THE ECOLOGY OF PSAMMOBIOTIC CILIATES OF SOUTH WALES

by

J.M. Wright

Department of Zoology, University College of Swansea, Singleton Park, Swansea, SA2 8PP (1).

Résumé

Le nombre et la distribution des ciliés psammobiotiques des rivages sablonneux du Sud du Pays de Galles sont étudiés ici. La variation en nombre et en espèces montre des différences considérables entre les deux rives de la Baie de Swansea. Les populations de ces rivages manifestent un accroissement lié à la température alors que les ciliés se trouvant à Nicholaston semblent être indépendants de la température. Cette différence dans la dynamique des populations est attribuée aux différences d'exposition à l'action des vagues.

Introduction

The psammobiotic ciliates of British shores have been studied by El Maghraby and Perkins (1956), Lackey and Lackey (1963) and Hartwig and Parker (1977). Numerically, the ciliates are found to be the most abundant animal phylum in the marine sandy environment and Fenchel (1969) considered them to be, on occasions, the most important in terms of relative metabolic activity. This paper presents a study of the ecology of psammobiotic ciliates: in particular, their variation in numbers during a twelve month period.

Methods

The study was carried out on two sandy shores of the South coast of the Gower Peninsula, South Wales (Figs. 1, 2) over a period of twelve months. Quantitative samples were obtained at one station on each shore. The Swansea Bay sampling site is located at a position between Mean High Water Neaps and Mid Tide Level (M.T.L.) where the water table is constantly at the surface. At Nicholaston, the sampling site is located at M.T.L.; here, the water table is at the surface only immediately ahead of a rising or falling tide. Sand samples were obtained using four 'Perspex' (Polymethacrylate) corers of 30cm length and external diameter 40mm, internal diameter 36mm (supplied by G.H. Bloore Ltd.). At one end, the internal edge was bevelled to make entry into the sediment easier and reduce disturbance. Negative pressure, applied by sucking with the mouth

(1) Present Adress: Biological Sciences, Post Graduate School, Rivers State University of Science & Technology, P.M.B. 5080, Port Harcourt, Nigéria.

Cahiers de Biologie Marine
Tome XXV - 1984 - pp. 217-239.

at the upper end as the corers were gently pushed by hand into the sediment, further reduced disturbance. The top of the corer was sealed with a rubber bung after it had been inserted to a depth of 20cm. The tube was then 'broken' from the sediment by pushing it to an angle of approximately 50° to the vertical, it was then lifted out and sealed with a second bung at the lower end. As the tube is transparant, any failure to sample properly could be seen and the process repeated if necessary. Four cores were taken at each station, arranged at the corners of a 25cm square.

Cores were returned to the laboratory where the contents were allowed to slide out under gravity, in order to disturb the core as little as possible. The bottom 6cm of sediment was discarded and the remaining 14cm length split into seven sections at 2cm intervals. From each of these sections, a 2g sample of sediment was removed and sub-

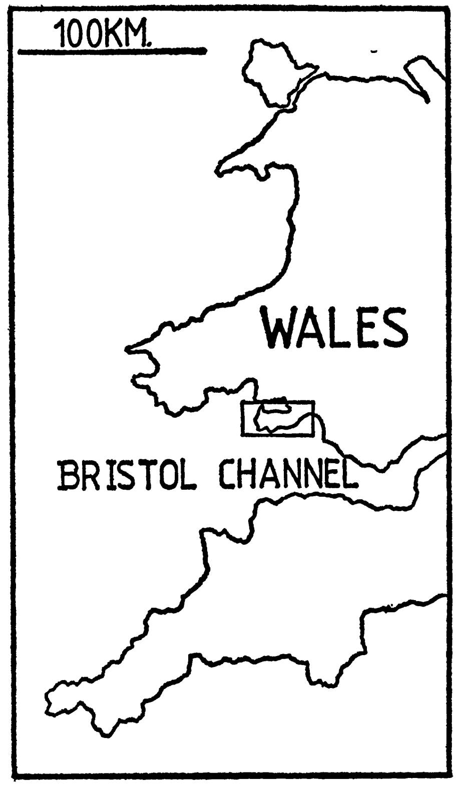

Fig. 1
South-West Britain, showing the location of the Gower peninsula.

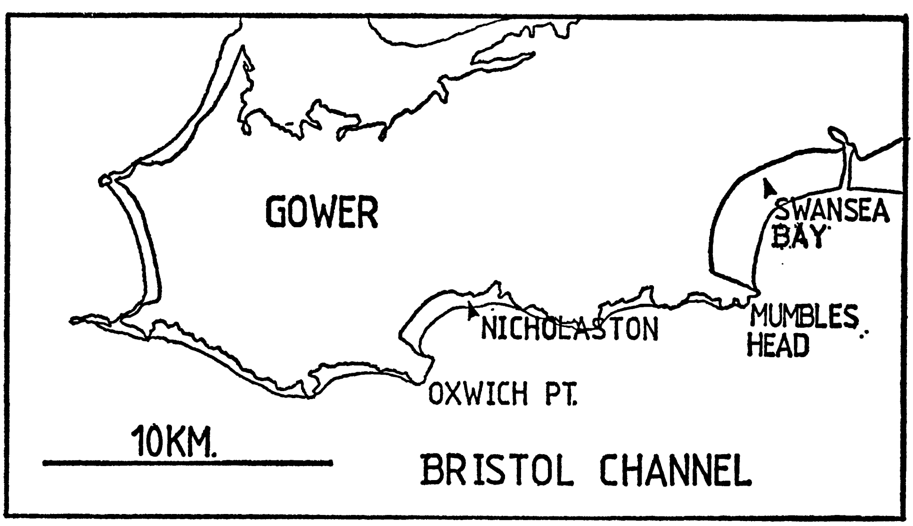

Fig. 2
The Gower peninsula (▲) sampling site.

sequently analysed for organic carbon content, using the method of Gaudette *et al.* (1974). The remaining sediment was subjected to Uhlig's sea-water ice technique for the extractions of ciliates (Uhlig, 1968). Identifications were made from living and stained specimens. Other parameters measured include por volume (Bruce, 1928), porosity (Webb, 1958), Redox potential (Fenchel and Riedl, 1970), hydrogen ion activity (Fenchel and Riedl, 1970) and mean grain size (Folk and Ward, 1957). Electrometric parameters were measured using a Pye Unicam Model 293 pH meter fitted with electrodes supplied by Russell ph Ltd. Mean grain size was measured using 21 half height, standard brass sieves of 200mm diameter in a quarter phi interval series, the coarsest being —1.00 ∅, the finest +4.00 ∅. The grain size data were analysed using an ICL 1904S at University College Swansea Computer Centre.

Results

All statistical parameters referring to the sediment are those of Folk and Ward (1957). The Swansea Bay sediment is a medium fine sand (Mz 2.03 ∅ = 0.25mm), moderately sorted (∅ I 0.56 ∅), with a nearly symmetrical distribution of fine and coarse grades (Sk I + 0.01) and an indication of better sorting in the central region of the distribution (Kg 1.12). The sediment from Nicholaston is a medium sand (Mz 1.57 ∅ = 0.34mm) well to moderately well sorted (∅ 0.50 ∅), with a nearly symmetrical distribution of fine and coarse grades (Sk I — 0.08); the distribution is approximately normal (Kg 1.05).

The organic carbon content of the Swansea site to a depth of 14cm over the sampling period had a mean of 0.07 p. 100 $\pm$ 0.03 with a range of values between zero and 0.17 p. 100. Higher values ((0.25 — 0.46 p. 100) were due to the occasional presence of coal particles; values greater than 0.17 p. 100 which coincided with the presence of black particles were discarded. During the sampling period, the amount of organic carbon did not follow a clear seasonal pattern. At Nicholaston, the mean organic carbon content was 0.05 p. 100 $\pm$ 0.02 with a range of values between zero and 0.13 p. 100; coal particles were not observed at this site. No seasonal cycle in organic carbon content was observed.

The pore volume at Swansea Bay had a range of values between 29 p. 100 and 49 p. 100 with a mean of 42.7 p. 100 $\pm$ 3.1 and at Nicholaston the range was between 33 p. 100 and 46 p. 100 with a mean of 39.6 p. 100 $\pm$ 3.5. The porosity immediately adjacent to the sampling cores in Swansea Bay showed a range of values between 17.8 p. 100 and 24.5 p. 100, with a mean value of 20.3 p. 100 $\pm$ 1.1. At Nicholaston, the range of values lay between 15.7 p. 100 and 26.7 p. 100, with a mean value of 18.3 p. 100 $\pm$ 1.2.

