SOME ASPECTS OF THE PRODUCTIVITY OF LAKE GRASSMERE, MARLBOROUGH, NEW ZEALAND AND ITS POSSIBLE UTILISATION

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A B S T R A C T

The growth of *Artemia salina* Branchiopoda, Anostraca in the concentrating ponds of a solar salt extraction plant was investigated during 1972/73. The aim of the study was to assess the possibility of harvesting the *Artemia* production of the ponds. A pronounced seasonal fluctuation in *Artemia* density in ponds with over 20 000/m^3 at the highest had a spring maximum and a late summer minimum. The spring upsurge was found to come from overwintering eggs and a small reservoir of overwintering adults. The proportion of females carrying eggs ranged from 98% in spring down to 2% in winter but the number of eggs produced per female showed a highly significant variation with salinity (over a 30 day period 231 eggs at 100 ppt and 89 eggs at 250 ppt). By counting the number of eggs present in mature females a sharp drop was shown to occur at salinities above 200 ppt. Hatching times and the percentage of eggs laid that do hatch were shown to be greatly influenced by salinity and temperature. At 26°C hatching times at 30 ppt salinity and 240 ppt were 2 and 5 days respectively. However, at 240 ppt less than 5% hatched. In contrast, at 7°C hatching times at 30 ppt and 150 ppt (max. at which eggs hatched) were 8 and 22 days respectively. It was concluded that increasing temperature reduced the inhibitory effect of high salinity.

Laboratory experiments showed that longevity of *Artemia* was greatest at 17°C and decreased at 7°C and 26°C but life and fertility tables constructed from the data showed a much higher fertility rate at 26°C than 17°C (rc = 0.305 and 0.207 respectively) and it was considered that the increased fecundity

at 26°C outweighed the shorter life span when considering production of Artemia.

Feeding trials using the unicellular flagellate alga Dunaliella euchlora showed that in a suspension of 4000 cells/ml adult Artemia assimilated 57% of ingested algae but as the density of algae was increased to 10 000/ml the efficiency of assimilation fell to 42%. Similar trials with juveniles (2 - 4 mm) showed a lower efficiency (54%) at 4000 cells/ml but higher (47%) at 10 000 cells/ml.

Lipid content of Artemia ranged from 18.3% during the spring algal peak down to 11% in autumn. Both swimming rate and feeding efficiency were found to be significantly affected by increasing viscosity as brine concentration increased. The swimming effort was found to increase by 33.7% between 60 ppt salinity and 300 ppt. A highly significant decrease in food uptake was found over the same salinities with consumption of algal cells in laboratory experiments falling from 26.2% of that available to 21.6%. The combination of increased effort and reduced food intake was considered to be partially responsible for the reduced vigour of Artemia populations at high salinities.

Experimental laboratory populations of Artemia reacted strongly when the algal growth rate in the culture was stimulated by fertilising and the addition of dried yeast. Stable populations of the equivalent of 860 000/m^3 were produced in the laboratory. These were easily maintained and showed no evidence of metabolite poisoning or lack of oxygen.

Production of the Artemia in the ponds showed that the maximum was reached in a pond with an annual range of salinity from 111 ppt to 188 ppt (winter and summer respectively) and

decreased in other ponds of higher average values. Mean daily production for the 14 month sampling period was 0.411 (g/m^3)/day with a range of from 1.53 (g/m^3)/day in spring to 0.006 (g/m^3)/day in autumn. Equivalent values for the most aline pond in the series were 0.049 (g/m^3)/day, 0.24 (g/m^3)/day and 0.003 (g/m^3)/day respectively. The very large ranges of salinity, caused by saltworks production methods, were considered to be very detrimental to efficient harvesting where a continuous production of Artemia may be needed.

The study of the Artemia production was supported by determination of water chemistry in the ponds and algal production over the study period. Nutrients selected for analyses were reactive nitrate, reactive silicate and orthophosphate. Nitrate levels ranged from 0.43 g/m^3 to 0.07 g/m^3 with a winter peak followed by a sharp spring drop and a summer low point. A similar pattern was found for orthophosphate concentrations but with a much larger range from 0.619 g/m^3 in winter to trace amounts during summer. Silicate levels varied directly with salinity and no evidence of high biological consumption was found.

The sediment of ponds at salinities over 150 ppt was cemented by precipitated calcium sulphate preventing development of turbidity even with strong wave action. Ph of the ponds varied between 8.0 and 8.5 but the onset of high spring algal growth was accompanied by a drop in pH that could not be readily explained. It may be due to strong bacterial growth.

The algae were dominated by two species, Dunaliella euchlora and D. salina. D. salina was confined to brines that were almost saturated but D. euchlora grew throughout the

series. Production of algae was estimated from laboratory incubator experiments. These suggested that primary production would be highest in salinities between 100 and 200 ppt. Growth trials of algae in artificial media showed that levels of reactive phosphate below 0.01 g/m^3 imposed strong restrictions on growth.

An annual budget of energy loss and gain was set up taking into account primary and secondary production and losses caused by Artemia respiration, faeces and egg production. Overall, for the most productive pond an ecological efficiency for conversion of algal energy into Artemia biomass of 19.1% was found.

A brief review of species of commercially cultivated shrimp was given consistent with the long-term possibility of using the Artemia production as a food, or food supplement, for growing shrimp.

Conclusions reached were that the crop of Artemia in the ponds, while they are being used to manufacture salt, is too sporadic to be easily harvested. The potential productivity in a carefully managed pond may be very high. Artemia can exist over a wide range of salinities but will perform well only within a restricted range.

INTRODUCTION

With the current worldwide emphasis on greater food production and more efficient use of existing productive environments, attention is being paid to the possibility of aquaculture, i.e. the controlled exploitation of water bodies (Doumenge 1972, Forster and Wickens 1972, Hudinaga 1969, Ritchie 1974, Swingle 1973, Tatum 1973).

The hypersaline environment, i.e. water with a salinity in excess of that of seawater, has been shown to be very fertile in some cases, supporting flora and fauna well adapted to surviving osmotic extremes (Artom 1905, Bayly 1967, Blanchard 1891, Edmondson 1969, Fisher 1902, Gilbert 1890, Heldt 1926, Jordan 1889, Kulkarni 1953, Rammner 1933, Relyea 1937).

In New Zealand saline ponds are very uncommon but Bayly (1967) has investigated two lakes with salinities of 6 ppt and 15 ppt. These ponds supported a restricted fauna including rotifers ostracods, copepods and Diptera. The salinities, however, do not compare with those in the Grassmere concentrating ponds which range from a minimum of 100 ppt to 312 ppt. Bayly (1972) distinguishes between land originating hypersaline waters and marine originating and divides the fauna present into "conformers that vary their body fluids to accommodate osmotic stress, and "regulators" that have positive mechanisms for maintaining their internal fluid balance against stress. Artemia salina falls into the latter group. Bayly recognises 100 ppt as a pond where the number of species present falls drastically and on the upper limit for most specialised insect groups, fish and higher Crustacea.

Lake Grassmere is located at 41° 44'S, 174° 10'E on the east coast of the South Island of New Zealand. It is a solar salt extraction plant formed from a lake bed and is divided into a series of ponds through which sea water flows and is evaporated (Insull 1948, Reid 1960). The brine supports obvious blooms of algae and vast numbers of the brine shrimp, Artemia salina. The blooms of algae are of two colours, red and green, and are found in high and low salinity brines respectively. Dense populations of Artemia feed on these algae and it has been suggested that they could be harvested as a crop (F. Doumenge, pers. comm.).

However, since Artemia is not itself an attractive product for human consumption, it has been suggested further that it could be fed to an edible marine species such as an edible shrimp, (I. Mannering, pers. comm., Fujinaga 1963). Another possibility would be the harvesting of resistant Artemia eggs for use as a tropical fish food. These should find a ready market in New Zealand as at present out total supply of Artemia eggs comes from Great Salt Lake, Utah, in the United States of America, (acquarium supplies retailers, pers. comm.).

To feed an edible shrimp population entirely on Artemia would require an enormous supply of Artemia. It probably would not be feasible to do this but Artemia could be used as part of a compounded diet containing such materials as casein, soy protein, collagen, sodium glutamate, yeast, inorganic mineral mixes, coarse fish meal and vitamin supplements (Broom 1969, Fujinaga 1963, Kanazawa, Shimaya, Kawasaki and Kashiwada 1970, Kanazawa, Tanaka, Techima and Kashiwada 1971, Sick, Andrew and White 1972, Wheeler 1967). The use of 40% - 60% Artemia in a blended food would greatly simplify the problems

of supplying micronutrients and vitamins to the shrimps that may otherwise be missing or in short supply in a purely artificial diet (Balazs, Ross and Brooks 1973).

Before any harvesting of Artemia in Lake Grassmere can be contemplated the levels of primary and secondary productivity of the ponds needs to be known and the annual range and times of maximum and minimum production determined. This is necessary information if Artemia is going to be used to feed a continually growing secondary consumer, e.g. cultivated shrimp.

The principal aim of the present study was to estimate the productivity of Artemia in the ponds and this has been supported by laboratory experiments on algal growth and an investigation of seasonal and interpond variations in selected pond nutrients.

The lake studies I carried out were divided into four phases. The first was concerned with monitoring physical factors likely to influence the flora and fauna of the lake waters. These included light, temperature, turbulence and sediment characteristics. The second phase was an investigation of the algae present, including measurement of seasonal changes in their densities. Since the ponds varied greatly and plant nutrient levels, laboratory experiments were performed to determine the conditions under which growth of algae was most vigorous. The main emphasis was contained in the third phase which was the study of Artemia population dynamics and production. As with the algal populations, knowledge of the limiting effects of physical conditions was obtained through laboratory experiments carried out at various salinity and food levels. In particular the effects of salinity and temperature acting together on breeding and egg hatching were

investigated. The overall productivity of the ponds has been summed up in the fourth phase of the thesis in which an energy budget has been compiled for each pond. The energy budget shows seasonal changes in production of both algae and Artemia as well as losses sustained on the conversion of algae energy to Artemia biomass available for harvest. The relative productivities of the ponds, covering a large salinity range should also provide a basis for making future decisions as to whether it is economically feasible to attempt to harvest Artemia from the ponds whose salinity is continually being raised due to evaporation during the salt making process. These ponds were also subject to intermittant pumping of water between the ponds which caused sudden changes in water characteristics.

Few salt lake ecosystems have been studies in detail, probably due mainly to difficulty of access to them since saline lakes often occur in arid desert regions where inland drainage and high evaporation combine to produce hypersaline conditions (Baid 1958, Goldman, Mason and Hobbie 1967, Hutchinson 1937, Meyer, Morrow, Wyss, Berg and Littlepage 1962, Rawson and Moore 1944). An exception is the lake described by Walker (1973) where the principal inflow of water was from subterranean seepage. Williams (1972) suggested that hypersaline lakes may provide ideal sites for carrying out production studies because they generally possess considerable habitat homogeneity and very low species diversity. Many studies of inland hypersaline lakes may not be readily compared to the Grassmere situation, since Lake Grassmere is evaporated seawater and as such has a different chemical complement to many inland lakes where local geological conditions produce waters rich in a few characteristic ions (Mason 1967, Walker 1973).

SECTION 1

THE PHYSICAL AND CHEMICAL ENVIRONMENT OF LAKE GRASSMERE

1.1 INTRODUCTION

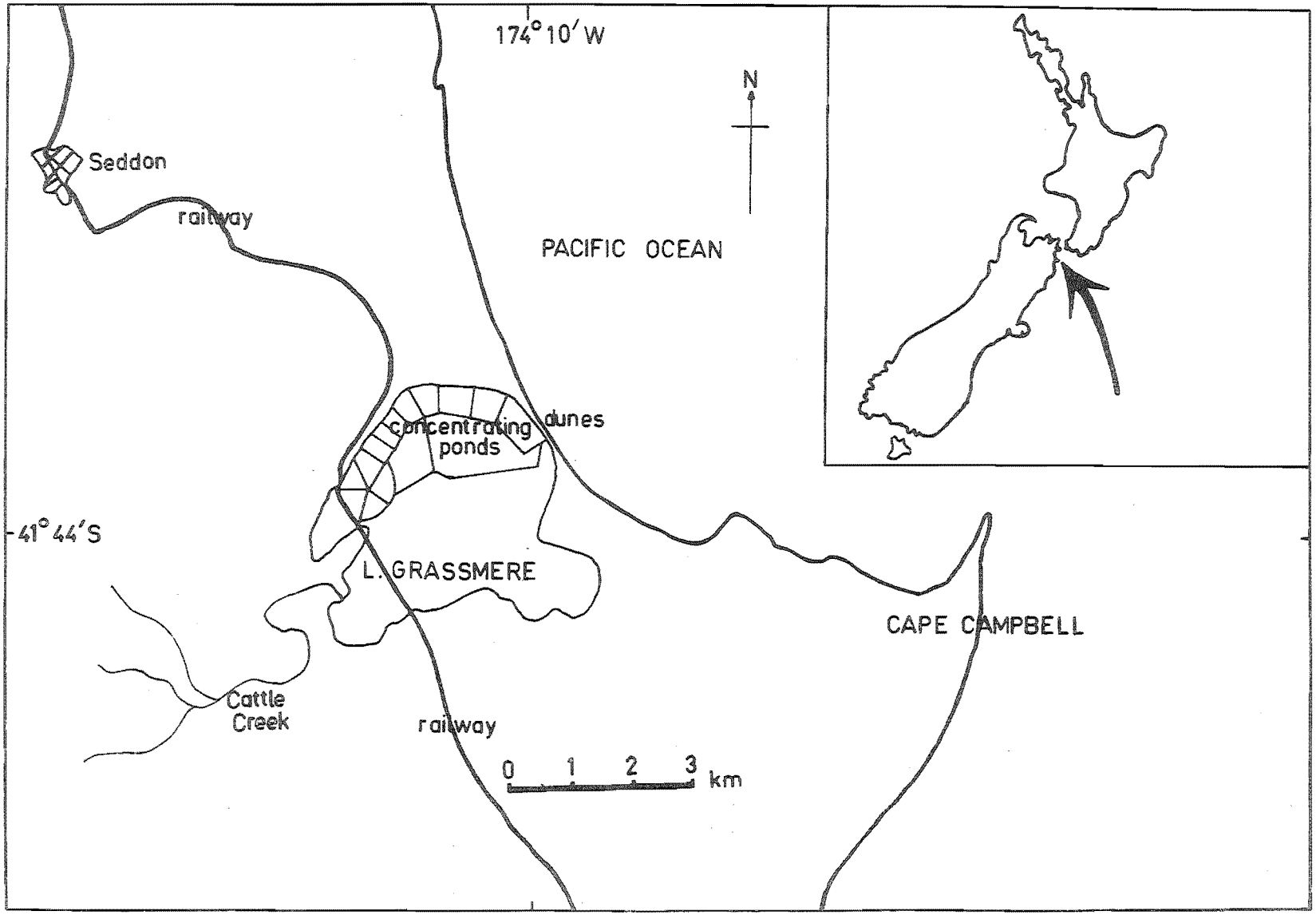
Lake Grassmere (41° 44'S, 174° 10'E) covers an area of 1782 ha. and is on the east coast of Marlborough, The South Island, New Zealand. It is a very shallow body of water, probably formerly a lagoon, separated from the Pacific Ocean by a bar of sand dunes about 100 m wide, (Fig. 1.1). To landward the lake is surrounded by rolling hills intensively grazed by sheep but with scrub-filled gulleys. The lake was originally fed by a small stream, Cattle Creek, of highly variable flow. Since the lake has been developed the stream has been diverted to avoid ponded areas. The region is sunny and windswept, due in part to its location at the base of Cape Campbell which projects out into the path of south westerly winds. Annual rainfall is low and evaporation very high aided by strong hot north-westerly winds that sweep the area during spring and summer.

It was for these reasons that the site was chosen for the establishment of a solar salt extraction industry. This process relies on the production of concentrated brine by evaporation of seawater through a series of shallow ponds. The final crystallisation of the sodium chloride fraction of the sea's chemical complement is performed in very shallow flat bottomed ponds that may be scraped by a mechanical harvester.

Worldwide, associated with brine pools, is found the Anostracan, Artemia salina and several characteristically hypersaline algae. Artemia is known to reproduce rapidly, withstand osmotic extremes, and be an extraordinarily useful

FIGURE 1.1

The location of Lake Grassmere relative to the rest of New Zealand


174° 10′ W
N
Seddon
railway
PACIFIC OCEAN
concentrating ponds
dunes
41° 44′ S
L. GRASSMERE
CAPE CAMPBELL
Cattle Creek
railway
0 1 2 3 km

food for other marine species, particularly the larval stages of other arthropods. This section is the first of five that investigate the lake with regard to the ecology, chemistry, flora and fauna, and energetics. The possibility of using the Artemia production will be discussed with reference to the results of these investigations.

The lake was visited during 1972 and 1973 on the following dates: 10 August 1972, 25 August 1972, 5 September 1972, 21 September 1972, 9 October 1972, 26 October 1972, 11 November 1972, 7 December 1972, 30 December 1972, 10 January 1973, 29 January 1973, 15 February 1973, 23 February 1973, 29 March 1973, 12 April 1973, 26 April 1973, 10 May 1973, 25 May 1973, 14 June 1973, 28 June 1973, 12 July 1973. 27 July 1973, 9 August 1973, 13 September 1973, 28 September 1973, 18 October 1973, 1 November 1973.

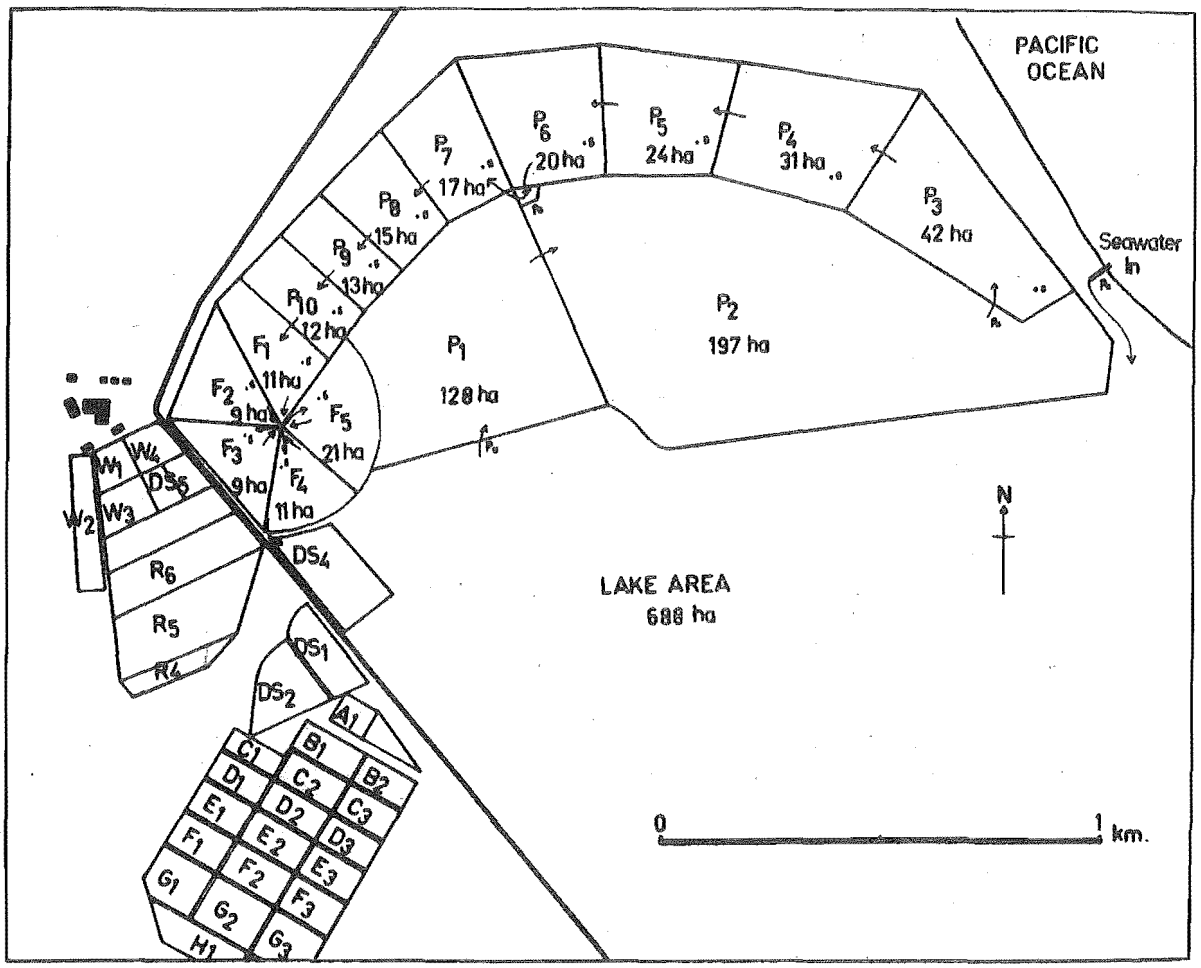
1.2 LAYOUT OF THE SALTWORKS

Approximately half of the total lake area has been subdivided into ponds by dykes of rubble and earth. The remaining half is unchanged and acts as a reservoir of water after it has been pumped in from the sea (Fig. 1.2). The main concentrating series is a chain of shallow ponds designated P1 to F5. Water flows by gravity from P1 to P6 and is then raised to P7 from where it again flows by gravity to F5. Ds_1 to Ds_5 are deeper ponds designed to store concentrated brine over winter by presenting a small surface area relative to the volume for minimum rain dilution. The depth of the concentrating ponds averages 0.75 m and that of the deep storage averages 4.6 m

The crystallising ponds are shown prefixed A to H in a large 91.1 ha. area. The ponds prefixed W are reservoirs

FIGURE 1.2

The layout of the ponds at Lake Grassmere


PACIFIC
OCEAN
P7
17 ha
P6
20 ha
P5
24 ha
P4
31 ha
P3
42 ha
P8
15 ha
P9
13 ha
P10
12 ha
F1
11 ha
F2
9 ha
F3
9 ha
F4
11 ha
F5
21 ha
P1
128 ha
P2
197 ha
Seawater
In
W1
W4
DS5
W2
W3
R6
R5
R4
DS4
DS1
DS2
A1
B1
B2
C1
C2
C3
D1
D2
D3
E1
E2
E3
F1
F2
F3
G1
G2
G3
H1
LAKE AREA
688 ha
N
0
1 km.

for wishing brine, a saturated brine used to free the harvested salt of dirt and plant particles without redissolving it. Ponds R1 - R6 are reconcentrating ponds. Buildings on the site are administration buildings, warehouses and a washing and bagging plant.

1.3 OPERATION OF THE PONDS

Seawater is pumped from the Pacific Ocean into the remaining unmodified lake bed where evaporation effects a pre-concentration. At intervals, but mainly early and late in the yearly cycle, brine from this area is pumped into P1 and P2 where further evaporation occurs. At a salinity of about 100 ppt water enters the main chain from P3 onward, again by being pumped, and progresses slowly towards the F series continually evaporating.

Early in the evaporating season, depending on the weather from October to November, concentrated brine is allowed to flow from deep storage back through the concentrating series to provide a boost in salinity for the coming season. Other deep storage water is run out into the crystallising ponds and evaporated until the sodium chloride portion of the mixture of salts in seawater has mostly crystallised out. Then the remaining solution, referred to as "bitterns", is disposed of into the sea.

Throughout the season there is a concentration gradient up the concentrating series with the most dilute being P1 and the strongest being the F series. The range is very variable depending on the intensity of evaporation and the entry of new water. During April and May when the autumn is setting in the crystallising ponds are harvested and the collected salt stacked on concrete slabs. This salt contains impurities

both inorganic and organic and has a pink appearance from the pigment of algae that florish in the final concentrating stages. Washing uses saturated brine that is recirculated from ponds that themselves show dense red algal blooms.

Over the season the colour of the ponds ranges from dark green to brilliant pink depending on the concentration at the time. Ponds P1 and P2 are almost always very muddy, and are frequently empty, but a crystalline crust ensures clarity in the rest of the ponds. For this reason, and the obvious vigour of the algal growth in P3 to F5, it was decided to restrict the physical and productivity measurements to ponds P3 to F5.

1.4 THE CLIMATE OF THE REGION

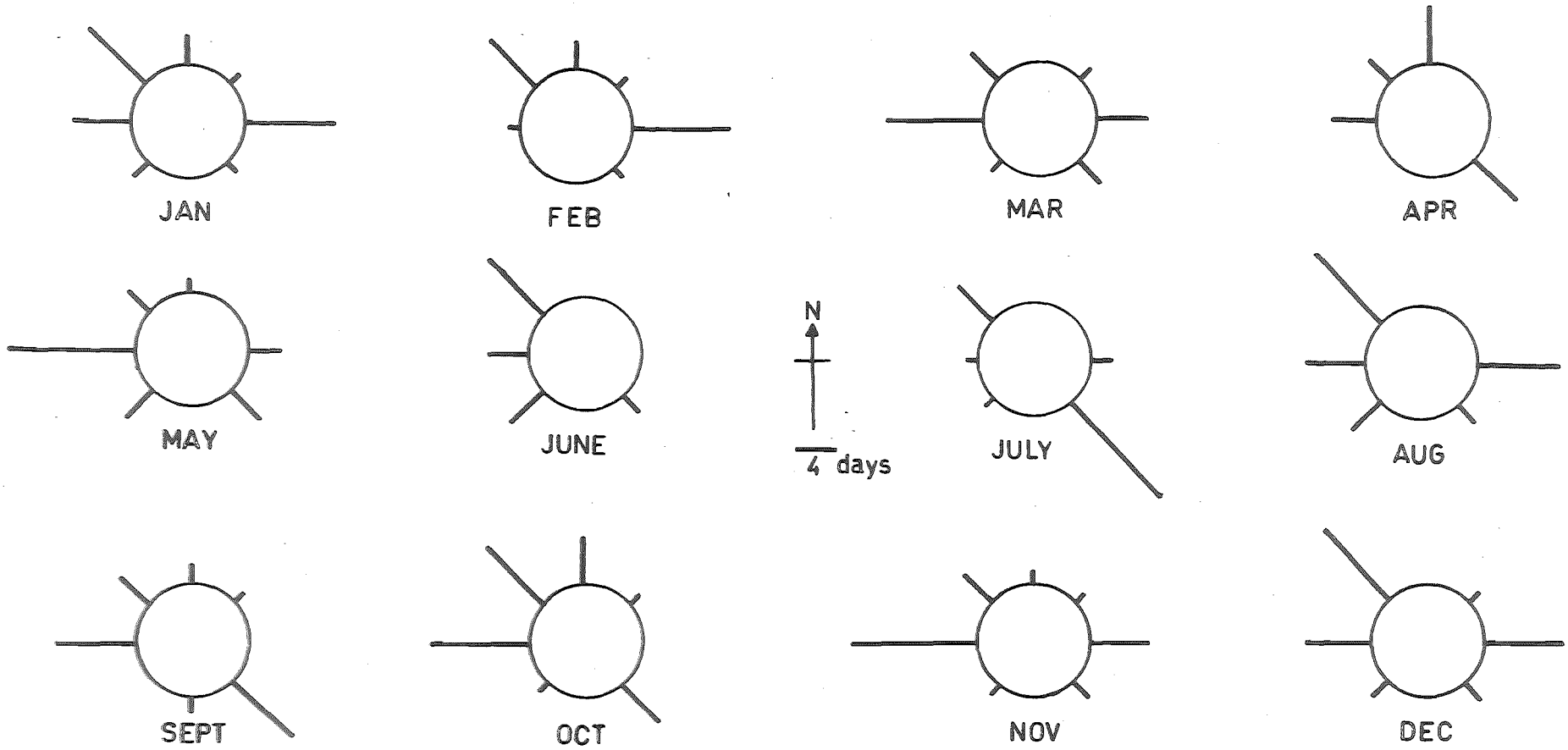
The climate of Lake Grassmere provides extremely good conditions for evaporation but the rate is dependent on the salinity becoming slower the higher the salinity. The importance of this to the concentrating ponds is that a fast rise in salinity occurs and the water warms in spring, and slower gains at the higher salinities occupy the bulk of the summer. In the following section all climatic data referred to were supplied by R. Butcher, Meteorlogical Observer, Lake Grassmere. This data is unpublished. Climatic records derived from the meteorological station at Lake Grassmere are presented for a year from November 1972 to October 1973.

(a) Wind

There are very few windless days at Grassmere during the summer but the proportion increased to about 25 percent over the winter months. During the summer months the main wind direction is west to north-west but with indications of an increasing easterly component in late summer, (Fig. 1.3.1).

FIGURE 1.3.1

Wind direction and frequencies at Lake Grassmere. The length of the line is proportional to the number of wind days recorded from each direction during 1972.


JAN
FEB
MAR
APR
MAY
JUNE
N
4 days
JULY
AUG
SEPT
OCT
NOV
DEC

Through autumn and into winter south-westerly and south-easterly directions became more predominant but northerly winds still occurred regularly. By the spring of 1973 the north to north-westerly component was again the dominant wind direction. Northerly gales of up to, and occasionally exceeding, Beaufort force 7, were regularly experienced over the summer.

(a) Evaporation

Evaporation was measured in a sunken pan for the same period and the results are displayed in Fig. 1.3.2. The loss of water is expressed as millimetres per month and is extremely high over the spring and summer seasons rising to 293 mm in January. From January to July a steady drop occurred until in July about 50 mm was lost. From this point, as spring advanced, the evaporation rate increased very rapidly reaching 200 mm per month in October. The heavy summer evaporation rates coincided with the abundant hot dry northerly winds and the rate decreased as easterlies and southerlies became more common.

(c) Precipitation

The rainfall over the period under consideration is shown in Fig. 1.3.3. At no time of the year does the precipitation per month exceed the evaporation and during mid-summer it lags far behind. During January at the peak of the evaporating season the rainfall for the month was 41.0 mm while the evaporation was 293 mm, a net loss of 252 mm for the month. Even in mid-winter the evaporation just exceeds the rainfall.

