# THE VERTICAL MIGRATION BEHAVIOUR OF ESTUARINE PLANKTON

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## ABSTRACT

A series of investigations on the vertical migration behaviour of estuarine zooplankton have been carried out in recent years. Several of these investigations have been carried out in collaboration with other zoologists and the detailed findings are being published separately. The work is reviewed here and an attempt is made to draw some general conclusions regarding the behaviour patterns observed. Attention is concentrated particularly on the behaviour of the copepod *Pseudodiaptomus*. Aspects investigated include behaviour in the field under natural conditions, light reactions and swimming speeds in the laboratory, reactions to layers of low salinity water, the role of endogenous rhythm in this behaviour and the significance of these behaviour patterns to the organisms.

Vertical migration behaviour occurs in almost all groups of animals represented in plankton. This behaviour is particularly well-marked in the plankton of estuaries. Some of the patterns observed seem to vary somewhat from those found in the sea or lakes. If plankton samples are taken during the hours of daylight in a South African estuary, very little zooplankton is obtained. If samples are taken at night much greater numbers of specimens are obtained and the composition of the plankton is found to differ markedly from that found during the day. Species which dominate the plankton during the day appear in small numbers in relation to other species at night and many species appear at night which do not occur at all during the day (Grindley 1970).

A series of studies has been carried out in recent years, some in collaboration with other biologists including Mr. A. Cannone, Miss R. Donaldson, Mr. A. Fricke, Mr. R. Hart, Dr. M. Jarvis, Mr. B. Lane and Mr. T. Wooldridge. Details of these investigations are being published separately but it seems appropriate to review this work here. In particular it appears desirable to try to draw some general conclusions from these various investigations and to discuss the possible significance of these behaviour patterns.

## PROCEDURE

Various sampling methods were used during these investigations including plankton nets, a hand-operated semi-rotary plankton pump, an engine-driven centrifugal plankton pump, van Dorn plankton samplers (6 litres and 2 litres) and a Clarke-Bumpus plankton sampler.

Experiments were carried out in the laboratory using various troughs and tubes and artificial sources of illumination, observations were made of the behaviour of plankton under natural diurnal light fluctuations and in constant darkness and constant light in controlled laboratories. Experiments were carried out in the field in glass tubes immersed in estuaries under natural light conditions, and with the apparatus devised specially to investigate the effects of salinity stratification in estuaries (Grindley 1964) under various conditions. Light intensities were determined by photometer including a submarine photometer of the Jerlov type. Hydrological and other environmental conditions were determined using standard oceanographic techniques.

Samples of zooplankton obtained usually included far too many organisms to allow counting of whole samples. Sub-samples were normally taken using a pipette technique perfected by Prof. Raymont and his co-workers at Southampton University (Conover 1957; Raymont & Carrie 1964). Counting was carried out under a binocular stereomicroscope in a small perspex counting tray divided into squares.

## RESULTS

### *Observations in Southampton water*

A study was made of the vertical distribution of estuarine zooplankton in Southampton Water during the day and night by pump sampling. Samples were taken at a series of depths from the surface to the bottom at three stations in the estuary. Hydrological conditions at the three stations varied from relatively uniform conditions at Calshot near the mouth of Southampton water to strong thermo-haline stratification at Eling near the top of the estuary.

Vertical migration was found to occur in a large number of different species including Copepoda and the larvae of various invertebrates. Some species provided inconclusive results and the Ctenophore *Pleurobrachia pileus* and Foraminifera apparently did not migrate. *Pleurobrachia* remained evenly distributed through the water column and Foraminifera remained near the bottom during both day and night. Experiments carried out in the field with the special apparatus described elsewhere (Grindley 1964) confirmed that the difference in vertical distribution of several *Acartia* species and the harpacticoid *Euterpina acutifrons,* were due to active migration behaviour.

Sampling at Eling when there was a difference between surface and bottom salinity of 15°/₀₀, with relatively low salinity water on the surface, indicated that the migrations of *Acartia bifilosa, Acartia discaudata, Centropages hamatus,* and various larvae were completely or almost completely inhibited while other species were affected to lesser degrees. The species that did apparently migrate up in considerable numbers into low salinity water included *Eurytemora hirundoides,* which is known to be euryhaline.

In general, the patterns of vertical distribution in Southampton water did not indicate a distinct movement of the whole plankton population, but rather a tendency of part of the population to spread towards the surface at night. Several species appeared to come up out of the bottom mud only at night, including Cumacea, Mysidacea, and crab megalopae. The total number of specimens of *Acartia* spp., gastropod larvae and lamellibranch larvae obtained in the water column was much greater at night, suggesting that a large part of these populations may rest on the bottom during the hours of daylight.

