A CONTRIBUTION TO THE BIOLOGY OF *PSEUDODIAPTOMUS HESSEI* (MRÁZEK) (COPEPODA: CALANOIDA) IN LAKE SIBAYA, SOUTH AFRICA

by

R. C. HART

Department of Zoology
Institute for Freshwater Studies
Rhodes University
Grahamstown
South Africa

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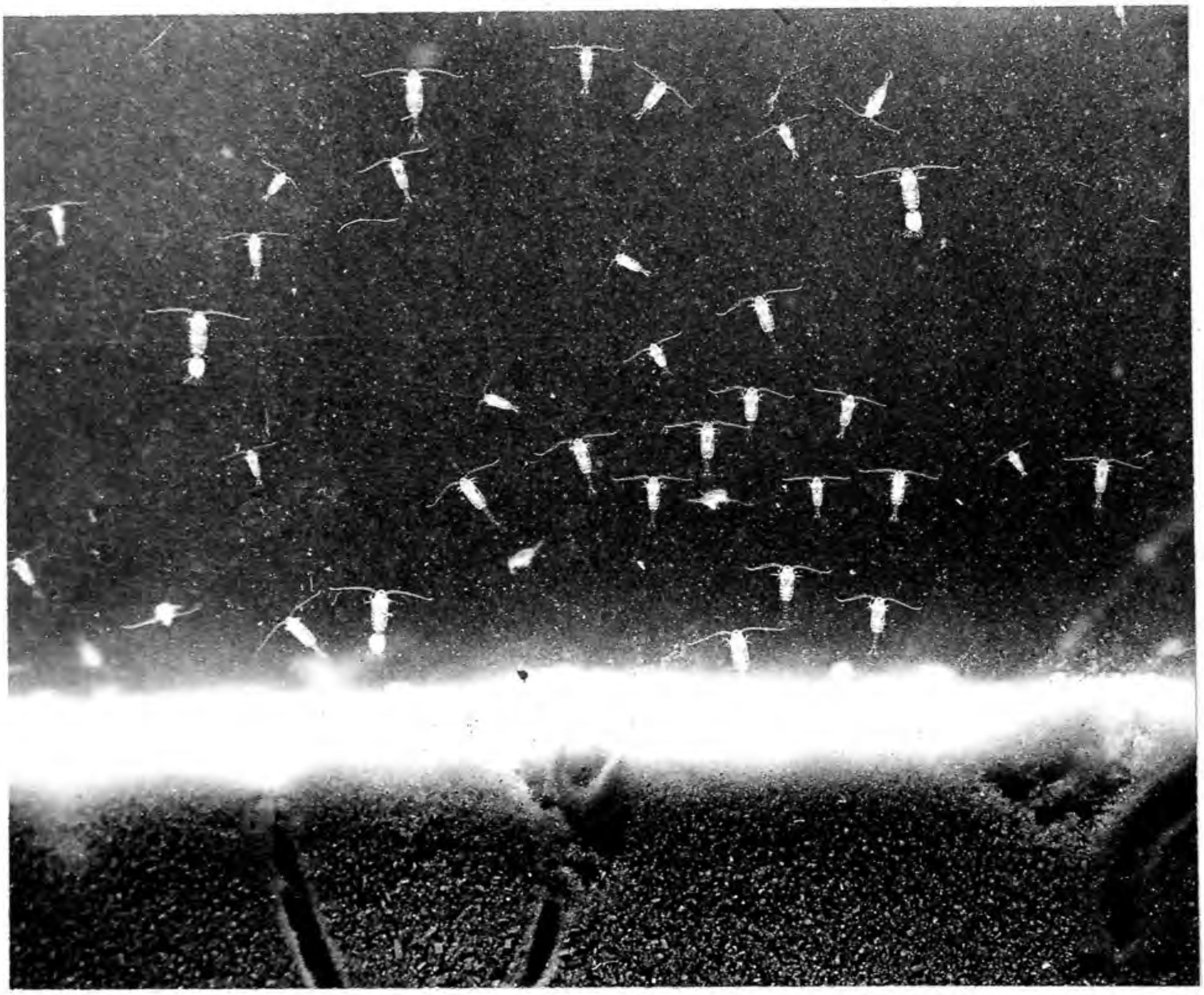

Frontispiece. Adult and copepodite stages of the calanoid copepod <u>Pseudodiaptomus hessei</u>. The photograph shows the calanoids at the interface of water and sand in a substrate bin. The flocculent sedimentary tripton is clearly visible as a whitish band. The majority of the calanoids are sedentary upon the vertical walls of the substrate bin.
Magnification approx. 8X

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RESUMÉ

Aspects of the biology of the calanoid copepod Pseudodiaptomus hessei are described, with particular reference to its vertical migratory behaviour.

The present investigations were carried out largely by means of Nansen-type plankton nets, but several new pieces of apparatus were developed and are described herein.

The daytime vertical distribution of P. hessei varies according to developmental stage and depth of water. In shallow areas of the lake the entire population is benthic or in very close association with the lake bed. In the deepest part of the lake (40m) the naupliar and early (i.e. C I - C III) copepodite stages are essentially pelagic, but the adult and late (i.e. C IV - C V) copepodite stages are predominantly benthic and may be quiescent or infaunal.

During the hours of darkness, the calanoids are distributed through the water column. The nauplii are consistently abundant in the surface waters but the distribution of the other stages is not regular. The distribution can be related to lunar intensity in many cases, with the post-naupliar stages frequently occurring deeper in the water column on bright moonlight nights and in the surface waters on overcast moonless nights.

The dusk ascent and dawn descent of the calanoids is clearly related to changes in light penetration in most individuals. The movements of a fraction of the adults occur in the apparent absence of adequate light cues. This behaviour is shown more extensively by the adult females. An endogenous activity rhythm has been shown in the species under laboratory conditions and it is suggested that this may play a part in the migratory movements.

A basic examination of the feeding methods, feeding appendages and food sources of adult and late copepodite stages has been made. Changes in feeding intensity through twenty-four have been examined in the field and under laboratory conditions. Using as an index of feeding intensity, the proportion of animals with food in their guts, it has been shown that a pronounced diel difference occurs in adult calanoids in the lake. Feeding is almost entirely restricted to the nocturnal presence of the calanoids in the water column. This difference exists in the pre-adult copepodite stages, but is not nearly as striking. The absence of feeding during daylight is not readily accounted for in terms of food availability and it is attributed to the quiescent or possibly infaunal existence of the adults.

A periodicity in egg hatching has been shown. Naupliar release from the parental egg sac is predominantly a nocturnal phenomenon in the hot and cool seasons. It is suggested that this may be important in attaining a favourable vertical distribution for the nauplii, and may be important in the distribution of the species.

A preliminary account of the seasonal cycle and population dynamics of *P. hessei* is given, based on data collected over two years at a single station. Seasonal changes in calanoid abundance are intermediate between those recorded in truly tropical areas and in temperate latitudes. Potential food sources show relatively little change.

The vertical migration of *P. hessei* is considered in relation to its apparent ecological significance and comparisons are drawn with observations made on the same species or other pseudodiaptomids in estuaries and lagoons elsewhere.

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Mr. R. Cross made the scanning electron micrographs of the feeding appendages of *P. hessei* and Professor B. Dussart has examined a sample of cyclopoid copepods from Lake Sibaya.

My wife has provided invaluable assistance in the field, often under arduous conditions at night, and was responsible for taking the majority of the photometric readings presented herein. Her careful determinations of phytoplankton and bacterioplankton abundance are gratefully acknowledged. My sincere thanks are due to her also for interpreting manuscripts into drafts and final copies and for preparing the figures. Her help and encouragement at all times is deeply appreciated.

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INTRODUCTION

Limnological studies in tropical and subtropical areas are poorly developed compared to their northern temperate counterparts. This is especially true in relation to zooplankton studies based on year round observations. It is startling to realize that detailed investigations of the biology and ecology of zooplankton in Arctic and Antarctic lakes probably outnumber those of tropical and subtropical lakes. In the vast continent of Africa, the major observations upon the plankton ecology of natural lakes are attributable mainly to the works of Talling (1957, 1964, 1965, 1966) and Burgis (1971). Only the latter author has been concerned with zooplankton ecology. By comparison, detailed studies of zooplankton in Arctic and Antarctic lakes have been made by Edmondson (1955), Comita (1956), McLaren (1961, 1964), Tash and Armitage (1967), Heywood (1970a, b) and Roff and Carter (1972).

Most of the general concepts concerning the ecology and biology of freshwater zooplankters have been based upon the northern temperate studies. The north temperate zooplankton have received extensive systematic and biological investigation. The seasonal behaviour of dominant species is known in a large number of lakes and the ecological energetics and production processes of many species have been studied. This much cannot be said of the tropical/subtropical freshwater zooplankton.

Apart from the systematic studies on various planktonic entomostraca (e.g. Fryer 1957 a, b, c, Kiefer 1934, Sars 1909, 1927, Harding 1942) and general statements concerning the zooplankton of particular lakes (e.g. Jackson _et al_, pp 45 - 47, 1963), little is known of the tropical African lake zooplankton. General limnological surveys of several lakes have been made with particular reference to the inland fisheries. These have resulted in the compilation of preliminary species lists and occasional biological notes concerning the invertebrate fauna. Detailed biological studies of the zooplankton are exceptionally few, especially considering the economic importance of various plankton-feeding fish in some of these lakes.

Other than the recent studies of Burgis (1970, 1971), the most detailed biological investigations of the zooplankton are those due to Worthington (1931) and Worthington and Ricardo (1936) who studied the vertical distribution and diel migration of several zooplanktonic species in Lake Victoria and other of the East African lakes.

At its inception in January 1968, the Lake Sibaya Research Station provided a permanent field laboratory from which continuous studies on various aspects of coastal lake limnology could be initiated. This field station, the first of its kind in South Africa, is built upon the shores of the largest natural freshwater lake in Africa, south of the Zambezi, and is briefly described by Allanson (1968). The lack of knowledge regarding the ecology of plankton in natural freshwater lakes in South Africa suggested the desirability of undertaking studies on both the phytoplankton and the zooplankton of the lake.

The studies undertaken by the present author and his wife, have, of necessity, been introductory in many respects. They have been the first of what is hoped will be many studies on the Lake Sibaya plankton, and have been the first plankton studies undertaken in a natural freshwater lake in Southern Africa. The investigations have been restricted in relation to available manpower, experience and facilities. Nevertheless, using traditional approaches some idea of the biology and seasonal behaviour of the numerically dominant organisms has been obtained and related to aspects of the physical and chemical limnology of the lake where possible.

The first serious limnological studies on Lake Sibaya were carried out in 1965 (Allanson 1969). These have been extended since then, particularly in relation to the physical and chemical limnology of the lake (Allanson and van Wyk 1969) and benthology (Boltt 1969a, b, Boltt et al. 1969). Prior to the studies initiated by the present author, very little was known of the Lake Sibaya plankton. Net tows had demonstrated the presence of various crustacean zooplankters in the surface waters at night. Hauls taken at intervals through the hours of darkness had demonstrated changes in zooplankton abundance at the surface. During daylight, the surface waters were apparently barren of crustacean zooplankton. Hauls taken in January and July over several years had shown that the calanoid copepod occurred in significant numbers during both the hot and cool seasons (Allanson, unpublished data). The phytoplankton had received no attention at all.

The presence of typically estuarine faunal components in Lake Sibaya (Allanson et al. 1966) was of great interest in relation to both the origin of the lake and the biology of the estuarine species in a freshwater lake. After publication of Allanson's et al. (1966) paper, the planktonic calanoid dominating the net haul collections was identified as Pseudodiaptomus hessei (Mrázek), a species dominating the plankton of most Cape estuaries (Grindley 1972). The species had not previously been known to occur in fresh water, although within the Pseudodiaptomidae various other species are reported from freshwater environments (Grindley 1965).

The presence of P. hessei in Lake Sibaya was noteworthy particularly in relation to its numerical abundance in this atypical habitat. P. hessei is the dominant species in Sibaya in terms of biomass and it is probably the most numerous single crustacean zooplankton species. Accordingly, the present investigation has been restricted primarily to this calanoid copepod. Early in the investigation, three aspects of the biology of the species seemed worthy of detailed study.

1. The ionic and osmotic regulation of the species.
2. The seasonal cycle of growth, reproduction and fecundity.
3. The vertical distribution of the species.

Ionic and osmotic regulation

P. hessei had been recorded only in estuarine systems or saline lagoons prior to its discovery in Lake Sibaya (Grindley 1963). Its presence in Lake Sibaya suggested that an analysis of its ionic and osmotic regulation might prove interesting, not only in relation to the biology of P. hessei, but in relation to the distribution of the pseudodiaptomids in general.

Growth, reproduction and fecundity

The importance of P. hessei in the plankton of Lake Sibaya was suggested by its dominance in terms of biomass. It appeared that analysis of the autecology and production processes of the calanoid would demonstrate, in part, the role of this plankter in the trophic network of the lake.

The vertical distribution

The diel vertical migrations of P. hessei in Lake Sibaya are pronounced. The migration pattern differs from the "classical" example given by Cushing (1951). More important, it differs in several important respects from the pattern of diel migration recorded for this species in estuarine systems (Grindley 1965, 1972). This much was evident from a study of the diel changes in vertical distribution made at the onset of the present investigations. In so far as could be judged, the migratory behaviour of P. hessei in Sibaya was of central importance to the general topic of vertical migration, especially in relation to the more recent ideas concerning the initiation and adaptive significance of such migrations. It was apparent that much could be gained by studying the migratory behaviour of P. hessei in Sibaya.

Grindley's observations upon the vertical distribution of P. hessei in shallow estuaries have shown that during daylight hours, the species may move out of the water column and onto, or even into, the bottom sediments. While adequate quantification of this movement has not been obtained (as recognized by Grindley himself (1972)), the evidence for such behaviour in estuaries is reasonable. It must be stressed that Grindley's observations were made in water of limited depth; the estuaries studied were generally only 1 - 3 metres deep (Grindley 1965). It was therefore of great interest to find that in Lake Sibaya, this movement onto the substrates occurred in the adult and late copepodite stages even in water of 40m depth. Under shallow, brightly illuminated estuarine conditions the movement of P. hessei onto the bottom substrates might be attributed to a photonegative response. A simple photonegative response is not as attractive in explaining this behaviour in Lake Sibaya, where the calanoids move into waters which are poorly illuminated. An assessment of the mechanisms underlying this behaviour was clearly necessary. It appeared that the planktonic mode of life might not be obligate in the older calanoids during daylight.

During the past decade or so, several positive advances have been made in understanding the significance of and mechanisms underlying vertical migratory behaviour. This is evident in the works of Siebeck (1960, 1964, 1969), Ringelberg (1961, 1964, 1969), Wynne-Edwards (1962), McLaren (1963), Harris (1963), McNaught and Hasler (1964, 1966), Hutchinson (1967), Miller (1970), Rudjakov (1970), Vlymen (1970) and Lincoln (1970), to mention those which, in the author's opinion, have done much to revive interest in vertical migration.[1]

The majority of modern workers agree that light initiates, directs and controls diel vertical migration, although the modus operandi is controversial. The older workers (with a few notable exceptions) interpreted the migration as an attempt by the animals to remain within a certain range of light intensities, the "optimal" or "preferendum" light intensities. The more recent workers have suggested that the rate of change of light intensity provides the stimulus to migrate. While this controversy will be taken up in detail at a later stage, the obvious importance of light is relevant to the immediate discussion.

Grindley's observations (1965, 1972) indicate that even in waters as shallow as 1 - 3m, P. hessei may not reach the surface waters until well after dark; he recorded peak numbers in the surface waters only at midnight, in many systems studied. The majority of animals are reported as leaving the surface waters before dawn. This pattern of vertical changes is, as Grindley emphasises, difficult to account for within the framework of an optically cued migration.

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[1] The works mentioned are those which are believed to be the most important in relation to their general applicability to vertical migration. More specific works are more numerous. Adequate reviews of the regional, seasonal and systematic aspects of vertical migration or vertical distribution are given in Cushing (1951), Baylor and Smith (1957), Bainbridge (1961), Banse (1964) and Hutchinson (1967).

In Lake Sibaya, however, notwithstanding the depth of water, the calanoids reach the surface waters fairly soon after sunset, and, those present in the surface waters leave at dawn. The pattern of movement is one which is clearly related to changes in light intensity.

From the literature it is clear that a concise and universal definition of the adaptiveness of vertical migration has been intangible. Only by studying the pattern in detail in one species was it thought possible to arrive at reasonably definitive answers to the enigmatic behaviour. The extension of conclusions obtained from one species to other species has been cautioned (McNaught and Hasler 1964). This, in itself, is somewhat incomprehensible. The diel vertical migration is a complex behaviour exhibited not by a restricted taxanomic group, but by a wide range of animals having one common factor - a planktonic mode of life. The existence of this behaviour in such diverse groups would suggest that a common denominator should be demonstrable, and significant attempts have been made to provide a universal interpretation of the adaptiveness of the migrations (e.g. David 1961, Wynne-Edwards 1962 and McLaren 1963).

The importance of diel vertical migration has been emphasized by many workers, who stress that for the behaviour pattern to have evolved in almost all planktonic animals, its significance must be profound (e.g. Grindley 1972). Others have questioned why an animal should spend so much of its energy moving often thousands of body-lengths daily (Worthington 1931, Marshall and Orr 1955a, Hardy 1956, Bainbridge 1961, Wynne-Edwards 1962). The recent work of Vlymen (1970) has suggested that the energetic cost of these migrations is considerably lower than generally believed. A similar conclusion had been reached previously by Hutchinson (1967). Nevertheless, the zooplankton contain geologically old groups and groups which reproduce reasonably rapidly. It would therefore be expected that adaptive selection would rapidly suppress the habit if it was of no adaptive significance. The likelihood that the behaviour pattern is an evolutionary relict seems remote.

In the attempts to relate vertical migration to feeding behaviour, the lack of evidence for interpretative purposes is particularly noteworthy. One of the most widely quoted theories to account for the significance of vertical migration is that of Hardy (Hardy and Gunther 1935, Hardy 1956). Hardy believes that the vertical migration will bring the zooplankton into new feeding areas at night. He sees it as a mechanism preventing depletion of food sources in a localized area and as a mechanism enabling unfavourable areas to be avoided for at least part of the 24 hour cycle. (Worthington (1931), on the basis of his studies on lacustrine zooplankton, had previously suggested the importance of feeding in relation to vertical migration. (p 443) "....hunger is the ulterior reason why the planktonic crustacea seek the upper layers...") Tacit in the hypothesis relating feeding to migration is the assumption that feeding is restricted mainly to the hours of darkness. More formally, McLaren (1963) has postulated the restriction of feeding to the warmer surface waters at night. However, the inadequacy of data concerning the relationship between vertical migration and feeding and the feeding behaviour of zooplankton in general, especially under natural conditions, is clearly stated by Rigler (in Edmondson and Winberg 1971, p 229)

"In recent years models of the dynamics of production (e.g. Cushing 1959) and a theory to account for the adaptive significance of diurnal vertical migration (McLaren 1963) have been created without an adequate knowledge of the feeding behaviour of zooplankton.

The authors were forced to make assumptions about the feeding behaviour of zooplankton since the existing observations were inadequate."

In recent years, much attention has been directed to the Arctic and Antarctic freshwater ecosystems. The biological simplicity of such systems (particularly the Antarctic lakes) has been considered to allow of a more thorough investigation of the biological interactions involved (Goldman 1970, Roff and Carter 1972). Worthington (1970, p 667) has said of the Arctic/Antarctic systems, "These fresh waters obviously have a high potential as laboratories and we shall look forward to learning more from them in future."

Tropical lakes also exhibit a simplicity commensurate with the lack of pronounced seasonal changes in solar radiation. In his classical study of vertical migration, Worthington (1931, pp 412 - 413) comments on the amenability of tropical lakes to studies of vertical migration. "Tropical lakes have considerable advantages over temperate lakes for such work as this in spite of their difficulty of access and the fact that their climatic conditions do not tend to stimulate the prolonged continuous activity in the field which such work demands. The chief advantage lies in the comparative uniformity of physical conditions, especially with regard to light."

Hutchinson, also, (1967, p 725) has pointed out that the complexity of vertical distribution and migration may increase in stratified systems. "Cases also are known in which the vertical distribution by day or by night varies systematically with the seasons and particularly with the development of thermal stratification in summer. It therefore may be supposed that thermal and chemical gradients as well as differences in illumination determine the position of the zooplankton."

Lake Sibaya, with its ephemeral and comparatively poorly developed physical and chemical stratification might therefore be expected to allow of a more simple appraisal of vertical migration than has been possible for markedly stratified lakes.

In classical terminology, the lake is undoubtedly oligotrophic. The low concentrations of chlorophyll throughout the year most probably reflect the paucity of plant nutrients, particularly free phosphorus and nitrogen, which are present in the lake waters in very low concentrations (Hart, unpublished data).

Notwithstanding the 10 ^{o}C seasonal change in water temperature of this subtropical lake, the standing crops of phyto- and zooplankton are not strikingly different. The lake supports low standing crops of phyto- and zooplankton, and numerically important species are few in number. Basically, therefore, the lake provides a very simple ecosystem, admirably suited to limnological investigation.

A consideration of the simplicity of the lake ecosystem suggested that this simplicity could be used to great advantage in studying the biology of _P. hessei_. In short, the lake provided a laboratory-type environment in which detailed studies could be made of the biology of _P. hessei_ under entirely natural conditions, and this has been the major aim of the present investigations. Using basically conventional techniques, a detailed study has been made of the vertical migration of _P. hessei_ and an attempt has been made to interpret these migrations within the framework of what is known of lacustrine limnology in general and of Lake Sibaya in particular. Questions arising from the field observations have been examined under laboratory conditions whenever this appeared necessary or potentially informative. However, for the most part, the present investigation is essentially a field study and the level of sophistication of laboratory studies has been dictated by the physical facilities available at the Research Station.

During the course of the vertical migration studies, data have been collected which have permitted a preliminary analysis of the seasonal behaviour and population dynamics of the calanoid. These data are reported in this work. No attempt has been made to investigate the ionic and osmotic regulation of _P_. _hessei_.

The pioneer-type studies undertaken on the plankton of Sibaya have been carried out under the primitive conditions which are inevitably associated with a new field station isolated from modern conveniences. (The Station is about 100km from the nearest railhead, and over 1000km from the parent institute.) As a result, many techniques and methods used during the study could undoubtedly have been replaced by superior ones under more favourable conditions. A large amount of time has had to be spent in making and maintaining equipment and the notoriously inclement disposition of the lake has severely affected the implementation of a rigidly planned research programme. These are problems appreciated by the field biologist who is not embraced by Vallentyne's (1969) definition of a limnologist. Nevertheless, the reader is asked to bear in mind the conditions under which this study was undertaken, while reading through the pages which follow.

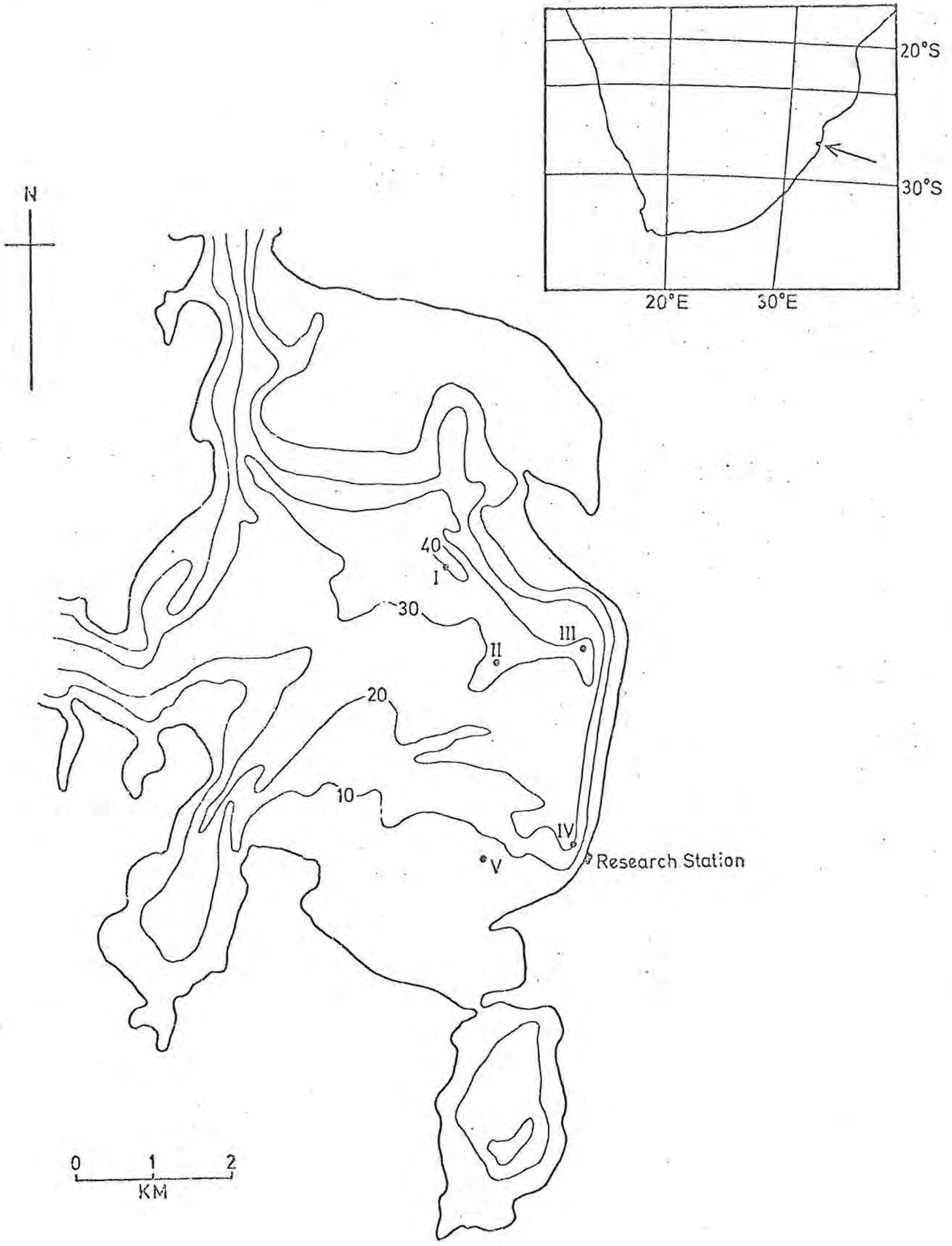


Fig. 1. Lake Sibaya: bathymetry and position of principal sampling sites. Depth contours at 10m intervals from Hill (1969). The northern and western arms of the lake are not illustrated. Inset - Southern Africa showing location of Lake Sibaya.

THE STUDY AREA

Lake Sibaya is the largest natural freshwater lake in Africa south of the Zambezi, lying in the coastal plain of Tongaland in northern Natal (see Fig. 1). The lake is situated very close to the Indian Ocean, separated from it only by a narrow range of coastal dunes which, in places, reach a height of over 100m. The surface of the lake is 21m above mean sea-level.

The lake is characterized by its lack of permanent thermal or chemical stratification (Allanson and van Wyk 1969, Minshull, Hart, Allanson, unpublished data). Any thermal stratification is of an ephemeral nature and is vertically depressed or broken down under wind stress. Oxygen levels are high at all depths with saturation values below 60% not having been recorded, even from the deepest waters in summer. Seasonally, temperatures range from 18 - 28°C, but summer temperatures in excess of 28°C have been recorded.

The waters of Lake Sibaya support a very low standing crop of phytoplankton, the volumetrically dominant species of which is the desmid Closterium ?pronum/aciculare. The general ecology of the phytoplankton has been examined by my wife and I during our residence at Lake Sibaya. The results of these investigations are being prepared for publication. The algal species studied show a fairly pronounced seasonal cycle of wax and wane, but standing crop values measured as chlorophyll, are reasonably stable throughout the year.

The crustacean zooplankton is represented by two cladoceran, four cyclopoid and one calanoid species. Bosmina longirostris and Moina sp. are primarily summer species but are present in the plankton throughout the year. Jointly, the four cyclopoid copepods numerically dominate the plankton throughout the year. The four major species are *Tropocyclops brevis* n. sp., *Mesocyclops leukarti aequatorialis* forma *micrura*, *Thermocyclops emini* and *Thermocyclops crassus consimilis* (Dussart 1972). The calanoid copepod *Pseudodiaptomus hessei*, is the most important single species. Numerically, this species contributes almost as much as the cyclopoid species combined and its comparatively large size places it as the volumetrically dominant species.

The waters of Lake Sibaya exhibit fairly low Secchi disc readings of 3 - 3.5m. This is somewhat incongruous in relation to the paucity of phytoplankton. Photometrically, 1% of midday incident light energy is recorded seasonally between 14 and 17m.

The lake is characterized further by its endorheic nature. No surface outlet is present. An adequate appraisal of the water balance is not available. Since surface run-off into the lake and inflow via streams is believed to be very little, the water level is thought to be maintained by direct precipitation onto the lake surface ($65km^2$) and by underground seepage. Seasonal fluctuations in lake level are directly comparable to the rainfall regime. Precipitation varies considerably from year to year in both timing and quantity, but records collected at the Research Station between 1968 and 1972 indicate that rainfall is most pronounced either in early summer (October) or late summer (April) but can be expected in small amounts in practically any month of the year.

LITERATURE REVIEW

The vast and confusing literature dealing with vertical migration in planktonic animals has been reviewed in several works, and it would be pointless to attempt a review here. Regional, seasonal and systematic reviews are given by Cushing (1951), Bainbridge (1961) and Hutchinson (1967). McLaren (1963) has examined the theories to account for the adaptive significance of vertical migration: Ringelberg (1964) has reviewed the experimental work performed on light and gravity responses of plankters under laboratory conditions. In the past decade, new and stimulating ideas have evolved and it is the object of this summary to review these ideas in so far as they are relevant to the present work.

a) The nature of the direct migratory stimulus

No serious workers today exclude light as the major abiotic factor influencing the migratory behaviour of most zooplankters. Of great significance is the revival of ideas previously held by Clarke (1930, 1933) who suggested that the causal stimulus in initiating migratory movements of certain species was the <u>change</u> in light intensity. For an extensive period, workers have been preoccupied with explaining the migrations as a response to remain within a certain optimal or preferential range of light intensities e.g. Russel (1926), Kikuchi (1930), Cushing (1951), Harris and Wolfe (1955) and Bainbridge (1961). This idea is tacit even in the recent works of Boden and Kampa (1967) and Kampa (1970).

"... diurnal vertical migrations of animals living at depths in the sea where light is appreciable are directly controlled by light and represent the animals' efforts to remain within a comfortable and/or useful photoenvironment" (Boden and Kampa 1967, p. 23).

Indeed, the day depth of various zooplankters is most easily accounted for in terms of an optimal light intensity. It is not so easy, however, to explain the dusk and dawn movements as responses to remain within a certain light intensity range. Siebeck (1960), Ringelberg (1961, 1964) and McNaught and Hasler (1964, 1966) have examined the role of changes in light intensity in relation to vertical movements particularly of freshwater zooplankters. Ringelberg (1961) has demonstrated that changes in light intensity provide the direct cause for vertical migration and has defined the causal stimulus as the "relative change in light intensity $\frac{\Delta I}{I}$ ". Irrespective of the causal stimulus, the final result of the migration is the same. However, as Ringelberg (1961, p. 494) points out:

"The biological meaning of the reaction may still be the maintaining of the initial light intensity. But the preferendum intensity is in this case not a causal but a finalistic explanation."

Nevertheless, the distinction between rate of change and preferendum intensity hypotheses is not simple and a considerable amount of data cannot be unequivocally explained by one or the other. For instance, migratory responses reported under conditions of total solar eclipse (e.g. Bright *et al* 1972) could be explained by either the rate of change or preferendum intensity hypotheses. However, the rate of change hypothesis is more acceptable as a physiologically valid causal stimulus on the basis of what is known of crustacean photosensory mechanisms.

It is generally believed that crustacean photoreceptor systems are incapable of measuring absolute light intensities (e.g. Ringelberg 1961, p. 498-9) even though intensity discrimination may be reasonably good. (McNaught and Hasler (1966) have reported a Weber-Fechner threshold ($\frac{\Delta I}{I}$) as low as 1.1% in the blue photosystem of *Daphnia*.) The apparent inability of crustacea to measure absolute light intensities, while generally accepted, has not been subjected to rigorous experimental attack. Until such analysis has been performed it appears justified to accept the relative rate of change of light intensity as the direct migratory stimulus in the absence of an alternative hypothesis, although it would appear prudent to bear in mind that significantly different responses may be exhibited by cladocerans with their compound eyes and copepods with their simple eyes.

b) Orientation to light and the importance of the underwater photoenvironment for depth control purposes.

Attempts to simulate migration under laboratory conditions are noted for their unreliability, particularly in copepods although greater success has been obtained in a cladoceran species (Harris and Wolfe 1955). It is clear from comparatively recent work that the inability of investigators to simulate migration in the laboratory has been a result of the oversimplified lighting conditions generally employed. Harris (1953) discussed the naturally occuring angular light distribution (A.L.D.) under water and subsequent work by Ringelberg (1964, 1969) on Daphnia magna and Siebeck (1969) on Mixodiaptomus laciniatus has demonstrated that this A.L.D. provides an orientation beacon for the cladoceran and copepod species investigated. The intensity of light under water provides a striking contrast between bright and dark at (ideally) 49° with the vertical. Light intensity between 49° and the vertical results from direct penetration and is very bright compared with that reflected light occuring outside the critical angle. This contrast in light intensity is an essential orientation beacon in the above-mentioned species, and by inference, in planktonic cladocera and copepoda in general.

McNaught and Hasler (1966) have considered the vertical distribution of four crustacean species in relation to the underwater photo-environments and optic sensitivity of the species. They have been able to relate the daytime vertical distribution of *Daphnia retrocurva* to the quantity and spectral quality of light to which the species is most sensitive. They suggest that the narrow-band visual pigments of *D. retrocurva* (the species has trichromatic sensitivity (McNaught and Hasler 1964)) are ideally suited to the detection of shifts in wavelength, both with time and depth. Determination of the Weber-Fechner $(\frac{\Delta I}{I})$ thresholds for light of different wavelengths has suggested that ultimately it might be possible to determine which wavelengths of light are most important in the migratory response and at what times in the diel cycle. Indeed, the spectral sensitivity of a species may, in some cases, be inferred from a knowledge of its day depth. For instance, McNaught and Hasler suggest that the deep mode of life of *Limnocalanus macrurus* points to the species having at least one visual pigment with maximum sensitivity in the blue.

These detailed interactions recorded between crustacean plankters and their photo-environment indicate strongly that simple laboratory studies cannot hope to achieve the level of complexity experienced under natural conditions. Clearly, laboratory studies of responses to optic stimuli must be carefully designed with due consideration of the factors discussed above.

It is not adequate to subject laboratory material to "point sources" of light or a "parallel beam" of light, and by increasing and decreasing the intensity expect to simulate a migratory pattern. In some cases this approach has given reasonable results and a considerable knowledge of the behavioural responses of *Daphnia magna* to light have been obtained in this way (Harris and Wolfe 1955, Ringelberg 1964). However, it would appear that a detailed study of the species in its natural environment has much to recommend it, especially since careful field studies generally result in a better appraisal of the selective advantages of the observed behaviour.

c) Pressure sensitivity and endogenous rhythmicity as modifying factors.

Considerable interest has been shown in pressure sensitivity of zooplankton in recent years. This must stem partly from Harris' (1953) proposal that vertical migration is an unavoidable consequence of using light for depth control purposes. His views were criticized because it was thought that depth control could be more simply effected by pressure sensitivity (McLaren 1963). Barosensitivity has been investigated in several planktonic animals. Knight-Jones and Qasim (1966) found no evidence of a pressure response in various freshwater cladocerans and copepods. Lincoln (1970, 1971) examined barosensitivity in Daphnia magna and Calanus helgolandicus. He obtained evidence for pressure responses in both species, although in D. magna the response was depressed in the presence of light. A priori, the selective advantage of pressure sensitivity in freshwater crustacean plankters is obscure. In the marine environment, barosensitivity might be expected to play an important depth-regulatory role by preventing the organism from sinking into waters too deep for subsequent movement into more superficial waters (for feeding or breeding). In the relatively shallow freshwater environments this does not appear to be a potential hazard, except in a restricted number of deep lakes. The existence of barosensitivity in freshwater crustacean plankters would therefore appear unnecessary and its role in modifying vertical migration or distribution limited.

Revival of Esterly's (1917) ideas of endogenous locomotory rhythmicity has resulted particularly from the demonstration of such rhythmicity in Daphnia magna and Calanus helgolandicus (Harris 1963). The existence of endogenous rhythmicity in other zooplankters has been recorded. Rudjakov (1970) has suggested that diel migrations are the result of innate alterations of phases of passive and active vertical displacements. Having examined the evidence for such a suggestion, Rudjakov proposes that diel vertical migrations are not the result of adaptations to a planktonic mode of life. The basic assumption upon which he has founded the theory is that the dawn descent is a passive movement. He appears to have overlocked the very clear evidence of the dawn descents being very closely correlated with changes in light penetration at dawn e.g. McNaught and Hasler (1964, 1966) and Boden and Kampa (1967).

Endogenous rhythmicity may play a part in initiating changes in locomotor activity in several species, but suggestions as to its universality as the causal agent in vertical migration are unwarranted. It is usefully invoked in several cases in explaining parts of the diel movements which are difficult to account for within a light-cued migration model. It is most improbable, however, that vertical migration can be unanimously attributed to endogenous locomotor rhythmicity.

d) The adaptive significance and environmental consequences of diel vertical migration

Many of the older workers questioned why zooplankters should expend so much energy performing diel vertical migrations, and concluded that it must be of great adaptive significance to the organisms. More recently it has been demonstrated theoretically that the energetic expenditure of these migrations is very small indeed (Hutchinson 1967). The problem has also been studied empirically by Vlymen (1970) who observed deceleration patterns following a leap by the calanoid copepod *Labidocera trispinosa*. He applied drag law formulae to determine energy expenditure in constant velocity swimming and in accelerating from rest to a given velocity. Using this approach, Vlymen has calculated that the maintenance of reported migratory speeds would expend less than 0.3% of the Basal Metabolic Rate.

In the light of the above works, it is no longer necessary to invoke a high energy expenditure in the migrations. In fact, only a very small selective advantage would be required to offset this slight energetic cost, although it is not suggested that the selective advantage is necessarily small.

McLaren (1963) has proposed an ingenious theory to account for the adaptive value of vertical migration. His arguments are based on the established relationships between copepod development rate, adult size and fecundity as temperature related functions. His hypothesis is based on the assumption that an energy bonus will accrue to animals feeding in the warmer surface waters and growing in the deeper cooler waters. This "bonus" energy can be directed into increased fecundity. Unfortunately, our present state of knowledge is such that his ideas are no longer entirely valid. Some of the assumptions upon which his hypothesis was based have subsequently been shown to be erroneous. This is particularly true in relation to his assumptions made concerning the restriction of feeding to the warmer surface waters. Experimental analysis of the effects of varying and constant temperatures on the growth of <u>Pseudocalanus minutus</u> (Lock and McLaren 1970) has failed to confirm any size advantage (and thereby increased fecundity) accruing from alternating temperatures, at least in this species under laboratory conditions. In view of the plateau in development rate recorded in <u>Diaptomus pallidus</u> (Geiling and Campbell 1972) McLaren's application of Bělehrádek's equation to relate various aspects of growth to temperature is cautioned. Tacit in McLaren's hypothesis is the assumption that there is a selective advantage in growing slowly and producing a greater number of slow-growing offspring. In nature, where conditions are continually changing, it may be that rapid growth and the production of a smaller number of offspring which will mature rapidly and reproduce earlier will be of greater selective advantage. In the light of these various criticisms, McLaren's hypothesis must be rejected. Nevertheless, his hypothesis must be rated as one of, if not the most significant attempt to define the adaptive value of vertical migration and the discussion and research which can be attributed directly or indirectly to his ideas is a fitting tribute to the theory.

Wynne-Edwards (1962) has suggested that the vertical migration of zooplankters may be a social "epideictic" display serving to plot the population density of the species which are then thought to limit their reproductive activity accordingly. These ideas have been the object of considerable criticism (McLaren 1963, Hutchinson 1967). Recently, the reversed migrations of the rotifer Asplanchna priodonta in a eutrophic environment have been attributed to interspecific competition between the rotifer and cladoceran species (Dumont 1972). Dumont proposes that the reversed migrations are initiated in response to species-specific or group-specific vibrations and his work suggests that inter-specific recognition is possible in these lowly metazoans. It would therefore appear prudent to withhold judgement on the social interactions envisaged by Wynne-Edwards, although intuitively his ideas in relation to zooplankton migration appear somewhat over-imaginative.

As originally proposed by Hardy and Gunther (1935) vertical migration in the sea was envisaged as a means by which the migrants could avoid toxic effects of dense algal patches. Later, Hardy (1956) took the view that the migratory movements would enable the migrants to exploit richer food areas and would mediate horizontal displacement into new feeding grounds. The consequences of vertical migration in the sea have been investigated empirically by Miller (1970) whose evidence does not match the theoretical treatment given by Hardy (loc. cit.). Using a vertically migrating parachute drogue as a model zooplankter, Miller has determined the extent to which vertical migration mediates horizontal displacement. Changes in zooplankton species composition determined by frequent net hauls in proximity to the drogue were used as an index of horizontal redistribution. The results of this novel approach have shown that while large-scale horizontal displacements may occur during reasonably short periods, this displacement is not accompanied by the expected changes in the zooplankton species composition. Zooplankton swarms or patches appear to maintain their integrity.

One of the simplest explanations of vertical migration is in terms of predator avoidance. This explanation is not favoured in explaining migration of marine zooplankters (McLaren 1963). In a lacustrine system, however, this model is more acceptable. It is most common to encounter zooplankters in deeper, darker waters during daylight. Potentially, this serves two functions. In the first place, it may keep the animals below the effective penetration depth of ultra-violet radiation, which is known to be lethal to Calanus (Marshall and Orr 1955a). Secondly, if the day depth of the animals is in reasonably dark water, the prey zooplankters will be less readily discerned by predators relying on visual recognition of their prey.

Granted, this predator avoidance may not be a reality in those species which do not appear to move into sufficiently dark waters. But in many copepods, the migration will take them into waters where even if they are not entirely in the dark, they will be apparently less vulnerable than if they were in brightly illuminated surface waters.

Younger stages of copepods are frequently captured nearer the surface during daylight than older stages. In this case, the smaller size of the younger stages probably reduces the chances of their being seen by predators. It also permits them to remain in what may be richer feeding grounds for a longer period of time. Surface area/volume considerations suggest that the energetic cost of the younger stages actively remaining in shallower waters will be less than that involved in the active maintenance of older stages at similar depths. In older stages, feeding may have to be restricted to the time during which they are in the surface waters and some ability to store food reserves in these later stages would appear necessary. In <u>Calanus</u>, for example, there is some evidence of increased fat content in successively older copepodite stages (Marshall and Orr 1955a).

Maly (1970) has examined the effect of predation on adult sex ratios of two diaptomids. General extension of his observations suggests that differential predation is a function of relative prey size and prey activity, and feeding behaviour of the predator. Larger and more active prey species are differentially captured by predators relying on visual prey recognition, while predation by passive predators is likely to be a function of prey abundance. By moving into deeper and darker waters, larger species or developmental stages of zooplankton are likely to avoid predation by visual predators while younger stages or smaller species are less likely to be seen in more brightly illuminated waters. Zaret (1972) has suggested that transparency of cyclomorphic cladoceran species may function to reduce visual recognition. It might be expected that younger stages or species inhabiting more illuminated layers during daylight would be more transparent than deeper living forms. However, a balance must develop here between transparency as an aid to invisibility and pigmentation to offset the harmful or lethal effects of ultra-violet radiation.

This brief survey of the more recent literature demonstrates clearly that the problem of vertical migration is by no means resolved. The more closely the problem is investigated, the more complicated appear to be the ramifications of this enigmatic behaviour. Two major problems are apparent - the direct and the ultimate causes of the migration. Laboratory work on _Daphnia_ has gone a long way in demonstrating the nature of the response to the direct migratory stimulus. However, our knowledge concerning the adaptive significance of the migration is still very limited and the ultimate reason for the migration is the subject of considerable speculation.

The present study has been concerned primarily with an analysis of the migratory behaviour of _P. hessei_. More specifically, an attempt has been made to determine the direct and ultimate causes of migration in this species.

Fig. 2. Motor Research Vessel "Tilapia" on the western littoral shores of Lake Sibaya.

METHODS

A wide range of methods have been employed during the course of the present study. Several of the techniques are standard practice in plankton studies, but others have been developed during the course of this study as and where the need for new or modified methods arose. It is proposed to deal firstly with conventional methodology, and secondly with special methods used in this study.

GENERAL METHODS

The field studies reported in this work were undertaken on Lake Sibaya in a 5.2m aluminium motor vessel, "Tilapia", powered by means of a 33 H.P. outboard motor (Fig. 2).

On all sampling dates, cloud cover, wind speed estimated on the Beaufort scale, and wind direction were recorded. During all routine samplings surface temperature was determined by means of a mercury in glass thermometer calibrated to 0.05°C. Temperature/depth profiles were obtained by means of a Wallace and Tiernan bathythermograph.

Stations

Fig. 1. shows the positioning of the five sampling sites used for most of the routine investigations. The stations are given in relation to the bathymetric features of the main basin of the lake, after Hill (1969). Various other sites were used for sampling purposes. The position of these other stations is given in the appropriate context.

Stations most regularly used for sampling purposes were permanently buoyed and sampling was undertaken while moored to the buoys. Other stations were marked with marker buoys and an anchor was used as a mooring on all but the calmest days. Where sampling was required at unmarked positions in the lake, a Sea-Scribe echo-sounder was used to establish station depth.

Sampling

Water bottles and plankton nets were used to sample the zooplankton in the water column. All samples were retained on #10 mesh (mean aperture 158µ). This mesh size was found to retain all the developmental stages of P. hessei with the exception of some of the first naupliar instar (N II).

a) Water bottles

In the early stages of the study, a 2 litre stainless steel Friedinger water sampling bottle was used. In the later stages of the study, a transparent 5 litre van Dorn sampling bottle was used for a restricted number of samplings.

The samples collected by means of water bottles were concentrated by pouring the entire contents quantitatively through a plankton bucket fitted with a large stainless steel window of #10 mesh. The concentrated samples were then transferred to 500ml screw top containers, and preserved by the addition of 40% formaldehyde to a final concentration of 5 - 10% formalin in lake water.

The major shortcomings of these water bottle samplers (particularly of the small volume Friedinger sampler) related to the small volumes collected and the impracticality of sampling the entire vertical column. These two limitations are serious ones where an analysis of the vertical distribution of the zooplankton is the major aim of the samplings, and especially when zooplankton abundance is low, as is the case in the present study area.

b) Nets

The majority of the samples collected during the course of this study was collected by means of a vertical closing net, constructed of #10 mesh bolting silk. Between 24/4/1970 and 5/5/1971 a vertical closing net of 30cm mouth aperture diameter and 1.5m total length was used. From 5/5/1971, a scale replicate of the original net was used, but the mouth aperture was reduced to 20cm. The net was conical in shape, with a canvas headpiece and tailpiece. A tripodal bridle was attached to the headpiece ring. A brass bucket (40ml capacity) fitted with a large window covered with #10 copper gauze mesh was secured to the tailpiece. The bucket was heavily weighted to ensure the rapid and regular descent of the net to the lower limit of the haul. The closing mechanism consisted of a cable trip arrangement which throttled the net approximately $\frac{1}{3}$ of its length from the mouth when triggered by means of a sliding messenger.

The net was lowered by means of a limnological hand winch attached to a davit which cleared the boat laterally by 50cm. The winch cable ran over a pulley driving a high quality meter wheel, calibrated to 0.1m.

During collections, the net was lowered rapidly, bucket first, to the preselected depth and then raised at approximately 0.3m/sec. The hauling rate was not standardized, but varied little with time. If split level hauls were being taken, the closing mechanism was activated as the net reached the preselected upper limit of the haul. The timing of net closure ensured that the net was not left open at the upper limit of the haul, and also precluded overspill and loss of portions of the catch during closure (Barnes 1949, Currie and Foxton 1956).

The collapsed net was raised rapidly to the surface, thoroughly rinsed down and the contents of the bucket decanted into screw-top containers and preserved. Standard post-sampling treatment of the net involved thorough flushing with tap water and subsequent drying.

The use of vertical net hauls in plankton sampling presents several difficulties. These relate chiefly to filtering efficiencies which are unlikely to be perfect. However, for the purposes of the present study, the paucity of crustacean plankters and the relatively large depth of water to be sampled precluded the satisfactory use of discrete depth pelagial samplers. Large volume samplers (e.g. Plankton trap or Schindler's sampler), whilst overcoming several of the problems involved with net sampling techniques, could not be used to sample a 40m water column adequately at the very short time intervals necessary to follow rapid migratory movements.

While it is appreciated that the net samples cannot give absolutely quantitative measures of zooplankton abundance, the results of the net samples are reported in absolute terms, assuming a filtration efficiency of 100%. While this assumption is not necessarily valid, common use is made of this convention in reporting results from net haul collections (Patalas 1969 and Carter 1969).

Notwithstanding the errors inherent in net sampling, net collections have enabled estimates to be made of the vertical distribution of the zooplankton populations throughout the entire water column. Samples taken by means of nets have enabled temporal changes in the vertical distribution and abundance of the zooplankters to be studied on a relative basis. In the light of various critisisms raised against the use of vertical net hauls, the comments of Tonolli (in Edmondson and Winberg 1971, p 5) are noteworthy.

"Despite uncertainties about the effective value of filtration, the net may be used in many cases , since even if it cannot guarantee completely quantitative evaluation, it permits relative

TABLE 1.

Net filtration coefficients for various developmental stages of P.hessei, assuming 100% sampling efficiency for the van Dorn Sampler.

	Net hauls 0-30m (942 litres)	van Dorn samples (35 litres)	van Dorn samples corrected to volume of net hauls	Filtration coefficient
Adult ♂	247	12	324	0.76
Adult ♀	158	10	270	0.59
Total Adults	405	22	594	0.68
Nauplii	1152	5	135	8.55*
CI	1044	43	1160	0.90
CII	566	59	1590	0.36
CIII	256	15	405	0.63
CIV	200	16	432	0.46
CV	124	3	81	1.40
Total copepodites	2190	136	3668	0.60
Total P. hessei	3747	163	4397	0.85

* The very low Naupliar catch in water bottle samples may be a reflection of an irregular vertical distribution masked in net hauls.

comparisons, valid within the same environment between analogous components of the population".

The entry of zooplankton into nets while they were being lowered, mouth upwards, has been reported (Bayly 1962) although Smyly (1968a) found that very few zooplankton were captured during net descent. In an earlier work (Smyly 1961) he reported lower catches in a net used to "fish" on its descent than in a net used to "fish" on its ascent. In the present study the net was lowered mouth upwards and used to capture zooplankton on its ascent. Sporadic checks on the entry of zooplankton during lowering indicated that insignificant numbers were captured during this process. Maximal errors of approximately 0.5% were recorded.

Filtration efficiency

A limited amount of evidence is available to indicate that filtration efficiency of the nets used in Sibaya is reasonably high. In the first instance, as a result of the oligotrophic nature of the lake in terms of algal biomass, clogging of the nets was never observed. Secondly, in a series of collections made simultaneously with water bottle and vertical net hauls, a reasonably high mean filtration coefficient of 0.85 was obtained (Table 1). Within each developmental stage of P. hessei, however, there was considerably greater latitude in this filtration coefficient.

The mean filtration efficiency of the nets used in the present study area compares favourably with estimates obtained by other workers. For example, Smyly (1968a) records filtration efficiencies of 50 - 75% and Kibby (1971) reports a mean efficiency of only 36%.

Coefficient of variability at a single station

The coefficient of variability for replicate hauls was calculated from a series of 9 replicate hauls made between 30m and the

TABLE 2.

P.hessei: Mean percentage deviation in catch of nine pairs of replicate hauls made at Station III on alternate nights (5/5/71 - 25/5/71).

Pair no.	Adult catch Replicate 1	Adult catch Replicate 2	Mean Percentage Deviation
1	390	442	12.5
2	218	306	33.6
3	110	102	7.7
4	262	414	45.0
5	295	259	13.0
6	253	265	4.6
7	238	202	16.4
8	228	311	30.8
9	405	357	12.6
Mean	266	295	19.6

surface. The hauls were made on alternate days between 5/5/71 and 25/5/71 at Station III. Each replicate haul was made within a few minutes of its predecessor and total counts of the catch of adult P. hessei were made.

The catches of replicate hauls in the nine pairs are presented in Table 2, together with the mean percentage deviation for each pair of catches. (Mean percentage deviation

$$= \left(\frac{N_1 - N_2}{N_1} \times \frac{100}{1} + \frac{N_1 - N_2}{N_2} \times \frac{100}{1} \right) \times \frac{1}{2}$$

where N_1, N_2 represent the larger and smaller numbers of the pair).

Table 2 shows that the mean percentage deviation for replicate hauls varies from 5 - 45%, with an overall mean percentage deviation of approximately 20%. The mean percentage deviation is similar to that recorded by other workers. Heywood (1970a) recorded variation of 26 - 52%, Chapman (1969), 13 - 25% and Bayly (1962), 9 - 40%. The 4th sample pair in the present series increases the range considerably. All others are below 34%.

Characters used in the determination of developmental stage in P. hessei

Descriptions of post-embryonic development have been published for several pseudodiaptomids. Johnson (1948) has described development in P. euryhalinus. Grice (1968) has studied the development of P. coronatus while Alvarez and Kewalramani (1970) have studied naupliar development in P. ardjuna. In the species adequately studied, the first naupliar stage is apparently suppressed and the eggs hatch directly into N II. As in other calanoid copepods, N VI passes into C I, and C VI is the sexually mature adult.

Characters used in the separation of the copepodite stages of P. hessei in the present study have been based upon observations made on the Sibaya material, and to a limited extent upon unpublished data of Grindley (pers. comm.). Individual calanoids from a sample taken from Sibaya were examined. Number of pairs of legs, number of urosome segments and total length were recorded for a large number of individuals. These data were plotted on a scatter diagram relating size to number of pairs of legs and urosome segments. The data resulted in discrete groups of points on the scatter diagram; each group could be related to a particular developmental stage. These characters were checked in laboratory raised calanoids and are summarized below. Determination of developmental stage was based on these characters.

Adult males are easily recognized by their geniculate antenna and jointed caudal setae. The adult females are characterized by the genital segment on the urosome and their sword-shaped central caudal setae (Grindley 1963).

	No. pairs legs	No. urosome segments	Mean length (μ)
C I	2	2	410
C II	3	2	520
C III	4	2	580
C IV	5	3	685
C V♂	5	4	770
C V♀	5	3	870
C VI♂	5	5	920
C VI♀	5	4	1090

Laboratory treatment of samples

For counting purposes the sample was transferred to a # 10 plankton bucket. In this bucket the sample was rinsed gently to remove the supernatant formalin solution. From the bucket the sample was transferred either to the counting chamber or to the subsampling vessel.