(d) Insolation

The Lake Grassmere has a high number of sunshine hours per year, as does the coastal strip north and south. For the

FIGURE 1.3.2

Evaporation measured in mm from a sunken pan evaporimeter

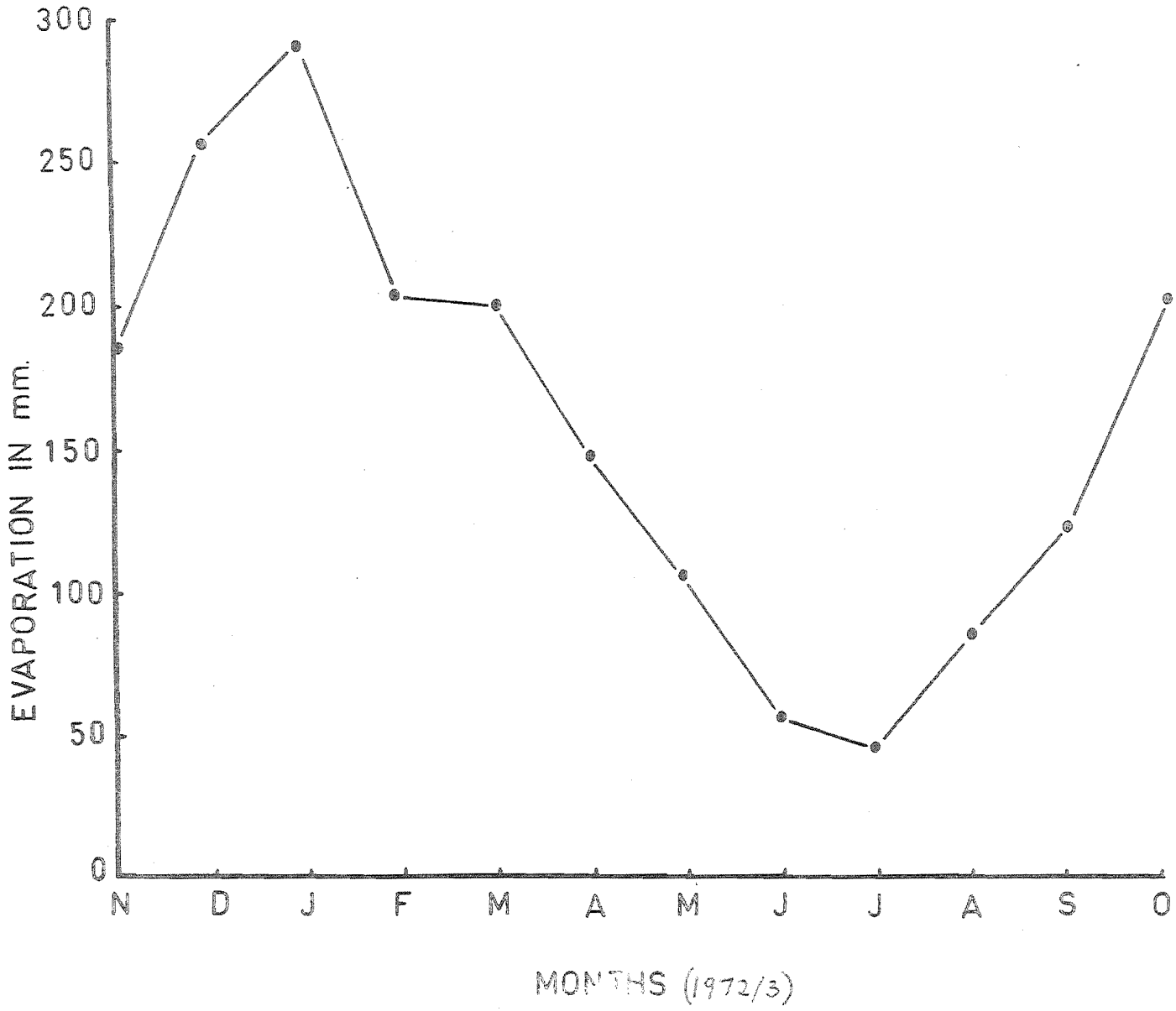
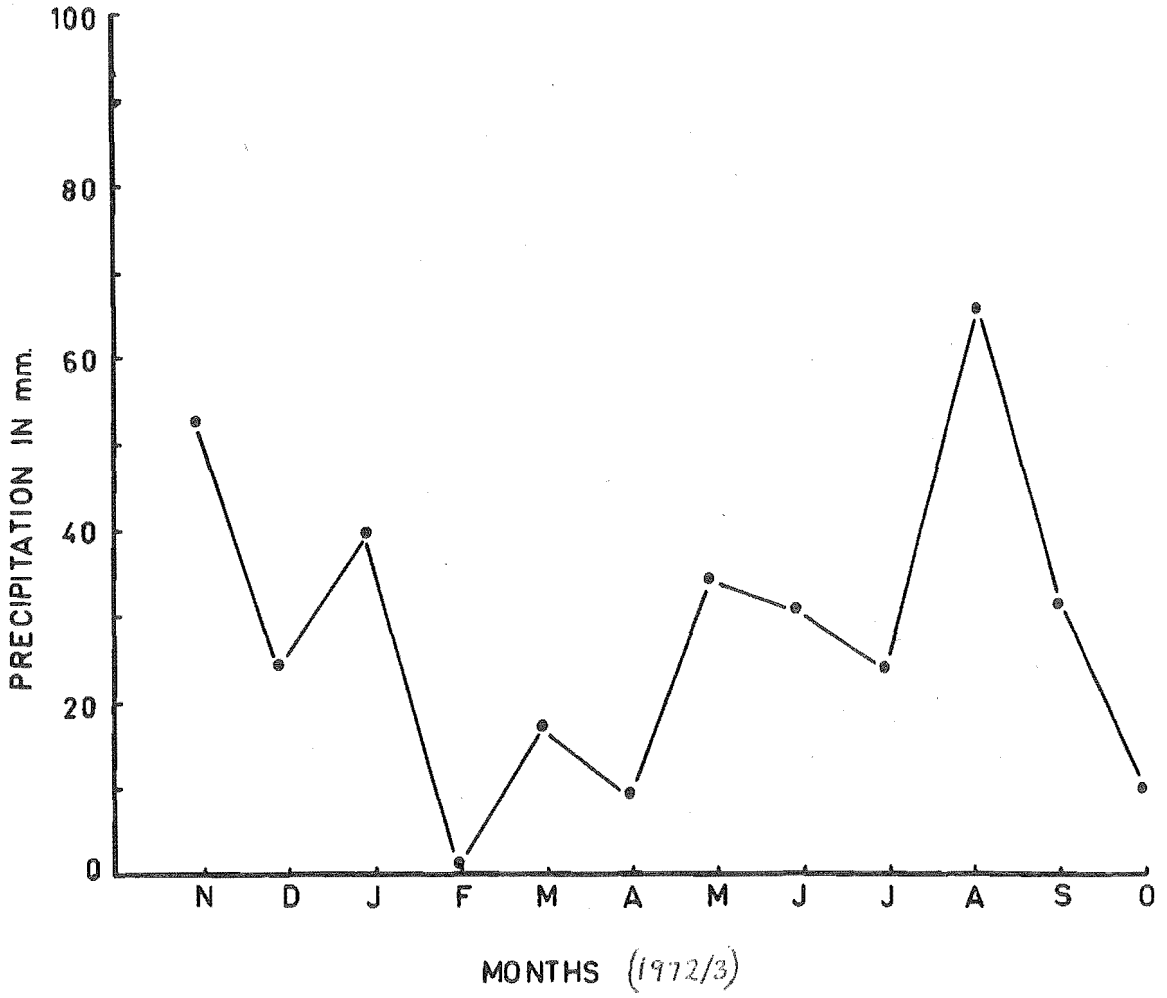

300
250
200
150
100
50
0
EVAPORATION IN mm.
N
D
J
F
M
A
M
J
J
A
S
O
MONTHS (1972/3)

FIGURE 1.3.3

Monthly rainfall recorded at the Lake Grassmere meteorological station


100
80
60
40
20
0
PRECIPITATION IN mm.
N
D
J
F
M
A
M
J
J
A
S
O
MONTHS (1972/3)

Total for Month (hours)		Mean per day (hours)	Energy equivalent (kJ/m^2)
Nov.	185	6.2	23.2×10^3
Dec.	241	7.8	23.0×10^3
Jan.	264	8.5	22.3×10^3
Feb.	259	9.2	21.1×10^3
Mar.	164	5.3	12.4×10^3
Apr.	161	5.4	10.5×10^3
May	146	4.7	7.0×10^3
June	139	4.6	5.2×10^3
July	169	5.5	6.4×10^3
Aug.	156	5.1	8.9×10^3
Sept.	172	5.7	12.6×10^3
Oct.	225	7.3	17.4×10^3
Total	2281		

Table 1.1 Insolation at Lake Grassmere from November, 1972, to October, 1973.

Data collected by N.Z. Meteorological Service, Kaikoura. Conversion from Langleys to kJ/m^2 used the factor, 1 calorie = 4.19 J.

period November 1972 to October 1973 the total was 2281. Table 1.1 shows the total for each month, the average number of hours per day for that month, and the energy equivalent of the radiation striking a flat surface. Equipment for this last parameter is not available at Grassmere and the values listed were obtained from Kaikoura, 70 km south of Grassmere. The number of sun hours recorded at the New Zealand Meteorological Service station in Kaikoura corresponded closely to that at Grassmere and it is considered that the associated energy input values are valid for Grassmere.

(e) Relative humidity

Lake Grassmere, on the east coast of New Zealand, is in a rain shadow brought about by the presence of the Southern Alps that interrupt the westerly wind flow and collect the contained moisture. The descending air on the easterly side of the Alps is compressionally heated and arrives at the coast as a warm, low humidity wind. Although the average relative humidity for the year was 72% readings of 30 - 40% relative humidity were regularly recorded during north-westerly winds. These low values of humidity enhance evaporation greatly and go a long way towards explaining the rates shown in Fig. 1.3.2.

1.5 SALINITY VARIATIONS

Extremely high intermolecular binding forces confers on water the very high coefficient of latent heat of evaporation of 2263 J/g at 100^{o}C. Water's closest molecular relative, hydrogen sulphide, H_2S, requires only 552 J/g at -61^{o}C. In addition to the great deal of thermal energy required to evaporate water, the addition of electrolyte

solutes decreases the partial pressure of water vapour above the solution in accordance with Raoult's law:

$$P = Po\ (1 - 0.000537\ S)$$

where Po is the vapour pressure of pure water and S is the salinity of the solution in parts per thousand, (Horne 1969).

METHOD

Salinity was measured with an Auto Lab model 601 extended range inductive salinometer from water collected and stored unfrozen in polythene

RESULTS

Table 1.2 shows the salinities in each of the concentrating ponds over the sampling period. At the beginning of the period the brines were relatively dilute after winter. By October the salinity was increasing and surpassing 200 ppt in the top half of the series. During December the highest salinities of the year were recorded, 312 ppt in F3 on 7 December 1972, and 301 ppt in F4 on 30 December 1972. In general, over the whole December/January period the salinity in the F series averaged just under 300 ppt. The rapid increase in salinity of the upper half of the concentrating series was aided by the management practice of running concentrated brine back through the series from the deep storage ponds when it had been retained over the winter.

The salinities in the lower half of the concentrating series showed a more steady increase with rather indistinct peaks at the 10 January 1973 sample and the 29 March 1973 sample.

By April 1973 the salinities in all of the ponds had begun to fall. This was encouraged by the withdrawal of brine from the F series for storage and crystallisation,

	P3	P4	P5	P6	P7	P8	P9	P10	F1	F2	F3	F4	F5
10/8/72	109	113	113	116	118	124	132	140	148	156	158	152	161
25/8/72	110	111	117	119	125	131	136	143	154	160	171	169	167
5/9/72	108	112	117	117	122	134	127	140	149	166	169	152	172
21/9/72	118	126	142	133	135	134	137	143	159	162	168	171	184
9/10/72	134	149	163	168	176	187	194	200	205	211	199	206	215
26/10/72	144	162	171	179	186	192	201	216	214	229	241	240	243
11/11/72	158	161	176	181	189	205	204	221	213	243	286	282	279
7/12/72	166	166	170	183	186	210	207	214	219	298	312	282	283
30/12/72	163	177	187	192	204	207	212	227	231	267	299	301	191
10/1/73	169	188	189	200	209	219	231	233	241	277	280	284	288
29/1/73	151	154	171	185	193	189	203	208	217	255	258	242	265
15/2/73	160	161	169	182	202	201	207	216	224	247	251	269	276
23/2/73	171	172	179	188	200	198	208	211	232	247	261	273	281
29/3/73	177	182	203	200	217	193	224	240	226	275	295	270	298
12/3/73	172	186	190	202	214	227	231	246	243	261	277	288	291
26/4/73	126	182	191	201	209	197	232	230	249	257	268	267	271
10/5/73	118	166	171	183	201	216	234	236	248	259	261	267	280
25/5/73	124	132	168	171	189	211	228	226	231	239	242	252	261
14/6/73	116	123	142	159	164	182	200	218	221	230	233	240	233
28/6/73	104	131	142	151	147	162	178	210	201	222	232	226	229
12/7/73	107	130	141	145	152	158	162	176	179	188	192	199	204
27/7/73	112	121	124	129	129	132	137	142	150	161	162	170	172
9/8/73	117	126	129	122	136	140	141	146	154	172	169	181	174
13/9/73	115	118	123	118	132	142	140	150	157	193	192	198	182
28/9/73	122	138	144	151	150	166	170	172	181	200	206	212	216
18/10/73	113	129	152	150	163	173	181	188	201	209	226	233	229
1/11/73	122	146	142	163	171	170	189	200	196	224	259	266	263

Table 1.2 Salinity in parts per thousand of each concentrating pond over the sampling period

and the replacement of the water from the main lake bed and ponds P1 and P2. The lowest recorded salinity for the year was in P3 on 28 June 1973 of 104 ppt. At this salinity the calcium sulphate crust had dissolved and the water was turbid.

From this point on an increase similar to that in 1972 started but the rate was slightly slowed reflecting the effects of a cooler damper spring.

The "isosaline" lines on Table 1.2 show that for a large part of the year ponds above P6 have salinities higher than 200 ppt and only during spring and late autumn are there any ponds with salinities lower than 150 ppt.

1.6 DEPTH OF THE PONDS AND WATER MOVEMENTS

The depth of the ponds, although fixed at a maximum of about 0.75 m by the height of the dykes, is very variable throughout the season. The lower P series are lowered towards the end of the evaporating season as brine is withdrawn from the end of the chain of ponds for retention in deep storage.

Water is pumped from P6 to the higher P7 and flows to F1 by gravity. F2, F3, F4 and F5 may be individually controlled by a system of sluice gates and are occasionally independently emptied as the salinity approaches that suitable for further processing. P1 and P2 function as bulk storage of preconcentrated seawater. This is normally completely pumped into P3 at some time during the evaporating season.

In addition to the intentional water movements, wind induced flow may be rapid during periods of gale force winds.

1.7 WAVE ACTION

The Grassmere area is prone to strong winds, (section 1.4), which cause considerable wave action on the ponds. Wave heights of up to 32 cm have been recorded during a wind of

Beaufort force 6. Prolonged winds also tend to cause piling up of water at the downwind end of the ponds and to cause water to flow through the concentrating series. This may be reversed when the wind moderates and causes a certain degree of mixing between adjacent ponds.

Wave action produces a stable head of foam on the high salinity ponds. This may accumulate to a considerable depth in ponds whose salinity is over 240 ppt. A quantitative estimate of the degree of "foaminess" was made according to the methods of Miyake and Abe (1948), Klein (1959) and Mason (1967).

METHOD

A 50 ml. sample of lake water was placed in a 125 ml glass graduated cylinder. The sample was shaken through a 20 cm vertical distance at four cycles per second for 15 seconds. The time was taken from the end of shaking until the first piece of surface is cleared of foam.

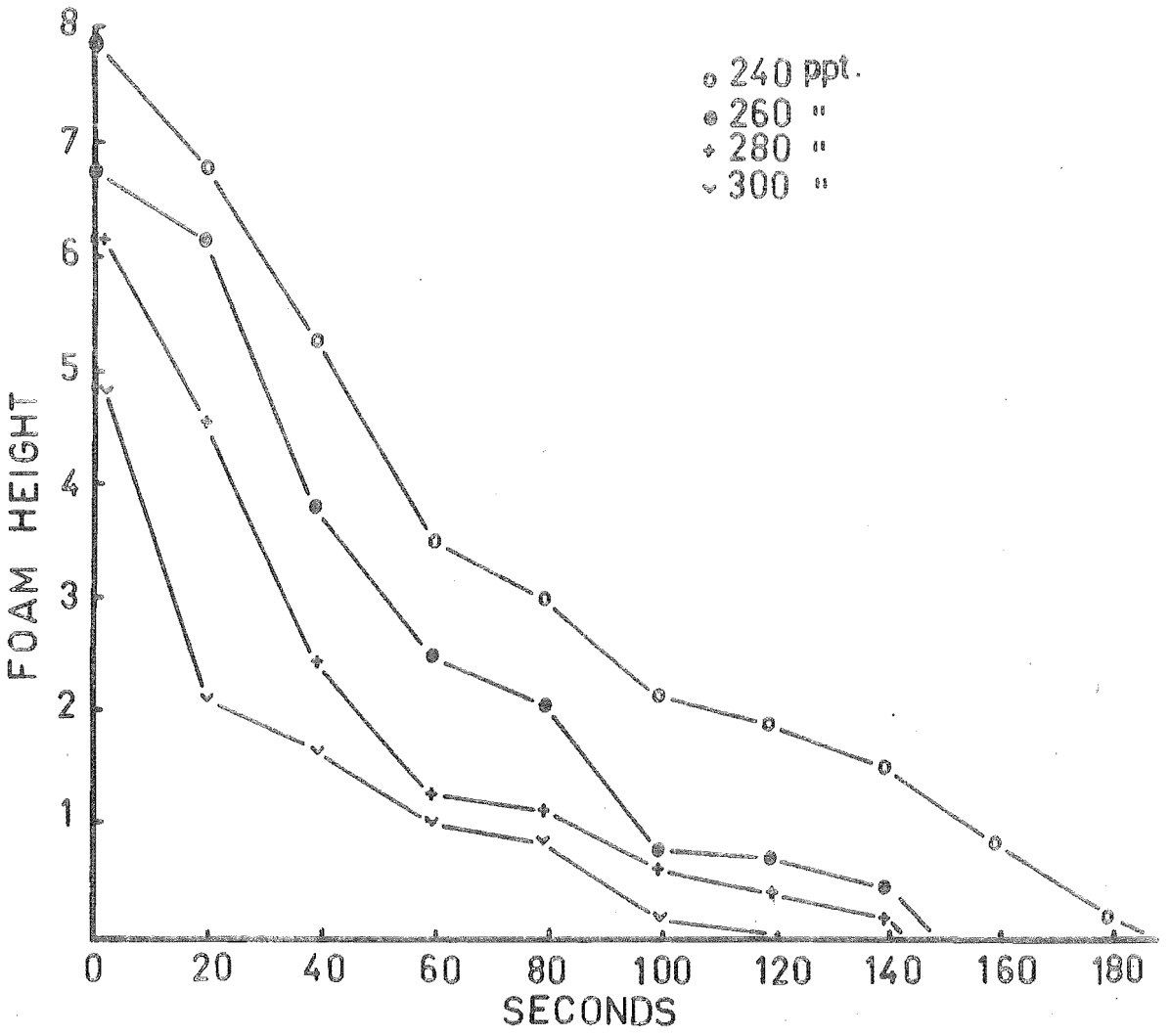
RESULTS AND DISCUSSION

The time taken for the foam to break up is compared with salinity in Fig 1.4. Four salinities were used; 240 ppt, 260 ppt, 280 ppt, 300 ppt. After shaking, the head of foam varied directly with the salinity being lowest for 240 ppt, (4.4 cm) and highest for 300 ppt (7.8 cm). Initially there was a rapid decrease in foam depth and this was followed by a slower decrease of what remained. The total length of life of the foam varied directly with the salinity. The 240 ppt foam survived 120 seconds and the other three 141 seconds, 150 seconds and 184 seconds respectively.

On the ponds after the depth of foam exceeded 15 cm it was generally blown away in large chunks. This aspect is probably the most important since the foam contained large

FIGURE 1.4

Foam head lifetimes measured after a standard shaking period for brine of four salinities


240 ppt.
260 "
280 "
300 "
FOAM HEIGHT
SECONDS
0
20
40
60
80
100
120
140
160
180
1
2
3
4
5
6
7
8

numbers of Artemia salina eggs that had been floating on the water surface.

Normally the Artemia eggs formed a ring around the pond margins as they were blown ashore in the absence of foam. It is virtually impossible to estimate accurately the loss of eggs but, considering the number of suitably windy days, it may be considerable.

1.8 SEASONAL AND DIURNAL TEMPERATURE VARIATIONS

Temperature increase has two important effects on the brine of the Grassmere ponds. The first of these is that gases are less soluble as the temperature is raised. The second is that, in general, water soluble salts are more soluble as the temperature is raised.

METHOD

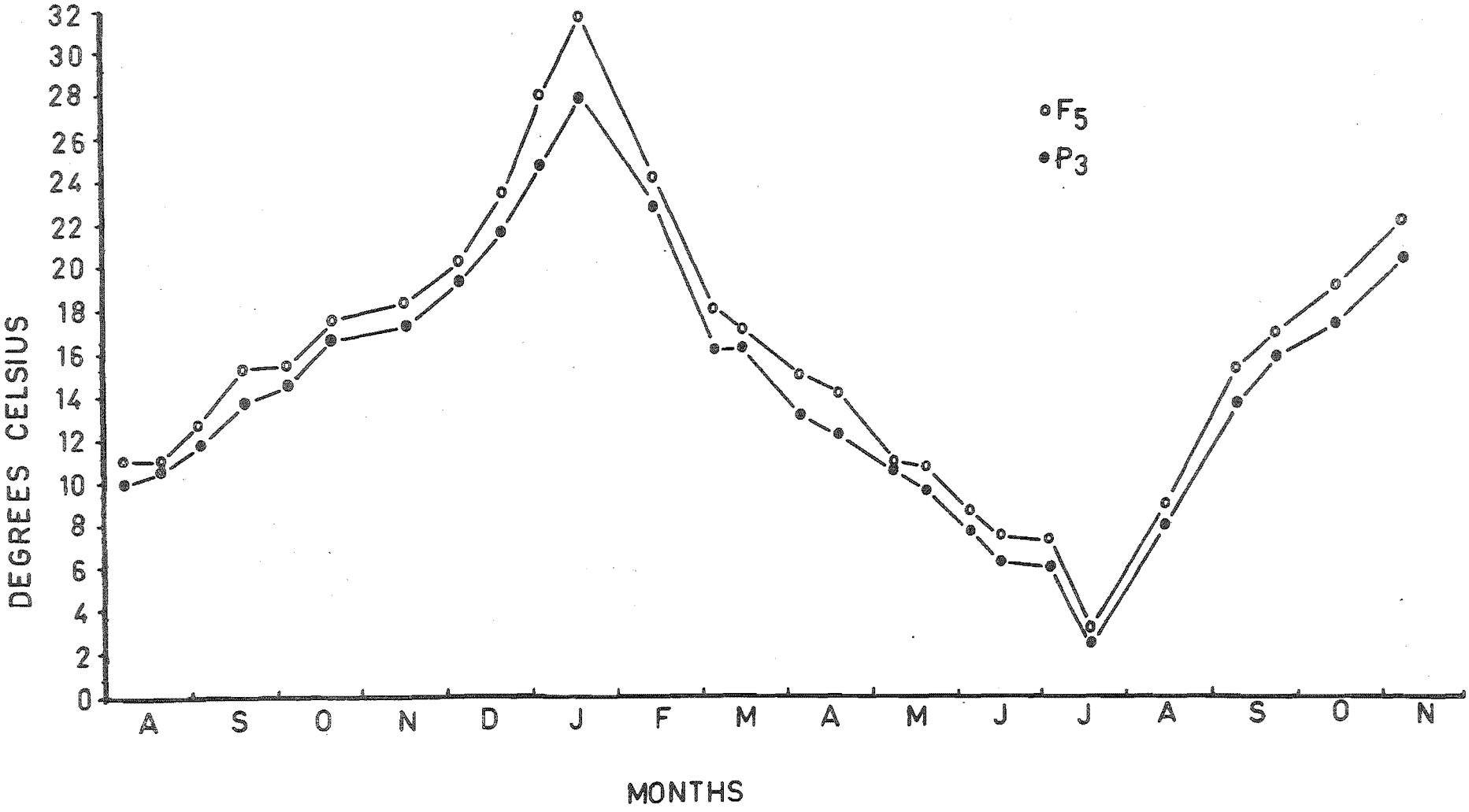
A mercury-in-glass thermometer accurate to 0.1^{o}C was used for measuring water temperatures at each visit, by wading out into the pond 20 metres and immersing the thermometer to a depth of 200 mm. Temperatures were measured at 1300 hours $\pm$ 1h.

RESULTS

Fig. 1.5 shows that the temperature range over the sampling period from August 1972 to November 1973 was large. It is immediately apparent that there is a difference between the highest and lowest salinity ponds, possibly because as the brine concentration rises its specific heat falls. For clarity only two ponds have been plotted but the rest fit in according to their salinity. The extreme low value of 3^{o}C (12/7/73) was recorded after a series of frosts had chilled the water over the previous week. The peak temperatures for the year of 31^{o}C in F5 and 28^{o}C in P3 were recorded at the end of January, (29/1/73). The spring rise was underway when

FIGURE 1.5

Temperature range of the brine in concentrating ponds P3 and F5 between August 1972 and November 1973


DEGREES CELSIUS
32
30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
0
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
MONTHS
F5
P3

sampling began in August 1972 but the almost linear rise came to an abrupt peak in January and was followed by a similarly rapid fall throughout the autumn and into the winter. The 1973 spring rise was more rapid than that in 1972 and by November 1973 the water temperature was four degrees higher than the year before.

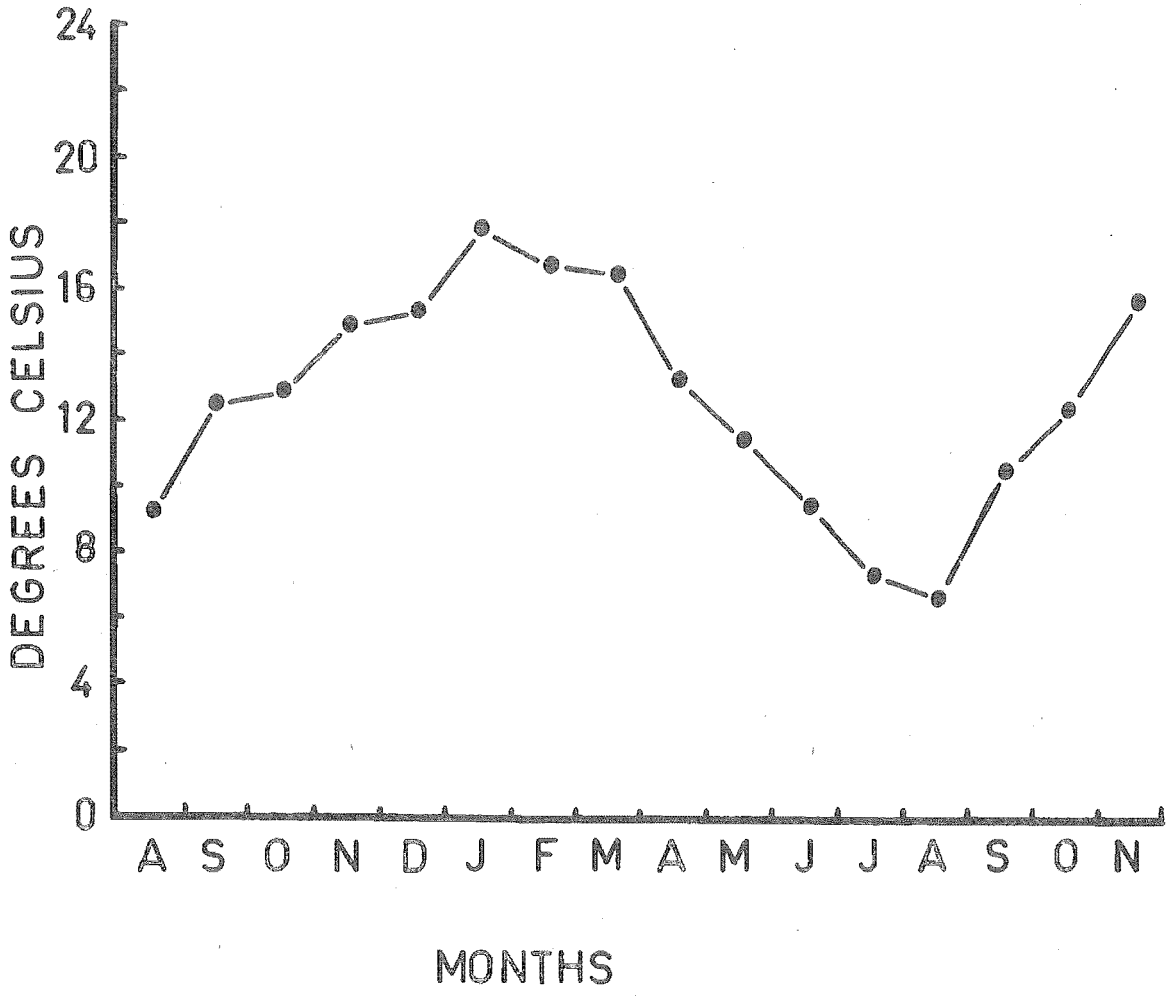
The monthly mean air temperatures recorded at Lake Grassmere for the same period are shown in Fig. 1.5.1. The maxima and minima times correspond to those of the ponds and, as with the ponds, a more rapid spring temperature rise is shown in the 1973 season than in 1972.

1.9 LIGHT PENETRATION

The concentrating ponds are very shallow and there is little likelihood of any problems being experienced with lack of light at any stage except where extreme turbidity is present. Generally, throughout the year, the bottom sediments were cemented by a precipitated salt and the water remained extremely clear. Algal blooms reduced the transparency in spring but measurements showed that, at the minimum, 80% of the incident radiation was reaching the substrate. Readings of light intensity were taken using a wide spectrum photocell embedded in araldite. The cell was lowered to the bottom and the reading read off a meter. The instrument was constructed at the University of Canterbury, Department of Zoology. At some periods, notably during late winter, salinity had decreased to the extend in P3 that the substrate was loosened by the re-dissolving of the binding material. During this period wind induced turbulence caused dense turbidity and the amount of incident radiation reaching the bottom of the ponds decreased to about 15%. Turbidity was, however, an unusual

FIGURE 1.5.1

Mean monthly air temperatures recorded at Lake Grassmere between August 1972 and November 1973


24
20
16
12
8
4
0
DEGREES CELSIUS
A S O N D J F M A M J J A S O N
MONTHS

event and for most of the year light would not be likely to be limiting primary production.