### *Observations in South African estuaries*

Studies were made of the circadian fluctuations of zooplankton in four different estuaries and lagoons in South Africa. Sampling was carried out in the Klein River lagoon at Hermanus (a closed estuary), at Schrywershoek at the southern end of the Langebaan lagoon (a hypersaline lagoon), at Langebaan near the mouth of the Langebaan lagoon (strongly tidal lagoon) and in the Swartkops estuary at Port Elizabeth (a tidal estuary). In each example plankton samples were taken and environmental conditions recorded at the surface every hour over a 24-hour period.

Vertical migration appeared to occur in almost all of the species of zooplankton observed. No evidence of migration was detected in the case of cirripede nauplii, copepod nauplii, and the isopod *Paridotea ungulata.* Differences were observed between the patterns of migration of different species. *Pseudodiaptomus hessei* appeared at the surface in large numbers only during the night whereas *Paracartia africana* also appeared in fairly large numbers during the day. Some species, including Cumacea, Ostracoda and decapod 'mysis' larvae, only appeared at the surface for part of the night. Nematodes started to appear at the surface during the afternoon.

Observations on the behaviour of adult males and females and the five copepodite stages of *Pseudodiaptomus hessei* indicated that the adults migrated more strongly. In *Paracartia africana* higher proportions of adult males and females migrated than did copepodite stages. In the mysids *Rhophalopthalamus terranatalis* and *Mesopodopsis slabberi* the adults and juveniles responded differently to moonlight.The adults were found to leave the surface when exposed to full moonlight whereas the juveniles still appeared at the surface.

Most species appeared at the surface during the night for a long period and there was no good evidence of any species migrating only at flood tide. In observations in the Swartkops estuary there was some evidence of higher proportions of certain species at the surface during flood tides but this effect appeared to be subsidiary to the main diurnal migration pattern. The patterns of vertical migration of most species observed in these four estuaries differed from the type usually described. The plankton only rose *after* dark, reached peak concentrations at the surface at some time during the night and descended *before* dawn.

*Observations at different levels*

Observations of vertical migration in the Klein River lagoon at Hermanus were made at three different levels during a 24-hour period by the author and Mr. A.J. Cannone then at the University of Cape Town. Sampling was carried out at the surface and near the bottom using a plankton pump with two hoses fixed to a surface float and a plate on the bottom respectively. The bottom mud surface was sampled by means of an instrument in the form of a sledge which scraped a thin layer of bottom mud and detritus by means of an adjustable blade into a plastic bag.

Observations were concentrated on the planktonic copepod *Pseudodiaptomus hessei* which dominates most Cape estuaries (Grindley 1963). It was found that *P. Hessei* was most abundant at the surface during the night and that it occurred only rarely at the surface during the day. The numbers of *P. hessei* were also found to increase in the water near the bottom at sunset and in the early morning. The simultaneous increase in numbers of *P. hessei* in both surface and bottom waters suggests that there must be a contribution to the population in the water from bottom mud.The presence of a population of *P. hessei* in close association with loose detritus and mud on the bed of the estuary was established using the sledge sampler. Laboratory observations indicated that when exposed to light they settled on the bottom or even wriggled into loose sediments of detritus. The sampling of *P. hessei* in the bottom mud was not reliably quantitative, but there appeared to be some evidence of lower numbers in the mud during the night. It would thus appear that the numbers of animals in the water column are supplemented during the night by upward migration from the bottom mud.

*Observations in deep water*

*Pseudodiaptomus hessei* and other species of zooplankton in South African estuaries usually occur in water only a few meters or even less in depth. In Lake Sibayi in Tongaland, *P. hessei* occurs in water 40 m deep. Observations of the vertical migration behaviour of this species in deep water in Lake Sibayi were made in collaboration with Mr. R. Hart of Rhodes University and Mr. T. Wooldridge of the Port Elizabeth Museum with the assistance of several colleagues. A series of samples was taken, using a van Dorn sampler at 4 m intervals from surface to bottom on two occasions providing a picture of the pattern of migration over the 24-hour cycle. It was found that in deep water upward migration commenced early, probably in response to low light intensity at those depths. Large numbers only appeared at the surface during the hours of darkness. Downward migration commenced well before dawn and was thus apparently not in response to a light stimulus. They became concentrated towards the bottom during the day.

*Reactions to light in the laboratory*

Observations of the reactions to light of *Pseudodiaptomus hessei* were carried out in the laboratory in collaboration with Dr. M.J.F. Jarvis of the University of Cape Town. An apparatus was constructed in which the copepods were kept in a trough of water through which a beam of light of variable intensity could be directed. The Copepods were found to move actively away from the source of light when using various intensities of white light. Similar reactions were obtained using various wave-lengths of light and using polarized light.