The redox potential discontinuity (R.P.D.) occurs between the values of +200mv and —100mv (Fenchel and Riedl, 1970); it is considered to begin at +200mv or less. At the Swansea Bay site, the redox potential varied between +398mv at the surface and —70mv at 14cm depth; the R.P.D. was observed to make a migration

TABLE 1

The mean number of ciliates for four cores to a depth of 14cm, adjusted to give numbers per square metre:

	No. m^{-2}	±1 Standard Deviation
Swansea Bay		
1979 March	5.75×10^4	5.5×10^4
April	1.8475×10^5	1.4767×10^5
May	3.015×10^5	1.3436×10^5
June	3.1725×10^5	2.144×10^5
July	6.5975×10^5	6.6259×10^5
August	5.2925×10^5	1.7194×10^5
September	5.2375×10^5	2.3318×10^5
October	3.705×10^5	1.0534×10^5
November	3.385×10^5	9.396×10^5
December	2.7025×10^5	1.6556×10^5
1980 January	2.9675×10^5	1.2117×10^5
February	7.085×10^5	5.1455×10^5
Nicholaston		
1979 March	9.5×10^3	5.07×10^3
April	3.4×10^3	9.93×10^3
May	5.975×10^4	1.691×10^4
June	6.575×10^4	3.695×10^4
July	2.325×10^4	1.864×10^4
August	9.0×10^3	4.83×10^3
September	2.85×10^4	7.3×10^4
October	2.39875×10^6	4.75686×10^6
November	3.575×10^4	4.635×10^4
December	2.5×10^3	1.9×10^3
1980 January	2.625×10^4	1.489×10^4
February	6.65×10^4	3.88×10^4

towards the surface during the warmer months of the sampling period (Pearson correlation coefficient $r = 0.725$, 9 d.f., 5 p. 100) being found at approximately 7cm in June 1979. At Nicholaston the redox potentials had a range of values between +438mv and +78mv at 14cm depth. However the value usually remained around +398mv throughout this depth no matter what the time of year.

The pH of the sediment at the Swansean Bay site had a range of values between 6.6 and 8.1 units. The profile was generally one of increasing pH with depth. At Nicholaston, the pH had a range of values between 6.6 and 7.9 units, being either constant or increasing with depth.

The water table at the Swansea Bay site is always at the surface regardless of the state of the tide. The slope of the beach is gentle and at the site position there is a layer of impervious clay at a depth of 30-40cm. The station is considered to be in the zone of saturation (Salvat, 1966, 1967). At Nicholaston, the water table lies below the sampling depth at the time of low water. The slope of the beach is steeper than that of Swansea Bay and, at the site position, there is a layer of larger particles of the gravel grade (Folk, 1954), measuring approximately 5-10cm, at a depth of 40cm. The water table is at the surface shorewards of rising and falling tides. The site is considered to be in the zone of resurgence (Salvat, 1966, 1967).

Changes in ciliate populations (see Table 1)

A comparison of these figures with those of previous authors shows that they are within the same range for the intertidal area:

Author	Number per square metre
Brotskaja 1951	$2 \times 10^4 - 4.7 \times 10^5$
Fenchel 1969	6.8×10^5
Burkovsky 1968	$<2.6 \times 10^6$
Burkovsky 1970	4.34×10^6
Hartwig 1973	$3.544 \times 10^5 - 3.3344 \times 10^6$ to 10cm in sandflat
	$9.27 \times 10^4 - 8.526 \times 10^5$ to 60cm in beach slope
Hartwig, Gluth and Wieser 1977	$3.7 \times 10^4 - 2.117 \times 10^6$ to 8cm
present work	$3.4 \times 10^3 - 2.40 \times 10^6$ to 14cm

The range of values obtained for the Nicholaston site ($3.4 \times 10^3 - 2.40 \times 10^6$) is greater than that for Swansea Bay ($5.75 \times 10^4 - 7.09 \times 10^5$) due to a single core taken at Nicholaston during October 1979:

Depth in cm	Core 1	Core 2	Core 3	Core 4
0-2	6	28	5	5
2-4	3	10	1	0
4-6	0	0	0	0
6-8	5	1	0	0
8-10	9500	1	3	3
10-12	3	1	2	0
12-14	17	0	1	0

The results for core I give an adjusted value of $9.534 \times 10^6 m^{-2}$, providing the highest estimate for any core taken at either Swansea Bay or Nicholaston.

The total number of ciliates at Swansea Bay (Fig. 3) reaches its maximum during the warmer months of the year and shows a positive correlation with the averaged maximum air temperature (Figs. 4, 5) for the thirty days preceding a sampling date ($r = 0.634$, 9 d.f., 5 p. 100). The highest number of ciliates was recorded in February; a second maximum occurred in July coinciding with the temperature maximum. The minimum number occurred in March, corresponding with a low temperature. The high number of ciliates obtained in February corresponded with a sharp rise in temperature during the 30 days preceding the sampling date. The average maximum temperature for February 1979 for that period was 5.3°C whilst, in February 1980, the corresponding temperature was 9.3°C.

At Nicholaston, the total number of ciliates was variable showing

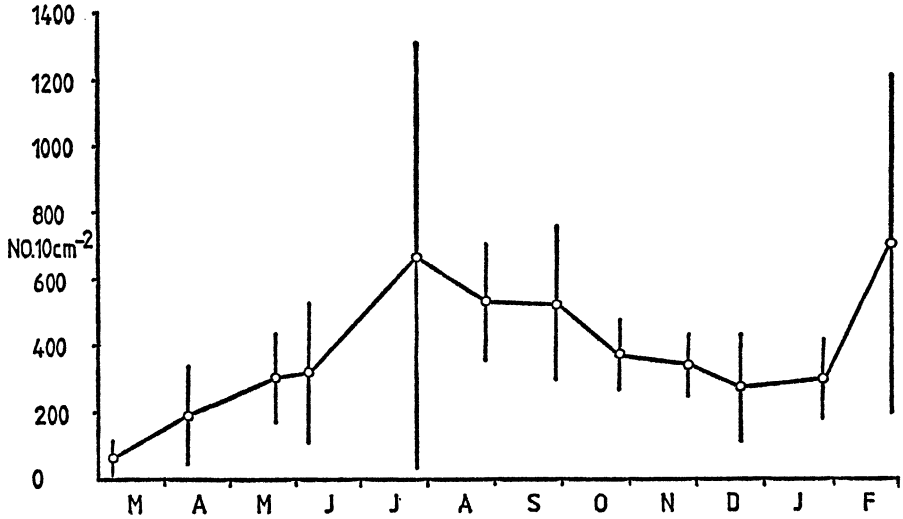

Fig. 3
The total ciliate numbers at Swansea Bay.

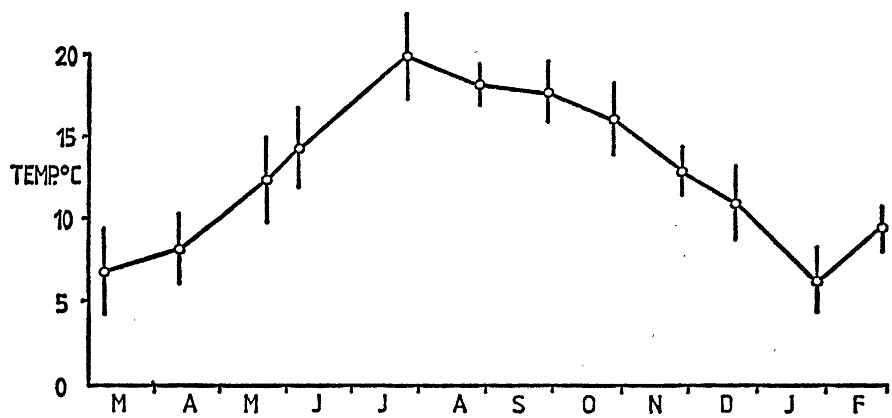

Fig. 4
The average maximum air temperature for the 30 days preceding a sampling date at Swansea Bay.

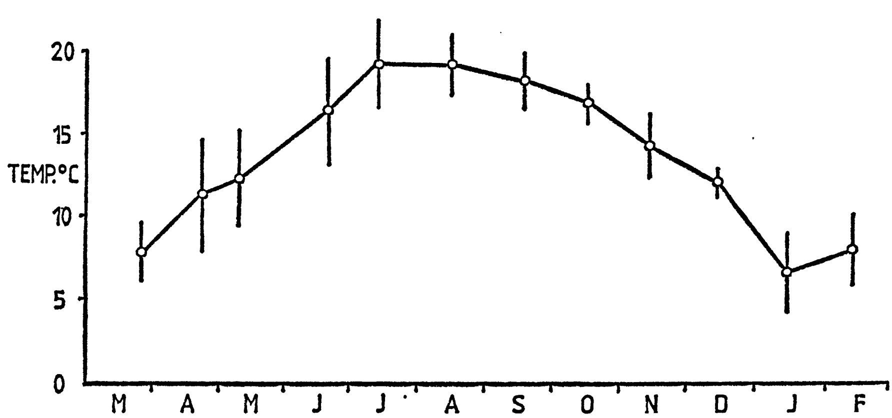

Fig. 5
The average maximum air temperature for the 30 days preceding a sampling date at Swansea Bay.