1.10 SEDIMENTS OF LAKE GRASSMERE

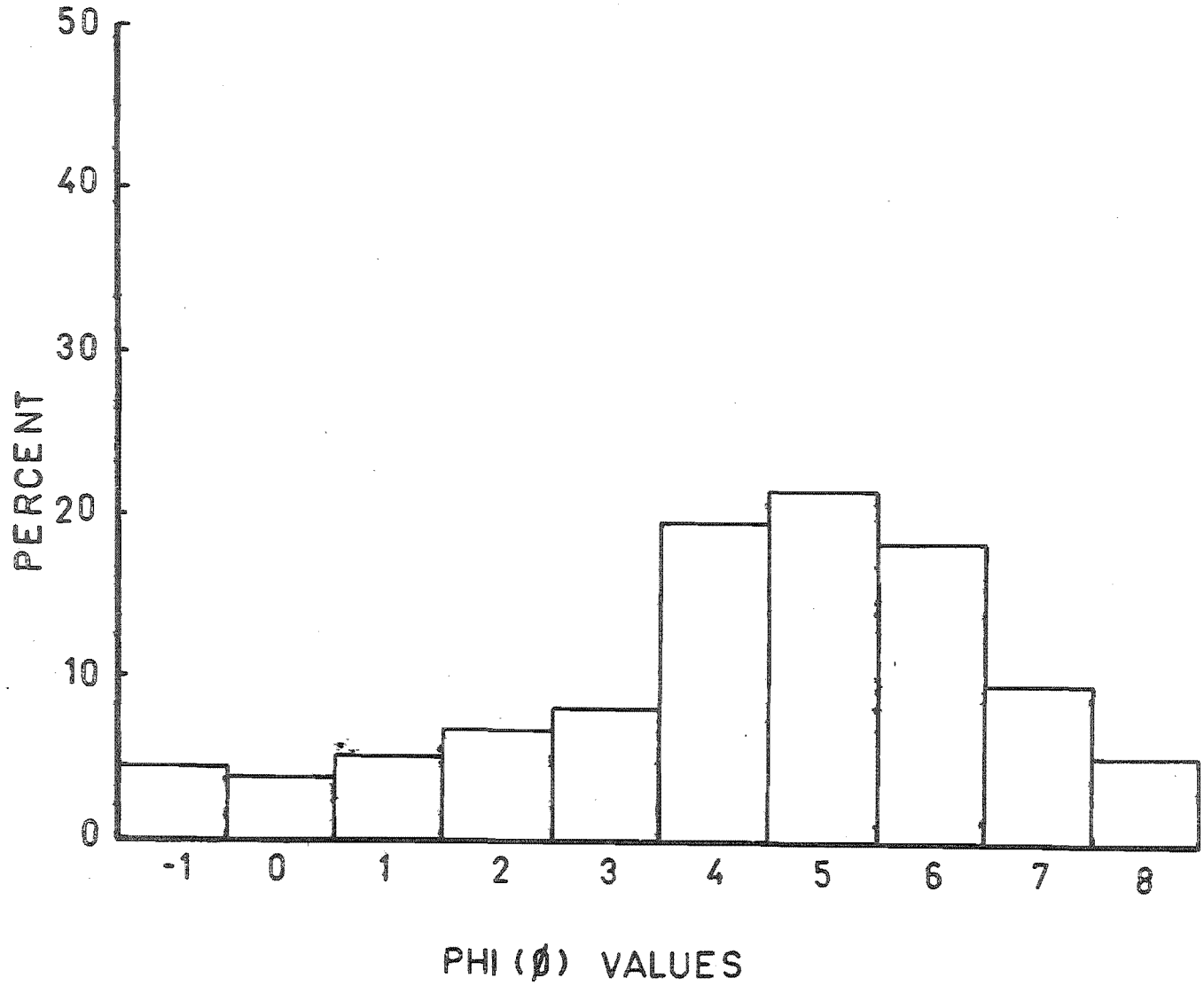
Sediment of the ponds were investigated because of the extreme turbulity at times of low salinity.

Sediment samples were taken from the bed of each pond using a hand corer that withdrew a 40 mm diameter core. There was no layering over the length of the core. The core from P7 was typical of the series and was investigated for grain size distribution by shaking through a series of sieves in a Rotap shaking machine for 30 minutes. The material that passed through the finest sieve, smaller than 0.062 mm, was further investigated by the pipette method. The fine material was suspended in a 1000 ml cylinder with a dispersant (sodium hexametaphosphate), to inhibit flocculation. The mixture was then well stirred and 20 ml pipette samples taken as the material settled in the cylinder (Morgans 1956). As the coarser material settles more rapidly, successive pipette samples show progressively finer grains. The water is evaporated off and the weight of solid material per sample carefully weighed.

The distribution of sediment grain sizes is shown in Fig. 1.6 as the percent of each phi (Ø) class present where phi is the negative log to the base 2 of the particle diameter in millimetres. The distribution is moderately well sorted with a maximum percentage of Ø5 sized grains. But there is also a large percentage of very fine material that is mainly responsible for creating dense turbidity when disturbed. The fineness also promotes the formation of anaerobic conditions at a shallow depth. Below five centimetres the sediment was

FIGURE 1.6

The distribution of particle sizes measured in phi (Ø) units for the Lake Grassmere sediment. Ø = $-\log_2$ of diameter in mm.


50
40
30
20
10
0
PERCENT
-1
0
1
2
3
4
5
6
7
8
PHI (Ø) VALUES

densely blackened by sulphide deposits and had a very strong sulphurous smell.

The sulphide was derived from the activities of anaerobic "sulphur" bacteria that reduce sulphate to sulphide when sulphate is used as a hydrogen acceptor in the absence of oxygen. Nitrate, nitrite and carbon dioxide may also serve in this capacity. The reduced product of the reactions accumulate in the sediment and modify it by further reaction. The most obvious one is the formation of black metallic sulphide by reaction with hydrogen sulphide.

1.11 THE EFFECT ON THE LAKE SEDIMENT OF PRECIPITATED CALCIUM SULPHATE

When seawater is evaporated the major contained salts precipitate out in the following order: calcium carbonate, calcium sulphate, sodium chloride, magnesium chloride, magnesium sulphate, sodium bromide, and potassium chloride (Borchert 1965). Calcium carbonate is present in only very small amounts, approximately 0.177 g/Kg seawater (Peterson 1966), but both calcium sulphate and sodium chloride are present in large amounts, 1.75 g/Kg and 29.69 g/Kg respectively, (Horne 1969).

Deposition of calcium carbonate begins at about 65 ppt salinity and is virtually complete by the time calcium sulphate begins to crystallise at about 150 ppt salinity. But deposition of calcium sulphate occurs over a wide range of salinities well beyond the point (310 ppt) at which sodium chloride crystals begin to appear and is found in all concentrating ponds. These values are approximate only since they vary considerably with water temperature. However, there were only very small amounts of calcium carbonate present in the crystalline mass, as shown by effervescence of

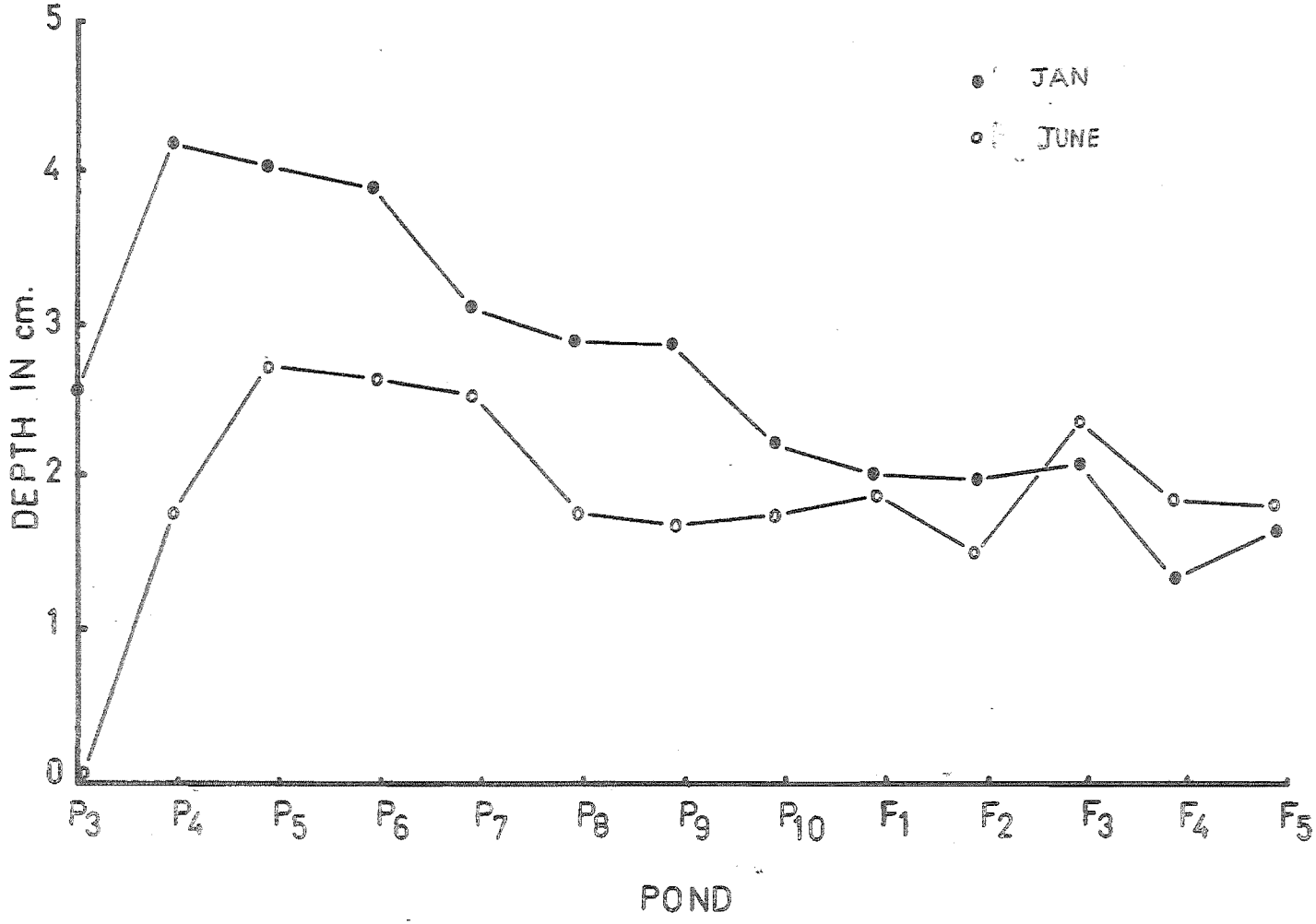
pulverised samples with dilute hydrochloric acid, since most would have been lost during earlier concentration in the main lake. The amount of deposited calcium sulphate varied from pond to pond with a maximum occurring near the beginning of the concentrating series. Fig. 1.7 shows the mean depth of the crust in ponds P3 - F5 in January 1973, the period of maximum evaporation, and in June 1973 when salinities were near their lowest. In January the amount deposited was maximal in P4 but was still being laid down in F5. Here sodium chloride was on the point of being crystallised out. In June losses had occurred in P3 - P9 but the rest were unchanged.

The initial effect of calcium sulphate precipitation is to cement the grains of substrate into a firm mass. However, the deposit continues to grow, the calcium sulphate becomes purer and forms a pavement of crystals strong enough to be walked upon. At the same time that this crust is formed, the pond water becomes very clear and remains so during severe wave action. Until the crust formed the sediment was unstable and algae could not attach to it but after the crust was well established, a green mat of Dunaliella euchlora, a unicellular alga, began to grow.

The crust was stable only as long as the salinity of the brine remained above that necessary to initiate precipitation. In P3 during May 1973 the influx of lower salinity brine, necessary to replace that being drawn off from F4 and F5, resulted in a drop in salinity to 118 ppt and a rapid break up of the crust. This had several effects. The first was that the sediment became loosened and the water became strongly turbid. The second was a loss of algae from the substrate and the appearance of masses of floating detached

FIGURE 1.7

The mean depth of the calcium sulphate crust in ponds P3 - F5 in January 1973 and June 1973


5
4
3
2
1
0
DEPTH IN cm.
JAN
JUNE
P3
P4
P5
P6
P7
P8
P9
P10
F1
F2
F3
F4
F5
POND

alga that blew to the lee shore where they dried out. A third effect was the release of hydrogen sulphide gass from the anaerobic sediments that had formed beneath the crust. This sediment was blue/black, and the smell was very strong in the vicinity of the pond. Elemental sulphur was found in a line around the shore when the most rapid break up of the crust occurred.

From these observations it appears that the minimum salinity that can be tolerated without causing drastic changes in the ponds is about 150 ppt and it is likely that unless the bottom of the ponds were to be artificially sealed off from the silty sediment, any ponds used for rearing Artemia would have to be kept at this salinity or higher.

1.12 REACTIVE NITRATE

INTRODUCTION

The sampling of reactive nitrate and orthophosphate concentrations alone cannot give a complete estimate of all of the forms of nitrogen and phosphorus available to the flora of the ponds. The data obtained are presented to show trends of seasonal concentrations of selected ions in relation to fluctuations in algal abundance and no firm opinion may be given, on the basis of the data available, as to whether the lack of nitrogen or phosphorus compounds is imposing a limit on the algal growth. Even though the amounts of free ions present at any time may be very small, the recycling rate may be very high and support a large standing crop of algae.

The supply of inorganic nitrogen compounds in a system such as Lake Grassmere originates from the breakdown of proteinaceous matter, mainly to ammonia, (NH_3), which is oxidised initially to nitrite, (No_2^-) and finally to

nitrate (No_3^-). Bacteria are responsible for much of this, but it may also occur photochemically, and rapidly, in shallow, well illuminated water, (Horne 1969). A secondary source of ammonia is the waste products of plankton metabolism. Other forms of nitrogen present in lake waters recognised by Vollenweider (1971) include gaseous nitrogen (N_2, N_2O, No), organic compounds (amino acids, peptides and polypeptides and dissolved albumin) and unidentified inorganic and organic compounds adsorbed on to particles. Evidence exists that some blue green algae can fix atmospheric nitrogen (Lund 1965).

METHODS

Water samples were taken in 200 ml polythene bottles at mid depth of the ponds, (approx. 40 cm). The bottles had been previously cleaned in hot potassium dichromate/sulphuric acid solution. The samples were filtered through a Millipore filter funnel fitted with a Whatman GF/C filter paper (0.4 μm) and frozen to -20^{o}C within 8 hours. After thawing, nitrate concentrations were determined by the colourimetric method described in Appendix (1) (APHA 1965). As a check on the possible loss of nitrate during frozen storage a sample of freshly removed water was divided and the nitrate in one half measured within two hours. The other half was frozen and analysed after two weeks' storage. No difference in nitrate levels was found between the two samples.

RESULTS

Nitrate levels during the year ranged from 0.43 g/m^3, (F4 on 9/10/72) to 0.07 g/m^3, (P4 on 29/1/73). Three trends were apparent. The first was an increase in nitrate level as the salinity increased up the concentrating chain. The second was the pronounced seasonality of nitrate levels found, with a winter peak, spring drop, summer low, and slow autumn

	P3	P4	P5	P6	P7	P8	P9	P10	F1	F2	F3	F4	F5
10/8/72	0.23	0.26	0.29	0.22	0.27	0.31	0.26	0.25	0.25	0.23	0.31	0.34	0.29
25/8/72	0.29	0.28	0.27	0.23	0.26	0.28	0.22	0.26	0.26	0.27	0.29	0.29	0.28
5/9/72	0.18	0.20	0.22	0.19	0.23	0.26	0.19	0.21	0.25	0.28	0.28	0.27	0.26
21/9/72	0.18	0.19	0.20	0.17	0.22	0.21	0.23	0.21	0.14	0.20	0.21	0.28	0.20
9/10/72	0.16	0.13	0.15	0.14	0.18	0.14	0.09	0.16	0.07	0.22	0.13	0.43	0.07
26/10/72	0.14	0.15	0.16	0.16	0.21	0.19	0.12	0.14	0.11	0.21	0.18	0.30	0.21
11/11/72	0.17	0.16	0.14	0.14	0.18	0.19	0.13	0.10	0.14	0.22	0.23	0.26	0.27
7/12/72	0.13	0.12	0.13	0.12	0.13	0.17	0.14	0.09	0.11	0.19	0.18	0.21	0.29
30/12/72	0.13	0.11	0.18	0.19	0.11	0.14	0.17	0.13	0.18	0.17	0.21	0.19	0.20
10/1/73	0.10	0.09	0.11	0.10	0.10	0.13	0.11	0.09	0.14	0.13	0.17	0.21	0.23
29/1/73	0.11	0.07	0.08	0.11	0.12	0.15	0.13	0.12	0.13	0.16	0.15	0.21	0.21
15/2/73	0.13	0.14	0.11	0.10	0.11	0.12	0.13	0.14	0.16	0.12	0.16	0.15	0.14
23/2/73	0.12	0.12	0.11	0.12	0.16	0.14	0.15	0.19	0.19	0.23	0.26	0.21	0.19
29/3/73	0.11	0.16	0.14	0.16	0.21	0.20	0.19	0.13	0.14	0.18	0.23	0.31	0.22
12/4/73	0.16	0.19	0.22	0.24	0.29	0.28	0.24	0.19	0.23	0.29	0.34	0.37	0.34
26/4/73	0.16	0.18	0.20	0.23	0.27	0.26	0.29	0.21	0.28	0.31	0.31	0.41	0.32
10/5/73	0.18	0.21	0.24	0.29	0.34	0.37	0.31	0.24	0.28	0.34	0.32	0.30	0.26
25/5/73	0.22	0.24	0.26	0.31	0.30	0.29	0.32	0.27	0.31	0.39	0.36	0.32	0.31
14/6/73	0.26	0.23	0.21	0.24	0.24	0.26	0.27	0.26	0.29	0.27	0.29	0.31	0.32
28/6/73	0.21	0.20	0.23	0.23	0.25	0.26	0.24	0.27	0.33	0.30	0.29	0.27	0.31
12/7/73	0.23	0.21	0.22	0.24	0.24	0.23	0.21	0.23	0.28	0.26	0.31	0.25	0.32
27/7/73	0.22	0.24	0.26	0.29	0.26	0.26	0.29	0.29	0.20	0.21	0.27	0.26	0.28
9/8/73	0.14	0.19	0.21	0.26	0.19	0.23	0.22	0.24	0.27	0.25	0.27	0.29	0.28
13/9/73	0.11	0.09	0.12	0.21	0.17	0.19	0.20	0.21	0.22	0.26	0.25	0.22	0.26
28/9/73	0.09	0.08	0.09	0.12	0.15	0.18	0.17	0.21	0.23	0.24	0.29	0.29	0.28
18/10/73	0.11	0.12	0.10	0.11	0.14	0.20	0.13	0.19	0.19	0.20	0.21	0.26	0.24
1/11/73	0.08	0.09	0.10	0.09	0.11	0.16	0.14	0.16	0.19	0.18	0.21	0.22	0.26

Table 1.3 Determination of reactive nitrate expressed as grams per cubic metre of water.

autumn recovery. The third trend was a difference in amplitude of the seasonal variation between the less saline and most saline ponds. In F4, the most saline, the range was from 0.29 and 0.28 in August, 1972, to 0.14 and 0.19 in February, 1973, whereas in P4, near the beginning of the series, the range was from 0.26 and 0.28 in August, 1972, to 0.09 and 0.07 in January 1973.

DISCUSSION

Nitrogen occurs in the sea mainly as nitrate, nitrite, and ammonium, nitrate being by far the most abundant and stable form, (Horne 1969). Nitrite and ammonia are often present in extremely small concentrations and are difficult to measure even with sophisticated analytical techniques.

Apart from these three, other nitrogenous compounds such as urea, uric acid, and amino acids are present and may be used directly by some algae. However, they are usually rapidly converted to ammonia and their concentrations remain exceedingly low, (Raymont 1963).

Water samples taken from the water entering Lake Grassmere from the open sea in September and March had nitrate levels of 0.21 g/m^3 and 0.16 g/m^3 respectively.

Determinations by Harvey (1955), of nitrate from South Pacific surface waters showed levels of 0.21 g/m^3 in April/May, Harvey (1928), working in the English Channel, found maximum values of 0.100 g/m^3 in winter and, because of high utilisation by phytoplankton, only trace amounts remained at the peak of the early summer bloom. Dakin and Colefax (1935) found a maximum value of only 0.040 g/m^3 off the New South Wales coast in surface waters due to a strong temperature inversion preventing replenishment from deeper waters. Neverthless, a strong algal growth was supported with almost all available

nitrate being used.

These examples show that the nitrate uptake may be rapid and almost complete and it is unlikely that the levels remaining at all times in the Lake Grassmere concentrating ponds would limit growth. The lowest levels, recorded on several occasions, were about 0.07 g/m^3.

The "isoconcentration" lines on the table of nitrate levels (Table 1.3), shows a high general level of nitrate at the beginning of the sampling period, presumably arising from winter breakdown of phytoplankton and zooplankton, but an accelerating drop as spring arrived. A summer low, consistent with heavy demands by the resident algae continued until about April when a steady rise began. This culminated in a winter high that coincided with the demise of the algal population and the return of nutrients to the water by their decay and the breakdown of complex molecules.

1.13 REACTIVE PHOSPHATE

Phosphorus plays a vital role in photosynthesis as part of adenosine diphosphate, (ADP), and adenosine triphosphate (ATP). Particularly in the Krebs cycle, ATP is used as a source of energy in incorporating inorganic carbon into complex, high energy, organic molecules. Phosphate very often limits the ultimate algal biomass and in view of this importance, it may be understood why, of all the dissolved nutrients, levels of phosphate are most closely related to the concentrations of chlorophyll, (Ketchum and Corwin 1965). Phosphorus is present in many forms in seawater, dissolved inorganic, dissolved and particulate organic and particulate organic absorbed into mineral and vegetable detritus. Lean (1973) recognises four forms of phosphate; dissolved inorganic phosphate, dissolved high molecular weight organically bound phosphate, low molecular

weight organically bound phosphate (MW 250), and very high molecular weight molecules (over 5 x 10^6 and possibly colloids). The form of phosphorus tested for during this project, is orthophosphate.

The phosphorus cycle cannot be considered a closed one since there may be a considerable interchange of phosphate with detrital and mineral particles whether suspended in the water column or as a stable substrate. Where the sediment is finely divided and phosphate is abundant, interchange between the bound up particulate phase and the free reactive phase may be very rapid, (Pomeroy, Smith and Grant 1965). Since both elements are essential for algal growth it follows that the situation may arise where phosphorus depletion may limit growth whereas nitrate remains in ample quantities.

METHOD

Reactive phosphate was measured by the method of Strickland and Parsons (1968), in which the sample reacts with a composite reagent containing molybdic acid, ascorbic acid and trivalent antimony. The resulting phosphate complex is reduced forming a blue solution which was measured at 8850Å using a Bausch and Lomb Spectronic 20 colourimeter. At very low phosphate levels extraction of the blue complex into isobutanol improved accuracy. Water samples were collected as for those used for nitrate analysis and frozen to -20°C within 8 hours after collection. A comparative analysis was made between a fresh sample and one thawed after two weeks storage. There was a slight loss of phosphate over the frozen storage period, averaging 1 - 1.5%, but insufficient to cause appreciable errors in the analytical estimates.

Analyses of total phosphate in pond sediments were made using the method of Muir (1952), where the sediment, which

	P3	P4	P5	P6	P7	P8	P9	P10	F1	F2	F3	F4	F5
10/8/72	0.012	0.044	0.036	0.101	0.299	0.120	0.222	0.092	0.116	0.200	0.082	0.075	0.117
25/8/72	0.033	0.030	0.049	0.099	0.272	0.100	0.107	0.040	0.070	0.097	0.102	0.066	0.114
5/9/72	0.02	0.041	0.04	0.012	0.100	0.025	0.11	0.014	0.03	0.04	0.05	0.03	0.12
21/9/72	0.020	0.04	0.035	0.012	0.055	0.029	0.075	0.015	0.008	0.015	0.024	0.026	0.067
9/10/72	0.019	0.029	0.037	0.009	0.007	0.010	0.040	0.010	0.010	0.013	0.030	0.009	0.015
26/10/72	0.019	0.020	0.020	0.010	0.010	0.007	0.015	0.007	0.015	0.007	0.007	0.004	0.009
11/11/72	0.015	0.020	0.019	0.015	0.007	0.008	0.009	0.007	0.009	0.007	0.006	tr	0.008
7/12/72	0.019	0.015	0.006	0.010	0.002	0.004	0.006	0.009	0.009	0.004	tr	tr	tr
30/12/72	0.009	0.010	0.005	0.007	0.004	0.005	tr	0.007	0.008	0.004	0.003	0.003	0.007
10/1/73	0.015	0.015	0.015	0.009	0.015	0.009	0.006	0.009	0.010	0.003	0.007	0.009	0.008
29/1/73	0.062	0.054	0.03	0.023	0.03	0.015	0.015	0.015	0.015	0.015	0.015	0.015	0.015
15/2/73	0.043	0.062	0.044	0.036	0.062	0.032	0.033	0.029	0.017	0.013	0.014	0.007	0.008
23/2/73	0.039	0.072	0.061	0.042	0.051	0.015	0.026	0.022	0.021	0.018	0.011	0.006	0.009
29/3/73	0.036	0.039	0.049	0.049	0.057	0.044	0.031	0.037	0.029	0.023	0.012	0.009	0.014
12/4/73	0.037	0.047	0.03	0.055	0.062	0.062	0.047	0.047	0.047	0.037	0.015	0.008	0.037
26/4/73	0.023	0.052	0.022	0.050	0.043	0.060	0.042	0.061	0.008	0.026	0.009	0.008	0.006
10/5/73	0.071	0.126	0.049	0.051	0.068	0.012	0.051	0.047	0.009	0.010	0.017	0.004	0.004
25/5/73	0.235	0.619	0.085	0.006	0.015	0.006	0.062	0.038	0.006	0.006	0.030	tr	tr
14/6/73	0.377	0.552	0.166	0.010	0.019	0.007	0.052	0.033	0.009	0.008	0.029	tr	0.003
28/6/73	0.282	0.476	0.233	0.032	0.030	0.010	0.044	0.029	0.015	0.015	0.019	0.002	0.002
12/7/73	0.271	0.299	0.262	0.041	0.032	0.027	0.031	0.026	0.020	0.015	0.015	0.007	0.005
27/7/73	0.252	0.230	0.261	0.051	0.044	0.029	0.030	0.021	0.023	0.019	0.016	0.007	0.006
9/8/73	0.201	0.221	0.172	0.034	0.030	0.025	0.029	0.023	0.021	0.016	0.013	0.005	0.005
13/9/73	0.198	0.162	0.101	0.029	0.024	0.025	0.021	0.020	0.011	0.016	0.012	0.010	0.005
28/9/73	0.200	0.081	0.030	0.041	0.021	0.020	0.020	0.009	0.012	0.014	0.012	0.009	0.007
18/10/73	0.132	0.044	0.021	0.009	0.009	0.008	0.009	0.009	0.008	0.007	0.009	0.008	0.006
1/11/73	0.066	0.039	0.006	0.006	0.007	0.006	0.005	0.007	0.008	0.006	0.007	0.008	0.006

Table 1.4 Determinations of reactive phosphate expressed as grams per cubic metre of wate

was cemented together with deposited calcium sulphate, was pulverised and mixed with fused sodium carbonate. The phosphate was released into the carbonate melt and prepared for analysis by dissolving in water.

RESULTS

Phosphate levels, Table 1.4, ranged from trace amounts to 0.619 g/m^3 detected on 25 May 1973, (P4). Several trends were apparent. Firstly, a decrease in phosphate was found as salinity increased up the concentrating chain of ponds, (i.e., P3 - F5). This decrease contrasted sharply with the increase noted for nitrate concentrations. The second trend, that of seasonal variation, showed a winter peak, spring drop, summer low and a rapid autumn recovery. The fluctuations were more severe than with nitrate, however, and superimposed on the overall change, were numerous short-lived fluctuations. In ponds P3 and P4 during May and June 1973, there was a sudden rise in phosphate levels which apparently was derived from the break-up of the calcium sulphate crust that had been covering the bottom of P3. At that time, water was being drawn through the chain of ponds and the biggest rise centred on P4 as enriched water from P3 was being drawn through. There was only minor disruption of the $CaSO_4$ layer in P4 and although the effect could be noticed in P5 it was not apparent in later ponds in the series.

Thirdly, a higher amplitude of seasonal variation in phosphate concentrations was found in the lower salinity ponds compared with the very saline F series ponds. This is similar to the findings for nitrate although the ranges in P3 of 0.09 g/m^3 - 0.377 g/m^3 and F5 of trace amounts - 0.177 g/m^3 were more extreme than for nitrate levels.

Analysis of the sediment crust at three dates, (29/1/73,

26/4/73 and 12/7/73), showed mean values of 0.37 g phosphate/ kg.

DISCUSSION

Since only one form of phosphorus was being measured the data had little predictive value. Nothing was known of the rate of interchange of phosphate with the sediment or the degree to which phosphate had entered into the formation of organic colloids. The most rapid drop in phosphate levels occurred in spring and coincided with the most active algal growth period of the year. It is possible, therefore, that phosphate could be a limiting factor for algal production. The further fall to undetectable amounts in summer followed by a steady rise throughout the autumn is characteristic of an alga/nutrient interaction (Ketchum 1954, Hutchinson 1957). Although the most important form of phosphorus for algae is inorganic phosphate (Vollenweider 1971), overbeck (1962) has shown that Chlorella pyrenoidosa, among others, is capable of secreting ectoenzymes that cleave pyrophosphates and glycophosphates. Most detailed work on phosphate levels in lakes refer to deep freshwater bodies or saline lakes formed by inland drainage and often with the aim of detecting the effect of eutrophication (Vollenweider 1971). Practically no information is available on the situation of Lake Grassmere, a very shallow and highly saline pond system.

The phosphate contained in the sediment appears to be a substantial reserve but was not available to the algae until the binding calcium sulphate layer had redissolved. To overcome this the salinity could be maintained at a level that does not permit the formation of $CaSO_4$ deposit, but this would leave the very fine unconsolidated silt composing the bed of Lake Grassmere, (Section 1.9), open to wave action, which when severe

causes extreme water turbidity, (Section 1.8).

1.14 REACTIVE SILICATE

Silicate is probably the most variable common element in the sea (Armstrong 1965) and is greatly affected by biological processes being the principal element in the skeleton of diatoms and many Protozoa. The ion occurs both in the dissolved state and as suspended particulate silica, but the ratios of these are very changeable. Although the form of occurrence is fairly well known the exact chemical species are unclear. Sillen (1961) considered that since silicic acid is a very weak acid, at the normal marine pH only 5% of the silica could be in the form of silicic acid, H_3SiO_4. Since silicon is biologically significant, like nitrate and phosphate, a seasonal trend should be found if this element is being consumed and returned on the death of the consumer. Frequently the concentration changes of silicate are erratic and not well correlated with the seasons because the principal consumers, the diatoms, characteristically exhibit sporadic blooms, (Armstrong and Butler 1960).