A square, transparent perspex tray (internal dimensions 7.0 x 7.0 x 2.0cm) with sides flared outwards at 10° to provide an optically clear base, was used as a counting chamber. A series of guidelines was scored on the underside of the base at 1 cm intervals giving a $1cm^2$ grid.

Counting Counting was performed under a Cooke, Troughton and Simms binocular dissecting microscope, using a total magnification of 12.5x for all counts of adult and late-stage copepodites. Higher magnification (15x or 25x) was used for counting the nauplii and early-stage copepodites.

Subsampling In samples in which enumeration of total numbers was impractical owing to the numbers involved, subsampling was employed. However, in practically all cases, all adult calanoids were counted. The subsampling technique used was slightly modified from the method described by Allanson and Kerrich (1961). An octagonal vessel was used and the sample was stirred by means of an L-shaped glass rod. In the present study, however, the sample was stirred by hand while an aliquot sample of 25ml was withdrawn by means of a wide mouthed (4mm diameter) pipette.

Subsampling Errors In all net samples collected during the present study, total counts were made of adult males, ovigerous and non-ovigerous adult females. In the case of numerically large samples, subsequent fractions of $\frac{1}{8}$, $\frac{1}{4}$ or $\frac{1}{2}$ by volume of the total sample were taken for analysis of the pre-adult stages of P. hessei or other crustacea not reported upon in this work. With very little extra labour it was possible to make counts of the adult calanoids in these subsamples. Therefore, for the majority of net samples in which subsampling was used, counts of adult P. hessei were made for both

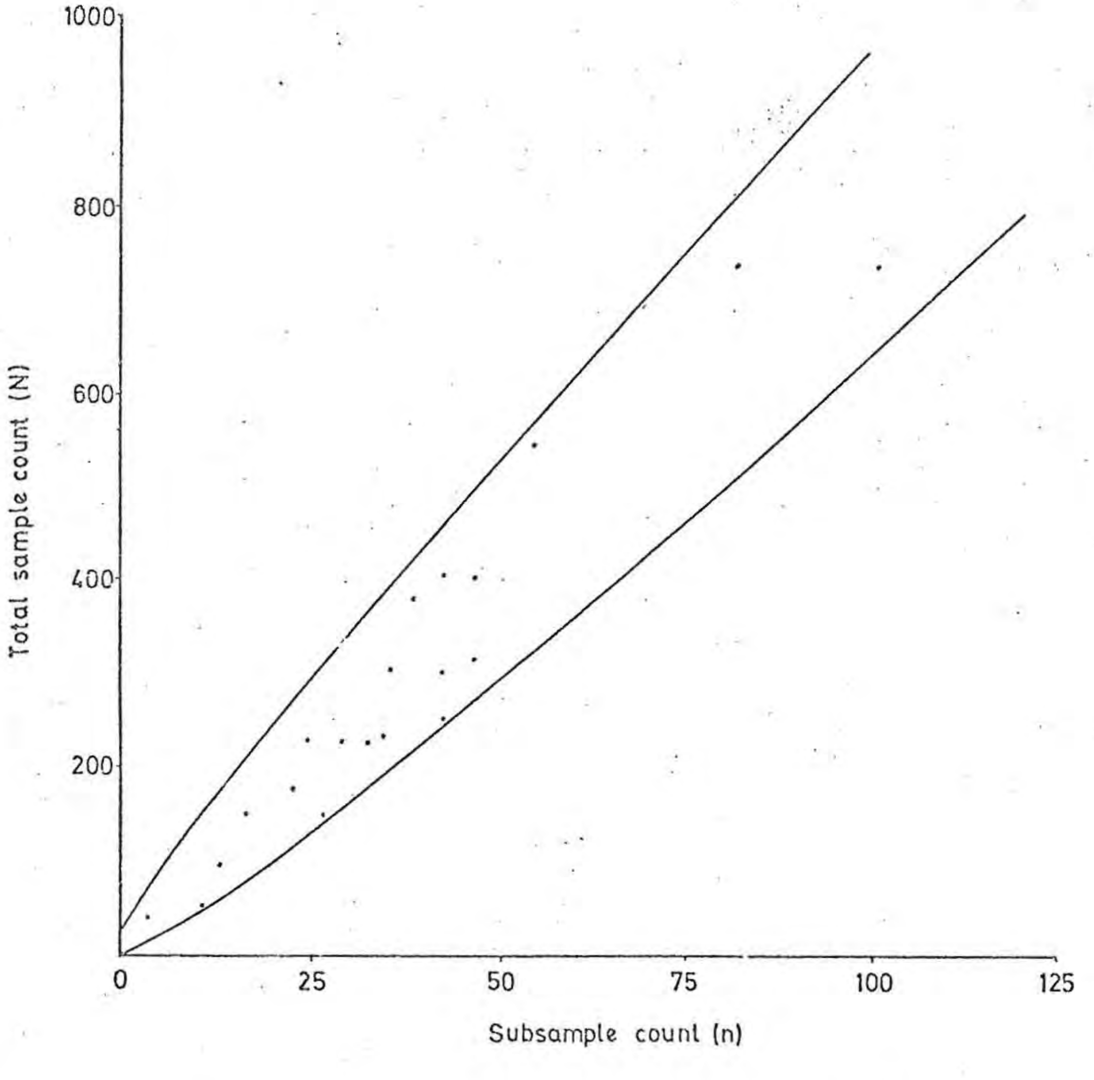


Fig. 3. 95% confidence limits for total sample counts based upon $\frac{1}{8}$th subsamples.

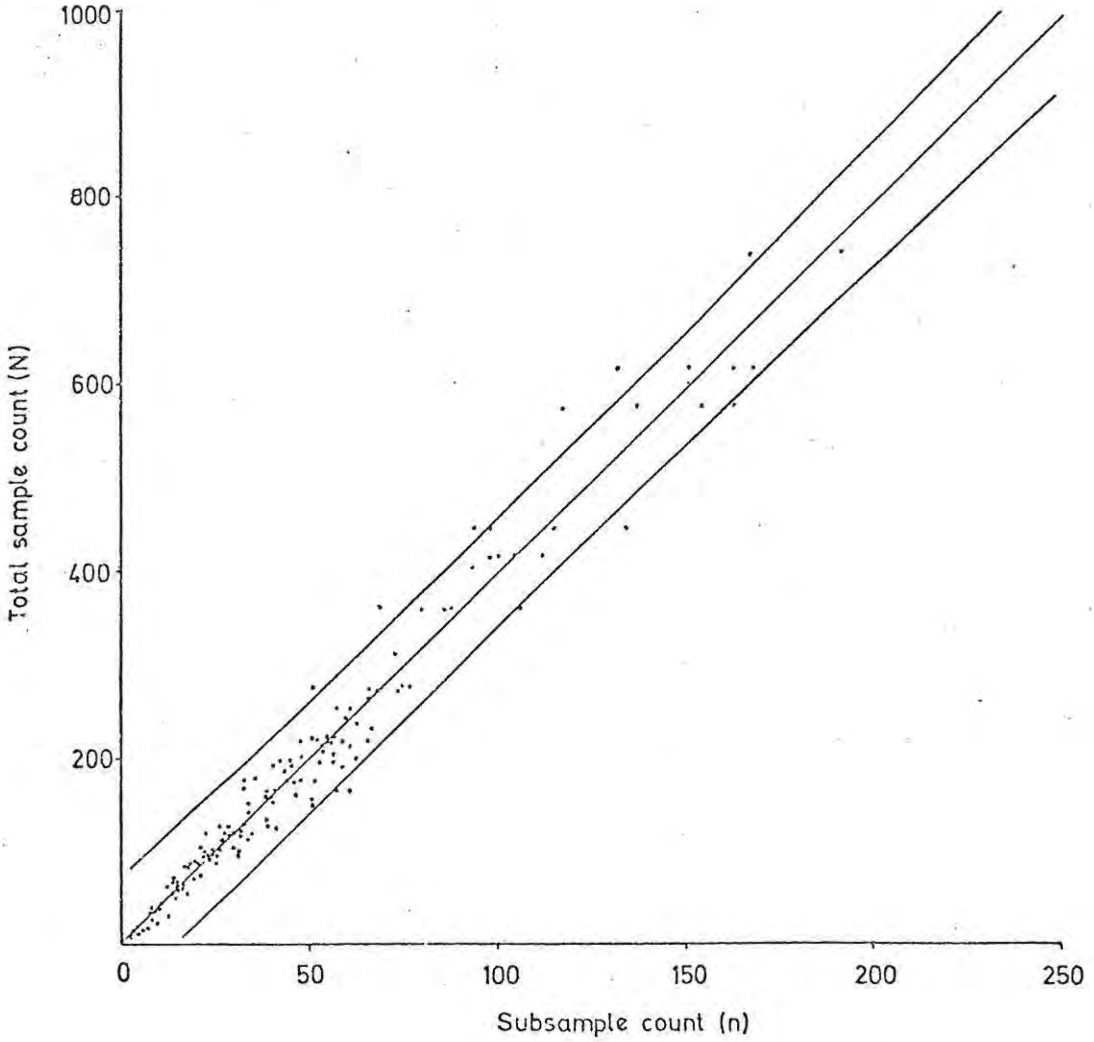


Fig. 4. 95% confidence limits for total sample counts based upon $\frac{1}{4}$ subsamples. The regression line is given by $y = 3.919x + 2.439$.

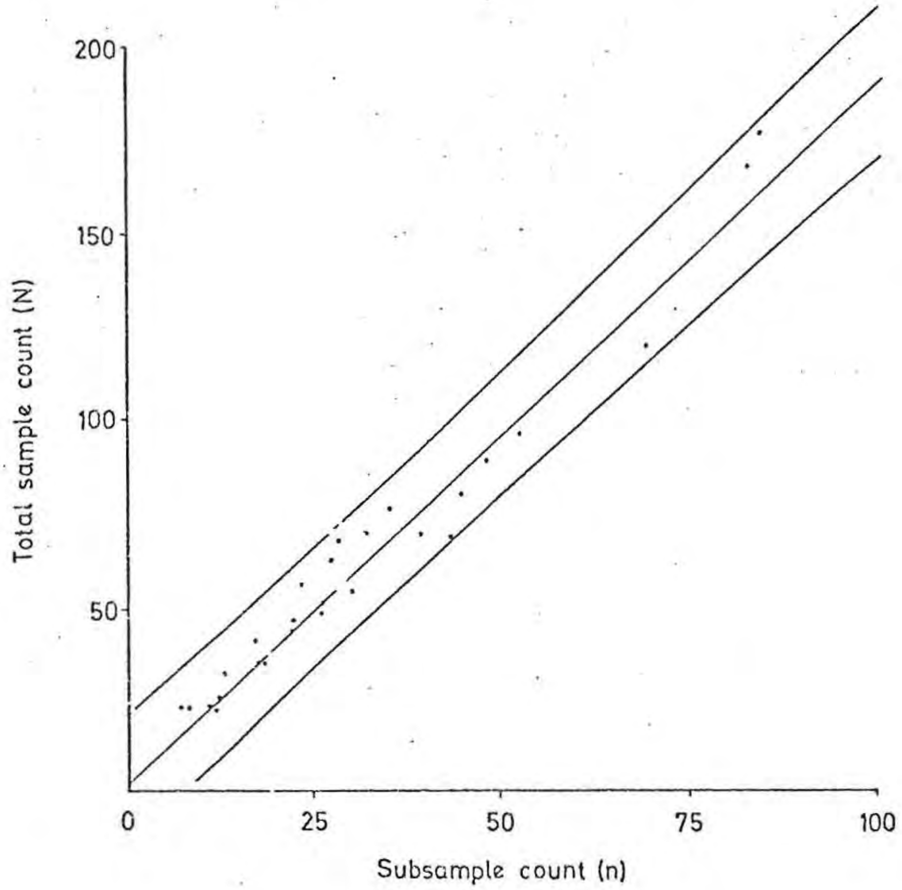


Fig. 5. 95% confidence limits for total sample counts based upon $\frac{1}{2}$ subsamples. The regression line is given by $y = 1.861x + 3.068$.

the subsample fraction and the entire sample. These data have enabled an assessment of the errors involved in subsampling to be made for the entire duration of the study. Figs 3, 4 and 5 show the relationships between subsample counts and the total count of the parent sample.

Allanson and Kerrich (1961) have examined the reliability of using subsamples $\frac{1}{8}$th by volume of the parent sample to estimate the total frequency of a species in the total sample. They have determined that when the subsample count (n) is less than 150, the confidence limits for the subsample count can be obtained from standard tables of the Poisson distribution. The corresponding estimate and confidence limits for the parent sample are obtained by multiplication. In subsample counts greater than 150, the 95% confidence limits of n are given by $\frac{n}{1.16}$ to $\frac{n}{0.84}$. The 95% confidence limits given in Fig. 3 have been determined using Allanson and Kerrich's procedure.

In the present study, the majority of subsampling has been based on fractions $\frac{1}{4}$ or $\frac{1}{2}$ by volume of the parent sample. Experimental analysis of the errors involved in using $\frac{1}{4}$ or $\frac{1}{2}$ subsamples has not been done. There is no evidence to suggest that the rules developed by Allanson and Kerrich for $\frac{1}{8}$ subsamples can be extrapolated linearly for use with $\frac{1}{4}$ or $\frac{1}{2}$ subsamples. Accordingly, conventional regression analysis (Snedecor and Cochran (1967)) has been used to determine the 95% confidence limits of the parent sample counts based on $\frac{1}{4}$ or $\frac{1}{2}$ subsample counts. These confidence lines are shown in Figs 4 and 5. The assessment of subsampling error has been based upon adult calanoid data. There is some evidence to suggest that this assessment can be applied to the pre-adult stages. Biased subsampling of different stages may occur, but the extent of such bias appears to be insignificant.

Subsample counts of the pre-adult stages of <u>P</u>. <u>hessei</u> were based on a minimum count of 50 individuals of any one copepodite stage, or 75 nauplii. (Numerically small samples were counted in entirity.) The 95% confidence limits given in Figs 3, 4 and 5 give percentage errors of 29%, 28% and 17% respectively for subsample counts of 50 individuals. The percentage accuracy of the estimate increases as the subsample count is increased. These values (29%, 28% and 17%) therefore represent the <u>maximum</u> errors introduced by subsampling practice.

The conclusions reached during the present study have been based upon vertical differences in calanoid abundance far greater than the variation attributable to subsampling error. It is clear, therefore, that while error is introduced by subsampling, the error is of little significance in the totality of the observations, and, for most practical purposes, can be ignored.

SPECIAL METHODS

During the course of the study, various special sampling techniques and sampling apparatus were developed to cater for special problems which arose. Early in the study it became apparent that the adult calanoids and late copepodite stages were reaching the lake bed, or immediately overlying water, during daylight. It became of primary importance to develop an adequate and simple method of capturing the calanoids in close proximity to, or upon, the substrate/water interface. While two conventional techniques have been applied for this purpose, they are discussed in this section as a matter of convenience. Detailed diagrams of the construction of the sampling devices designed during the present study are given in the appendix. These diagrams are annotated and may be referred to in relation to the descriptions in the text.

Van Veen Grab

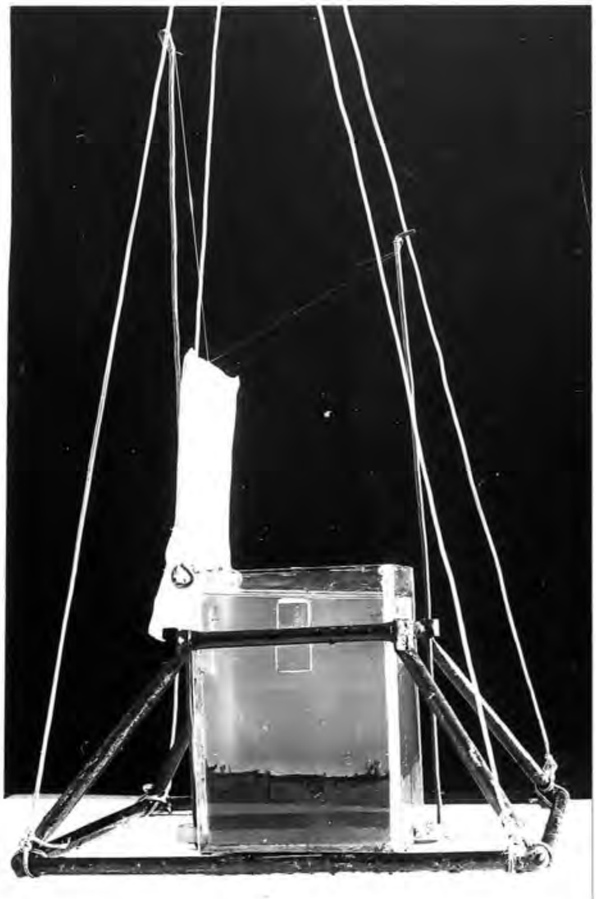
Initially, a van Veen grab of 225cm^2 bite, fitted with rubber flap valves (Boltt 1969a) was used. However, the effective separation of copepods from the mass of substrate collected was impractical. Further, the currents set up by the sampler on its descent (Wigley 1967) were likely to disturb the calanoids off the substrate as a result of the well developed rheotactic response observed in *P. hessei* during the present study.

Vertical Bottom Sampler (Appendix 1)

Some idea of the abundance of the copepods on the substrates was obtained from samples collected with a "vertical bottom sampler" designed and built during the study. This apparatus consisted of a square perspex column (15 x 15 x 30cm) with an upper and lower horizontal sliding door. These doors were cocked in the open position during descent and were triggered automatically upon reaching the lake bed when the weight of the sampler was taken off the cable. After triggering, the doors, powered by strong rubber bands, slid along grooves and closed the sampler. Valuable introductory data were obtained with this apparatus, but problems associated with water-tight sealing were insurmountable when the apparatus was used on hard sandy bottoms. On soft flocculent bottoms, penetration below the level of the lower door was possible and the substratum enclosed effectively sealed the lower door. However, in view of the predominantly sandy nature of the lake bed, a more reliable sampling technique was required.

Jenkin's surface-mud sampler

A Jenkin surface-mud sampler (Mortimer 1942) was used with some success on sand but the very small sampling area and its immense weight precluded its extensive operation.



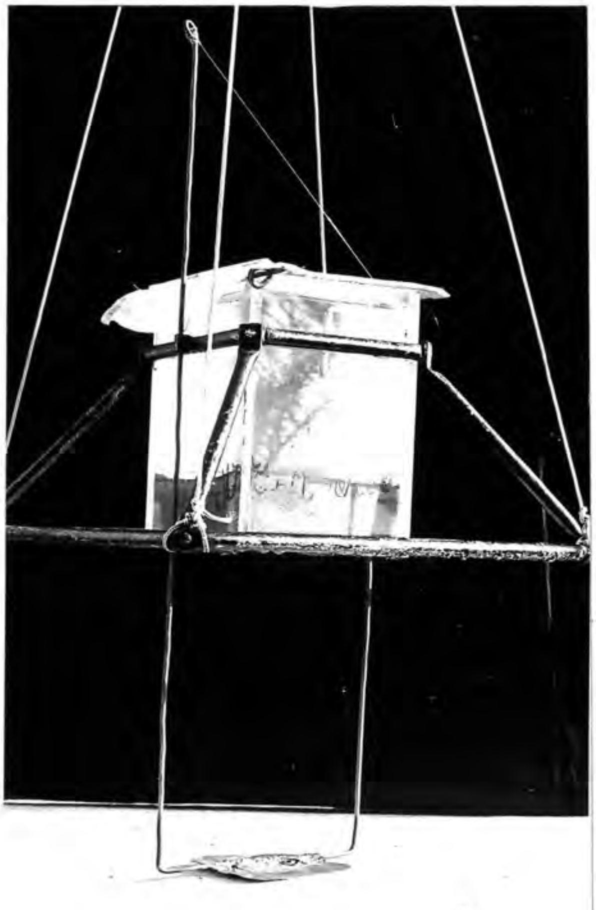


Fig. 6. Substrate bin in the open (upper photograph) and closed positions. The littoral sand introduced as a substrate is clearly visible. The burrows of various benthic crustaceans can be seen. The shallow dark band above the sand is the flocculent tripton which collects in the bins.

Substrate Bin (Fig. 6, Appendix 2)

Calanoid populations on the lake bed and in the waters immediately overlying the lake bed have been successfully monitored by means of the "substrate bin". This apparatus consists of a perspex box (15 x 15 x 22cm) with a base, fitted into a tubular metal framework. The perspex box is fitted with a hinged upper lid of #10 mesh bolting silk stitched onto a wire framework and glued onto the perspex wall along the hinging surface. The lid is connected to an "automatic" opening and closing device by means of nylon fishing twine. The closing device consists of a "square-U" shaped wire with one upright section approximately twice as long as the other. This wire runs through eyes on the sides of the perspex box and is provided with a broad metal foot attached to the horizontal section of the "U" below the base of the perspex box. A nylon line runs from the end of the longer wire to the face of the lid parallel with the hinging plane, and a shorter cord runs from the shorter upright of the "U" to the same point on the lid. As the bin is lowered onto the substratum, the weight of the apparatus is taken by the foot on the trigger wire and this forces the wire to slide up the walls of the box until the base of the box rests upon this foot on the lake bed. In the process, the cord from the longer upright of the "U" is tightened and raises the hinged lid. The bin is therefore in the open position while it is on the substrate and closes automatically as it is raised off the substrate, and the weight is taken off the foot.

Estimates of copepod abundance as assessed by these substrate bins depend upon prior vertical movements of the calanoids into the containers. For this reason, it was necessary to lay these traps on the evening before the requisite sampling date. By doing this, the substrate bins effectively sampled the calanoids which reached

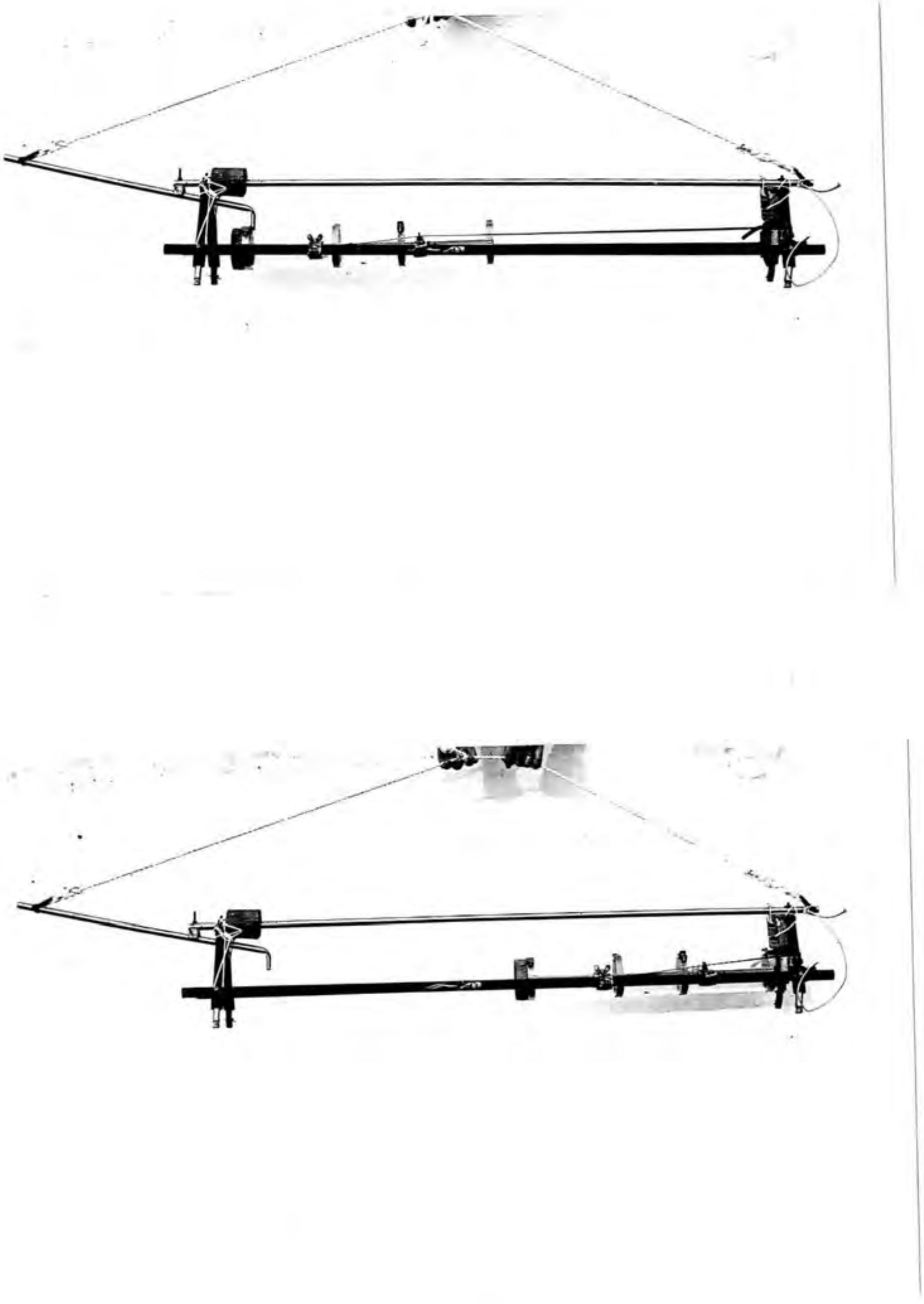


Fig. 7. Horizontal Bottom Sampler in the open (upper photograph) and closed positions.

the substrate as a result of their descent at dawn. Before the bins were layed, a layer of littoral sand substrate about 4 - 5cm deep was introduced into the bins. The absolute depth of substrate was of no importance since the estimates of abundance have been interpreted as numbers per unit area of substrate and not per unit volume of overlying water.

Horizontal Bottom Sampler (Fig. 7, Appendix 3)

Towards the very end of the study, a simple horizontal bottom sampler was designed and constructed. This consisted of a perspex tube (50cm x 7cm diameter) which was mounted upon and ran along two horizontal rails. These two rails, together with an upper third rail, were mounted on triangular leg frames. The leg frames were of such a length as to allow the perspex tube to run horizontally along the lake bed cutting slightly into the interfacial detritus. The trailing end of the perspex tube was sealed with #10 mesh copper gauze. The leading edge of the perspex tube sealed, on closure, against a sponge rubber faced metal plate fitted onto the leg tripod. The tube was powered by means of powerful rubber springs. The sampler was triggered automatically when its weight was taken off the lowering cable on reaching the lake floor.

This sampling device was designed to sample animals off undisturbed and entirely natural lake substrates. It provided useful corroboration of the substrate bin results.

Treatment of samples collected in association with sediments.

Removal of calanoids from the samples taken from natural or artificial substrates or sediments in the various ways described above was performed in two stages. The first stage was carried out in the field, immediately after collection. The sample was decanted through a plankton bucket fitted with a large #10 mesh window. As

Fig. 8. Magnesium sulphate flotation of Pseudodiaptomus hessei. The calanoids are visible as a distinct band at the surface.

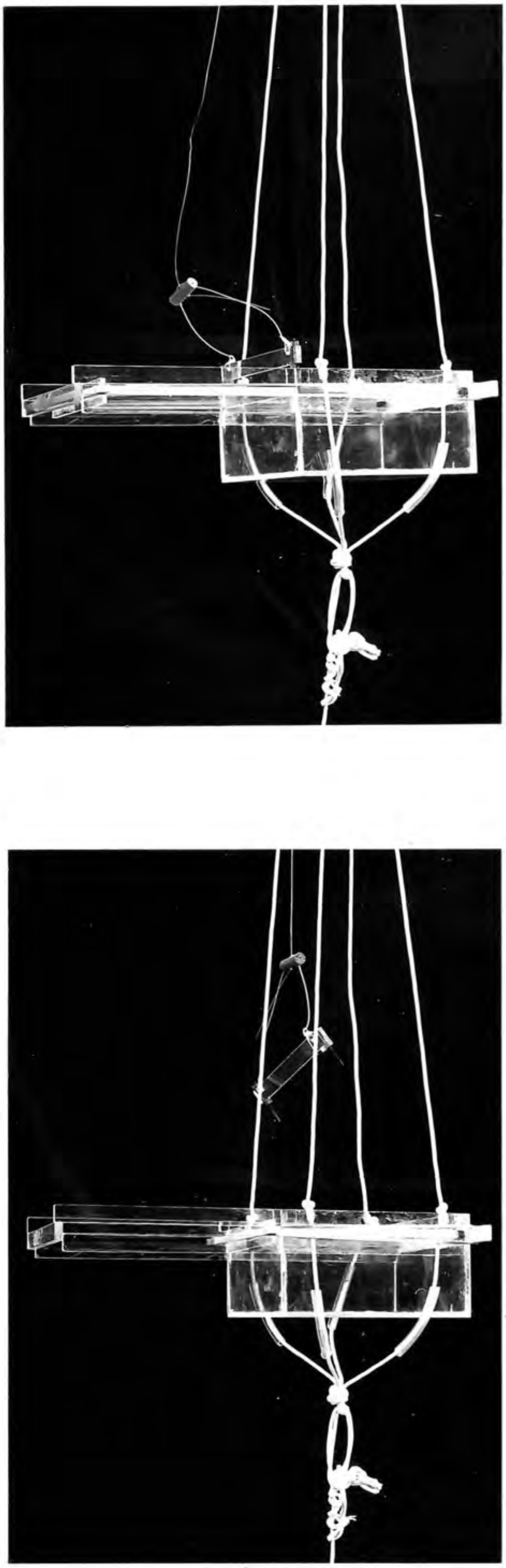


Fig. 9. Suspended Tray in the open (upper photograph) and closed positions.

little substrate as possible was decanted in this initial filtration. The resulting sample was preserved immediately. The remaining substrate was added to the plankton bucket and elutriated twice with filtered lake water to remove any copepods remaining upon and adhering to the substrate. These washings were combined and preserved for subsequent analysis.

Several checks were made to estimate the number of copepods remaining after successive rinses. It was found that less than 5% of the animals remained after initial decanting and single elutriation. This fraction was lowered to generally less than 1% after the second elutriation.

The second stage was performed in the laboratory where further separation of copepods and detritus was carried out either by filtration through various sized meshes (4, 22, 32, 40, 44 meshes per cm.) or by $MgSO_4$ flotation (Smyly 1964) in a separatory funnel, after removal of supernatant formalin.

Where collections were made with the specific aim of examining gut contents, graded filtration was used to remove the detritus and separate the calanoids. However, for most of the work, where diel variation in numerical abundance was being estimated, $MgSO_4$ flotation was used. This flotation technique was found to be exceptionally satisfactory in the present study (see Fig. 8).

<u>Suspended Tray</u> (Fig. 9 , Appendix 4)

The suspended tray was designed to determine the settling intensity of calanoids on substrates suspended at different depths in the water column. This apparatus consists of a shallow perspex tray (internal dimensions 15 x 15 x 6cm) fitted with a horizontal sliding upper lid. The whole unit is suspended horizontally at any depth in the water column by means of a heavy base weight, a submerged float ~1m above the tray and a surface float. The sliding

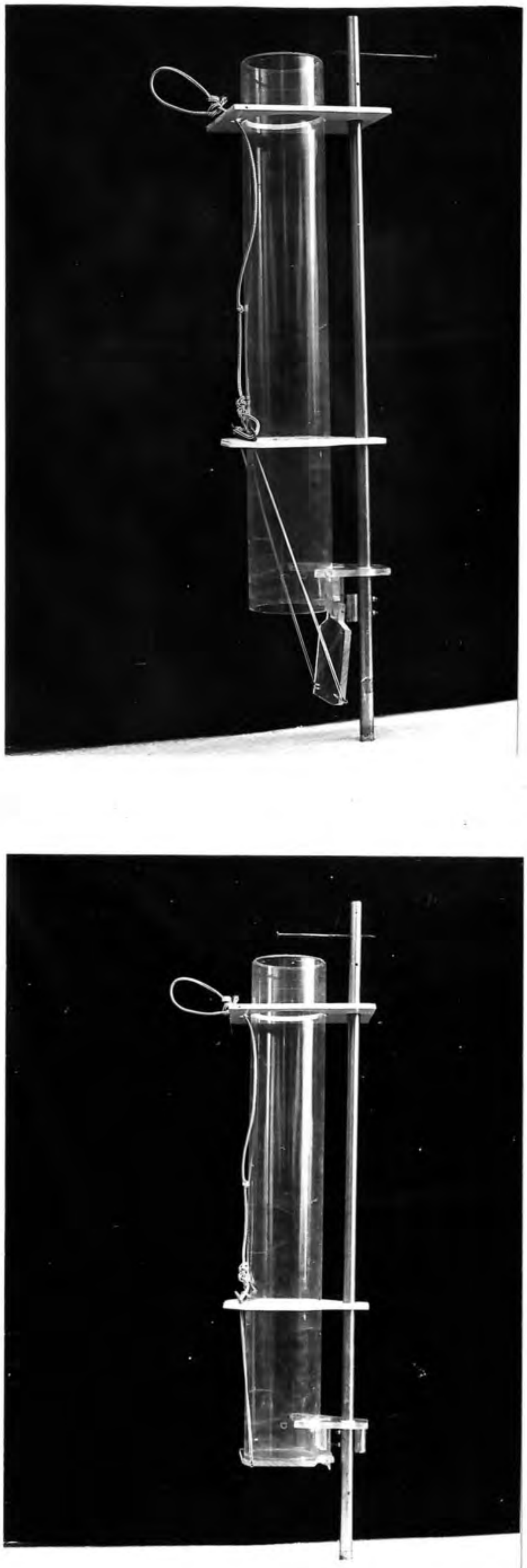


Fig. 10. Aquarium Sampler in the open (upper photograph) and closed positions.

upper lid is cocked open against the pressure of rubber bands by a trigger mechanism which is activated from the surface by means of a trip line. Eight trays were constructed, and suspended at 5m depth intervals over the deepest area of the lake.

The trays were either provided with a shallow layer of littoral or deep-water substrate or left empty. The collection of calanoids in these trays depends upon the vertical migratory movements into the trays at dawn. Accordingly, it was necessary to position the trays in the lake at least one evening before the requisite sampling date.

Aquarium Sampler (Fig. 10, Appendix 5)

Vertical migration studies under laboratory conditions required an adequate sampling technique. Photographic techniques have been used successfully by Harris (1963) and Harris and Wolfe (1955). In the present study, however, photographic techniques were unsuccessful and another technique had to be developed.

To this end, a transparent perspex tube (50cm x 7cm diameter) was modified to make a water bottle sampler which would always sample at the same depth within the experimental vessel. Calanoid abundance in the upper levels ($\frac{2}{3}$) of the water column in a large glass tank could be determined with this apparatus.

The tube was fitted with a hinged lower lid. This lid was kept parallel with the long axis of the tube by means of a trigger on a metal pipe running the length of and extending beyond either end of the perspex tube. This pipe ran through eyes on the perspex tube. The lid was maintained in the open position by means of the trigger, against the pressure of rubber springs. The trigger mechanism was fixed onto the long metal pipe to give a standard clearance of 12cm between the lower end of the perspex tube and the bottom of the tank. The length of the rod prevented sampling closer than 12cm off the bottom of the experimental container.

During sampling, the apparatus was lowered into the aquarium until the vertical rod touched bottom. The vertical rod was then turned through 90° by means of a handle at its upper end. This movement released the trigger mechanism and the lid closed. An adequate seal was maintained by increasing pressure between the lid and the tube by means of a tensioning cord while the apparatus was removed from the aquarium. Sample volume was determined by decanting the contents of the sampler into a measuring cylinder. The sample was then concentrated through a plankton bucket, preserved, and retained for subsequent examination.

Photometric equipment

While a consideration of this equipment could justifiably have remained in the general section, the development of some highly sophisticated photometric equipment for the present study justifies its inclusion here.

Initially, light measurements were made by means of a submersible and deck cell photometer. The sensor units consisted of CdS cells connected to sensitive µ-ammeters by means of variable resistance shunts. This photometer enabled the percentage attenuation of light to be determined. However, changes in underwater light intensity at dusk and dawn could not be established accurately by means of this equipment and it was superceded by an alternate instrument.

The majority of light readings was made by means of a Hydro-Bios luxmeter. This submersible light meter was satisfactory except in relation to its lower sensitivity limits. The maximal sensitivity of 1 lux proved inadequate for the present study.

The most satisfactory photometric equipment was designed and developed by Dr. R.E. Boltt in conjunction with the Electronics laboratories of the Physics department of Rhodes University. The equipment was designed specifically to record very low light intensities with a minimal voltage requirement. The instrument is to be described in detail elsewhere. Basically, this photometer consists of a submersible sensor unit with seven sensitivity ranges. Light intensity on a full moon evening is sufficient to give almost full-scale deflection on the most sensitive range.

Unfortunately, this equipment was available for only a very short period and was used to make one set of measurements at dusk and one at midday.

Presentation of data

Since several collecting methods have been used in this study, it is necessary to devote some space to a discussion of data presentation. For the purposes of presentation it has been assumed that all the collecting methods are absolutely efficient unless otherwise stated. The main result of this assumption pertains to the widely different sample volumes which are, in some cases, compared.

Data collected from water bottle samples are illustrated by means of frequency polygons with a corresponding scale. In the portrayal of results collected from net samplings, histograms have been used to indicate depth/frequency distributions. Net collections are generally represented as numbers per m^3. Each panel of data is provided with a scale to avoid confusion. However, it is important to note that different scale axes may be used in consecutive panels and the reader is asked to bear this in mind. In some cases, net collections are illustrated as numbers under unit surface area. When this has been done, the scale inscription is altered accordingly.

In many of the figures, a comparison between numbers of calanoids in the water column and numbers on the substrates has been desirable. Resulting from the use of widely different methods of collection, the volumes sampled are accordingly very different. e.g. Net hauls versus substrate bins. The abundance of calanoids on the substrates during the day relative to their density in the water column has made it impractical for the purposes of illustration to bring the numbers to a unit volume of water as the difference can run to at least two orders of magnitude. In order to compare the water column collections with collections off the substrates the counts have been computed on a unit area basis. Water column counts are denoted as numbers below unit surface area and substrate counts are correspondingly calculated as numbers per unit area of substrate. It is important to note that these two are not mutually inclusive as would be implied by the common use of the convention "per unit area". The numbers per unit surface area involve the counts made of the water column populations below unit area but excluding the numbers per unit area on the lake bed. Similarly, the numbers per unit area of substrate relate to the population abundance as monitored by substrate bins, horizontal bottom sampler, Jenkin's tubes etc. and denote the numbers within a restricted distance above the lake bed. This distance varies from several centimeters in the case of the horizontal bottom sampler to approximately 20cm for substrate bin collections. Once the water column and substrate collections are computed on an areal basis, relative percentages in the water column and on the substrate may be calculated.

The percentages on the substrate relative to the percentages in the water column are plotted in a two-bar horizontal histogram below the depth/frequency histogram where this has been thought desirable or where data for this calculation have been available. The use of this method of presentation is best illustrated by means of an example. The example presented below is based upon the 0600hr sampling series during the 24hr station of 1-2/3/72. This is figured in the text (Fig 19).

Adult ♀, 0600hrs, 24hr station 1-2/3/72.

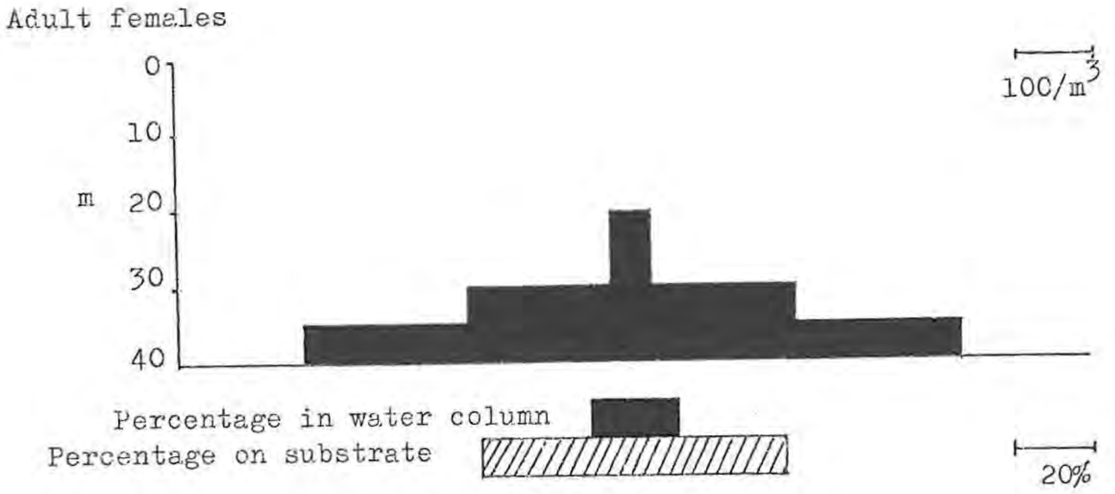
Net haul intervals	No. captured per haul	No. captured per 10m haul or $0.314m^3$*	No. captured per m^3
0-10m	0	0	0
10-20m	0	0	0
20-30m	14	14	45
30-35m	67	134	426
35-38.5m	95	271	864
Totals	176	419	

*The cross sectional area of the 20cm diameter net is $\pi \times 10^2 = 314cm^2$.
Each 10m haul therefore filters $\frac{1000 \times 314}{1000\ 000}$ $cm^3 = 0.314m^3$

Adult ♀ catch in substrate bin = 470 animals
Area of substrate bin 15 x 15cm = $225cm^2$
No. of animals per $314cm^2$ $\frac{470}{1} \times \frac{314}{225} = 656$

No. in water column under $314cm^2 = 0 + 0 + 14 + 67 + 95 = 176$
No. on substrate above $314cm^2 = 656$
Total no. on substrate and in water column = 176 + 656 = 832
% of ♀ calanoid population in water column = $\frac{176}{832} \times \frac{100}{1} = 21\%$
% of ♀ calanoid population on substrate = $\frac{656}{832} \times \frac{100}{1} = 79\%$

The following series of histograms demonstrate how these values have been illustrated in the rest of the text. The solid black histograms against the depth axis represent the vertical distribution of the water column population. Below this, the solid black and shaded histograms denote the percentage of the total population in the water column and the percentage on the substrate respectively.



It will be noticed that in the above diagram the vertical distribution is illustrated to a depth of 40m although the lower limit of the haul was at 38.5m. When, during a series of collections, the bottom depth varied during the course of the series, the maximum depth sampled has been used for illustrative purposes. In all cases, however, numbers per m^3 have been computed on the basis of the true net haul length. Only at Station I did bottom depths vary by 1 - 1.5m. At other stations the lake bed was fairly regular.

The above method of presentation of data depends only upon the relative numbers beneath unit area of surface and on unit area of substrate. It takes no account of the widely different volumes sampled. Percentage changes in abundance in the water column and substrate fractions of the populations are strictly comparable when these changes have been determined at the same station or different stations of equal depth. Under these conditions the percentage estimate is based on a constant ratio between water column sample volume and substrate sample volume. In the case of a station 40m deep, for example, numbers beneath $1m^2$ in the water column will have been determined from a volume of $40m^3$, whereas the numbers on $1m^2$ of substrate will have been estimated from a volume of $\sim 0.2m^3$ in a substrate bin. The ratio between these two volumes is constant for all stations of 40m depth. In the case of a series of stations of increasing depth, however, this ratio will increase with station depth. In a series of stations at 10, 20, 30 and 40m, for example, this ratio changes from 50 to 200. While this has no effect on the presentation of data, this being a function of unit area, it will be appreciated that with increasing depth, percentage estimates will be biased increasingly in favour of the water column fraction. In a 40m station, therefore, a figure indicating 100% abundance on the substrates represents an incredibly high concentration of calanoids on the substrate, relative to the density in the water column.

THE HORIZONTAL DISTRIBUTION OF PSEUDODIAPTOMUS HESSEI

Introduction

At the onset of the present study, two stations were sampled routinely. These were Stations III and IV, 30m and 20m deep respectively. Fortnightly samplings at these two stations over a period of several months demonstrated two points. Firstly, the temporal changes in zooplankton abundance were similar at both stations. Secondly, the standing crop estimates of the calanoid were consistently lower at the shallower station. Diel changes in vertical distribution were determined at these two stations and the results showed a markedly comparable pattern of events over 24 hours (see Figs. 14 and 15).

On the basis of these findings, and particularly in view of the research load carried at the time, it was decided to concentrate on the deeper station, and to ignore, for the time being, any horizontal variation that might be apparent. The findings up to the time of this decision suggested that the vertical distribution of the calanoid could be studied at the deeper station with a reasonable expectation of reliability. In view of later work, this has proved correct.

It was appreciated, however, that a realistic appraisal of population dynamics could not be expected from single station sampling. Nevertheless, it was anticipated that the single station sampling would enable the general seasonal pattern of events to be determined.

Later in the study, the horizontal distribution of the calanoid was examined in greater detail. Furthermore, the reliability of the initial routine single station samplings was tested by sampling at four additional stations, Stations I, II, IV and V, from November, 1971 to June, 1972.

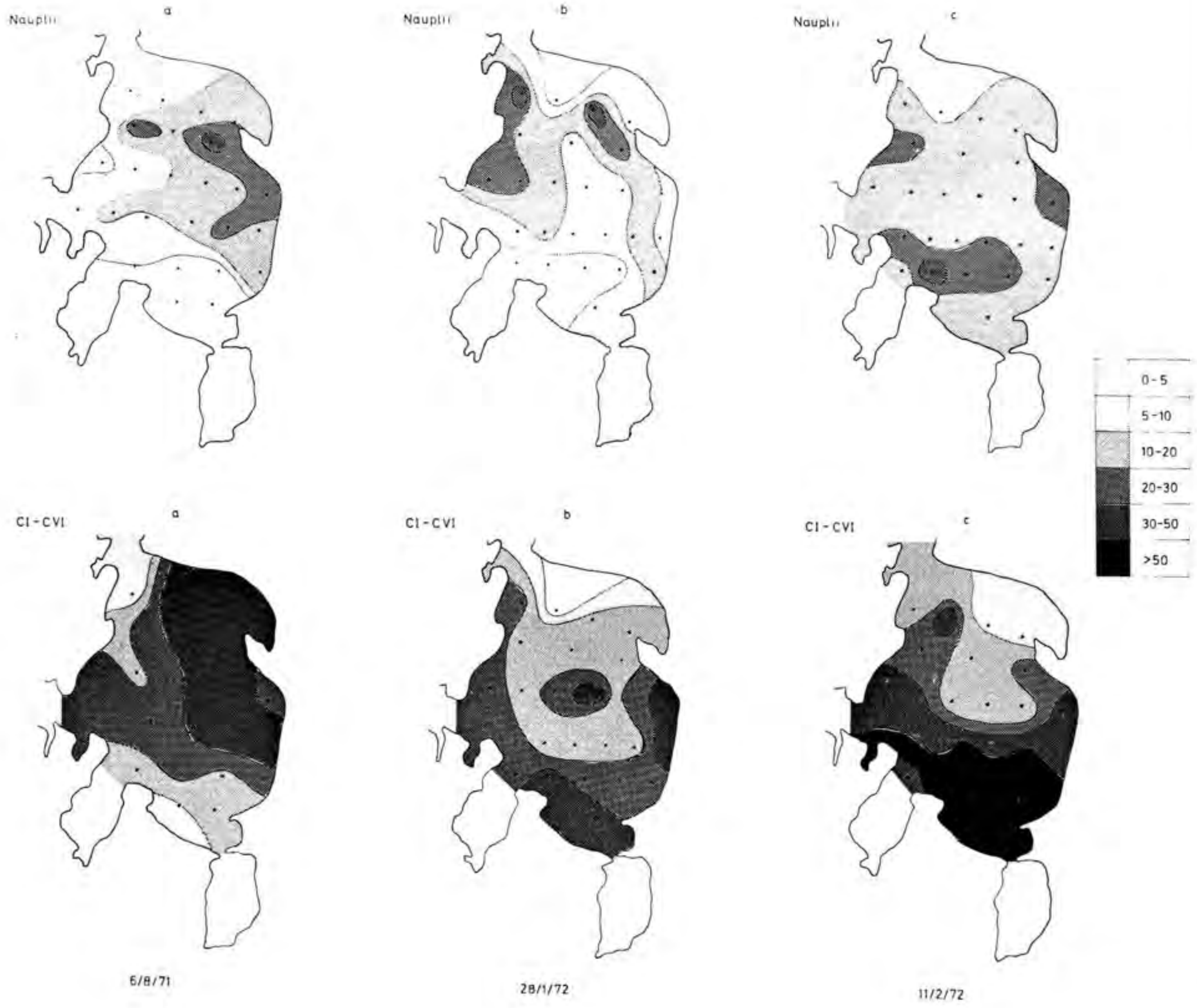


Fig. 11. The horizontal distribution of nauplii and copepodites of P. hessei on three sampling dates. Calanoid abundance expressed as catch per metre of net haul i.e. catch per 31 litres, assuming a filtration efficiency of 100%.

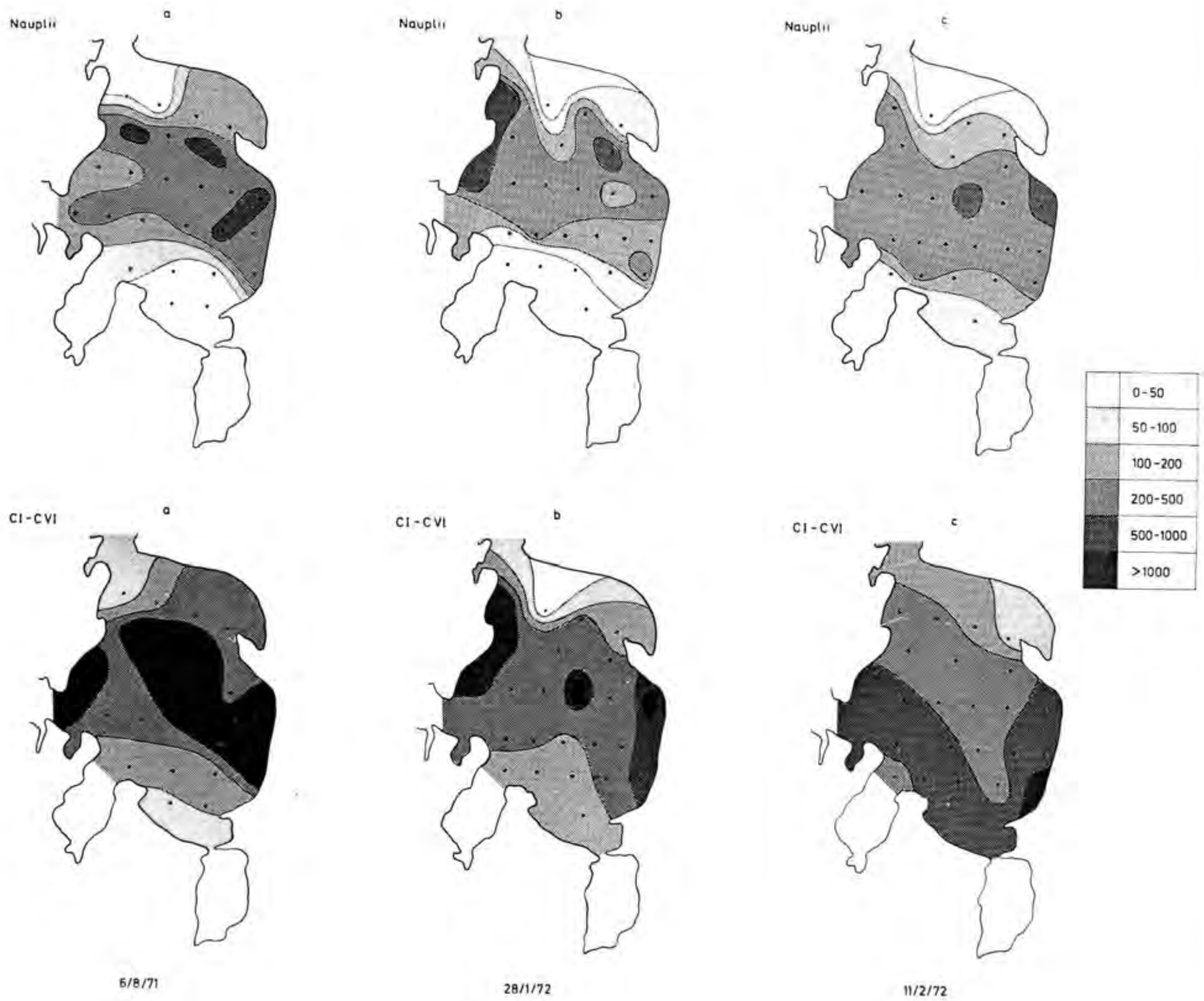


Fig. 12. The horizontal distribution of nauplii and copepodites of P. hessei on three sampling dates. Calanoid abundance expressed as catch per net haul i.e. catch under 314 cm^2, irrespective of length of vertical haul.

The horizontal distribution of P. hessei

The pattern of horizontal distribution and its changes have been examined over the main basin of the lake by means of three semi-synoptic surveys based on 25-station samplings. Collections were made at night by means of net hauls, from the lake bed to the surface. Each sampling series lasted for 6 - 8 hours, and therefore the results are, for all practical purposes, synoptic, and are referred to as such.

The developmental stages of P. hessei were counted separately, and although differences in their horizontal distribution exist, these are not readily intelligible. For the purposes of the present description, counts have been lumped into two categories viz. nauplii and copepodites I - VI. The horizontal distribution of nauplii and total copepodites on three occasions is shown in Figs 11 and 12. Fig. 11 shows the numbers per metre of net haul (i.e. numbers per unit volume of water filtered). Fig. 12 shows the numbers per net haul, irrespective of haul length (i.e. numbers per unit area of the lake surface).

In assessing the horizontal variation in abundance, the numbers of calanoids per unit volume (Fig. 11a, b, c) are more meaningful. Within the limits of the somewhat arbitrary iso-frequency intervals employed in compiling the figures, it is clear that a reasonably regular pattern underlies the horizontal variation. Fig. 11a shows a clear increase in abundance from south-west to north-east for nauplii and copepodites. Fig. 11b shows that naupliar populations are greater in the northern areas of the lake, whereas copepodites are most abundant in the southern areas. Fig. 11c shows a fairly even naupliar distribution over the entire lake, but a striking concentration of copepodites in the southern half of the lake.

Factors responsible for these striking patterns of distribution have been examined. It was impractical to undertake temperature recordings in conjunction with the surveys. However, there is very little likelihood that sufficient temperature differences exist horizontally over the lake to bring about this distribution. Bathythermograph records taken at Stations I - V at fortnightly intervals between November, 1971 and June, 1972 have demonstrated the uniformity of lake temperatures at these widespread stations. The maximum difference in surface temperature recorded between these stations was 0.5°C, but mean temperatures throughout the water column were considerably more uniform.