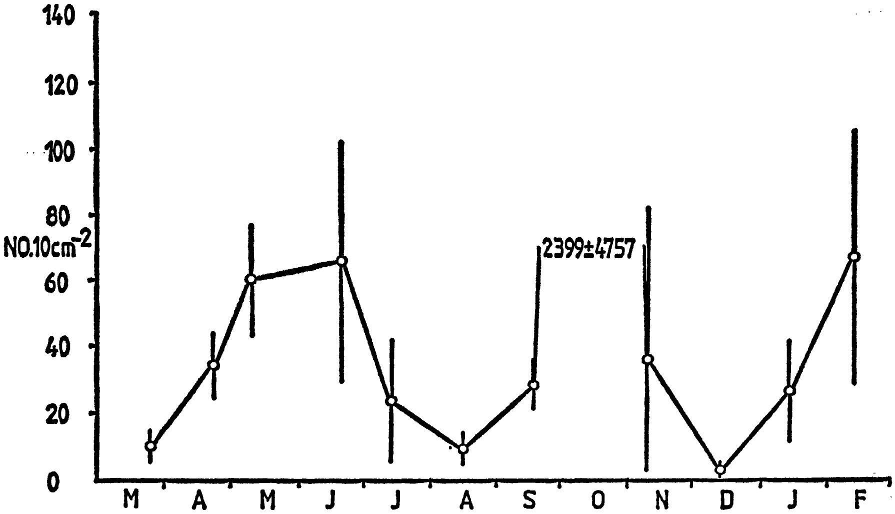

FIG. 6
The total ciliate numbers at Nicholaston.

several maxima, none of which coincided with the maximum in temperature (Fig. 6). The numbers did not show a correlation with temperature.

The mean population depth of these populations was calculated by taking the number of ciliates at a given depth interval, multiplying by the actual depth in centimetres and then dividing each product by the total number of ciliates for that core. A correlation was found between mean population depth and temperature at Swansea Bay ($r = 0.796$, 9 d.f. 1 p. 100), i.e. the population is found at a shallower depth with increasing temperature (Fig. 7). The percentage

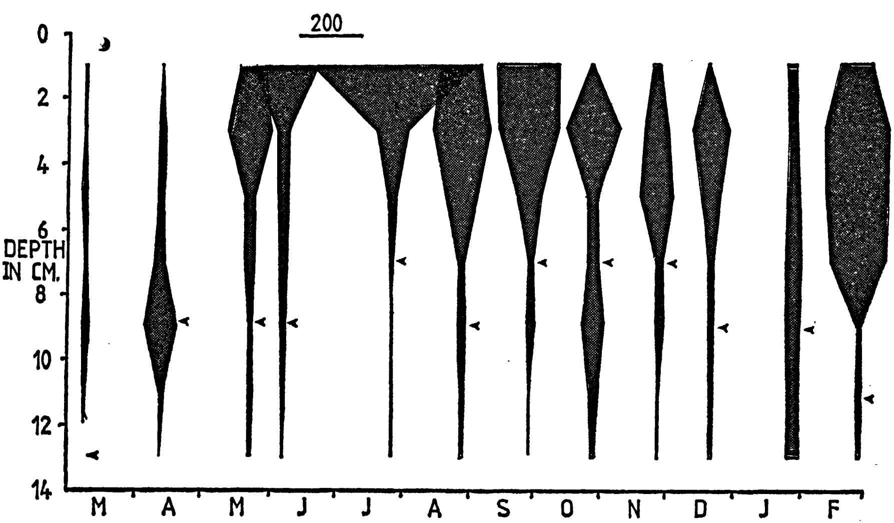

FIG. 7
Distribution of total ciliate population with depth at Swansea Bay. (◆) Begining of R.P.D.

of the population which occurs in the top 2cm also shows a correlation with temperature (r = 0.634, 9 d.f. 5 p. 100). At Nicholaston there was no observable relationship between mean population depth or percentage occurring in the top 2cm of sediment with temperature (Fig. 8).

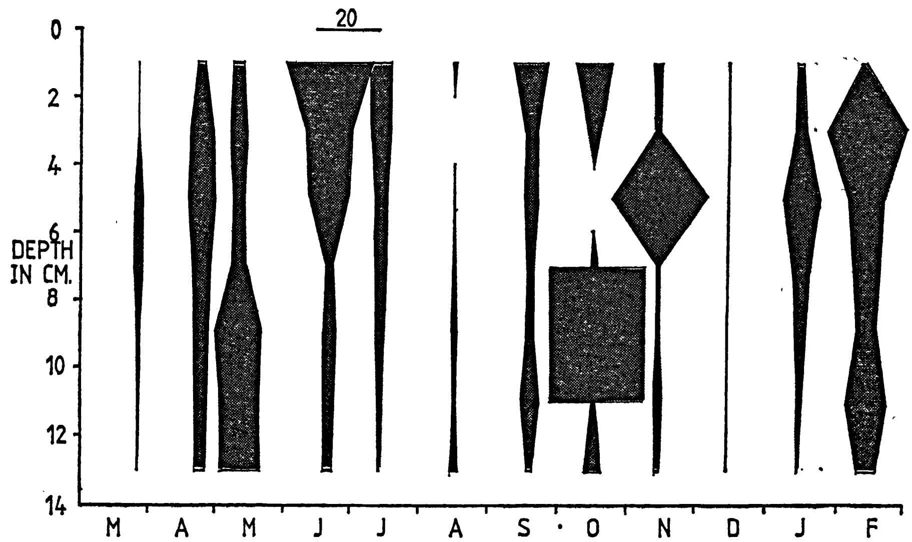

FIG. 8
Distribution of total ciliate population with depth at Nicholaston.

FAMILY TRACHELOCERCIDAE

The members of this family, comprising the three genera *Trachelocerca, Tracheloraphis* and *Trachelonema* account for 32.9 p. 100 of all the ciliates at the Swansea Bay site. The mean value for the sampling period was $1.24 \times 10^5 m^{-2}$ with a range of values between 8.0×10^3 and $6.42 \times 10^5 m^{-2}$. The numbers of Trachelocercidae show several peaks (Fig. 9); there is a correlation between numbers and average maximum air temperature (r = 0.705, 9 d.f., 5 p. 100). The peaks occur in September, June and February. The mean population depth shows a significant relationship with temperature (r = 0.757, 9 d.f., 1 p. 100): the population is nearer the surface during the warmer months. The percentage of the population occurring in the top 2cm of sediment also shows a significant relationship with temperature (r = 0.640, 9 d.f., 5 p. 100). At Nicholaston, the Tracheloceridae accounted for 20.4 p. 100 of the total ciliate numbers (ignoring the exceptional Core 1 of 17.10.79) or 2.1 p. 100 if this is included in the calculation. The mean value for the sampling period was $6.5 \times 10^3 m^{-2}$ with a range of values between zero and $4.6 \times 10^4 m^{-2}$. The numbers show no correlation with average maximum air temperature (Fig. 10), neither does the mean population depth nor the percentage occurring in the top 2cm of sediment.

TRACHELORAPHIS TEISSIERI Dragesco, 1960

This species is present on occasion in quite large numbers at the Swansea Bay site, whilst it is absent from the Nicholaston site. At Swansea Bay, it accounts for 5.3 p. 100 of the total ciliate population with a range of values between zero and $1.49 \times 10^5 m^{-2}$ and a mean of $2.0 \times 10^4 m^{-2}$. The numbers show no correlation with average air temperature being absent from the sampling site during the warmest months. The mean population depth shows a correlation with temperature ($r = 0.713$, 8 d.f., 5 p. 100) and the percentage occurring in the top 2cm of sediment also correlates with temperature ($r = 0.699$, 8 d.f., 5 p. 100).