METHOD

Samples were taken from each concentrating pond at each visit to Grassmere and also from the open sea near the intake to the main seawater supply. Collection details were as for nitrate samples. The analytical method used was from Strickland and Parsons (1968). Three determinations were selected as being typical of the levels found in the ponds over the sampling period. They were spring, 9/10/72, summer, 3/12/72, and autumn, 26/4/73.

RESULTS AND DISCUSSION

Microscopic examination of the ponds' flora and fauna

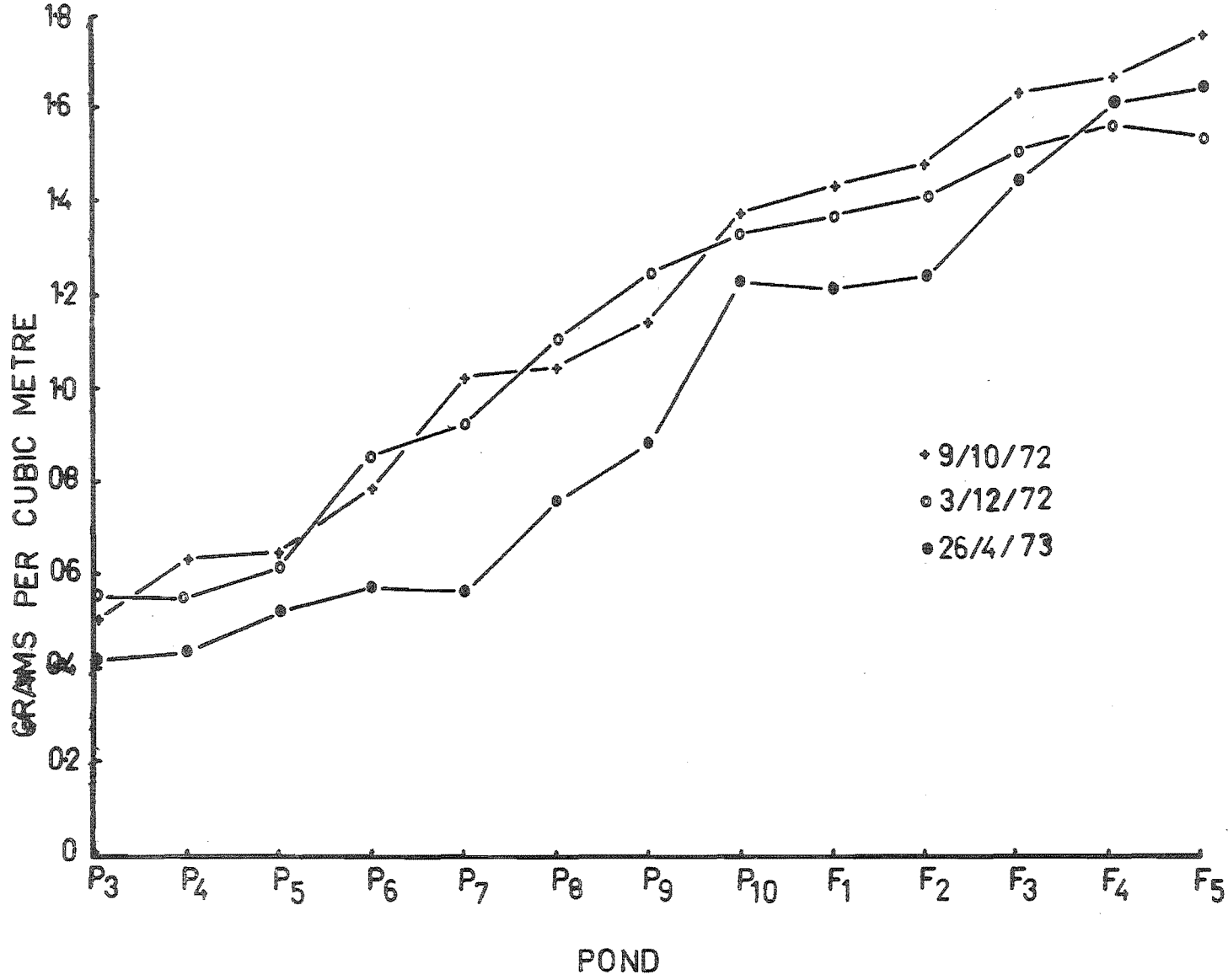
failed to disclose any organisms that would use silicon in large amounts. It was hoped that the level of silicon shown by the analyses would tend to confirm or refute this hypothesis. The graphs of concentration of silicon compounds (Fig. 1.8) showed steadily increasing concentrations proportional to the salinity increase up the concentrating ponds at about the rate that would be expected if the silicates were simply being concentrated by evaporation. It would not be expected that silicates would crystallise out at the concentrations achieved in the crystallising ponds since seawater is very under-saturated in respect of silicates, (Armstrong 1965). The concentration of reactive silicate in samples of seawater from the lake intake when seawater was being pumped in was 0.012 g/m^3. Such spot checks are not reliable, however, since the oceanic silicate levels exhibit pronounced seasonal and non seasonal fluctuations.

1.15 DISSOLVED OXYGEN

The solubility of gases, unlike that of most electrolytes, increases with decreasing temperature. Also, in aqueous electrolyte solutions gas solubility decreases with increasing concentration. The atmospheric gases are dissolved in seawater roughly in proportion to their abundance in the atmosphere but oxygen and carbon dioxide are in addition subject to perturbation by biological activity. These three functions that control the dissolved gas levels assume great importance in the Grassmere ponds. Being a solar salt plant, the ponds are laid out to absorb the maximum possible solar energy. As the evaporation proceeds during the summer the combination of temperature and concentration may produce very low levels of dissolved oxygen.

FIGURE 1.8

Determinations of reactive silicate in the ponds P3 - F5 on 9 October 1972, 3 December 1972 and 26 April 1973


GRAMS PER CUBIC METRE
0
02
04
06
08
10
12
14
16
18
P3
P4
P5
P6
P7
P8
P9
P10
F1
F2
F3
F4
F5
POND
9/10/72
3/12/72
26/4/73

METHOD

Water was taken at point 'S'(Fig 1.2), as for nitrate, from each pond at 1300 hrs. $\pm$ one hour, on each sampling date in 300 ml BOD bottles. Two samples were taken from each pond each visit. The sample was stored in dim light for 15 minutes until "fixed" by the addition of the manganous sulphate and alkaline iodide solution of the Winkler method of analysis. The method used was that described in Strickland and Parsons (1968).

RESULTS

The results (Table 1.5) show an extremely wide range of oxygen concentrations from 6.2 $m_g O_2/l$ on 27 July 1973, to 0.89 $m_g O_2/l$ on 29 January 1973. The values measured may be influenced by the photosynthetic activity of the algae at the time of sampling. Although 1300 hours is approximately the point of maximum isolation for the day. This does not necessarily guarantee maximum photosynthesis. Depletion of bicarbonate ions with water, low nutrient levels or light inhibition could have caused the peak photosynthesis to be earlier in the day. As would be expected, the highest oxygen tensions are formed in the lowest salinity ponds and during the coldest portion of the year but levels remain reasonably high until the water starts to rapidly warm up in late spring. The temperature was consistently high throughout summer and early autumn and oxygen levels were low all of this time. No stratification was found at any time of the year except for short periods when heavy rain had fallen in the absence of wind. The fresh rainwater formed a layer floating on top of the brine. This was a short-lived and rare event, however, and it is doubtful whether this had any effect on the oxygen levels.

	P3	P4	P5	P6	P7	P8	P9	P10	F1	F2	F3	F4	F5
10/8/72	5.32	5.16	5.29	5.11	5.07	4.94	4.88	4.86	4.37	4.21	3.96	3.93	3.62
25/8/72	5.17	5.29	4.96	5.03	4.88	4.68	4.72	4.37	4.15	3.63	3.49	3.41	3.02
5/9/72	5.26	4.98	4.77	4.74	4.12	3.86	3.79	3.67	3.72	3.45	3.24	3.08	3.12
21/9/72	4.64	4.43	4.19	3.31	3.74	3.45	3.13	3.16	3.02	2.84	2.45	2.41	2.32
9/10/72	4.28	4.06	3.73	3.75	3.32	3.04	2.89	2.71	2.78	2.43	2.31	2.27	2.22
26/10/72	4.14	3.78	3.59	3.27	3.32	3.15	2.71	2.43	2.06	2.12	1.96	1.89	1.71
11/11/72	3.24	3.13	3.15	2.72	2.58	2.67	2.76	2.26	2.01	1.82	1.83	1.78	1.44
7/12/72	3.02	3.06	2.48	2.30	2.20	2.21	1.52	1.39	1.22	1.01	0.91	1.13	0.99
30/12/72	2.81	2.42	2.11	1.24	1.31	1.22	1.21	1.20	1.16	1.14	1.11	0.92	1.11
10/1/73	2.52	2.48	1.86	1.72	1.81	1.77	1.42	1.02	1.11	1.08	1.00	0.99	0.92
29/1/73	2.21	1.83	1.67	1.74	1.3	1.12	1.18	1.09	1.23	1.12	1.08	1.04	0.89
15/2/73	2.34	2.12	2.02	1.81	1.90	1.97	1.42	1.31	1.36	1.22	1.12	1.06	1.00
23/2/73	3.10	2.62	2.22	2.11	2.19	2.00	1.78	1.62	1.58	1.60	1.36	1.20	1.21
29/3/73	2.90	2.78	2.49	2.32	2.14	2.19	2.13	2.11	2.00	2.02	1.82	1.44	1.01
12/4/73	3.52	3.13	2.68	3.22	2.92	3.02	2.84	2.63	2.41	2.00	1.69	1.48	1.32
26/4/73	4.82	4.61	4.12	4.08	3.87	3.75	3.94	2.93	2.72	2.19	2.26	1.82	1.54
10/5/73	4.77	4.59	4.31	4.02	4.19	3.97	3.62	3.44	3.09	2.47	2.19	2.02	1.91
25/5/73	5.34	5.14	4.76	4.31	3.82	3.62	3.71	3.33	2.62	2.31	2.37	2.23	2.20
14/6/73	5.88	5.55	5.01	4.18	4.22	4.26	3.88	3.56	3.12	2.82	2.67	2.21	2.32
28/6/73	5.74	5.8	4.6	4.51	4.62	4.72	4.99	3.51	3.52	3.48	3.34	2.91	2.92
12/7/73	6.19	5.29	5.02	4.83	4.46	4.28	4.15	4.02	3.76	3.59	3.39	3.16	3.02
27/7/73	6.24	5.13	4.78	4.61	4.27	4.49	4.38	4.16	3.82	3.84	3.71	3.80	3.81
9/8/73	5.46	5.6	5.24	5.10	4.89	4.62	4.60	4.31	3.70	3.83	3.99	4.11	3.90
13/9/73	5.28	5.26	2.16	3.66	3.50	3.39	3.41	3.28	3.37	3.49	3.44	3.40	3.41
28/9/73	5.33	4.99	4.63	4.49	4.30	3.89	3.82	3.91	3.36	2.83	2.99	2.91	2.82
18/10/73	5.01	5.06	4.81	4.63	4.51	4.26	3.91	3.82	3.67	3.81	3.52	2.99	2.90
1/11/73	4.92	4.71	4.28	4.41	4.40	3.87	3.80	3.61	3.30	2.96	2.72	2.84	2.52

Table 1.5 Oxygen tensions in milligrams per litre in each concentrating pond over the sampling period.

DISCUSSION

Although the overall values for oxygen in the pond waters are low, there is still a readily available supply since the ponds are very shallow and the region is very windy. This provides the ideal conditions for gas interchange with the waters. Anaerobic conditions exist just below the surface of the sediment, a very fine silt, and under the normally impervious crust of precipitated calcium sulphate. The presence of free oxygen in the waters was demonstrated by the rapid oxidation of sulphides to free sulphur when the black sub-crustal ooze was disturbed. This was noticed by Emery (1969) working on a coastal lagoon with a similarly fine sediment that had a sulphide odour when disturbed.

The lines of equal oxygen tension on Table 1.5 show that for only short periods in the lower salinity ponds does the oxygen tension rise above 5 mg/l of water and for most of the summer months there is less than 3 mg/l. Between November and January there was a rapid drop in oxygen levels. This corresponded with the periods of maximum salinity and highest temperatures but no proof exists to show that these were the sole factors operating. Oxygen tensions are close to the theoretical values for the conditions with some evidence of undersaturation of the highest salinities.

A similarly rapid rise in oxygen levels took place during the autumn. During the winter, with little evaporation and increasing rain dilution, levels very slowly rose between May and August until the effects of the 1973 spring became apparent. But from this point on the decrease in oxygen levels was slower than for the corresponding period in 1972 and at the close of sampling on 1 November 1973 the oxygen tensions

in the ponds were up to 1 mg/l higher than for 7 November 1972.

1.16 pH.

INTRODUCTION

In addition to the major salts dissolved in seawater, specifically those of strong acids and bases such as NaCl and $MgSO_4$, there are a large number of salts of weak or slightly dissociated acids, e.g., borates and silicates. The anions of such salts readily combine with protons provideing a buffering action to the system when H^+ or OH^- ions are added from biological reactions. Free protons are generally captured and hydrated forming a hydronium ion, H_3O^+, generally abbreviated to H^+. The equilibrium constant for dissociation of water is temperature dependent, (Horne 1969), so the H^+ concentration decreases at low temperatures.

The various forms of carbon dioxide, CO_2^-, HCO_3^-, CO_3^{2-}, exercise the greatest control over the H^+ concentration but Sillen (1961) feels that the H_3BO_3 - H_4SiO_4 system is also highly important.

In the vast oceans the amount of metabolising material relative to the bulk of the water is small and except in highly fertile surface layers the pH remains very close to the theoretical. By contrast, in a shallow water mass like the Lake Grassmere ponds perturbation of pH by photosynthetic and respiratory reactions may be very marked.

METHOD

Measurements of pH were made at about 1300 hrs on each visit to the ponds, using a Radiometer type 23 pH meter. For pH measurement a 20 m subsample was taken from the algal water sample (section 2.3). Before each measurement the meter was calibrated against a standard buffer composed of equal parts

of potassium dihydrogen phosphate and disodium hydrogen phosphate (pH 6.87), (Strickland and Parsons 1968).

RESULTS

The graphs shown in Fig. 1.9 are those for the extremes of the range of concentrating ponds, P4 being the lowest salinity pond that had a stable substrate cemented by crystalline $CaSO_4$, and F5 being the most saline at the end of the concentrating chain. P3, the first pond (Fig. 1.2) was not included in the overall consideration because of occasional saturation of the water with hydrogen sulphide caused by stirring of the fine, anaerobic substrate by strong winds. This occurred unpredictably when $CaSO_4$ was partially redissolved as low salinity water was introduced to the concentrating series.

In pond P4 at the beginning of sampling, 10 August 1972, the pH was falling and this fall continues, apart from a brief rise at the start of October, until a low point of pH 8.0 was reached on 11 November 1972. A rapid rise to pH 8.45 in January was the beginning of a period of relative stability during which the pH ranged between 8.35 and 8.45. This held throughout midsummer and autumn but by midwinter (June and July), a peak of pH 8.5 was recorded. The arrival of spring coincided with a slow fall in pH which gradually accelerated until by November the lowest pH of the study period, 7.9, was recorded.

When the values recorded for F5 are compared with those for P4 the same general trends are apparent. The same fluctuations were seen in both ponds but those of the more saline F5 were much less in amplitude. However, the low point in the summer of 1972 is displaced by more than a month to 30 December 1972. A slow rise stabilised at about pH 8.25

FIGURE 1.9

Determination of pH in ponds P4 and F5 taken at 1300 hours $\pm$1 hour throughout the study periods

SAMPLING DAY KEY

1 = 10/8/72
2 = 25/8/72
3 = 5/4/72
4 = 21/9/72
5 = 9/10/72
6 = 26/10/72
7 = 11/11/72
8 = 7/12/72
9 = 30/12/72
10 = 10/1/73
11 = 29/1/73
12 = 15/2/73
13 = 23/2/73
14 = 29/3/73
15 = 12/4/73
16 = 26/4/73
17 = 10/5/73
18 = 25/5/73
19 = 14/6/73
20 = 28/6/73
21 = 12/7/73
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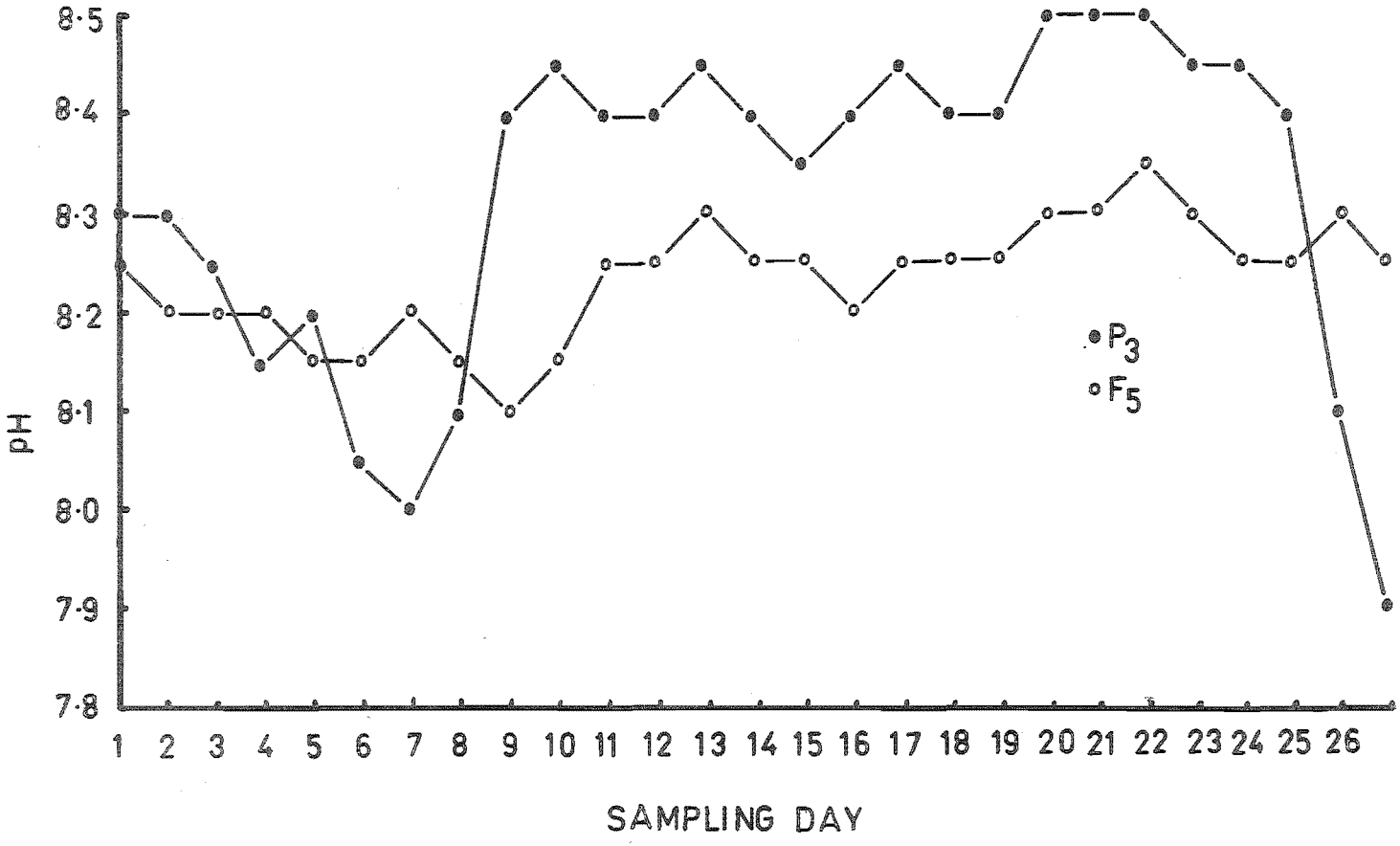
23 = 9/8/73
24 = 13/9/73
25 = 28/9/73
26 = 18/10/73
27 = 1/11/73


8·5
8·4
8·3
8·2
8·1
8·0
7·9
7·8
pH
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26
SAMPLING DAY
P3
F5

compared with 8.4 in P4. As in P4 the highest pH recorded during the study period occurred in July but it was not long lived and a fall similar to that seen in P4 began in early spring. A rise in mid-October interrupted this but when sampling was discontinued in November the pH was again falling.

DISCUSSION

The low pH measured in summer in P4 could be correlated with the rapid onset of the spring bloom of Dunaliella euchlora The rapid rise in pH during December similarly corresponded with the demise of the bloom and the partial exhaustion of nutrients from the water. Further circumstantial evidence that the algal bloom has an effect on the pH was shown by the displacement of the low point of the pH in F5 where the onset of the phytoplankton bloom was affected by the very high salinity.

A small drop in pH was found in both P4 and F5 during April 1973 but, as with the main drop, it was displaced by several weeks in F5. This may correspond to a partial recovery of the Dunaliella population after the summer low period.

The drop in pH was apparently related to the onset of intense algal growth. This relationship on its own is unusual since normally the increase in photosynthesis is accompanied by a rise in pH due to depletion of bicarbonate ions by the alga (Emery 1969). But the period when the pH was falling also coincided with the rapidly increasing salinity of the ponds, rising temperatures and the very rapid increase in Artemia numbers. The possibility exists that the pH variation could be brought about by some chemical interaction as concentration by evaporation proceeded. The change in pH was larger in P4 where the more rapid evaporation was

occurring. The period of falling pH during spring coincided with the period of increasing respiration of bacteria, Protozon and Artemia as the water began to warm up. The respiratory output of CO_2 would tend to depress the pH. The detailed records of bacterial and Protozan respiration are not available to support this theory. Excretary products of Artemia may also have some effect but it is difficult to imagine them producing the profound effects shown in Fig. 1.9. A literature search did not reveal any similar records therefore no firm hypothesis can be advanced to account for the variations.

SUMMARY

(1) Lake Grassmere has an average of 2281 hours of sunshine annually and the prevailing winds are dry north-westerlies. These conditions promote rapid evaporation of water throughout the pond series where salinities during the summer range from 160 ppt to 312 ppt.

(2) The ponds are approximately 0.75 m deep and prone to strong wave action. Associated wind induced water movement occurs between ponds.

(3) A wide annual range of water temperatures were found, ranging from $3^{o}C$ in July to $31^{o}C$ in January. Pond temperatures followed air temperatures closely.

(4) Sediments were five silts derived from the erosion of local hillsides. The median particle size was phi 5 but a large percentage of finer material caused dense turbidity durning wave action.

(5) Turbidity of the water was reduced or eliminated as the salinity increased to about 150 ppt and calcium sulphate

precipitated out as a crust bonding the sediment into a firm mass. In all ponds except P3 this condition persisted throughout the year but in P3 the crust redissolved in winter. Under the crust, anaerobic conditions developed.

(6) Reactive nitrate was abundant at most times of the year with concentrations ranging from 0.43 g/m^3 (F4 on 9/10/72) to 0.07 g/m^3 (P4 on 29/1/73).

(7) Reactive orthophosphate showed a much wider range of concentration than nitrate, ranging from trace amounts during early summer to 0.619 g/m^3 (25/5/73 in P4). This suggests that phosphate levels may affect algal frowth rates, but other forms of phosphorus and their transformations would have to be investigated before a definitive answer could be given.

(8) Analyses for dissolved silicate showed that the concentrations present varied with salinity ranging from 0.4 g/m^3 (P3 on 26/4/73) to 1.8 g/m^3 (Fs on 9/10/72). No evidence of biological uptake of silicate in large quantities was found.

(9) Oxygen dissolved in the water was greatly affected by salinity and temperature. A wide range of oxygen concentrations (6.2 mgO_2/l (P3 on 27/7/73) to 0.89 mgO_2/l (F5 on 29/1/73)) was found. It was concluded that dissolved oxygen levels were near saturation, at the conditions prevailing, at all times of the year.

(10) The pH of the ponds showed unusual fluctuations whereby values fell at the times phytoplankton populations began to bloom. These falls in pH also coincided with rapidly increasing salinity, rising temperatures, and very rapid increase in Artemia numbers. Fluctuations

were larger in the lower salinity ponds with a range in P4 from 7.9 (1/11/73) to 8.5 (12/7/73), and in F5 from 8.1 (30/12/72) to 8.3 (23/2/73).

SECTION 2

THE ALGAE OF THE LAKE GRASSMERE CONCENTRATING PONDS

2.1 INTRODUCTION

GENERAL BIOTA OF THE PONDS

The Macrofauna of the ponds P3 - F3 was totally dominated by Artemia and the microfauna by protozon. Macroflora was represented by a filamentous blue-green alga, tentatively placed in the Oscillatoriaceae, and microflora by bacteria and the two species of Dunaliella. In ponds P1 and P2 a slightly more diverse biota was observed when the seawater was in the process of preconcentration. With salinity at 81 ppt additonal macrofauna included; Copepoda (2 spp), Ostracoda (1 sp), and Nematoda (1 spp). Microflora included Chlorophyta (2 spp) and Chrysophyta (2 spp). Also found near P1 and P2 were two adults of the brine fly, Ephydrella sp. No larve were found in the ponds.

When the water in P1 and P2 was pumped into P3, at a salinity of approximately 125 ppt, the additional biota had disappeared.

Results of the salinity determinations from ponds P3 - F5 have shown that salinity is very high throughout the year, reaching saturation levels during summer in the F series ponds. In this harsh environment three species of algae were found, two unicellular flagellates and one filamentous form.

Two flagellates were members of the Volvocales, family Polyblepharidaceae, Dunaliella salina Teodoresco 1905, and Dunaliella euchlora Lerche 1937, and the filamentous form was a blue-green of the family Oscillatoriaceae.

Both species of Dunaliella have two flagella of equal

length at the anterior end of the cell. The chloroplasts are cup-shaped, one per cell, and possess a single pyrenoid. An eyespot is present but no contractile vacuoles. The smaller of the two flagellates, (D. euchlora), frequently formed amorphous palmellae of immobile cells within a common matrix.

Asexual reproduction was by longitudinal fission in the swimming phase, and by repeated division of the protoplast forming up to 16 zoospores in the palmella. Sexual reproduction was by isogamous, biflagellate zoogametes forming a thick walled, red pigmented zygote. Sexual reproduction was only observed in D. euchlora.

The cells have no well defined outer wall but instead there was a diffuse mucoid layer. Cell shape varied somewhat from ovoid to pyriform sometimes with lateral compression.

Dunaliella salina cells, Plates 2 and 3, show the typical cup-shaped chloroplast but the cell contents are frequently obscured by haematochrome, a red carotenoid pigment. The eyespot is small and one third the distance from apex to base of the cell. Mean size was 14 µm long and 9 µm at the maximum width. Green pigmented cells were formed at intermediate salinities but at very high salinities haematochrome masking was universal. The green form was originally described as a separate species, D. viridis Teodoresco 1905, but when it was shown that environmental factors were responsible for the change the two were synonymised (Smith 1944).

Dunaliella euchlora, Plate 1, is considerably smaller that D. salina being 9 µm long by 4 µm broad. The chloroplast is similar but the eyespot is adjacent to the flagellar basal body and is not always visible. Cell colour is always green in the vegetation phase. Haematochrome masking occurs only during sexual reproduction, when gametes may be red or green,

PLATE 1

A pair of recently divided Dunaliella euchlora. Prominent is the chloroplast appearing as parallel lines (C). Several large pale starch granules, (S), surround a pyrenoid, (P), and a lipid globule, (L), is visible near the cell wall. The nucleus, (N), is large and the nucleolus, (N_1), is visible in one cell. The point of attachment of the flagella is designated (F). The gelatinous sheath surrounding both cells is faintly visible, (G). Several small vacuoles, (V), are clustered between the nucleus and chloroplast.

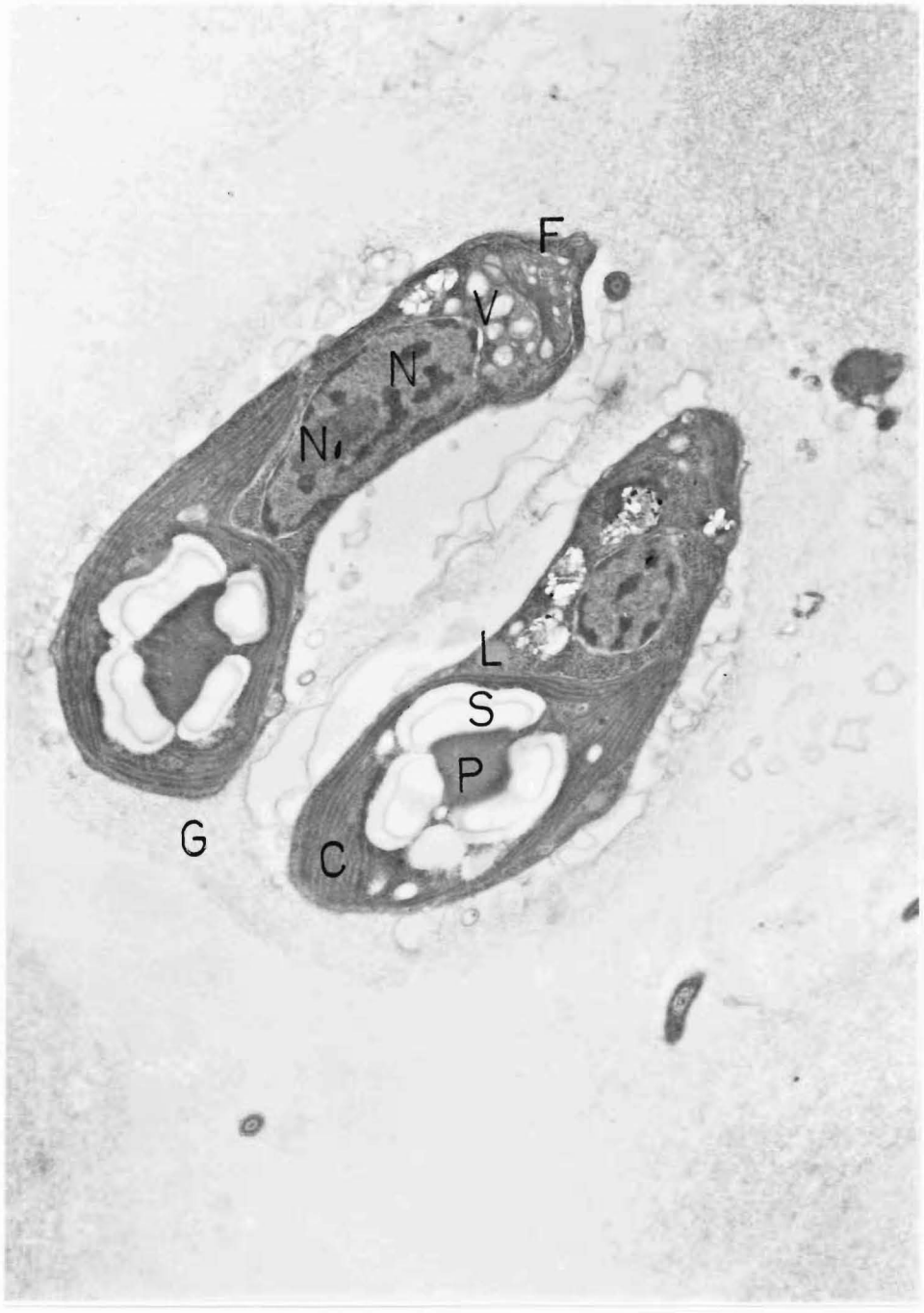

F
V
N
N
L
S
P
G
C

PLATE 2

A single vegetative cell of Dunaliella salina. Starch granules, (S), are irregularly dispersed throughout the cell and lipid globules, (or possibly pigment material), (L), are large and shown adjacent to the nucleus, (N). Mitochondria, (M), are visible at three points around the nuclear membrane. The chloroplast, (C), is diffuse and may be seen around the starch granules. Ribosomes, (R), fill the spaces between the lipid globules and small vacuoles, (V), occupy other pockets, particularly adjacent to the nucleus, the cell membrane is represented as a very thin layer surrounded by a thick gelatinous sheath, (G).