Food availability in terms of total nanoplankton cells and bacterioplankton "units" (see p 165) was assessed for the surface waters during the January survey. Very little variation was observed in these counts. The mean, range, standard deviation and standard error of these counts over 25 stations are given below.

	Nanoplankton cells	Bacterioplankton "units"
Mean	139.4	625.3
Range	112 - 220	524 - 784
Std. Error	5.693	16.867
Std. Deviation	28.465	84.334
n	25	25

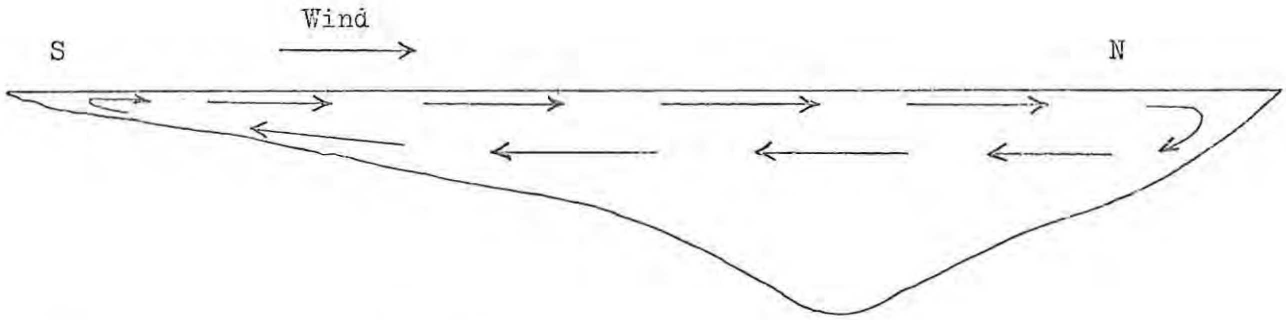
If the uniformity of nanoplankton and bacterioplankton observed in the surface waters is exhibited at different depths, then the effect of food availability on the horizontal distribution of <u>P. hessei</u> must be considered slight. (Observations to be presented later suggest that nanoplankton and bacterioplankton are the most likely food sources of <u>P. hessei</u>.)

Temperature and food availability show no indication of affecting the horizontal distribution of the calanoids in Sibaya. This is in contrast to the observations made on the planktonic crustacea of Lake Ontario by Patalas (1969), who demonstrated the importance of horizontal temperature variation in controlling the horizontal zooplankton distribution. Patalas suggested that temperature modified development rates of the zooplankton and also affected their food supply, by affecting the growth rate of food organisms. This resulted in the horizontal variation in abundance of the species studied.

In Sibaya, the changes in calanoid distribution are attributable mainly to wind induced currents moving the waters of the lake. An examination of current-induced changes was made possible by the fortuitous occurrence of severe winds on the night of 2/2/72. South westerly winds of gale force, accompanied by rain and cold weather, lashed the lake for several days after this date. Several days after the storm abated, it was possible to undertake a survey. The changes in distribution, evident between Fig. 12b and 12c which occurred within 14 days, are most plausibly related to the extensive water movements which accompanied the storm.

Comparison of Figs. 12b and 12c shows that the naupliar distribution is more uniform after the storm. In the copepodite stages, there is a striking concentration in the southern areas of the lake. Notwithstanding the concentration of copepodites after the storm, there is also evidence from Figs. 12b and 12c that the resulting distribution is less patchy.

The pronounced concentration in the southern end of the lake, as a result of strong south westerly winds would be unexpected on the basis of the work reported by Langford and Jermolajev (1966). In the lakes studied by these workers, plankton were generally moved in the direction of the wind and concentrated on, or near, the windward shores. The lakes studied by them were often stratified when their observations were made. In Sibaya, the lack of thermal stratification is probably more conducive to the development of reverse currents than internal seiches. Allanson (pers. comm.) has recorded reverse currents in Sibaya even after fairly light northerly or southerly winds. These currents are generally recorded below 10 or 12m. On the basis of what is known of the current systems in Lake Sibaya (Allanson, unpublished data) a reasonable model can be erected to account for the changes in distribution apparent between the January and February surveys. During the storm, the following current movements are envisaged:-



It is reasonable to assume that these currents would continue for some time after the storm had abated.

As will be shown in subsequent sections, P. hessei undertakes extensive diel migrations. During daylight, the animals are in the deeper waters, but at night they are distributed through the water column. At night, therefore, they will move up into turbulent waters, and, depending upon their vertical position within the water column, will be subjected either to the surface northerly drift or the reverse current. Since the calanoids exhibit a nocturnal (midnight) sinking, they will spend a proportionately shorter time in the uppermost waters than in deeper waters, and will therefore be affected mostly by the reverse current. Laboratory observations have shown that the post-naupliar calanoids swim strongly against strong water currents but are apparently little affected by slower currents. As a result of this differential reaction to fast and slow currents, and the proportionately greater time the copepodites are exposed to the weaker reverse currents, those stages with some swimming prowess will be concentrated in the southern end of the lake. The nauplii, on the other hand, are comparatively poor swimmers and will be at the mercy of the water movements and turbulence. This will result in their distribution throughout the water mass. The comparatively uniform naupliar distribution evident in Fig. 12c is obviously a reflection of this.

Within the framework of this model, it is likely that sampling undertaken several days before the survey was made would have demonstrated a concentration further north, as would sampling carried out several days later.

These observations demonstrate the extreme lability of the calanoid populations. This has important bearing upon single station sampling. It is evident that a single station in Sibaya can, at best, give only a very general idea of zooplankton abundance. It also suggests that reliable sampling for production estimates must be based on more stations than can be effectively dealt with by two workers. However, specific aspects of the biology of a species can undoubtedly be based on sampling at a restricted number of stations. As a result of the rapid redistribution effects, different sub-populations are likely to be sampled on each occasion, so that a representative idea may be obtained even at a single station.

The synoptic survey results indicate that deep water stations are least affected by changes in distribution. In the shallow northern and southern areas of the lake, pronounced depletion or concentration effects are evident (Figs. 11 and 12). At deep water

TABLE 3

The coefficient of dispersion of various age groups of *P. hessei* as determined from the three synoptic survey collections.

	6/8/1971			28/1/1972			11/2/1972		
	$\frac{\text{Variance}}{\text{Mean}}$	χ^2 d.f = 23	P	$\frac{\text{Variance}}{\text{Mean}}$	χ^2 d.f = 24	P	$\frac{\text{Variance}}{\text{Mean}}$	χ^2 d.f = 24	P
Nauplii	5.50	126.6	< 0.001	7.47	179.2	< 0.001	2.25	54.1	< 0.001
C_{I-III}	4.09	94.1	< 0.001	7.29	174.8	< 0.001	32.9	789.6	$\ll 0.001$
C_{IV-V}	0.80	18.3	~ 0.75	2.72	65.3	< 0.001	6.99	167.8	< 0.001
Adults	2.21	50.9	< 0.001	2.18	52.4	< 0.001	1.80	43.1	< 0.01
Total *P. hessei*	7.94	182.6	< 0.001	7.43	178.4	< 0.001	30.76	738.3	$\ll 0.001$

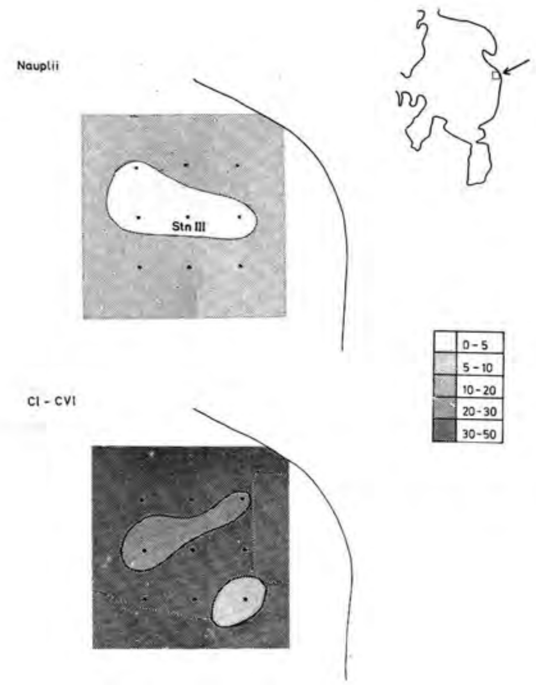


Fig. 13. The horizontal distribution of nauplii and copepodites of P. hessei around Station III (2/2/1972). The abundance is expressed as numbers per metre of net haul (i.e. approximately 31 litres, assuming 100% filtration efficiency).

stations, the changes are less pronounced. The routine stations have been, for the most part, deep water stations and the results obtained at these stations are therefore likely to be more representative of general seasonal changes in abundance than would samples collected from shallow stations.

Superdispersion and infradispersion

The concepts of superdispersion and infradispersion have been used fairly extensively to describe the horizontal distribution of zooplankton (e.g. Comita and Comita 1957). These concepts based upon Fischer's coefficient of dispersion ($\frac{\text{variance}}{\text{mean}}$) are strictly applicable to the horizontal distribution within a limited vertical plane, but have been used in describing the horizontal distribution based on vertical net hauls of reasonable length (e.g. 0 - 40m, Ricker 1937). On the basis of the synoptic surveys described above, these concepts would appear to be of limited value in describing the distribution of P. *hessei*. On all three synoptic survey dates all age groups of P. *hessei* are very significantly superdispersed (Table 3) apart from the age group C IV - C V, which during the 6/8/71 survey, shows a random to slightly infradispersed distribution. However, examination of the iso-frequency maps shown in Figs. 11 and 12 reveals extensive changes in the overall distribution pattern even though the calanoids are superdispersed at all times.

Small scale horizontal distribution

The synoptic surveys have demonstrated the horizontal distribution over the entire area of the main basin of Lake Sibaya. Small scale horizontal distribution has been examined around Station III on 2/2/72. These observations, based on bottom to surface net hauls, are shown in Fig. 13. Adjacent sampling sites were separated from each other by approximately 300m. These data may be compared with the more extensive synoptic survey findings of 28/1/72 (Fig. 11b).

Variations in abundance were evident around Station III. Notwithstanding the existence of these variations, the general pattern of abundance is readily accommodated within the lake-wide abundance pattern shown in Fig. 11b.

Considerable interest has been shown in the mechanisms which bring about the horizontal distribution patterns observed in zooplankton. On a lake-wide scale Patalas (1969) has been able to correlate the large scale horizontal distribution of zooplankton in Lake Ontario with temperature differences existing across this lake. On a spacially smaller scale, Stavn (1971) has examined the distribution of Daphnia within simulated Langmuir circulations. He has been able to show that the distribution of Daphnia in such spirals can be attributed to a combination of differing behaviour patterns in fast and slow currents in the presence or absence of light.

The origin of patchiness in P. hessei is not attributable to temperature variations and there is little likelihood that it results from large scale differential food availability. A priori, the role of Langmuir circulations in modifying the small scale distribution of the calanoid would appear to be slight. In Sibaya, current reversals have been recorded to a depth of approximately 20m during Force 3 - Force 4 conditions (Allanson, unpublished data). It is plausible, therefore, that this is the lower limit to which Langmuir circulations are effective at similar wind velocities. As will be demonstrated in the succeeding section, the copepodite stages of P. hessei are chiefly below this depth during daylight in sufficiently deep areas of the lake, or else closely associated with the lake bed in stations shallower than 20m. Accordingly, it might be expected that these stages will be little influenced by Langmuir circulations during daylight. At night, when the calanoids migrate into superficial waters, they will come under the potential influence of the spirals. However, the winds generally drop considerably after nightfall, thereby reducing the velocity and depth of the Langmuir spirals and, supposedly, the influence that these spirals will have on the calanoids.

Wind induced currents undoubtedly play a major role in modifying the distribution of P. hessei. This is clearly evident from the synoptic survey findings. However, further elucidation of the horizontal distribution, its origin and changes, is clearly required. Lake Sibaya, by virtue of its homogeneous nature and extensive subjection to wind stress, provides an ideal situation for a detailed study of this aspect of plankton distribution.

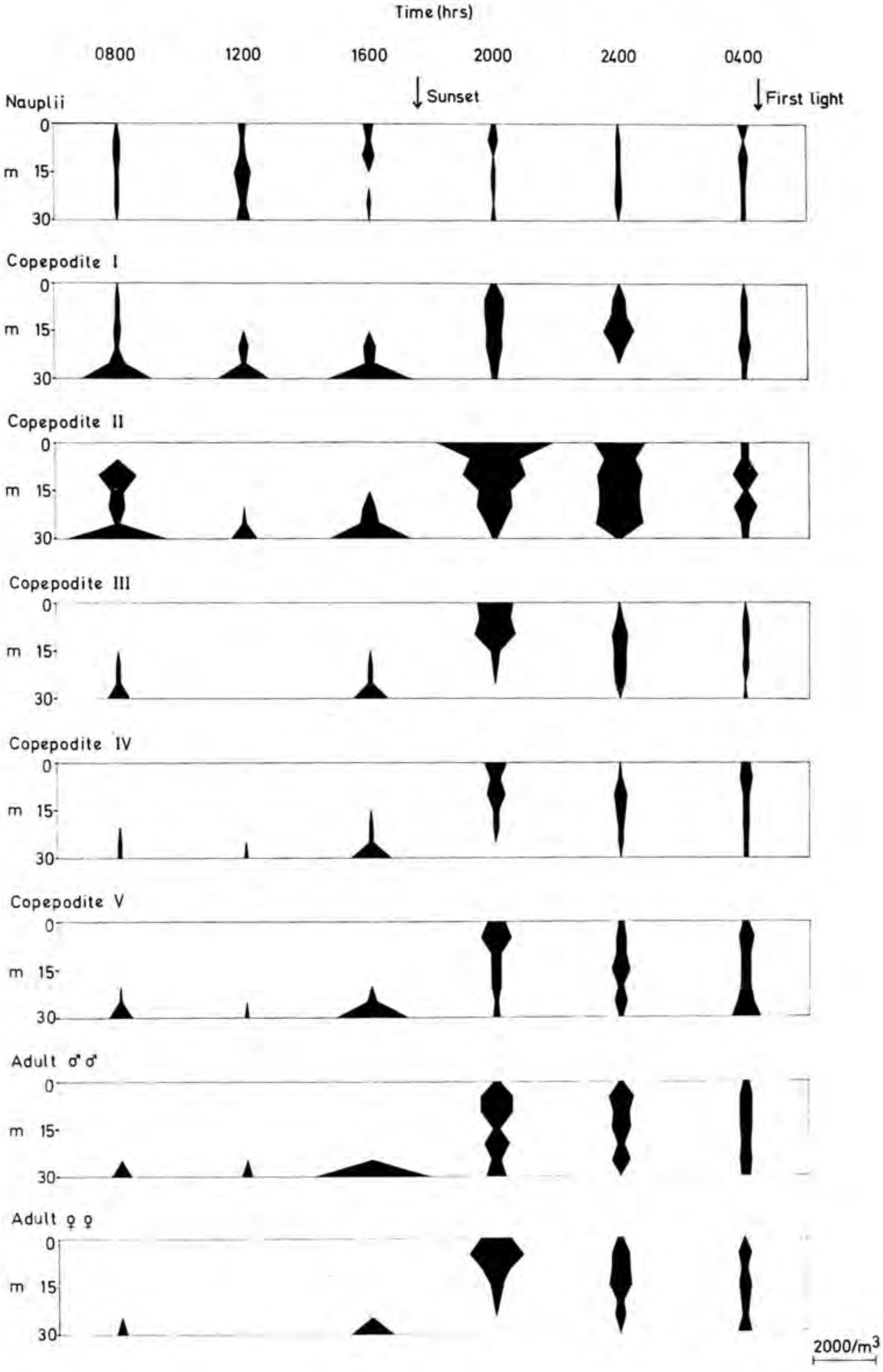


Fig. 14. P. hessei: Changes in vertical distribution during 24 hours at Station III, 10 - 11 April, 1970. Developmental stages illustrated sequentially. Collections made with a Friedinger sampler.

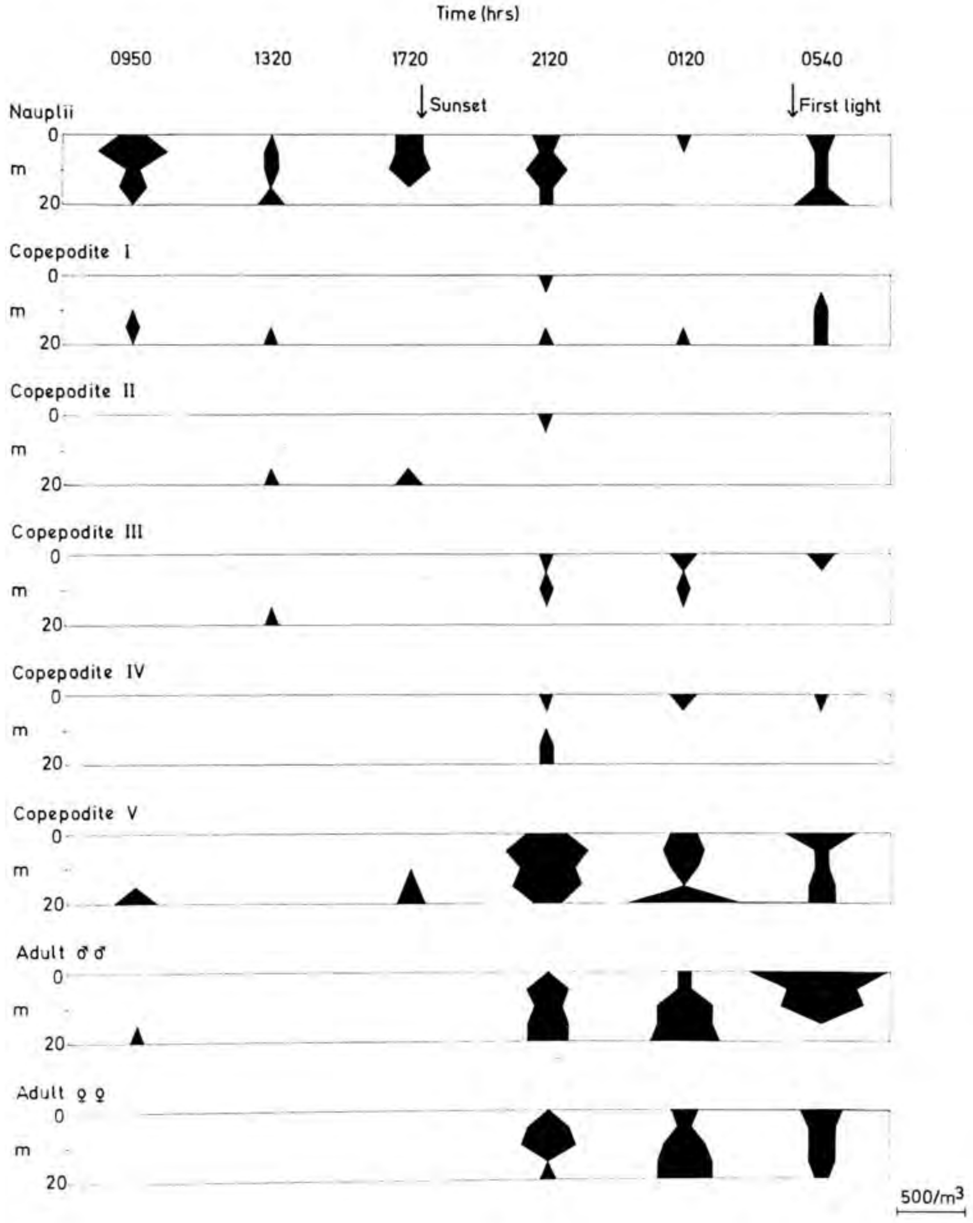


Fig. 15. P. hessei: Changes in vertical distribution during 24 hours at Station IV, 10 - 11 April, 1970. Developmental stages illustrated sequentially. Collections made with a Friedinger sampler.

THE DAYTIME VERTICAL DISTRIBUTION PATTERN OF PSEUDODIAPTOMUS HESSEI

Introduction

In April, 1970, a twenty-four hour sampling series was undertaken at two stations (Station III and Station IV), in order to establish the diel changes in vertical distribution of the planktonic crustacea. Collections were made by means of a 2 litre Friedinger water sampler. The diel changes in distribution recorded in the different developmental stages of *Pseudodiaptomus hessei* are given in Figs. 14 and 15, for Stations III and IV respectively. The existence of diel changes in vertical distribution of *Bosmina longirostris*, *Moina* sp. and the cyclopoid copepods was also established by this series, but the migratory movements of these species are not described in the present work.

The vertical distribution of the different stages of *P. hessei* shown in Figs. 14 and 15 was most interesting in relation to the apparent absence of the adult and later copepodite stages from the water column during the hours of daylight. The conspicuously low catches during daylight were open to two explanations. The calanoids could either be reaching the lake sediments, where sampling was impossible, or they could be avoiding the sampling device.

Although avoidance of sampling gear is known (*vide* Smyly, 1968b), subsequent work on the species in Lake Sibaya has shown that this is not sufficiently pronounced to result in the diel changes in distribution recorded. This is in accord with most previous observations where workers were concerned with avoidance behaviour.

The movement of the same species of calanoid onto the sediments of shallow estuaries (1 - 3m deep) has been recorded by Grindley (1965). Similarly, Worthington and Ricardo's (1936) studies on the vertical distribution of zooplankton in several East

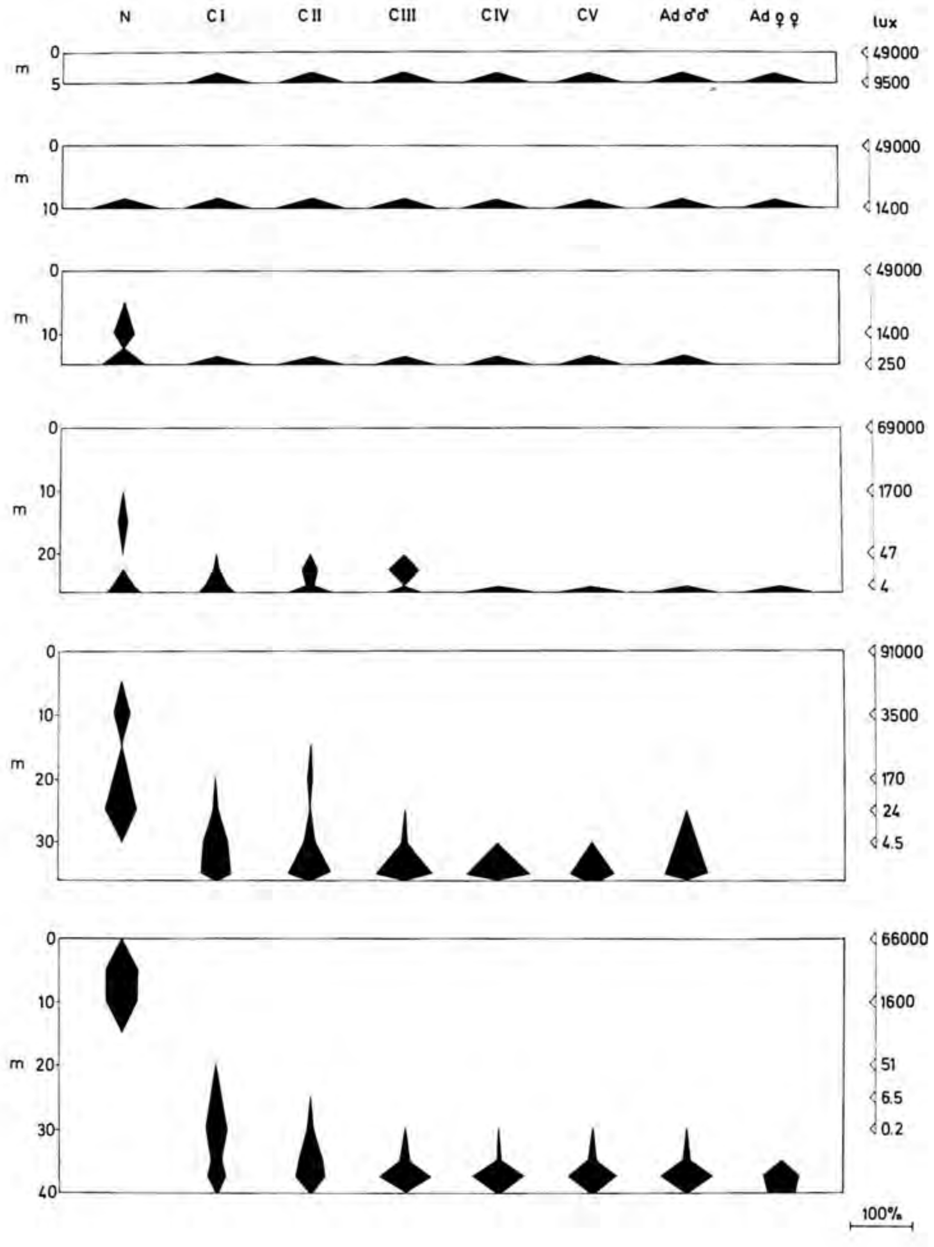


Fig. 16. P. hessei: Percentage vertical daytime distribution of developmental stages at six stations of increasing depth, 22 March, 1971. Lux values indicated on right hand margin. Collections made with Friedinger sampler and vertical bottom sampler. Samples collected between 1000 and 1500hrs.

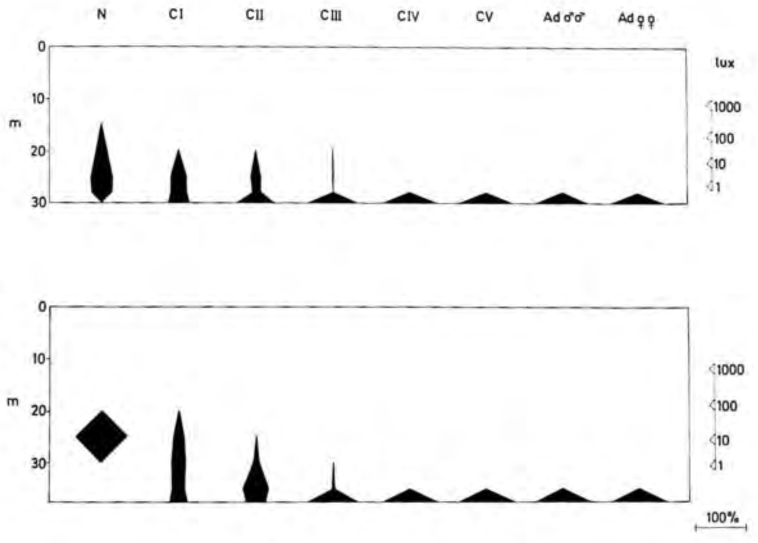


Fig. 17. *P. hessei*: Percentage vertical daytime distribution of developmental stages at two stations, 3 September, 1971. Lux values indicated on right hand margin. Collections made with van Dorn sampler and Jenkin sampler. Samples collected between 1100hrs and 1300hrs.

African Lakes have led them to conclude that two planktonic crustacean species moved onto the bottom (at 15m) in Lake Naivasha. It seemed likely, therefore, that movement onto the substrates could account for the absence of the older stages of P. hessei from the water column during daylight hours.

The daytime distribution pattern

Several special daytime sampling series were undertaken to assess critically the daytime vertical distribution of the calanoid. Various collection techniques were used, and simultaneous light measurements were made where possible.

Fig. 16 shows the percentage vertical distribution of different developmental stages of P. hessei at several widely spaced stations on a North/South transect from Station I to the southern end of the lake. Water column samples were collected by means of a Friedinger water bottle. Attempts were made to determine the density of the calanoids on the substrates using the vertical bottom sampler (p 42). Water column collections indicate the progressive proximity of successively older stages to the lake bed. At very shallow stations, all stages of the calanoids were captured only on the lake bed. The low catches of animals on the deep water substrates are most probably the result of inefficiencies in the bottom sampler. Subsequent work has demonstrated the abundance of the calanoids on the lake bed in deep water as well as in shallow water, and it was realized at the time that the vertical bottom sampler was not entirely efficient.

A more restricted sampling series (shown in Fig. 17) was carried out using a Jenkin sampler to assess bottom-dwelling populations and a transparent van Dorn water bottle to assess the pelagial component. This series confirmed the paucity of older stages of P. hessei in the water column; the substrate collections made

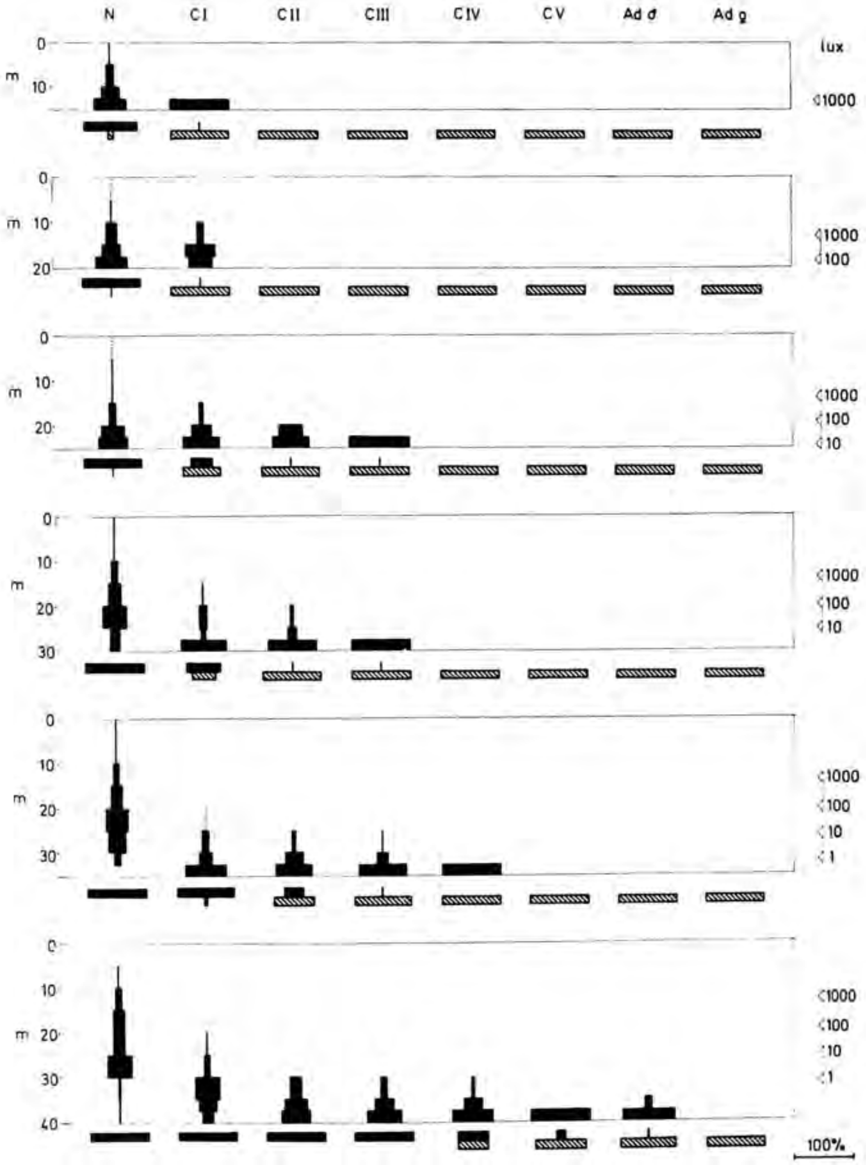


Fig. 18. Percentage vertical daytime distribution of developmental stages at six stations, 16 March, 1972. Distribution in the water column represented by histograms in panels. Two bar histograms below the panels represent the percentages of animals in the water column (solid black) and on the substrates (shaded). (See text on pp 53 - 57 for derivation.) Isolumes of 1000, 100, 10 and 1 lux indicated where applicable on right hand margin. Dotted lines are used where the number of animals captured in a particular depth stratum was insignificantly small. Net haul and substrate bin collections. Samples collected between 1030hrs and 1330hrs. Wind - Force 2, Easterly.

with the Jenkin sampler showed clearly the pronounced association of the older calanoids with the lake sediment. At both the 30m and 40m stations, copepodites IV, V and adult _P_. _hessei_ were captured _only_ on the substrates.

The most detailed analysis of the daytime vertical distribution of _P_. _hessei_ is based upon net haul and substrate bin collections at six stations of increasing depth. Net hauls (over very short intervals near the lake bed), together with substrate bin collections and light recordings were made on a transect between Station I and Station III. The percentage vertical distribution of different developmental stages is presented in Fig. 18. While the following description is based upon Fig. 18, the general pattern evident in Figs. 16 and 17 is comparable.

The variation in daytime vertical distribution in different sexes and developmental stages of P. hessei.

The vertical strata occupied by the developmental stages of _P_. _hessei_ vary considerably. The predominant pattern is one of an increase in day depth in the progressively older stages (Fig. 18). Since this may bring them into association with the substrate, the vertical distribution is necessarily truncated and accordingly compressed.

Nauplii are present practically throughout the water column, although their densities in the surface 5 or 10 metres are low. Numbers on the substrates are relatively low at stations of 15m and deeper. They are not encountered on the substrates below 25m and are, in fact, absent from the deepest waters at the 35m and 40m stations. Maximum abundance lies between 20m and 30m, between approximately 100 lux and 5 lux.

Stage I copepodites are mainly on the substrates at stations shallower than 25m but do not occur on the 40m substrates. In pelagial waters they are found mainly below 15m and are most abundant between 30m and 35m at light intensities below 5 lux.

Stage II copepodites are restricted to the substrates at stations shallower than 20m and are most abundant in the water immediately overlying the substrates at 40m, although they do not occur on the sediments at this depth.

Stage III copepodites are entirely benthic at stations shallower than 20m, with only very low percentages inhabiting the water column at stations between 25m and 35m deep. However, the entire population is pelagic at the 40m station.

Stage IV copepodites are entirely benthic at stations shallower than 30m and although some individuals are present in the water column between 32.5m and 35m at the 35m station, the pelagial fraction is less than 1% of the total. At 40m, however, approximately half the population is pelagic.

Stage V copepodites are predominantly benthic. At the 40m station only a very small percentage of this stage is pelagic, and these individuals are below 37.5m.

Adult males and females are predominantly benthic at all stations. Very low percentages of adult males are present in the pelagial waters below 35m. In the collections shown in Fig. 18, adult females were not captured in the water column. From other collections it has been noticed that where adult females do occur off the substrates during daylight hours, these are mainly non-ovigerous females. Ovigerous females have almost never been encountered off the substrates during daylight hours when the sun is high. The significance of this observation is not known. This distribution pattern may play some part in the reproductive biology of the species. Since sufficiently detailed investigations of the vertical distribution of other freshwater calanoids which reach poorly illuminated substrates during daylight are lacking, it is not possible to compare these observations with those of independent works.

Worthington and Ricardo (1936) have reported that egg-bearing females of Cyclops hyalinus were not encountered above 10m in Lake Naivasha at midday. They believe the adults of this species reach the bottom sediments during daylight. However, in view of the shallowness of their station, it is not possible to dismiss the effects of light intensity alone in bringing about this pattern, although Beadle's (1932) data on photosynthesis might be taken to indicate rapid light attenuation in this lake. McNaught and Hasler (1966) have reported that during daylight, Limnocalanus macrurus may be either benthic or within a few metres of the bottom in Lake Michigan (at a 40m station) but unfortunately their data were not analysed by sex or reproductive state.

Seasonal variations in daytime vertical distribution

Although routine daylight vertical collections have not been undertaken on a seasonal basis, collections from different times of the year are available. From these collections it is clear that no significant seasonal changes are involved, and the available data indicate the generality of the pattern described above. For example, one collection was made during a period of strong thermal differentiation, with a thermal gradient of 3.8°C over 34m.[1] The vertical distribution under these conditions was indistinguishable from that of other daytime collections made during homothermal periods.

Seasonal changes in the daytime vertical distribution of

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[1] The occurrence of such a pronounced thermal gradient is not a regular feature in Lake Sibaya. This was by far the largest thermal discontinuity recorded between 1969 and 1972.

crustacean zooplankton have been reported by many workers in temperate lakes (Carter 1969, Langford 1938, for example). In temperate latitudes important seasonal changes in incident illumination levels and in the thermal structure of lakes would be expected. In the present study area, seasonal changes in incident light intensity are not very pronounced. The similar distribution patterns observed at different seasons are therefore not unexpected.

Daytime vertical distribution under various weather conditions

The vertical distribution of *P. hessei* has been studied under two widely different weather conditions, separated by several days. On 7/1/1972, the vertical distribution was studied at Station I in bright, clear, calm and sunny conditions, with incident light intensity in excess of 100,000 lux. At the same station on 13/1/72, the distribution was determined in conditions of total overcast, wind and intermittent rain, with incident light intensity of only 38,000 lux. The distribution patterns observed for the different stages on the two dates were indistinguishable. The 1 lux isolume lay at 30.2m and 27.0m at midday on the two respective dates.

These observations contrast with the conclusions reached by Cushing (1951). The results reviewed by him have indicated that the plankton occur much nearer the surface under windy and rainy conditions. Cushing suggests that "the effect of weather is firstly to cut off the light by breaking the surface, and secondly to make the upper layers physically uninhabitable." The first of these postulated effects appears to play no determinable part in modifying the distribution of *P. hessei*.

Variation in distribution during daylight hours

The preceding description of the day depth of *P. hessei* has related mainly to the pattern as observed between 1000hrs and 1400hrs,

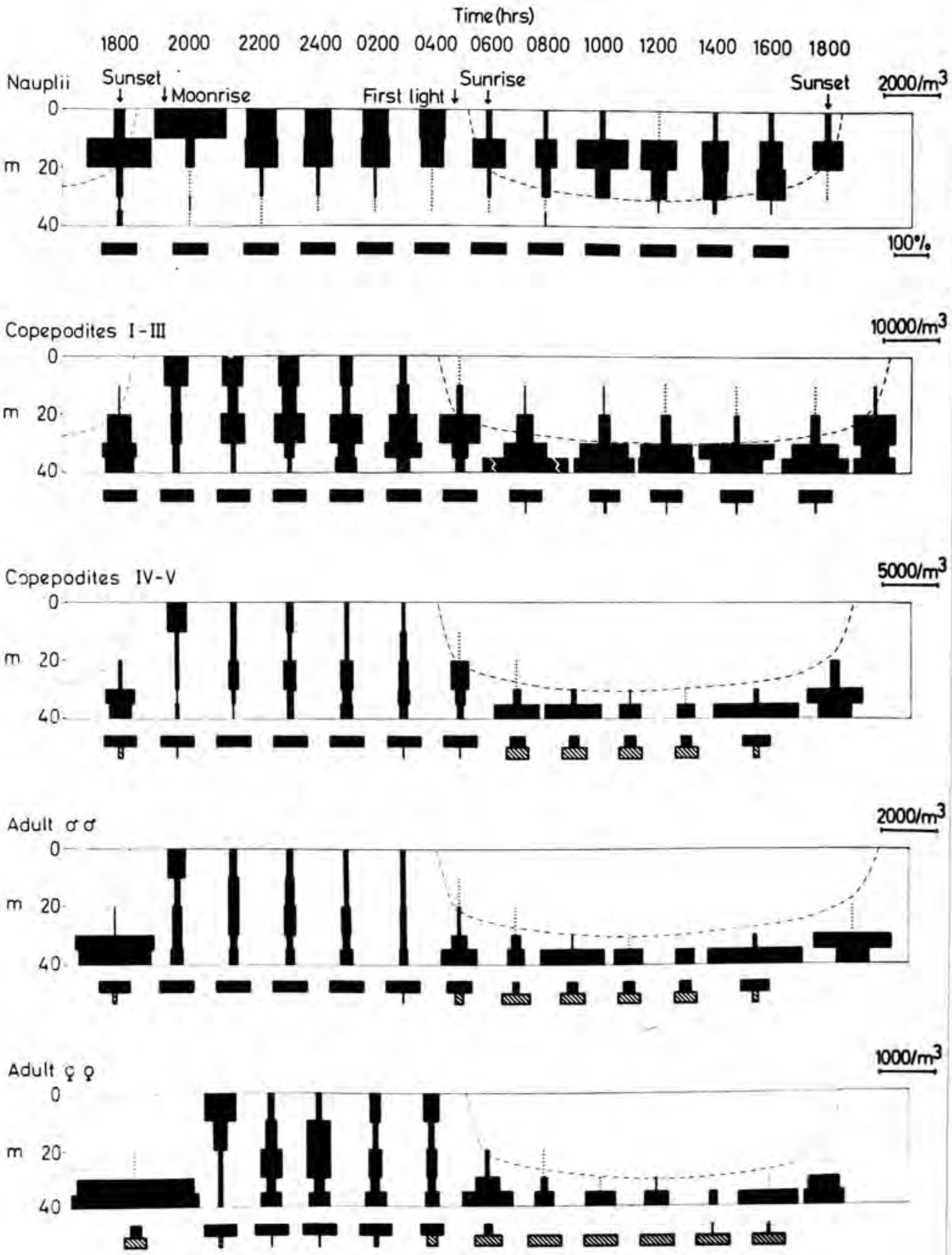

Fig. 19. P. hessei: Changes in vertical distribution at Station I during 24 hours, 1 - 2 March, 1972. Developmental stages illustrated sequentially with respective scales. 1 lux isolume indicated by means of dashed line. Net haul and substrate bin collections.

when the sun is high. However, an examination of the distribution through daylight hours (excluding the dusk and dawn periods), is informative. Fig. 19 shows the vertical distribution of different stages through 26 hours. The distribution of the various stages from 0800hrs to 1600hrs is very similar and demonstrates the apparently static nature of the distribution. This contrasts with the changes in distribution through daylight hours reported for other zooplankton (reviewed by Cushing, 1951). Small vertical changes in distribution, not apparent from the present sampling techniques, may be significant, and, in default of further information, it is unwise to stress unduly the apparently static distribution which has been observed. However, in comparison with other studies, where equally long hauls have been employed, the distribution of P. hessei is remarkably constant through the day.

The species shown most clearly to exhibit day to day and hour to hour changes in its vertical distribution is the marine calanoid Calanus finmarchicus. This is undoubtedly a pelagic species which does not occur regularly on interfacial sediments, although detailed observations of the vertical distribution of the species in very shallow waters might show otherwise. In this connection it is interesting to note that Kos (1969) reports large masses of Calanus glacialis, C. plumchrus and C. cristatus among algae near the bottom and digging themselves into the ooze in Possjet Bay, Sea of Japan. Unfortunately the depth at which these observations were made is not stated in the abstract. Reference to Bartholomew (1958) indicates that Possjet Bay ranges in depth from 0 - 50m. It would therefore appear that these observations were made in comparatively shallow waters.

On the basis of what is known of the daytime distribution of P. hessei, it may be appropriate to describe the calanoid as facultatively planktonic, certainly in the adult and late copepodite stages. The constancy of its daytime vertical distribution might then be ascribed to the facultatively planktonic mode of life of the species.

The daylight substrate association or "benthic" existence of P. hessei.

The preponderence of the older calanoids on the lake substrates during daylight is most interesting. The significance of this association and the mechanism underlying it are obviously worthy of analysis, since this pattern is not commonly reported in the literature.

It is necessary to determine whether the benthic association of the calanoids in the deepest waters results from a purely photonegative reaction. Given a greater depth of water (e.g. 70 - 100m) would the adults continue migrating until they reached the lake bed, or would they assume a typically pelagic day depth?

Two points must be considered in relation to these alternatives.

1. The typical habitat of this calanoid species.
2. The light intensity in the deep waters.

P. hessei is typically an estuarine species. In its normal habitat it is therefore encountered in water of limited depth. Many estuaries in which the species occurs are shallower than 3m. The deepest estuarine system in which P. hessei is known to occur is Lake Nhlange (50km. to the north of Lake Sibaya) which has a maximum depth of 31m (Hill 1969). The vertical distribution of the species in this lake is unfortunately unknown. The presence of the species in shallow estuaries would suggest that bright light intensities do not restrict the species' success. Grindley (1972) has reported that the species digs itself into the bottom sediments when subjected to bright light. Comparable behaviour has not been observed for the Sibaya populations of the species, although extensively sought under

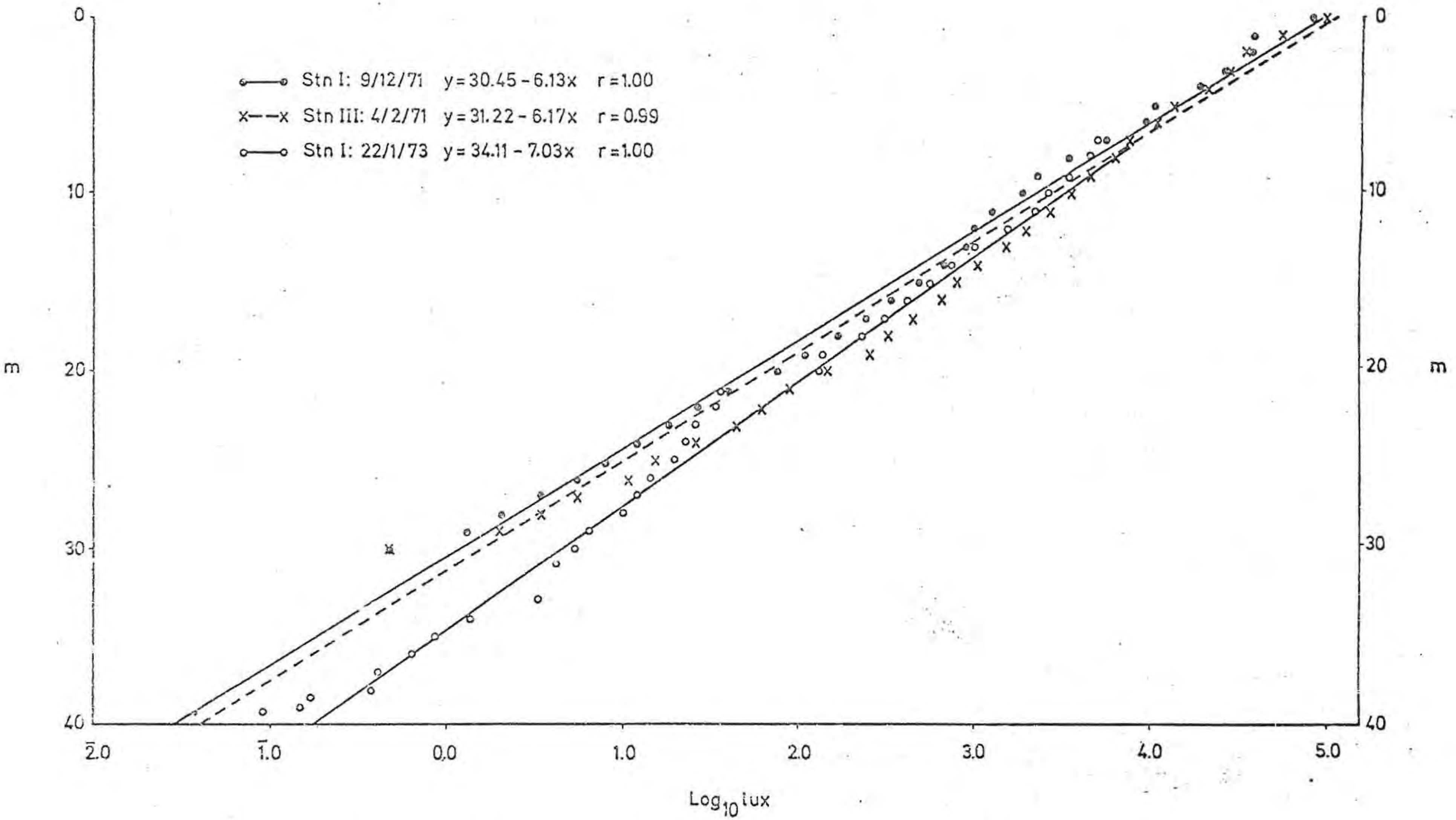

Figure 20. Relationship between log lux and depth in the open waters of Lake Sibaya.

both field and laboratory conditions.

Some idea of the midday light intensities below 30m in Lake Sibaya has been obtained, firstly by linear extrapolation of light penetration data obtained with the Hydrobios luxmeter and secondly by direct measurement with Dr. R.E. Boltt's photometer. These data are shown in Fig. 20. Extrapolation of the luxmeter readings gives estimates of light intensity at 40m of 3×10^{-2} to 4×10^{-2} lux. Direct measurements with Dr. Boltt's photometer gave a value of 9×10^{-2} lux at 39.3m. The discrepancy between the extrapolated and direct values is not unreasonably large and is most probably due to slightly different calibration of the two instruments or to temporal differences in lake transparency. Concurrent calibration of the two instruments has not been possible owing to mechanical failure of the luxmeter.

Although light threshold values are unknown in P. hessei, and in calanoids in general, there is every likelihood that light of this intensity can be discerned by P. hessei.

No records of the vertical distribution of P. hessei in waters deeper than 40m exist. In the absence of such information, an attempt has been made to estimate the depth at which the adults might be expected to be pelagic, given adequately deep waters. The modal depths of the nauplii, C I and C II stages at the 40m station (Fig. 18) increase in a regular fashion. By assuming that the modal depths of subsequent stages will show an equally regular increase, linear extrapolation of the modal depths of nauplii, C I and C II indicates that modal concentrations of adult P. hessei might be expected between 55 and 65m in waters of "unlimited" depth. This depth stratum (55 - 65m) would be the expected pelagial day depth of P. hessei.

Continued linear extrapolation of the luxmeter light penetration data shown in Fig. 20 gives expected values of 15×10^{-5} and 41×10^{-7} lux (based on the mean of both regression lines) for the upper and lower limits of the theoretical modal depth. Extrapolation of Dr. Boltt's photometer readings gives corresponding values of 13×10^{-4} and 50×10^{-6} lux.

Vertical migrations of marine crustacea at depths of 500 - 1000m have been recorded (cited in Waterman, 1961). This implies that they perceive illumination at intensities of not more than about 1×10^{-6} lux. A threshold estimate of 10^{-5} to 10^{-6} lux has been recorded in the prawn Palaemonetes (cited in Waterman, 1961). In freshwater crustaceans, eyeless Daphnia magna have been reported to respond to light intensities of 5×10^{-3} lux (Harris and Mason 1956). In Parry Sound, the daytime median distribution depth of adult Limnocalanus macrurus is generally between 55 and 75m except during spring and early summer, when the adults occur nearer the surface. The median distribution depths of all stages of Senecella calanoides are generally below 60m except in March (Carter 1969). In Lake Michigan in August, L. macrurus only appears off the bottom (40m) at sunset, at a light intensity of 2×10^{-2} lux at 35m (McNaught and Hasler 1966). In Lake Ontario, L. macrurus is concentrated in the 75 - 100m stratum at midday in September (Patalas 1969). In Lake Lucerne, the average depth of adult Diaptomus laciniatus is below 70m during midmorning and the younger stages (apparently late copepodite instars) are below 50m during the same period (Worthington 1931). These observations, for the most part made in lakes more transparent than Sibaya, suggest that P. hessei might be expected to move into deeper waters if this was possible in Lake Sibaya. Nevertheless, if P. hessei was pelagial at 55 or 65m, it would be reasonable to assume that it was living at the extreme lower limit of its visual acuity.

In the light of these arguments, the profundal benthic existence of adult P. hessei might represent little more than a simple photo-negative response, although considerable visual sensitivity by the adult calanoids is necessarily inferred by this interpretation.

Substrate preferences

Although it is unlikely that an animal which is planktonic by night should be dependent upon substrate type, an investigation of substrate preferences in the species was made in order to assess more rigorously the "benthic" association.

Substrate choice experiments were made under laboratory conditions using a clear perspex choice chamber system with sliding partitions. Experiments were carried out in complete darkness and in diffuse indoor light. Exposed littoral sand and profundal mud covered with flocculent tripton were offered as alternatives. In some experiments a third choice was offered, viz. bare perspex. No consistent results were obtained in several experiments.

Field experiments using suspended trays have supplemented the laboratory observations. Suspended trays (p 49) containing profundal mud, littoral sand, or exposed with no introduced substrate, were set out near the lake bed at a 20m station overnight. They were retrieved at mid-morning on the following day. Approximately equal numbers of calanoids were found on all substrate types in several replicate collections. Although this approach has several limitations, the absence of any consistent preference or avoidance of any of the substrate types investigated suggested that substrate type is immaterial to the calanoids.

The field results alone could be criticised on the basis of not accounting for a possible over-riding effect of light forcing the calanoids to remain on any substrate once reached. The labora-

TABLE 4.

Catches of P. *hessei* in suspended trays at increasing depths at Station I on two dates.

	7/12/1971				9/12/1971			
Depth m.	Adult ♂	Adult ♀	CI-CV	Total P. *hessei*	Adult ♂	Adult ♀	CI-CV	Total P. *hessei*
5	3	40	42	85	2	12	30	44
10	9	45	85	139	27	49	187	263
15	7	53	86	146	30	56	317	403
20	18	77	156	251	26	87	192	285
25	45	121	261	427	*31	69	199	299
30	81	244	555	880	*79	133	442	654
35**	201	126	258	585	115	255	905	1275
40	295	819	1974	3088	353	966	1287	2606

* Closing of lids not entirely satisfactory.

** Several shrimps (*Caridina nilotica*) were captured in this suspended tray. The disproportionately low calanoid catch may be related to disturbance by *Caridina*.

tory studies, however, have confirmed the absence of substrate preference in a system where light cannot override the other responses. In view of the planktonic nature of the calanoids at night, the lack of obvious substrate preferences was not unexpected.

The relative importance of substrate and light intensity in the daytime vertical distribution.

If it is assumed that the calanoids migrate downwards at dawn until they reach a solid substrate, it would not be unreasonable to expect them to settle on solid substrates suspended in the water column. If, on the other hand, they were moving downwards in avoidance of high light intensities, it might be expected that they would not remain on artificial substrates suspended in the water column at light intensities within the critical intensity range. In designing apparatus to investigate these alternatives, the height of the vertical walls of the apparatus (suspended trays) was restricted as far as possible. This was done in order to restrict the extent of upward swimming necessary for the calanoid to leave the artificial substrates.

In view of the apparent insignificance of substrate type, described above, experiments were carried out using littoral sand, from which the copepods could be most easily separated for counting.

Trays were suspended overnight at 5m intervals at Station I and retrived around midday. Results of two series of collections made at Station I are given in Table 4. It is assumed for the present purposes that the catches in each tray result from the downward migration of the calanoids at dawn. Starting with a uniform vertical distribution through the water column, the catch in the tray at 5m should represent all animals present in the 5m above the tray. This catch may be denoted by n. The catch in the 10m tray should be 2n, in the 15m tray 3n, etc., to 8n in the 40m tray. Collections in the 5, 10, 20 and 40m trays should therefore yield successively doubled catches, if the initial vertical distribution is uniform, and if the animals, once reaching a substrate in daylight, remain there.