TRACHELORAPHIS HAMATUS Wright, 1982

At the Swansea Bay site, this ciliate accounts for 14.7 p. 100 of all the ciliates encountered with a range of values between zero and $2.05 \times 10^5 m^{-2}$ and a mean of $5.58 \times 10^4 m^{-2}$. There is no correlation

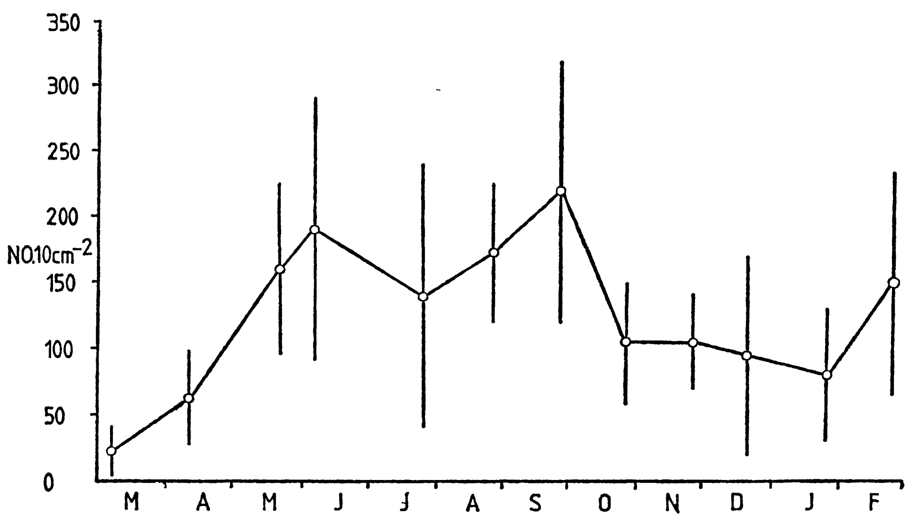

Fig. 9
The numbers of Trachelocercidae at Swansea Bay.

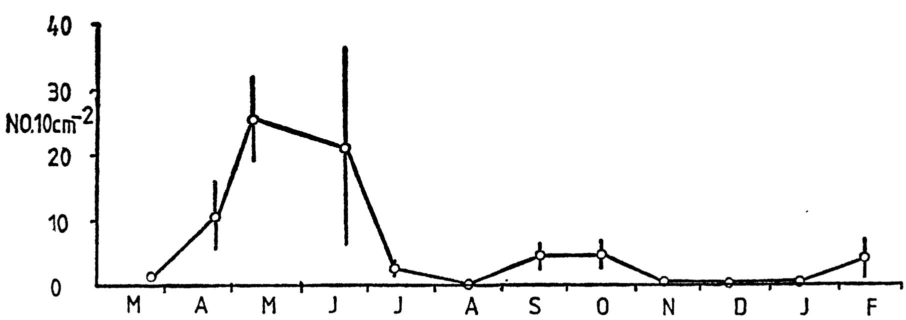

Fig. 10
The numbers of Trachelocereidae at Nicholaston.

between numbers and temperature although there is an observable peak during September otherwise, the trend is one of increase during the survey. There is a correlation between mean population depth and temperature ($r = 0.761$, 9 d.f., 1 p. 100) and also between the proportion occurring in the surface layers of sediment and temperature ($r = 0.615$, 9 d.f., 5 p. 100). At Nicholaston, this species accounts for 1.4 p. 100 (or 0.1 p. 100) with a range of values between zero and $6 \times 10^3 m^{-2}$ and a mean of $4.4 \times 10^2 m^{-2}$.

TRACHELORAPHIS DITIS Wright, 1982
TRACHELORAPHIS CONFORMIS Wright, 1982

These two species have been considered as one group during the survey due to their similar appearance in life. At Swansea Bay, they

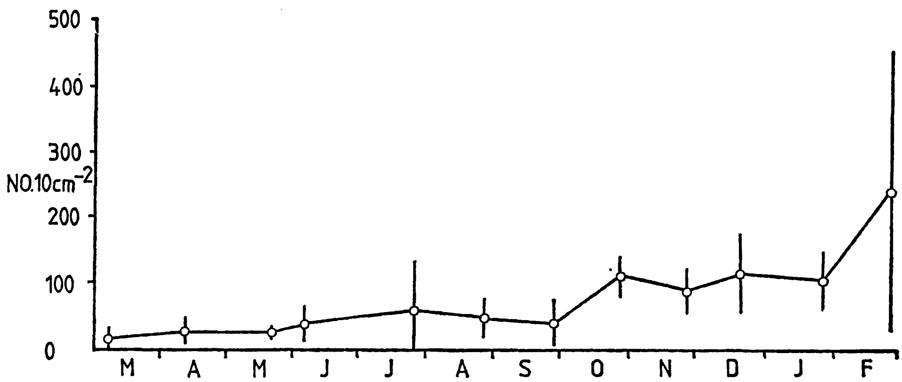

Fig. 11
The numbers of Loxodidae at Swansea Bay.

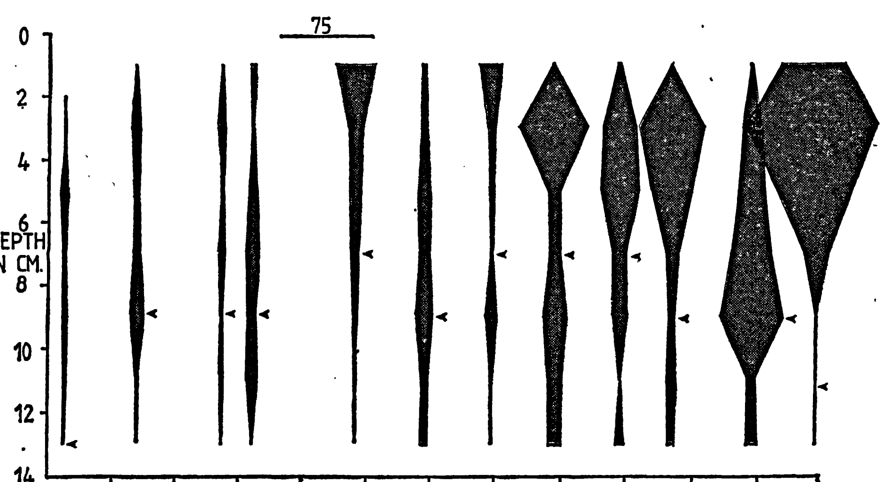

Fig. 12
Distribution of the Loxodidae with depth at Swansea Bay. (◆) Beginning of R.P.D.

account for 10.8 p. 100 of the total ciliate population. The range of density values lay between zero and $3,35 \times 10^5 m^{-2}$ with a mean value of $4.10 \times 10^4 m^{-2}$. The variation in numbers and temperature are related and show a significant correlation ($r = 0.751$, 9 d.f., 1 p. 100). There is a correlation between mean population depth and temperature ($r=0.830$, 9 d.f., 1 p. 100) and also between the percentage occuring in the top 2cm and temperature ($r=0.674$, 9 d.f., 5 p. 100). At Nicholson, this group accounts for 13.2 p. 100 (or 1.8 p. 100) of the total. The range of values lay between zero and $4.0 \times 10^4 m^{-2}$ with a mean value for the survey of $4.22 \times 10^3 m^{-2}$. There is no correlation between temperature and numbers, although this group is absent in the cooler months. Neither the mean population depth or the percentage occurring in the top 2cm of sediment correlate with temperature.

TRACHELONEMA OLIGOSTRIATA Raikov, 1962

This species accounts for fewer than 0.3 p. 100 of the ciliates observed at the Swansea Bay site. The range of values lay between zero and $1.8 \times 10^4 m^{-2}$ with a mean value of $1.27 \times 10^3 m^{-2}$. This species is present for nine months of the sampling period, producing a peak in numbers during July; however, there is no correlation between numbers and temperature, nor is there a significant relationship between temperature and either mean population depth or the percentage occurring in the top 2cm. At Nicholaston, this species makes up 0.3 p. 100 (or less than 0.1 p. 100) of the ciliate population and occurs in only three months of the sampling period.

FAMILY LOXODIDAE

For the purposes of this report the Loxodidae is taken to consist of the genera *Remanella, Kentrophoros* and *Ciliofaurea.* At the Swansea Bay site, individuals of the genera *Kentrophoros* and *Ciliofaurea* occur occasionally whilst the genus *Remanella* occurred regularly throughout the sampling period and accounted for over 99 p. 100 of the family. The Loxodidae accounted for 20.0 p. 100 of the ciliates recorded at the Swansea Bay site with a mean of $7.57 \times 10^4 m^{-2}$ and a range of values between zero and $5.32 \times 10^5 m^{-2}$. The Loxodidae show a temporal relationship rather than a correlation with temperature: the regression with time is significant ($r = 0.844$, 10 d.f., 0.1 p. 100) (Fig. 11). The mean population depth of the Loxodidae (Fig. 12) does not correlate with average maximum air temperature, but the percentage of the population occurring in the top 2cm of sediment does correlate with temperature ($r = 0.631$, 9 d.f., 5 p. 100). At Nicholaston, the Loxodidae are an unimportant constituent of the total ciliate population and account for 0.2 p. 100 (or fewer than 0.1 p. 100).

KENTROPHOROS CANALIS Wright, 1982

This species occurs only very occasionally at Swansea Bay and not at all at Nicholaston.

REMANELLA MULTINUCLEATA Kahl, 1933

This species accounts for fewer than 0.1 p. 100 of the ciliates at Swansea Bay and does not occur at all at Nicholaston.

CILIOFAUREA MIRABALIS Dragesco, 1954

This ciliate was found during a single month's sampling at Swansea Bay (in February 1980) when it occurred in densities of $1.4 \times 10^3 m^{-2}$ and accounted for 0.3 p. 100 of the total ciliate population. It does not occur at Nicholaston.