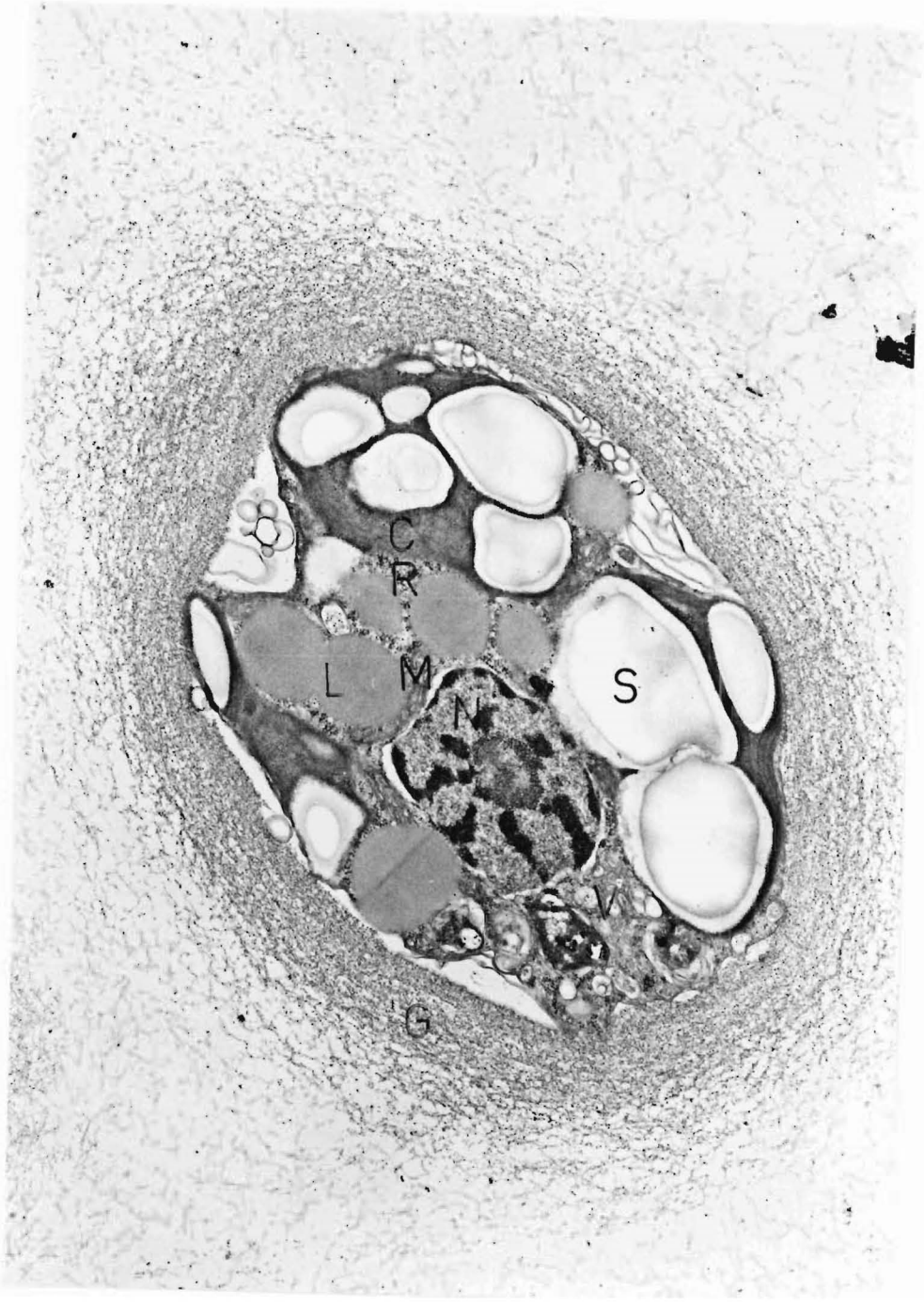
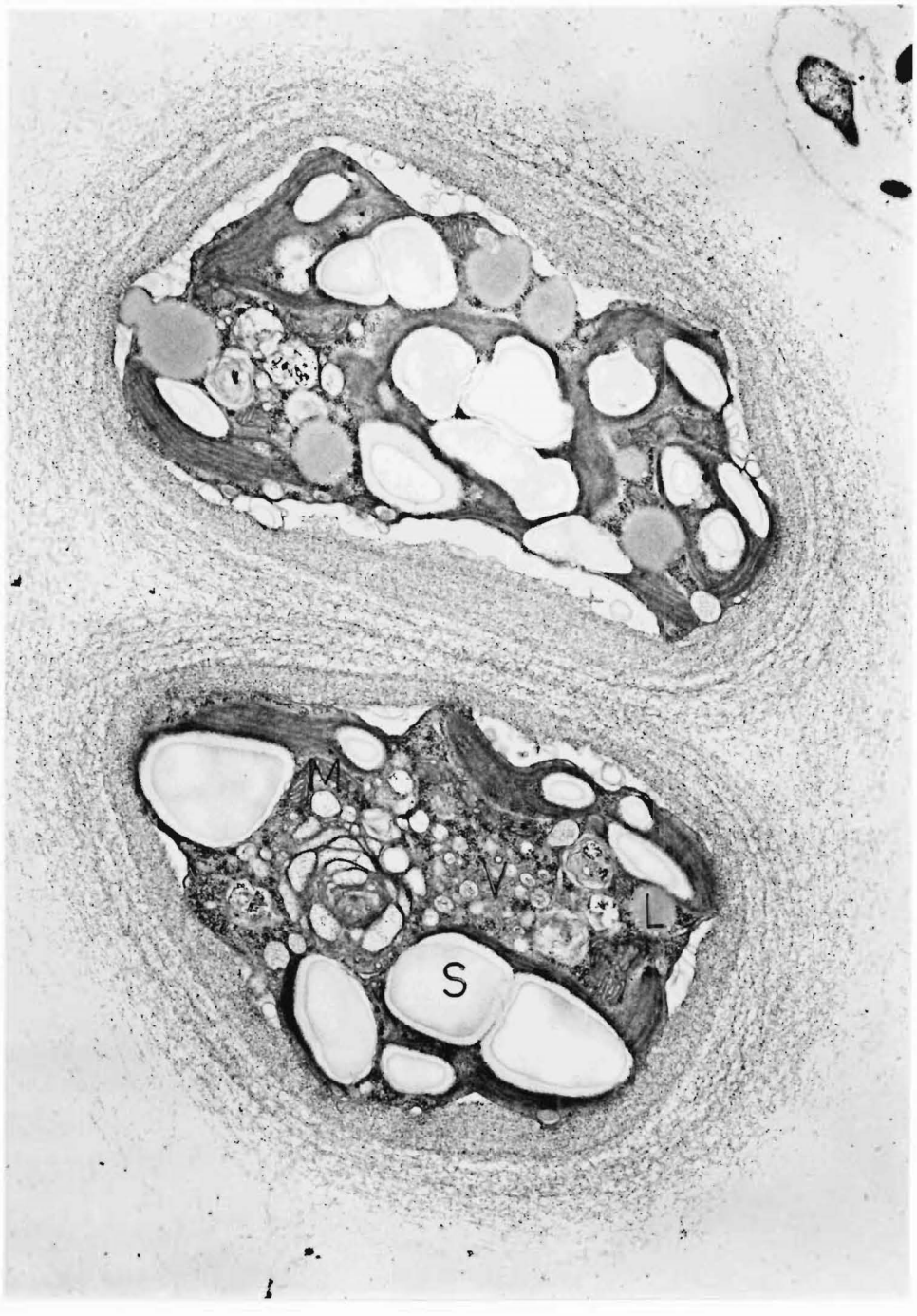

C
R
L
M
N
S
V
G

PLATE 3

A pair of recently divided Dunaliella salina. Much the same as plate 2 but showing mitochondria, (M), particularly clearly and numerous small vacuoles, (V). Starch granules, (S), and lipid or pigment globules (L), are abundant but no nuclear material is visible. The division of the gelatinous sheath is almost complete and pronounced layering is apparent in the material.


M
V
L
S

and in the resting zygote which is deeply pigmented. D. euchlora readily forms palmellae in which cells divide rapidly near the centre while flagellate vegetative cells are released from the edges.

The third alga present was a member of the family Oscillatoriaceae and order Cyanophyta or blue-green algae. It took the form of long chains of very small, 1.5 μm long x 2 μm wide, cylindrical cells surrounded by a well defined membrane. No chloroplast was present but the pigment and granular materials were distributed evenly throughout the protoplasm. The filaments were unbranched, very fragile, and characteristically grew in tangled masses. A thin gelatinous sheath was visible surrounding the filament. No heterocysts or spores were present and multiplication was by fragmentation of the filaments. These characteristics are typical of the Oscillatoriaceae, (Smith 1951). The alga has been tentatively identified as an Oscillatoria? species, but does not fit well with any currently described species.

2.2 REPRODUCTION OF DUNALIELLA EUCHLORA AND D. SALINA

Asexual reproduction of D. euchlora was observed in two circumstances. The first of these was as a palmella, a loosely aggregated mass of algal cells enclosed in a thin mucilaginous sheath. Division of cells was most rapid near the centre of the palmella but here no flagella were formed. Cells near the edges had extended flagella and were swimming off into the water column. The palmellae commonly composed up to 10% of the standing crop of algae in the ponds but were not extensively grazed by Artemia. This form of reproduction, therefore, provided a constant steady supply of vegetative cells.

The second form of asexual reproduction was simple longitudinal fission. This occurred in free swimming vegetative cells. After division each cell received one of the pair of flagella and the second was rapidly regenerated.

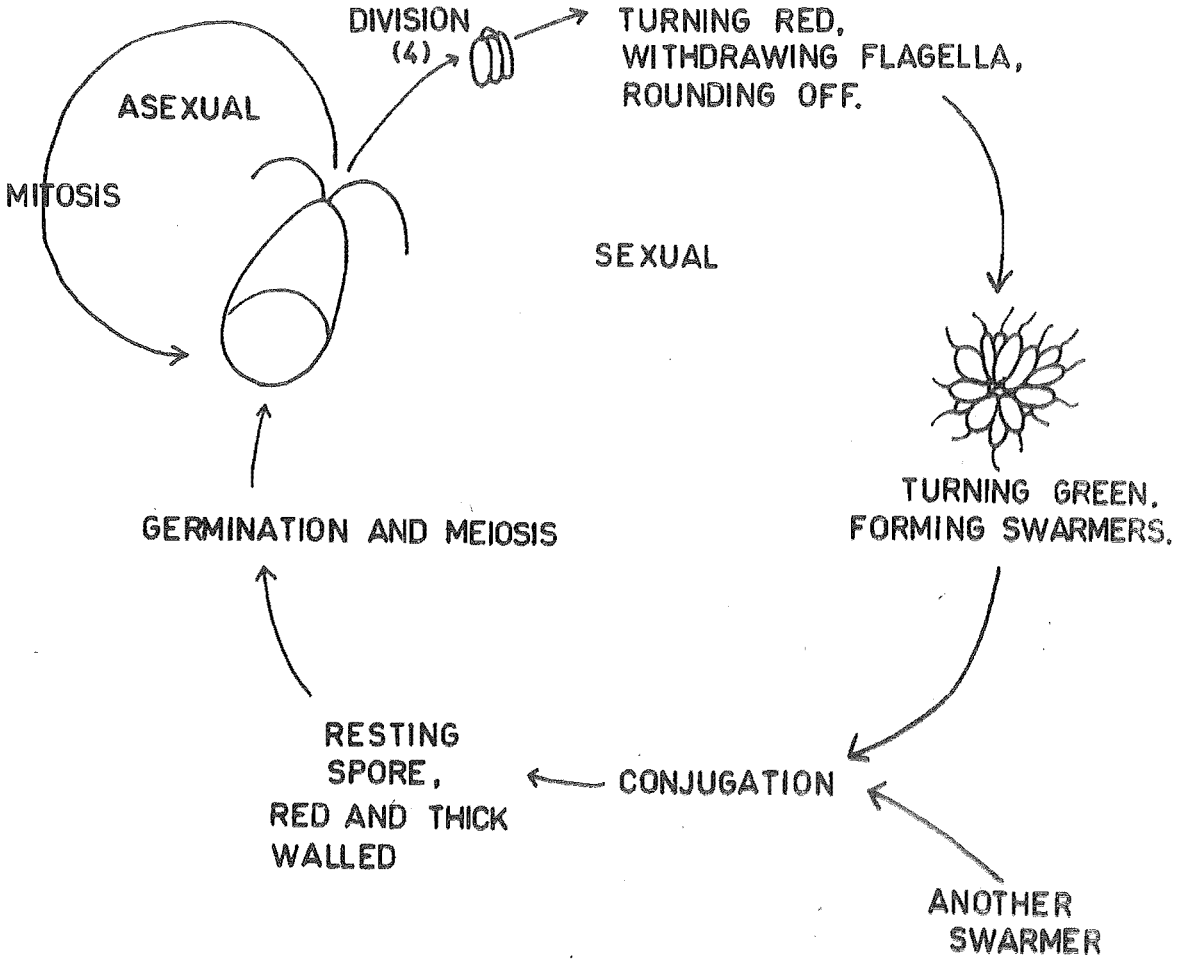
Sexual reproduction in D. euchlora was detected in the concentrating ponds during mid and late summer. Laboratory trials showed that it could be induced by maintaining cultures at high temperatures, (over 28^{o}C), or by providing salinities greater than 190 ppt and a medium lacking reactive orthophosphate. Sexual reproduction did not occur at salinities approaching saturation in the F series ponds. The onset of sexual reproduction was indicated by the appearance of red patches on the substrate crust of the concentrating ponds. Table 2.1 shows the time of the appearance of sexually reproducing algae. In the diagram " - " represents absence and " + " presence. The onset of sexual reproduction corresponded fairly well with the 200 ppt isohaline in Table 1.2 and the periods of low orthophosphate concentration shown in Table 1.4.

In reproducing sexually D. euchlora that were attached to the substrate first divided into four cells, (Fig. 2.1). These rounded off and then turned red due to the spread of the carotenoid pigment, haematochrome, through the cell starting with the area immediately surrounding the nucleus. The next stage consisted of a large number of divisions so that the original cell was transformed into a mass of very small isogametes. These slowly recovered the original green of the vegetative cell and were released by rupture of the former cell membrane. Conjugation then took place with other gametes. Fusion took about 20 minutes and occurred after gametes had attached at the flagellate end of cells. The

FIGURE 2.1

The sexual and asexual reproduction cycles of

Dunaliella euchlora


DIVISION
(4)
TURNING RED,
WITHDRAWING FLAGELLA,
ROUNDING OFF.
ASEXUAL
MITOSIS
SEXUAL
TURNING GREEN,
FORMING SWARMERS.
GERMINATION AND MEIOSIS
RESTING
SPORE,
RED AND THICK
WALLED
CONJUGATION
ANOTHER
SWARMER

	P3	P4	P5	P6	P7	P8	P9	P10	F1	F2	F3	F4	F5
10/8/72	-	-	-	-	-	-	-	-	-	-	-	-	-
25/8/72	-	-	-	-	-	-	-	-	-	-	-	-	-
5/9/72	-	-	-	-	-	-	-	-	-	-	-	-	-
21/9/72	-	-	-	-	-	-	-	-	-	-	-	-	-
9/10/72	-	-	-	-	-	-	-	-	-	-	+	-	-
26/10/72	-	-	-	-	-	-	-	+	+	+	-	-	-
11/11/72	-	-	-	-	-	+	+	+	+	+	+	-	-
7/12/72	-	-	-	-	-	+	+	+	+	+	-	-	-
30/12/72	-	-	-	+	+	+	+	+	+	+	-	-	-
10/1/73	-	-	-	+	+	+	+	+	+	+	+	-	-
15/2/73	-	-	+	+	+	+	+	+	+	+	-	-	-
23/2/73	-	-	+	+	+	+	+	+	+	+	+	-	-
29/3/73	-	-	+	+	+	+	+	+	+	+	+	-	-
12/4/73	-	-	+	+	+	+	+	+	+	+	-	-	-
26/4/73	-	-	-	-	+	+	+	+	+	+	+	-	-
10/5/73	-	-	-	-	-	-	+	+	+	+	+	-	-
25/5/73	-	-	-	-	-	-	+	+	+	+	-	-	-
14/6/73	-	-	-	-	-	+	+	+	+	+	-	-	-
28/6/73	-	-	-	-	-	+	-	+	+	-	-	-	-
27/7/73	-	-	-	-	-	-	-	+	-	-	-	-	-
9/8/73	-	-	-	-	-	-	-	-	-	-	-	-	-
13/9/73	-	-	-	-	-	-	-	-	-	-	-	-	-
28/9/73	-	-	-	-	-	-	-	-	-	-	-	-	-
18/10/73	-	-	-	-	-	-	-	-	-	-	-	-	-
1/11/73	-	-	-	-	-	-	-	-	-	-	-	-	-

Table 2.1 Ponds containing sexually reproducting D. euchlora, "+", and ponds where none was found, "-".

zygote rounded off, withdrew flagella and formed a thick walled, deep red, resting stage. Germination of the resting stage was preceeded by meiotic division to produce four new vegetative cells.

In D. salina only vegetative multiplication was seen. No palmellae were formed and no resting stages were seen at any period of the year.

Very little information is available regarding multiplication in Dunaliella species although Teodoresco (1906) observed conjugation in D. salina. This took 10 minutes for complete fusion and the formation of a four flagellated form. MacDougal (1914) also noted conjugation in samples of D. salina from the Salton Sea, California, but as with Teodoresco, he could not deduce any more. Lerche (1937) confirmed that both D. euchlora and D. salina undergo sexual reproduction and the processes are essentially similar to those described above.

2.3 ALGAL BIOMASS IN THE PONDS

Dunaliella euchlora existed in two phases in the Lake Grassmere ponds; a free-swimming flagellated cell and a sessile palmella stage. Artemia fed almost exclusively on the motile form by filter feeding. In the concentrating ponds up to salinities of approximately 290 ppt the alga present was almost exclusively Dunaliella euchlora with very small amounts of the oscillatoriacean which was not ingested by Artemia.

In the most saline pools both species of Dunaliella existed with the highly pigmented species, D. salina often in greater concentrations and producing vivid red blooms, (Plate 4). Although the red colour of the water indicated a bloom, the density of the pigment was not always proportional to the

PLATE 4

An aerial view of part of the concentrating series and factory buildings at Lake Grassmere. Shown are part of ponds P1, P10, F2, F3, F4 and F5, (Fig. 1.2). Deep storage pond Ds 1 is shown at top right. A *Dunaliella salina* bloom is well developed in F3 judging by the red colour. Slight pigmentation is also visible in F2 and F5. The small ponds to the lower right are saturated brine used to wash harvested salt. The saturated solution supports dense blooms of *D. salina*. The white piles are harvested salt awaiting processing and bagging, (approx. 150 000t).

Photograph: V.C. Brown

density of cells in the water because the red carotenoid pigment is very water soluble and leaches from both dead and living cells. The accumulation after several minor outbreaks tended to produce the impression of a major bloom whereas the actual number of D. salina cells was not very large. Very dense, deep red growth of D. salina appeared only at saturation salinity just before the water was pumped off into deep storage or to crystallising ponds. In view of this management practice the occurrence of major blooms of D. salina may be considered a transitory event rather than a permanent feature of the concentrating series. In the present study a bloom is identified as a period of very high production of algae but not necessarily associated with a very high density of standing crop. This distinction is made because generally throughout the concentrating series blooming of the algae is accompanied by an increase in Artemia biomass that consumes the increased production. Thus, even though production of algae may be high, the water may retain its clarity. The exceptionally dense crops of D. salina in saturated brine achieve these numbers because Artemia breeds and feeds very much less rapidly in this environment than at lower salinities.

SEPARATION OF PHYTOPLANKTON FROM ZOOPLANKTON AND DETRITUS

Water samples for algal density and biomass determinations were taken in 1 litre plastic containers from the point marked 'S' in Fig. 1.2. The containers were immersed to a depth of 400 mm and allowed to fill. In establishing these stations random sampling consisting of five samples were taken around the margins of each pond on the first two sampling occasions. They were all analysed as described below and showed no difference in the distribution of algal cells

throughout each pond. Vertical samples at the sites did not show any stratification in the water column. The almost continual wind induced water circulation was considered to be responsible for the good mixing.

The water was passed through a 0.1 mm mesh plankton net which filtered out all Artemia adults, nauplii and eggs, and the larger protozoa. It also removed most of the detrital material that consisted mainly of cast exoskeletons of Artemia. The filtrate was then examined microscopically and the volume of organisms other than algae, such as protozoa, estimated, (Gillbritch 1952). Since all organic material was going to be included in the estimate of organic carbon, and specifically the algal carbon was being measured, the estimated volume of protozoa was used as a correction factor and subtracted from the results of the algal biomass determination. The shapes of the protozoa were regarded as prolate spheroids and the volume of cell material calculated. This was a correction factor which varied between two and six present depending on the season.

DETERMINATION OF BIOMASS BY WET COMBUSTION

The method described by Strickland and Parsons (1968) which employs a sulphuric acid/potassium dichromate oxidant was used. They state: "Results given by this method are in terms of glucose carbon. The true carbon content of particulate organic material would only approach this value if all of the carbon were present as carbohydrates. Normally, results will be high or low according to the nature of the organic material but the average composition of phytoplankton and detritus is such that the true carbon content is within 10 - 20 percent of the oxidation value given by the present procedure. The oxidisable carbon is a realistic measure of the energy stored

in a crop."

The decision to use a wet combustion method for determining algal biomass rather than a pigment extraction method was made for several reasons: both Dunaliella euchlora and D. salina exhibit periods of intense red carotenoid pigment continually, but at varying intensities, frequently masking the nucleus only in vigorous cells but totally masking the contents of senescent cells, and thick walled cysts. D. euchlora is predominantly green in vegetative form but strong red pigment production occurs when sexual reproduction is about to take place. When environmental conditions are becoming limiting, particularly at high salinities and low reactive phosphorous levels, the sessile phase of D. euchlora may also develop intense red pigmentation.

The presence of intense red carotenoid pigment makes chlorophyll estimation very difficult through its masking effect. If the proportion of red pigment is constant this may be able to be used in estimations but this is also extremely variable. The number of variables makes pigment analysis of doubtful value even discounting the possible interference from dissolved pigment. It was concluded that organic carbon analyses would prove superior in this situation.

METHOD

One litre of water that previously had been passed through a 0.1 mm mest net to remove zooplankton was drawn through a millipore filter funnel fitted with a 4.5 cm Whatman GF/C glass fibre filter. The filters had previously been subjected to 500^{o}C for 30 minutes to burn off any residual organic material. A moderate vacuum, (200 mm. Hg)$_{1}$, was used to prevent algae being ruptured and their cell contents being

drawn through the filter. After the filter had been sucked dry the vacuum was released and it was flushed with two applications of 0.25 M sodium sulphate solution to remove most of the sodium chloride from the lake water. Between applications the filter was sucked dry. The removal of chloride from the material to be oxidised is important since chloride interferes with the dichromate oxidant by reducing it to chromate. The balance of the chloride was removed by the next step which was heating with 70 percent phosphoric acid. The preheated filter was heated with the oxidising mixture until no more reduction of dichromate to chromate was taking place. The reduction of the dichromate was determined by measureing the extinction of a blank dichromate/sulphuric acid solution against the reduced sample with a Bausch and Lomb "Spectronic 20" spectrometer. The extinction found was corrected for absorbance by trivalent chromium, (E corrected = 1.1E found), and then applied to the equation:

$$mgC/m^3 = \frac{E \times F \times v}{V}$$

where V = volume in litres of lake water used, F is a factor determined by combustion of a solution of pure glucose, v = volume of dichromate oxidant used and mgC/m^3 is the oxidisable carbon per cubic metre of water.

RESULTS

The standing crops of algae on 27 occasions and in 13 ponds are shown in Table 2.2. At the beginning of the study period the spring increase for 1972 was just beginning and on this date, 10/8/72, the highest algal biomasses were found in ponds P7 and P8, (1210 mg/m^3 and 1370 mg/m^3 respectively). At this time standing crops in the very saline F series were much smaller than those in the concentrating series and the

lowest biomasses were found in F3 and F5, (290 mg/m^3 and 220 mg/m^3 respectively).

After 8th August, an increase in algal growth became evident although the start of this increase was retarded in the F series where it was not found until the 9th September sample. The highest biomasses in the early spring period were found in ponds P8 - F5 on 21st September but the biomass of algae in ponds P3 to P7 continued to rise to a peak about 11th November. At the time the algal biomass was falling in the high salinity ponds, with the exception of F4 and F5 which were showing sporadic blooms of the red pigmented alga, Dunaliella salina. Except for these blooms, algal biomasses continued to fall throughout summer and early autumn and did not begin to rise again until late autumn. This increase continued into the 1973 winter and spring.

DISCUSSION

The peak abundance of algae in the Grassmere ponds is high by oceanic standards although similar values have been recorded in surface waters at times of high productivity. Riley (1941a) found values for total organic carbon content of 3100 mg/m^3 in the top one metre in Long Island Sound, Eastern U.S.A. which he interpreted as the spring maximum for the area. A somewhat lower figure was found by Jenkins (1956) when sampling at 50 m off Plymouth, England. Here 1500 mg/m^3 was recorded and at the same time at the surface 1000 mg/m^3 was found. Miyake, Kigoshi, Sigiura and Sarohushi (1954) published records of up to 2000 mg/m^3 off the Japanese coast during August. This figure was challenged by Strickland (1960), however, who considered that zooplankton and detritus had been included in the sample. The levels of organic carbon found in the Grassmere ponds are by no means exceptionally

	P3	P4	P5	P6	P7	P8	P9	P10	F1	F2	F3	F4	F5
10/8/72	920	1110	1020	950	1210	1370	1020	830	600	710	290	380	220
25/8/72	980	1480	1310	1120	1390	1920	1070	1070	740	870	420	510	430
5/9/72	1690	1820	1240	1480	1620	1610	920	1000	790	980	1000	690	310
21/9/72	1470	1780	1720	1920	1880	860	1140	1260	1200	1080	1210	970	920
9/10/72	1620	2270	2210	1880	2210	620	720	970	820	990	710	1020	1080
26/10/72	1510	2470	1920	1690	1460	420	660	610	470	620	560	680	1690
11/11/72	2020	2660	2110	1070	1310	210	490	230	260	310	490	520	820
7/12/72	1520	2090	1140	770	680	160	140	290	360	120	360	630	290
30/12/72	970	1000	690	520	400	270	110	220	160	130	410	820	1040
10/1/73	620	720	1060	390	320	420	360	280	200	160	370	1030	1670
29/1/73	1060	880	1440	680	300	280	320	240	170	230	220	600	620
15/2/73	270	680	720	260	210	210	180	220	130	180	290	890	480
23/2/73	180	410	610	290	340	220	170	290	80	140	260	130	210
29/3/73	100	380	480	190	240	260	210	380	220	370	340	720	830
12/4/73	90	110	170	130	200	390	420	510	690	1010	1260	1080	1880
26/4/73	120	260	380	460	670	840	300	410	540	830	720	690	2040
10/5/73	160	190	690	310	190	280	190	270	260	410	270	140	1030
25/5/73	260	420	770	380	270	100	80	100	110	160	210	280	620
14/6/73	140	640	830	620	890	140	110	190	240	180	240	360	210
28/6/73	330	820	970	870	1230	270	420	610	360	340	140	420	110
12/7/73	260	1110	820	1090	1440	1040	660	750	330	440	290	380	160
27/7/73	390	1630	1290	1990	1680	1280	1290	1620	1610	620	540	470	220
9/8/73	620	1890	2640	2080	2030	1920	2000	2060	2610	1670	920	660	320
13/9/73	760	2020	2270	2820	2610	2390	2180	2290	2840	1790	1220	740	230
28/9/73	1440	2110	2010	2160	1990	2290	2000	2310	1920	1410	1010	920	460
18/10/73	1720	2000	2310	2000	1740	1690	1460	1920	1270	1060	1000	710	630
1/11/73	2280	1640	1970	2060	1670	1480	920	870	1020	690	830	620	1090

Table 2.2 Biomass of algae expressed as milligrams of oxidisable carbon per cubic metre.

high as the figure of 2000 mg/m^3 of chlorophyll as recorded by Talling, Wood, Prosser, and Baxter (1973) indicates. Converted to mgC/m^3 using the equation suggested by Strickland (1960) this gives a value of 120 gC/m^3, (Grassmere maximum approximately 2.9 gC.m^3).

2.4 DISTRIBUTION OF ALGAE IN RELATION TO SALINITY

Looking down on the Grassmere complex at almost any time between spring and early winter the first impression is the variety of colour in the ponds. The most saline ponds in the concentrating series P1 - F5 normally appear dull pink, Plate 4, whereas the least saline and moderately saline ponds look blue/green. Meanwhile the saturated brine used for washing the crystalline salt prior to drying and bagging shows an intense red colour that also occurs in small puddles of saturated brine around the base of the storage slabs. This immediately suggests that the two algae responsible for producing these colours, Dunaliella euchlora (green) and Dunaliella salina (red) have different salinity optima.