While the vertical distribution is undoubtedly not uniform through the water column prior to the dawn descent (see Figs. 14, 15 and 19), Table 4 shows that significant increases in catch are generally obtained from the successively deeper collections. In the 7/12/1971 series, the postulated doubling (in total P. hessei) is evident between the 5, 10 and 20m collections. This suggests that movement off the shallower trays does not occur. In the 20m versus the 40m catch, 12-fold and 9-fold increases are evident for the two dates. These very large increases between the 20m and 40m collections are unexpected and may be a result of initial uneven vertical distribution of the calanoids. They could also be taken to indicate that there is movement of the animals off the midwater trays (those at 20 - 30m for example) and subsequent arrival in the 40m levels.

It is significant that animals are found in reasonably large numbers in the shallower collections. Animals in the 5m tray would be subjected to midday light intensities in excess of 10,000 lux, and those at 10m to 2000 lux. These intensities are considerably greater than those apparently "selected" by the calanoids when they have access to sufficiently deep water. If bright light was deleterious to the organism, some "distress" response or agitation might be expected, the most likely result being an increase in locomotor activity. If this occurred, it could be expected that random movements would result in the calanoids leaving the trays. Once clear of the horizontal area presented by the trays, the animals would be in the pelagial waters. Once in the open waters, either active locomotion and/ or passive sinking should result in their movement into deeper waters.

Irrespective of their subsequent behaviour or future in the water column, they would not be captured in the suspended trays in any significant numbers.

The results given in Table 4 demonstrate that significant numbers are captured in the trays suspended near the lake surface, suggesting the unlikelihood of large scale movements out of the suspended trays. As a result of these observations, it could be postulated that a thigmokinetic reaction overrides the photic response on well illuminated substrates. Such a mechanism would obviously have a strong selective value in relation to visual discrimination of the calanoids by predators. Movement of the animals in brightly illuminated waters would enhance their visual recognition by potential predators. If they merely remained quiescent on the bottom, however, predation by forms relying on visual recognition of prey would be considerably reduced (Maly 1970).

Evidence for massive horizontal redistribution of _P. hessei_ has been presented. The transportation of large numbers of the calanoid into relatively shallow areas of the lake has been demonstrated. The postulated selective advantage of this thigmokinetic response, under conditions of bright light intensity, would therefore be very real. The shallower waters of Lake Sibaya accommodate most of the juvenile cichlid population (Bruton, 1973). Predation upon the calanoids could be very large in the absence of adequate protective responses.

The collection of calanoids in the shallow suspended trays is open to another interpretation. It can be argued that presence of a bright overhead light source would prevent any active ascent by a negatively phototactic animal. In this way, therefore, the very response directing the calanoids into deeper, darker waters also "traps" them in shallow, brightly illuminated areas. If this

TABLE 5.

Daytime activity of *P. hessei* on the lake bed at various depths, assessed in terms of recruitment into substrate bins exposed after sunrise for 2 and 5 hour periods. The bins were positioned near Station I. The effects of any horizontal patchiness were reduced as far as possible by positioning the bins within 300 m of each other.

	38.5m		32.5m		27.5m	
Exposure Retrieval time	2 hrs. 1048hrs	5 hrs. 1353hrs	2 hrs. 1115hrs	5 hrs. 1420hrs	2 hrs. 1145hrs	5 hrs. 1455hrs
Adult ♂♂	217	308	8	18	1	0
Adult ♀♀	31	77	4	4	0	0
CI-CIII	163	177	120	40	218	52
CIV-CV	337	502	80	66	7	2

results in a quiescence then the overall result, which is likely to be of selective value, as argued above, remains the same. The obvious success of the calanoids in brightly illuminated, shallow estuaries (*vide* Grindley 1972) indicates that the species is adequately adapted to succeed in such systems, although the importance of its "burrowing" behaviour (Grindley, *loc. cit.*) is not known.

Daytime activity on the deep water substrates.

It has been suggested in preceding pages that the daytime benthic association of adult *P. hessei* may be a function of the light sensitivity of these calanoids, resulting in their movement into the darkest possible waters. Also, it has been shown that if the calanoids arrive at a brightly illuminated substrate during the course of their dawn migration, they will remain there, apparently "oblivious" of the incident light intensity (suspended tray results). However, it was apparent that the suspended tray results depended in part upon various assumptions which were not necessarily valid and it appeared necessary to examine the relationship between light intensity and daytime activity in another way. Substrate bins, exposed after the dawn descent and subsequently retrieved after various intervals, have provided further information about the daytime activity of the calanoids on the natural lake bed. Recruitment of calanoids into the bins during daylight has been used as a relative index of their locomotor activity.

Table 5 shows recruitment into bins exposed at different depths for 2 and 5 hour periods. Significant recruitment of adults is restricted to the deepest station, where light intensity values are very low (4×10^{-2} to 9×10^{-2} lux - Fig. 20). No significant recruitment of adult and late copepodite stages occurs at 27.5m, where midday light intensities of 1 - 3 lux are generally recorded. This set of results shows clearly that daytime locomotor activity

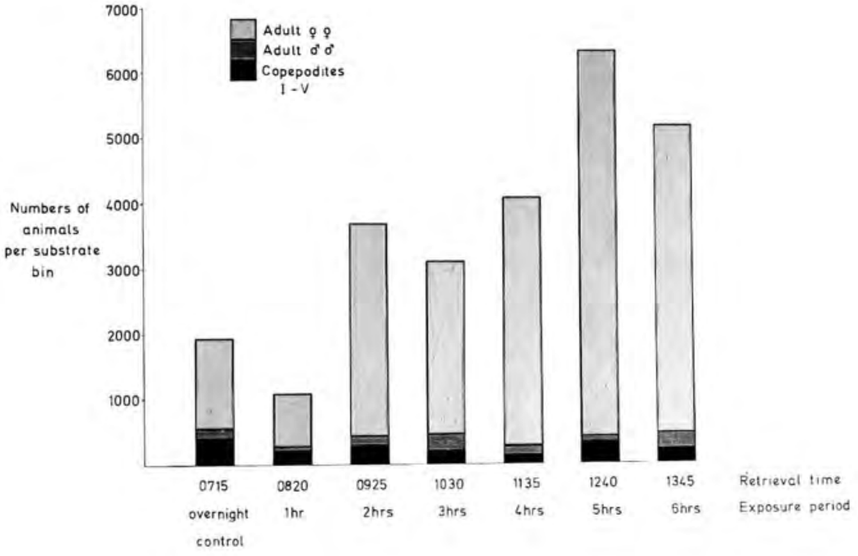

Fig. 21. *P. hessei*: Recruitment of adult and copepodite stages into substrate bins on the lake bed at 39m, during daylight. See text (p. 96) for further explanation.

(assessed as recruitment) is related to depth, and by implication, light intensity. These results therefore offer support for the conclusions based on suspended tray results.

There are difficulties involved in using recruitment rate as an index of locomotor activity, however. If the calanoids were continually active during daylight, it would be reasonable to expect that immigration to and emigration from the substrate bins would balance one another. That calanoids are in fact captured in significant numbers suggests that immigration may exceed emigration. An assessment of changes in substrate bin catch during daylight was therefore made to determine the immigration and emigration pattern more accurately. One substrate bin was exposed overnight and retrieved well after sunrise, by which time the dawn descent is completed. The catch in this bin was taken to represent the expected calanoid abundance per unit area of the lake bed and is labelled as the control in Fig. 21. Six bins were then exposed simultaneously (between 0720hrs and 0745hrs) and retrieved serially at hourly intervals. The calanoid catches after 1, 2, ... 6 hours are shown in Fig. 21, in which the 0715hrs histogram represents the control (overnight) catch.

Fig. 21 shows that after 1 hour, the total calanoid catch is approximately $\frac{1}{2}$ of the control, but that it increases with time to a total of more than three times the control catch after 5 hours (1240hrs histogram). If the catches are considered in relation to age and sex, it is clear that the increases in total catch are almost entirely attributable to recruitment of adult females into the bins. The preponderance of females tends to mask changes in catch of the males and copepodites but close examination of these data shows that only the adult female catches increase reasonably consistently over the six hour period. The percentage changes in adult male catch between consecutive collections exceed the percentage changes of the female or copepodite catches, but the changes in the male and copepodite catches are erratic, showing no consistent increase or decrease.

Circumstantial evidence indicates that P. hessei is predated upon or physically disturbed by the goby, Glossogobius giurus which is the commonest benthic fish in deep water in Sibaya (Bruton 1973). Capture of this fish in a substrate bin is invariably associated with lower calanoid catches than obtained in simultaneous collections in which the fish is not caught. Presumably the goby will also disturb the calanoids on the natural lake bed. If this premise is correct, the daytime entry of the calanoids into the substrate bins may be a function of this disturbance. Since the bins are not regularly frequented by gobies or other fish, they provide a comparatively undisturbed environment. Calanoids entering the bins as a result of extraneous disturbance (as opposed to spontaneous locomotion) will enter an area in which they may remain undisturbed until their dusk ascent. An increasing calanoid population would therefore be expected and the increasing female calanoid catch may be explained on this basis. However, this proposed explanation does not account for the comparatively stable catch of adult males and copepodites. Neither does this interpretation account for the differential catch in successively deeper stations (Table 5). The reasons for these differences are unclear but it is likely that differential visual sensitivity between sexes and developmental stages are involved in part.

The importance of these results to the present investigation is that they show that calanoids are active in varying degree over the deep-water substrates during daylight, although this activity is not necessarily spontaneous and may be induced by predator-avoidance or physical disturbance. Of greatest relevance is the fact that such activity, be it spontaneous or otherwise, is not apparent on shallower, better illuminated substrates. If, indeed, the calanoids are active on shallower, brightly illuminated substrates, the vertical component of their locomotion is apparently insufficient to allow them access into the substrate bins (the tops of which are ~20cm above the lake bed). In even brighter conditions, the 7 cm walls of the suspended tray apparently restrain their exit. In essence, therefore, these data support the hypothesis that the benthic association of the calanoids is a direct result of their light sensitivity, and that given access to deeper waters, this species might be expected to show a typically pelagic day-depth in all its developmental stages.

Feeding on the substrates

One last point must be raised in relation to the daytime association of the calanoids with the profundal sediments. Extensive microscopic examination of the behaviour of the calanoids in association with natural lake sediments has been made under laboratory conditions. A feature consistently observed during many hours of observation was the occurence of extensive ingestion of sedimentary material by calanoids sedentary upon this substrate. Filter currents were conspicuous; ingestion of stained (methyl red) and unstained flocculent sedimentary tripton was observed; faecal pellet production was seen. There was no doubt whatsoever that the calanoids were ingesting particulate material derived from, or in close proximity to, the interfacial deposits. This flocculent material was shown to have a very high chlorophyll, total Nitrogen and phosphate-phosphorus content. These laboratory observations pointed most strongly to the bottom areas being rich feeding grounds for the calanoids. However, subsequent field work has demonstrated that these food sources are not used by the older calanoids in natural conditions, and therefore the migration of calanoids onto the lake bed could not be interpreted as a behavioural adaptation allowing exploitation of these apparently rich food sources. The feeding behaviour of *P. hessei* is discussed in detail in a subsequent section.

Day depth control in *P. hessei*

It has been shown that the developmental stages of *P. hessei* maintain their day depth with some rigidity in Lake Sibaya. In the open waters of the lake, only three abiotic cues are available for depth control purposes during daylight hours.

1. Vertical changes in hydrostatic pressure.
2. Vertical changes in the spectral composition of light.
3. Vertical changes in light intensity.

No biotic cues are known which could be used by *P. hessei* to maintain its vertical position.

1. Pressure

It has long been recognised that vertical changes in hydrostatic pressure provide the simplest and most consistent environmental cue for depth-regulatory purposes under water. However, barosensitivity is not a universal feature of zooplankton in general and only a limited number of species have been shown to be sensitive to realistic pressure changes. Barosensitivity is seemingly less common in freshwater copepods and cladocerans than in their marine counterparts. Knight-Jones and Qasim (1966) found no pressure responses in various freshwater cladocerans and copepods. *Daphnia magna* responds vigorously to large increases in pressure under conditions of total darkness, but the response is markedly depressed in the presence of light (Lincoln 1971). In *Calanus helgolandicus*, Lincoln (loc. cit.) has found evidence for fairly sensitive pressure reception, seemingly unaffected by light. In this species, the overt threshold is approximately 0.7 bar.

Barosensitivity has not been examined in P. hessei and although on the basis of Lincoln's findings, it is possible that P. hessei may exhibit barosensitivity, the very precise depth regulation of this species during daylight would seemingly require greater sensitivity to pressure changes than that reported for C. helgolandicus. Until sensitivity to small changes in pressure is demonstrated, the significance of pressure reception for depth-regulatory purposes in comparatively shallow freshwater environments will remain questionable, certainly in relation to its use for the purposes of depth control during daylight.

2. Spectral composition of light

Changes in the spectral composition of light during its penetration through water are well known. Generally speaking, maximum transmission occurs in the blue or green wavelengths, while red light is most rapidly attenuated. Changes of this nature could conceivably be used by the calanoids to determine their vertical position. Such a mechanism of depth control would depend upon the ability of the photoreceptors to assess the relative proportions of energy of different wavelengths. This would, in turn, dictate a bi- or multi-chromatic vision similar in principle to the trichromatic system reported for Daphnia retrocurva (McNaught and Hasler 1966). However, there is no evidence for a multi-chromatic visual system in copepods, and even if multi-chromatic vision was present, other requirements (not matched by the known complexity of copepods) are involved in using the system for depth regulation. In short, there appears to be little likelihood that copepods are able to use changes in the spectral quality of light for the purposes of depth regulation, although the possibility is somewhat stronger in cladocerans.

It is interesting, nevertheless, that adults and late copepodites of P. hessei show a reasonably clear photonegative response to blue light under laboratory conditions, although their responses to white, red and green light are not consistent (see Appendix 6). McNaught and Hasler (1966) have postulated the existence of a visual pigment with maximum sensitivity in the blue wavelengths in Limnocalanus macrurus, the older stages of which are benthic during daylight, at least during part of the year. This apparent blue sensitivity in P. hessei is logical in view of its vertical distribution. It is clear that even though a multichromatic sensitivity is not necessarily involved, the visual acuity of a species may be related to the predominant wavelength reaching the depths which it inhabits by day.

3. Light intensity

Recent workers (Siebeck 1960, Ringelberg 1961, 1964, McNaught and Hasler 1964) have stressed the importance of light intensity changes as the direct migratory stimulus, certainly at dusk. However, for the purposes of depth control during daylight, the rate of change of light intensity is an inappropriate and meaningless stimulus. The older idea whereby zooplankton were assumed to remain at an optimum intensity provides a simpler explanation for the means by which zooplankton regulate their day depth. The most serious objection to the optimum intensity hypothesis relates to the absence of any known mechanism whereby the optimum intensity can be determined, as it is generally accepted that crustacean photo-receptor systems are unable to measure absolute light intensities (Ringelberg 1961, Waterman 1961, McNaught and Hasler 1964).

This has led McNaught and Hasler to state (1966, p 194) "However, the earlier idea of an optimum intensity might best be considered nothing more than a handy ecological correlation and likely is not a valid explanation for the basic mechanisms of depth control. Detection of changes in intensity of the order of 1% of background would enable zooplankton to appear to follow an "optimum". Today the basic question concerns the visual receptors and their function in depth control." Unfortunately, examination of crustacean visual receptors has not as yet provided adequate information as to how potential optical cues are used in depth control.

The simplest reference point for depth regulation using light intensity might be the depth at which light *of a particular quality* is just perceived. Given that each successive developmental stage is increasingly photosensitive, the present explanation might account for the observed distribution of *P. hessei* in Lake Sibaya.

For *P. hessei* (as for all zooplankters) the most serious difficulty imposed by living at its limit of visual sensitivity relates to loss of orientation should gravitational influences happen to displace it into waters which are "totally" dark. This difficulty could be overcome if some additional mechanism allowed for orientation to gravity. In *Daphnia*, Harris (1953) has suggested that the eye may function as a statocyst. In copepods, no special gravity receptors are known, but in *P. hessei* (as in several other calanoids studied) the free-fall position of living unanaesthatized individuals is "tail" first, the first antennae acting as "parachutes". This natural falling position could be used for orientation to gravity. A calanoid sinking into waters in which no light was visible could swim *upwards* using this orientation mechanism. Thus day depth control in *P. hessei* might be envisaged as an alternation of upward and downward swimming about this critical, just discernable light intensity, or, alternatively, active ascent following passive sinking.

This explanation, albeit conjectural, permits a simple interpretation of the observed daytime distribution of *P. hessei* without the need to invoke the ability to measure absolute light intensity.

The dominance of the species in shallow estuarine habitats (Grindley 1963) which are often brightly illuminated, requires comment in relation to the clear photo-sensitivity exhibited by this species in the deep waters of Lake Sibaya. The wide distribution of this species[1] indicates that it is highly adaptable, occurring in tropical to almost temperate conditions and in a wide range of salinities.

Its success in shallow brightly-illuminated estuaries and lagoons may be a function of this obvious adaptability expressed in relation to its light tolerances. However, there is a possibility that substrate contact may in part be responsible for this tolerance. Thigmokinesis seemingly invokes an insensitivity of the calanoids to the incident light intensity. This is certainly the impression gained from laboratory studies. Upon contact with a substratum, the calanoids become seemingly insensitive to the light source. (Since there is an apparent cessation of locomotory activity upon contact with a substrate, I have referred to the mechanism as thigmokinesis rather than as thigmotaxis - Kenneth 1963).

The viewpoint taken above is based on the assumption that the ancestral form of *P. hessei* was adapted to a deep-water environment (i.e. a marine ancestry) and that colonization of estuarine

[1] *P. hessei* was first described from material collected from the mouth of the Congo River. Grindley (1963) records it as abundant in estuaries and lagoons on the west and south coasts of South Africa as far east as the Kleinmond estuary ($33\frac{1}{2}^{\circ}$S, 27°E). Since then it has been discovered in many of the more northerly estuaries on the east coast of South Africa, as far as the Mocambique border (Kosi estuary system, 27°S, 33°E). Examination of the estuaries and lagoons of Mocambique will most probably reveal its presence even further north.

habitats was a secondary phenomenon. There are several extant marine forms, at least one of which (P. nudus) occurs off the coast of South Africa (Grindley 1963). Conversely, the photo-sensitivity of the species in Sibaya may have been a secondary development, with the estuarine stock from which the Sibaya population arose having been considerably less sensitive to light. The former explanation would seem more probable in view of what is known of the behaviour of P. hessei under estuarine conditions. However, a final conclusion must await a comparison of the visual sensitivity of the estuarine populations with that evident in P. hessei from Lake Sibaya.

THE NIGHT-TIME VERTICAL DISTRIBUTION OF PSEUDODIAPTOMUS HESSEI

The majority of vertical migration studies in freshwater lakes has been based upon observations made either during a single diel cycle, or, in some cases, during several diel studies made at irregular intervals through the year. Regular sampling of the vertical distribution of freshwater zooplankton in relation to seasonal changes in environmental variables has not been undertaken to any great extent. McNaught and Hasler (1964) have investigated the diel migrations of Daphnia spp. extensively on a seasonal basis and have related the migrations to changes in light intensity. Carter (1969) has examined the daytime vertical distribution of various copepods on a seasonal basis. Neither work enables an assessment to be made of the factors responsible for the distribution although McNaught and Hasler's observations clearly demonstrate the importance of changes in light intensity in regulating changes in the vertical distribution between day and night. Temporal changes in zooplankton abundance have been correlated with numerous abiotic and biotic environmental variables in Lake Maggiore (Goldman et. al. 1968). Regrettably, these authors did not examine the vertical distribution of the zooplankton during their otherwise very extensive observations on the biotic and abiotic environment in the upper 30m of the lake.

In the present study, the night-time vertical distribution of P. hessei has been determined on a seasonal basis, and an attempt has been made to relate this where possible to various environmental variables. In the preceding section, the daytime vertical distribution of P. hessei has been described. From the observations presented it would appear that the vertical distribution during daylight is reasonably static and, more important, predictable from day to day. This predictability suggests that intensive studies of the daytime vertical distribution are unlikely to provide much information about the modifying influences of the environment upon the vertical distribution, apart from the master influence of light intensity and possibly thigmokinesis in the case of the adult and immediately pre-adult calanoids.

Preliminary observations on the night-time vertical distribution (Figs. 14 and 15) indicated that the nocturnal distribution of the calanoids was dynamic and it appeared likely that intensive examination of this distribution might indicate interactions between the calanoids and their environment.

Changes in vertical distribution through the hours of darkness

Changes in vertical distribution during the course of one night must be considered before seasonal changes in vertical distribution are examined. The overall pattern of diel migration in *P. hessei* (Figs. 14, 15 and 19) corresponds most closely to the "nocturnal" pattern described by Hutchinson (1967), although in some developmental stages the pattern is more appropriately ascribed to Hutchinson's "twilight" migration type.

The most detailed observations of vertical changes through one night, given in Fig. 19, show that after sunset the calanoids of all stages are most abundant in the upper waters, although in the copepodite instars, some animals are present throughout the water column. The calanoids remain distributed throughout the water column during the hours of darkness, with the exception of the naupliar stages which remain predominantly in the upper 20m. The copepodite stages show a clear sink during the course of darkness. This "midnight" sink (Cushing 1951) or "nocturnal" sink (Hutchinson 1967) results in the modal concentration depth of the adults moving from the 0 - 10m stratum at 2000hrs to the 35 - 40m stratum by 0200hrs. This nocturnal sinking is commonly reported in plankton and is generally believed to result either from a decrease in activity and corresponding passive sinking, or from random locomotor movements in the absence of a directional (photic) stimulus. Either will, as a result of gravitational influences, result in a net downward movement. The increasing rapidity of this sinking in successively older (and larger) calanoid stages is consistent with either of the alternative explanations. The larger stages with smaller surface area/volume ratios would be expected to gravitate more rapidly (on a weight for weight basis).

The series under consideration was made two days after full moon. Since moonrise occurred at 1915hrs, the calanoids were subjected to bright moonlight for practically the entire night. The nocturnal "sinking" in the present series can therefore be explained also on the basis of a negatively phototactic response. However, the reality of nocturnal sinking on moonless nights is evident from Fig. 14 and particularly Fig. 15. The series shown in Figs. 14 and 15 were undertaken four days after new moon. Moonset occurred at 2030hrs. In view of the limited lunar intensity and its brief temporal influence upon the plankton, the nocturnal sinking observed in these series cannot be accounted for on the basis of negative phototactic behaviour. In Fig. 15, the 2100hrs distribution was recorded after moonset and a clear nocturnal sinking is evident in the numerically abundant stages between 2100hrs and 0100hrs.

It is clear that any attempt to study seasonal changes in night-time vertical distribution must take into account those changes which occur during the course of one night. In the present study, the majority of samples were collected from $1\frac{1}{2}$ - 3 hours after sunset (Table 7), thereby reducing the potential intra-night variation

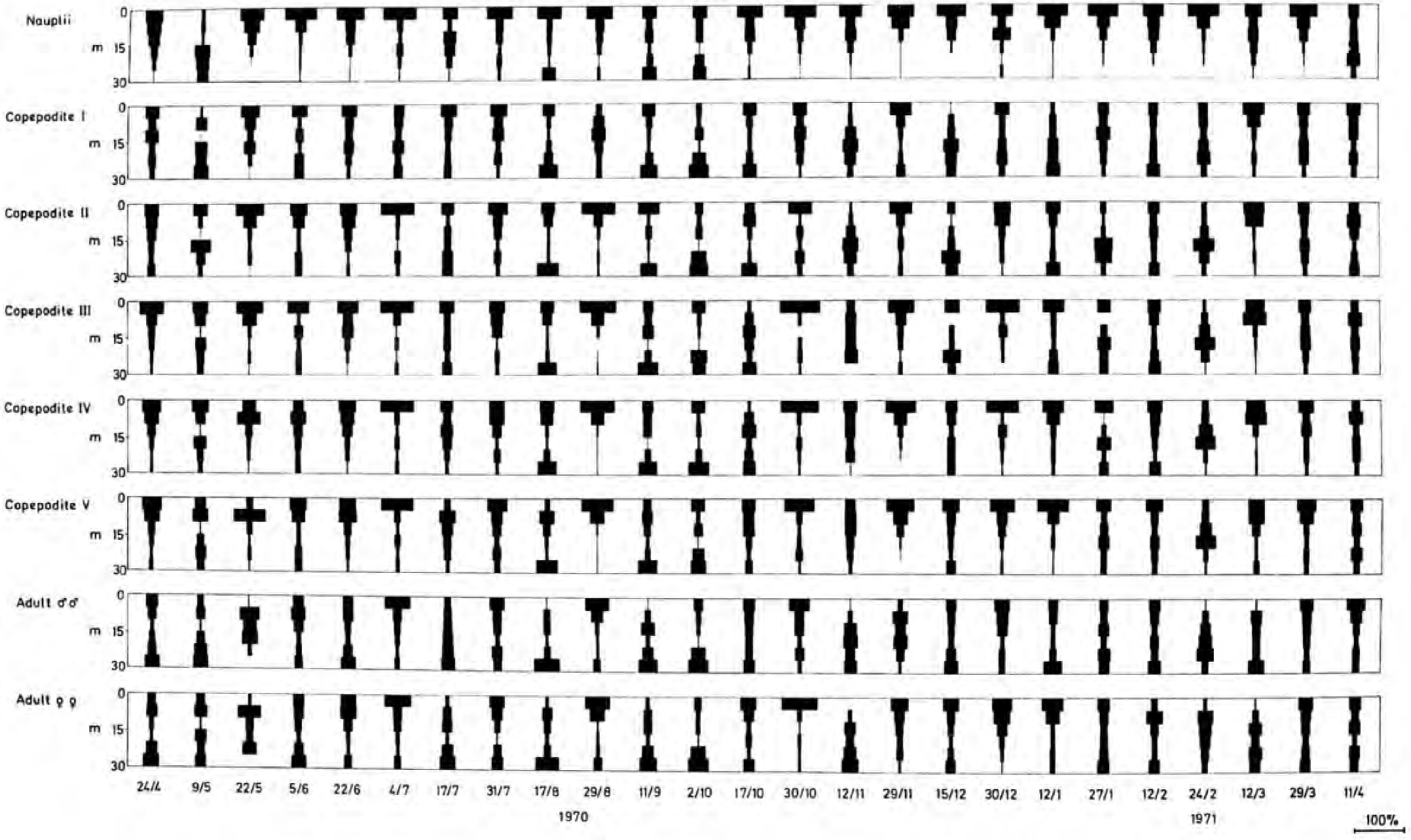

Figure 22. P. hessei: Percentage vertical night-time distribution of developmental stages at Stn. III during 1970-1971. Collections made by means of net hauls between 2000 and 2130 hrs.

to a considerable extent.

Seasonal variation in the vertical distribution of P. hessei.

During 1970 - 1971, a series of 25 collections was made at approximately fortnightly intervals at Station III. The vertical distribution was assessed by vertical net hauls made sequentially through successive 5m strata. The results of these collections are shown in Fig. 22. Percentage vertical distribution has been used to obviate difficulties of illustration which would otherwise have arisen as a result of seasonal changes in population age-structure and total abundance. The resulting histograms are more readily comparable one with another. Seasonal changes in calanoid abundance and population age-structure per se are examined in a later section of this work.

Nauplii Naupliar distribution was very similar throughout the year. Nauplii were maximally abundant in the surface waters on all but three sampling dates. They were seldom present in large numbers below 15 - 20m.

Copepodite I The distribution of this stage was not very regular. Modal concentrations were generally recorded in either the very surface or very bottom waters. However, this stage was normally present throughout the water column.

Copepodites II - V These stages were frequently most abundant in the surface waters but on most sampling dates they occurred throughout the water column.

Adults The distribution of adult calanoids resembled that of the copepodite II - V stages. In the case of adult males, maximum abundance was more frequently in the bottom waters than in the surface waters. The vertical distribution pattern for both ovigerous and non-ovigerous females was very similar, although not shown separately in Fig. 22.

TABLE 6.

P. hessei: Frequency of occurrence of population modes of various age groups in relation to depth. Aggregate data determined from 25 early evening collections at Station III during 1970 - 1971.

Depth stratum	Nauplii	CI	CII	CIII	CIV	CV	Adult ♂	Adult ♀	Total
0-5	22	12	16	16	16	16	8	12	122
5-10	0	0	1	2	5	6	3	5	22
10-15	0	2	0	0	2	1	0	2	7
15-20	1	3	4	2	1	1	1	0	13
20-25	1	1	1	3	0	1	2	1	10
25-30	1	7	3	3	3	3	11	7	38
n	25	25	25	26*	27*	28*	25	25	

* Where n is greater than 25, a bimodal distribution has been encountered on one or more sampling dates.

TABLE 7

Biotic and abiotic factors recorded during 25 night-time samplings at Station III during 1970/1971. See text for further explanation.

Date		24/4	9/5	22/5	5/6	22/6	4/7	17/7	31/7	17/8	29/8	11/9	2/10	17/10	30/10	12/11
Time of sampling		2030	2030	2030	2015	2010	2015	2145	2030	2030	2030	2045	2100	2030	2005	2035
Hours and minutes after sunset		3.00	3.12	3.18	3.09	3.04	3.03	4.27	3.06	2.54	2.48	2.57	3.00	2.18	1.47	2.05
Wind speed (Beaufort Scale)		1	0-1	2	2	1	2	2	1	2	2	2	1-2	1	0-1	0
Wind direction		E	Var.	NW	SW	NE	SW	N	ENE	E	E	SE	NE	Var.	S	-
Moon phase on sampling date		Full- Last Qu.	New- 1st Qu.	Full	New	Full- Last Qu.	New	Full	New	Full	New	1st Qu.- Full	New	Full- Last Qu.	New	Full
*Presence of absence of moon at time of sampling		P	A	A	A	A	A	A	A	P	A	P	A	A	A	P
Cloud cover		0/10	0/10	0/10	5/10	0/10	0/10	9/10	3/10	0/10	0/10	9/10	2/10	10/10	3/10	3/10
Relative light intensity		4	2	2	2	2	2	1	2	6	2	3	2	1	2	5
Surface Temperature °C			22.2°	22.0°	20.7°	19.3°	18.85°	18.7°	18.05°	18.95°	20.05°	19.95°	21.45°	20.8°	21.95°	23.05°
Temperature gradient (0-30m)		0.1°		0.15°		0.15°		0.05°		0.2°		0.6°		1.1°		0.8°
Phytoplankton cells	0-5m	473	476	386	362	373	366	380	442	458	361	408	350	242	348	375
	30m	416	414	450	360	408	408	334	502	459	487	362	397	280	327	300
Chlorophyll a (ug/l)	0-5m	2.92	2.42	3.18	1.53	2.37	3.54	2.83	3.25	2.74	1.82	2.92	1.51	2.83	2.13	1.63
	30m	1.94	1.66	2.59	2.01	2.96	3.04	2.30	3.60	4.00	3.69	2.95	2.65	1.94	2.94	2.34
Cell volume	0-5m	465	534	296	460	806	704	689	1039	1238	868	1116	382	190	168	162
	30m	532	575	326	514	736	735	697	1285	1365	1254	756	884	280	384	283

*P = Present
A = Absent

TABLE 7

iotic and abiotic factors recorded during 25 night-time samplings
t Station III during 1970/1971. See text for further explanation.

	17/7	31/7	17/8	29/8	11/9	2/10	17/10	30/10	12/11	29/11	15/12	30/12	12/1	27/1	12/2	24/2	12/3	29/3	11/4
	2145	2030	2030	2030	2045	2100	2030	2005	2035	2030	2015	2020	2030	2030	2030	2015	2020	2020	2010
	4.27	3.06	2.54	2.48	2.57	3.00	2.18	1.47	2.05	1.42	1.21	1.14	1.24	1.24	1.36	1.39	1.56	2.20	2.22
	2	1	2	2	2	1-2	1	0-1	0	3	3	2	1	1	2-3	0	2	3	2
	N	ENE	E	E	SE	NE	Var.	S	-	ENE	NE	NW	NE	E	S	-	ENE	SE	SW
	Full	New	Full	New	1st Qu.-Full	New	Full-Last Qu.	New	Full	New	Full-Last Qu.	New	Full	New	Full	New	Full	New-1st Qu.	Full
	A	A	P	A	P	A	A	A	P	A	A	A	P	A	P	A	P	A	P
	9/10	3/10	0/10	0/10	9/10	2/10	10/10	3/10	3/10	0/10	10/10	10/10	10/10	0/10	0/10	0/10	6/10	7/10	10/10
	1	2	6	2	3	2	1	2	5	2	1	1	5	2	6	2	5	1	5
5°	18.7°	18.05°	18.95°	20.05°	19.95°	21.45°	20.8°	21.95°	23.05°	24.65°	25.7°	26.4°	26.2°	26.6°	26.5°	26.3°	26.3°	26.5°	25.15°
	0.05°		0.2°		0.6°		1.1°		0.8°		0.3°		0.75°	1.4°		0.6°		0.8°	0.1°
	380	442	458	361	408	350	242	348	375	388	415	758	878	1499	1143	889	504	376	421
	334	502	459	487	362	397	280	327	300	274	401	628	902	626	1023	789	278	313	361
	2.83	3.25	2.74	1.82	2.92	1.51	2.83	2.13	1.63	2.30	2.50	3.28	2.04	2.08	2.06	1.97	2.38	2.40	4.32
	2.30	3.60	4.00	3.69	2.95	2.65	1.94	2.94	2.34	2.62	2.83	3.03	2.81	1.89	2.34	1.99	2.36	3.78	3.20
	689	1039	1238	868	1116	382	190	168	162	115	271	240	351	420	398	509	291	293	435
	697	1285	1365	1254	756	884	280	384	283	185	314	340	450	350	394	464	354	367	459

*P = Present
A = Absent

The frequency of occurrence of the modal concentration depth in different depth strata is given for the various developmental stages in Table 6, which indicates clearly the regularity with which the calanoids are encountered most abundantly in the surface waters.

While the nauplii show a regular vertical distribution pattern throughout the year, the copepodite stages do not. Complete inversions of the distribution pattern may occur between consecutive samplings. However, Fig. 22 shows that the vertical distribution of the C II to C VI stages is generally similar on any one sampling date. Very clear examples of this similarity are given in the distributions of 4/7, 31/7, 17/8 and 29/8. When adults are maximally abundant in the surface waters, the same distribution is exhibited by the C II - C V stages: conversely, when the adults are concentrated in the deeper waters, so are the C II - C V stages. This regularity in the vertical distribution of different stages on any one date suggests that the distribution of the different stages might be related to one or more causal factors common to the instars involved.

Net phytoplankton counts, soluble phosphate and chlorophyll a analyses of 0 - 5m and 30m samples were made generally on the morning preceding the zooplankton sampling. Monthly analyses of dissolved oxygen, pH, alkalinity and chloride at 0, 15 and 30m depths were made in conjunction with bathythermograph records. Surface temperature, wind speed and direction, cloud cover and lunar phase were recorded on all dates when zooplankton hauls were made. Some of these data are given in Table 7. Detailed graphical and numerical examination of the vertical distribution of P. hessei has been made in relation to these various biotic and abiotic variables. This detailed analysis provides little more information than that evident upon concurrent visual inspection of Fig. 22 and Table 7.

The relationships between the vertical distribution and the environmental variables are briefly outlined below. Reference is made to the detailed analyses only where correlations are evident.

Abiotic factors

1. Sampling time in relation to sunset

In view of the changes which occur in the vertical distribution during the course of the night, differences in vertical distribution between sampling series might plausibly be related to the time interval between sunset and sampling. This is not borne out by the data in Table 7, however. Many contrasting pairs of collections were made at similar times after sunset. The strikingly different distribution patterns of 17/8 and 29/8 for example, were both recorded just less than 3 hours after sunset.

2. Correlation with lunar periodicity

Routine samples were collected generally within a few days of either new or full moon (Table 7) as a result of the fortnightly sampling interval employed. Some of the alternate series showed a periodicity in pattern which could be related to lunar periodicity *per se* but rhythmicity was not evident overall.

3. Correlation with lunar intensity

Changes in the vertical distribution pattern were most closely related to lunar intensity. The series of 31/7 to 11/9 showed a fairly regular pattern in relation to lunar intensity in the C II - C VI stages, with larger numbers in the surface waters on moonless nights and in the deeper waters at full moon. However, there were other series which did not correspond and where large numbers were found in surface waters under full moon conditions (e.g. 12/1) or in deeper waters under new moon conditions (e.g. 2/10). The relationship between night-time vertical distribution and light intensity has been examined critically. A reasonably clear correlation exists between the modal depth of adult male and adult female calanoids and a relative light intensity scale of 1 - 6 based upon moon phase and cloud cover at the time of sampling.

The modal depth of the adults is in almost all cases in the surface waters on moonless nights and near the lake bed on bright moonlit nights. In the older copepodite stages, a similar relationship exists but the co-ordinate plots contain several apparently irregular data-points. In the early copepodite stages, the correlation is not clear and the modal depths of the nauplii are almost invariably in the surface waters, irrespective of relative light intensity.

The adult calanoids, which have been shown to be very sensitive to light intensity during daylight (see preceding section) are apparently equally sensitive at night. The youngest stages appear to be least influenced by light, a feature reflected also in their daytime vertical distribution.

The avoidance of surface waters on bright moonlight nights by adult P. hessei is dissimilar to that recorded in other freshwater copepods. Eudiaptomus gracilis and Cyclops strenuus (stages unknown) are reported to collect in the upper 30cm under moonlight conditions (Lozeron 1902, cited in Hutchinson 1967). Comparable behaviour is not apparent in P. hessei as far as can be judged from the sampling techniques used.

Avoidance of surface waters on bright moonlit nights has been recorded in various marine crustacea and age-dependency is involved in some cases. Ritz (1972a) has shown that late stage phyllosoma larvae of Panulirus longipes cygnus are present in surface waters in much greater concentrations on dark nights than on bright moonlit nights. The difference is not pronounced in the younger stages, however. Ritz (1972b) has gone so far as to suggest that midnight sinking may be a result of negative phototaxis on bright moonlight nights. If the depression of *P. hessei* under bright moonlight conditions is a phototactic response, it implies a very low threshold of perception for this species.

4. Correlation with lake temperature

No changes in the vertical distribution pattern, which can be related to seasonal changes in lake temperature or temperature/depth profiles are evident from the seasonal vertical hauls.

5. Correlation with wind speed

Within the limited range of weather conditions under which sampling was carried out, there is no obvious correlation between vertical distribution and wind speed. The populations might be expected to be deeper in the water column under turbulent conditions but routine sampling under such conditions has not been carried out.

6. Correlation with pH, Oxygen and Chloride

Vertical changes in oxygen, chloride and hydrogen ion concentration are limited through the hydrographic seasons in Lake Sibaya. The vertical distribution of *P. hessei* shows no correlation with these parameters.

Biotic factors

1. Correlation with chlorophyll concentration

The vertical distribution of the calanoids shows no consistent correlation with the limited differences in chlorophyll concentration between surface and bottom waters. There are occasions where the modal depth of the calanoid population is deeper when chlorophyll values are greater in the deeper water (e.g. 17/8), but the reverse is also true on other sampling dates (e.g. 29/8). There is no clear evidence for either avoidance of or attraction to denser algal populations.

2. Correlation with distribution of other zooplankton species.

Vertical distribution of the two cladoceran species and cyclopoid copepods was determined in conjunction with that of P. hessei. Bosmina longirostris and Moina sp. were predominantly captured in the waters adjacent to the lake bed, with small numbers present through the rest of the water column. The distribution of the cyclopoid copepods (which were not specifically differentiated but counted as a group) was very similar to that of the calanoid nauplii, with a regular surface or near-surface modal concentration. Apart from the similarity in distribution between cyclopoids and nauplii of P. hessei, no clear correlation exists between the distribution of P. hessei and other crustacean plankters. Since Mesocyclops leukartii aequatorialis is a frequent component of the cyclopoid species, there is probably some predation by this species on P. hessei. Fryer (1957d) and Smyly (1961) have reported the carnivorous nature of this cyclopoid species. In most samples collected in Lake Sibaya, some M. leukartii were observed to be grasping nauplii and early copepodites of P. hessei. These observations suggested that the cyclopoid was predating upon the calanoid fairly extensively. Recently, Comita has illustrated an example of M. edax grasping a copepodite instar of Diaptomus siciloides (Comita 1972, Fig. 12). He suggests that this grasping behaviour is a result of adding preservative to the sample and that it has no predatory significance. While he presents reasonable arguments for taking this viewpoint, the predatory nature of many cyclopoids is widely recognized. If the grasping behaviour was merely an artefact arising from preservation it might be expected that more individuals would behave similarly. The low frequency of this observation in any single sample would be more intelligible if it did in fact have some predatory significance.

The foregoing discussion implicates light as the most important single factor influencing the night-time distribution (at least in adult calanoids). The apparent lack of correlation between the vertical distribution and other environmental variables must be attributable mainly to the comparatively homogeneous vertical structure of Lake Sibaya. However, it may well be, on the basis of Saunder's (1971) arguments, that the zooplankton are responding to short term changes in biotic or abiotic variables which are not apparent from the present investigation. In the case of P. hessei analysis of hour to hour changes in distribution in conjunction with extremely sensitive light readings, will, I believe, demonstrate more clearly the effect of light on the distribution of the calanoid. Undoubtedly it is necessary to examine not only the incident light conditions, but also the immediately preceding light history of the calanoids, if an adequate understanding of the distribution is to accrue. Such an approach has not been possible in the present study, primarily because sufficiently sensitive photometric equipment was not available. The equipment developed by Dr. R.E. Boltt (p 53) can doubtless be applied to advantage in the future.

Calanoid densities on the lake bed at night

The close association of the older calanoids with the lake substrates during the hours of daylight has been considered in the previous section. In this context it is appropriate to question whether all the calanoids leave the lake substrates at night and whether they reach the substrates again during the hours of darkness. This aspect has not been considered on a seasonal basis, but may be examined in relation to the 24 hour station series of March, 1972 (Fig. 19).

Substrate bin samples taken at two-hourly intervals through the course of the night have shown clearly that the calanoids move off the substrates after sunset. Furthermore, from Fig. 19 it is clear that most of the stages do not come into contact with the substrates again during the hours of darkness. Nauplii and early copepodites were not captured in the bins at night. Adult males and copepodites IV - V were first captured on the substrates just before first light (0400hrs series), but only in very small numbers. However, some adult females were captured on the lake bed between 2000hrs and 0200hrs, and by 0400hrs a large percentage of the total catch was captured in the substrate bins. The adult females captured on the lake bed at night were almost all ovigerous specimens. While the difference in catch between non-ovigerous and ovigerous females may have some biological significance, the relatively greater population of ovigerous than non-ovigerous females in all samples in the present sampling series precludes further assessment of this possibility.

From the observations presented, it is clear that the calanoid distribution during the hours of darkness is dynamic in comparison with the daytime distribution. Apart from limited catches of adult females on the lake bed, the entire population is in the water column during the night and significant numbers reach the substrates only in the period immediately preceding dawn, at the earliest. Locomotory movements are clearly maintained in varying degree, certainly by some individuals, since calanoids of all stages are captured in the surface waters throughout the night.

A priori, the avoidance by P. hessei of superficial waters during moonlit nights appears to be of limited selective advantage in Lake Sibaya, although it potentially serves to reduce visual recognition by predators. However, it is possible that this behaviour is a carry-over from the estuarine existence of this species where the trait may have been important in reducing the displacement of the species to sea for at least part of the tidal cycle. Grindley (1972) has reported some evidence which suggests that in Richard's Bay (a strongly tidal estuary approximately 180km south of Sibaya) the species is being continually displaced to sea, where it is apparently unable to survive. Only in those areas of the estuary furthest from the sea are high percentages of ovigerous females recorded. Unfortunately, Grindley does not give his detailed findings but tacit in his observations is the suggestion that P. hessei may not be well adapted to estuarine systems. This is difficult to reconcile with his earlier statements recording the numerical dominance of P. hessei in most Cape estuaries (Grindley 1963).

CHANGES IN THE VERTICAL DISTRIBUTION OF PSEUDODIAPTOMUS HESSEI DURING THE DUSK AND DAWN PERIODS

Introduction

In the preceding sections the daytime and night-time vertical distributions of the calanoids have been described. It has been demonstrated that during the day, the animals are in the deeper waters, and, in the case of the later developmental stages, concentrated upon the bottom sediments. By contrast, the night-time distribution is one in which the calanoids are distributed in varying abundance throughout the entire water column. The migratory movements involved in bringing about these changes form the basis of this section.

Extensive replicate studies of the dusk and dawn movements could not be made in view of the limited manpower available. However, the 25 night-time samplings, described in the preceding section, which demonstrated the invariable occurrence of calanoids in the surface waters after nightfall, provide clear evidence of the regularity with which the calanoids undertake a dusk ascent. In view of the predictable occurrence of the migrations, it was clear that the dusk and dawn movements could be studied to advantage by means of a few detailed sampling series. This has been the approach used.

Dusk and dawn are critical periods in the diurnal light cycle, representing as they do, the periods of maximum rate of change of light intensity. Only by examining the movements of the calanoids in detail during these periods is it possible to determine the direct cause of diel migration.

The dusk and dawn migrations of the calanoids were studied by means of stratified vertical net haul samples taken at short time intervals. Changes in light penetration were assessed concurrently. Initially, observations on light changes were made by following the changes in depth at which 1% of the surface incident light intensity

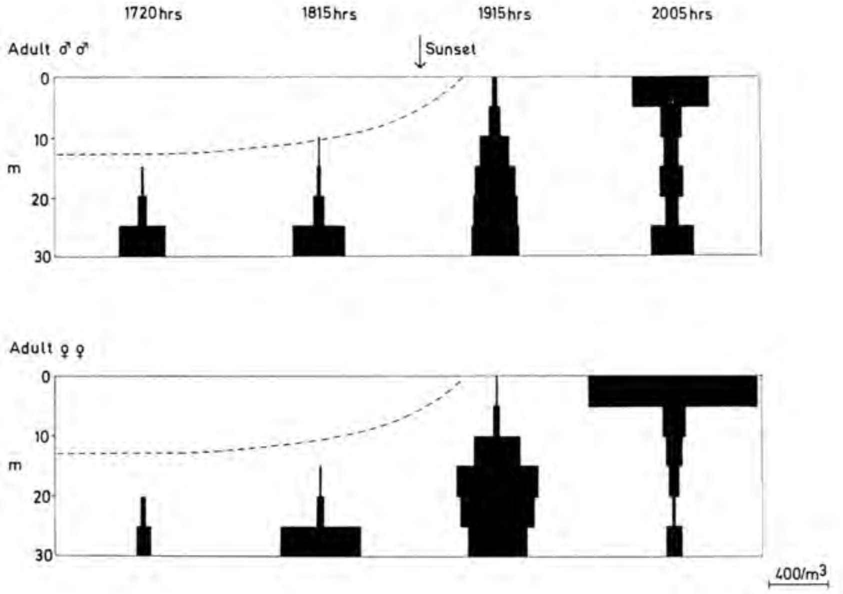

Fig. 23. P. hessei: Changes in vertical distribution at dusk, determined at Station III, 23 January, 1971. Penetration depth of 1% incident light indicated by means of dashed line. Net haul collections.

occurred. Subsequently, when a luxmeter became available, changes in depth of the 1 lux isolume were followed with time.

The sampling times indicated on the figures for dusk and dawn series represent the median sampling time: a series started at 1600hrs and completed at 1630hrs would be labelled 1615hrs. In the dusk series, net hauls of the lowermost strata were carried out first and then taken progressively closer to the surface. In the dawn collections sampling began in the surface waters. The vertical sequence of sampling therefore matched the direction of calanoid movement.

DUSK MOVEMENTS

Station III series (Fig. 23)

In this series, the vertical movements of the adult calanoids were determined in relation to changes in the penetration depth of 1% of incident light intensity.

Both adult males and adult females exhibited similar vertical movements, reaching the uppermost waters only after sunset. The changes in distribution were initially very small (between 1720 and 1815hrs) but with the increasingly rapid fall off in light penetration the distribution pattern changed equally rapidly. In the adult males, for instance, the modal concentration was in the very deepest waters between 1720hrs and 1815hrs. Between 1815hrs and 1915hrs there was a conspicuous upward movement and by 2005hrs the modal concentration was in the surface stratum. In the case of the adult females, the modal concentration depth changed more gradually from the deepest waters at 1815hrs, to the middle waters at 1915hrs and then to the surface waters at 2005hrs.

From this series, it was evident that the migratory movements were closely related to changes in light penetration. Two other significant points emerged. Firstly, the increase in calanoid catch

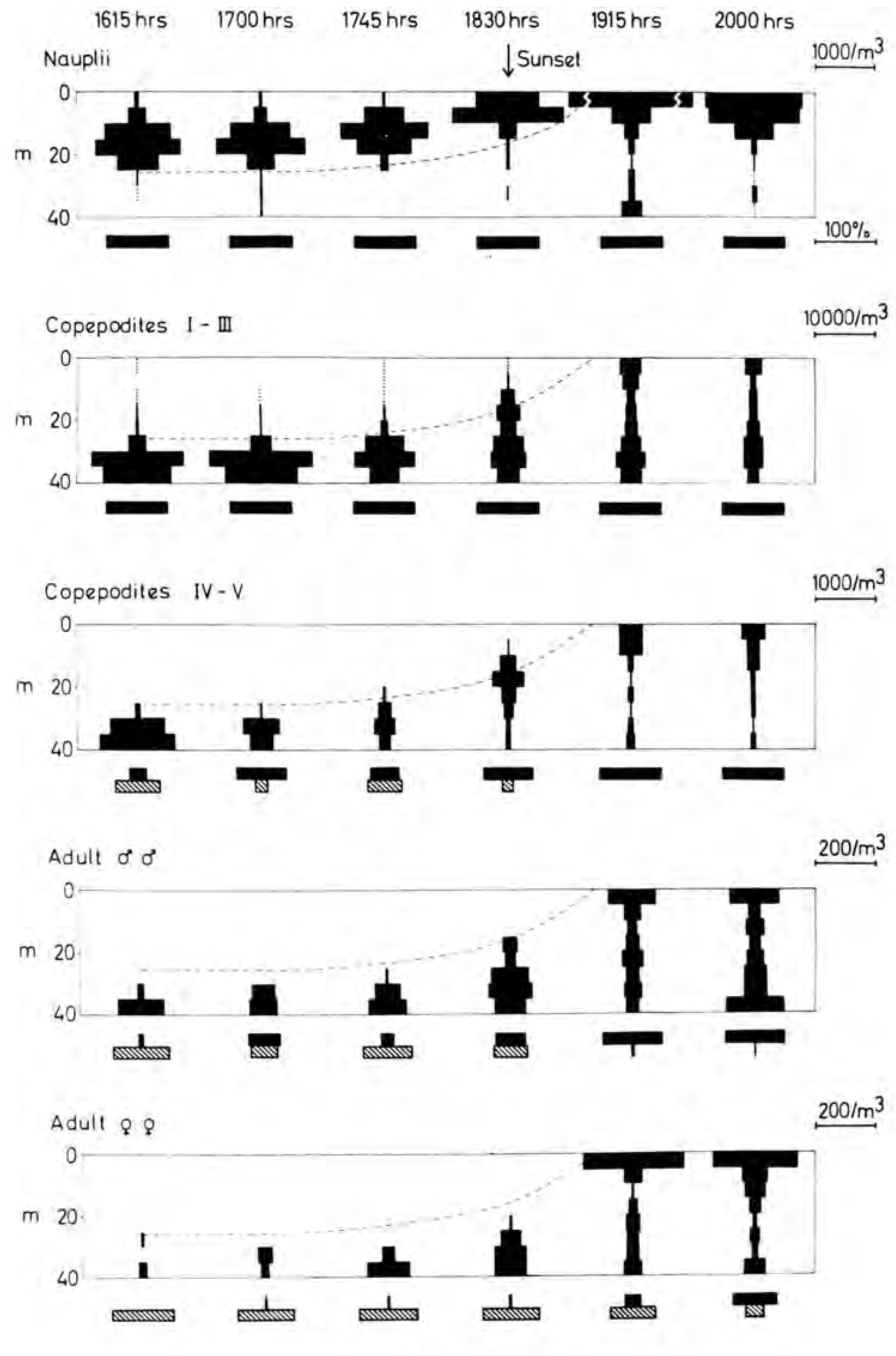

Fig. 24. P. hessei: Changes in vertical distribution at dusk, determined at Station I, 15 February, 1972. 1 lux isolume indicated by means of dashed line. Net haul and substrate bin collections.

with time, and secondly, the continued ascent of the calanoids after sunset. This continued directional movement after sunset was irreconcilable with the idea of suprathreshold rates of change in light intensity providing the direct migratory stimulus (Ringelberg 1961, 1964). It suggested the possibility that the calanoids were responding phototactically to very low light intensities or else, once initiated by some (presumably) photic stimulus, the migratory movement could continue independently of the causal stimulus. It was clearly necessary to re-examine the dusk movements in conjunction with more sensitive photometric equipment.

Station I series (Fig. 24)

The most detailed study of the dusk movements was carried out at Station I using a net and substrate bins to collect samples. Changes in light penetration were determined by means of a luxmeter. These collections have permitted analysis not only of the calanoid movements in the water column but also movements off the substrates.

Nauplii

The naupliar population was entirely pelagic and mostly above the 1 lux isolume in this series. The modal concentration depth of the nauplii moved upwards after 1700hrs; by sunset a large number were found in the surface waters and at 1915hrs, the modal concentration was recorded in the surface stratum. The presence of a discrete group of nauplii in the deepest waters during the 1915hrs sampling is noteworthy, particularly in view of their restricted vertical distribution until this time. While nocturnal fragmentation and downward movement of Daphnia longispina and Thermodiaptomus galeboides populations has been observed in Lake Victoria by Worthington (1931), temporal considerations indicate the unlikelihood of a similar occurrence in the present series. It is most improbable that nauplii, with their restricted locomotory ability, could have moved at least

25m in less than one hour.

C I - C III

In the early copepodite stages, the population was almost exclusively in the water column. There was no significant movement until 1700hrs; after this time there was a conspicuous ascent which brought them into the uppermost waters by 1915hrs, although large numbers were still present in deeper waters. These stages were almost entirely below the 1 lux isolume until 1745hrs. However, by sunset, a fairly large number of the young copepodites was above this isolume. At 2000hrs, these stages were fairly uniformly distributed through the entire water column.

C IV - C V

The late copepodite stages were below the 1 lux isolume until sunset, at which time there were several above it. These stages remained mainly below 30m until 1700hrs. Between 1745hrs and 1830hrs there was a conspicuous upward movement, which resulted in a clear modal concentration at the surface by 1915hrs. These stages were maximally abundant on the substrates until 1745hrs (apart from the 1700hrs series)[1]. After 1745hrs there was a rapid movement off the substrates, until by 1915hrs they were entirely pelagial.

Adult males

The adult males were below the 1 lux isolume at all sampling times and were captured mostly on the substrates until 1915hrs; even at sunset, more than 50% of the population was benthic. Despite the predominance of the animals on the substrates, vertical movements into and within the water column were evident between 1745 and 1830hrs.