*The speed of swimming of Pseudodiaptomus hessei*

Observations of the speed of swimming of *Pseudodiaptomus hessei* were made under laboratory conditions in collaboration with Miss. R. Donaldson of the University of Cape Town. Observations were carried out using a directional light source as a stimulus to cause horizontal swimming in a glass trough and upward and downward swimming in a vertical glass tube. It was found that in short bursts of movement in a horizontal direction a speed of 26,5 cm/s could be reached by adult females. Over longer distances speeds ranged from 1,5 cm/s to 9,0 cm/s for adult males and females. Distances were usually found to be covered in a series of bursts of swimming activity, with intermittent rests. Speed of vertical swimming of adult males and females was found to range from 0,25 to 4,5 cm/s in an upward direction. The speed of passive sinking of adult females was found to be 0,25 to 0,5 cm/s.

*Attempts to obtain vertical migration in the laboratory*

Attempts were made to obtain vertical migration behaviour in vertical glass tubes under laboratory conditions. Experiments were conducted under various conditions but, as has been found by many other biologists using other species, normal vertical migration behaviour did not occur in the laboratory. Despite various attempts to simulate natural light conditions employing graded diffusion screens and suspended pigments in the water column all that could be obtained was a rhythm of activity. It was found that during the night there was more activity and that rather more animals were found in the upper part of the tube than during the day. However, the bulk of the population under experimental conditions remained in the lower part of the tube. Observations were complicated by the tendency of *Pseudodiaptomus hessei* to settle on the glass sides of the experimental tubes.

*Experiments in the field*

Experiments were carried out with specimens of *Pseudodiaptomus hessei* in glass tubes immersed in the Langebaan lagoon and in the Milnerton estuary in collaboration with Mr. A. Fricke of the University of Cape Town. Because of the difficulties in obtaining a natural pattern of migration under laboratory conditions, it was necessary to resort to observations of the movements of *Pseudodiaptomus hessei* in glass tubes suspended in estuaries. In this way the natural gradient of light in the estuary is reproduced in the experimental tube. Under these conditions, a natural pattern of migration was obtained.

*Experiments using a new apparatus*

Although a glass tube suspended in an estuary allows the natural gradient of light to be reproduced, it does not allow for observations of the effects of salinity stratification on vertical migration behaviour. Field observations had indicated that layers of low salinity water might play a significant role by affecting the migration behaviour of estuarine zooplankton so it appeared desirable to devise an apparatus which would allow experiments on the effects of salinity stratification under field conditions. An apparatus was devised (Grindley 1964) consisting of a transparent perspex tube divided into chambers by sliding trapdoors, and with an injection mechanism for introducing living zooplankton. The apparatus is controlled from the surface by means of four cords. It is completely transparent and panels of fine nylon netting down one side allow free exchange of water so that any stratification is reproduced within the experimental tube.

In darkness and near dawn, the mean percentage of *Pseudodiaptomus hessei* appearing in the top chamber was highest (mean 53,8%) while in sunlight and shaded daylight, it was least (mean 23,9%). In the presence of a layer of low salinity water on the surface less than 1% of the *Pseudodiaptomus* appeared in the top chamber both in sunlight and in darkness. No consistent differences in the migration behaviour of the sexes or developmental stages of *Pseudodiaptomus* were apparent. Migration appeared to increase with decreasing light intensity. Upward migration appeared to be inhibited by too great a salinity gradient (salinity difference of more than about 10°/oo) while below this critical value migration was not inhibited (Grindley 1964).

*Observations of an endogenous rhythm of activity*

Observations were made over periods of several days on the rhythms of activity of *Pseudodiaptomus hessei* in vertical glass tubes in collaboration with Mr. A. Fricke of the University of Cape Town. Observations were made under three different conditions: with the tube in constant darkness, with the tube in constant light and with the tube out of doors in natural light but shielded with a diffusion screen in an attempt to simulate a natural light gradient.

Observations were made of the numbers of specimens appearing at various levels in the tubes at three-hour intervals throughout the period of observation. Observations in darkness were made with a shielded red light which was found not to disturb the copepods. A strong rhythm of activity was found to occur under natural light conditions; weak rhythms of activity were found to persist in constant darkness and constant light, suggesting that there is an endogenous rhythm of activity in *Pseudodiaptomus hessei*.