METHOD

Lake Grassmere pond water taken in September 1973 was adjusted to the following salinities with distilled water, 100, 150, 200, 250, 300 ppt. Saturated brine, (about 312 ppt), was also prepared by evaporation of lake water at room temperature. The levels of nitrate and phosphate in the solutions were adjusted to 0.08 g/m^3 and 0.01 g/m^3 respectively by the addition of sodium nitrate and potassium hydrogen phosphate. Two series of five 500 ml Erlenmeyer flask cultures were set up. One was inoculated with Dunaliella euchlora and the other with D. salina. The cultures were kept at room temperature, (25°C $\pm$5°C), with

light supplied by two 65 watt cool white fluorescent tubes for 30 days with the salinity being adjusted daily and the nutrient levels every fourth day. Sampling of the algae was by shaking the container and extracting three one ml pipette samples. Numbers present were counted with a haemocytometer and the mean of ten counts recorded. When cell density was very small 10 ml samples were centrifuged down and resuspended in 0.5 ml of solution.

RESULTS

Fig. 2.2 shows the growth of the population of Dunaliella euchlora, expressed as cells/ml, in the six salinities used. Growth was most vigorous at the lowest salinity, 100 ppt, after an initial lag period of five days. The logarithmic growth phase extended from day 10 to day 20 when the population began to stabilise at about 18000 cells/ml. Growth rates at 150, 200 and 250 ppt were slower and the logarithmic growth stage was not so pronounced. However, in 150 ppt and 200 ppt the final stable density was similar to that found at the lowest salinity. The growth rate in the 250 ppt culture matched those at 150 and 250 ppt until on day 20 it levelled out at about 12000 cells/ml.

Growth rate in the 300 ppt solution was much slower than at lower salinities and numbers had increased to only 7000 cells/ml by the 26th day. A similar situation was found in saturated brine but with a still lower final density of 3700 cells/ml.

Results of a similar set of trials carried out with D. salina are shown in Fig. 2.2.1. They show a decline in cell numbers rather than an increase as in D. euchlora in the 100 ppt cultures. A small increase in numbers from 1000 cells/ml to 2800 cells/ml was found at 200 ppt and a slow

FIGURE 2.2

Growth of Dunaliella euchlora in culture at salinities of 100, 150, 200, 250, 300 ppt and saturated brine

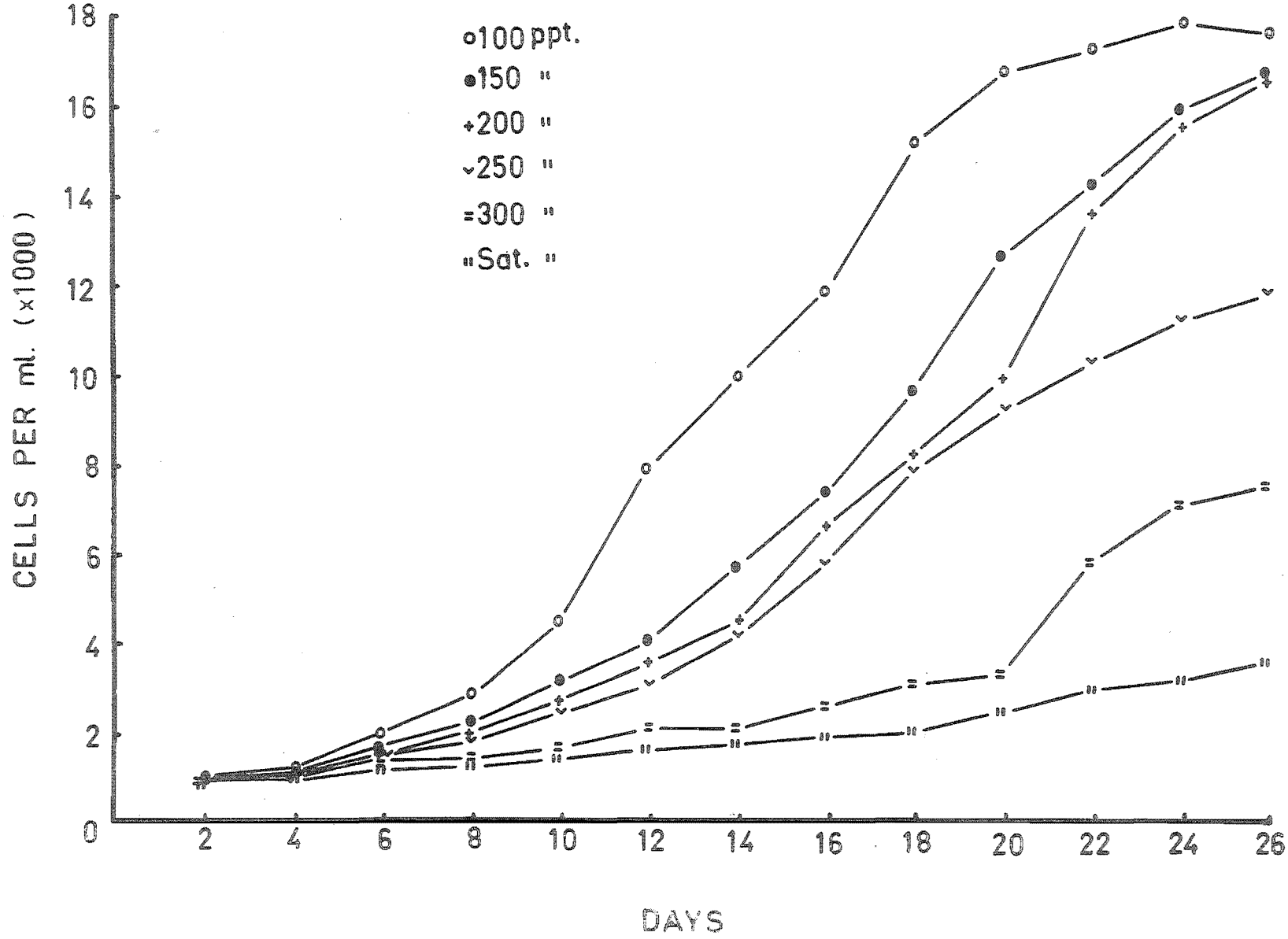
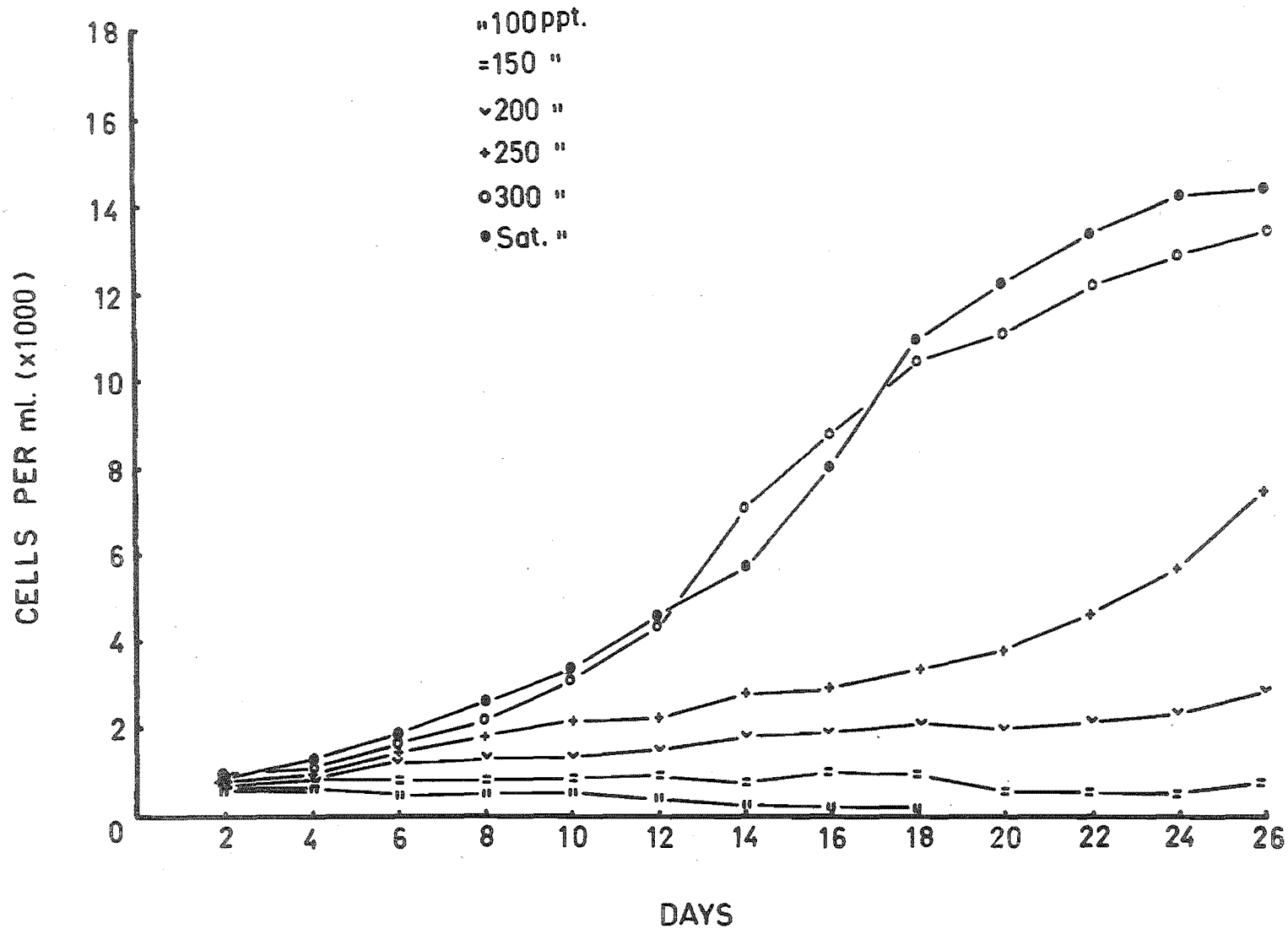

CELLS PER ml. (x1000)
DAYS
o 100 ppt.
• 150 "
+ 200 "
v 250 "
= 300 "
" Sat. "
0
2
4
6
8
10
12
14
16
18
20
22
24
26

FIGURE 2.2.1

Growth of Dunaliella salina in culture at salinities of 100, 150, 200, 250, 300 ppt and saturated brine


"100 ppt.
=150 "
˘200 "
+250 "
o300 "
•Sat. "
CELLS PER ml. (x1000)
0
2
4
6
8
10
12
14
16
18
2
4
6
8
10
12
14
16
18
20
22
24
26
DAYS

increase which was showing signs of an increased rate late in the experimental period, was observed in the 250 ppt solution. A very rapid logarithmic increase took place in both the 300 ppt solution and the saturated brine. The increase in cell numbers was initially faster in the saturated brine but slowed after the twelfth day and the number in the 300 ppt culture moved fractionally ahead. This was reversed after the 18th day and the final count put the numbers in the saturated brine about 2000 cells/ml ahead of those in the 300 ppt solution.

DISCUSSION

There is a large difference between the salinity optima, as measured by population density, of D. euchlora and D. salina. That for D. euchlora lies somewhere between normal oceanic salinity, (35 ppt), and 200 ppt, although at Lake Grassmere it lies between 100 ppt, (the minimum salinity found), and 200 ppt. The optimum for D. salina is at the extreme salinity of saturated brine, although growth is still good somewhat below saturation. Gibor (1956) compared several "strains" of D. euchlora, identified as D. viridis, obtained from the concentrating ponds of the Leslie Salt Company on San Francisco Bay and found that they had different optima. Over all, however, growth was found to be most vigorous at about 100 ppt salinity although it occurred from fresh water up to 220 ppt. When testing D. salina, Gibor found that the range of salinities that supported good growth was between 35 ppt and saturated brine with maximum multiplication rate at 150 ppt. This range is much larger than at Grassmere. Gibor found that both D. euchlora and D. salina could be acclimatised to salinities outside their normal range with prolonged culture. In the

present study acclimation of algae to different salinities in the ponds could have affected the results of experiments. This would be difficult to examine and control for because rapid changes in salinity covering a wide range occur as a result of salt works operations.

McLachlan (1959) also found that a large variation in growth between cultures of D. euchlora could be explained by the presence of two strains. They were indistinguishable morphologically but their growth rates differed by 100 percent in laboratory culture using modified ASP medium.

2.5 NUTRIENT REQUIREMENTS OF ALGAE

The two major macro-nutrients that are considered to influence the growth rates of algae are nitrate, Section 1.11, and phosphate, Section 1.12. To estimate the minimum concentrations of these nutrients necessary for vigorous growth of Dunaliella euchlora and D. salina a set of solutions was set up containing controlled amounts of nitrate and phosphate.

METHOD

The culture solution used was the modified ASP medium described by McLachlan (1959) which had potassium hydrogen phosphate as the phosphorus source and potassium nitrate as the nitrate source and a full range of inorganic micronutrients. The media were set up in four series of five 250 ml Erlenmeyer flasks each containing 200 ml. Two of the series were tested each two days for nutrient levels, and the other two series were undisturbed except for the removal every second day of small volumes for cell counts as in 2.4. On the basis of the analyses of the control flasks, fresh nutrient salts were added to the experimental series to maintain the original concentrations.

EXPERIMENTAL SERIES (1)

nitrate g/m^3	phosphate g/m^3
0.8	0
0.8	0.001
0.8	0.010
0.8	0.100
0.8	0.200

EXPERIMENTAL SERIES (2)

nitrate g/m^3	phosphate g/m^3
0	0.200
0.01	0.200
0.10	0.200
0.50	0.200
1.00	0.200

Incubation was for 16 days at 26°C 15 cm from the light source of two 65 watt fluorescent tubes. The experiment was carried out with D. euchlora and D. salina at salinities determined in section 2.4 as being good for growth. They were 150 ppt for D. euchlora and 300 ppt for D. salina.

RESULTS

Great difficulty was experienced in maintaining nutrient levels as bacterial populations began to develop in the flasks but it was felt that at least an approximation to the stated levels was adhered to. The upsurge in bacterial populations was intially rapid and their consumption of nutrients was high. However, within a few days the culture system stabilised and the bacterial population became constant (as determined by microscopic examination) and nutrient levels could be well controlled. From this point on the experimental

conditions, as stated in the method, were fulfilled. Figs 2.3 and 2.3.1 show the increase in numbers of D. euchlora with limited phosphate and limited nitrate respectively. When no nitrate or phosphate was present, cell numbers stayed constant for a short period and then began to decline. Low levels of phosphate (0.001 g/m^3) and nitrate (0.01 g/m^3) both resulted in very slow growth of algae with only 5100 cells/ml and 380 cells/ml respectively being present after 16 days incubation. However, there was no substantial difference in growth rate at the three highest mentioned levels.

When D. salina was cultivated under identical conditions, except for a higher salinity, a similar drop in cell numbers was found when either of the nutrients was totally absent, (Figs 2.4 and 2.4.1). Marked growth inhibition was found when phosphate levels of 0.001 g/m^3 and 0.010 g/m^3 were present but growth was fractionally faster at the higher phosphate level. At the 0.100 g/m^3 and 1.00 g/m^3 phosphate concentration there was rapid multiplication and no significant difference between the two treatments.

When the nitrate concentration was varied, (series 2) total absence caused a stead drop after a brief period of multiplication in the first four days. An increase in concentration to 0.01 g/m^3 produced slow growth but with a ten times increase to 0.1 g/m^3 the cell density was approximately doubled. At the high nitrate concentrations of 0.5 g/m^3 and 1.00 g/m^3 growth was again stimulated and similar.

DISCUSSION

The results indicate that inorganic phosphate levels of 0.001 g/m^3 have a strong inhibitory effect on the multiplication of both Dunaliella euchlora and D. salina. It also appeared

FIGURE 2.3

Growth of Dunaliella euchlora in culture at a salinity of 150 ppt and five different phosphate concentrations

FIGURE 2.3.1

Growth of Dunaliella euchlora in culture at a salinity of 150 ppt and five different nitrate concentrations

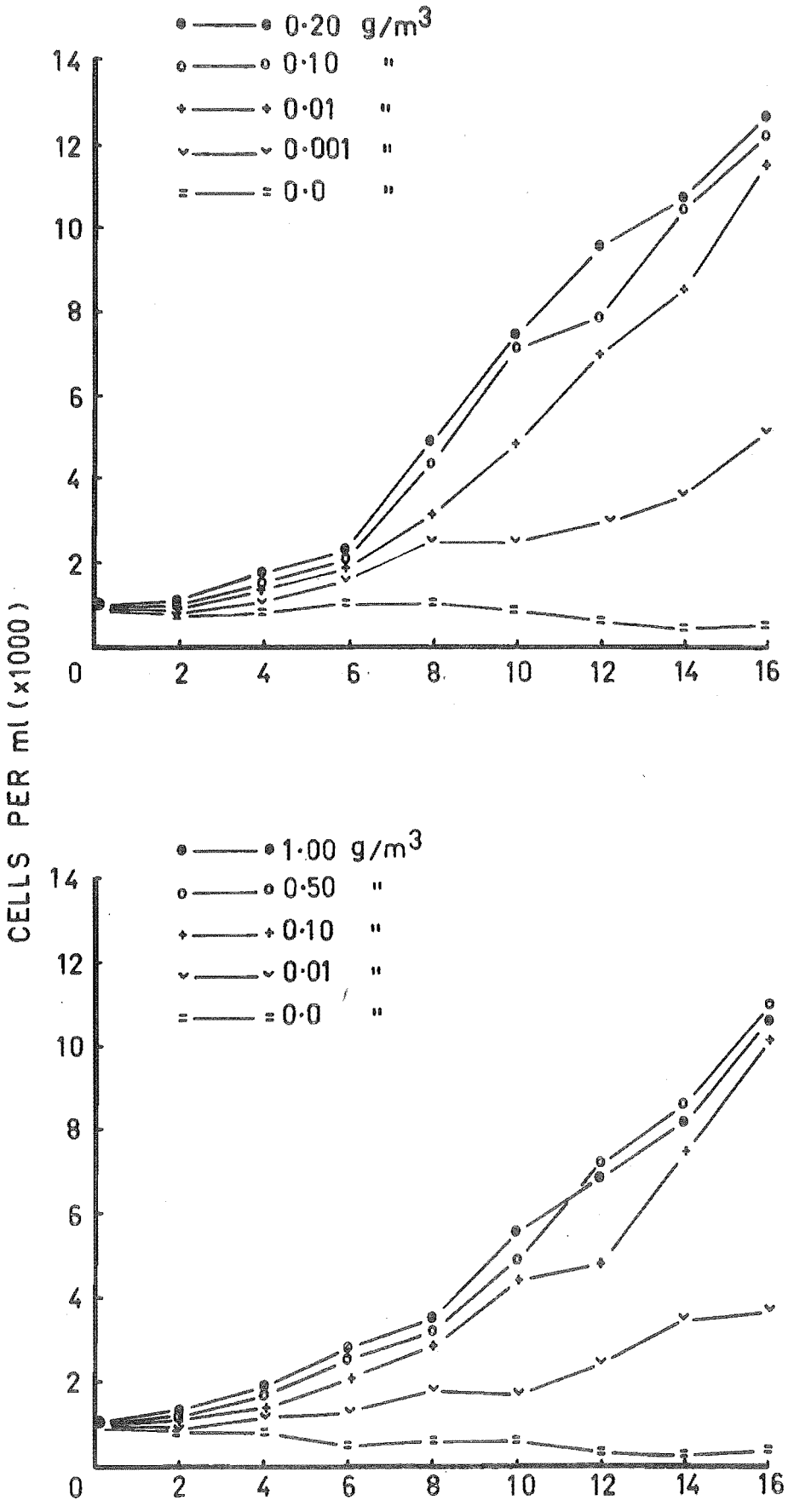
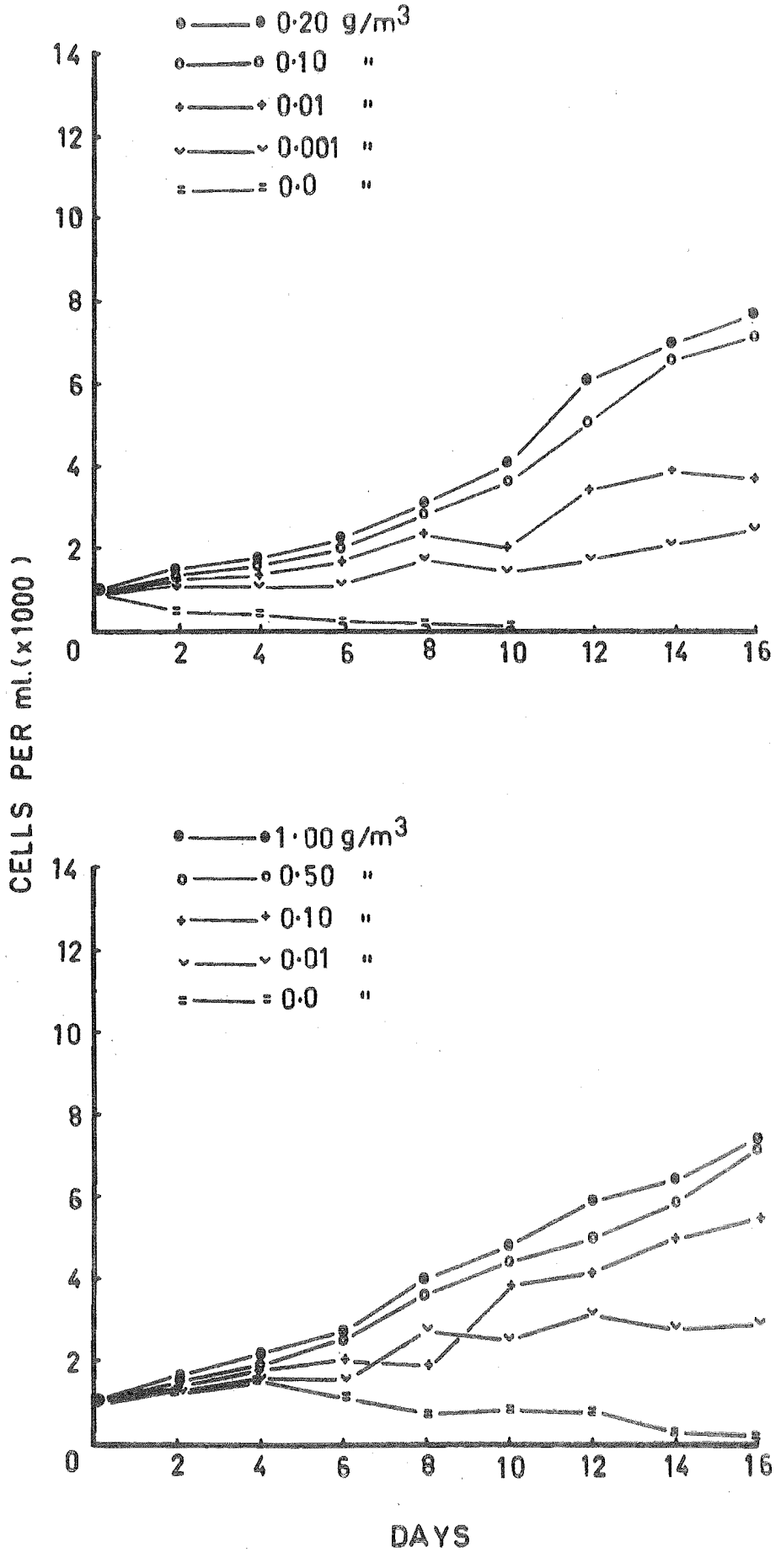

0·20 g/m3
0·10 "
0·01 "
0·001 "
0·0 "
1·00 g/m3
0·50 "
0·10 "
0·01 "
0·0 "
CELLS PER ml (x1000)
0
2
4
6
8
10
12
14
16

FIGURE 2.4

Growth of Dunaliella salina in culture at a salinity of 300 ppt and five different phosphate concentrations

FIGURE 2.4.1

Growth of Dunaliella salina in culture at a salinity of 300 ppt and five different nitrate concentrations


0·20 g/m3
0·10 "
0·01 "
0·001 "
0·0 "
1·00 g/m3
0·50 "
0·10 "
0·01 "
0·0 "
CELLS PER ml.(x1000)
DAYS
0
2
4
6
8
10
12
14
16

that whereas D. salina was moderately inhibited by 0.01 g/m^3 of phosphate, D. euchlora grew well and multiplied at nearly its maximum rate. It is a risky venture to transpose the findings from small cultures to a large pond environment since only two major macronutrients were being controlled and there was no way of telling how much change there was in the amounts of micronutrients that are necessary for healthy growth. Bacterial growth in the cultures may also have caused variations in the nutrient balance that would not occur in the ponds. However, comparison of the algal populations in the Grassmere ponds with the phosphate determinations does tend to reinforce the belief that levels of phosphate below and about 0.01 g/m^3 are imposing some restriction on the multiplication rate.

There is no clear correlation between nitrate levels and algal growth in the ponds, Table 1.3, and it is not possible to see a similar type of inhibition in the ponds as that suggested by the culture experiments. It seems likely that if phosphate is the limiting factor in algal growth it is overshadowing the nitrate effect.

2.6 PHOTOSYNTHETIC RATES

Determination of gross and net photosynthetic rate by the "light and dark bottle" method is an old established and well documented routine that does not require rediscription here. The method that was adopted here was that described by Strickland and Parsons (1968). Chemical analysis was by the Winkler method, without modification. It was initially hoped to perform determinations in the field but after trials the rates were determined in a laboratory incubator because of problems associated with high levels of oxygen saturation

in the brine ponds. These often caused bubbles to form unpredictably at an early stage of incubation and reliable production estimates could not be obtained. This problem was overcome by frequent monitoring of the light bottles in the laboratory situation.

METHOD

From one litre of water taken from each pond at point 'S' and 400 mm depth two 250 ml B.O.D. bottles, one clear and the other opaque black, were filled after the water had been filtered through a 0.1 mm mesh at the lake edge. The light bottles were placed in an incubator consisting of a water bath at lake temperature illuminated by four 65 watt cool white fluorescent tubes. The dark bottles were left in a darkened water bath at a similar temperature. The incubation period was six hours.

At the end of the period a Winkler determination was performed on all of the samples and the titre of sodium thiosulphate used in the calculations as detailed below:

$$\text{Gross photosynthesis } (MgC/m^2/hr = \frac{605 \times f \times (Vlb - Vdb)}{N \times PQ}$$

$$\text{Net photosynthesis } (MgC/m^2)/hr = \frac{605 \times f \times Vlb - Vlw)}{N \times PQ}$$

f is a correction factor for iodine liberation not coincident with the dissolved oxygen present, Vlb, Vdb and Vlw are the thiosulphate titres of the light bottle, dark bottle and unconfined lake water respectively. N represented the normality of the thiosulphate, (0.01 N), and PQ the photosynthetic quotient for the algae which was taken as 1.2, (Strickland and Parsons 1960).

To measure primary production of the thin mat of the sessile stage of Dunaliella euchlora present on the pond substrates, shallow cores, 8 cm in diameter, were cut from

the crust. Two were taken from each pond. One was rubbed clean of algae and the other left as it had been. Each was then placed in a shallow 500 ml glass container which was filled with Millipore filtered water from the pond of origin (Whatman GF/C paper, 0.4 μm). The containers were then incubated in the normal manner for six hours and the carbon production calculated as above. The water above the substrate sample was substantially free of Dunaliella cells except for those being shed from the sessile phase.

RESULTS

The total primary production of both pelagic and benthic algae is expressed as production per 6h in Table 2.3.

Most algal productivity arises in all ponds from the pelagic forms of both D. euchlora and D. salina. The benthic form of D. euchlora plays its most important part at intermediate salinities (150 ppt - 250 ppt) where there is a stable substrate. However, pelagic algae are still the dominant primary producers at these salinities. At salinities approaching saturation, growth of benthic D. euchlora is greatly reduced. Full details of relative productions of benthic and pelagic algae are shown in Table 4.4.

