchel 1969). The strong water movement between the breaker zone and the bar top at Julebæk causes high water input into the sediment and a low organic content. Consequently, the oxygen content of the interstitial water is high, even at summer temperatures. Relocation of sediment is high in this area, and drainage of interstitial water occurs regularly at the highest parts. The low water movement in the trough causes low water input to the sediment and a rather high organic content. Therefore, at higher temperatures the sediment is reduced immediately below the surface. In winter, the sediment is oxidized to several cm depth due to low temperatures and a somewhat larger water movement. Relocation of sediment is relatively low in the trough. The stations seaward of the breaker zone are in these respects intermediate between those on the higher parts of the bar and those in the trough.

B. pilosa and *B. sarsi* are very well adapted to the changing conditions in the sediments of exposed beaches. They have no need for a burrow with connection to the sediment surface as they obtain their supply of oxygen from the interstitial water and their food from sand grains which they efficiently clean for adhering organic matter. At higher temperatures they dig fast enough to keep pace with an eventual erosion or accretion of the sediment (Nicolaisen & Kanneworff 1969). However, we have frequently noted that the animals become very sluggish when the temperature is close to 0 °C. In winter, this may cause many animals to leave the bottom by accident when erosion takes place.

As the demand for oxygen of *Bathyporeia* increases strongly with temperature (Fish & Preece 1970b, and own unpublished results) the oxygen content of the interstitial water is especially critical in summer. As *B. pilosa* always was present on the air-exposed parts of the Julebæk profile in summer the species must be tolerant to water drainage from the sediment. This agrees with the experimental findings of Preece (1971b). The absence of *B. sarsi* from these parts of the bar is most likely due to a lesser tolerance to this factor, although this has not been tested experimentally.

Field investigations performed by Khayrallah & Jones (1980a) showed that *B. pilosa* rarely occurs in sediments with a median particle diameter outside the range of 150-220 μm or with a silt and clay content greater than 2 %. Animal density was not correlated with median particle diameter or silt and clay content within these ranges. Judging from these results, the small variations in grain size composition on the main part of the Julebæk profile are unlikely to have influenced the distribution of *B. pilosa* and *B. sarsi* significantly. In this context it is noteworthy that in winter high densities were found at the deepest stations where the median particle diameter was lowest.

B. pilosa is very tolerant to low salinities. Thus, it is found in the Bay of Finland at salinities of about 4.5 ‰ (Segerstråle 1943) and the experimental studies of Preece (1970) also showed a large tolerance to low salinities. To our knowledge, *B. sarsi* has not been reported from the Baltic proper. Furthermore, the surface salinities of the northern Øresund seems to be close to the lower limit of the salinity tolerance of this species (unpublished results). It therefore seems possible that the limited breeding success of *B. sarsi* in summer at Julebæk may, at least in part, be due to low salinities in combination with high temperatures. It seems likely, however, that the main source of mortality is predation, mainly by juvenile flounder and plaice which are numerous at Julebæk from July to October. At Barsebäck on the Swedish coast of the Øresund we have frequently found that 0-group flounders in July have their stomachs completely filled with *B. pilosa*, which is the only *Bathyporeia* species present at this locality. Later on they change diet. This agrees with the findings of Sasdy (1972, quoted in Persson 1982). It is noteworthy that at Julebæk mortality mainly takes place in the reproductive period.

The nocturnal swimming activities of *Bathyporeia* are partly associated with reproductive activity (Watkin 1939b, Colman & Segrove 1955b, Fincham 1970a,b, Preece 1971a), but they also allow the animals to seek and locate more favourable living conditions. The response of *B. pilosa* to variations in current speed have been investigated by Khayrallah & Jones (1980a). They found that with increasing current speed active swimming decreased and passive drifting increased. At current speeds above 2.5 cm/sec most of the animals drifted passively. Reduced swimming activity of *B. pilosa* at low temperatures was demonstrated by Preece (1971a).