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[1] In the 1700hrs series a goby (Glossogobius giurus)(Teleosti) was captured in the substrate bin. The low substrate bin catch at this time is thought to be due to disturbance or predation by this fish. This results in an overestimation of the water column fraction of the population in the two-bar histograms.

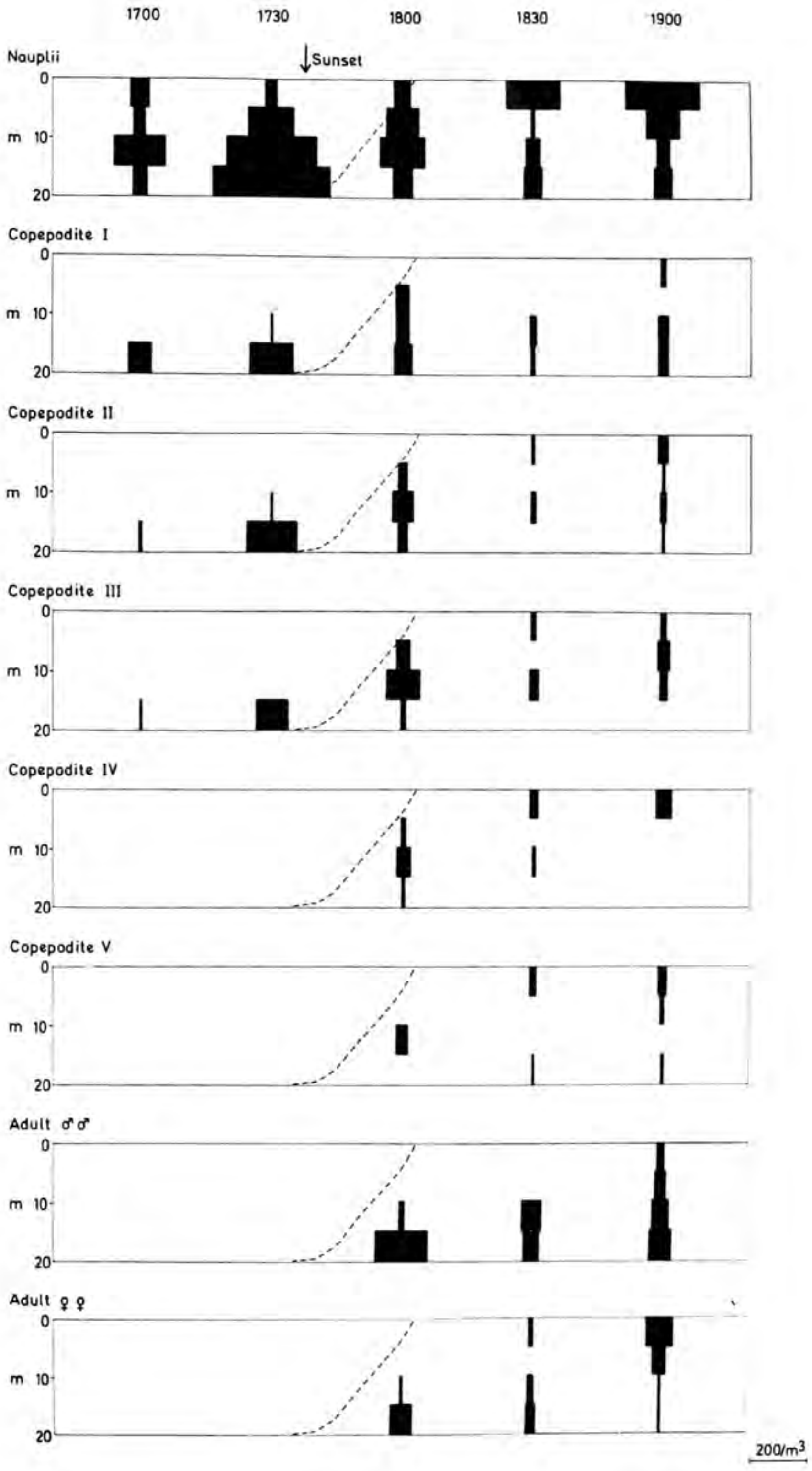


Fig. 25. P. hessei: Changes in vertical distribution at dusk, determined near Station IV, 14 September, 1971. 1 lux isolume indicated by means of dashed line. Net haul collections.

Only after sunset, however, was the majority of adult males found in the water column. By 1915hrs there was a clear concentration mode in the surface waters, although individuals were present throughout the water column.

Adult females

The adult females in the pelagial waters exhibited a movement which was similar to that reported for the adult males. Migratory movements were most pronounced between 1830hrs and 1915hrs i.e. after sunset. The pelagial females remained below the 1 lux isolume.

In their benthic association, the females showed a pattern unlike that of any other stages. They were found on the substrates in far greater proportions and for a far longer time than was the case with adult males. At sunset, 98% of the females were still on the substrates and even at 2000hrs, 29% remained on the lake bed. The existence of this relatively high proportion on the lake bed at night could result from a non-migratory fraction, although evidence presented earlier (pp 117-118) contradicts this idea. Notwithstanding the significant proportion of females on the substrates after sunset, the pelagial females are most abundant in the very surface waters. This might indicate that a portion of the female population starts its ascent considerably later than sunset. This is difficult to reconcile with an optically initiated and directed migration.

Station IV series (Fig. 25)

The series undertaken at this shallower station was carried out in conjunction with Jenkin sampler collections of the bottom populations. Measurements of the 1 lux penetration depth were determined simultaneously with the net hauls. Population densities were extremely low, resulting in a somewhat irregular pattern of vertical distribution. Nevertheless, the general pattern of movements is apparent. (The substrate collections are not incorporated

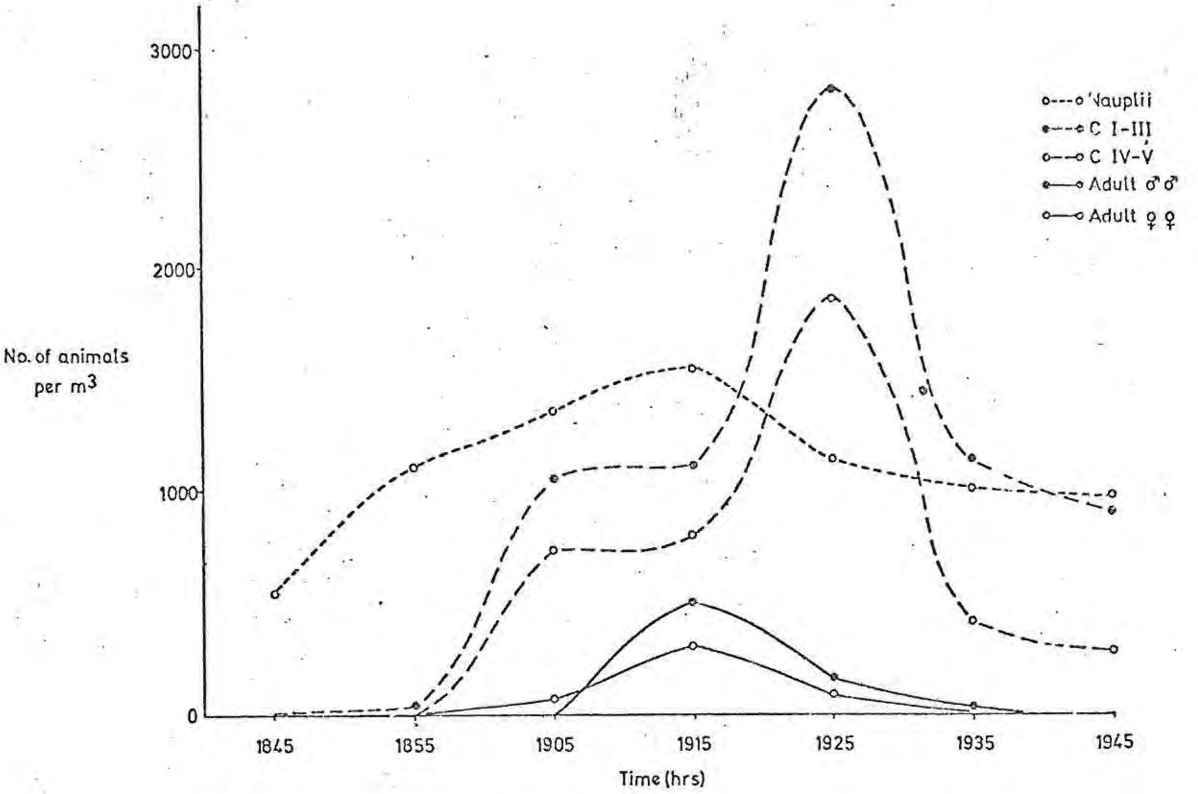


Fig. 26. *P. hessei*: Arrival of various age groups into surface 0 – 5m waters at dusk, 23rd February, 1972. Net haul collections at Station I. Sunset occurred at 1830hrs.

in Fig. 25 owing to the low numbers captured.)

Nauplii were present throughout the water column at all sampling times but a fairly clear upward movement was evident between 1730hrs and 1830hrs. This upward trend between 1730 and 1830hrs was also shown by the first three copepodite stages, although the low densities resulted in a rather patchy distribution. Of interest in the fourth and fifth copepodite stages and in the adults, was their complete absence from the water column between 1700 and 1730hrs. It is likely that their movement off the substrates and into the water column occurred only after sunset. The adults were mostly at least 10m below the 1 lux isolume.

Most conspicuous population movements were evident after 1730hrs when the 1 lux isolume showed a relatively rapid rate of movement upwards. An indication of the change in depth of the 1 lux isolume before sunset can be obtained by interpolating the data given in Fig. 24, from which it can be seen that the changes in depth of the 1 lux isolume were initially slow until approximately 1 hour before sunset. In the hour preceding sunset and for about half an hour after, changes in light penetration were very rapid.

Arrival in the surface waters

The arrival of calanoids in the uppermost 5m at dusk has been assessed by net hauls through the 0 - 5m column at 10 minute intervals at Station I. The results of this sampling series are given in Fig. 26. Sampling was started approximately 15 minutes after sunset.

Nauplii were present at 1845hrs, increased in abundance until 1915hrs, and then decreased. Early (C I - C III) and late (C IV - C V) copepodites were present at 1905hrs, reached maximal numbers at 1925hrs and then decreased in abundance. Some adult males were present at 1905hrs; adult males and females were most abundant at 1915hrs, but

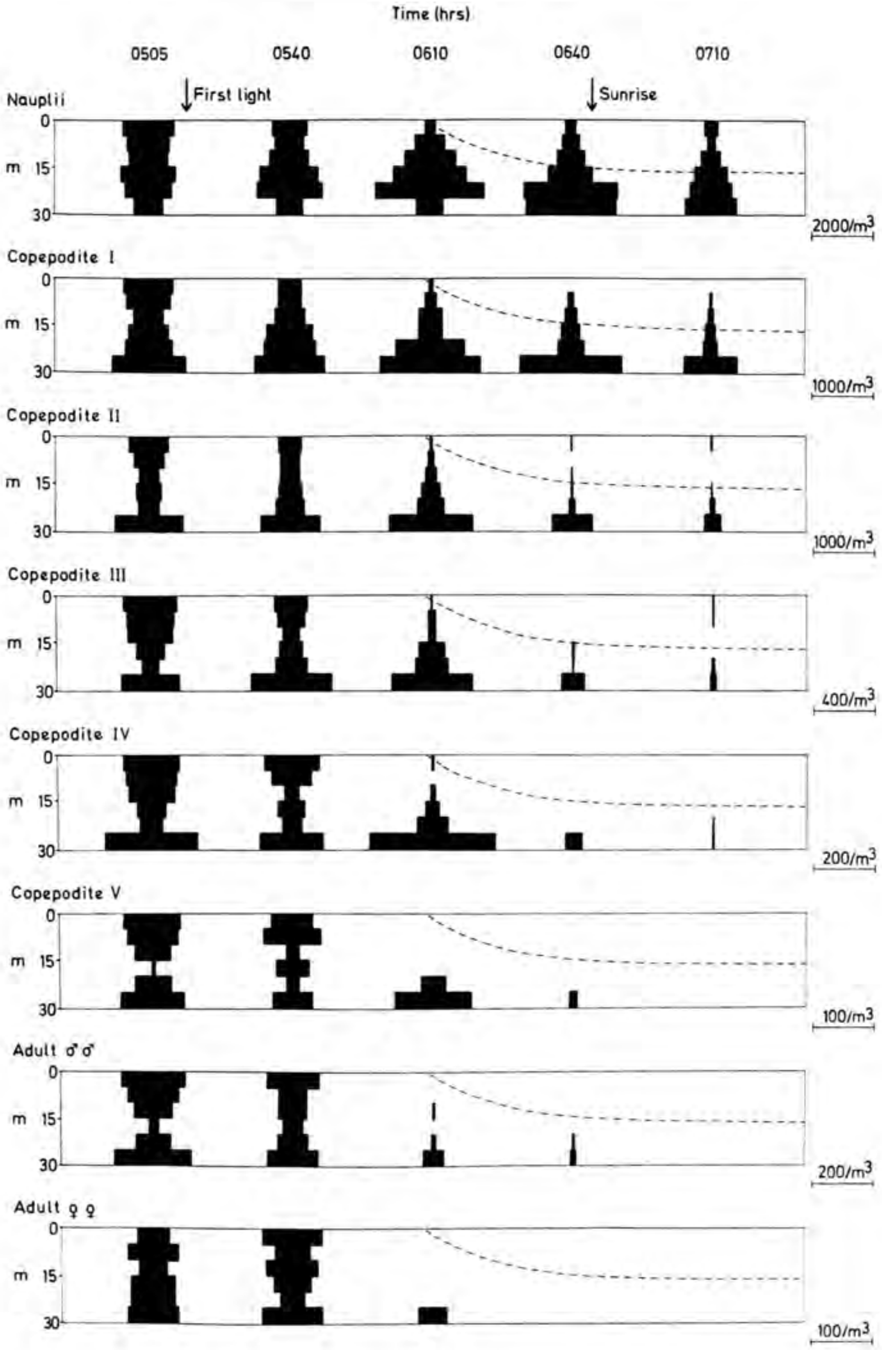


Fig. 27. P. hessei: Changes in vertical distribution of various age groups at dawn, 27 May, 1971, determined at Station III. Penetration depth of 1% incident light indicated by means of dashed line. Net haul collections.

by 1935hrs no adults were captured in the surface 5m.

These data indicated that the arrival of the different age classes of the calanoid at the surface waters was not entirely synchronous, but the time differences were not large. Of considerable interest was the rapid movement out of the surface waters following the period of peak accumulation. Whether this represented a valid emigration or resulted from horizontal patchiness is not known. The series was carried out under moderately windy conditions with evidence of considerable current movements in the surface waters. Under these circumstances, it is possible that the decrease in calanoids at the surface reflected an active avoidance of the currents.

DAWN MOVEMENTS

Station III series (Fig. 27)

Calanoid movements in the water column at dawn were assessed from net hauls in relation to changes in penetration depth of 1% incident light intensity.

Nauplii

Nauplii were present throughout the water column during the entire series, but a conspicuous downward movement was initiated after the first grey light of dawn. Before sunrise the nauplii were concentrated in the deepest waters. Light was first detected photometrically at the surface 35 minutes before sunrise, when the nauplii were most abundant in the 20 - 25m stratum. By sunrise, when 1% incident light was recorded at 14.6m, the nauplii had reached their day depth.

C I - C III

The early copepodite stages showed a general pattern of change closely resembling that of the nauplii. These stages were fairly numerous in the surface waters at 0505hrs, but by 0540hrs their

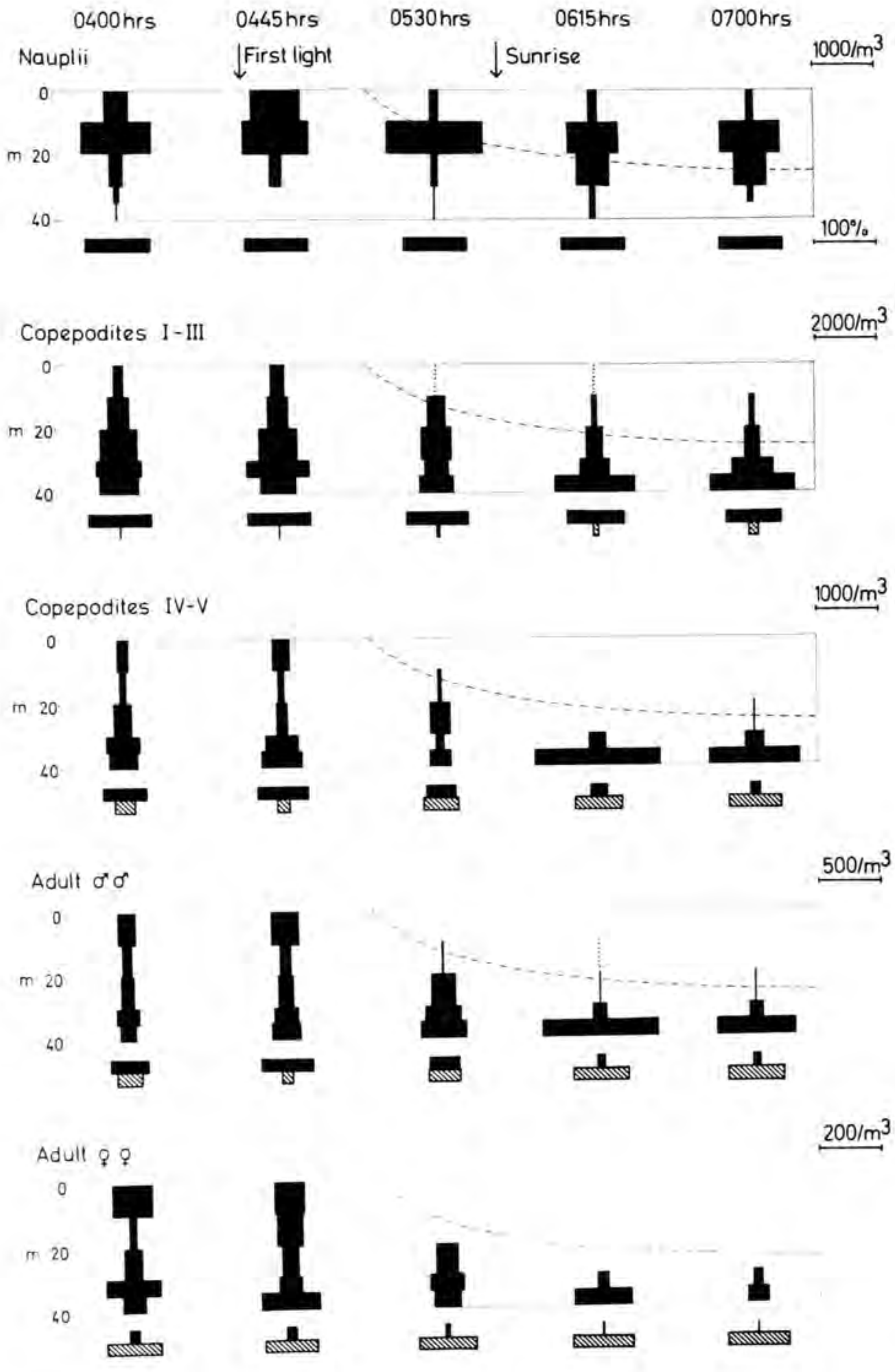


Fig. 28. P. hessei: Changes in vertical distribution at dawn, 19 February, 1972, determined at Station I. 1 lux isolume indicated by means of dashed line. Net haul and substrate bin collections.

distribution had been clearly depressed and by 0610hrs they were most abundant in the deepest waters. By 0710hrs comparatively few C I individuals were present above 15m, and insignificant numbers of C II and C III were captured above 25m.

C IV - C VI

The late copepodites and adults showed a pattern similar to that observed in the younger copepodites. The movement out of the water column was, however, progressively more rapid in successively older stages. In the adults, there were indications of a slight upward movement between 0505hrs and 0540hrs, suggestive of a dawn rise.

The decrease in total catch between 0610hrs and 0640hrs in all post-naupliar stages is very marked. This is undoubtedly related to their movement out of the water column and onto the lake sediments as will be shown for the Station I collection series (Fig. 28).

Station I series (Fig. 28)

Dawn collections at Station I involved substrate bin collections, net hauls and light penetration measurements (in lux). The data obtained have shown that calanoid movements out of the water column are related to their arrival on the lake bed. The general pattern of change is clear despite the coarseness of the net hauls.

Nauplii

The entire naupliar population was pelagial during the entire series. Between 0400hrs and 0700hrs the nauplii were most abundant within the 10 - 20m column. After the first grey light of dawn a large number of nauplii were present in the surface waters but movement into deeper waters by the majority of the animals resulted in their occurrence chiefly below the 1 lux isolume until after sunrise when this isolume lay deeper than the bulk of the population.

C I - C III

Most of the early copepodites were present in the deeper waters during the sampling period with the majority below the 1 lux isolume. After sunrise, the animals were concentrated in the deepest waters, with a very small proportion (chiefly the oldest) on the substrates, and some (the youngest) closer to the surface.

C IV - C V

These stages were present throughout the water column at 0400hrs, with a significant proportion on the lake bed. At 0530hrs the majority was on the lake bed with the pelagial fraction below 20m. After sunrise most of this age group was on the substrate or just above the lake bed. These stages were predominantly well below the 1 lux isolume and by 0700hrs only 15% of the population was pelagial.

Adult males

Adult males were distributed throughout the water column at 0400hrs, with reasonably large numbers on the lake bed. (In this series there was a sensible movement upwards at 0445hrs after the first dawn light. This upward movement was accompanied by an increase in the pelagial component and a concomitant decrease in the benthic component.) By 0530hrs, only insignificant numbers were captured above 20m, and the majority of the males were captured in the deepest waters and on the lake bed. The distribution was depressed still further, until by 0615hrs - shortly after sunrise - a mere 12% of this population was pelagial, and these were mostly below 35m.

Adult females

The adult females exhibited a pattern closely resembling that of the adult males, but the concentration of females on the substrates was considerably greater than the males. Before sunrise

92% of the females were on the substrates and by 0700hrs, scarcely 1% remained in the water column.

Endogenous rhythmicity under laboratory conditions

Several observations made during the dusk and dawn collections suggested that a factor other than light might be responsible for the timing of the dusk and dawn movements in some individuals. Movement of some adult females off the lake substrates well after sunset in the dusk series was irreconcilable with a light initiated migration, although other females performed migrations which closely paralleled the decrease in light penetration (Fig. 24). Likewise, in the dawn series, large numbers of C IV and C V and adult calanoids had reached the substrates well before first light (Fig. 28). This suggested that either the calanoids had "prejudged" the arrival of first light, or that "nocturnal sinking" had brought them into contact with the lake sediments well before any light initiated movements could occur. If the nocturnal sinking alone had resulted in their arrival on the lake bed at 0400hrs it was difficult to understand why larger numbers of animals had not reached the substrates by 2400hrs or 0200hrs (vide Fig. 19). An attempt was therefore made to determine whether an endogenous rhythmicity was involved.

Diel changes in locomotor activity were determined in two large glass aquaria (90 x 45 x 45cm) filled with lake water. One aquarium was kept in continuous darkness and the second was subjected to a natural light/dark regime. Calanoids were collected from the centre of these aquaria by means of the aquarium sampler (see p 51) at two-hourly intervals through 24 hours. The experiments were performed twice. In the first series, calanoids were captured by means of substrate bins from Station I and kept in the aquaria for 4 - 27 hours before the start of the experiment. In the replicate series, net hauls and substrate bins were used to capture calanoids;

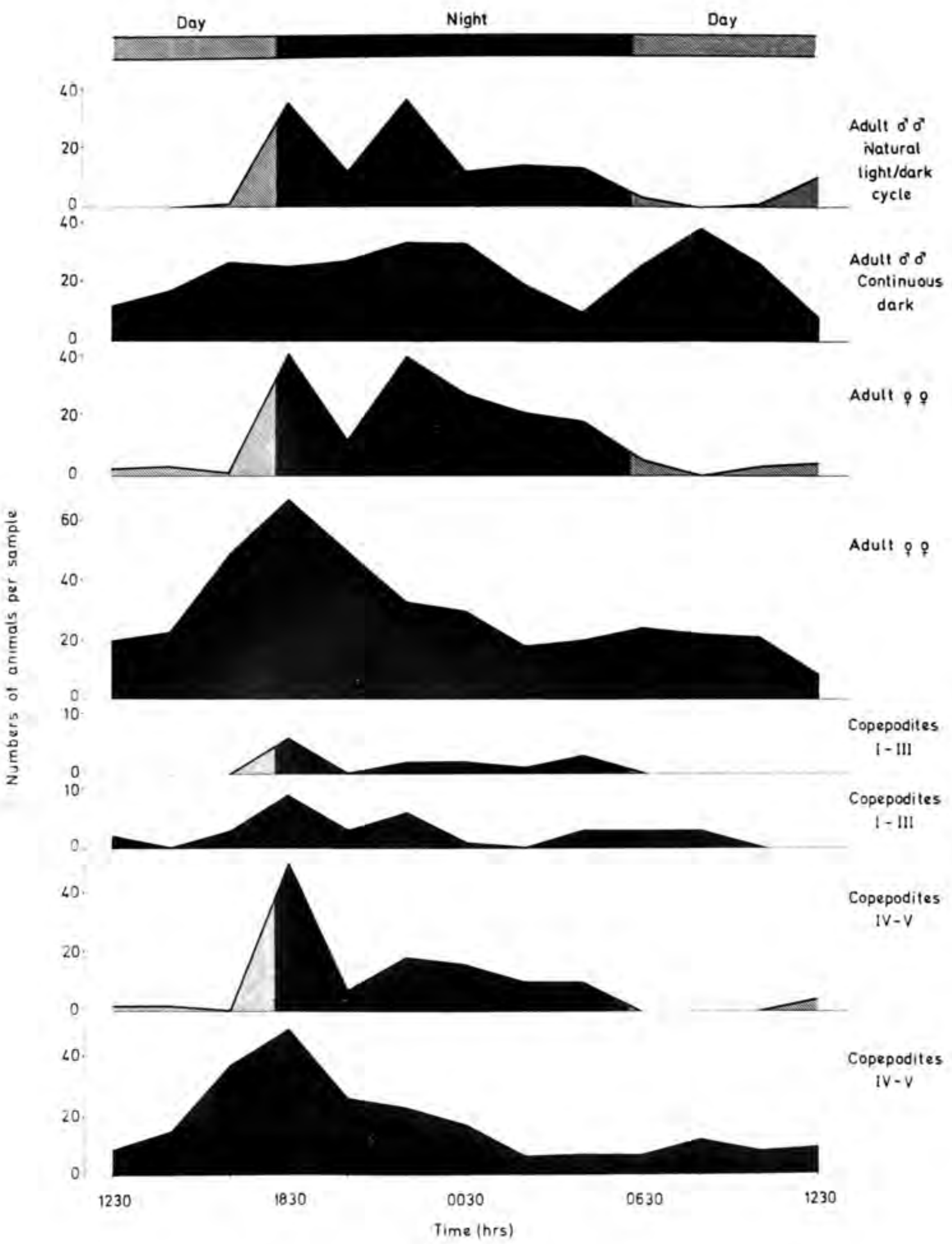


Fig. 29. *P. hessei*: Diel changes in activity in animals subjected to a natural light/dark cycle in comparison to animals held in continuous darkness. Presence of animals in water column used as index of activity. See text for further explanation.

the animals were kept in the aquaria for 20 - 44 hours before the experiment was started. In both series, an attempt was made to standardize the starting numbers in the two aquaria by adding the catch of equal numbers of bins or net hauls to each. Starting concentrations of calanoids were too large for depletion effects to modify successive samplings.

Total catch in the water column in the centre of the aquaria provided a simple index of locomotor activity. During periods of low activity, the calanoids were essentially sedentary on the sides or bottom of the aquaria. They were only captured by the aquarium sampler when they were active in the water column. Results of the two series are given in Figs. 29 and 30. Activity is shown in relation to time of day for different age groups and sex for the two experimental light regimes.

In the first experiment (Fig. 29) animals subjected to the natural light/dark regime exhibited an activity pattern clearly related to changes in illumination. With the onset of darkness, there was a marked increase in the number of animals present in the water column and, with time, these numbers decreased in a fashion entirely comparable with the nocturnal sinking observed in the lake dwelling calanoids. This pattern was evident for adults and copepodites. In the calanoids held under continuous darkness, a similar increase in activity was evident in adult females and copepodites, but it occurred considerably before natural dusk. Nocturnal "sinking" was evident in the adult females and copepodites, but daytime activity was higher under the conditions of continuous darkness. This may, however, be an artefact resulting from dissimilar total starting populations in the two aquaria. In the adult males held under a continuous dark regime activity was high throughout the twenty-four hour period.

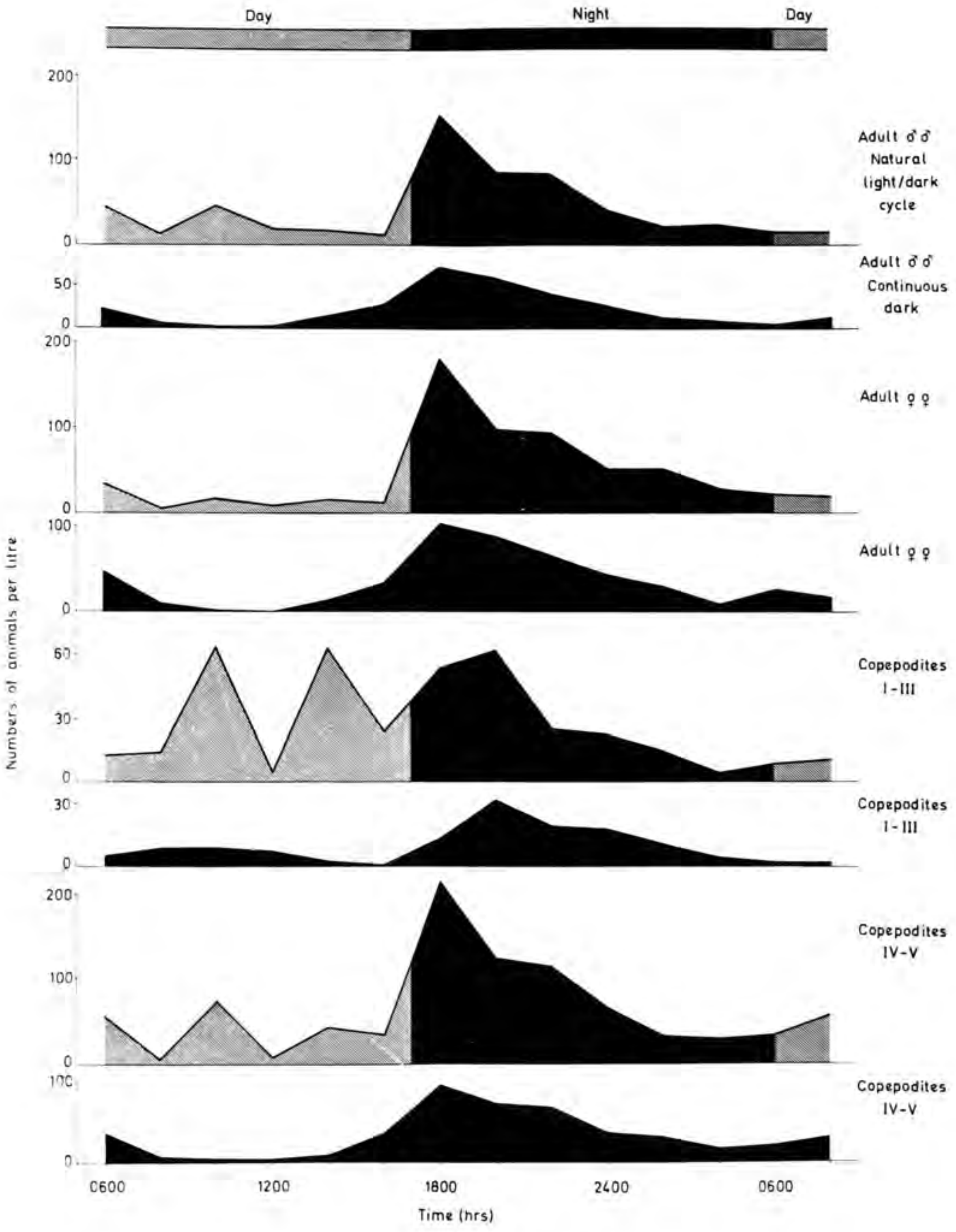


Fig. 30. *P. hessei*: Diel changes in activity in animals subjected to a natural light/dark cycle in comparison to animals held in continuous darkness. Presence of animals in water column used as index of activity. See text for further explanation.

This series indicated a fairly marked similarity in activity in animals subjected to a natural light/dark cycle and those kept under continuous darkness. This suggests the existence of an endogenous rhythmicity, albeit somewhat out of phase with the natural light regime.

The second set of experiments (which was more carefully controlled in view of previous experience) is shown in Fig. 30. There is a striking similarity in the activity patterns irrespective of the light regime, apart from somewhat irregular changes in daytime activity shown by the younger copepodite stages held under a natural light/dark cycle. Increased activity at dusk is synchronous in both aquaria (as far as can be judged by the intersampling interval employed). The existence of an endogenous activity/locomotor rhythm is strongly suggested on the basis of the two sets of results.

Discussion of dusk and dawn migratory movements in relation to changes in light intensity and endogenous rhythmicity.

Changes in the vertical distribution of the majority of the calanoids at dusk and dawn are clearly related to changes in light intensity. This is certainly not an unexpected result. However, there are indications that some of the calanoids may migrate in the absence of a light cue. The general pattern of migratory movements is evident upon inspection of changes in vertical distribution represented in histogram form. However, the movements of the calanoids may be examined with greater sensitivity if changes in the distribution depth of the median individual are considered. The median distribution depth provides the most accurate non-parametric point co-ordinate for describing changes in distribution. The finite nature of the water column imposes certain limits on the extent of migrations. Pronounced concentration or depletion effects are therefore evident as a result of the migrations and these are adequately

TABLE 8.

Rates of movement of different age groups of P. hessei at dusk in relation to rate of change of light penetration. All rates are expressed as m/hr. Data based on dusk series of 15/2/72 at Station I. Positive values indicate ascent, negative values, descent. Calanoid movement is determined from changes in the median distribution depth of the pelagial component of the population between successive samplings. Calculations of movement rates have been based on the absolute time of sampling the specific depth stratum in which the median individual was encountered. Rate of change of light intensity reflects the rate of movement of the 1 lux isolume and provides an indirect indication of the rate of change of incident light intensity.

Age group	1615 - 1700hrs	1700 - 1745hrs	1745 - 1830hrs	1830 - 1915hrs	1915 - 2000hrs
Nauplii	-0.1	+4.0	+8.3	+3.8	-3.8
CI - CIII	0	+2.3	+5.5	+2.3	+1.0
CIV - CV	+1.6	+2.8	+13.0	+14.2	-1.6
Adult ♂	+2.3	-0.4	+5.9	+16.2	-8.1
Adult ♀	+3.0	-3.7	+4.3	+26.0	-2.1
1 lux isolume	0	+3.5	+9.9	+32.0	-

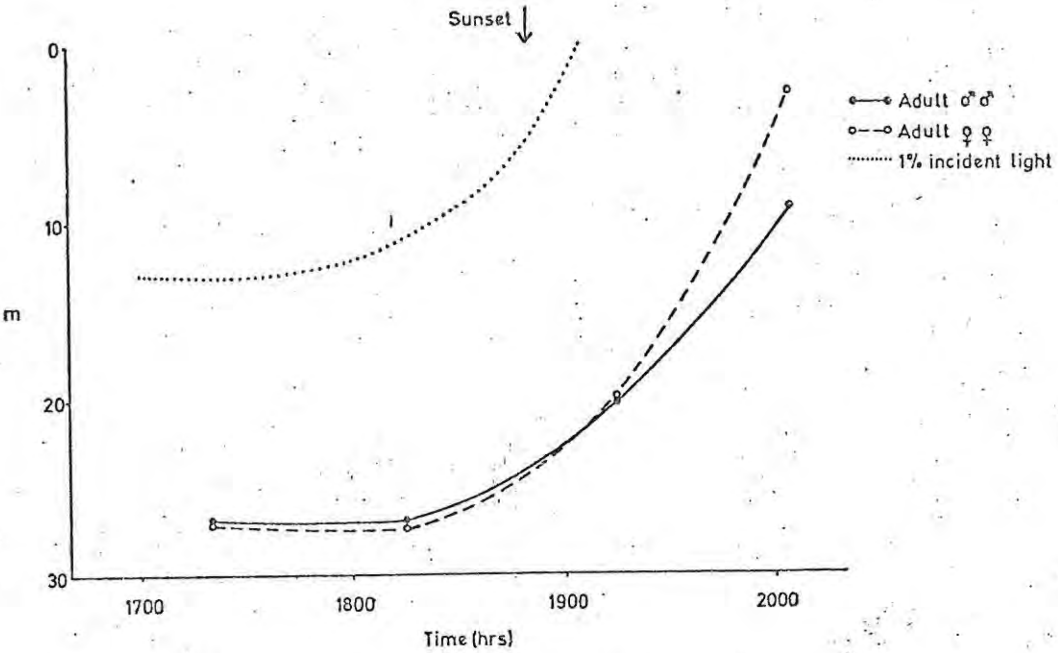


Fig. 31. Vertical displacements of the median distribution depths of adult P. hessei in relation to changes in the penetration depth of 1% incident light intensity levels at dusk. Station III series, 23/1/71.

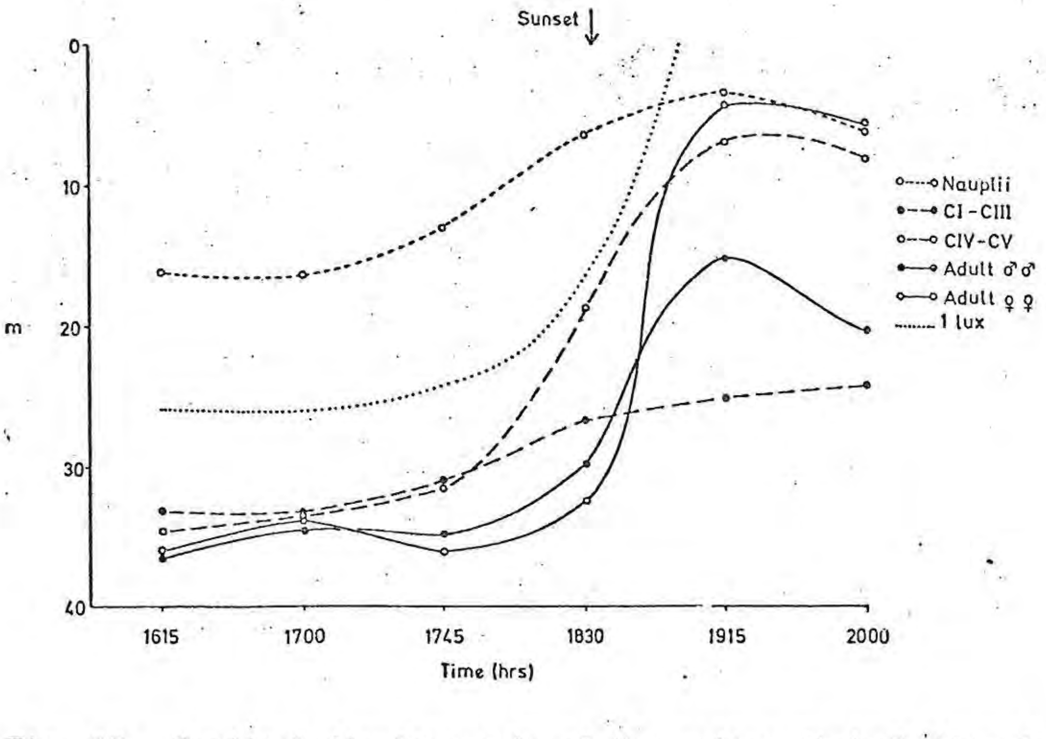


Fig. 32. Vertical displacements of the median distribution depths of different age groups of P. hessei in relation to changes in depth of the 1 lux isolume at dusk. Station I series, 15/2/72.

accounted for when use is made of the median distribution depth. Movements of the median individual are given in relation to changes in light penetration in Figs. 31, 32, 33 and 34 for the Station III and Station I dusk and dawn series respectively. In calculating the median depths, the benthic fraction of the population has been ignored. The major result of so doing is to underestimate the rate and extent of movement in the older stages but this does not invalidate the conclusions reached.

Dusk

If changes in the median distribution depth of the calanoids are examined in relation to changes in light penetration (Figs. 31 and 32 and Table 8) there is in general a noticeable parallelism between the movements of the median and the changes in light penetration. This is clearly shown in the case of the adults and late copepodite stages. The restricted movements of the early copepodite stages (as reflected by the median) are seemingly incongruous compared to the more pronounced movements of the weaker naupliar stages. In general, the movements of the younger stages occur before those of older stages (as reflected in Figs. 24, 25 and 32). This is commensurate with the suggestion that each successive stage of P. hessei is increasingly photosensitive. That the migratory movements are seemingly staggered to some extent might be taken to indicate that each stage is attempting to remain within its optimum light intensity or at the limit of its visual sensitivity, but might also merely reflect their differential sensitivity. There are, however, difficulties associated with this point of view.

The degree of synchrony involved in their arrival at the surface (Fig. 26) is difficult to reconcile with this interpretation unless it is a reflection of their different swimming abilities. It is clear that the migratory movements are not initiated until a certain low level of light intensity is reached with the setting of the sun. Nevertheless, at dusk, the animals can and do outswim the particular isolume below which they are normally restricted. This is clear for the pre-adult copepodite stages in which a small but significant part of the population moves into waters brighter than those occupied less than an hour previously (Fig. 24). Restricted sensitivity of the luxmeter has prevented measurements being made of changes in penetration of light energy values less than 1 lux, but such isolumes would follow in general the pattern recorded in the 1 lux changes although attenuation would be more rapid in the final period before darkness. In this respect, the movements of the median adult calanoids would more closely parallel the anticipated changes in light penetration of lower energy level isolumes.

The migratory movements of the older stages of P. hessei are performed at extremely low light intensities, and in some individuals, seemingly in the absence of an adequate light stimulus. On 18th September, 1972, a series of light measurements was made at Station I at sunset, using the photometer developed by Dr. R.E. Boltt. The light values recorded as the sun set below the horizon are given below.

depth	lux
20.5m	5×10^{-1}
25.6m	1×10^{-1}
28.8m	9×10^{-2}
29.3m	6×10^{-2}
32.3m	4×10^{-2}

These values may be interpolated into the dusk series of February, 1972 (Fig. 24). In this series, at sunset, the 1 lux isolume was recorded at 16m. The 1830hrs distribution shows that

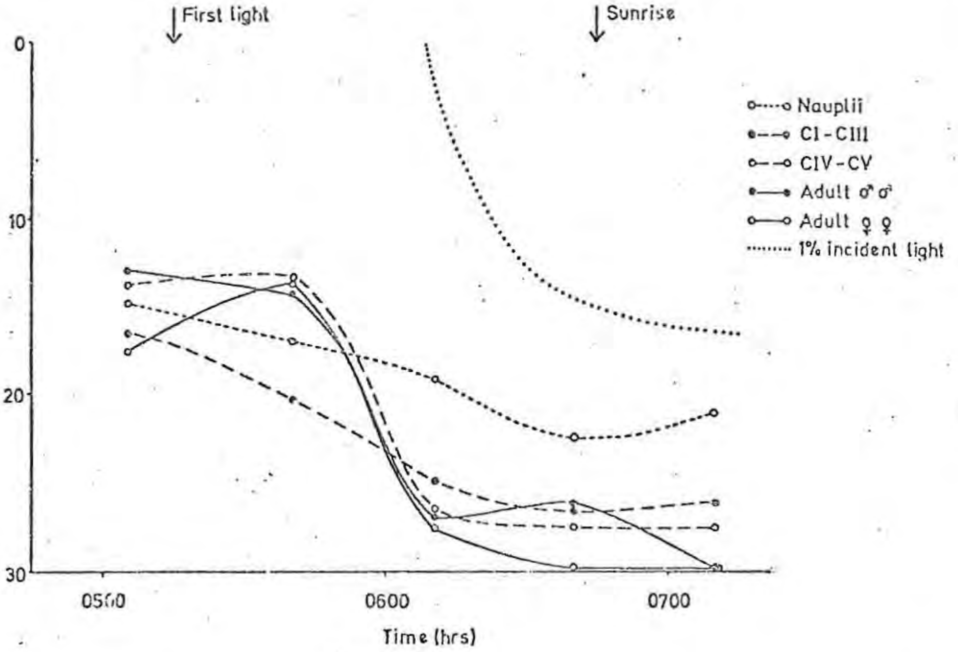


Fig. 33. Vertical displacements of the median distribution depths of different age groups of P. hessei in relation to changes in the penetration depth of 1% incident light intensity levels at dawn. Station III series, 27/5/71.

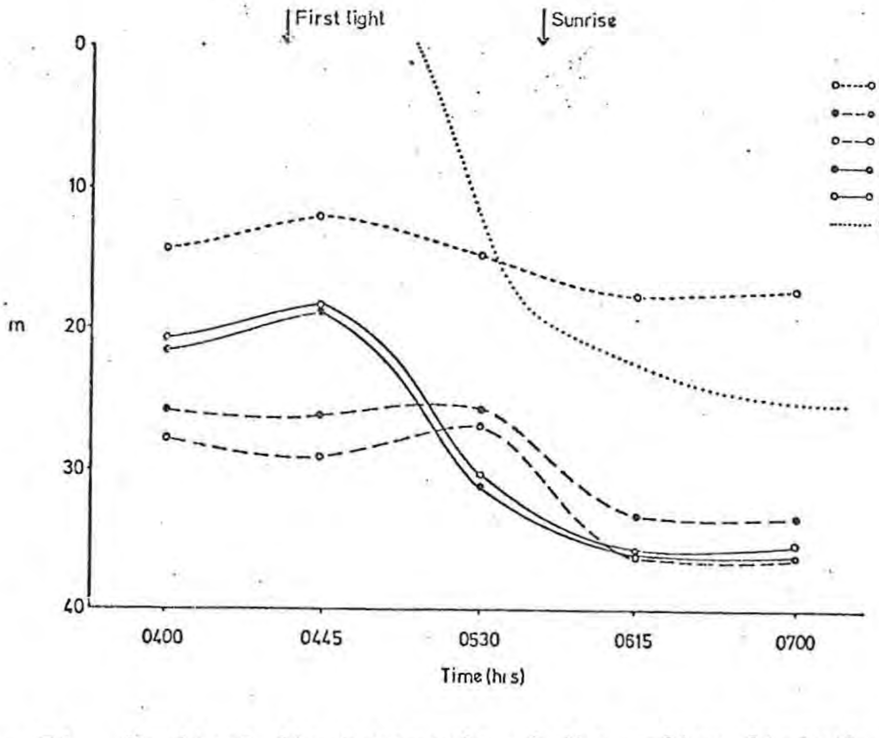


Fig. 34. Vertical displacements of the median distribution depths of different age groups of P. hessei in relation to changes in depth of the 1 lux isolume at dawn. Station I series, 19/2/72.

the majority of all calanoid stages (excluding the nauplii) are below 1 lux. The younger copepodite stages are predominantly in waters of less than 1×10^{-1}lux, the older copepodites mainly in slightly brighter waters. The pelagial adults are predominantly in waters darker than 1×10^{-1}lux; many adult males (more than 50%) and almost all adult females are still upon the substrates at intensities considerably below 4×10^{-2}lux. The majority (75%) of adult females are on the substrates even at 1915hrs (45 minutes after sunset), when it would be unlikely that any sensible light energy was present on the lake bed. The movements of this fraction of the female population are entirely discordant with the rate of change hypothesis or the optimum intensity hypothesis, or any hypothesis which involves light as a direct causal stimulus.

There is no reason to believe that the substrate bins are grossly unreliable in assessing movements onto or off the lake sediments. The bins are entirely transparent, allowing any light changes to be transmitted to the calanoids within. The openings are wide and should provide no barrier or obstacle to the movements of the calanoids out of the bins at dusk. If these arguments are acceptable, then the movement of part of the adult female population out of the bins in the absence, seemingly, of adequate light cues, is unlikely to be artefactual. The movements of this fraction of the calanoid population can be ascribed only to endogenously controlled changes in locomotor activity.

Dawn

The dawn movements of pelagial calanoids at two stations of different depth are very similar and are clearly correlated with changes in light penetration. The movements of the median individual are shown in relation to changes in light penetration in Figs. 33 and 34.

TABLE 9.

Rates of movement (m/hr) of different age groups of P. hessei at dawn in relation to rate of change of light intensity. For further explanation, see caption to Table 8. The positive values indicate ascent i.e. dawn rise. Data based on dawn series of 19/2/72 at Station I.

Age group	0400-0445 hrs	0445-0530 hrs	0530-0615 hrs	0615-0700 hrs
Nauplii	+4.0	-3.9	-3.9	+0.7
CI - CIII	-0.5	+0.7	-9.4	-0.1
CIV - CV	-2.4	+3.4	-10.7	+0.1
Adult ♂	+5.6	-14.9	-6.0	0
Adult ♀	+4.2	-13.0	-7.5	+0.9
1 lux isolume	-	-30.7	-12.0	-4.1

As a result of the nocturnal sinking of the calanoids, the median distribution depth lies fairly deep before dawn and the magnitude of subsequent movements is necessarily reduced compared to the dusk movements. Notwithstanding the reduction in magnitude, the maximum rate of displacement of the median distribution depth at dawn (Table 9) is comparable to the values recorded at dusk (Table 8).

Fig. 34 shows a small rise in the median distribution depths of adults and nauplii between 0400hrs and 0500hrs. It is also shown by the adult females in Fig. 33. This has been interpreted as an ephemeral dawn rise. It is generally believed that the dawn rise is a simple positive phototactic response by dark-adapted animals to a low light intensity. This interpretation matches the observations on P. hessei. However, as a result of the very pronounced sensitivity of this species to light, and possibly the rapid increase in light intensity which is experienced in these latitudes where twilight is practically non-existent, the ascent is terminated rapidly. The reduced magnitude of the dawn rise is therefore entirely commensurate with the conditions and species involved. While it could be objected that the net haul intervals are too large to permit the demonstration of a dawn rise, the existence of this rise on two separate sampling dates, at the same time in relation to the diurnal light cycle, argues strongly in favour of its validity. The positive values shown in the first two columns of Table 9 are referable to this dawn rise.

There is some evidence that the dawn descent is not initiated simultaneously by all stages. From Fig. 34, for example, it is evident that the adults start their descent earlier than the preceding copepodite stages, suggesting that photosensitivity may be progressively increased in successive stages (although the nauplii are seemingly inconsistent in this regard). However, a similar trend is not apparent from Fig. 33.

The presence of many copepodite IV and V stages and adult males on the lake substrates before first light is interesting. More striking is that the majority of adult females are on the sediments at this time (vide Fig. 28). The relative proportions of the developmental stages on the sediments increases in relation to their size. This suggests that their presence on the sediments may be a function of nocturnal sinking; the heavier, larger stages "sinking" onto the sediments in greater numbers. It could also result from a "prejudging" of first light through an endogenous rhythmicity. If the latter explanation is correct, then in both dusk and dawn movements, a part of the population must be migrating in the absence of a light stimulus.

Two important points emerge from the preceding pages, both related to the direct migratory stimulus. Firstly, in those calanoids in which the migratory movements are clearly related to changes in light intensity, it would be interesting to know in what way the calanoids are responding to light intensity. Is the stimulus to migrate a function of rate of change of light intensity as held by Ringelberg (1961, 1964) and McNaught and Hasler (1964, 1966) for instance, or are the calanoids remaining at all times within an optimum intensity range? Secondly, the calanoids which migrate in the apparent absence of an adequate light stimulus indicate that mechanisms other than light may be directly responsible for initiating their movements.

Let us consider, firstly, the movements which occur at apparently perceptible levels of illumination. The major difficulty in explaining the migrations as "attempts" to remain within an optimum light intensity is in the apparent inability of crustacean photoreceptors to measure absolute energy levels. To obviate this difficulty, I have suggested earlier that given progressively increased sensitivity in successive stages, and assuming each stage to be living at the limit of its visual acuity, the staggered day-depth of P. hessei could be explained. A similar mechanism is not as easily invoked to explain the dusk and dawn movements. If, at dusk, each stage moved upwards to remain at the level of its visual acuity, the "outswimming" of particular isolumes would not be expected. Also, it might be expected that the arrival of successive stages at the surface would match their visual sensitivity. This is not achieved. Similarly, at dawn, it would be expected that the adults would be the first to descend, with the other stages following in sequence. This is not strictly in accordance with the observations. However, this expected staggering of arrival or departure might be masked at dusk and dawn as a result of the very rapid changes in light intensity at this time of day, and also to some extent by the inter-sampling interval.

Ringelberg (1961, 1964) and McNaught and Hasler (1964) give evidence for accepting rate of change of light intensity as the direct migratory stimulus, certainly in the cladoceran species studied. McNaught and Hasler have shown for natural populations of Daphnia that a linear or near-linear relationship exists between the rate of vertical movement and the rate of change of log light intensity. This relationship applies in three distinct movements during the diel cycle viz. dusk ascent, dawn rise and descent to day depth.

It is apparent that unequivocal evidence for either the rate of change or optimum intensity hypotheses will be difficult to obtain. There is clearly a delicate balance between the two hypotheses. Beeton (1960) has considered them inseparable, since changes in light intensity would force a given species to move in order to remain within its zone of optimum intensity. Final conclusions are unwarranted in respect of P. hessei, although I favour the rate of change hypothesis on the basis of work done on cladocera.

Having discussed the migrations which take place at sensible levels of light energy, it is of interest to consider the dusk and dawn movements which occur in darkness. These are mainly exhibited by a portion of the adult female population although not entirely restricted to the female calanoids. These movements are most plausibly explained on the basis of involving endogenously regulated changes in locomotor activity. Evidence for internally regulated changes in locomotor activity in the copepodite stages I - VI of P. hessei has been presented. Seemingly, the adult females rely on this internally regulated migratory trigger to a far greater extent than the other stages whose migrations are more clearly related to changes in illumination. The significance of this is not known, but the females are considerably larger than the males and presumably more conspicuous to would-be predators. There might therefore be selective pressures upon the females to undertake the migrations under darker conditions than males or younger stages. If this was the case, the importance of endogenous rhythmicity would be in allowing the migrations to take place in very dark conditions i.e. after sunset and before daybreak.