Productivity rates varied over a wide range with strong seasonal trends being apparent. Vigorous spring growth was shown in the lower P series ponds between the beginning of sampling, (August 1972), and the beginning of December. The onset of increased growth in the F series occurred later but was beginning to show by 5th September 1972. In the middle ponds, particularly P8 - F1, growth was beginning to slow down by 9th October 1972. The fall off in production had extended over the whole range of ponds by 10th January 1973. A gradual fall in rates was seen throughout summer and autumn

	P3	P4	P5	P6	P7	P8	P9	P10	F1	F2	F3	F4	F5
10/8/72	0.93	1.13	1.04	0.97	1.23	1.39	1.04	0.85	0.62	0.72	0.30	0.38	0.23
25/8/72	0.98	1.51	1.34	1.14	1.43	1.95	0.99	1.09	0.76	0.88	0.42	0.51	0.44
5/9/72	1.73	1.85	1.36	0.95	1.66	1.64	0.93	1.02	0.97	1.01	1.02	0.71	0.32
21/9/72	1.49	1.79	1.74	1.96	1.89	0.86	1.16	1.28	1.22	1.09	1.22	0.98	0.93
9/10/72	1.64	2.30	2.49	1.91	2.25	0.64	0.74	0.98	1.01	1.01	0.74	1.04	1.09
26/10/72	1.53	2.49	1.95	1.71	1.48	0.42	0.67	0.62	0.47	0.62	0.56	0.62	1.72
11/11/72	2.04	2.69	2.14	1.09	1.34	0.22	0.49	0.23	0.26	0.30	0.50	0.53	0.83
7/12/72	1.55	2.13	1.16	0.77	0.68	0.16	0.14	0.03	0.37	0.12	0.37	0.64	0.30
30/12/72	0.98	1.02	0.69	0.52	0.41	0.27	0.11	0.23	0.16	0.14	0.43	0.08	1.06
10/1/73	0.63	0.74	1.07	0.41	0.32	0.42	0.37	0.28	0.21	0.16	0.37	1.04	1.69
29/1/73	1.07	0.89	1.45	0.96	0.30	0.28	0.32	0.25	0.17	0.23	0.23	0.62	0.64
15/2/73	0.28	0.68	0.74	0.26	0.21	0.21	0.17	0.21	0.14	0.17	0.30	0.30	0.49
25/2/73	0.19	0.42	0.62	0.30	0.33	0.23	0.16	0.30	0.09	0.14	0.26	0.14	0.21
29/3/73	0.11	0.38	0.49	0.20	0.25	0.26	0.21	0.38	0.22	0.37	0.37	0.72	0.84
12/4/73	0.09	0.11	0.17	0.14	0.21	0.28	0.42	0.51	0.69	1.02	1.28	1.09	1.89
26/4/73	0.12	0.26	0.38	0.47	0.69	0.79	0.30	0.42	0.54	0.38	0.76	0.59	2.08
10/5/73	0.16	0.20	0.68	0.32	0.19	0.29	0.19	0.28	0.26	0.42	0.28	0.14	1.04
25/5/73	0.26	0.42	0.77	0.38	0.28	0.10	0.07	0.11	0.11	0.16	0.21	0.27	0.64
14/6/73	0.14	0.65	0.84	0.64	1.64	0.14	0.11	0.19	0.25	0.19	0.25	0.37	0.21
28/6/73	0.33	0.83	0.98	0.89	1.24	0.28	0.42	0.62	0.37	0.33	0.14	0.42	0.10
12/7/73	0.26	1.13	0.38	1.46	1.06	0.76	0.76	0.34	0.46	0.46	0.30	0.38	0.16
27/7/73	0.42	1.66	1.29	1.11	1.71	1.29	1.29	1.64	1.65	0.64	0.54	0.47	0.23
9/8/73	0.63	1.92	2.68	2.12	2.06	1.94	2.02	2.09	2.92	1.69	0.93	0.67	0.32
13/9/73	0.77	2.06	2.30	2.84	2.66	2.43	2.22	2.32	2.87	1.82	1.23	0.76	0.23
28/9/73	1.46	2.13	2.04	2.19	2.02	2.19	2.32	2.01	2.34	1.96	1.43	0.93	0.47
18/10/73	1.74	2.02	2.34	2.03	1.76	1.72	1.48	1.96	1.28	1.16	1.02	1.47	0.63
1/11/73	2.32	1.76	2.01	2.08	1.69	1.49	0.93	0.89	1.04	0.69	0.84	0.61	0.74
TOTAL	24.59	35.27	35.28	32.06	30.65	23.21	19.66	22.13	20.59	17.70	14.86	16.58	19.89
MEAN	0.91	1.31	1.31	1.19	1.13	0.86	0.73	0.82	0.77	0.65	0.55	0.61	0.74

Table 2.3 Net production of algae expressed as grams of carbon per cubic metre per 6 hour incubator period

but by 14th April 1973 there was evidence of a slow increase in productivity. The increase became rapid after the end of July 1973 and the highest productivities of the sampling period were found in August and September 1973. Exceptions to this pattern were found in P3 and F5. P3 lagged well behind P4 in production during spring 1973 but began to catch up by 18th October 1973 and by 1st November 1973 was showing the highest daily production of the concentrating series. F5, and to a lesser extent F4, showed a similar slow start to the growing period. It is likely that the inhibition in P3 was caused by turbidity of the water in the absence of a gypsum crust whereas the inhibition in F4 and F5 was probably the result of high salinities.

The effect of high salinity in F5 is also shown by periodic short lived blooms of the red Dunaliella salina. These were signified by rapid production increases seen on 26th October 1972, 10th January 1973, 12th April 1973 and 26th April 1973.

DISCUSSION

A strong relationship exists between the declining levels of dissolved phosphate, Table 1.4, and the decrease in phytoplankton production, Table 2.3, particularly with regard to the summer depletion of phosphate. It therefore seems likely that the phosphate levels in the ponds may exert an influence on primary production. There was no clear cut relationship with levels of nitrate.

WIND STIRRING EFFECTS

Wind induced wave action has its maximum effect when the crust of calcium sulphate has been redissolved by low salinity seawater. The best example was in P3 between 14 June 1973 and 28 September 1973. Net algal production in the

very turbid water failed to increase during the spring as rapidly as that in the adjacent ponds and it was not until the crust had been re-established in November 1973 that productivity matched that of nearby ponds. With the stirring of the sediment, nutrient levels, particularly of phosphate, were enhanced.

Artemia growth was not as greatly affected as would be expected considering the low algal producticity.

A linear regression analysis was considered as a statistical means of showing a correlation between the amount of dissolved phosphate present and the growth of the algae. This type of analysis, however, is only successful if there can be demonstrated a simultaneous change of both components. It does not show a significant correlation when there is a lag between a change in the nutrient levels and a change in algal growth. This analysis would work well in a lake where the level of phosphate was stable and showed slow changes over the season with similar slow algal reactions, but in the Grassmere ponds changes occur more rapidly and in both directions. The changes, caused in part by pumping of large amounts of water from pond to pond and from the sea to ponds, could take place in a matter of hours. With only fortnightly samples, the period taken for the algal production to vary with the changes in nutrient levels could not be accurately estimated. At no time could the relationship between algae and the nutrient regime be considered totally stable. A trial linear regression was attempted but because of the above reasons proved inconclusive.

The highest levels of carbon fixation, 2.92 ($g^{C}m/^{3}$)/6h and 2.87 ($g^{C}m^{3}$)/6h, (F1 9/8/73 and 13/9/73 respectively), are similar to those that have been found in artificially fertilised

or polluted environments. For example, Hepher (1962) found levels of 0.37 - 0.5 (g^C/m^2)/hour in fertilised fish ponds in Israel, and Knopp (1959) estimated fixation of 0.31 (g^C/m^2)/hr in the polluted River Main, Germany. Rates of 0.6 - 1.13 (g^C/m^2)/hr were determined from sewage oxidation ponds by Bartsch and Allum (1957) and Johnson, Mathiesen and Røen (1962) demonstrated production rates of 5 - 6 (g^C/m^2)/Day from polluted Danish lakes.

One of the obvious similarities of the Grassmere ponds to ponds used for fish rearing and sewage oxidation is their shallowness, and it is not particularly meaningful to compare the production of Grassmere to that of oceanic or lake regions except where data is provided for the productivity of surface waters.

A somewhat similar saline system was investigated by Walker (1973). His production estimates showed a very strong summer peak of carbon fixation with a maximum of 2.9 (g^C/m^2)/ Day in March 1970 and an annual daily mean between December 1969 and November 1970 of 1.181 (g^C/m^2/Day. The annual total amounted to 435 (g^C/m^2)/year proving to be the most productive non-polluted inland water body yet investigated.

SECTION 3

ARTEMIA SALINA (BRANCHIOPODA : ANOSTRACA)

3.1 INTRODUCTION

The sub-class Branchiopoda contains about 800 described species belonging to four orders, Anostraca, Lipostraca, Notostraca and Diplostraca. The Anostraca includes about 175 species, known generally as the fairy shrimps. Artemia salina, probably the best known representative of this group, is a fairly generalised crustacean having homonomous metamerism of the thorax, abdomen, nervous system and heart. There is no carapace and the head is distinctly separated from the thorax. The mandibles do not have palps and the second maxillae are reduced. Each of the 11 anterior segments bears a pair of simple, leaf-like limbs. This simplicity is considered to be a secondary rather than a primitive feature. The posterior segments are limbless but the first two are fused and form the gonopore, and uterus in the female.

The first antennae are simple but the second are heavily built and in the male form claspers for copulation. The exoskeleton is very soft and rigidity is maintained through turgor pressure.

DIGESTIVE SYSTEM

Food travels up a short ectodermal foregut and enters a long, tubular midgut which gives rise to two bulbous dorsal caecae that pass forward into the head capsule. The midgut progresses to a long thin hindgut terminating in an anus with a well developed sphincter muscle.

CARDIO-RESPIRATORY SYSTEM

The heart extends through all 18 body segments and possesses ostia in each. Blood flows towards the anterior and

posterior but most flows anteriorly. The swimming appendages are richly supplied with blood vessels and oxygen exchange takes place over most of their surfaces but especially across the exite.

REPRODUCTION

Gonads are paired and eggs are transported via a short oviduct into a median uterus that communicates to the exterior by a broad ectodermal vagina. Males have paired penes attached to long thin testes located laterally in the abdomen. To copulate, the male approaches the female dorsally and seizes her just posterior to the limbs using the highly developed second antennae. Males may stay mounted for days, and during that time the metachronal rhythm of the limb movements of each partner slowly come into phase. At irregular intervals the male mates by wrapping its body around the female so the penes become opposed to the gonopore. Eggs thus fertilised may be laid to hatch externally or may be retained to hatch *in utero* and produce ovoviviparous young. Egg laying predominates over ovoviviparous birth in four circumstances; at the beginning of spring, when a young female first lays, when the environmental conditions are particularly severe, and at the end of the female's reproductive life. Ovoviviparity commonly occurs when food is abundant and the population is increasing rapidly. Some populations of *Artemia* reproduce parthenogenetically, (Barigozzi 1934b).

THE EGGS

The eggs constitute a survival and dispersal phase since they may dry up and remain dormant in mud for over five years and still retain full viability. In *Artemia* two types of eggs are produced, so called summer and winter eggs, that differ mainly in the thickness and texture of the tough shall. Prior

to being laid the egg undergoes total cleavage and blastoderm formation and may hatch in less than 18 hours if conditions are optimal. An extreme case of this occurs in another anostracan, Chirocephalus sp. where sections of the egg show the primordia of the two metameres behind the head, and hatching will occur within two hours. The life of dry (14% water content) eggs may be greatly extended by storage at low temperatures or under vacume, (Whitaker 1940b, Dempster 1960).

Anostracans are never found in the sea and it is probable that much of their widespread distribution is from eggs that have become stuck to the feet of wading birds. Local dispersal no doubt also occurs by wind transport as the eggs are very light.

GEOGRAPHIC DISTRIBUTION

Artemia salina is found worldwide wherever brine pools occur, either naturally or as part of industry such as the solar salt plant at Lake Grassmere, (Artom 1920b, 1922, Baid 1958, Barigozzi 1934a, 1946, Barnard 1929, Blanchard 1891, Fockler 1937, Gauthier 1928, Haas and Goldschmidt 1946, Kulkarni 1953, Perrier 1954, Popova 1925, Relyea 1937, Sars 1895). Not only brine is inhabited, but natron lakes in Egypt, Arabia, and South America also support Artemia. The principal dissolved salts in natron lakes are frequently sodium nitrate and magnesium sulphate. A fairy shrimp, Branchinecta granulosa has been found on Lagotellerie Island on the Antarctic peninsula in temporary pools. This constitutes the highest form of aquatic invertebrate life on the Antarctic continent, (Llano 1962). Because Artemia can tolerate very high salinities it can exploit environments which are unavailable to other competitive or predatory species.

SYSTEMATICS OF THE GENUS ARTEMIA

Long periods of existence in isolated and dissimilar environments with infrequent infusions of new individuals have allowed Artemia to produce numerous local variants. With the rise of modern biology many of these were located and described as species of the genus Artemia. Discovery of Artemia is credited to Linnaeus but the first formal description was by Shaw (1791) who named it Cancer stagnalis. This was later changed to Cancer salinus and then redescribed by Leach as Artemia salina. Since then 24 species have been described differing from each other in morphological details:

Artemia salina	Leach
A. arietina	Fischer
A. asiatica	Walter
A. bivalvens	Artom
A. cagliaritana	Artom and Heymans
A. elegans	Simon
A. fertilis	Verrill
A. franciscana	Kellogg
A. gracilis	Verrill
A. guildingi	Thompson
A. intermedia	Simon
A. jelskii	Abonyi
A. konica	Verrill
A. koppeniana	Fischer
A. milhauseni	Fischer
A. monica	Verrill
A. oudneyi	Lieven
A. partenogenetica	Artom
A. principalis	Simon
A. proxima	King
A. sessuata	King
A. typica	Artom
A. univalvens	Artom
A. urmiana	Gunther
A. vectensis	Hutchinson (fossil)

A new genus was subsequently erected by Abonyi (1915), for two species, Callonella jelskii and C. dybouskii which apparently could survive in freshwater.

Discrimination of many of the species named above was based on the ratio of the length of the cephalothorax to

abdomen, and on the appearance of the caudal furcae. Specimens living at high salinities develop large caudal furcae densely covered in setae but the size and density of the setae declines with decreasing salinity until at very low salinities very few setae are present (Abonyi 1915, Sciacchitano 1925b). The relative length of the abdomen to cephalothorax also shortens with a reduction in salinity (Gilchrist 1956). Most of the species were described in the middle nineteenth century but towards the end of this year, and during the first part of the twentieth century, workers demonstrated "transmutations" between "species" by varying the salinity of the environment (Schmankewitsch 1875c, 1877b, Sciacchitano 1927a).

It is now generally agreed that Artemia salina is the only valid species present save physiologically distinct local varieties that are still recognised. Artemia may also be highly polyploid, 3n to 8n chromosome numbers have been counted (Goldschmidt 1952).

USES OF ARTEMIA

Humboldt (date unknown), in his Personal Narratives described the harvesting and consumption of Artemia by Arabs who called the brine shrimps "Loul" or "Fezzan Worm". Similarly Jensen (1918) mentioned that American Indians formerly harvested Artemia from Great Salt Lake, Utah, and used it as a dried storage food. This is possible because the internal salt concentration of Artemia departs very little from the average value for Crustacea of about 0.8 ppt whereas that of the external media varies between 30 and 300 ppt. Artemia was also used by Arab salt makers to "clear" salt ponds as the shrimps take up finely divided mineral and vegetable particles.

Artemia is also an excellent food for newly hatched

commercially grown shrimp, an otherwise very difficult stage to feed in culture. The rapid turnover of Artemia provides a ready supply of naupliar and metanaupliar stages when bred in bulk cultures. Adult Artemia may also be used in shrimp or prawn rearing at a later stage either whole or, more commonly, as part of a blended diet formulated to provide a balanced intake. Artemia eggs are also sold commercially to be hatched for aquarium fish food.

3.2 FECUNDITY

The rapid increase in Artemia numbers in spring is due to hatching of resistant eggs that have overwintered. After these animals have sexually matured further increase is from their very prolific egg production. The way that Artemia may take advantage of a temporary abundance of algae suggests a very flexible egg production rate.

Numerous authors including Artom (1906, 1925a), Goldschmidt (1952), Haas and Goldschmidt (1946), and Mathias (1932) have reported parthenogenesis in Artemia but this has not been observed at any time in the Grassmere stocks. Attempts to induce parthenogenesis by isolating groups of females did not succeed and eggs produced in the ovaries did not traverse the oviducts. In aquaculture there are advantages to be gained by using either sexually reproducing or parthenogenetic stocks. Where sexual reproduction is occurring there is greater scope for genetic recombination and the differential survival of variants that thrive best in the prevailing environment. On the other hand, in parthenogenetic stock every animal is a female and breeding may be exceptionally intense providing a rapid build up of the population. Artemia females tend to be slightly larger than males and a parthenogenetically reproducing

female population may have a slight advantage in biomass.

3.2.1 THE PROPORTION OF FEMALES CARRYING EGGS

Random subsamples were taken from routine collections and inspected for the percentage of females carrying eggs. It might be expected that there would be an annual cycle of fertility and possibly differences in ponds of differing salinities. The results, displayed Fig. 3.1, (which are mean values for the concentrating series P3 - F5) showed a great seasonal range from 98% in spring to 2% in midwinter.

There was no substantial difference in the timing and percentage of females carrying eggs over the whole range of ponds. In addition to the main annual cycle of egg carrying females, there was evidence of a small rise in mid November 1972, and again at the end of December.

3.2.2 NUMBER OF EGGS PRODUCED PER FEMALE

Although females may be carrying eggs, the importance to the population is only realised when they are laid. To determine the rate of release of eggs, Lake Grassmere water was adjusted to five known salinities, 50, 100, 150, 200 and 250 ppt. Five beakers were filled with water of each salinity and young mature females added to each. Food supply was unlimited and the temperature 22 - 25^{o}C. The cultures were inspected daily for eggs or ovoviviparous nauplii arising from eggs hatching within the uterus. After 30 days the experiment was ended and the average production for each set of five Artemia calculated.

RESULTS

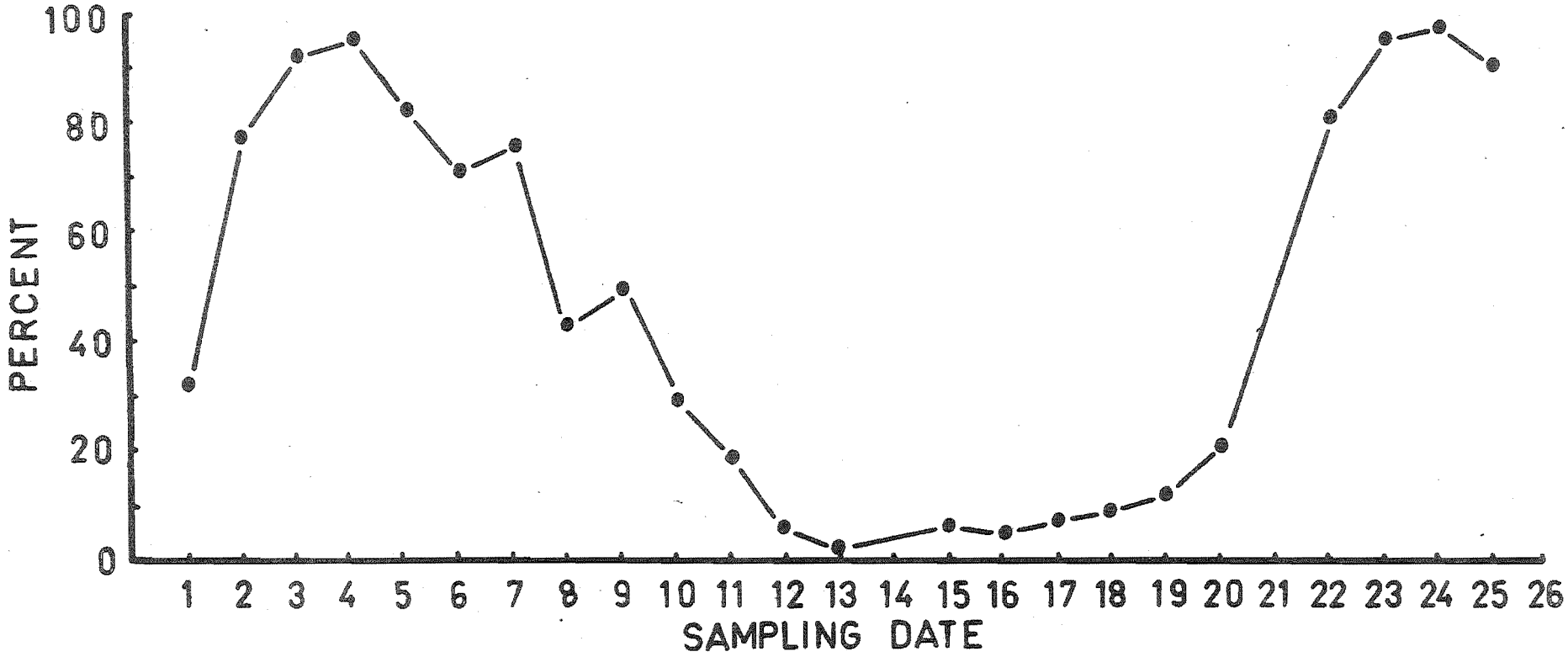
Eggs were not released regularly but in small clutches of five to ten at two or three day intervals. The results, (Table 3.1), have been subjected to an analysis of variance which showed a highly significant difference between the

FIGURE 3.1

The percentage of female *Artemia* carrying eggs. Mean values for all ponds.

SAMPLING DAY KEY

1 = 10/8/72	14 = 29/3/73
2 = 25/8/72	15 = 12/4/73
3 = 5/4/72	16 = 26/4/73
4 = 21/9/72	17 = 10/5/73
5 = 9/10/72	18 = 25/5/73
6 = 26/10/72	19 = 14/6/73
7 = 11/11/72	20 = 28/6/73
8 = 7/12/72	21 = 12/7/73
9 = 30/12/72	22 = 27/7/73
10 = 10/1/73	23 = 9/8/73
11 = 29/1/73	24 = 13/9/73
12 = 15/2/73	25 = 28/9/73
13 = 23/2/73	26 = 18/10/73
	27 = 1/11/73


100
80
60
40
20
0
PERCENT
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26
SAMPLING DATE

columns at the 1% level, and suggests that salinity affects egg laying. There is a fairly obvious drop in numbers between the 200 ppt and 250 ppt solutions and evidence of a peak at 100 ppt. The small drop between the 100 ppt and 50 ppt may not be of great significance. The hypothesis (Khmeleva 1969), that approximately 100 ppt is approaching the optimum for Artemia growth and multiplication has also been reinforced on numerous other occasions when culturing for other experiments (personal observation).

FEEDING OF ARTEMIA DURING LABORATORY EXPERIMENTS

Dense bulk cultures of Dunaliella euchlora were set up in 21 flasks and supported on modified ASP medium. These cultures were used to feed small experimental groups of Artemia. Food algae were added daily to the Artemia. Since the D. euchlora was capable of surviving over a large range of salinities the bulk cultures were adjusted to the same salinity as that being used for the Artemia populations before any additions were made. The additions of algae to the Artemia cultures were made so that there was food present at all times. The volume of algae culture added was determined by consumption rate of Artemia. This is not by any means a natural situation, since food supplies fluctuate widely, but in the absence of very large culture vessels to support few Artemia this was the only practical alternative.

Salinity	50	100	150	200	250
Animal 1	188	221	168	176	87
2	169	232	174	187	112
3	202	197	252	149	81
4	281	241	201	172	84
5	192	263	184	159	79
Total	1032	1154	979	843	443
X	206	231	195	169	89

	Sum of s.	D.F.	Var.	F.	F0.01
BSS	12427	4	3109.25	4.88**	4.22
WSS	15307	24	637.79		

Table 3.1 Egg production of Artemia at five salinities for 30 day periods and analysis of variance of the results.

3.2.3 NUMBER OF EGGS PRESENT IN INDIVIDUAL ARTEMIA

Since it appeared that the numbers of eggs present in the uterus of female Artemia varied with the salinity of the ponds it was decided to take samples from a range of salinities and count and compare the egg numbers.

METHOD

One hundred mature females were taken from each concentrating pond in January 1973, and preserved in 5% formalin. Eggs were counted through the transparent wall of the uterus.

RESULTS AND DISCUSSION

Fig. 3.2 shows the relationship between the average number of eggs per female and the salinity of the 13 ponds P3 - F5 (140 ppt - 282 ppt). Little variation in average number, about 45 - 55 eggs per animal, was seen until a salinity of about 215 ppt was reached. A steady reduction in numbers occurred as salinities increased above 215 ppt until at the highest salinity, 282 ppt, the number was only about 20 eggs per animal. This result may not have reflected the effects of salinity alone but possibly also a lower food supply. Reference to table 2.2, the production of algae, shows that during January production was much lower in the higher salinity ponds P7 to F3, but also during this period there was a temporary bloom of Dunaliella salina. Subsequent aquaria experiments with unlimited food and high salinities still showed much the same trend of decreasing egg numbers and it is concluded that salinity was having the dominant effect.

3.3 EGG HATCHING IN ARTEMIA RELATED TO TEMPERATURE AND SALINITY

INTRODUCTION

Artemia salina produces two types of egg; a thin shelled,

lightly-pigmented form, and a thicker, tougher shelled type with dense pigmentation (Mathias 1932). Apart from their appearance, the eggs are identical, both having haematin pigmentation, Needham and Needham (1930), and two membranes internally. The first of these is immediately inside the shell and the second closely surronds the developing embryo, (Myint 1956).

When the eggs are laid the heavily shelled form acts as a resting stage and, although continually moist or immersed in water, will not hatch for up to four months. This is analogous to diapause in insect eggs. Prior to this state being entered the embryo is fully developed and capable of hatching within 24 hours.

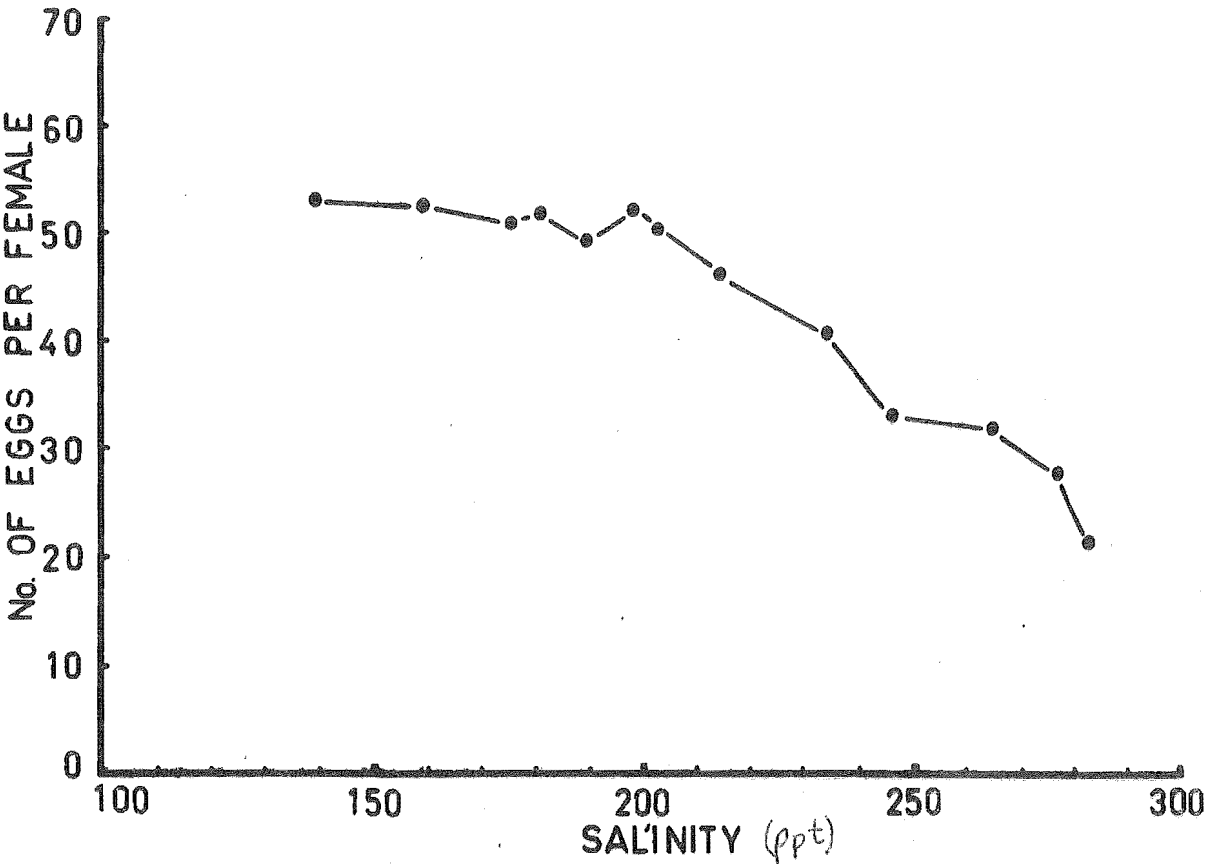
The lighter-shelled egg proceeds towards hatching immediately it is laid and will hatch at a rate determined by the environmental conditions. In this fashion it acts to provide a very rapid increase in numbers whereas the resting stage is a reserve that may overwinter and provide a boost to numbers in spring. Both forms are able to stand years of desiccation and last even longer when kept in a vacuum or at very low temperatures, (Whitaker 1940b). Hatching of both types of egg requires light, even if for only a short period, prior to or during immersion in the culture solution.

METHOD

Water was collected from the Lake Grassmere ponds and adjusted to the following salinities in parts per thousand: 30, 60, 90, 120, 150, 180, 210, 240. Three culture temperatures, 26°C, 17°C and 7°C were used. Eggs were collected at Lake Grassmere from concentrating pond P6 on 26 October 1972, and were approximately one year old at the time of the experiment. In spite of their age they still retained excellent viability.

FIGURE 3.2

The relationship between the number of eggs carried by female *Artemia* and the salinity of the ponds over a range of 140 - 282 ppt.


70
60
50
40
30
20
10
0
No. OF EGGS PER FEMALE
100
150
200
250
300
SALINITY (ppt)

Five hundred eggs ($\pm$ 5%) were placed in each of the eight salinities at each temperature and checked daily for hatching until no more hatching occurred. The cultures were allowed to run and the nauplii counted regularly until no more hatching was evident. There was no feeding of the nauplii.

RESULTS

The data collected are displayed as three graphs, one for each of the three temperatures, (Fig. 3.3.1, 3.3.2, 3.3.3). The time until hatching and the percentage of eggs that hatched were influenced by the lowering of the temperature. For example, at a salinity of 90 ppt hatching took place in less than two days at 26°C, seven days at 17°C and 20 days at 7°C. Also, at the highest temperature hatching times were almost constant at salinities ranging from 30 ppt to 100 ppt. At each of the lower temperatures hatching times differed considerably at different salinities, lengthening as the salinity was increased.

At a constant temperature, salinity has a direct influence on the rate of hatching and also on the percentage of eggs that hatch, but the most important factor shown in the graphs is that the effects of higher salinities is greater at lower temperatures. This aspect is brought out most clearly by consulting the right hand axis of each graph showing the percentage of eggs added that hatched at each salinity. Taking the 120 ppt culture as an example: after two and a half days at 26°C, 70% had hatched. At a similar salinity at 17°C, 60% had hatched in eight days, and at 7°C, 5% had hatched after 21 days. As previously mentioned, the Artemia egg has two membranes internally, one on the inside of the shell and the other around the developing nauplius. There is evidence that

FIGURE 3.3.1

Hatching time and percent of total eggs hatching at 26°C and over a salinity range of 30 - 270 ppt.