## DISCUSSION

Several features of the patterns of vertical migration observed in these studies appear to be of interest in relation to the biological mechanisms involved in this behaviour. In most species there was a clear difference between day and night behaviour as indicated by differences in vertical distribution. This was correlated with the periods of daylight and darkness. There were even differences between behaviour in darkness and in full moon-light in certain stages of some species. Most species in shallow water did not rise until *after* dark and remained in the surface water almost all night, descending again *before* dawn. In several species maximum numbers appeared at the surface near the middle of the night rather than at dusk or dawn. Even where observations were carried out in very deep water there was no evidence of downward scattering after dusk and although organisms started to rise from the bottom during the afternoon, their descent commenced in the early hours of the morning before there was any light stimulus for their downward migration.

A great many different patterns of vertical migration have been observed involving various zooplankton species elsewhere but several reviews of the subject, including Cushing (1951), Bainbridge (1961), Wynne-Edwards (1962), Raymont (1962) and Hutchinson (1967), have established a general pattern involving a late afternoon rise, a downward scattering during the period of total darkness followed by a temporary dawn rise before the descent to deep water for the day. These movements may be explained primarily as positive movements towards a source of low light intensity, scattering at night when there is no light stimulus and active downward swimming away from the high light intensity in daylight to the particular depth where they maintain their position.

The results obtained in the present work appear to require a modified explanation. The absence of sunset and dawn rises under most conditions and the rise to the surface of several species during complete darkness suggests that in these examples their behaviour may be controlled by an endogenous physiological rhythm and merely phased by changes in the environment. The experiments designed to investigate the existence of an endogenous rhythm of activity in *Pseudodiaptomus hessei* tend to support this view. However, there are many problems in interpreting work of this nature and the results obtained, although tending to indicate the existence of an endogenous rhythm of activity in *Pseudodiaptomus hessei,* cannot be regarded as conclusive at this stage. Harris (1963) has discussed the role of endogenous rhythms in vertical migration in other species.

The question of the timing of these migrations in relation to the tidal cycle and the period of darkness is very interesting. Zooplankton in estuaries tends to drift with tidal currents and so remain in water of similar salinity. The occurrence of vertical migration in estuaries however, means that the zooplankton may have to contend with relatively rapid changes of salinity. When the plankton rises it is liable to enter water of a salinity very different to that at the bottom or of that which it entered the previous night at a different phase of the tidal cycle. This could be avoided to some degree by the plankton rising at the same state of the tide and hence at a different time each night. Carriker (1951) has suggested that this occurs in the case of oyster larvae for example, and that by rising during the flood tide and sinking on the ebb they become dispersed upstream. The surge of plankton appearing on the flood tide in the observations at Swartkops might appear to be evidence of such behaviour but it appears to be subsidiary to the major circadian cycle of migration. It can also be explained by the tidal introduction of more abundant plankton from further down the estuary that had migrated to the surface earlier in response to the onset of darkness. This view is supported by the patterns of appearance of species at Schrywershoek, where both at high water and at low water there may be peak concentrations of certain organisms from further down and further up the lagoon respectively.

Diurnal vertical migration must be of profound significance to have evolved in almost all planktonic animals. Its survival value to estuarine planktonic animals is probably in helping to maintain their position in the estuary. Complex current patterns occur in estuaries where there are usually tidal oscillations and a net surface outflow of low-salinity water, and a compensating influx of saline water along the bottom which maintains the salinity gradient (Ketchum 1953).

By performing vertical migrations the planktonic animals drift alternately upstream and downstream tending to maintain their position in the estuary (Rogers 1940). In the case of river floods, however, the plankton would be in danger of being swept out to sea, if it rose to the surface. The inhibition of migration produced by a strong salinity discontinuity would however prevent this occurring. This may well be the reason for the evolution of this particular behaviour pattern. This behavioural mechanism would also reduce the coefficient of reproduction (Ketchum 1954), required to maintain a zooplankton population in an estuary, for a given exchange ratio of water escaping seaward at each tidal cycle.

The cumulative effect of tidal movements in the same direction during several successive nights could completely override the station-maintaining role of vertical migration behaviour in an estuary. There would appear to be an interesting field here for investigation by means of computer simulation models using tidal data which is in existence for several of our estuaries and comparing the results with existing plankton distribution patterns. The boundary between the true estuarine zooplankton and the tidally replaced neritic plankton should correspond to a particular value of tidal exchange ratio. Evidence that tidal replacement volume plays an important part in the biology of plankton in South African estuaries has recently been obtained in investigations being carried out in Richards Bay. It has been found that although large numbers of juvenile stages of *Pseudodiaptomus hessei* may be found in the middle regions of the estuary, high percentages of ovigerous females are only found in those parts of the system furthest from the sea. It would appear that it is only in these furthest reaches of the system that a significant percentage of the organisms are able to complete their life cycle without being displaced to sea where they cannot apparently survive.

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