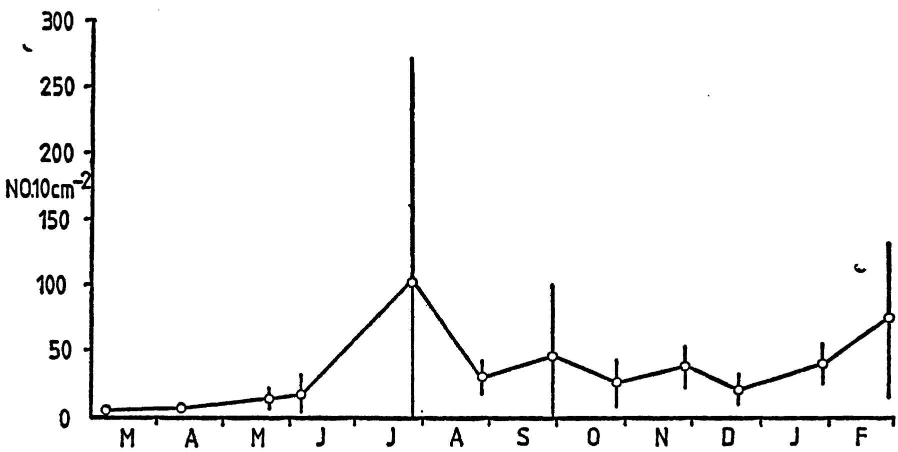

FIG. 13
The numbers of Geleidae at Swansea Bay.

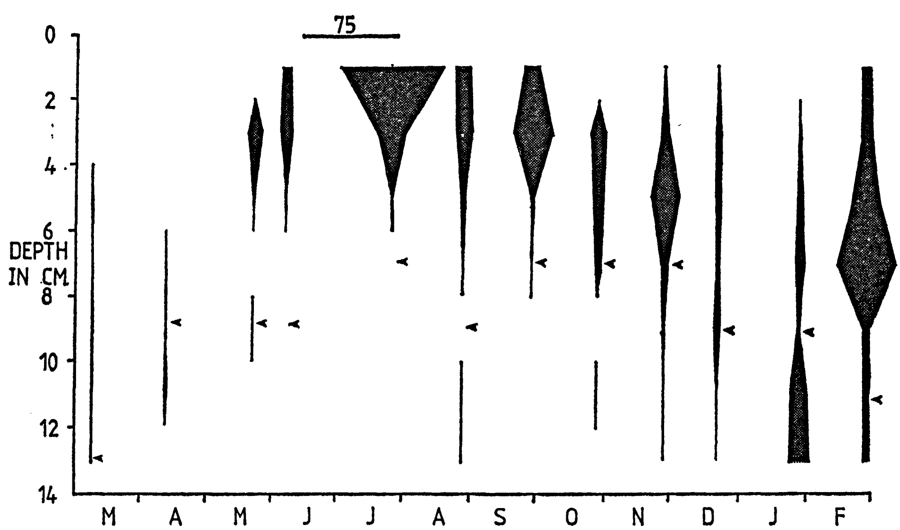

FIG. 14
Distribution of the Geleidae with depth at Swansea Bay. (◄) Beginning of R.P.D.

FAMILY GELEIDAE

The only members of this family encountered belong to the genus *Gelea*. At Swansea Bay, they account for 9.0 p. 100 of the total population. During the survey period, they had a mean density of $3.42 \times 10^4 m^{-2}$ with a range of values between zero and 3.57×10^5 m^{-2}. This family does not show a significant relationship with temperature but there is an apparent temporal increase (Fig. 13). However, the mean population depth (Fig. 14) does correlate with temperature ($r = -0.869$, 9 d.f., 0.1 p. 100); the percentage occuring in the top 2cm of sediment also correlates with temperature ($r = 0.746$, 9 d.f., 1 p. 100). At Nicholaston, the occurrence of Geleidae is rare; during the course of the survey none were recorded.

GELEIA NIGRICEPS Kahl, 1933

This species was encountered occasionally at Swansea Bay, it was not recorded from either site during the course of the survey.

FAMILY COLEPIDAE

All members of the Colepidae that were encountered during the survey belonged to the genus *Coleps*. At Swansea Bay, this family accounts for 11 p. 100 of the total ciliate population. The range of density values lay between zero and $5.35 \times 10^5 m^{-2}$ with a mean value of $7.35 \times 10^4 m^{-2}$. The numbers show a significant correlation with temperature ($r = 0.786$, 9 d.f., 1 p. 100). Mean population depth shows a correlation with temperature ($r = -0.923$, 8 d.f., 0.1 p. 100) and the percentage of the population occurring in the top 2cm of sediment also correlates with temperature ($r = 0.702$, 8 d.f., 5 p. 100). At Nicholaston, the Colepidae account for 5.7 p. 100 (or 0.8 p. 100) of the total population. The range of values lay between zero and $4.9 \times 10^4 m^{-2}$ with a mean of $1.8 \times 10^3 m^{-2}$. This family was present in only the six warmer months of the sampling period.

COLEPS PULCHER Spiegel, 1926

At Swansea Bay, this species accounts for 2.6 p. 100 of the ciliate population. The range of density values lay between zero and $1.37 \times 10^5 m^{-2}$ with a mean value for the survey of $1.00 \times 10^4 m^{-2}$. There is no correlation between numbers and temperature (Fig. 15), although the mean population depth, does correlate with temperature ($r = -0.893$, 8 d.f., 1 p. 100), being nearer the surface during the warmer months; there is no correlation between the percentage occurring in the top 2cm and the temperature. At Nicholaston, *C. pulcher* is comparatively rare and was present during two months of the survey in low numbers ($7.5 \times 10^2 m^{-2}$) on both occasions.

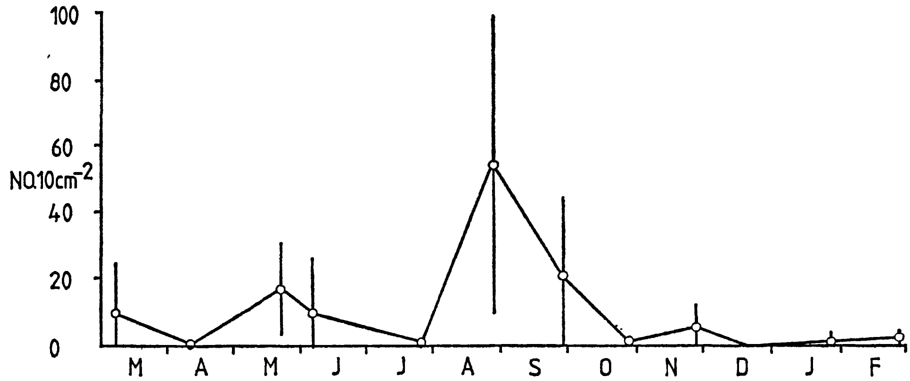

FIG. 15
The numbers of *Coleps pulcher* at Swansea Bay.

COLEPS SIMILIS Kahl, 1933

This species accounts for 8.8 p. 100 of the ciliates at Swansea Bay with a range of values between zero and $5.33 \times 10^5 m^{-2}$ and a mean of $3.35 \times 10^{4-2}$. The numbers (Fig. 16) show a correlation with temperature ($r = 0.727$, 7 d.f., 5 p. 100). The mean population depth also correlates with temperature ($r = —0.739$, 7 d.f., 5 p. 100) as does the percentage of the population in the surface layers ($r = 0.744$, 7 d.f., 5 p. 100). At Nicholaston, this ciliate accounts for 5.3 p. 100 (or 0.7 p. 100) of the total ciliate population. The range of values lay between zero and $4.40 \times 10^4 m^{-2}$ with a mean for the survey of $1.69 \times 10^3 m^{-2}$. This species was present during six months of the sampling period.

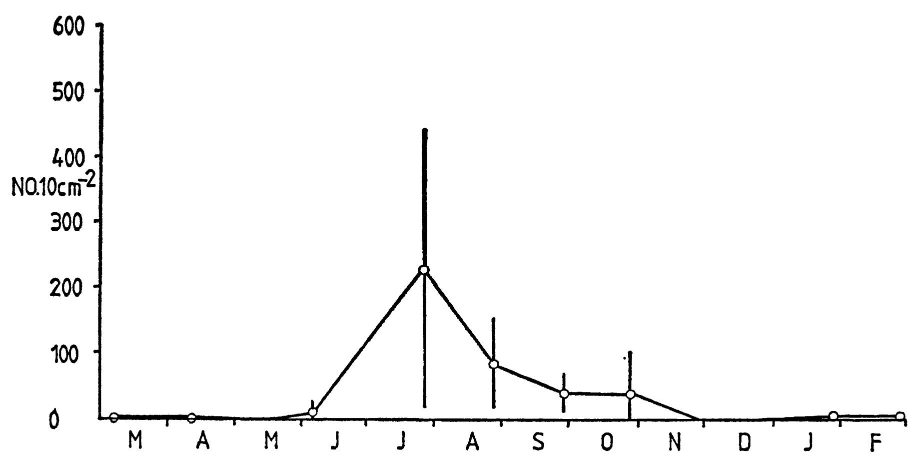

FIG. 16
The numbers of *Coleps similis* at Swansea Bay.