Utilization of an internal clock mechanism would be of particular significance if it enabled the females to "pre-judge" dawn and to move downwards before increasing illumination made them visible to predators. The major difficulty involved in an active descent would be in the absence of a night-time orientation beacon. In active ascent it is entirely feasible that the "free-fall" position provides for orientation to gravity in conditions of total darkness. However, no equally simple means is known whereby swimming could be directed downwards in darkness. A priori, involvement of a reversed response to the ascent orientation mechanism would appear unnecessarily complicated. However, movements out of the surface waters before dawn could be achieved by a decrease in activity, leading to passive sinking. This activity decrease could be internally regulated, although, in general, activity rhythms increase rather than decrease at dawn. It is possible, therefore, that the presence of calanoids on the lake bed is a result merely of their nocturnal sinking.

Grindley (1972) reports that P. hessei wriggles into loose sediments of detritus when exposed to light. Thus the calanoid might move into total darkness, in which case endogenous rhythmicity would be of considerable importance in initiating the migrations since a photic cue might be irrelevant to an infaunal rather than epifaunal calanoid. Comparable behaviour has not been observed in P. hessei populations in Sibaya, but this is not to say that it does not exist. In fact, observations to be presented upon diel variations in feeding are most satisfactorily explained by assuming an infaunal existence of adult and near-adult stages of P. hessei during daylight.

There remains one further point to be discussed in relation to the dawn descent of the calanoids. Several authors have previously considered the possibility that the dawn descent is merely a passive sinking phase. This possibility has been recently revived by Rudjakov (1970). He presents data on sinking rates which indicate the feasibility of this interpretation. However, the observed descent rates of P. hessei in nature are not matched by laboratory determinations of passive sinking. Clearly gravity will be of some influence in the dawn descent, but some component of active swimming is also required. I believe that considerable caution is required in interpreting laboratory estimates of sinking rate. In the first instance, the natural environment is likely to be reasonably turbulent and this is likely to result in reduced sinking rates compared to those recorded in a still tube of water in the laboratory. Secondly, narcotized calanoids, in my experience, do not sink with outstretched first antennae which, in the natural free-fall position provide a considerable parachute effect. For these reasons, I believe that laboratory determinations of sinking rate are likely to be overestimates and may suggest that sinking is of greater importance than is really the case.

Discussion of the mechanisms which bring about the migratory responses, while fascinating, does not necessarily lead to an understanding of the adaptive significance of the migration. It is most unlikely that diel migration is without adaptive significance, however intangible such significance might appear. Harris (1953) has suggested that diel migration is an unavoidable side effect of an optically controlled depth-regulation. Tacit in his hypothesis is the assumption that depth regulation may be adaptively significant but that the migratory movements themselves are not necessarily so. However, irrespective of the direct causal factors involved, the diel migration must surely be considered of indirect significance if it achieves the purpose of depth regulation. Likewise, it can be argued that if crustacean visual physiology initiates an increased locomotor activity in response to supra-threshold rates of change in light intensity, then this too, must be of adaptive significance. In the preceding pages, vertical distribution and the migratory behaviour of P. hessei has been described, and where possible an attempt has been made to interpret the observations in relation to the causal mechanisms involved. The observations provide a basis from which to examine the question of vertical distribution and migration in relation to its functional and adaptive significance.

FEEDING BIOLOGY AND DIEL VARIATION IN FEEDING ACTIVITY

Introduction

The relationship between vertical migration and feeding behaviour has attracted considerable attention, particularly in relation to marine environments (Hardy and Gunther 1935, Harvey et al. 1935, Gauld 1951, 1953, Marshall and Orr 1955a, Hardy 1956, and McLaren 1963). Many zooplankters live by day below the photosynthetic zone and since many species are herbivorous, it is not surprising that their movement into surface or near-surface waters at night has been interpreted as a feeding response. Carnivorous species which also migrate, were assumed to be following their prey. However, considering the importance attributed to this relationship between migration and feeding, it has received surprisingly little attention under natural conditions. Gauld (1951, 1953) examined the feeding behaviour of Calanus finmarchicus in relation to its vertical distribution and time of day. He found that under natural conditions, very few calanoids contained food during daylight, but that at night, most did. Under laboratory conditions faecal pellets were produced both by day and by night, leading Gauld to conclude that the low proportion of fed animals by day was not the result of an intrinsic feeding rhythm, but rather a reflection of the low food content of the waters occupied by day. Some field evidence was obtained in support of this conclusion.

Most subsequent work on the feeding biology of crustacean zooplankton has been concerned primarily with estimates of filtration rate, assimilation, food selectivity and various factors affecting the above. (e.g. Marshall and Orr 1955b, 1956, Conover 1960, 1966a, b, Nauwerck 1963, Mullin 1963, Anraku 1964, McMahon and Rigler 1965, Richman 1966, Burns and Rigler 1967, Burns 1968, 1969a, b, Sorokin

1968, Schindler 1968, Gliwicz 1968, 1969, McQueen 1970, Schindler 1971). Apart from Gliwicz's studies, most of these investigations have been carried out predominantly under laboratory conditions and the feeding behaviour under natural conditions has been somewhat neglected.

By and large it has been assumed that in planktonic entomostraca, feeding will occur more or less continuously in nature, as long as food is present, although it has also been noted in certain laboratory studies that zooplankton will swim through seemingly rich food sources without feeding. The relationship between feeding, vertical distribution of consumer and time of day does not appear to have been studied in a freshwater system in the same way that Gauld examined it in the marine environment.

Notwithstanding the numerous laboratory studies of zooplankton feeding behaviour, our basic understanding of this important aspect of the trophic dynamics of aquatic ecosystems is inadequate. As recently as 1963 it was necessary for McLaren to make assumptions concerning the feeding behaviour of zooplankton, as existing observations were inadequate.

During the course of the present study, it was observed that adult and late copepodite stages of P. hessei collected during daylight seldom contained food in their guts, whereas at night the majority of calanoids had conspicuously full guts. The regularity of this observation and its obvious relevance to the question of vertical migration suggested that a basic examination of the feeding biology of this species should be undertaken. It was clear that an adequate appraisal of the relationship between feeding and migration demanded some knowledge of the feeding behaviour and migrations of the consumer and of the vertical distribution of the food organisms in the water body under consideration.

Aspects of the feeding biology of *P. hessei* and the food resources of this calanoid are described in the following pages. The techniques used have been simple but satisfactory for the purpose of examining the feeding behaviour of *P. hessei* as it relates to the vertical distribution of this calanoid and to its migrations in a natural system.

Feeding mechanism

The feeding mechanism of adult and late copepodite stages of *P. hessei* has been studied by microscopic examination of the calanoid in dense algal cultures and in solutions of coloured foodstuffs. Without the aid of a stroboscope or compressorium only a general idea has been obtained of the appendages involved and their respective functions. In general, however, the feeding mechanism of *P. hessei* resembles that described for *Calanus* by Cannon (1928, in Marshall and Orr, 1955a). In *P. hessei* rapid vibrations of the antennae 2 and the mandibular palps create a vortical current on either side of the animal. This current passes laterally towards the posterior. A counter current moving anteriorly effectively brings the food particles into contact with the filtering appendages. The food particles are collected by the posterior feeding appendages and passed forwards, presumably along a median food groove. Particles are either ingested after brief masticatory movements involving the mandibular appendages or else discarded by rapid flexing, apparently of the antennae 2.

Setation of the filtering appendages

The basic structure and setation of adult *P. hessei* appendages has been described by Grindley (1963). However, one aspect of the morphology of the mouthparts not described by Grindley is the setulation of the anterior appendages.

Fig. 35. Antenna 2 of adult ♂ P. hessei (x400).

Fig. 36. Mandible of adult ♀ P. hessei (x400)

Fig. 37. Maxilla 1 of adult ♀ P. hessei (x450).

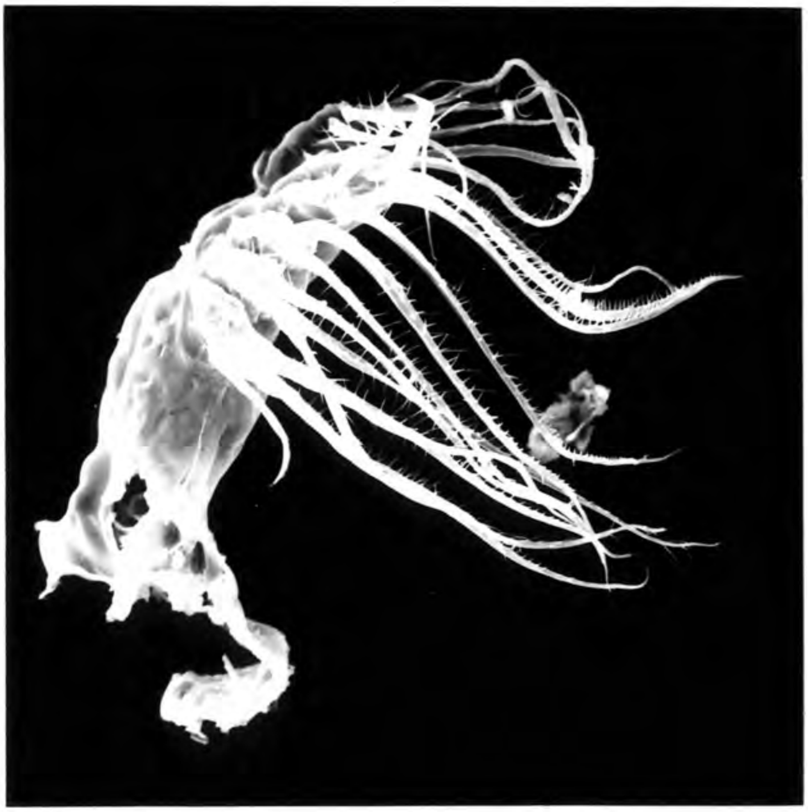


Fig. 38. Maxilla 2 of adult ♀ P. hessei (x700).

This setulation has been examined using Scanning Electron Microscopy of freeze dried material. The appendages were dissected and mounted separately. The anterior appendages of P. hessei (excluding the antennae 1) are shown in Figs. 35 - 41. Setulation is restricted to the appendages involved in filtering out the food particles and is absent from those appendages primarily involved in the production of filter currents.

Antennae 2 (Fig. 35) This appendage is primarily involved with the production of filter currents and as such, setulation is not expected. The setation of this appendage is both limited and very simple.

Mandibles (Fig. 36) The mandibular palp functions chiefly in producing filter currents, and as such setulation would be superfluous. The gnathal lobe is a masticating organ and bears no setae or setules.

Maxilla 1 (Fig. 37) Superficial examination would suggest that the broad area presented by this complicated appendage would be a very effective comb. However, the setae are irregularly supplied with setules and therefore would be able to filter out only larger particles if used as a filter comb at all. In C. finmarchicus this appendage is reported to have several functions. Firstly, it may be involved in the production of filter currents. Secondly, the maxillular setae sweep suspended particles towards the posterior end of the filter chamber. Lastly, the heavy spines on the appendage are thought to scrape off food particles collected on the maxilla 1 and push them towards the mouth (Cannon, loc. cit.). In view of the absence of extensive setulation on this appendage in P. hessei, it is clearly not used as a primary filter comb.

Maxilla 2 (Figs. 38 - 40) This is generally accepted as the major filtering organ in herbivorous calanoids (Lowndes 1935, Marshall and Orr 1956, Anraku and Omori 1963, and Heywood 1970b). In P. hessei

Fig. 39. Maxilla 2 of adult ♀ P. hessei (x500).

Fig. 40. Detail of setulation of Maxilla 2 of adult ♀ P. hessei (x3000).

Fig. 41. Maxilliped of adult ♂ P. hessei (x500).

it is richly furnished with regularly-spaced setules, of similar arrangement to that reported in C. finmarchicus (vide Marshall and Orr 1956, Fig. 2). These delicate setules are fairly regularly spaced along the length of the primary setae, at intervals of 2 - 4μ. In fresh, wet material, the arrangement of the setae is more regular than shown in Figs. 38 and 39. The appendage presents a far more uniform paddle shape and it is reasonable to assume that in life, the setules form a very effective mesh. Fig. 40 shows in detail the arrangement of these setules. The regularity of their spacing is noteworthy. An interesting comb-like structure of unknown function can be seen at the bottom centre of Fig. 40.

Maxilliped (Fig. 41) Basically a simple appendage, this structure is furnished with complicated combs, spines and setae, but setulation is very limited. Its structure suggests that this appendage is used for processes other than filtration.

Natural food of P. hessei in Lake Sibaya

P. hessei, like the majority of calanoids, is essentially a filter feeder. No evidence is available to indicate that filter feeding is anything but obligate in this species in Lake Sibaya. The general nature of the food ingested by the calanoids has been investigated using direct and indirect methods.

(i) Filtration rates

An estimate of food ingestion is readily determined by assessing changes in cell concentration after exposure of the food source to a population of calanoids. Where the taxonomy of autotrophic and heterotrophic components is known, an accurate idea of the species composition of the food may be obtained (Gliwicz 1968, 1969). While this degree of sophistication is not possible with the Sibaya material, the consumption of broad food categories viz.

nanoplankton, bacterioplankton and net phytoplankton can be estimated.

In determining absolute filtration rates, the use of various control measures is imperative. However, where used to indicate only the nature of the food consumed, the experimental procedures may be simplified considerably. Inverted microscope estimates of net plankton, nanoplankton and bacterioplankton abundance were made on a sample of lake water into which a number of calanoids were then introduced ($N = 50$). The experimental vessel (volume = 1200ml) was kept in the dark and agitated manually at intervals of 30 to 45 mins. After four and eight hours, subsamples of the water were removed and algal and bacterial numbers assessed. These data were used to determine filtration rates, using the equation for exponential decrease given by Gauld (1951). Over both four and eight hour periods, filtration rates of approximately 1 ml/calanoid/hour were obtained for both nanoplankton (30µ largest dimension) and bacterioplankton "units" (see p 168). Grazing upon net phytoplankton was negligible.

These experiments, using naturally occurring food species at natural concentrations demonstrate the importance of the smaller particulate material as food sources. This is in accordance with the morphology of the feeding appendages as described.

(ii) Gut content analysis

Direct examination of the contents of the fore-gut in a manner similar to that employed by Fryer (1957d) has substantiated the results of filtration studies. The great bulk of the fore-gut contents consist of bacterial and nanoplankton elements, especially the former. Bacterial aggregations associated with diffuse masses of flocculent apparently detritic material made up a large portion of the fore-gut content. Only occasional net phytoplankton were seen.

(iii) Faecal pellet analysis

Several scores of faecal pellets have been examined during the course of the study. The pellets consisted mainly of compacted bacterial material, interspersed periodically with empty diatom frustules and undigested filaments of the blue green alga *Anabaenopsis*. Empty skeletons of circular nanoplankton components similar in shape to *Chlorella* frequently occurred. The low proportion of intact algal cells in the faecal pellets suggests that algal cells ingested are generally assimilated. Only occasional recognisable remains of net algae were observed. *Synedra acus* was the most frequently recorded net algal fragment. It is not known whether the compacted bacterial cells which made up the bulk of the pellets represented the natural intestinal flora, or whether they represented undigested bacteria grazed from the water. The former appears the more likely explanation in view of the high assimilation of bacteria reported in other copepods (Sorokin 1968).

Radio-isotope work is necessary to extend these highly qualitative observations into a meaningful quantitative study of calanoid nutrition (*vide* Marshall and Orr 1955b, 1956, Sorokin 1968, Schindler 1971, who have studied the food spectrum of calanoids).

Vertical distribution of food in Lake Sibaya

Estimates of standing crop and biomass of various components of the primary producers and consumers of Lake Sibaya have been made at Station III on a seasonal basis.

The methods used for the analysis are to be published elsewhere. However, basic descriptions of the methods used are given below. Net phytoplankton were sedimented using Lugol's iodine and nanoplankton and bacterioplankton were sedimented with a modified Lugol's iodine solution (*Volvox* fixative in Johansen, 1940) and

TABLE 10

Mean standing crop estimates for various phytoplankton groups and species and chlorophyll *a* in relation to depth. Figures based on mean data of 1969 - 1972, for Station III. The number of sampling dates is given by N.

SPECIES (Cells or colonies per litre)	N	SURFACE WATER (0-5 m)	MIDDLE WATER (15 m)	BOTTOM WATER (30 m)
BLUE-GREEN ALGAE				
Merismopedia sp.	30	480×10^{2}	-	367×10^{2}
Anabaena sp. A	69	56×10^{2}	-	39×10^{2}
Anabaena sp. B	69	77×10^{1}	-	53×10^{1}
Anabaenopsis sp.	69	3161×10^{2}	-	2350×10^{2}
GREEN ALGAE				
Closterium pronum/aciculare	69	646×10^{2}	-	781×10^{2}
Scenedesmus sp.	30	34×10^{2}	-	72×10^{2}
DIATOMS				
Synedra acus	69	121×10^{2}	-	278×10^{2}
Melosira g. granulata	69	426×10^{2}	-	477×10^{2}
Melosira g. angustissima	69	32×10^{2}	-	50×10^{2}
Other diatoms	30	793×10^{2}	-	1365×10^{2}
CHLOROPHYLL (µg/l)				
Chlorophyll *a*	54	2.6	2.7	2.8
Chlorophyll *a* corrected for phaeophyton	33	1.7	-	1.9

counted under an inverted microscope. Chlorophyll concentrations were determined spectrophotometrically in cold methanol extracts (Talling 1965). Bacterial activity was assessed by means of broad spectrum culture media, under laboratory and in situ conditions. Investigations were based in all cases upon samples taken from surface waters and waters close to the lake bed. Waters of intermediate depth were studied in some cases.

Net phytoplankton and chlorophyll

Chlorophyll concentrations and standing crops of the dominant net phytoplankton species were determined fortnightly over two years at Station III. A 5m plastic hose was used to collect an intergral sample of the 0 - 5m column (Lund, Kipling and Le Cren, 1958). A 2 litre Friedinger water bottle was used to collect water ~1m above the lake bed. These investigations indicated clearly that total algal standing crops and chlorophyll values were similar for surface and deep waters, although the algal species showed a consistent tendency for a slight numerical increase in the deeper waters. In only the blue-green algae were the standing crops in the surface water consistently higher than those in deep water. These data are summarized in Table10 and show clearly that the standing crop of primary producers (as chlorophyll) is very low indeed. The algal species studied showed a regular seasonal cycle of wax and wane, although these changes could not be related to the more erratic fluctuations in chlorophyll concentration. (Table 7 shows the seasonal changes in chlorophyll content of surface and bottom waters during 1970 - 1971).

Nanoplankton and Bacterioplankton

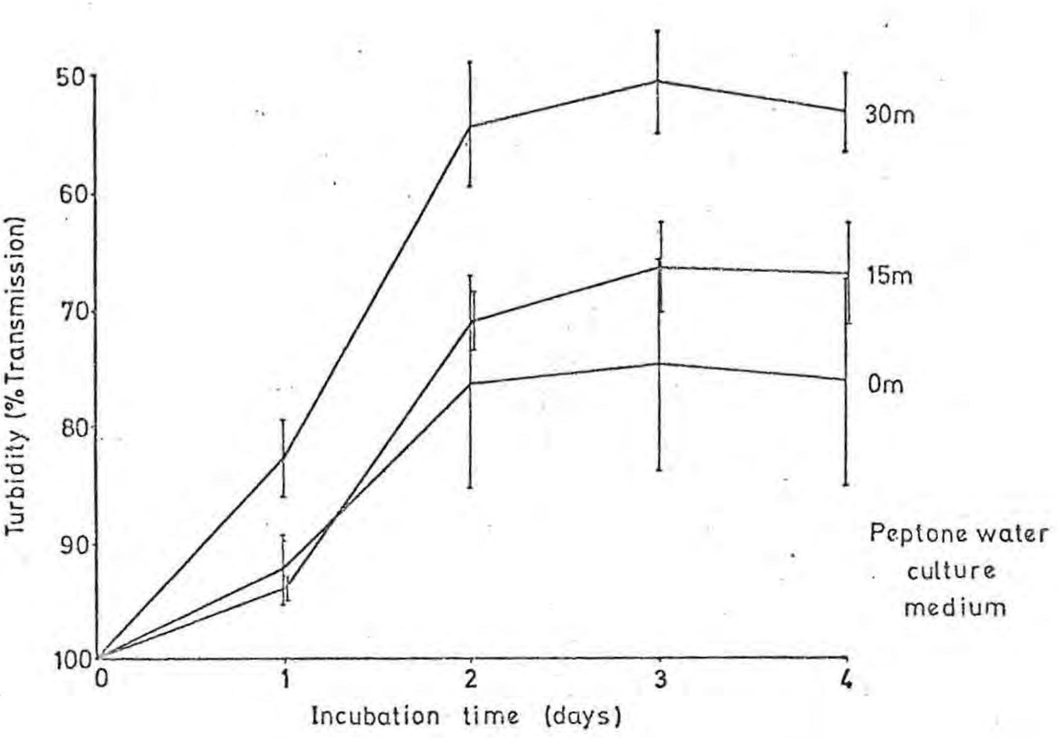
Nanoplankton estimates were based on total counts of all algae of which the greatest dimension did not exceed 30µ (Hutchinson 1967). Bacterioplankton estimates were made of bacterial colonies

TABLE 11.

Mean standing crop estimates (in numbers/ml.) for nanoplankton and bacterioplankton in relation to depth. Aggregate data for Stations I and III indicated separately. The number of determinations is given by N.

	STATION III	
20/7/71 - 27/10/71	0m-5m	30m
Nanoplankton cells	2389	2343
Bacterioplankton units	9100	9661
N = 7		

	STATION I		
15/12/71 - 5/6/72	0m	19m	38m
Nanoplankton cells	4050	3330	4248
Bacterioplankton units	13050	11772	13104
N = 10			



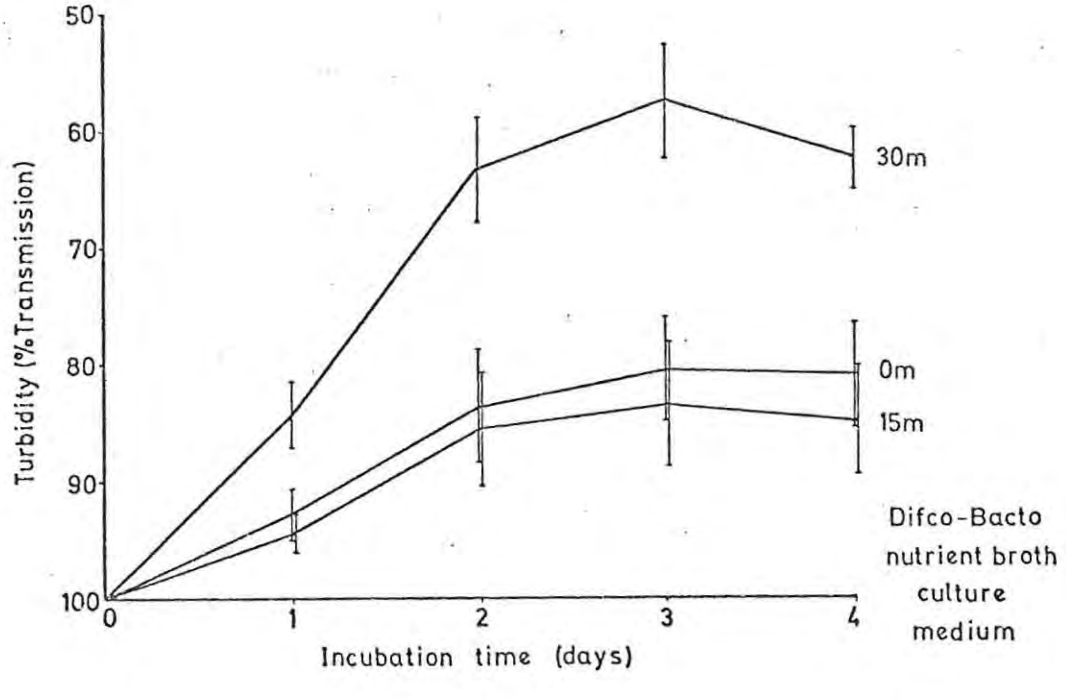


Fig. 42. Heterotrophic activity as reflected by turbidity changes in two culture media, inoculated with lake water from three depths. The mean and standard deviations of 5 series of incubations using water samples collected at Station III are shown.

or agglutinations. Counts were weighted in relation to colony size. Small colonies (<10μ) were given a numerical value of 1; largest colonies (>20μ) were given a value of 3. The resulting counts have been termed bacterioplankton "units". Individual bacteria were not counted.

The changes in nanoplankton cell counts and bacterioplankton "unit" counts were followed over a period of one year. Mean counts during this period are given in Table 11. Nanoplankton counts were similar for surface and bottom waters, but intermediate waters consistently contained fewer cells. Bacterioplankton showed the same pattern with reasonably similar counts in the surface and bottom samples and lower values in intermediate waters.

Culture techniques were also used to determine the heterotrophic activity of suspended bacteria collected from surface, middle and near-bottom waters. Water samples were collected in a pre-sterilized evacuated home-made sampler. Broad spectrum culture media (nutrient broth and peptone water) were inoculated in test tubes with lake water from different depths. A water bath placed over a paraffin refrigerator burner was used as an incubator. Temperature was regulated as far as possible by raising or lowering the water bath. Mean incubation temperatures were $30^{\circ} \pm 3^{\circ}C$. Bacterial activity was determined indirectly by turbidity development, assessed in an Eel colorimeter. While the techniques were simple, sterility of controls was achieved entirely satisfactorily. The results are therefore comparable, and indicate the relative heterotrophic activity of bacterial communities from different depths. Fig. 42 shows the mean results of 5 series of incubations. Maximum bacterial activity was obtained from deep water samples, and either surface or mid-water samples gave intermediate values.

Bacterial activity was also measured <u>in situ</u>. Test tubes containing culture media were inoculated with water from three depths and plugged with cotton wool. The test tubes were packed into 1200ml polyethylene bottles with cotton wool. The bottles were sealed and suspended in the lake at the depths at which the water samples had been collected. After three days the tubes were collected and turbidity was determined. The results of the in situ incubations were similar to those obtained under laboratory conditions. The mean percentage transmission of these samples after 3 days incubation is given below.

	1m	15m	30m
Nutrient broth	83	87	68
Peptone water	71	74	64

The major point arising from these data is that the vertical distribution of primary producers and consumers within the pelagial of Lake Sibaya, is one of small variation. This arises from the lack of thermal stratification and the extensive mixing brought about by wind generated currents.

Primary production in Lake Sibaya

An initial estimate of primary production was obtained by Professor B.R. Allanson in January, 1973, using radio-carbon light and dark bottle techniques. A net primary production intergral of $30.29mgC/m^2/hr$ was obtained for the open waters of the lake. The compensation point was recorded at 16m. The light and temperature regime experienced in this subtropical lake might be expected to provide favourable conditions for primary production, particularly since the algal populations are not subjected to the so-called "shock" factor of annual stratification and overturn (Round 1971). However, the low primary production together with the annually low algal standing crop might be taken to indicate that one or more of the essential plant nutrients is a limiting factor in the primary production of Sibaya. This idea is supported by the geology of the area and by seasonal analyses of phosphate and nitrate. Orthophosphate values are generally below 5µg/l throughout the year and nitrate levels are barely detectable; values in excess of 0.01µg/l have not been recorded (Hart, unpublished data). The entire area overlies deep sand deposits and all influent streams drain from sandy catchment areas.

It is interesting to note that by feeding upon two different energy resources (viz. nanoplankton and bacterioplankton), P. hessei is utilizing two different trophic levels simultaneously. The ability of this calanoid to do so may, in part, be responsible for the success of this species in an environment in which primary production is very low.

Diel variation in feeding in P. hessei

Adult and late copepodite stages of P. hessei collected off the lake sediments during daylight hours were seldom observed to have food in their guts. By comparison, most calanoids collected in net hauls at night had conspicuously full guts. This pronounced difference was entirely unexpected in view of the uniform vertical distribution of potential food sources, described above.

The question of diel variations in feeding intensity in copepods (and zooplankton in general) has attracted considerable attention (Gauld 1951, 1953, Marshall and Orr 1955a, McLaren 1963). Hardy (1956) has postulated that vertical migrations of zooplankton may be simple feeding migrations. McLaren (1963) has proposed that an energy bonus would accrue to zooplankton vertically migrating in thermally stratified systems if feeding was restricted to the warmer surface waters i.e. if a diel variation in feeding existed.

It is clear that, in general, the feeding behaviour of zooplankton may be inseparably associated with their migratory behaviour. In the marine environment where pronounced vertical changes in food availability are experienced, Hardy's (1956) hypothesis is obviously realistic. In the unstratified waters of Lake Sibaya, the diel changes in the vertical distribution of P. hessei are associated with changes in the proportion of animals with food in their guts. However, these changes are not matched by similar vertical changes in algal or bacterial standing crop. It was obvious that the initial observations on diel variation in feeding had to be confirmed. The evidence for such confirmation is presented in the following pages. Results of field and laboratory studies are presented separately.

Methods

Three techniques have been used to assess diel variations in feeding. The majority of the field observations have been based simply upon the presence or absence of food in the gut. A limited series of radio-isotope experiments was also undertaken. The question of diel variation in feeding has also been examined under laboratory conditions using faecal pellet production and presence or absence of food in the gut as indices of feeding behaviour. The radio-isotope studies and the laboratory studies are given in context in subsequent pages.

1. Presence or absence of food in the gut

The presence or absence of food in the gut is a subjective measure of feeding. Nevertheless, it gives a good indication of large-scale changes in feeding. It has been used by Gauld (1951, 1953) in his studies on Calanus finmarchicus and is undoubtedly the simplest method of determining the extent to which feeding takes place under entirely natural conditions. In the present study, animals were collected by various means at different times of the day and immediately preserved with formalin. Samples were kept in the dark in a cool place and examined within 24 - 48 hours. In the Sibaya material, distinct differences in quantity and colour of food were evident between the daylight and night samples, particularly in the adult and late copepodite stages of the calanoid. Animals collected at night had conspicuously full guts. The midgut contained a compacted mass of green or greenish yellow material which was immediately obvious upon microscopic examination. Generally, the gut was either very full or empty; only occasionally did the gut appear slightly filled. By comparison, animals collected during daylight were predominantly without food in the gut. When food was present, it was generally present in small amounts and was of a darker colour (greenish brown to brown). A simple yes/no criterion was employed in quantifying the observations. If any food was visible in the gut, the animal was counted as fed. No distinction was made between markedly or slightly filled guts. In view of the thousands of calanoids which required examination, it was obviously impractical to dissect out gut contents. The differences were, however, sufficiently pronounced on the basis of simple external examination.

Three potential sources of error may be involved in determining feeding in this way.

a) Gut clearance during processing.

b) Spontaneous defaecation upon preservation.

c) Transparency of food.

a) Gut clearance rates in relation to processing time. It is evident that if an actively feeding animal is kept without food for a period exceeding the normal passage time of food through the gut, the animal will have an empty gut. It could therefore be incorrectly concluded that the animal was not feeding. It was important, therefore, to establish the gut clearance rate of the calanoids and to ensure that the time taken to collect and preserve the calanoids did not exceed this time.

Gut clearance rates of animals exposed to natural food sources at natural concentrations varied from 10 to 15 minutes. This gut clearance rate is considerably shorter than that reported for Calanus finmarchicus (Gauld 1953), Diaptomus oregonensis (Richman 1966), D. gracilis (Kibby 1971) and McMahon and Rigler's (1965) estimates for Daphnia magna.

The time interval between collection and preservation of samples taken using different techniques did not vary to any significant extent. In both substrate bin collections and net haul collections, the time interval between the filtration of the calanoids out of their surrounding environment, and preservation, did not exceed 2 - 3 minutes. Thus, the time interval between collection and preservation was at all times considerably less than the gut clearance rate recorded. There is little likelihood, therefore, that large-scale gut clearance would have occurred in the interval between collection and preservation.

b) Spontaneous defaecation during preservation. Gauld (1953) reported spontaneous defaecation during preservation in C. finmarchicus. He found that this defaecation was very erratic and could introduce errors into the results. Accordingly, he kept his material alive for examination. This necessitated keeping the calanoids for at least 20 minutes before starting examination of the first specimens. This was entirely impractical with the Sibaya material; gut clearance rates alone could have seriously affected the results. The striking diel differences to be reported support the conclusion that in P. hessei spontaneous defaecation is not a serious factor. If it were, the diel differences would not be expected, unless the extent of sponta-

TABLE 12.

The proportions and percentages of P. hessei containing food in their guts, in relation to time of day.

STAGE	NET HAULS		SUBSTRATE BINS	
	Midday 35-38m	Midnight 0-38m	Midday 38m	Midnight 38m
Adult ♂♂	$\frac{3}{100}$ 3%	$\frac{256}{279}$ 92%	$\frac{0}{137}$ 0%	$\frac{0}{0}$ -
Adult ♀♀	$\frac{4}{51}$ 8%	$\frac{173}{205}$ 85%	$\frac{7}{100}$ 7%	$\frac{0}{0}$ -
CI - CV	$\frac{12}{50}$ 24%	$\frac{269}{350}$ 77%	$\frac{10}{100}$ 10%	$\frac{0}{0}$ -

TABLE 13.

Proportions and percentages of P. hessei containing food at midday, in relation to the substrate type used in the substrate bin.

STAGE	LITTORAL SAND	SAND FROM LAKE BED AT 39m.	MUD FROM LAKE BED AT 35m.
Adult ♂♂	$\frac{0}{73}$ 0%	$\frac{0}{81}$ 0%	$\frac{0}{83}$ 0%
Adult ♀♀	$\frac{3}{171}$ 2%	$\frac{5}{152}$ 3%	$\frac{3}{172}$ 2%
CI - CV	$\frac{2}{100}$ 2%	$\frac{6}{100}$ 6%	$\frac{4}{100}$ 4%

neous defaecation itself varied dielly. Several experiments reported below demonstrate that there is no reason to believe that it does.

c) Transparency of food. Algal cells compacted in the gut are conspicuous by virtue of their colour and opacity. If the calanoids were consuming a hypothetically transparent food source, they might appear to have empty guts. In the present study, there is evidence that diel variations in proportions of fed and unfed animals occur in the presence of identical food sources. It is unlikely, therefore, that false conclusions have been drawn as a result of food transparency, particularly since animals collected with food during daylight (when there is a lower incidence of feeding) generally contained dark-coloured gut contents.

In spite of the subjective nature of the observations, there is little probability that they are seriously in error. The potential sources of error can be excluded in some cases. In many cases the results obtained provide in themselves support for assumption of their validity, as they would not be obtained if a systematic error was present. This will become evident as the observations are presented.

Field studies based on the presence or absence of food in the gut and the validity of substrate bin results.

The diel differences in the proportion of fed and unfed animals are large, particularly in the case of adult calanoids. The extent of this difference is shown in Table 12, in which midday and midnight collections made with nets and substrate bins are compared. The absence of calanoids from the substrate bins at midnight is as a result of their migratory behaviour. Similarly, the low catches in midday net hauls reflect the vertical distribution pattern.

The data given in Table 12 demonstrate the pronounced changes which occur between day and night. During daylight, very few animals are captured with food in their guts. This is true, whether they are caught in the water column or on the substrates. At night, the majority of the animals contain food.

The net haul sample results are obviously realistic. There is little or no possibility of obtaining high "percentage fed" values if these are not in fact real. It is only the low values which warrant examination.

Extensive observations of calanoids in association with sedimentary substrates have been made in the laboratory. Calanoids were consistently seen to filter off particles of very fine flocculent material collected from sediment taken from the lake bed. These observations originally led to the suggestion that the calanoids might be utilizing the flocculent material as a food source. This, in turn, suggested that the low proportion of calanoids with food in their guts, collected in substrate bin samples, might arise from the artificiality of the substrate introduced into the bins. The possibility that the substrate bin results are artefactual has been examined and the evidence demonstrating the validity of the results, drawn from several separate approaches, is given in (i) - (v) below, before the major observations are presented.

(i) Use of natural substrates in the bins

The littoral sand substrates normally used in the substrate bins were replaced with natural substrates collected off the lake bed with a Van Veen grab. Bins in which littoral sand (from 0m), profundal sand (from 39m) and profundal mud (from 35m) were used as substrates, were positioned on the lake bed at 39m. The proportions of fed and unfed animals at midday, collected from these bins after an overnight exposure, are given in Table 13. No difference in

TABLE 14.

Comparison between the proportions and percentages of P. hessei containing food collected at midday from substrate bins exposed in the lake for varying lengths of time.

STAGE	OVERNIGHT EXPOSURE	8 DAY EXPOSURE
Adult ♂	$\frac{0}{73}$ 0%	$\frac{0}{237}$ 0%
Adult ♀	$\frac{3}{171}$ 2%	$\frac{11}{495}$ 2%
CI - CV	$\frac{2}{100}$ 2%	$\frac{12}{300}$ 4%

TABLE 15.

Proportions and percentages of P.hessei containing food in relation to time of day. Daytime values determined from animals collected from substrate bins exposed at 38m. Night-time values determined from animals restrained to substrate bins until after dark, by means of sealing lids fitted to the bins during daylight. Both sets of bins exposed at 38m.

STAGE	DAYLIGHT 38m	NIGHT 38m
Adult ♂♂	$\frac{0}{90}$ 0%	$\frac{14}{60}$ 23%
Adult ♀♀	$\frac{10}{112}$ 9%	$\frac{23}{60}$ 38%
CI - CIII	$\frac{13}{150}$ 9%	$\frac{46}{177}$ 25%
CIV - CV	$\frac{33}{200}$ 17%	$\frac{25}{107}$ 23%

proportions of fed and unfed animals exists. χ_c^2 (Siegel 1956, p. 107) is not significant at the 95% level. Total catch per bin was similarly unaffected by substrate type (see also p. 88)

(ii) Temporal changes in "artificial" substrates exposed on the lake bed.

Exposure of the substrate bins on the deep lake bed for as little as 4 - 6 hours, results in a conspicuous accumulation of flocculent tripton. If the exposure is increased to several days this flocculent material compacts on the originally introduced substrate, forming a layer which may reach several centimetres in depth. A complex fauna and flora appears within several days, and it is superficially difficult to distinguish the few centimetres of sedimentary material from that occurring on the natural lake bed. Calanoids collected from bins exposed for this length of time would supposedly have available to them, the food sources available on undisturbed natural sediments. In Table 14 the proportions of fed animals collected from substrate bins exposed for $\frac{1}{2}$ a day and 8 days are given. There is no significant difference between the two samples.

(iii) Proportions of younger stages with food.

If food was a limiting factor within the substrate bins, it would be expected that the feeding of different developmental stages should be affected similarly. Yet, in practically all substrate bin collections, the proportions of earlier developmental stages with food were considerably greater than those of the later stages (Table 16, for example). This might be taken as evidence against food limitation within the bins, assuming that the food requirements of the younger stages are similar to those of the adults.

(iv) Feeding changes in calanoids confined to substrate bins until after nightfall

At night, the entire calanoid population moves out of the substrate bins into the overlying pelagial water. In situ estimates of feeding within the substrate bins are therefore not possible at night unless calanoids are forcibly confined to the substrate bins until after dark. This procedure has been used to assess the diel changes in feeding which take place within the confines of the bins. Proportions of fed and unfed animals were determined from a bin sample collected and preserved at midday. A replicate bin was retrieved at midday, sealed by means of a transparent perspex lid, and returned immediately to the lake bed (at 38m). The sealed bin was retrieved again $1\frac{1}{4}$ hours after sunset and the calanoids removed and preserved. The results of the day and night samples are given in Table 15. Despite the small numbers involved, conspicuous changes in the percentages of animals with food are evident. The diel changes are not as pronounced as those normally recorded in free-living calanoids (vide Table 12). Nevertheless, it will be appreciated that during the $5\frac{1}{2}$ hour period in which the bin was sealed, sedimentation of potential food sources would be expected. Therefore, when the calanoids moved into the water overlying the substrate within the substrate bin in their normal dusk ascent, they moved into waters which were probably somewhat depleted of food. The smaller difference between day versus night results in this experiment is explicable when viewed in this manner. Notwithstanding sedimentation effects, day versus night results differ significantly when tested by means of χ^2_c (in 2 x k contingency tables, Siegel 1956, p. 107), in the case of the adults and early copepodite stages. (Adult males $p > 0.001$, Adult females $p = 0.02 - 0.01$, C I - C III $p > 0.001$, C IV - C V $p = 0.5 - 0.7$).

(v) Collections of animals off natural undisturbed substrates.

With the construction of the horizontal bottom sampler (p. 46) it was possible to collect large numbers of calanoids off natural

TABLE 16

Diurnal variation in proportion and percentages of *P. hessei* containing food. Calanoids were collected by means of substrate bins, horizontal bottom sampler and net hauls at Station I, 24/5/72. Sunrise was obscured by cloud cover, but occurred at approximately 06.30 hrs, sunset at 17.00 hrs.

		SUBSTRATE BIN		HORIZONTAL BOTTOM SAMPLER		NET HAULS	
0600	Adult ♂	26/119	22%	51/324	16%	12/12	100%
	Adult ♀	65/150	43%	32/200	16%	4/4	100%
	CI-III	15/38	40%	56/100	56%	147/263	55%
	CIV-V	21/50	42%	48/192	25%	23/37	62%
0800	Adult ♂	8/114	7%	37/468	8%	5/10	50%
	Adult ♀	31/150	21%	48/281	17%	0/1	0%
	CI-III	16/57	28%	52/100	52%	64/135	47%
	CIV-V	17/59	29%	42/100	42%	19/29	67%
1000	Adult ♂	9/139	6%	12/221	5%	0/2	0%
	Adult ♀	46/138	33%	28/200	14%	0/0	-
	CI-III	9/33	27%	45/100	45%	59/143	41%
	CIV-V	33/87	38%	83/176	47%	2/10	20%
1200	Adult ♂	10/100	10%	7/148	5%	0/0	-
	Adult ♀	40/114	35%	16/86	19%	0/0	-
	CI-III	26/58	45%	69/100	69%	12/27	45%
	CIV-V	50/99	50%	76/144	53%	0/0	-
1400	Adult ♂	15/109	14%	19/201	10%	0/1	0%
	Adult ♀	48/117	41%	120/269	45%	0/0	-
	CI-III	43/77	56%	77/100	77%	17/42	41%
	CIV-V	55/113	49%	118/154	77%	0/0	-
1600	Adult ♂	22/109	20%	40/200	20%	0/2	0%
	Adult ♀	97/194	50%	151/300	50%	0/0	-
	CI-III	36/50	72%	34/56	61%	56/131	43%
	CIV-V	63/93	68%	97/148	66%	0/2	0%
1800	Adult ♂	NO SAMPLE TAKEN		11/14	79%	35/37	95%
	Adult ♀			58/81	72%	24/27	89%
	CI-III			1/1	100%	165/270	61%
	CIV-V			1/1	100%	49/63	78%

substrates where natural physical, chemical and biotic factors would be expected. Collections of calanoids off the natural lake substrates during daylight hours have provided the most adequate confirmation of results obtained from substrate bin collections. Table 16 gives the results of serial daylight collections of calanoids off lake sediments and from the pelagial waters. It shows the comparability of substrate bin, horizontal bottom sampler and to some extent net haul collections in relation to the percentage of animals with food in their guts. Comparison of substrate bin and horizontal bottom sampler results by means of the Wilcoxon matched-pairs signed-ranks test leads to the conclusion that the results are significantly different with respect to the percentages of calanoids with food. Be this as it may, the daytime substrate values are still low relative to the pelagic night-time values obtained in the same series.

Comparison of the 1600hrs and 1800hrs samples taken with the horizontal bottom sampler shows a marked increase in the proportion of animals with food. However, this increase may be artefactual, on the following grounds. The horizontal bottom sampler, in the open position, could act in some way like a net descending horizontally or at times, slightly obliquely. There was no provision in its construction to ensure that the collecting tube was kept closed until it was activated on the lake bed. Since, by 1800hrs. the dusk ascent of the calanoids was well advanced (sunset was at 1700hrs), there is no guarantee that the 1800hrs sample does not represent animals captured in the water column and not off the substrates. For this reason, and since the sample involved is so small, it would appear justified to ignore this set of results.

The net collections at 1800hrs show a marked increase in the proportion of adults with food. This strongly suggests that feeding is closely correlated with movement of the calanoids into the pelagic waters.

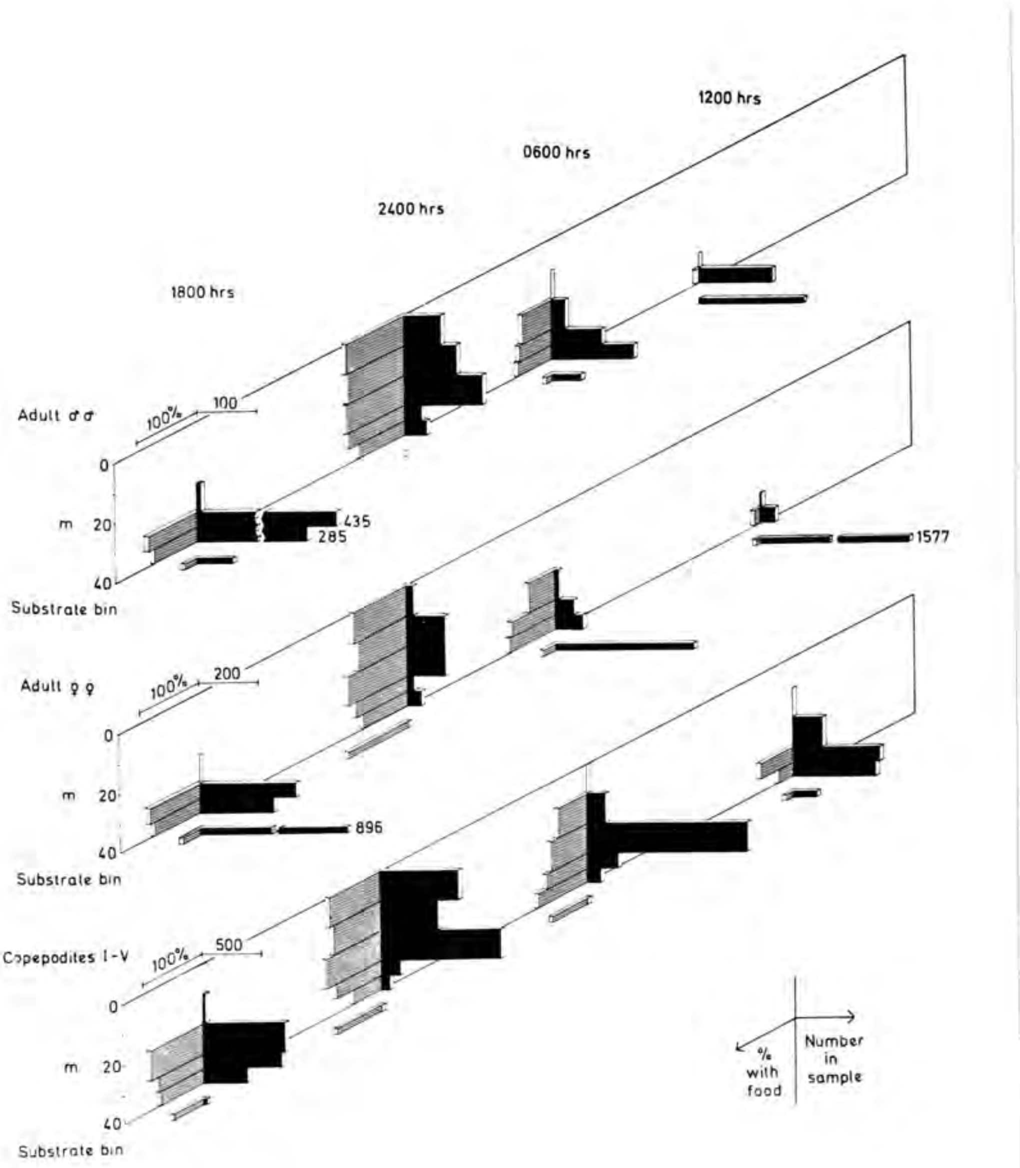


Fig. 43. *P. hessei*: Diel changes in percentages of animals with food in guts in relation to their vertical distribution. Samples collected by means of net hauls and substrate bins, 1 - 2 March, 1972, at Station I. Vertical distribution indicated in solid black; percentage fed indicated by cross-hatching.

The observations presented in the preceding pages provide evidence that the low percentage of adult calanoids with food during daylight is not an artefact arising from the use of substrate bins. It is clearly a valid feature of the feeding biology of P. hessei. Differences occur between daytime samplings, depending on sampling equipment. Nevertheless, these differences are small in comparison to the overall diel changes which have been recorded. Having provided justification for using results obtained from substrate bin samples, it is possible to examine the overall circadian pattern of feeding as it relates to the vertical distribution of P. hessei.

Results

The most complete investigation of changes in feeding in relation to vertical distribution and time of day is shown schematically in Fig. 43. The vertical distribution and its temporal changes are represented on the x axis and depth on the y axis. The percentages of animals containing food are shown on the z axis. The 3 - dimensional format allows the comparison of vertical distribution with changes in percentages of animals with food, in relation to the time of day. Fig.43 shows that large percentages of calanoids are fed when they are in the water column at night whereas when they are on the lake bed at midday, very low percentages contain food. The figure shows that high feeding intensity is associated with the presence of the calanoids in the water column, irrespective of whether they are in the very surface or very deepest waters. Differences are evident between the adults and copepodites but the general pattern is consistent.

These observations were made during a single circadian series. However, a large quantity of data collected over a period of some five months are available to confirm the general conclusions which emerge from Fig. 43.

TABLE 17.

Proportions and percentages of *P. hessei* containing food, captured in the water column by day and by night, by means of net hauls. These are aggregate data, based on collections made between February and June, 1972. Data collected 1½ hours either side of sunset or sunrise are excluded. The low numbers of adults captured by day is a reflection of their vertical distribution. The relatively low number of younger stages in the night samples is a function of sampling intensity.

	DAYLIGHT	NIGHT
Adult ♂♂	$\frac{8}{116}$ 7%	$\frac{575}{627}$ 92%
Adult ♀♀	$\frac{8}{105}$ 8%	$\frac{345}{405}$ 85%
CI - CV	$\frac{292}{619}$ 47%	$\frac{269}{350}$ 77%

TABLE 18.

Proportions and percentages of *P. hessei* containing food, captured off substrates by day and by night by various means. These are aggregate data for February to June, 1972. Data collected 1½ hours either side of sunrise or sunset are excluded. The low number of calanoids captured by night is a reflection of their vertical distribution.

	DAYLIGHT SAMPLES		NIGHT SAMPLES	
	Substrate Bin	Horizontal Bottom Sampler	Substrate Bin	Horizontal Bottom Sampler
Adult ♂♂	$\frac{108}{1523}$ 7%	$\frac{229}{1829}$ 12%	$\frac{31}{34}$ 91%	-
Adult ♀♀	$\frac{413}{1803}$ 23%	$\frac{574}{2018}$ 28%	$\frac{44}{53}$ 83%	-
CI - III	$\frac{225}{485}$ 46%	$\frac{319}{548}$ 58%	$\frac{2}{3}$ 67%	-
CIV - V	$\frac{359}{811}$ 44%	$\frac{519}{927}$ 66%	$\frac{70}{71}$ 99%	-

TABLE 19.

Proportions and percentages of P. hessei containing food, captured in the water column and on the substrates using various methods, during the dusk and dawn periods (i.e. 1½ hours either side of sunset and sunrise). These are aggregate data, based on several collections.

	DAWN			DUSK	
	Net Samples	Substrate Bin	H.B.S.*	Net Samples	Substrate Bin
Adult ♂♂	$\frac{78}{136}$ 57%	$\frac{27}{199}$ 14%	$\frac{51}{324}$ 16%	$\frac{267}{347}$ 77%	$\frac{61}{239}$ 26%
Adult ♀♀	$\frac{94}{130}$ 72%	$\frac{24}{100}$ 24%	$\frac{32}{200}$ 16%	$\frac{242}{296}$ 82%	$\frac{166}{400}$ 42%
CI - CIII	$\frac{147}{263}$ 56%	$\frac{0}{0}$	$\frac{56}{100}$ 56%	$\frac{368}{620}$ 60%	$\frac{15}{38}$ 40%
CIV - CV	$\frac{23}{37}$ 62%	$\frac{0}{0}$	$\frac{48}{192}$ 25%	$\frac{49}{57}$ 86%	$\frac{21}{50}$ 42%
CI - CV	$\frac{147}{225}$ 65%	$\frac{31}{160}$ 19%	$\frac{0}{0}$	$\frac{235}{300}$ 78%	$\frac{40}{80}$ 50 %

* Horizontal Bottom Sampler.

TABLE 20.

Proportions and percentages of P. hessei containing food in relation to time at dawn. The results are based upon collections made by means of substrate bins (Station I, 19/2/1972).

	0400hrs	0410hrs	0445hrs	0530hrs	0615hrs	0700hrs
Adult ♂♂	$\frac{8}{8}$ 100%	$\frac{23}{25}$ 92%	$\frac{23}{25}$ 92%	$\frac{19}{50}$ 38%	$\frac{3}{50}$ 6%	$\frac{0}{50}$ 0%
Adult ♀♀	$\frac{0}{0}$	$\frac{41}{50}$ 82%	$\frac{43}{50}$ 86%	$\frac{15}{50}$ 30%	$\frac{9}{50}$ 18%	$\frac{3}{50}$ 6%
Copepodites I - V	$\frac{23}{24}$ 96%	$\frac{49}{50}$ 98%	$\frac{50}{50}$ 100%	$\frac{15}{50}$ 30%	$\frac{9}{50}$ 18%	$\frac{3}{50}$ 6%

Table 17 shows the proportions and percentages of animals containing food present in the water column by day and by night. In the adult calanoids particularly, there is a striking difference between the daylight and night collections. Practically all calanoids collected from pelagial waters at night contain food, whereas the proportion of adults with food during daylight is very low. In the pre-adult copepodite stages a significant difference exists, but is less striking than in the case of the adults.

A similar diel difference in feeding is evident in calanoids captured off the lake bed, as shown in Table 18. During daylight, relatively few adults contain food. This is apparent in both horizontal bottom sampler and substrate bin results. Very few calanoids are captured on the lake bed at night. Nevertheless, those that are captured almost all have food in their guts. It will be realized, however, that the calanoids collected on the lake bed at night have probably just sunk into the bins out of the pelagic waters as a result of their nocturnal sinking. Their presence on the substrates is "incidental" and in all probability the food they contain was ingested in the pelagic waters.

It is clear that pronounced differences exist in the proportions of adults with food by day and by night. Accordingly, it is of interest to examine the feeding intensity during the transition between day and night and night and day.

The proportion of calanoids with food in their guts during the dusk and dawn periods is shown in Table 19. At dawn, the percentage of adults containing food is considerably higher in the pelagic (i.e. net) samples than in samples collected off the substrates. At dusk this is also apparent if the net and substrate bin results are compared. Changes in the proportion of calanoids with food at dawn are given in Table 20, which shows a steady temporal decrease in the proportion of fed calanoids. The results suggest that feeding is chiefly carried out in pelagic waters and that as the calanoids reach the lake substrates, the intensity of feeding decreases. Dusk collections have shown a similar pattern, with a high proportion of pelagic calanoids containing food, whereas the benthic component is poorly fed.