The information on the behaviour of *Bathyporeia* in the water column is important for understanding the distribution on the beach. When a bore is formed after collapse of a breaker there is a net onshore movement of water across the surf zone (Ingle 1966). Part of this water surplus moves seaward toward the breaker zone as a bottom return-current. The movements of stained sand grains showed that the bottom water tended to move toward a breaker zone from both sides. Passive drifting will, therefore, tend to concentrate the animals in the surf and breaker zone. When the temperature is close to 0 °C digging-in can only be accomplished in the relatively calm water of the trough and at the deep end of the profile. The somewhat higher temperatures at the deep end of the profile increases the animals' ability to dig in.

Based on the above information we interprete the distribution patterns of *B. pilosa* and *B. sarsi* at Julebæk as follows:

The increase in temperature around the beginning of April leads to an increase in swimming activity and digging ability of the animals, and both species are moved by the near-bottom currents toward the breaker and surf zones where the temperatures is higher. This move contributes significantly to an important early rise in rate of various life processes (e.g. maturation of gonads, feeding and growth). During summer the temperature and oxygen conditions limit the animals to the breaker and surf zones. The mortality during summer is mainly due to predation, although the temperature and salinity conditions together with desiccation on the top of the bar may be partly responsible in the case of *B. sarsi*. In winter the animals disappear from the high parts of the bar, due to the combined effects of low temperature and increased relocation of sediment by increased water movement. The animals are carried into the water column and, due to their sluggishness at low temperatures, they are only able to rebury in the calmer areas of the trough and, mainly, the stations at the seaward end of the profile. Mortality is low at this time of year due to the absence of predators and to low temperatures.

On the nearly tideless Julebæk beach the distributions of *B. pilosa* and *B. sarsi* are very similar, the main difference being the absence of *B. sarsi* from the air-exposed parts of the bar. The populations of both species are essentially limited to the stations which are permanently covered by water. This is in marked contrast to the distribution of the two species on beaches of Western Europe with pronounced tides, where they occur in the middle and upper parts of the tidal zone (Fish & Preece 1970a, Colman & Segrove 1955a, Ladle 1975, Vader 1965, Holme 1949, Watkin 1942, Salvat 1967). When the two species occur together in significant densities (Salvat 1967, Vader 1965) the distribution of *B. pilosa* extends to a higher tidal level than that of *B. sarsi*. This supports our assumption that *B. pilosa* is more tolerant to environmental stress than *B. sarsi*.

The distributions of the two species on tidal beaches have been correlated with the variation in several sediment properties, including those used in the above discussion (Salvat 1967, Khayrallah & Jones 1980a, Khayrallah & Jones 1980b), but the major controlling factors may very well differ with locality.

Seasonal changes in distribution of *Bathyporeia* have been described earlier. At La Vigne (southern French Atlantic coast) Salvat (1967) found a seaward displacement in summer of the upper limit of distribution of *B. pilosa*, and assumed it to be caused by high temperatures. A seaward displacement in summer of *B. pilosa* was also found by Fish & Preece (1970a) at the coast of Wales. Persson (1982), working at the Swedish coast of the Baltic, found a seaward move in autumn of *B. pilosa* and assumed it to be caused by an active search for better feeding conditions. At the coast of Northumberland Ladle (1975) found that the population of *B. sarsi* was displaced seawards in April-May. The lack of a common trend in annual distribution changes indicates that the controlling factors operate differently at the various localities.

The maximum densities of *B. pilosa* at Julebæk are within the range of maximum densities previously reported from the tidal zone of western Europe (Salvat 1967). From the Baltic proper densities as high as 19000 *B. pilosa* per m^2 have been reported (Persson 1982). The highest densities of *B. sarsi* at Julebæk (4 April 1973) are, to our knowledge, the highest densities reported for this species. Thus, on the basis of population densities there is nothing to suggest that the low salinities and the near absence of tides at Julebæk are unfavourable to the two species. This invalidates the assumption of Salvat (1967) that *B. pilosa* is exclusively an intertidal species.

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