FAMILY AMPHILEPTIDAE

LITONOTUS ANGUILLA Kahl, 1930

This species did not occur at the Swansea Bay site during the survey. At Nicholaston it accounts for 0.9 p. 100 (or 0.1 p. 100) and occurred during three months of the sampling period.

FAMILY SCAPHIDIODONTIDAE

CHILODONTOPSIS VORAX (Stokes, 1894)

This species accounts for fewer than 0.1 p. 100 of the ciliates at Swansea Bay and at Nicholaston 3.2 p. 100 (or 0.4 p. 100), occuring in four months of the sampling period.

FAMILY PLEURONEMATIDAE

All the members of this family found during the survey belong to the genus *Pleuronema*. At Swansea Bay, they accounted for 5.8 p. 100 of all the ciliates encountered. The range of density values was between zero and $2.34 \times 10^5 m^{-2}$ with a mean of $2.19 \times 10^4 m^{-2}$. The numbers (Fig. 17) do not correlate with temperature, neither does the mean population depth nor the percentage occurring in the top 2cm of sediment. At Nicholaston, they account for 11.7 p. 100 (or 1.6 p. 100). The numbers do not correlate with temperature neither does the mean population depth or the percentage occurring in the top 2cm of sediment.

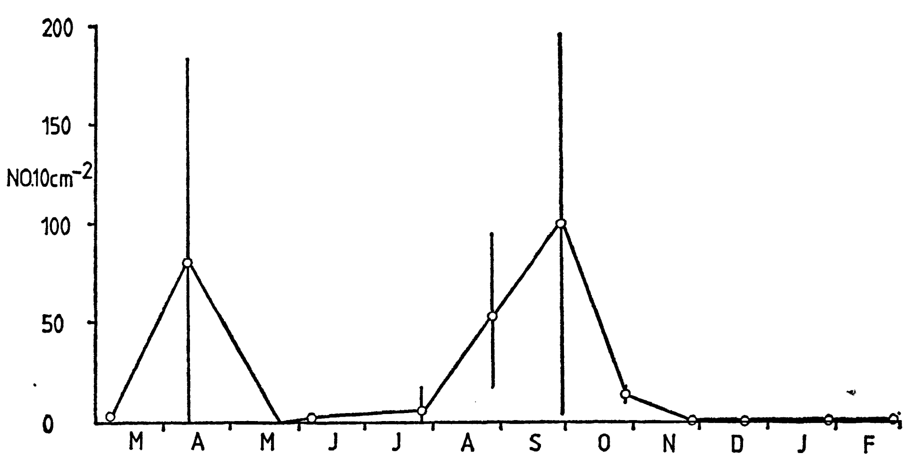

FIG. 17
The numbers of Pleuronematidae at Swansea Bay.

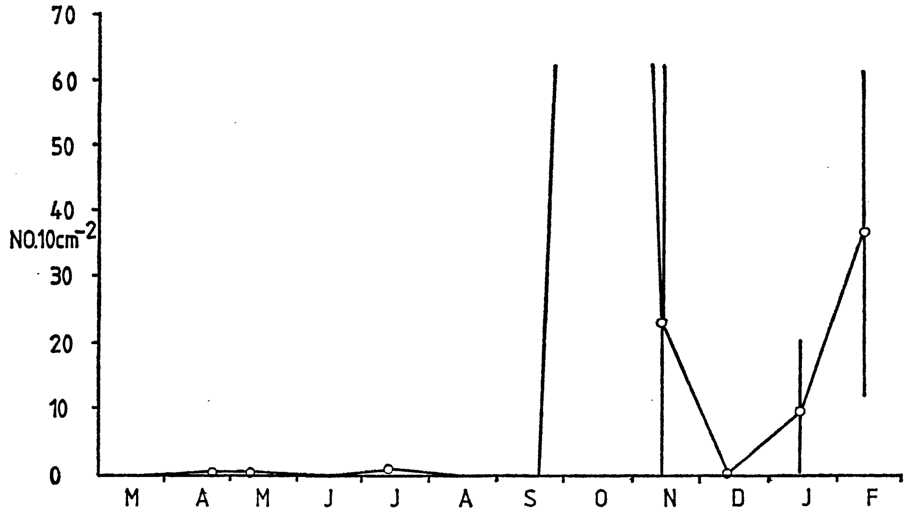

FIG. 18
The numbers of *Euplotes bathcatus* at Nicholaston.

TABLE 2

Family	Swansea Bay	Nicholaston 1	Nicholaston 2
Summary of families as a percentage of the total number of ciliates			
Colepidae	11.4	5.7	0.8
Trachelocercidae	32.9	20.4	2.8
Loxodidae	20.0	0.2	<0.1
Geleidae	9.0	0	0
Pleuronematidae	5.8	11.7	1.6
Condylostomatidae	<0.1	7.0	1.0
Euplotidae	4.9	21.7	89.1
	< <84.0%	66.7%	95.3%
Summary of species as a percentage of the total No. of ciliates			
Coleps pulcher	2.6	0.4	0.1
C. similis	8.8	5.3	0.7
Litonotus anguilla	0	0.9	0.1
Tracheloraphis teissieri	5.3	0	0
T. hamatus	14.7	1.4	0.2
T. ditis & T. conformis	10.8	13.3	1.8
Trachelonema oligostriata	0.3	0.3	<0.1
Remanella multinucleata	0.1	0	0
Ciliofaurea mirabalis	0.3	0	0
Chilodontopsis vorax	<0.1	3.2	0.4
Peritromus faurei	0.3	0.9	0.1
Euplotes balteatus	4.9	19.9	88.8
	< <47.7%	45.6%	92.2%

Columns 1 and 2 of the Nicholaston values refer to the inclusion of core 1 of 17.10.79.

FAMILY CONDYLOSTOMATIDAE

This family comprises the genus *Condylostoma* for the purposes of this survey. At Swansea Bay, they account for fewer than 0.1 p. 100 of the total ciliate population, a range of values between zero and $2.0 \times 10^3 m^{-2}$ with a mean value of $1.9 \times 10^2 m^{-2}$. They were present in only six months of the sampling period and then consisted of few animals.

At Nicholaston, the Condylostomatidae account for 7.0 p. 100 (or 1.0 p. 100) of the total number of ciliates. The range of values was between zero and $2.56 \times 10^4 m^{-2}$ with a mean value for the survey of $2.23 \times 10^3 m^{-2}$. They do not correlate with temperature for numbers, mean population depth or percentage occurring in the top 2cm.

FAMILY PERITROMIDAE

Other species besides *Peritromus faurei* Kahl, 1932 occurred during the survey but only as individuals.

PERITROMUS FAUREI Kahl, 1932

This species accounts for 0.3 p. 100 of the ciliates of Swansea Bay being found in low numbers during three months of the sampling period. At Nicholaston it accounts for 0.9 p. 100 (or 0.1 p. 100), again occurring in only three months of the sampling period.

FAMILY EUPLOTIDAE

This family consists of the genera: *Euplotes, Diophrys, Discocephalus* and *Uronychia*. Of these, *Euplotes* is the most important and accounts for over 99 p. 100 at Swansea Bay and 90 p. 100 at Nicholaston.

EUPLOTES BALTEATUS (Dujardin, 1841)

The genus *Euplotes* was on occasion so numerous that they were counted using a Sedgwick-Rafter counting chamber. At Swansea Bay, this species accounted for 4.9 p. 100 of the total number of ciliates encountered and occurred in six months of the sampling period, becoming particularly abundant in the latter part of this period. At Nicholaston, it accounted for 19.9 p. 100 (or 88.8 p. 100) of the total ciliate population. It occurred in eight months of the period but showed no correlation with temperature (Fig. 18). The mean population depth does not correlate with temperature but the proportion of the population occurring in the surface layers does ($r = 0.852$, 4 d.f., 5 p. 100).

For a summary of the families and species as a percentage of the total number of ciliates see Table 2.

DISCUSSION

Since Fauré-Fremiet (1950, 1951, 1958) first based an ecological classification of benthis interstitial ciliates on their occurrence in beaches of particular grain size it has been possible to place some ciliates in more than one of the three categories Microporal, Mesoporal or Euryporal (Hartwig 1973). Fauré-Fremiet (*loc. cit.*) considered that the species typical of the microporal group are characterised by a long and flattened shape, thigmotactic behaviour, elongate caudal regions, a creeping or jerky movement and by being generally fragile. Mesoporal species are found in coarser sand and the Euryporal species may be found in either Micro- or Mesoporal sands.