From the data presented, it is apparent that pronounced diel differences occur in the feeding of P. hessei, and further, that these variations are intimately associated with the vertical distribution of the species. In the adult calanoids, which have been shown to reach and settle on the lake bed during daylight, feeding is seemingly terminated during their benthic phase. But at dusk, as they move into the overlying waters, the proportion of adults with food increases dramatically. At dawn, the process is reversed. In the pre-adult stages, however, which are (depending upon the stage) either entirely pelagic or less exclusively benthic during daylight, larger proportions contain food by day than in the adults.

Various lines of evidence have suggested that the food resources of Sibaya are not significantly different vertically. The enigma of the diel variation in feeding in P. hessei is in the fact that this variation occurs in the face of an apparently adequate food supply. Laboratory studies were initiated in an attempt to determine the reasons for the circadian feeding rhythm.

However, before the laboratory studies are described, the results of a series of radio-carbon feeding experiments carried out in situ are given.

2. Radio-carbon feeding studies

Radio-isotope tracer methods have been applied in an attempt to confirm the results based on presence or absence of food in the gut. Tracer studies were carried out as far as possible under field conditions, where natural conditions of illumination, temperature, food availability and zooplankton density would be experienced by the experimental animals.

Numerous workers have employed radio-isotope techniques to estimate filtration rates, assimilation rates, food species etc. in copepods and cladocera. (e.g. Sorokin 1968, Marshall and Orr 1955b 1956, Schindler, D.W. 1968, Schindler, J.E. 1971, McMahon and Rigler 1965, Richman 1966, Richman and Rogers 1969, Burns 1969b.) These studies have been carried out mostly under laboratory conditions. For the purposes of the present study, however, daytime in situ experiments were obviously required if the visual observations were to be confirmed or supplemented. Daytime feeding was studied in sealed substrate bins on the lake bed. Prior to starting the experiment, the bins were exposed overnight to collect tripton and calanoids. By doing this it was reasonable to expect that the food materials collected would be those naturally occurring in appropriate quantities, and that the calanoid densities would be comparable to those existing on the natural lake bed.

The procedures employed in assessing diel variation in feeding are described in detail in Appendix 7. In essence, calanoids were exposed to radio-carbon labelled pelagic waters at night in one series, which was performed under laboratory conditions. In a second, daytime series, the tripton and suspended material collected in a substrate bin was labelled, and calanoids were exposed to this labelled material in a substrate bin which was sealed and returned to the lake bed. Potential food sources were labelled in the dark

TABLE 21

Feeding intensity (expressed as dpm/animal) in *P. hessei* subjected to radiocarbon labelled flocculent detritus and *pelagial water*, in relation to time of day. Daytime feeding intensities were measured *in situ*. See text for further explanation.

Material labelled	Flocculent tripton	Flocculent tripton	Flocculent tripton	Pelagial water	Millipore filtered water
Time of day	Day	Day	Night	Night	Night
Exposed at	40 m	10 m	Lab	Lab	Lab
Amount of radioactivity in suspension (dpm/1)	89614	107586	186065	746868	0
Total radioactivity in suspension and solution (uCi/1)	0.040	0.048	0.084	20.723	16.697
	UPTAKE BY ADULT *P. HESSEI*				
dpm/sample	0	55	76	1117	244
No. of calanoids/sample	200	200	200	203	137
Gross uptake per animal (dpm)	0.00	0.275	0.380	5.502	1.781
Self-adsorption per calanoid (dpm)	-	-	-	1.781	1.781
Net uptake from suspended material (dpm/animal)	0.00	0.275	0.380	3.721	0.00
	UPTAKE BY MIXED *P. HESSEI* POPULATION				
Replicate (1)					
dpm/sample	877	1650	1400	2337	244*
No. of calanoids/sample	11466	7064	5161	381	137
Gross uptake per animal (dpm)	0.076	0.233	0.271	6.134	1.781
Replicate (2)					
dpm/sample	265	2085	-	1278	-
No. of calanoids/sample	3032	6242	-	187	-
Gross uptake per animal (dpm)	0.087	0.334	-	6.834	-
Gross mean uptake (dpm/animal)	0.081	0.283	0.271	6.484	1.781
Self absorption per calanoid (dpm)	-	-	-	1.781	1.781
Net mean uptake from suspended material (dpm/animal)	0.081	0.283	0.271	4.703	0.000

*Using self adsorption value of adult calanoids. Self adsorption value of younger stages highly suspect: see appendix 7.

using ^{14}C glucose and ^{14}C acetate.

Results

The results of these experiments are given in Table 21.

Self-adsorption of ^{14}C

The available data indicate that self-adsorption is proportional to the concentration of radio-activity to which the calanoids are exposed. Self-adsorption figures have been determined at 0.25, 6.7 and 16.7 μCi/l; uptakes equivalent to 0.9, 1.3 and 1.7 dpm per adult calanoid per hour were obtained at these respective concentrations.

For mixed copepodite stages, a single self-adsorption value of 11.9 dpm/animal was obtained in a solution containing 16.7 μCi/l. This value was so incongruously large as to be highly suspect and therefore the adult self-adsorption values have been used for all corrections.

Absorption of ^{14}C from ingested particulate material

Uptake of ^{14}C from the labelled flocculent tripton, both in the *in situ* exposures during daylight and in the laboratory system at night, is very low. Uptake figures of 0 - 0.38 dpm/animal were obtained for adult calanoids. Uptake values of 0.08 - 0.27 dpm/animal were obtained for mixed populations. Self-adsorption of ^{14}C in these exposures is theoretically zero, since no radio-activity was theoretically available in soluble form. The radio-activity added to the substrate bins reflects that bound up in the washed flocculent material. In practice, however, it is likely that some leaching of ^{14}C from the flocculent material occurred during the *in situ* exposure. At the level of radio-activity involved, even if the entire radio-active component had been in soluble form (i.e. 0.04 to 0.08 μCi/l) self-adsorption would have been very low. At most, self-adsorption could amount to the total uptake. For the purposes of Table 21 any self-adsorption from the flocculent tripton exposures has been ignored.

In marked contrast, ^{14}C uptake from labelled components of pelagial waters is pronounced. Adults exposed to labelled pelagial waters absorbed radio-carbon equivalent to 5.5 dpm/animal/hour, of which 1.8 dpm/animal/hour was attributable to self-adsorption. In a mixed population of P. hessei uptake amounted to 6.5 dpm/animal/hour. Using the adult self-adsorption value of 1.8 dpm/animal/hour, the uptake referrable to ingestion of labelled particulate material is 3.7 dpm/animal/hour in the adult calanoids and 4.7 dpm/animal/hour in the mixed calanoid population.

It was not possible to repeat the experiments to confirm the initial findings. However, the results indicate very clearly the greater uptake from the labelled pelagial components at night than from the labelled flocculent tripton by day or by night. As a result of the inadequate retrieval of ^{14}C from the flocculent tripton for assay purposes (see Appendix 7) and because of the suspect self-adsorption value, the results have to be treated with caution. Standing as they do, however, they confirm the more extensive visual observations of diel changes in numbers of animals containing food. Certainly, there is nothing in the results which contradicts the field results obtained by visual examination of the calanoids.

3. Laboratory Studies

The data collected under field conditions demonstrate unequivocally that a relationship exists between feeding and vertical distribution with a restriction of feeding to the pelagic waters in the case of the adult calanoids. Several lines of evidence suggested that the reduced feeding during daylight was not necessarily a reflection of food inavailability. Superficially, it was not possible to determine whether the feeding changes were associated with the migratory movements per se or with time of day per se.

Laboratory studies were therefore initiated in an attempt to establish the causal factors involved in the diel changes in feeding.

Two possibilities existed;

1. The feeding of adult calanoids was restricted to darkness by means of an endogenous feeding rhythm.
2. The feeding of the adult calanoids was inseparably associated with the locomotory activity involved in their nocturnal migrations.

Apart from visual observations under laboratory conditions of calanoids feeding while sedentary, the second possibility appeared more consistent with the observed results. The calanoid stages found in pelagial waters during daylight and which would therefore be maintaining station by locomotory activity, were those in which the diel variation in feeding was least pronounced. Further, the general association between locomotion and feeding in calanoids is widely accepted (reviewed by Jorgensen 1966). (This is not to state that filter feeding is automatic in a swimming animal, however.) The principal objection to this simple explanation lay in the visual observation of feeding in sedentary calanoids under laboratory conditions.

The idea of innate feeding rhythms in copepods has been raised (Wimpenny 1938, Gauld 1951) although its existence has been rejected in subsequent investigations (Gauld 1953, Richman and Rogers 1969). The issue is one of considerable application to McLaren's (1963) thesis and has been investigated in *P. hessei*. Changes in feeding upon interfacial sedimentary and/or pelagial food sources has been studied in relation to time of day.

(a) Feeding rhythmicity in substrate bins

Substrate bins exposed for several days on the lake bed at Station I were returned to the laboratory with their associated fauna and flora. One series was subjected to the natural light/dark regime

TABLE 22

Proportions and percentages of *P. hessei* containing food under laboratory conditions. The calanoids were kept in undisturbed substrate bins under two different light regimes.

	CONTINUOUS DARK		NORMAL LIGHT/DARK CYCLE	
	Day	Night	Day	Night
Adult ♂ ♂	$\frac{30}{53}$ 57%	$\frac{21}{50}$ 42%	$\frac{13}{121}$ 11%	$\frac{12}{17}$ 70%
Adult ♀ ♀	$\frac{38}{53}$ 70%	$\frac{9}{50}$ 18%	$\frac{18}{84}$ 21%	$\frac{47}{65}$ 72%
CI-CIII	$\frac{35}{44}$ 80%	$\frac{7}{10}$ 70%	$\frac{30}{100}$ 30%	$\frac{13}{16}$ 71%
CIV-CV	$\frac{84}{93}$ 90%	$\frac{62}{78}$ 80%	$\frac{35}{100}$ 35%	$\frac{53}{59}$ 90%
CI-CV	$\frac{119}{137}$ 87%	$\frac{69}{88}$ 78%	$\frac{65}{200}$ 33%	$\frac{66}{75}$ 88%
CI-CVI	$\frac{187}{243}$ 77%	$\frac{99}{188}$ 53%	$\frac{96}{405}$ 24%	$\frac{125}{157}$ 80%

and the other bins were kept under continuous darkness. The two series were subsampled at 1400hrs and 2200hrs over a period of two days. Subsampling involved siphoning off a portion of the bin contents through a plankton bucket and returning the filtered supernatant to the bins. The calanoids were preserved and examined.

The combined results of both days are shown in Table 22 for each experimental light regime. In the calanoids maintained under the natural light/dark cycle, there is a clear increase in the percentage of animals with food in the night-time collections, in all stages examined. In the case of the adult calanoids, the magnitude of this change is almost comparable with that observed under natural conditions. In the adults kept under continual darkness, the daytime values are larger than the night-time values, although the day and night values of the pre-adult stages are not conspicuously different. Comparison of the daytime values recorded under each experimental light regime demonstrates widely different results. If an endogenous feeding rhythm was a reality in the species, these differences would be unexpected.

(b) Feeding rhythmicity in pelagial waters

The feeding intensity of calanoids exposed to pelagic waters as a food source has been studied over 24 hours. Faecal pellet production was used as an index of feeding intensity.

P. hessei were collected from substrate bins and sorted according to age and sex. Batches of adult males, adult females and copepodite stages IV - V were placed into 40ml plastic tubes within a 50ml beaker containing crustacean free lake water. The solid base of the central plastic tube had been replaced with a mesh sufficiently coarse to allow faecal pellets to pass through it but fine enough to prevent loss of experimental animals. Two replicate series were prepared. One series was subjected to a natural day/night

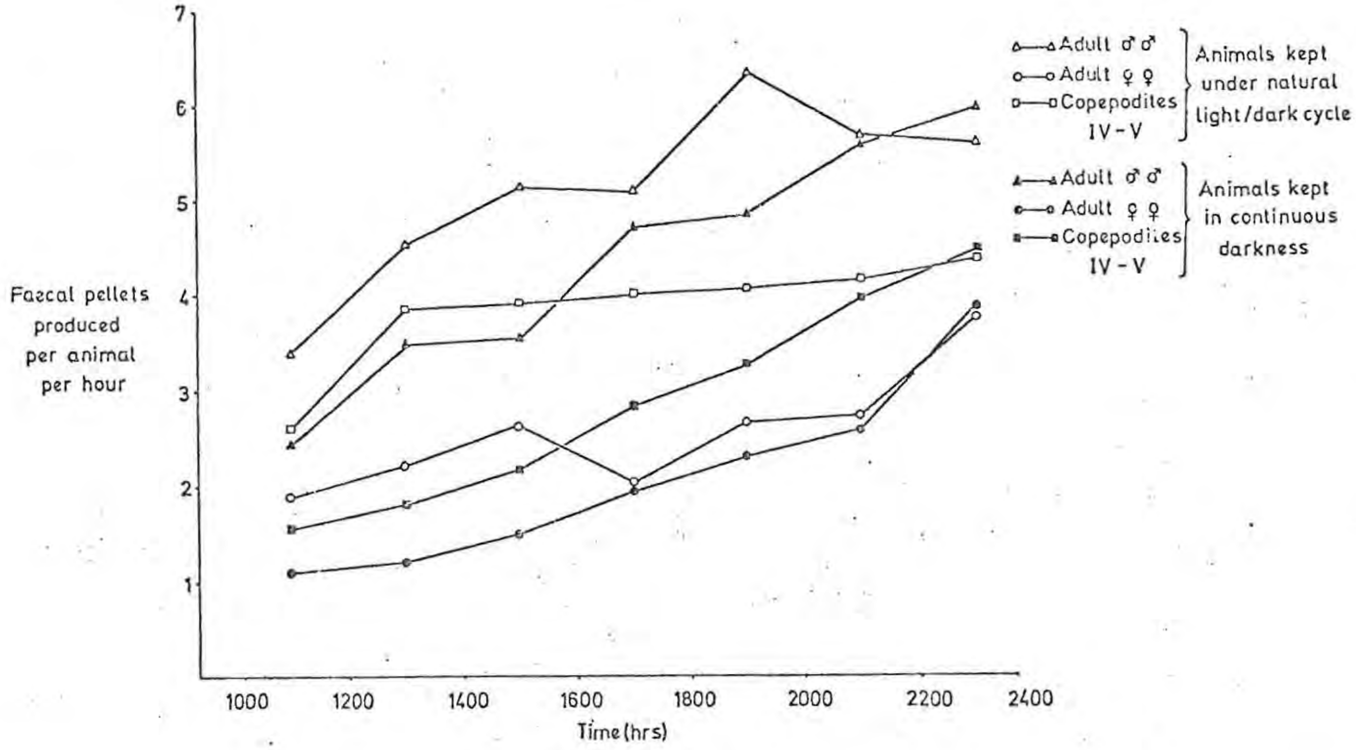


Fig. 44. P. hessei: Faecal pellet production of adult and late copepodite stages under laboratory conditions, between 1000hrs and 2400hrs. Open symbols - animals subjected to natural light/dark regime. Closed symbols - animals subjected to continuous darkness.

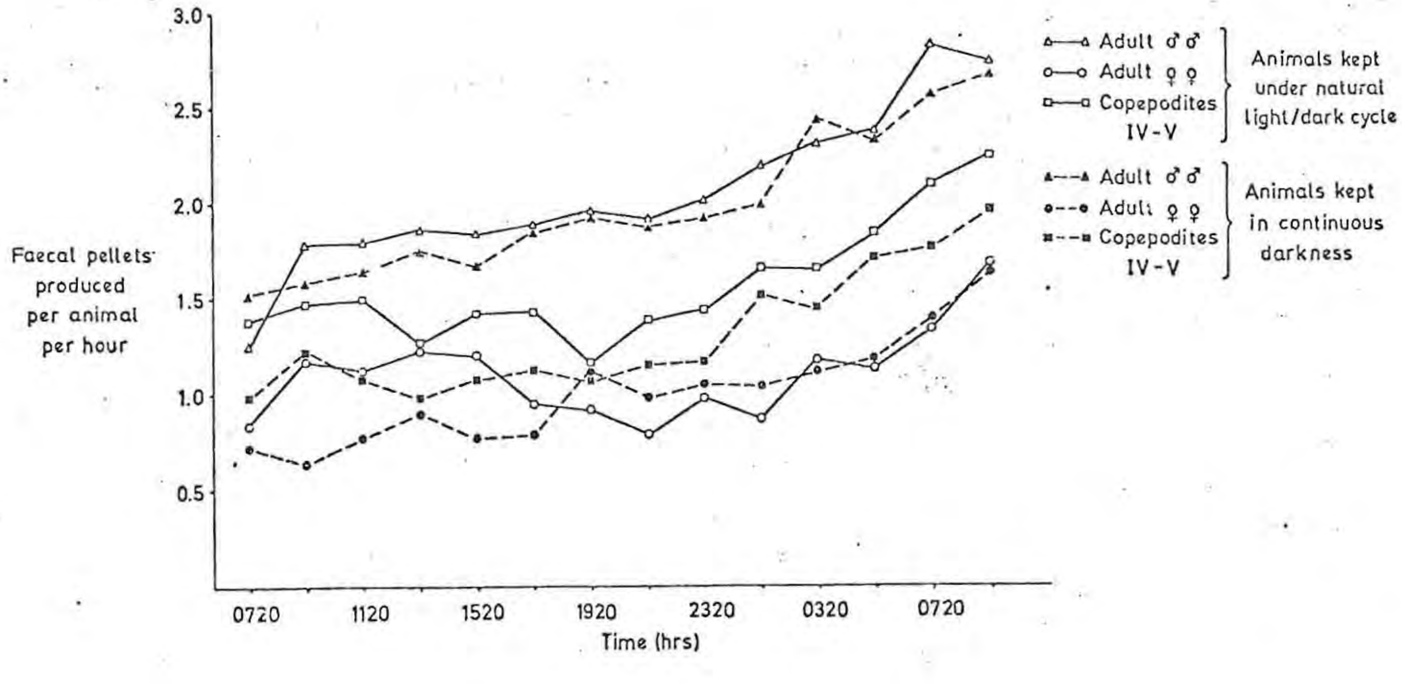


Fig. 45. P. hessei: Faecal pellet production of adult and late copepodite stages under laboratory conditions, through 24 hours. Open symbols - animals subjected to natural light/dark regime. Closed symbols - animals subjected to continuous darkness.

regime, with diffuse indoor daylight used as the daytime light source. The second series was kept under continuous darkness, interrupted briefly only when the faecal pellets were being collected or the water agitated to resuspend potential food particles.

At intervals of two hours, the central containers were briefly agitated within the beakers to dislodge all the material on the mesh into the beaker. The central tube was then transferred rapidly to fresh lake water in a second beaker. The brief aerial exposure of the calanoids resulted in no mortalities. Faecal pellets from each beaker were sedimented with Lugol's iodine in an inverted microscope counting cell and counted within 1 - 2 hours, to reduce the possibilities of pellet disintegration. Serious depletion of food within the small volume of water was avoided by the two-hourly replacement of lake water. Sedimentation of food particles was countered as far as possible by agitation of the central tube within the beaker at intervals of 30 - 45 minutes.

The variation in faecal pellet production is shown over 12 hours in Fig. 44 and over 24 hours in Fig. 45. In the first experiment 30 calanoids were used in each 40ml tube; in the second series 50 animals were used per tube. The figures show that faecal pellets were produced throughout the study period. Pellet production rate was not affected to any great extent by the experimental light conditions, although the number produced per calanoid was in most cases lower in animals kept in continuous darkness. Figs. 44 and 45 both show a general pattern of increasing pellet production during the course of the experiments. The significance of this is not known. There is evidence for several copepod species that feeding intensity is markedly affected by the volume of water available per animal (Marshall and Orr 1955b, Mullin 1963). Since the crowding effect in the present experiments was considerable, changes in feeding intensity over the experimental period might be artefactual.

Jointly, the laboratory studies demonstrate clearly that no intrinsic feeding rhythm exists. Feeding occurs irrespective of whether the calanoids are sedentary or planktonic. Both pelagic and benthic food sources are consumed by day or by night in conditions of darkness or in light. In short, the laboratory studies do not permit an immediate interpretation of the field results.

Discussion

The entire question of diel variation in feeding in the adult calanoids is most perplexing. It has been shown that feeding in adult *P. hessei* is related to their presence in pelagic waters and therefore to their migratory movements. The fact that they contain food at night and not by day is, in itself, probably incidental, but since their presence in the water column in synonomous with night, vigorous distinction between feeding "at night" and feeding "in the water column" has not always been made. To summarize, the laboratory and field results together provide the following facts.

1. The proportion of adult calanoids with food is considerably greater when the adults are pelagic by night than when they are benthic by day.
2. In the pre-adult stages, which show less strictly the division into benthic and pelagic "phases", the diel differences are not as pronounced.
3. The food sources available to the benthic calanoids are not ingested during daylight under natural conditions, but when calanoids are confined with this as the only food source they will ingest it after dusk in the natural environment. Under laboratory conditions they will ingest the same material more extensively when it is dark than when it is light.
4. Under conditions of diffuse indoor lighting or total darkness,

calanoids exposed to pelagic food sources will continue producing faecal pellets throughout twenty-four hours, irrespective of the light regime.

On the basis of these facts it is clear that the diel variation in feeding observed under natural conditions is neither the result of an intrinsic feeding rhythm nor does it arise as a result of the hypothetical inseparability of feeding and active locomotion. Sedentary animals produce faecal pellets throughout the day.

Notwithstanding the concentration of calanoids upon the lake bed during daylight, it is unlikely that serious depletion of food will occur within the narrow zone of water above the sediments. Large populations of calanoids restricted to substrate bins and therefore isolated from the continuous tripton fall-out in the lake show diel changes in feeding intensity. The same evidence suggests that hypothetical changes in food quality with depth are unlikely to be the cause of the diel feeding changes. Ryther (1954), McMahon and Rigler (1965), Mullin (1963) and Conover (1956, 1966b) have shown for various entomostracan groups that feeding ceases or its intensity is depressed when senescent cultures are used as food sources. McMahon and Rigler (1965) have suggested that food might be undesirable for four reasons.

(i) It may inhibit feeding.

(ii) It may be toxic.

(iii) It may be indigestible.

(iv) It may be deficient in some essential nutrient.

The food sources of deeper waters and in association with the lake sediments are consumed by the calanoids, optionally in the case of the earlier copepodite stages. In adults restricted to substrate bins, these sources are ingested. It appears, therefore, that possibilities (i) - (iii) above are not applicable. Calanoids kept in the laboratory for one month with interfacial sediments and overlying water provided as a food source, survived and produced eggs. After a month the experiments were discontinued. These observations exclude possibility (iv).

The only explanation which fits the field results is that feeding is associated with locomotory activity and is therefore restricted to the calanoids which are present in the water column. In the adults, therefore, feeding is restricted to the hours of darkness. In pre-adult copepodites which are not as exclusively associated with the lake sediments during daylight, a smaller or greater proportion of the animals captured will contain food. This explanation is also consistent with what is known of the daytime activity of the calanoids on the lake bed and the endogenous rhythmicity demonstrated in relation to their locomotory activity. Having reached this conclusion, one discrepancy remains to be resolved and this relates to the fact that sedentary calanoids will feed under laboratory conditions.

Two possibilities exist to explain the fact that calanoids on the lake bed do not ingest particulate material. Firstly, it is probable that extra-cellular products of metabolism are excreted by the tripton-bacteria-algae complex which forms the flocculent sedimentary layer on the lake bed. If various toxic or inhibitory products are excreted by day (i.e. during illumination, however dim) but not by night, then most of the observations can be reconciled, provided that a similar diel difference in excretory products is not evident in the pelagic micro-organisms.

The second possibility is that the adults do not feed during daylight under natural conditions because they are quiescent on the lake bed or may be infaunal. Grindley (1972) reports that P. hessei may dig itself into loose detritus when subjected to bright light.

Under natural conditions, Kos (1969) records various species of Calanus digging into marine ooze. Calanopia americana has also been recorded as digging itself into sedimentary material (Clarke 1934). Infaunal existence is, of course, extensively documented in cyclopoid and harpacticoid copepods. If P. hessei is, in fact, in interstices in the lake substrate, then clearly it would be unable to filter-feed. This is, to my mind, the more likely explanation of the absence of feeding in adult P. hessei during daylight. Unfortunately, unequivocal evidence for such behaviour has not been obtained, but circumstantial evidence supports this viewpoint. Core samples and substrate bin samples have been scrutinized for evidence of infaunal calanoids. Substrate bins, raised after an overnight exposure on the lake bed, initially appear to contain but a few calanoids, which are clearly visible "anchored" onto the vertical perspex walls (as shown in the frontispiece). However, if the bin is tapped sharply, large numbers of calanoids, previously not visible, appear from the substrate. Numerous bins have been examined for evidence of epibenthic calanoids, but since calanoids are difficult to see against the flocculent tripton, their apparent absence from the surface cannot be taken as direct evidence that they are in the substrate. If the calanoids are, in fact, in rather than upon the sedimentary layer, then clearly they are just below the surface as their mass appearance is not accompanied by large scale disturbance of the interfacial sediments.

If the calanoids are in the sediments under natural conditions, then it should be possible to induce similar behaviour under laboratory conditions. Numerous attempts to do this have failed. Neither calanoids subjected to bright sunlight out of doors nor calanoids kept under diffuse indoor lighting show any evidence of "burrowing". In aquaria in which a deep layer of flocculent sediment is provided, calanoids swim into the substrate, but their disappearance is momentary. I attribute the lack of success in invoking this behaviour to the unnatural illumination to which the calanoids were subjected in these experiments. In natural conditions, calanoids and other entomostraca are subjected to a very specific angular distribution of light under water and this provides an essential orientation beacon - the dorsal light contrast.

Accordingly, attempts were made to demonstrate the existence of burrowing under more natural light conditions by confining the calanoids to a substrate bin and exposing the bin on the lake bed. Unfortunately, only free-diving techniques could be used to examine the enclosed calanoids. This restricted the depth at which observations could be made to several metres only. The bins were accordingly exposed close to the shore and underwater observations only showed a marked concentration of calanoids on the vertical wall of the bin furthest from the shore (? littoral avoidance). It is conceivable that the sequence of events at dawn is necessary to invoke burrowing behaviour and that attempts to isolate this particular behavioural component are futile.

It is regrettable that this question could not be resolved satisfactorily. Self contained underwater breathing apparatus (SCUBA) methods are anticipated in the future. Notwithstanding the lack of direct evidence, I believe the "burrowing" hypothesis to be the most satisfactory explanation of the observed diel changes in feeding intensity in the adult calanoids. Alternatively, the lack of feeding may result from a daylight quiescence in natural populations sedentary on the lake bed. Either explanation is consistent with various other observations made.

The pronounced diel changes in feeding in the adult calanoids in the lake are of considerable significance in assessing the adaptiveness of the diel vertical migrations. The changes are of particular relevance to McLaren's (1963) hypothesis. In the adult calanoids, the restriction of feeding to the hours of darkness meets one of McLaren's requirements. However, although feeding is restricted to the hours of darkness, it may occur at any depth through the water column (Fig. 43). McLaren's hypothesis necessitates the restriction of feeding to the warmer (food-rich) surface waters. In Sibaya the surface waters are seldom distinctly warmer than the deeper waters and, likewise, the food potential of the waters is not markedly different vertically. Younger stages of P. hessei do not exhibit the distinct diel changes in feeding which are necessary in McLaren's model. On most counts, therefore, McLaren's model is not applicable to P. hessei in Sibaya.

The existence of vertical migrations by P. hessei in the face of very slight vertical changes in food availability are not easily accounted for as simple feeding migrations. In the adults feeding and migration are apparently related, yet if the migration was simply a feeding excursion, it seems unlikely that it need be so pronounced. An ascent of only several metres would bring them into waters which are, superficially, not markedly different in their food potential from the very surface waters. The migration would, therefore, appear to have some deeper significance.

DIEL PERIODICITY OF EGG HATCHING IN PSEUDODIAPTOMUS HESSEI AND THE DETERMINATION OF EGG DEVELOPMENT RATES

Introduction

It is obvious that any behaviour pattern or biological process showing a regular diel periodicity is of considerable interest when assessing the significance of diel vertical migration. Thus it was of great interest when a periodicity in egg-hatching was observed in P. hessei. The reality of this occurrence has been examined under laboratory conditions at both summer and winter temperatures and using female calanoids collected from the water column at night and from lake substrates by day.

To reduce repetition, the question of egg development rates is also examined in this section, although for the greater part, these data are used in the following section relating to the population dynamics of P. hessei.

Methods

Egg development rates were determined using the techniques used for rotifers (Edmondson 1960, 1965) and copepods (Burgis 1970). Ovigerous females of P. hessei were individually placed into 40ml plastic specimen tubes with about 35ml of lake water, previously filtered through #20 silk to exclude crustacean zooplankton. In the absence of thermostatically controlled water baths, temperature fluctuations were reduced as far as possible by storing the specimen tubes in a container of water provided with a max/min thermometer. Max/min. temperatures were recorded at each inspection, and from these a mean temperature has been computed. While this effected only a crude measure of temperature control, wide variations were reduced. Temperature remained for the most part ±2°C around the mean. The females were examined at varying intervals of time through

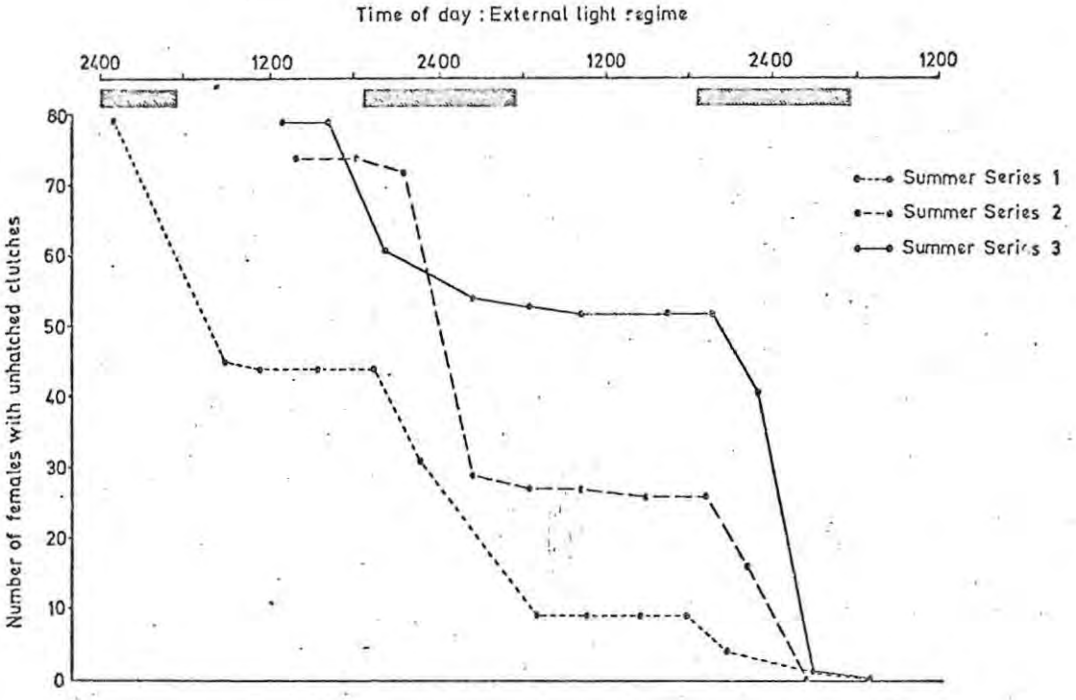


Fig. 46. Egg hatching of P hessei in relation to time of day during summer. Series 1 - females collected in vertical net hauls at 2300hrs, 21/1/73. Experiment started at 0100hrs, 22/1/73. Series 2 and 3 - females collected in substrate bins at 1200hrs and 1100hrs, 23/1/73 and 25/1/73 respectively and experiments started at 1400hrs and 1300hrs on 23/1/73 and 25/1/73. Mean incubation temperature 26.9°C. See text for further explanation.

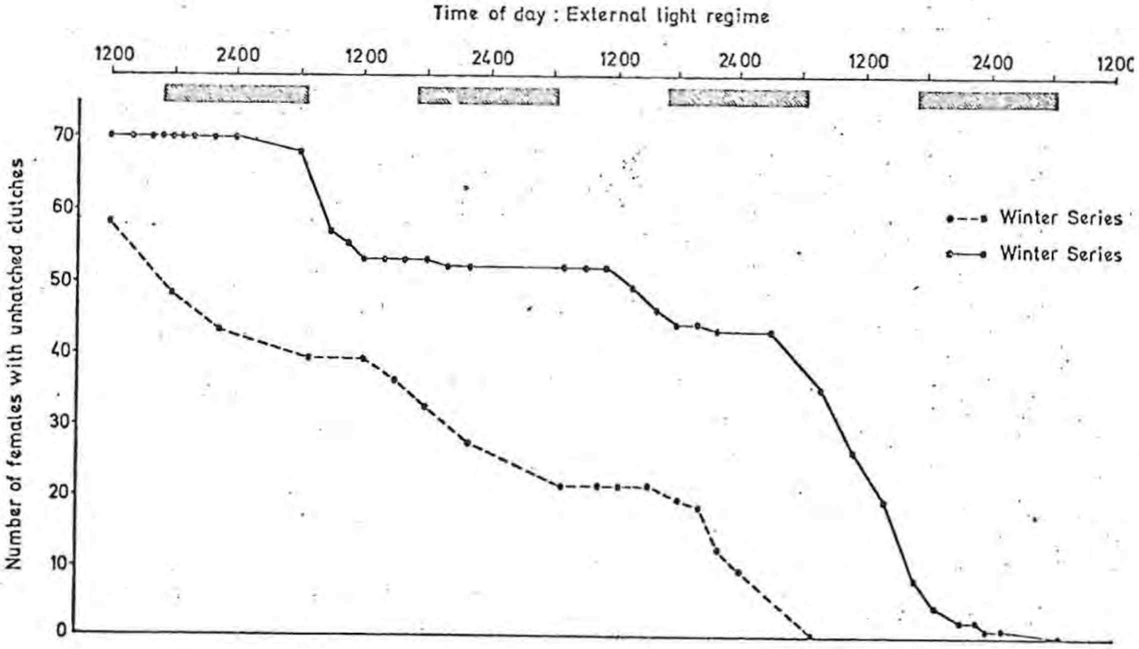


Fig. 47. Egg hatching of P. hessei in relation to time of day during winter. Series 1 - females collected in substrate bins at 1000hrs, 6/6/72 and experiment started at 1200hrs, 6/6/72. Series 2 - females collected in substrate bins at 1000hrs, 14/6/72 and experiment started at 1200hrs, 15/6/72. Mean incubation temperature 19.0°C.

the 24 hour cycle. At each examination it was noted whether the female was carrying her egg sac, whether the eggs had hatched into nauplii and whether a second clutch had been produced after the hatching of the first.[1] In P. hessei, nauplii apparently hatch while the egg sac is attached to the female and nauplii of each batch hatch synchronously. The eggs constituting any given clutch are laid within a reasonably short time.

Results and Discussion

The results relating the numbers of females carrying original clutches after the start of the experiment, to time of day, are given in Figs. 46 and 47, for summer and winter respectively.

In summer, the periodicity of hatching is striking (Fig. 46). Relatively few clutches hatched during daylight hours. Had it been practical to make observations at closer intervals, it is likely that the correlation between hatching and time of day would be even closer.

The first winter series (Fig. 47) showed maximum hatching during the hours of darkness (at least $\frac{44}{56}$ clutches hatched during darkness). In the second series, hatching was maximal during daylight hours ($\frac{50}{70}$ clutches hatched during daylight.) The discrepancy between these two winter series may be artefactual. In the second series the copepods were held in a substrate bin in the laboratory for 24 hours before the individual females were isolated. The mean development time of eggs in this series is considerably greater than in the first series, although mean temperature was only 0.4°C cooler.

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[1] The term "first" or "original" clutch is applied to the clutch carried by the female at isolation. "Second" clutches are those produced secondarily in the laboratory. Use of the word original does not necessarily carry the connotation of the first clutch ever produced by the female.

It is generally agreed that temperature plays the major role in affecting development rate of copepod and rotifer eggs. From the published data on the effect of temperature on copepod egg development, it is highly unlikely that a temperature decrease of 0.4°C would result in the observed increase in development time. On the basis of this reasoning it is possible to question the validity of the second winter series. However, irrespective of the timing of egg hatching in relation to time of day, a pronounced periodicity is unquestionably involved in all series. It is this periodicity and its usual occurrence at night (4 out of 5 series) which is of great interest.

Data have been presented which demonstrate the ascent of the calanoids at dusk to the upper waters of the lake. The majority of adult females move into and remain in the water column during the hours of darkness. Given this migration pattern and a nocturnal periodicity in egg hatching, the species is provided with a logical and adaptive mechanism for distributing their planktonic young.

It has been shown that the nauplii of P. hessei live closer to the surface than any successive stages. As a result of this vertical distribution, the nauplii are influenced by the surface or near-surface currents to a proportionately greater extent than any subsequent stages. Accordingly, the horizontal distribution of the species is likely to be brought about primarily by the naupliar stages. By virtue of their relatively small size, the surface area/volume ratio of the nauplii is better suited for the maintenance of a pelagic existence than that of subsequent stages. Clearly, once in the surface waters, the nauplii can be passively distributed far and wide. If horizontal transport of the nauplii is to be achieved, it is necessary for the nauplii to be deposited in the surface waters as their own locomotory ability is limited, particularly in the youngest stages. The hatching periodicity shown by P. hessei nauplii is ideally suited to ensure their occupancy of the surface waters. If they hatched continuously through 24 hours, those hatching by day would be unlikely to reach surface or near-surface waters of their own accord. This conclusion undoubtedly holds true for deep water environments although in shallow estuarine conditions the limited swimming ability of the nauplii might be adequate to enable them to reach the surface. It would be interesting to know whether this hatching periodicity occurs in marine pseudodiaptomids. It is in the oceanic environment that the aforementioned dispersal mechanism would be of greatest selective advantage and in which it most probably evolved. A priori, the selection pressures which might have selected for the development of this behaviour would not be expected in comparatively small and shallow freshwater lakes, and would be even less likely in very shallow estuaries.

The hatching periodicity and consequent "release" of nauplii in superficial waters might also be important in ensuring that these stages have ready access to food in those environments in which pronounced vertical changes in algal biomass occur. In Lake Sibaya, there are seldom pronounced quantitative vertical changes in food availability, but qualitative changes may be significant.

The determination of egg development rates in relation to temperature

Since egg production in relation to other population parameters can be used to obtain estimates of production (see Burgis (1971) and Edmondson and Winberg (1971), for practical examples), it is of great importance to be able to determine egg development rates at different temperatures. Egg development rates have been studied in rotifers (Edmondson 1960, 1965) and copepods (Burgis 1970) by assuming that mature females of a population are constantly laying eggs. If this assumption is met, then the clutches carried by a random selection of females will be at a variety of developmental stages and will therefore hatch continuously. Thus, if the number of females carrying unhatched clutches is plotted against time, a straight line should result, and, extrapolated to the time axis, gives a mean development time from laying to hatching.

In the case of P. hessei, the assumption relating to the continuous nature of egg laying cannot be met. If it is assumed that the development rate of eggs carried externally in an egg sac is purely temperature dependent (the evidence for the validity of this assumption being reasonable), then the periodicity in hatching must reflect a similar periodicity in egg laying. Indeed the extrusion of second clutches is almost entirely restricted to the hours of darkness (see below) and there is every reason to believe that first clutches are also layed at night.

It may be that, if examined critically, other species will also show a periodicity in egg laying. Burgis (1970) shows egg development as a function of temperature in her Fig. 1A (p. 743). If the data points of this figure are examined, some evidence of periodicity is evident. This is most noticeable in the data points of lower temperatures e.g. 15°C and 20°C. Development is too rapid in the higher temperatures for a clear diel pattern to emerge. Another factor which may mask hatching periodicity in Burgis' data is that the starting time of her experiments is unknown.

In the summer series 2 and 3 for P. hessei shown in Fig. it will be noticed that starting time is matched against time of day. The data are not plotted against time from the start of the experiment. Had they been plotted in this way, an erroneous idea of development rate would have been obtained (as illustrated by series 1 in the same figure). If Burgis' data could be related to time of day, a clearer periodicity might emerge. The present investigation

TABLE 23

Time of laying of second clutches in *P. hessei* and the percentage of females laying second clutches

	WINTER DATA				SUMMER DATA					Overall mean percentages
	Series 1	Series 2	Total	Mean Percentage	Series 1	Series 2	Series 3	Total	Mean Percentage	
No. of second clutches layed by DAY	5	17	22	40%	8	6	8	22	10%	16%
No. of second clutches layed at NIGHT	28	5	33	60%	63	68	65	196	90%	84%
Percentage of females laying second clutches	59%	86%		74%	90%	100%	92%	94%		87%

might serve to caution against indiscriminate application of this technique to determine egg development. Pilot surveys are obviously required to determine the validity of the assumptions upon which the method is based.

Production of second clutches in *P. hessei*.

Observations of individual females were continued after hatching of the original clutches. In the second winter series the animals were examined for nine days after the original clutches had hatched. The data on formation of second clutches are given in Table 23, in relation to time of day. A large percentage of females layed a second clutch of eggs under laboratory conditions (94% and 74% for summer and winter respectively)[1]. In the second winter series, where observations were continued long enough, the development time of ten of these second clutches could be determined directly to within several hours (directly in the sense that both time of egg laying and time of hatching were accurately known). For these ten clutches, a mean development time of 80.4 hours (range 74.5 - 84 hours) was obtained.

The estimation of egg development rates in *P. hessei*

It has been shown that conventional techniques are not suitable for the determination of egg development rates in *P. hessei* as in this species egg laying is not continuous (either within the individual or within the population). The extrusion of second clutches in *P. hessei*, and by implication first clutches as well, is almost entirely a nocturnal event (Table 23). It is reasonable to assume that egg laying is essentially random <u>during the night</u>, with different females laying their clutches at various times between nightfall and

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[1] As a matter of interest, 13% of the females in the second winter series produced third clutches.

daybreak. On the basis of this assumption, an estimate of egg-development rate can be made.

In summer series 1 (Fig. 46) a sample of calanoids was collected just before midnight and by 0100hrs a number of ovigerous females had been individually isolated. On the basis of the assumption that the clutches carried by these females had been extruded at random on the evening of collection or other evenings previously, it is apparent that this random selection of females (if the sample is sufficiently large), will contain some females whose clutches have just been extruded and others whose clutches are just ready to hatch. If these clutches are examined regularly until they have all hatched, then the time until hatching of the last clutch will provide an estimate of egg development time, albeit based on a very small proportion of the sample starting number. On the basis of the first summer series in which the collection was made at night, a development time of 54 hours is obtained.

However, in cases where females are isolated during daylight, there are neither females whose clutches have just been layed nor females whose clutches are just ready to hatch. All clutches are more intermediate in their development as the clutches involved are those which were extruded one or several nights previously. Therefore, to use these data to estimate egg development rate it is necessary to extrapolate back to the time at which eggs were layed. Since it has been assumed that clutch production occurs throughout the hours of darkness, midnight can be taken as the starting point as this reference point is likely to define some measure of central tendency about the nocturnal dispersion in egg-laying time. Using midnight as a reference point, the clutches which are least developed are assumed to have been laid at midnight prior to the daytime collection of the calanoids and the interval between this midnight and the time at which all clutches have hatched will give an estimate of egg development rate.

Using this extrapolation method, the second and third summer series give egg development times of 50½ and 55 hours and the first and second winter series give egg development times of 79½ and 102 hours. In the irregular second winter series, egg laying occurred mainly by day (Table 23) and therefore midday probably represents a better starting point than midnight. If this correction is made, an estimate of 90 hours is obtained. However, in view of the irregular periodicity evident in this second winter series, the extrapolation estimate has been ignored. The indirect estimate of egg development rate in the first winter series (79½ hours) is very close to the direct estimate of 80.4 hours determined in ten second clutches in which both egg laying time and egg hatching time were observed directly (see p. 210).

If the three indirect summer estimates are averaged, a mean development time of 2.2 days is obtained. Mean development time at winter temperatures is 3.3 days, based on the indirect estimate of the first series (79½ hours) and the direct estimate of the second (80.4 hours).

Egg development times in *P. hessei* in relation to naupliar distribution

At summer and winter temperatures (i.e. at average incubation temperatures of 27°C and 19°C) there is very clear evidence that egg hatching or "naupliar release" is almost entirely confined to the hours of darkness (apart from the suspect second winter series). If egg development is purely temperature dependent, eggs layed at temperatures between 20°C and 25°C (i.e. intermediate between summer and winter determined values) would be expected to show a development time somewhere intermediate between 2.2 days and 3.3 days. For arguments sake let us take as an example the situation where eggs are layed at midnight and take 2.5 days to hatch. Hatching will then occur at midday when the parent female is on the lake bed and the proposed selective advantage of hatching in the surface waters will not accrue. By the same reasoning, at winter temperatures when egg development takes 3.3 days, eggs layed at midnight will hatch after sunrise, when the females will again be on the lake bed. Yet the observations upon egg hatching at winter temperatures have shown that egg hatching is in fact almost entirely restricted to the hours of darkness. This leads me to the conclusion that more is involved than can be ascertained at present. The present estimates have been based upon the assumption that egg laying is continuous through the night. Use of this assumption was necessary to obtain an estimate of egg development rate. However, it may be that P. hessei shows peak laying over a shorter time interval[1] at night and slight seasonal shifts in the time of occurrence of this peak could result in maximal egg hatching during the night at all temperatures. Harding, Marshall and Orr (1951) and Marshall and Orr (1955a) have reported seasonal and regional changes in time of egg laying in Calanus, showing that a mechanism of ensuring that nauplii hatch predominantly at night is not impossible in P. hessei. A better understanding of the problem must await a seasonal investigation of this behaviour. However, I am of the opinion that the nocturnal egg-hatching periodicity observed is not an incidental or fortuitous result occuring only at these two temperatures.

The existence of a demonstrable egg-hatching and egg-laying periodicity clearly suggests that the selective advantages for these mechanisms are real and the natural outcome of this periodicity provides a logical distributive function. Whether egg-hatching periodicity will occur by day or by night at temperatures other than those at which the phenomenon has been studied remains to be seen.

[1] Mullin 1968

However, I believe that this periodicity will result in the release of at least part, if not all, of the naupliar stock during the hours of darkness, at other temperatures.

TABLE 24

P. hessei: Comparison of standing crop (nos. per m^3) of various age classes determined from samples taken at a single station (Station III) and mean values obtained from 25 stations sampled synoptically, for three sampling dates.

DATE	CATEGORY	LAKE MEAN n=25	STANDARD DEVIATION	STN. III n=1	RANGE OVER 25 STATIONS
Synoptic survey of 6/8/1971	Nauplii	391	262	713	96 - 1111
	CI-CIII	620	284	688	159 - 1242
	CIV-CV	125	56	105	25 - 239
	Adults	147	102	159	41 - 494
	Total	1283	570	1666	385 - 2624
28/1/1972	Nauplii	378	300	318	6 - 1102
	CI-CIII	429	316	911	54 - 1688
	CIV-CV	196	130	395	48 - 468
	Adults	173	110	194	19 - 424
	Total	1163	525	1815	153 - 2777
11/2/1972	Nauplii	542	197	685	207 - 1175
	CI-CIII	1064	1056	768	137 - 4529
	CIV-CV	245	234	80	57 - 1102
	Adults	183	102	159	41 - 436
	Total	2033	1411	1691	710 - 5870

THE SEASONAL CYCLE AND POPULATION DYNAMICS OF PSEUDODIAPTOMUS HESSEI IN LAKE SIBAYA

Introduction

The seasonal cycles of African lucustrine zooplankton have received very little attention. The study on Thermocyclops hyalinus in Lake George (Burgis 1971) represents the most thorough investigation reported to date. This work has subsequently been compared with a temperate study on Cyclops strenuus abyssorum (Burgis and Walker 1972). This comparison has illustrated the sustained high levels of production in the tropical lake compared to the seasonal nature of production in the temperate system.

While comparisons cannot readily be made with the work of Burgis and Walker (loc. cit.), the present study provides some preliminary information about the seasonal cycle in a lake system intermediate between those compared by Burgis and Walker, in respect of its annual thermal regime.

Representativeness of Station III

The longest observations on the seasonal cycle of P. hessei have been carried out at Station III. In view of the pronounced horizontal patchiness observed in the lake, it is necessary to examine the representativeness of these data. Between November, 1971 and June, 1972, routine collections were made at stations I - V. For this period, therefore, the Station III estimates can be compared with mean values for Stations I - V. Also, the Station III data can be compared with lake mean values obtained from 25 stations sampled during the three synoptic surveys.

(i) Station III compared with synoptic survey results

Table 24 compares the standing crop of various developmental stages of P. hessei at Station III, with lake mean standing crops.

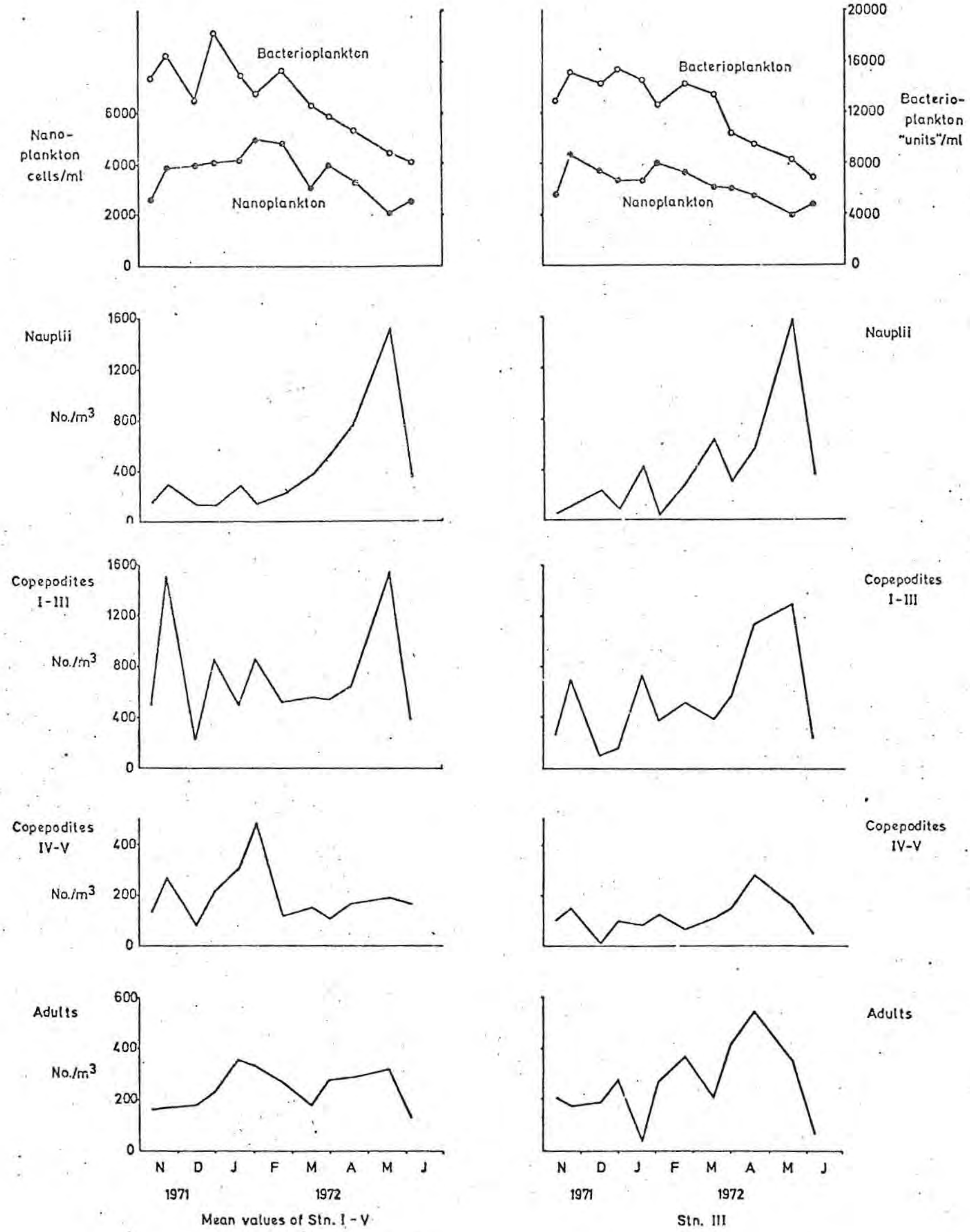

Fig. 48. Seasonal changes in total standing crop of P. *hessei* in relation to changes in nanoplankton and bacterioplankton standing crops in the surface waters. Mean data collected from Stations I - V are given in the left hand panel. The right hand panel shows the Station III data.

From this table it is clear that standing crop estimates based upon single station sampling may vary by a factor of three from the lake mean values. In the majority of cases, however, the Station III estimates are fairly close to the lake mean data, and are well within one standard deviation of the mean.

(ii) Station III compared with mean of Stations I - V

Twelve routine collections at Stations I - V have shown the extent to which erratic fluctuations in standing crop may occur independently at these five stations. The fluctuations are most pronounced at the two most offshore stations. If Station III results are compared with the lake mean determined from Stations I - V (Fig. 48), similar changes are clearly apparent in the naupliar and early copepodite standing crops. The resemblance in the late copepodite and adult standing crops is not so clear.

Thus, while not giving an absolutely reliable estimate of seasonal changes in standing crop, the data collected at Station III give a general idea of the seasonal changes in this species, certainly in respect of the nauplii and early copepodite stages. Since these younger stages will reflect fairly closely the breeding intensity, it is justified to report the seasonal changes observed at Station III.

Seasonal changes at Station III (Fig. 49)

The general pattern of change in standing crop in all four age categories is one of erratic fluctuations between consecutive sampling dates. For the most part, these fluctuations are of limited extent. Underlying these fluctuations is a pattern which essentially resembles the changes in lake temperature and changes in precipitation. (Surface temperature has been used as a simple index of lake temperature.)