The shores at Swansea Bay and Nicholaston are both within the range described for microporal (between 0.4 and 0.12mm) and therefore might be expected to support a similar ciliate fauna when, in fact, not only do they have a different fauna but also a different ecology. This difference in ecology is explicable by a consideration of the relative exposure of the two shores.

The two sampling sites are characterised by a moderately sorted sediment with a nearly symmetrical distribution and no excess of coarse or fine grades. The Swansea Bay sediments are leptokurtic: that is, the central region is better sorted than the 'tails', which suggests that the sediment is tending to become bimodal (Folk and Ward 1957). The Nicholaston sediments are mesokurtic: that is, the central region is as well sorted as the 'tails' and they are thus unimodal. The percentage of fines ($<63\mu m$) is greater at Swansea Bay than at Nicholaston. This, along with the larger mean grain size, suggests that a higher energy source prevails at Nicholaston.

Wind data supplied by the Meteorological Office, Bracknell, were taken at Mumbles Head (Swansea Bay), an exposed head-land lying between the two sites and thus broadly applicable to both of them. They indicate that winds blowing from 221°-280° (the prevalent direction) account for 34.4 p. 100 of all wind for the period 1969-1979. The two localities are affected by such winds to different degrees, the Nicholaston locality being afforded the least shelter by headlands. This is reflected in the slightly larger grain size, lower fines content and steeper beach slope at Nicholaston.

Burkovsky (1971) considered that the ciliates which tend to dominate exposed beaches are protected by well developed penicular and fibrillar skeletal structures. Hartwig and Parker (1977) believed that those species with a short body and a more compressed or rounded shape are more resistant to exposure. Similarly, the ciliates of depositing shores (characterised by fine sediments) make up a fauna which is equivalent to the microporal group of Fauré-Fremiet (*loc. sit.*) in their morphology as typified by such species as *Trachelo-raphis prenanti* f. *oligocineata* Raikov and Kovaljeva, 1968, *Pseudo-*

prorodon arenicola Kahl, 1933, *Condylostoma remanei* Spiegel, 1928, *C. fjeldi* (Hartwig and Parker, 1977).

Hartwig (1973), when studying the ciliate fauna of the Island of Sylt (North Sea), made a distinction between ecological groups of ciliates based not only on the grain size of sediments but also on beach position. On a typical medium wave beaten beach the shore could be divided into the sand flat, which is almost fully saturated, a region between the sand flat and beach slope at the landward part of the beach, and the beach slope which is saturated only immediately shorewards of a rising and falling tide. Each of these regions has a typical fauna, a larger number of species being found in the sand flat than in the beach slope. When comparing beaches of different exposure, Hartwig observed that both highly exposed and sheltered shores had fewer species than a shore of medium exposure.

The two shores in this survey differ in exposure, Nicholaston being more exposed than Swansea Bay. As a result of this exposure, the beach slope is steeper at Nicholaston and so the water table is at the surface only immediately landwards of a rising and falling tide; at Swansea Bay, the beach slope is gentle and the water table is always at the surface. The movement of the water table at Nicholaston produces variable ecological gradients during a tide.

This difference in stability of gradients results in the markedly different ecology of the two ciliate populations. At the Swansea Bay locality, the total ciliate population is dependent on temperature, reaching a maximum in the warmer months, whilst at Nicholaston the numbers are independent of air temperature. This can be explained by the lack of buffering of temperature variations due to the absence of a water table. In considering the families and species regarded as ecological groups at Nicholaston, none show a significant relationship between numbers and temperature. At Swansea Bay, several groups show a significant relationship with temperature: Trachelocercidae, Colepidae, *Coleps similis* and *Tracheloraphis ditis* and *T. conformis*. The Condylostomatidae and Euplotidae are independent of temperature in as far as they occurred at irregular intervals throughout the sampling period. A third category includes those groups which occurred throughout the sampling period but are not significantly related to temperature: Loxodidae, Geleidae, Pleuronematidae, *Tracheloraphis teissieri, T. hamatus, Trachelonema oligostriata* and *Coleps pulcher;* of these, the Loxodidae showed a significant increase with time.

As part of the study, the organic carbon content was measured (using the titration method of Gaudette *et al.*, 1974) and, for an eight month period, the numbers of motile diatoms and flagellates extracted by Uhlig sea-water ice technique (Uhlig, 1968) were recorded. Neither of these groups of data significantly correlated with temperature at either Swansea Bay or Nicholaston; however, flagellate numbers did show a significant decrease over the time during which they were sampled. Dale (1974) found a significant correlation between bacterial numbers, as revealed by acradine orange staining, and the amounts of organic carbon and nitrogen when grain size was the controlled parameter in a partial correlation analysis. Therefore, the organic carbon content is a measure of the numbers of bacteria present. Bacteria are a major constituent of the diet of many ciliates (Fenchel 1968, 1969) and, if it is assumed that their division rate is dependent on temperature, then the relative accuracy of the titration method for the given range of organic carbon contents is called into question.

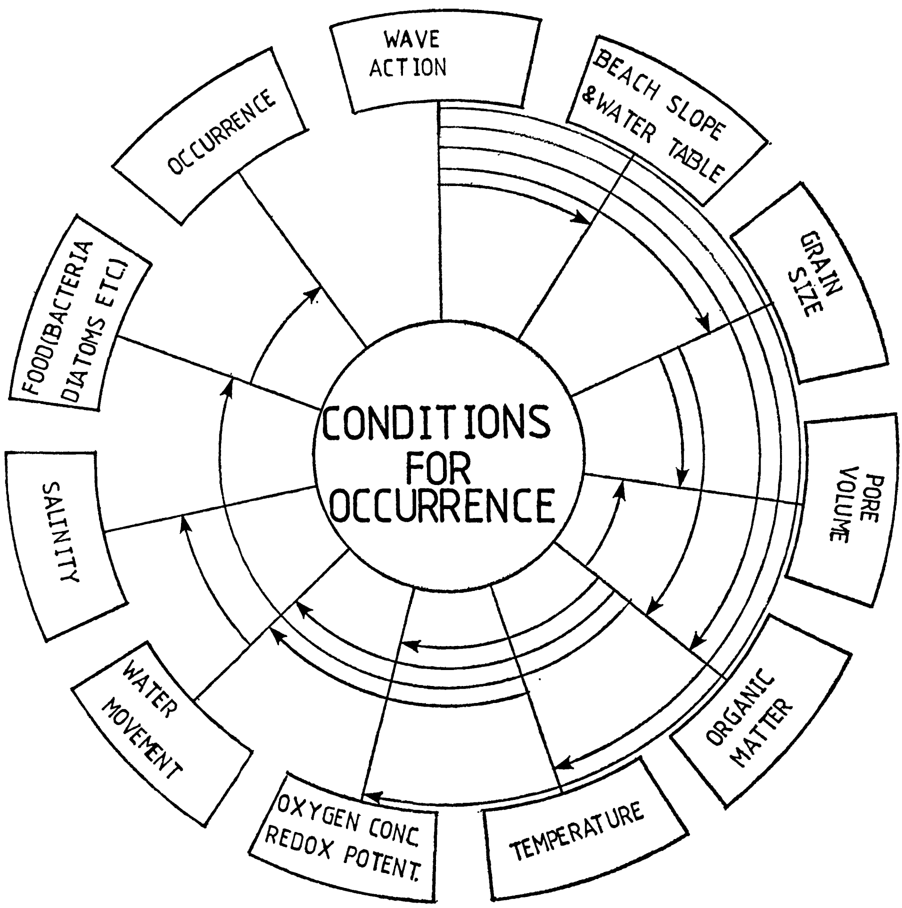

FIG. 19
The interrelationships of various factors affecting the conditions suitable for occurrence of ciliates.

The groups of ciliates which depend on temperature are presumably utilising food organisms which also depend on temperature and are therefore seasonal, whilst the second group of ciliates are able to utilise intermittent food supplies. The third group, of which the Loxodidae show a significant temporal variation and the Geleidae a pronounced temporal trend, tend to produce maxima in spring and autumn: Pleuronematidae, *Coleps pulcher, Tracheloraphis hamatus* (with a third peak in February 1980) and *T. teissieri* with a peak in spring and a second peak in December, *Trachelonema oligastriata* has a single peak in June. Burkovsky (1979) studied a seasonal succession of ciliates and found that during the warmer months, larger omnivorous ciliates produce large populations although the diversity is reduced. The first stages of the succession are characterised by the frequent change in dominating species related to a corresponding change in environmental conditions. The varying dominance of the third category of ciliates observed at Swansea Bay may well be following a succession; however, the sampling interval is large and not suitable for the definition of any succession at Swansea Bay.

At Swansea Bay, in addition to the relationship between numbers and temperature for certain groups, it has been shown for most groups that there is a significant temperature-related migration towards the surface during the warmer months, whilst at Nicholaston there are no groups that show this migration. Similarly, at Swansea Bay most groups show a significant migration into the top 2cm of sediment whilst at Nicholaston only *Euplotes balteatus* shows this movement. The observed migrations at Swansea Bay are related to corresponding changes in environmental factors as typified by the R.P.D., which has been shown to move up or down (Fenchel 1971, Ott and Machan 1971).

Hartwig, considering many of the factors upon which the abundance of a ciliate population depends, produced a scheme based on Burkovsky (1971) in which the effect of wave action and therefore exposure is given prime importance. The energy input to a site, in the form of wave action, affects grain size and therefore pore volume, organic matter content, bacterial numbers and chemical or physico-chemical parameters such as redox potential and pH. Many of these factors are inter-related, depending on temperatures and ultimately the presence or absence of th water table (Fig. 19 after Burkovsky 1971 and Hartwig 1973).

Summary

The number and distribution psammobiotic ciliates occurring on two sandy shores in South Wales is described. The variation in numbers and species shows considerable differences between the two shores. The Swansea Bay populations show a temperature related increase whilst those ciliates occurring at Nicholaston seem to be independent of temperature. This difference in population dynamics is ascribed to differences in exposure to wave action.

REFERENCES

BROTSKAJA, W.A., 1951. — The littoral micro-benthos of the White Sea. *Trudy Vsesoyuznogo gidrobiologicheskogo obshchestva*. 3, *pp.* 179-193. (en Russe).

BRUCE, J.R., 1928. — Physical factors on the sandy beach. Part I. Tidal, climatic and edaphic. *J. mar. biol. Ass. U.K.*, 15, *pp.* 535-552.

BURKOVSKY, I.V., 1968. — Quantitative data on the vertical distribution of psammophilic infusoria in the Velikaya Salma (Kandalaksha Bay, the White Sea). *Zoolog. Zhurnal*, 47, *pp.* 1407-1410. (en Russe).

BURKOVSKY, I.V., 1970. — The ciliates of the mesopsammon of the Kandalaksha Gulf (White Sea). I. Acta Protozool., 7, *pp.* 475-489. (en Russe).

BURKOVSKY, I.V., 1971. — Ecology of psammophilous ciliates in the White Sea. *Zool. Zhurnal,* 50, *pp.* ELFT-EAQL. (en Russe).

BURKOVSKY, I.V., 1979. — Seasonal and primary successions in marine psammophilous ciliates. *Zoolog. Zhurnal,* 58, *pp.* 469-476. (en Russe).

DALE, N.G., 1974. — Bacteria in intertidal sediments: factors related to their distribution. *Limnol. Oceanogr.,* 19, *pp.* 509-518.

DRAGESCO, J., 1954. — Diagnoses préliminaires de quelques ciliés psammophiles nouveaux. *Bull. Soc. zool. Fr.,* Ser. V, 79, *pp.* 57-62.

DRAGESCO, J., 1960. — Ciliés mésopsammiques littoraux. *Trav. St. biol. Roscoff,* N.S. 12, *pp.* 1-356.

DUJARDIN, F., 1841. — Histoire naturelle des Zoophytes. Infusoires, *pp.* 1-678, Paris.

FAURÉ-FREMIET, E., 1950. — Ecologie des cités psammophiles littoraux. Bull. Biol. France-Belgique, 84, *pp.* 35-75.

FAURÉ-FREMIET, E., 1951. — The marine sand dwelling ciliates of Cape Cod. Biol. Bull., 100, *pp.* 59-70.

FAURÉ-FREMIET, E., 1958. — Le cilié *Condylostoma tenuis* n. sp. et son algue symbionte. Hydrobiol., 10, *pp.* 43-48.

FENCHEL, T., 1968. — The ecology of marine microbenthos. II. The food of marine benthic ciliates. Ophelia, 5, *pp.* 73-121.

FENCHEL, T., 1969. — The ecology of marine microbenthos. IV. Structure and function of the benthic ecosystem, its chemical and physical factors and the microfauna communities with special reference to the ciliated Protozoa. Ophelia, 6, *pp.* 1-182.

FENCHEL, T., 1971. — The reduction-oxidation properties of marine sediments and the vertical distribution of the microfauna. *Vie, Milieu* 22, *pp.* 509-521.

FENCHEL, T. and RIEDL, R.J., 1970. — The Sulfide System: a new biotic community underneath the oxidised layer of marine sand bottoms. *Mar. Biol.,* 7, *pp.* 255-268.

FOLK, R.L., 1954. — The distinction between grain size and mineral composition in sedimentary rock nomenclature. *J. Geol.,* 62, *pp.* 345-351.

FOLK, R.L. and WARD, W., 1957. — Brazos river bar: a study in the significance of grain size parameters. *J. sed. Geol.,* 27, *pp.* 3-26.

GAUDETTE, H.E., FLIGHT, W.R., TONER, L. and FOLGER, D.W., 1974. — An inexpensive titration method for the determination of organic carbon in recent sediments. *J. sed. Geol.,* 44, *pp.* 249-253.

HARTWIG, E., 1973. — Die Ciliaten des gezeitensandstrandes der Nordseeinsel Sylt. II. Ökologie. *Mikrofauna Meeresboden,* 21, *pp.* 1-171.

HARTWIG, E., GLUTH, G. and WIESSER, W., 1977. — Investigations on the ecophysiology of *Geleia nigriceps* Kahl (Ciliophora, Gymnostomata) inhabiting a sandy beach in Bermuda. *Œcologia* (Berl.), 31, *pp.* 159-175.

HARTWIG, E. and PARKER, J.G., 1977. — On the systematics and ecology of interstitial ciliates of sandy beaches in North Yorkshire. *J. mar. biol. Ass. U.K.,* 57, *pp.* 735-760.

KAHL, A., 1930-1935. — Urtiere oder Protozoa I: Winpertiere oder Ciliata (Infusoria), eine Bearbeitung der freilebenden und ectocommensalen Infusoria der Erde, unter Ausschluss der marinen Tintinnidae. *In:* Die Tierwelt Deutschlands un der ungrenzenden Meeresteik (ed. F. von Dahl), *pp.* 1-884, Jena: Gustav Fischer.

LACKEY, J.P. and LACKEY, E.W., 1963. — Microscopic algae and protozoa in the waters near Plymouth in August 1962. *J. mar. biol. Ass. U.K.,* 43, *pp.* 797-805.

MAGHRABY, A.M., EL, and PERKINS, E.J., 1956. — Additions to the marine fauna of Whitstable. *Ann. mag. nat. Hist.,* 9, *pp.* 481-496.

OTT, J.A. and MACHAN, R., 1971. — Dynamics of parameters in intertidal sediments. *Thalassa Jugoslavica,* 7 (1), *pp.* 219-229.

RAIKOV, I.B., 1962. — Les ciliés mésopsammiques du littoral de la Mer Blanche (U.R.S.S.) avec une description de quelques espèces nouvelles ou peu connues. *Cah. Mar. Biol.,* 3, *pp.* 325-361.

RAIKOV, I.B. and KOVALJEVA, V.G., 1968. — Complements to the fauna of psammobiotic ciliates of the Japan Sea (Posjet Gulf). *Acta Protozool.* 6, *pp.* 309-333.

SALVAT, B., 1966. — *Eurydice pulchra* Leach, 1815 et *Eurydice affinis* Hansen, 1905 (Isopodes, Cirolanidae). Taxonomie, éthologie, écologie répartition verticale et cycle reproducteur. *Acta Soc. Linn. Bordeaux,* Série A, 103, *pp.* 1-77.

SALVAT, B., 1967. — La macrofaune carcinologique endogée des sédiments meubles intertidaux (Tanaidacés, Isopodes et Amphipodes), éthologie, bionomie et cycle biologique. *Mém. Mus. natn Hist. nat.,* Paris, ser. A, *Zoologie,* 45, *pp.* 1-275.

SPIEGEL, A., 1926. — Einige neue marine ciliaten. *Arch. Protistenk.* 55, *pp.* 184-190.

STOKES, A.C., 1894. — Notices of presumably undescribed infusoria. *Proc. Amer. phil. Soc.,* 33, *pp.* 338-345.

UHLIG, G., 1968. —Quantitative methods in the study of the interstitial fauna. *Trans Amer. micros. Soc.,* 87, *pp.* 226-232.

WEBB, J.E., 1958. — The ecology of Lagos Lagoon V. Some physical properties of Lagoon deposits. *Phil. Trans. Roy. Soc.,* Series B, 241, *pp.* 393-419.

WRIGHT, J.M., 1982. — Some sand dwelling ciliates of South-Wales. *Cah. Biol. Mar.,* 23, *pp.* 275-285.