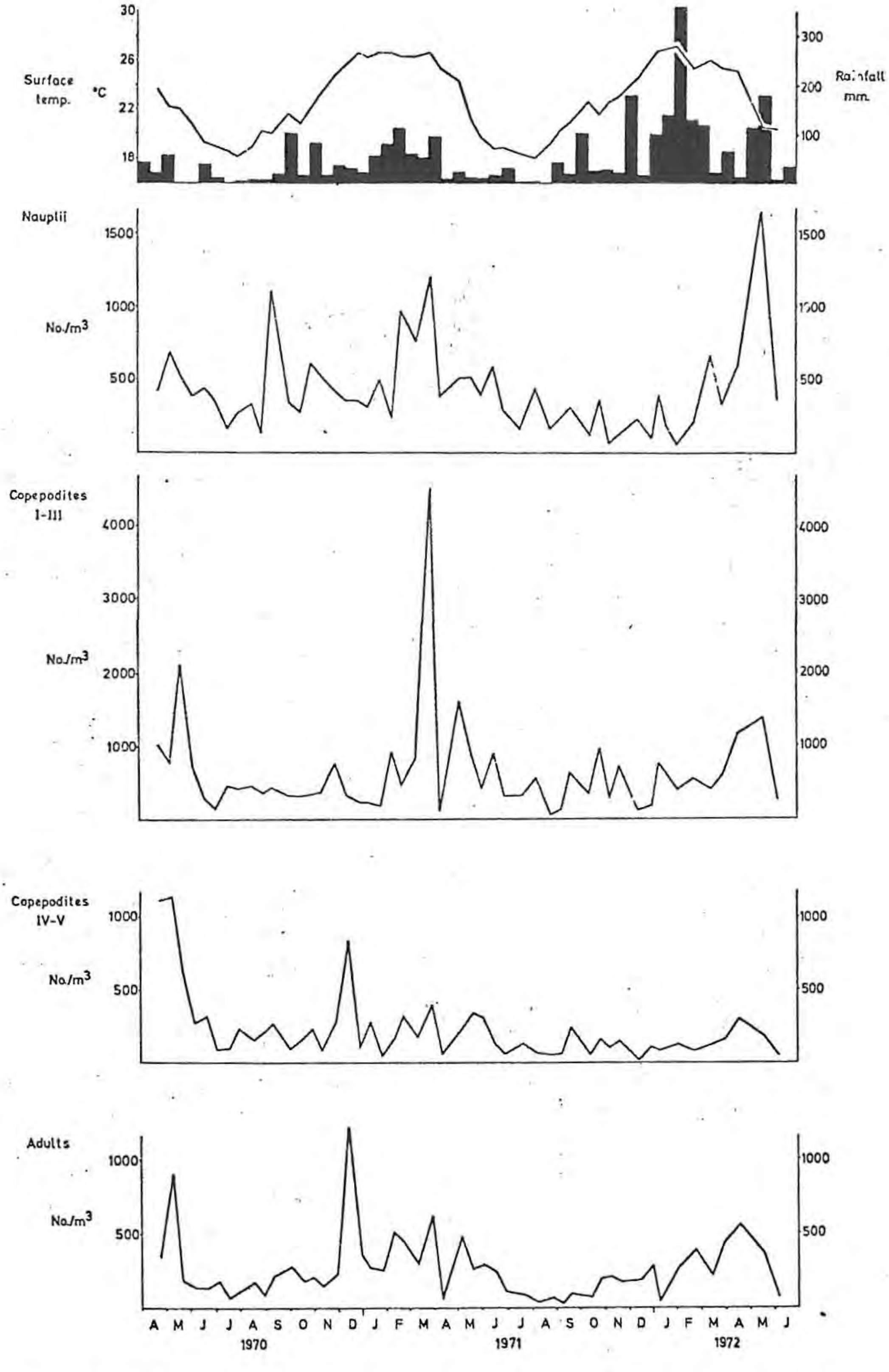

Fig. 49. P. hessei: Seasonal changes in standing crop of nauplii, copepodites I - III, copepodites IV - V and adults during 1970-1972, at Station III. Seasonal changes in surface temperature at this station, together with rainfall records collected at the Research Station, are shown in the top panel.

Routine determinations of algal standing crops (cell counts and chlorophyll a) were made on samples collected generally on the morning preceding the zooplankton hauls. Chlorophyll a is very low (annual mean in the surface waters is less that 2µg/l) and fluctuates erratically. No intelligible seasonal change occurs. No clear correlation exists between chlorophyll a content and calanoid standing crop at Station III during the study period. Seasonal changes in calanoid abundance occur despite the absence of concomitant changes in chlorophyll content.

Changes in nanoplankton and bacterioplankton numbers were determined between July, 1971 and June 1972. The changes in standing crop in surface waters are shown in Figs. 48 and 50. These changes can be related to changes in lake temperature. However, the steady decline in nanoplankton and bacterioplankton standing crop from mid-February, 1972 occurs at a time when the naupliar and early copepodite standing crops are increasing steadily (Fig. 48). Therefore, the decreasing standing crop of nano- and bacterioplankton may reflect not only the decreasing lake temperatures, but also grazing by the calanoid.

Overall changes in calanoid standing crop are small compared with those reported in temperate lakes, but larger than the lake mean range reported by Burgis (1971) for a tropical lake. During the 27 months of observation, total P. hessei standing crop (as numbers per m^2) varied by a factor of 22 from the lowest to the highest.

Breeding is continuous throughout the year. As a result, cohort structure is not readily followed. The calanoids develop rapidly at the temperatures involved and fortnightly samples do not demonstrate cohort succession. Indeed, a series of collections made at Station III on alternate days over a period of 31 days (May-June, 1971) did not enable the cohort structure to be followed. A

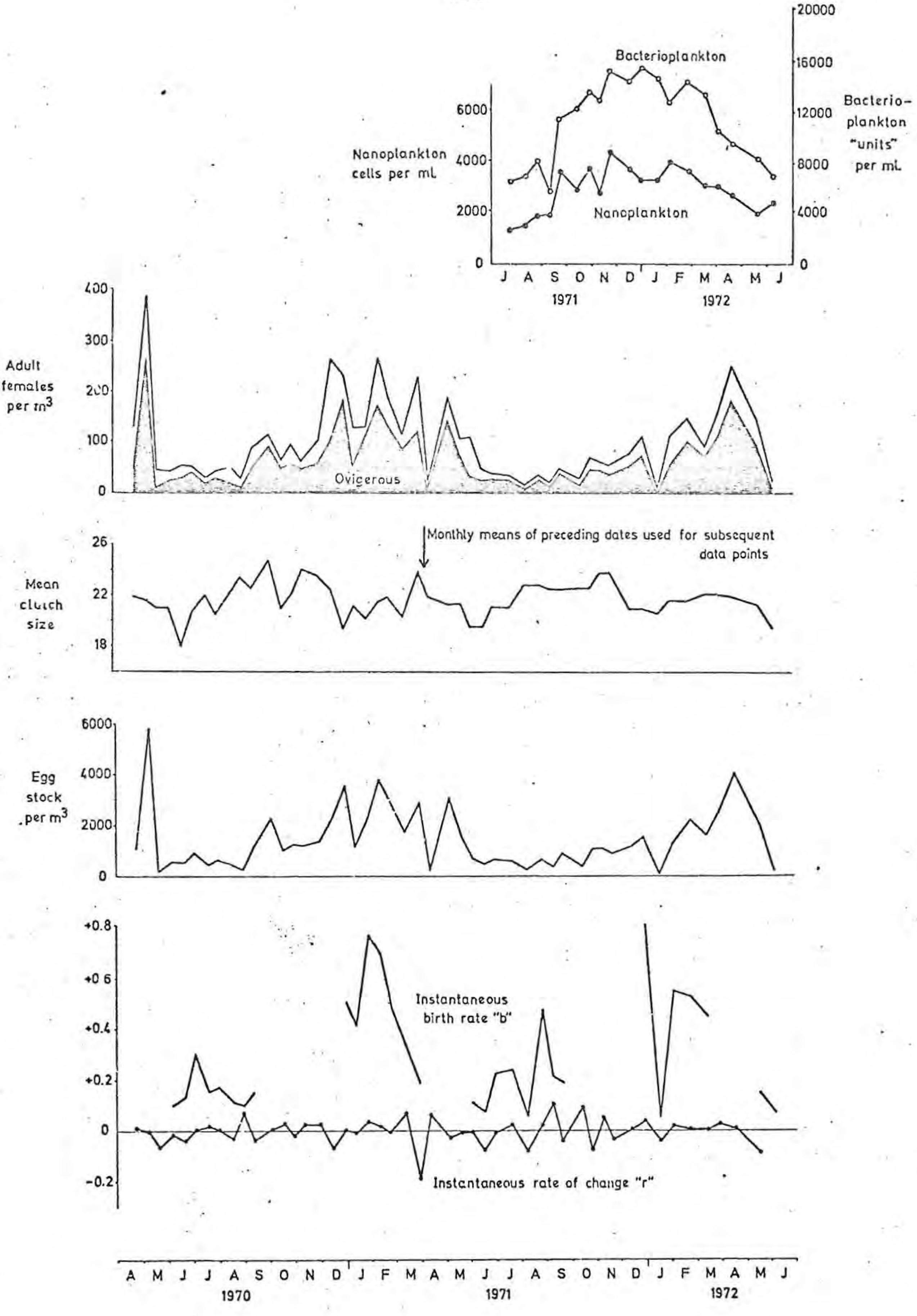

Fig. 50. Seasonal changes in adult female standing crop, mean clutch size, egg stock, instantaneous birth rate and instantaneous rate of change of P. hessei at Station III during 1970-1972. Changes in surface water standing crops of nanoplankton and bacterioplankton at Station III during 1971-1972 are given in the uppermost panel.

series of laboratory experiments has shown that development rate from egg laying to adult is 23 days at circa 23°C.

Population dynamics of *P. hessei*

From a knowledge of egg stock, egg development rates and standing crop numbers, several population parameters can be derived. The relationships used in determining these parameters are given below (after Cummins *et al.* 1969).

The finite birth rate, B. $\frac{\text{Eggs/m}^3\text{/day}}{\text{Popln. nos/m}^3}$ = Eggs/individual/day

The instantaneous birth rate, $b = \log e\ (1 + B)$

The instantaneous rate of change, $r = \frac{\log e\ N_t - \log e\ N_o}{t}$, where

N_o is the initial standing crop number, N_t is the standing crop number after time t in days.

The instantaneous death rate, $d = b - r$.

Adult female populations

Fig. 50 shows the standing crop of ovigerous and non-ovigerous females during 1970 - 1972. Egg bearing females were present throughout the year and an average of 63.4% of all females were ovigerous. The adult female population showed an extended summer peak in standing crop in 1970/1971, but this peak was delayed in the 1971/1972 summer. These peaks lasted well into the cool season. The changes in adult female standing crop show a resemblance to changes in lake temperature although as would be expected there is a lag period.

Clutch size and egg stock

Mean clutch sizes (Fig. 50) were determined from 20 females per sample on all samples taken until March 1971. After this date, the monthly means of the preceding year were used. Seasonal changes in egg stock (Fig. 50) have been computed from the standing crop of ovigerous females and mean clutch size.

Egg development rates

Egg development rates have been determined at summer and winter temperatures. These determinations have been described in the preceding section (pp 203 - 214). The following egg development rates have been applied in estimating the finite birth rate.

Lake Temp.(^{o}C)	Development (days)	
26, 27, 28	2.2	Based on summer determination at 27°C.
18, 19, 20	3.3	Based on winter determination at 19°C.

No attempt has been made to calculate egg development rates at intermediate temperatures (e.g. McLaren 1966).

Instantaneous birth rate (b) and instantaneous rate of population change (r)

These two population parameters are illustrated in Fig 50. The instantaneous birth rate (b) is shown only during the mid-summer and mid-winter periods, where data on egg development rates are available. The instantaneous birth rate is considerably higher in summer than in winter, as would be expected on the basis of the adult female population. The instantaneous rate of population change fluctuates minimally about the horizontal axis ($r = 0$), with no pronounced or extensive seasonal changes. This suggests the existence of a relatively stable population, with recruitment being balanced for the most part by mortality of one sort or another. Calculations of mortality (d) from the relationship $d = b - r$ result in values of d very close to those of b as a result of the very low values of r. For Station III, mean b in 1970 - 1972 was 0.1707 ± 0.0997 (S.D.) and 0.4791 ± 0.2236 (S.D.) at winter and summer temperatures respectively. Corresponding mean values of d were 0.1843 ± 0.0939 (S.D.) and 0.4850 ± 0.1950 (S.D.). It is apparent that, notwithstanding the considerably higher values of b during summer than during the cool season, the increased production is defrayed by a corresponding increase in mortality. Thus, large standing stocks of P. hessei are not built up with a resulting "pooling" effect of energy and nutrients. Instead, there is a constant re-cycling of the available nutrients allowing for sustained production, albeit at low levels.

In relation to the population parameters discussed above, three potential sources of error must be mentioned. Firstly, these parameters depend upon strictly qualitative collections and net hauls are unlikely to provide this rigour. Secondly, the size of the total population is underestimated by the loss in catch of the first naupliar instar. Since the proportion of this stage in the water column must vary with time, no standard correction factor can be applied to make amends for this loss in catch. Lastly, there is evidence that net collections may be undersampling the adult females. In a total of 126 net hauls between January and June 1972, the mean adult sex ratio of males to females was 1.616. For 50 substrate bin collections made during the same period, this ratio was only 0.235. In 16 horizontal bottom sampler samples in May/June 1972, the ratio was 1.184. The widely different ratios might be taken to indicate either an undersampling of females in net hauls or an oversampling of females in the substrate bins. In view of the continued recruitment of adult females into substrate bins during daylight (pp 94 - 98) oversampling of females in substrate bins may be involved to a greater extent than undersampling in net hauls. However, until this discrepancy can be resolved, the possibility remains that net hauls give an underestimate of the female population, thereby affecting the reliability of the calculations.

Since there are potential sources of error associated with the determination of these population parameters, the values obtained from Station III collections must be treated as preliminary. Notwithstanding the limitations involved, it may be said with some degree of certainty that the P. hessei population in Lake Sibaya is reasonably stable. In comparison with the work reported from temperate lakes, this is an important feature.

The dominant species of net phytoplankton in Sibaya show a clear and fairly regular seasonal succession (Hart, unpublished data). The constancy of chlorophyll a through the year probably reflects the fact that one algal species follows another without any marked change in total chlorophyll. However, the senescence of one species followed by the increase in another undoubtedly provides the substrate for an important bacterial based detritus (tripton) chain. Because this chain is always being stimulated (or nearly so) by the products of algal succession, food resources for a filter feeder never seriously decline to bring about numerical control. In a species such as P. hessei which feeds upon both primary producers and primary consumers simultaneously, food will be available in reasonable amounts throughout the year.

This is in contrast to the marked seasonal changes in food availability which affect temperate zooplankton populations. The limited seasonal changes in standing crop of P. hessei can be logically accounted for on the basis of food availability, reflecting the thermal and illumination regimes, of this lake. The present observations are in many respects intermediate between those recorded in tropical and temperate lakes in general.

FINAL DISCUSSION

Vertical migration has been the subject of considerable interest for many years. Much of this interest has stemmed from speculations regarding the energetic cost of the migratory movements (e.g. Worthington 1931, Bainbridge 1961). Notwithstanding the more recent realization that the energetic cost of these movements is relatively insignificant (Hutchinson 1967, Vlymen 1970), the migratory behaviour of zooplankton retains its fascination, and an examination of its functional significance is clearly warranted.

Earlier workers, for the most part, interpreted the migratory movements in relation to tangible selective pressures, such as feeding and predator avoidance. More recently, attempts to determine the significance of migratory movements have resulted in the consideration of more subtle and cryptic advantages. Thus, McLaren (1963) has postulated that an "energy bonus" would accrue to a species migrating in thermally stratified waters, provided that feeding was restricted to the warmer waters. David (1961) has suggested that migratory movements, by ensuring mixing of populations, may serve to inhibit "the formation of too many species with too little capacity to survive changes in the environment."

Attempts to determine a universal significance of vertical migration have met with varying degrees of success, but for the most part, irregularities or variations in migratory behaviour shown not only between systematic groups but also within them, have prevented the establishment of a universal definition of significance. Similarly, the lack of fundamental evidence has severely hampered solution of the problem. Indeed, in view of the widely different selective pressures on marine, estuarine and fresh-water zooplankton, it might be expected that no universal interpretation need be demonstrable.

For these reasons, I believe that an understanding of the ecological significance of vertical migration will depend upon intensive studies of a single species or group of related species in relation to their particular environments. The observed advantages of migration to this species or group of species need not necessarily apply to others. Nevertheless, the widespread occurrence of this behaviour is difficult to reconcile with any ideas of a species-specific or group-specific advantage, though the primary evolution of this behaviour pattern may have been of more widespread advantage. However, the paucity of fossil records (Waterman and Chace 1960) prevents an adequate assessment of Crustacean evolution and thereby precludes further examination of such questions.

The present study provides some basic groundwork from which to examine the ecological significance of migration. Clearly, much more data are required before the question can be resolved entirely satisfactorily. In particular, an examination of the importance of predation on this species (as on zooplankton in general) is urgently required. Nevertheless, it seems appropriate at this stage to consider the ecological significance of the vertical migratory behaviour of P. hessei

In so doing, it is necessary to bear in mind that the present study has been made in a somewhat atypical environment, and, further, that the temporal isolation of P. hessei in Lake Sibaya is geologically insignificant. Thus, some of the aspects of its vertical distribution are more readily intelligible in relation to its ecology in estuaries than in the truly lacustrine environment.[1] Where this is seemingly

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[1] It is generally accepted that the Temoroidea, to which the Pseudodiaptomidae belong, is primarily a marine group, in which the invasion of brackisk and fresh waters is a secondary phenomenon (Hutchinson 1967). There is every reason to believe that the present lucustrine populations of P. hessei in Sibaya were derived from the estuarine populations of this species, as the present lake almost certainly represents a drowned estuary cut off from the sea. Thus, there is no reason to suggest that estuarine P. hessei were derived from an ancestral fresh-water stock.

the case, I have discussed the feature in relation to its significance in estuaries, drawing largely upon Grindley's studies.

It is probable that the migratory movements themselves, however spectacular or otherwise they may be, are not directly significant. Rather, it is the cyclic alternation of depth which they provide which is of ecological value to the migrating organisms. If considered in this manner, the basic issue concerns the functional significance of the day-time and night-time distributions. This may not be a complete explanation, but it does provide us with a directive in examining the ecological value of the migrations.

The movement into deeper waters by day in all stages of P. hessei serves several potential functions. It reduces the visibility of the species to predators relying on visual discrimination of their prey. The potentially deleterious effects of ultra-violet radiations are avoided or reduced, and the external metabolites of photosynthesizing phytoplankton are avoided to some extent. Physical damage caused by excessive turbulence is prevented at least during daylight (and in other species depressed distributions have been recorded at night under stormy conditions (Cushing 1951).) The sedentary existence of adult calanoids at all depths in Sibaya is likely to affect their energy budget favourably. This may be more important in fresh water with its reduced density. Also, it may be more important in tropical/subtropical areas where metabolism is likely higher as a result of the higher temperatures, although the metabolic physiology of tropical/subtropical copepods is largely unknown. The benthic existence of adult P. hessei results in their existence in an almost entirely two-dimensional environment during daylight. The importance of this in allowing for intraspecific contact and increased chances of mating is difficult to assess. In turbid waters this may be of considerable potential value, although other lines of evidence suggest that the calanoids are quiescent or possibly infaunal during daylight. Records of pairs in copula (in preserved samples) collected during the present study show that mating occurs both on the lake bed by day and in the water column by night, but the low number of observations precludes further analysis.

It has been shown that in the shallow waters of Sibaya, all stages of P. hessei are sedentary or else in very close association with the lake bed. Under estuarine conditions, this vertical distribution is likely to be of considerable importance in reducing the possibility of their being washed out to sea. If the calanoids are in fact in, rather than merely on, the sediments, this would enhance even further, the maintainance of the populations in a tidal estuary. It is interesting to note that P. coronatus (an American species) is able to attach to various substrates and can withstand considerable current action without being dislodged (Jacobs 1961). In Sibaya, tidal influences are absent, but it has been suggested above that the daytime benthic existence of the adults may offer other advantages.

The vertical distribution of P. hessei in Lake Sibaya is such that the youngest stages will be influenced by wind induced currents for a proportionately greater period than the older stages, and thus play the major role in the horizontal distribution of the species. This was clearly evident from the synoptic survey findings reported earlier in this work. That the younger stages provide the distributive phase is logical in relation to the smaller energetic cost of maintaining a pelagic existence in the smaller stages and also in relation to their numerical abundance. The vertical distribution of the younger stages is also such that these immature, growing stages are able to feed continuously. Certainly, there is evidence that the early copepodite stages feed throughout the day and night to a greater or lesser extent, whereas in the adult calanoids, feeding is almost entirely restricted to the hours of darkness. That adult females are able to satisfy their own nutritional requirements and also produce eggs from a temporally restricted feeding period suggests that their filtration and assimilation efficiency is comparatively high.

The ascent of P. hessei into surface waters at night is commensurate with a striking initiation of feeding in the adult animals. In this respect, therefore, the migration of the adults may take the connotation of a simple feeding excursion. However, it is questionable why the adults need perform such extensive migrations in Sibaya for the sole purpose of feeding, since it has been shown that food is present throughout the water column with no marked vertical differences in quantity. That the adults feed in the near-bottom pelagic waters at the outset of their dusk ascent suggests that neither do qualitative differences in food resources dictate their dependence upon the very surface or near-surface food organisms.

Observations have been presented which show that naupliar hatching from the parental egg-sac is restricted to the hours of darkness, almost entirely during summer and at least in some cases during winter. (If the one set of winter observations is artefactual as has been suggested earlier, then the great majority of clutches hatch at night during winter also.) These observations suggest very strongly that the nocturnal ascent serves a distributive function and implies a direct ecological significance involved in the migrations of the adult females. The release of nauplii in the upper waters may also be related to their feeding requirements.

A priori, the significance of naupliar release in upper waters under estuarine conditions (if indeed estuarine populations of P. hessei show this behaviour) is questionable, as it would result in the loss of a significant proportion of nauplii to sea under certain tidal conditions. Indeed, Grindley (1972) has suggested that in Richards Bay, only in the reaches furthest from the sea, is a significant proportion of the P. hessei population able to reach maturity.

If this interpretation is correct, it would appear that the dominance of P. hessei in South African estuaries (Grindley 1963) is likely to be a reality only in those estuaries with small tidal replacement volumes. This suggests that the species is better adapted to blind estuaries or the quiet reaches of tidal estuaries, although mechanisms are apparently involved in reducing the losses of the species under conditions of river flooding. Thus, Grindley (1964) reports that P. hessei does not migrate through strong salinity discontinuities.

The apparent inability of a euryhaline species such as P. hessei (which occurs in essentially fresh water in Sibaya and hypersaline lagoons) to survive in the sea is somewhat incongruous. A similar case is reported in P. (Pseudodiaptallcus) euryhalinus which breeds in waters of salinity ranging from 1.8°/oo to 68.4°/oo, but is seemingly restricted to coastal lagoons and estuaries (Johnson 1939). The restriction of these species from the sea is presumably brought about by factors other than water chemistry. It would be interesting to know whether P. euryhalinus is also sedentary during daylight. If so, the daytime benthic association may be obligatory in these species and thereby restrict them to waters of limited depth. In this respect, it is interesting that several marine species are encountered chiefly in shallow neritic waters (Grindley 1963, 1969). It would be useful to know their vertical distribution.

Clearly, the pseudodiaptomids provide an ideal group for comparative studies of vertical migratory behaviour and indeed for comparative studies of their overall biology. Several species which have been studied are very hardy (Jacobs 1961, Grindley and Grice 1969, present study) and ideally suited to laboratory experiments.

There is one further aspect of vertical migration which may be of wider significance to vertical migrants in general and which seemingly applies to P. hessei in Lake Sibaya. Available evidence suggests that sensible photosynthesis is restricted to the upper 15 metres or so in Lake Sibaya. In areas of the lake shallower than this, the great majority of all stages of P. hessei are benthic during daylight. In deeper waters, where the younger stages show a truly pelagic distribution, most of the calanoids are encountered below 15 metres. Thus, notwithstanding the fact that the pre-adult stages feed to a greater or lesser extent during daylight, the grazing pressure on algae in the photosynthetic zone is cyclically reduced as as result of the diel migrations. This may be important in providing the phytoplankton populations with a "recovery" period. Thus, the diel migration may provide a subtle mechanism reducing over-exploitation of food resources. Saunders was clearly thinking along similar lines when he said (1971, p. 31) "Another control system that exists is that of light-forced photosynthesis and the light cued zooplankton migration which results in a coupled producer-grazer control system.

The present study has raised several interesting possibilities in relation to the control and selective advantage of vertical migration in P. hessei. The problems of day depth, dusk and dawn movements, night-time distribution etc. have been discussed in context. However there is one further point which needs to be raised, and this concerns the use of laboratory studies.

Although this is primarily a field study, several attempts have been made to induce the vertical migratory movements under laboratory conditions. These are briefly outlined in Appendix 8.

These attempts have been almost entirely unsatisfactory, for reasons outlined in the appendix. Similarly, an examination of feeding behaviour under laboratory conditions has given results which are incomparable in many respects with those obtained in the field; the discrepancies are attributed to the unnatural lighting conditions employed. These laboratory studies on feeding tend to overestimate significantly the daily filtration rate, and any studies on the energy transformation of this species will have to take such factors into consideration. The importance of the light quality, quantity and direction to this species is apparent.

These observations suggest that laboratory studies of feeding behaviour may, alone, be inadequate in other species and stress the importance of concurrent field investigations. This has been recognized by previous authors and significant attempts have been made to overcome the practical difficulties associated with field investigations (e.g. Gliwicz 1968). Nevertheless, it is equally clear that some features of behaviour can only be studied under laboratory conditions. In such cases, it may well prove worthwhile to simulate naturally occurring underwater light conditions where there is any likelihood that the behaviour under consideration may be influenced by light.

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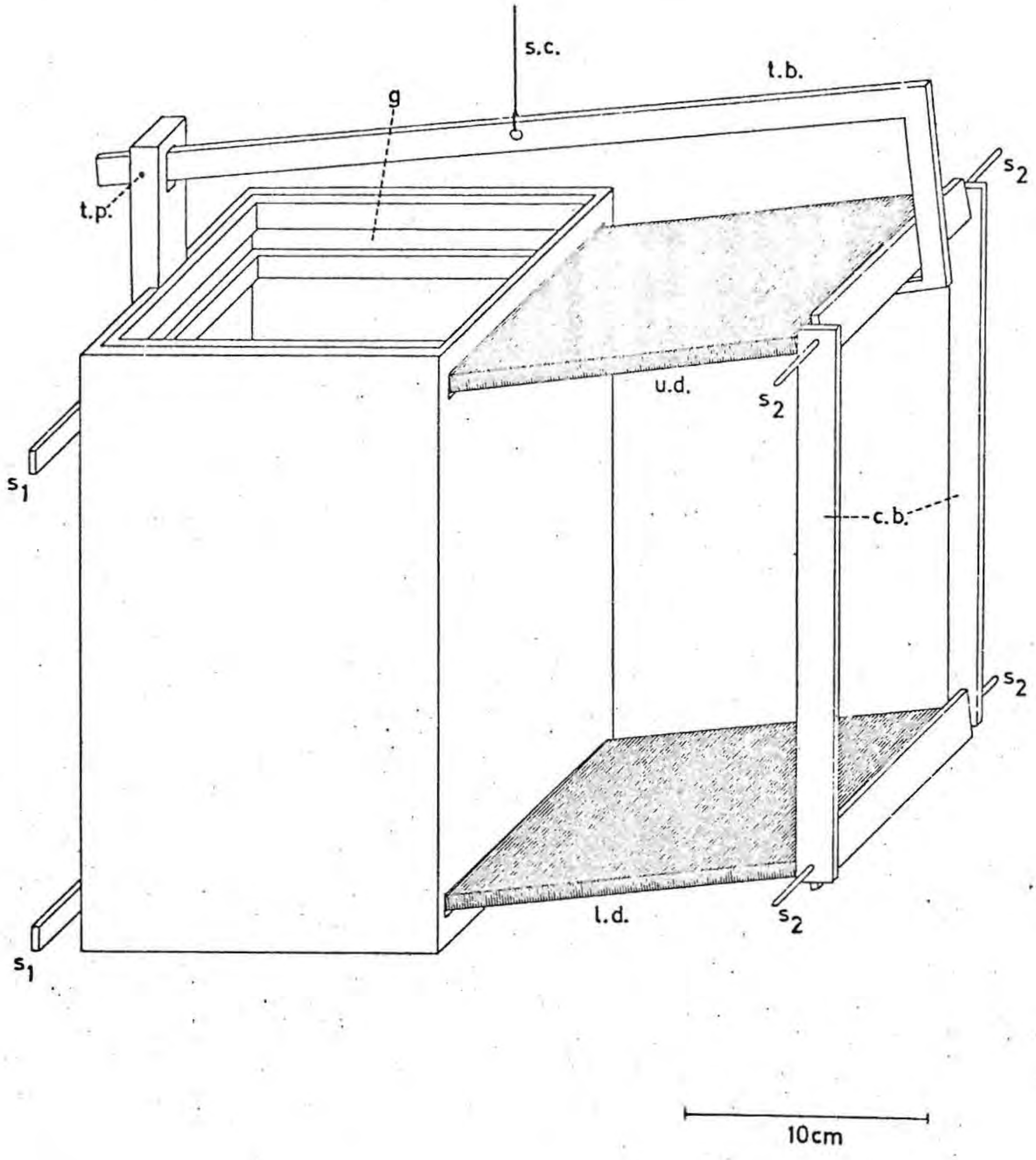
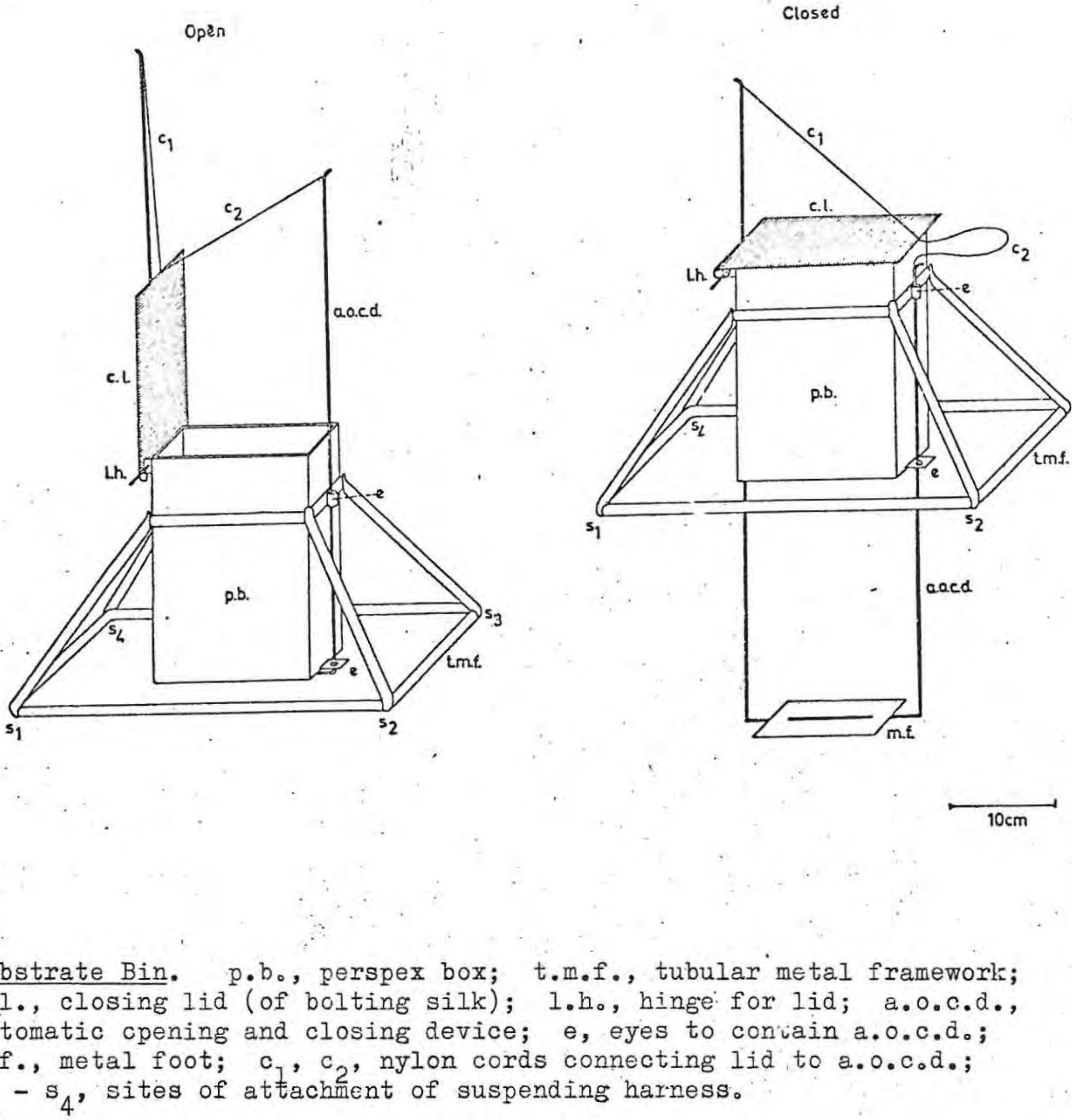
APPENDIX 1



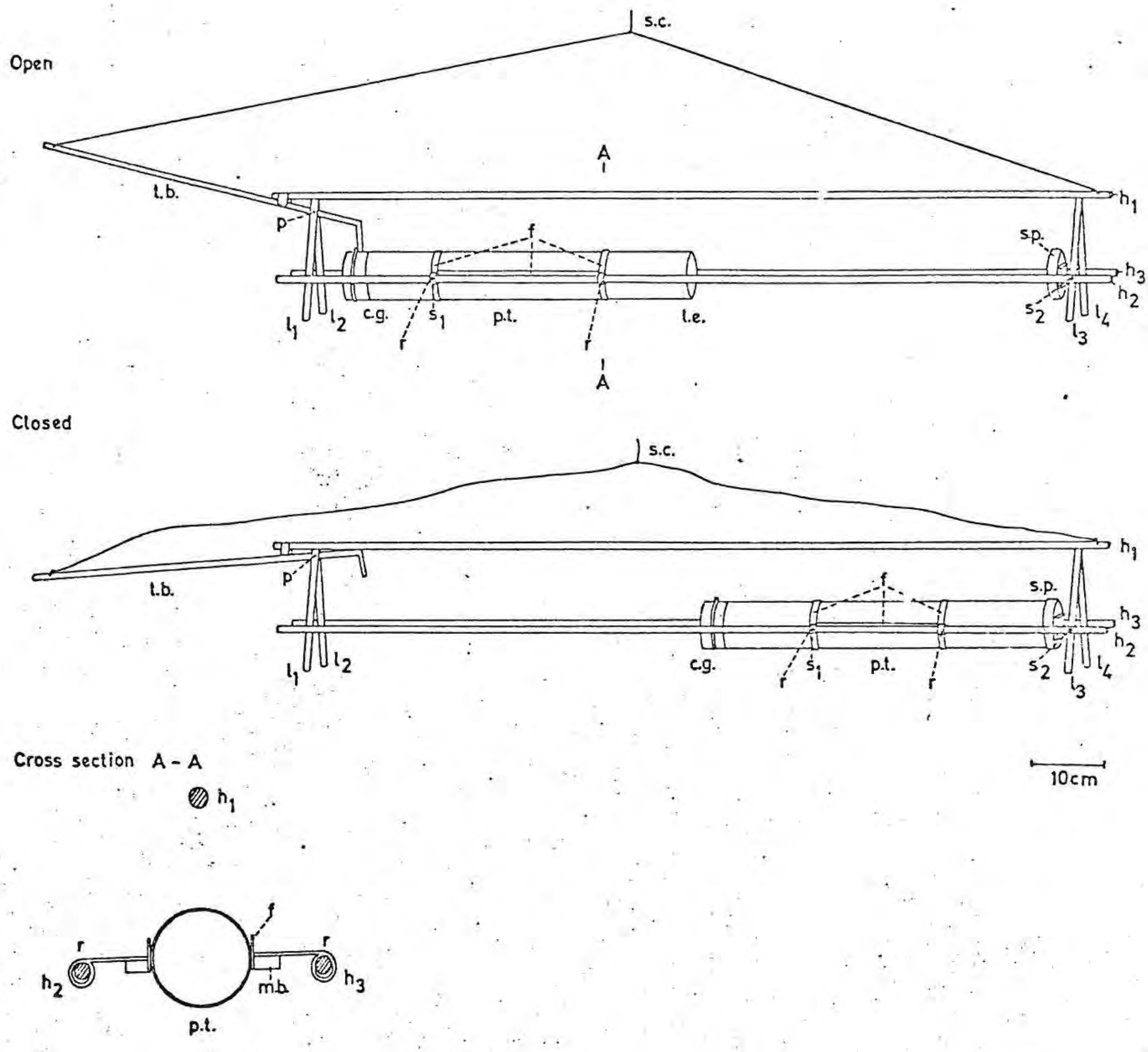
Vertical Bottom Sampler. u.d., upper door; l.d., lower door; s_1, s_2, points of attachment of springs; g, groove for sliding door; t.p., trigger pivot; s.c., suspension cable; t.b., trigger bar and cocking mechanism; c.b., coupling bars to synchronize upper and lower sliding doors.

APPENDIX 2



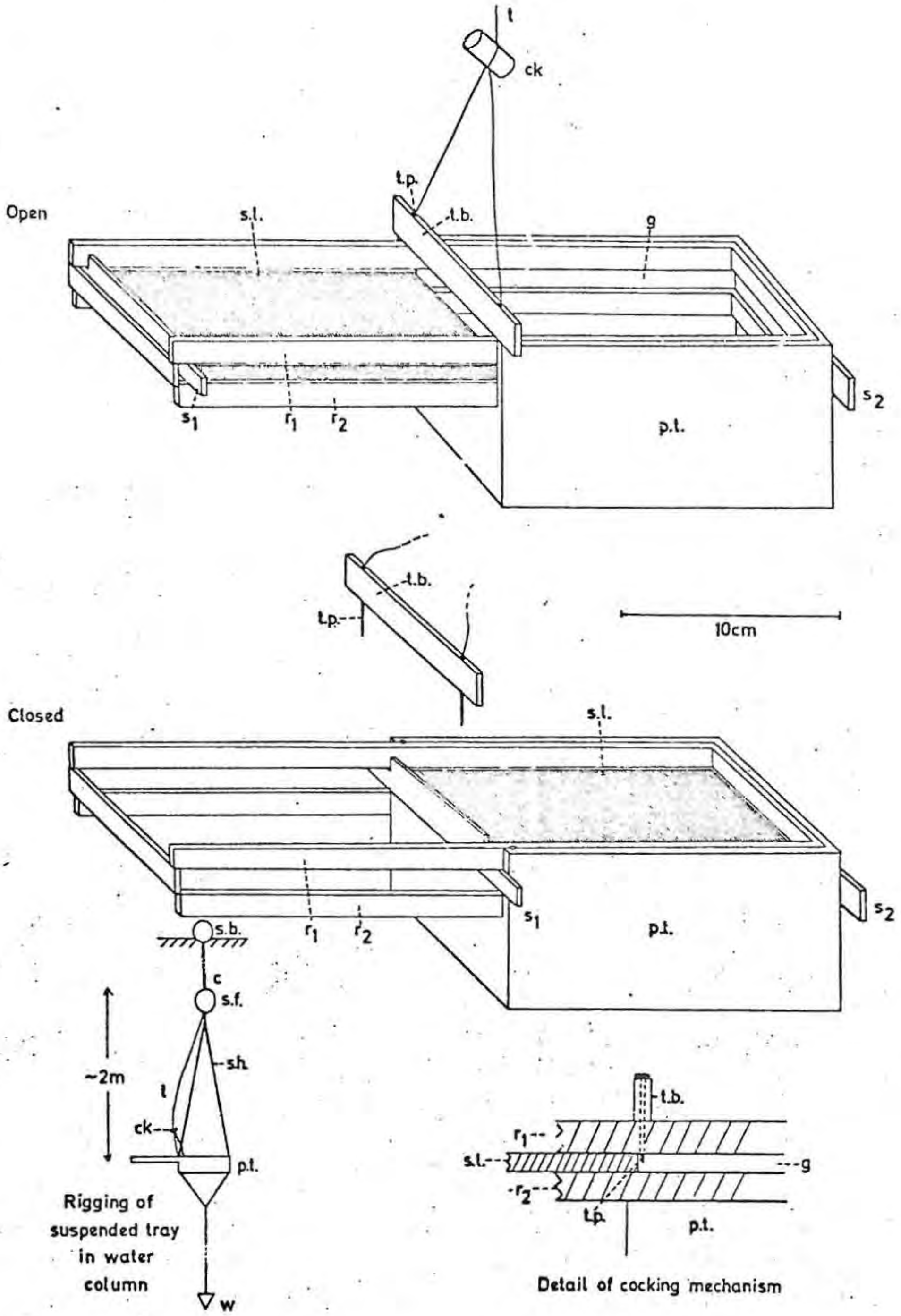
Substrate Bin. p.b., perspex box; t.m.f., tubular metal framework; c.l., closing lid (of bolting silk); l.h., hinge for lid; a.o.c.d., automatic opening and closing device; e, eyes to contain a.o.c.d.; m.f., metal foot; c_1, c_2, nylon cords connecting lid to a.o.c.d.; s_1 - s_4, sites of attachment of suspending harness.

APPENDIX 3



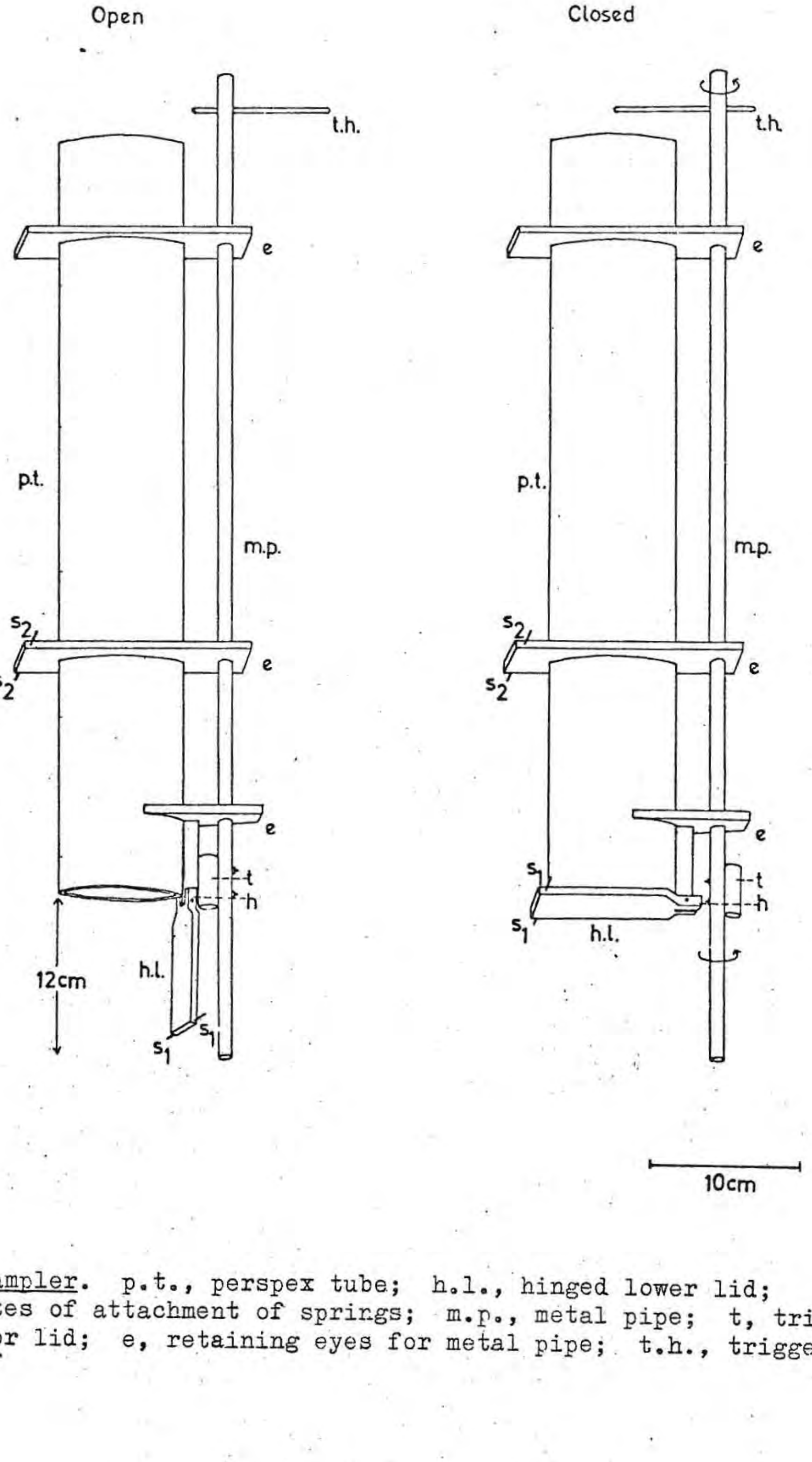
Horizontal Bottom Sampler. p.t., perspex tube; h$_1$, upper horizontal rail; h$_2$, h$_3$, lower horizontal rails; l$_1$ - l$_4$, legs; c.g., copper gauze on trailing end; l.e., leading edge; s.p., sealing plate for leading edge; t.b., trigger bar; p, pivot point; s$_1$, s$_2$, sites of attachment of springs; f, metal frame housing perspex tube; s.c., suspension cable; r, runners; m.b., mounting block for runners (r) and metal frame (f).

APPENDIX 4



Suspended Tray. p.t., perspex tray; s.l., sliding lid; s.h., suspending harness; w, base weight on lake bed; s.f., submerged float; s.b., surface buoy; c, cable to surface; t, trip line; s_1, s_2, sites of attachment of springs; t.b., trigger bar; t.p., trigger pin; ck, cork to keep trip line clear of closing mechanism; g, groove for sliding lid; r_1, r_2, upper and lower runners for sliding lid.

APPENDIX 5



Aquarium Sampler. p.t., perspex tube; h.l., hinged lower lid; s_1, s_2, sites of attachment of springs; m.p., metal pipe; t, trigger; h, hinge for lid; e, retaining eyes for metal pipe; t.h., trigger handle.

APPENDIX 6

Photonegative responses of P. hessei to light of different colours.

Light source	Chamber		
	1	2	3
White	40½%	32½%	27%
Green	36½%	25%	38½%
Red	33½%	24%	42½%
Blue	18%	20%	62%

The experiments were made in a perspex trough 45cm x 5cm x 5cm with two sliding partitions. Chamber 3 was furthest from the light source. Light was provided by a 35w microscope lamp. Green light was obtained using a VG 9 Schott filter and red light with a RG1/610 Schott filter. Blue light was obtained by passing light through a dilute solution of methylene blue.

The table gives the mean percentage distribution of two replicate series, using 100 - 150 animals per experiment.

APPENDIX 7

Radio-carbon techniques used in assessing diel feeding intensity in *P. hessei*.

Available evidence has shown that *P. hessei* consumes nanoplankton and bacterioplankton, and that these food sources are grazed at a similar rate. Accordingly, the determination of the feeding intensity in *P. hessei* was not restricted to the autotrophic food species.

Wright and Hobbie (1966) have shown that uptake of glucose in natural waters in the dark may be attributable to two distinct processes. At glucose concentrations below circa 500µg/l, substrate uptake is largely due to bacteria, and other heterotrophically feeding organisms in which permease active transport sites are present. At higher substrate concentrations, uptake is mainly a function of algal uptake as a result of diffusion. These findings were employed in the present investigation, and substrate concentrations were used which overlapped the requirements for both heterotrophic uptake and for uptake by diffusion processes. In this way it was hoped that by carrying out the exposure in the dark, a fairly broad spectrum of likely food organisms would be labelled either by heterotrophic uptake by active transport or by diffusion. Radiocarbon glucose and sodium acetate were used as isotope sources. Working solutions of 1µCi/ml were prepared, with substrate concentrations of 60µg/ml and 1.5µg/ml for ^{14}C glucose and ^{14}C acetate respectively. Higher specific activity solutions were not available.

Labelling the flocculent sedimentary material and detritus

The flocculent tripton collected in a substrate bin (4 litres) during an overnight exposure on the lake bed was thoroughly stirred and concentrated under reduced pressure onto Green's 995 Hydruro filter paper and made up to a final volume of 220ml. To this concentrate, 4ml of radio-active sodium acetate and 6ml of ^{14}C glucose were added in the dark. After 1 hour an aliquot of 20ml of the concentrate was removed and the balance of the concentrate was filtered again through Green's 995 filter paper, washed carefully with millipore filtered (0.45µ aperture) lake water three times, and made up with millipore-filtered water into two 100ml aliquots. The remaining 20ml aliquot was millipore filtered and the filter disc and filtrate aliquots were retained for radio-assay.

The 100ml aliquots of labelled floc were retained in the dark and taken as rapidly as possible onto the lake where substrate bins had been left exposed overnight to collect calanoids. The bins were raised and 100ml of labelled floc added to each. The contents were gently agitated to suspend the labelled floc through the bins: the bins were fitted with transparent perspex lids sealing against rubber gaskets, and returned to the lake bed. After an exposure of 1 hour, the bins were raised once again and a sample of the bin contents was taken for analysis of ^{14}C in the floc and in solution. The entire calanoid population was removed by filtration through a 10 plankton bucket and preserved immediately. In the laboratory, 100 adult males and 100adult females were individually removed from the thoroughly washed sample and placed into dioxane scintillation cocktail in a scintillation vial. The number of calanoids remaining in the balance of the sample was estimated by subsample counts. These calanoids were then transferred *en masse* to a second scintillation vial. As much water as possible was removed from the sample, and scintillation cocktail was added.

Replicate in *situ* exposures were made between 1300 and 1400hrs both at a 38m station and at a 10m station.

A single experiment was carried out at night. Calanoids were confined to a substrate bin on the lake bed by means of a sealing lid fitted at 1400hrs, and the entire bin was retrieved after nightfall and returned to the laboratory. The night-time feeding intensity was determined in the bin using labelled floc as described for the *in situ* daytime experiments.

Labelling the pelagial waters

Water was collected from 10m at Station I, returned to the laboratory and labelled in the dark by the addition of 20µCi of ^{14}C per litre. 10µCi of ^{14}C glucose and 10µCi of ^{14}C acetate were added to each of two replicate one litre samples several hours after sunset, and, after stirring, the samples were allowed to incubate in the dark for 1 hour. Animals collected from the substrate bins were introduced into the solution and after an exposure of one hour in the dark, were decanted through a plankton bucket, washed, formalinized, counted and sorted into scintillation vials to which scintillation cocktail was added.

^{14}C uptake of the lake water before introduction of the calanoids was determined by a parallel experiment; the ^{14}C fractions retained on a millipore filter disc after gentle washing, and in solution, were taken to indicate the relative uptake of ^{14}C into particulate material and that remaining in solution.

Self-adsorption values of the calanoids were determined at various concentrations of ^{14}C label in millipore filtered water. The procedure used was similar to the night-time feeding experiments, but millipore filtered lake water was used. Copepods exposed to this control solution for one hour were removed, preserved, washed and sorted into scintillation vials.

The samples were returned to the laboratories at Rhodes University for subsequent treatment. The samples of calanoid and flocculent material in cocktail solution were vibrated ultrasonically for 60 minutes to rupture the cell structure and solubilize the cell contents (c.f. Schindler 1971). In the samples containing flocculent material ultrasonication was not sufficiently effective in solubilizing the samples. Precipitation of the homogenized floc occurred within the scintillation vials, affecting the subsequent radio-assay. An attempt was made to counter this by retrieving the ultrasonicated particulate material on filter paper, and combusting it on a platinum basket in oxygen. The CO_2 resulting from this treatment was adsorbed in phenyl-ethylamine : methanol 1 : 1 V : V. However, the phenyl-ethylamine : methanol mixture reacted with the dioxane cocktail after several days, producing a pronounced colour which entirely quenched the samples and precluded radio-assay. Combustion could not be repeated on the floc samples using alternative procedures as all the available material had been used. However, prior to combustion attempts, all the material had been radio-assayed after straight-forward sonication, and these results have been used. While these results probably underestimate the radio-activity of the labelled flocculent material, they undoubtedly provide some indication of the relative isotope uptake.

In the calanoid samples, ultrasonication resulted in stable radio-assay counts. Some precipitation of the material occurred, but the particles were extremely small and it was assumed that most ^{14}C sources had been solubilized, excluding possibly the small fraction potentially bound in the exoskeleton.

Radio-carbon was assayed by means of a Beckman LS 133 Liquid Scintillation system using external standard ratio for quench calibration. Background estimates were carried out on material which had not been exposed to radio-isotopes. ^{14}C counting efficiencies for the homogenized flocculent material varied from 77 - 83%. With homogenized zooplankton samples counting efficiencies were consistently between 84% and 88%.

APPENDIX 8

Attempts to simulate migration under laboratory conditions

During the course of the present study, extensive attempts have been made to simulate migratory behaviour under laboratory conditions. Perspex tanks from 100cm x 25cm x 25cm and smaller, to tanks 2000cm x 45cm x 15cm have been employed. Light gradients have been obtained using Indian Ink suspensions; other experiments have been made using lake water only. Light changes have been brought about by increasing or decreasing the number of filters between the light source and the tank. Overhead and lateral light sources have been used, as well as illumination from below. Visual and photographic attempts have been made to follow the movements, either of individual calanoids or of large numbers of calanoids simultaneously. Experiments have been made by day and by night, at dusk and at dawn, indoors and out of doors. Torches, light bulbs and reflected sunlight have all been used as light sources. These experiments have all failed. One of the major problems encountered was the apparent indifference of the calanoids when they came into contact with a solid surface. On reaching a substrate, the calanoids invariably anchor to it by means of their antennae and regularly set up filtering currents. They become completely insensitive to a light beam directed onto them and sharp tapping of the surface on which they are anchored is necessary to get the animals to move. The only clear and reproducable response was that evident in animals which were dark adapted at night. Illumination of the dark adapted calanoids revealed them all to be swimming about throughout the vessel. As soon as they were illuminated, however, they moved obliquely onto the sides of the vessel (generally obliquely downwards irrespective of whether overhead or lateral illumination was applied). On reaching the walls of the vessel they stopped moving and appeared to be oblivious to light, whether it was of very low intensity (the yellow-red glow of a 1.5v torch with a flat battery) or the highly directional white light of a 6v torch fitted with new batteries. Until either of these light sources was turned off, the animals remained on the vessel walls. Only when the animals were again subjected to darkness, did they become active, and if illuminated again even as little as 5 - 10 minutes after their first light exposure, the majority were seen to be swimming about. The alternation between activity and thigmokinetic quiescence could be elicited in the same calanoids several times in succession at night, but inactivity was the order of the day.

It was the only predictable and reproducable response to light (or lack of light) which could be elicited under laboratory conditions in addition to the endogenous activity rhythms. Failure of other experimental approaches to the migratory behaviour are most plausibly attributable to the inability to simulate the underwater photo-environment naturally encountered by the calanoids. Both the angular distribution and wavelength composition of light are clearly of great importance to crustacean zooplankton (Ringelberg 1961 - 1964, Siebeck 1960, 1969 and McNaught and Hasler 1964, 1966). Also, the well developed endogenous activity rhythm in the species is likely to complicate the issue. The simulation of the natural photoenvironment was not possible with the equipment and facilities available at the research station.