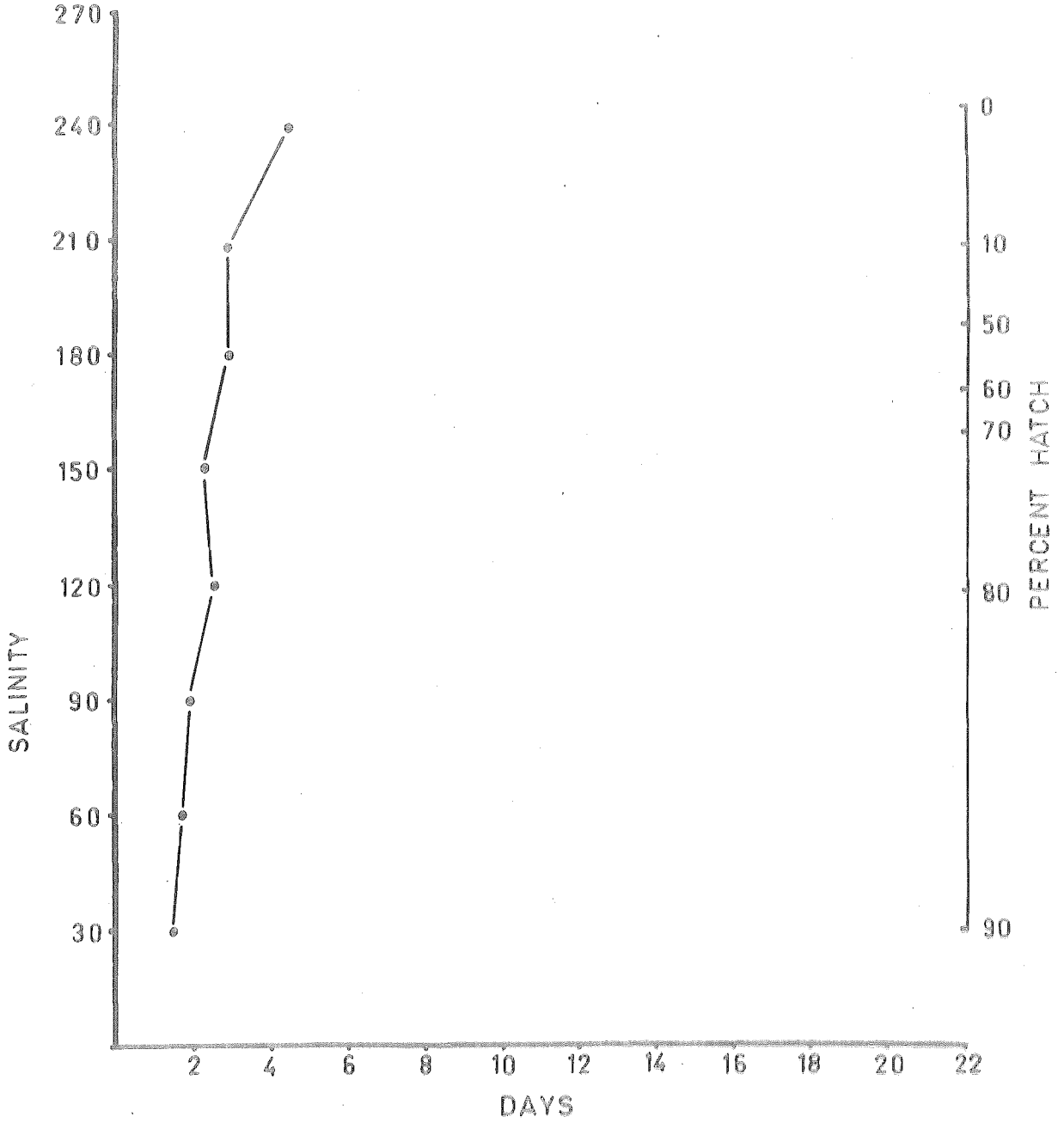

270
240
210
180
150
120
90
60
30
SALINITY
0
10
50
60
70
80
90
PERCENT HATCH
2
4
6
8
10
12
14
16
18
20
22
DAYS

FIGURE 3.3.2

Hatching time and percent of total eggs hatching at 17°C and over a salinity range of 30 - 270 ppt.

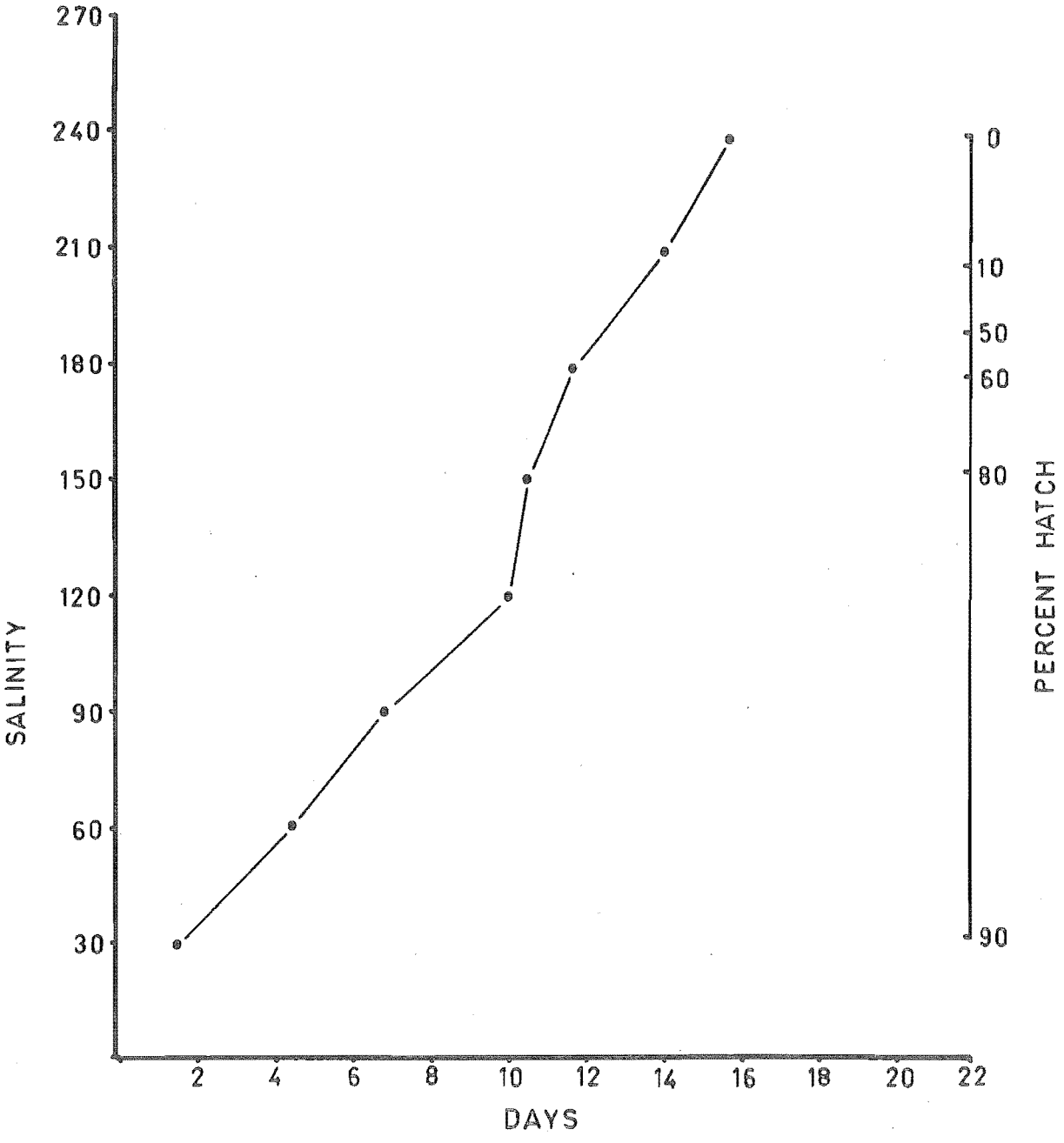
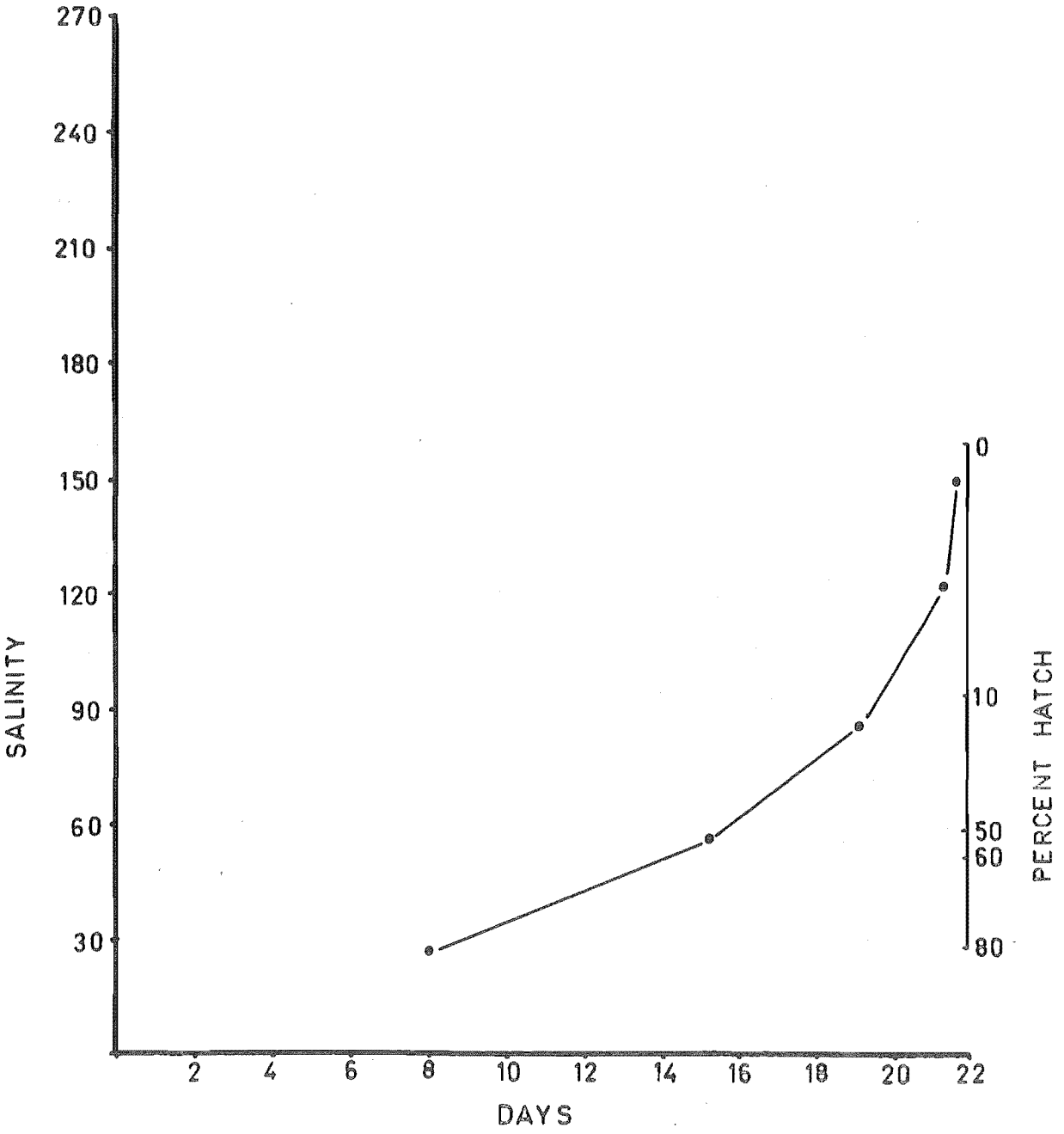

270
240
210
180
150
120
90
60
30
SALINITY
2
4
6
8
10
12
14
16
18
20
22
DAYS
0
10
50
60
80
90
PERCENT HATCH

FIGURE 3.3.3

Hatching time and percent of total eggs hatching at 7°C and over a salinity range of 30 - 270 ppt.


270
240
210
180
150
120
90
60
30
SALINITY
0
10
50
60
80
PERCENT HATCH
2
4
6
8
10
12
14
16
18
20
22
DAYS

high salinities have the effect of preventing the emerging nauplius from detatching from the inner membrane (Jennings and Whitaker 1941).

DISCUSSION

Many workers have performed experiments aimed at demonstrating effects attributable to salinity. Barigozzi (1939) raised Artemia cultures on a diet of Clamydamonas and found that development time was dependent on the salinity of the medium taking about one month and lengthening as the salinity was increased. Bond (1932) extended these experiments to the egg hatching period and further suggested that an increase in salinity retarded hatching, and lower salinities ultimately produced faster growing and larger adult Artemia. Evans (1913) defined the range over which hatching and early development could take place as 50 to 200 ppt. However, the later developmental stages and adults were found to survive over a larger range of from 40 ppt to 250 ppt. Boone and Baas Becking (1931) examined the effect of salinity on egg hatching and discovered that hatching had two stages after the egg shell had ruptured. The first was extrusion of the membrane enclosed nauplius and the second, ecdysis from the membrane. The second step could be greatly accelerated or retarded by varying the ionic complement of the culture solution. They determined optimal sodium concentrations of 0.48m and 0,24m for ecdysis and naupliar development respectively. Sciacchatino (1925) showed that both summer and winter eggs would hatch at almost any salinity but the resulting nauplii would only thrive in salinities near that of normal seawater or higher although the nauplii from winter eggs were more successful at low salinities.

If these results are applied to the situation existing

in the Lake Grassmere ponds, it should be found that the effects of high salinity may be diminished by an increase in water temperature. On the other hand, when the temperature begins to decline at the end of the season, egg hatching in the F. series of ponds may be almost totally curtailed.

3.4 THE LONGEVITY OF ARTEMIA AT THREE WATER TEMPERATURES

As with all invertebrates, the biochemical processes of Artemia are greatly affected by changes in body heat. The temperature of Artemia is heavily dependent on the water temperature of Lake Grassmere which passes through a wide range from about 5°C - 30°C. This implies a considerable range in metabolic rate and possibly a considerable difference in the length of life of individuals. The average length of life is also the turnover time for the population and is a major factor to be considered when planning a harvesting programme. The metabolic rate also affects the recovery time after heavy harvesting. A quick maturation of juveniles and a long reproductive life provides more scope for egg laying and the re-establishment of a stable population in the shortest time.

METHODS

Three cultures of 100 nauplii each were set up in Lake Grassmere water adjusted to a salinity of 140 ppt. These were then left at temperatures of 7°C, 17°C and 26°C. The Artemia were fed every second day from a bulk culture of Dunaliella euchlora (10 000 cells/ml) and the numbers present counted every four days. The concentration of Dunaliella cells was checked by haemocytometa counts and kept at a level (4000 - 7000 cells/ml) that provided good feeding conditions in the pond environment. After 18 days the nauplii had matured and some were ready to release eggs. To avoid natural increase upsetting the numbers,

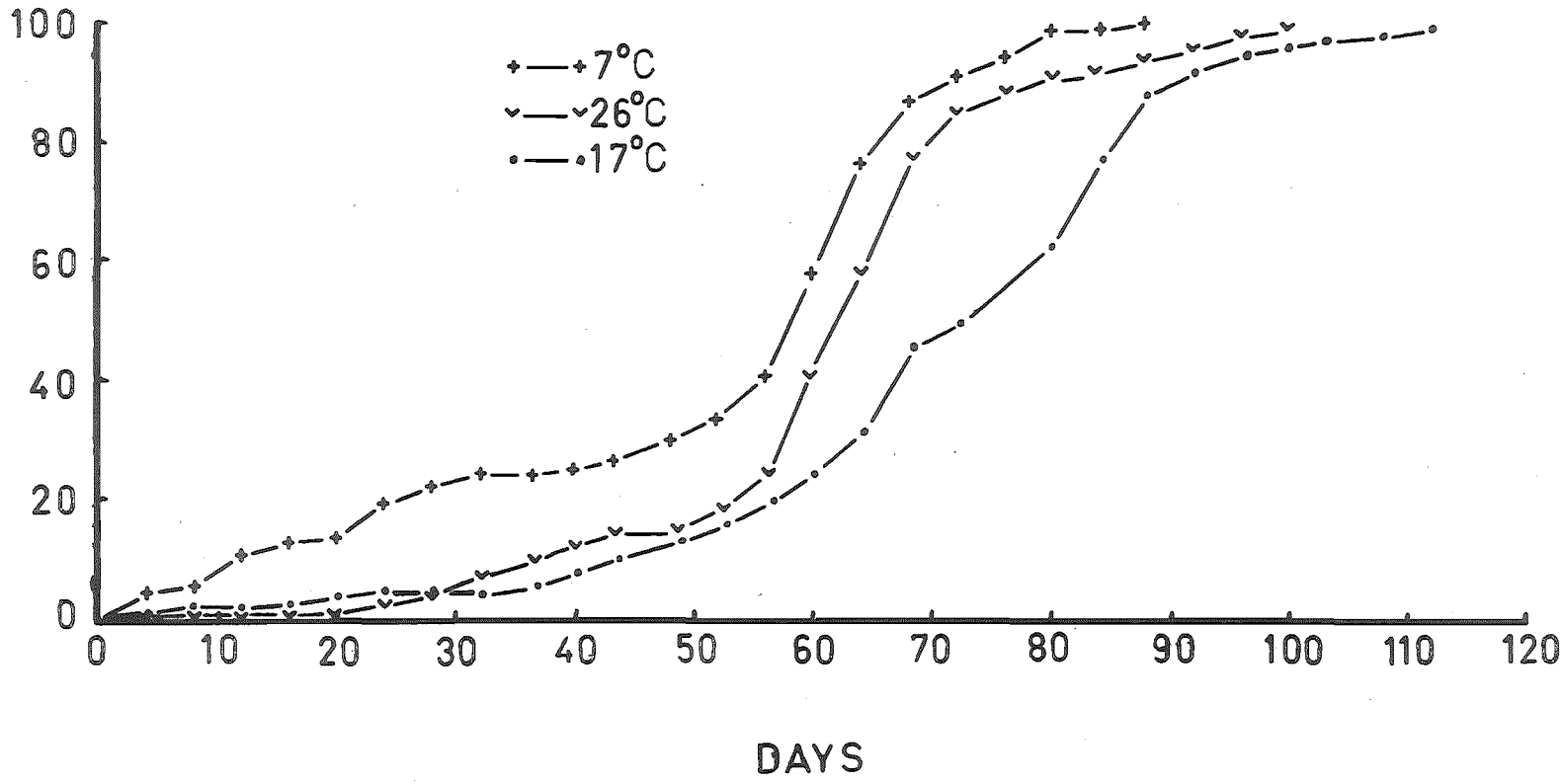
after each counting the entire content of the culture vessels were poured through a 2 mm sieve to retain all of the mature animals but allow free passage of the remaining material. The material which had passed through the 2 mm sieve was then poured through a 0.1 mm plankton net. This retained any eggs or nauplii that had developed in the four day period but did not retain the algae. This procedure was carried out every four days until all the adult Artemia had died. This procedure, therefore, provided information on length of life and times of maximum mortality. This handling of Artemia could have caused damage leading to premature death, but longevities found correspond with that found by other workers.

RESULTS

The decrease in numbers of nauplii initially placed in each culture is expressed as a cumulative frequency curve for each of the three experimental temperatures (Fig. 3.4). The points represent the state of the population at the end of each four day period. At the lower temperature, 7°C, mortality was high among nauplii, metanauplii, and young adults, and after 32 days 24% of the original population had died. By contrast, in the 17°C and 26°C cultures, only 4% and 7% respectively died in this time. A period of stability occurred in the 7% culture until about the 50th day when the death rate accelerated and 90% had died by the 72nd day. By the 84th day all were dead. Mortality rates in the 17°C and 26°C cultures were not very different until after the 56th day when a rapid increase in death rate occurred in the higher temperature environment. There was also an increase in death rate in the 17°C cultures at this time but it was of a smaller magnitude. By the 100th day the 26°C culture was empty and only 4% were living in the 17°C culture. By the 112th day these too had died.

FIGURE 3.4

Longevity of *Artemia* at temperatures of 26°C, 17°C and 7°C with unlimited food and at 140 ppt salinity.


100
80
60
40
20
0
7°C
26°C
17°C
0
10
20
30
40
50
60
70
80
90
100
110
120
DAYS

The low temperature caused high juvenile mortality and shortened maximum life span by approximately 28 days compared with the 17°C culture. Longest lived individuals occurred at the middle temperature of 17°C. At the highest and lowest temperatures death rate became very rapid in the middle age ranges with 65% of the populations dying over about 18 days.

DISCUSSION

Most estimates of the life span of Artemia salina are within the three to four months range. Khmeleva (1969) found that the average life span of Artemia from lakes in Crimea (Sivash, Vozensenovskoye Lake, Sasyk Lake) and from the Kuyal'nik Estuary near Odessa was 133 days after passing through 27 molts. These were determined at 20°C and with unlimited food. It is characteristic of all Crustacea that lowering of the environmental temperature prolongs the lifetime presumably by reducing the overall metabolic rate and slowing the "wearing out of the body".

Artemia obtains the bulk of its food by filter feeding, the rate of which depends on the activity of the animal, and a lowering of the environmental temperature would undoubtedly affect the rate of food ingestion. This is possibly most important in the naupliar and metanaupliar stages where the animal is metabolising very rapidly and retains practically no food reserves. Although Artemia nauplii do not feed during the first 48 hours . At 17°C there was slightly higher metanaupliar mortality than at 26°C (i.e., up to day 18), but at 7°C there was much higher metanaupliar mortality with possibly 18% of the population dying before maturity.

In the 17°C culture, once the early developmental stages had been completed, the death rate was lower than at 26°C and 7°C, at which temperatures death rates were very similar.

Despite this similarity, greater losses of metanauplii at 7°C meant that this culture died out by the 84th day compared with the 100th day for the 26°C.

Both the 7°C and 26°C cultures showed a period of high mortality between the 55th and 75th days. This increase was not so evident in the 17°C culture although there was a slightly increased death rate between the 80th and 90th days. The type of difference found between the 26°C and 17°C cultures may be expected in such circumstances when at the higher temperature the animals live rapidly, reproduce rapidly, and generally have a high turnover, whereas at a slightly lower temperature the same sequence of events takes place but all changes occur more slowly.

An interesting feature noted in the 17°C culture was that when the animals were approaching the end of their lives, old and weak Artemia sometimes spent three to five days slowly swimming before they died. In contrast, at 7°C old Artemia died very rapidly once they lost normal mobility. In the 26°C culture the feebly swimming phase was present but did not last as long as at 17°C.

Overall, it would appear that 7°C is approaching the lower limit for normal activity of Artemia. This is supported by the observations of Vorhies (1917) who noted that in Great Salt Lake, Utah, Artemia disappear when the water temperature drops below 6°C and young first appear in spring when the temperature reaches 9°C. He also considered that the maximum density of Artemia occurred at temperatures of 25 - 30°C.

3.4.1 LIFE AND FERTILITY TABLES

A more informative method of presenting the results displayed in Fig. 3.4 is to express them as a life table. This system, first elaborated in detail by Deevey (1947) has two

variants. An age specific life table is based on the fate of a single cohort, usually an entire generation that may be stationary or fluctuating. The second type known as a time specific life table is based on an imaginary cohort delimited by determining the age structure of a sample of individuals from a population where there is continual reproduction and considerable overlapping of generations.

Artemia are impossible to age accurately after the twelfth instar because there are no external morphological changes in later instars, simply an increase in size. The size of Artemia is extremely variable depending on salinity, temperature and food supply and cannot be used alone for age estimation. In addition, since there is continual reproduction, use of a time specific life table is impossible without introducing gross inaccuracies.

The experiments set up in section 3.4 produced, in effect, separate cohorts growing at three temperatures. Removal of all eggs and ovoviviparous nauplii maintained the purity of the cohort and provided the opportunity to construct an age specific life table for each culture. The known number of young produced over the life of the culture allowed the further elaboration of a fertility table similar to that devised by Laughlin (1965).

METHOD

Life tables, (Tab. 3.2, 3.4, 3.6) were set up for each culture with the following columns:

x,	the age classes in days.
lx,	the number alive at the beginning of each age class, i.e., out of the 100 original Artemia.
dx,	the number dying during the age interval, x.
Lx,	the number of animals alive between ages x and x+1.

$$Lx = \frac{l + lx+1}{2}$$

Tx, the total number of animal x age units beyond the age x.

$Tx = Lx + Lx+1 + Lx+2 \ldots Lw$ where w is the last age group.

ex, the expectation of life remaining for individuals of age x.

1000qx, the mortality rate per thousand at each age interval.

$$1000qx = 1000 \cdot \frac{dx}{lx}$$

Fertility tables, (Tab. 3.3, 3.5, 3.7) were set up with the following columns:

x, the age classes in days.

lx, the number of females in the population (assumed to be 50% until sexual characters were visable).

mx, half of the mean number of eggs laid per female per time interval (assuming 50/50 sex ratio).

$Mx = \frac{Nx}{2}$ where Nx is the total natality of a female of age x.

(lx . Mx) X 10 X 0.86, the total number of female births per ten day time interval assuming that 86% of the eggs produce breeding adults, (hatching success derived from separate trials).

Nt, the total number of female live births over the duration of the cohort's existence.

A quantitative value for the rate of increase may be obtained from the equation:

$$rc = \frac{\log_e Nt}{Tc}$$

Where rc is the capacity for increase, $\log_e$ Nt is the naperian log of Nt, and Tc is the mean time taken for females of the cohort to begin producing eggs, (modified from Andrewartha and Birch, 1954).

x	lx	dx	Lx	Tx	ex	1000qx
0-10	100	1	99.5	593	59.3	10
11-20	99	1	98.5	493.5	49.8	10.1
21-30	98	5	95.5	395	40.3	51
31-40	93	6	90.0	299.5	32.2	61.2
41-50	87	5	84.5	209.5	24.1	57.4
51-60	82	27	68.5	125	15.2	329.3
61-70	55	39	35.5	56.5	10.2	709.1
71-80	16	9	11.5	21	13.1	562.5
81-90	7	2	6.0	9.5	13.5	285.7
91-100	5	4	3.0	3.5	7.0	800
101-110	1	1	0.5	0.5	5.0	1000

Table 3.2 Life Table for 26^{o}C Culture.

x	lx	Mx	(lx.Mx) x 10 x 0.86
0-10	50	-	-
11-20	49	-	-
21-30	49	4.3	1812
31-40	47	6.7	2708
41-50	46	6.2	2452
51-60	43	6.0	2218
61-70	29	7.7	1920
71-80	11	6.4	605
81-90	5	6.9	296
91-100	4	5.4	182
101-110	1	3.4	29
	$\bar{X}$ mx =	5.8	12189 = Nt rc = 0.305

Table 3.3 Fertility Table for 26^{o}C Culture.

x	lx	dx	Lx	Tx	ex	1000qx
0-10	100	2	99	692	69.2	20
11-20	98	2	97	593	60.5	20.4
21-30	96	0	96	496	5.16	0.0
31-40	96	5	93.5	400	4.16	52.1
41-50	91	6	88	306.5	3.4	65.9
51-60	85	11	79.5	218.5	2.57	129.4
61-70	74	20	64	139	1.88	270.2
71-80	54	18	45	75	1.39	333.3
81-90	36	28	22	30	0.83	777.7
91-100	8	5	5.5	8.0	1.0	625.0
101-110	3	2	2	2.5	0.83	666.6
111-120	1	1	0.5	0.5	0.5	1000

Table 3.4 Life table for 17^{o}C Culture.

x	lx	Mx	(lx.Mx) x 10 x 0.86
0-10	50	-	-
11-20	49	-	-
21-30	47	3.3	1333
31-40	47	5.9	2384
41-50	44	4.5	1702
51-60	42	3.8	1372
61-70	39	6.2	2079
71-80	33	5.1	1447
81-90	24	4.9	1011
91-100	6	3.2	165
101-110	3	4.0	10
111-120	1	2.8	2.4
	$\bar{X}$ mx =	4.4	11505 = Nt rc = 0.207

Table 3.5 Fertility Table for 17^{o}C Culture.

x	lx	dx	Lx	Tx	ex	1000qx
0-10	100	8	95.5	494	4.94	80
11-20	91	6	88	398.5	4.38	65.9
21-30	85	9	80.5	310.5	3.65	105.9
31-40	76	1	75.5	230	3.03	13.1
41-50	75	7	71.5	154.5	2.06	93.3
51-60	68	31	52.5	83	1.22	455.9
61-70	37	26	24	30.5	0.82	702.7
71-80	11	10	6	6.5	0.59	909.0
81-90	1	1	0.5	0.5	0.5	1000.0

Table 3.6 Life table for 7°C Culture.

x	lx	Mx	(lx.Mx) x 10 x 0.86
0-10	50	-	-
11-20	46	-	-
21-30	43	-	-
31-40	41	2.0	705
41-50	40	1.7	584
51-60	37	1.4	445
61-70	23	1.9	375
71-80	9	2.1	162
81-90	1	1.3	11
	$\bar{X}$ Mx =	1.7	2279 = Nt rc = 0.123

Table 3.7 Fertility table for 7°C Culture.

RESULTS AND DISCUSSION

The conditions under which the experimental population were reproducing were probably more ideal then those encountered in the lake and the real value in the results lies in the relative performances at different temperatures. Comparing the populations reared at 27°C and 17°C, females survived longer at the lower temperature and showed a lower mortality per time period in the 60 - 90 day range. Although the numbers of eggs and ovoviviparous nauplii produced were lower, the larger number of surviving females produced a surprisingly high number of eggs. This impressive performance is somewhat diminished when the capacity for increase, rc is calculated and it is found that the value for the 17°C culture of 0.207 falls well behind that for the 26°C system of 0.305. The pitfall is in the time taken from egg hatching to the first reproduction of a resultant female, (14 days at 26°C and 20 days at 17°C).

Comparing the 7°C culture with the 17°C and 27°C cultures the first impression is of a very short reproductive period because of slow development in the metanaupliar stages and high mortality of adults at the peak of egg production. When this is combined with the very low number of eggs produced per female per day (1.7) it is found that overall egg production falls far short of that in the higher temperature cultures. The 30 day development period before egg laying is also very detrimental to the population's capacity for increase, and results in an rc value of only 0.123.

Although the level of Dunaliella viridis was kept as close as possible to that prevailing in Lake Grassmere, ca. 3000 - 4000/ml, other physical and biological factors, apart from temperature and light, could not be adequately controlled.

The netting of all offspring removed any intraspecific competition and other crowding influences, so any comparison with the dynamics of field populations must be made very cautiously. The trials do demonstrate the very large capacity for egg laying and increase in a very short time, and other personal observations have shown that the densities that can be acheived with adequate food supplies are extremely high, (ca. 800 000/m^3).

3.5 FEEDING RATE OF ARTEMIA

A knowledge of the rate of uptake of algal cells from lake water is essential when attempting to calculate the energetics and productivity of the *Artemia*/*Dunaliella* relationship in Lake Grassmere. This provides the basic information about the energy transfer from the primary producer to the first consumer level.

METHOD

The most difficult part to estimate in this section was the amount of food contained in the gut at any given time. I found the best way to circumvent this problem was to displace the material in the gut with a non-nutrient, inert substance consisting of a suspension of sand and clay that had been cleaned in warm potassium dichromate/sulphuric acid. *Artemia* were placed in this and readily consumed the particles which had replaced all the faecal material in the hindgut within 24 hours. A most convenient feature of *Artemia* faeces is that they are wrapped in a fine membrane and extruded in one or two millimetre lengths. These could be recovered with fine forceps for further analysis.

A series of algal cultures was prepared using the nutrient formula described in section (2). The densities of

these were adjusted to known numbers of cells/ml using a haemocytometer. The concentrations used were 10,000, 8,000, 6 000 and 4,000 cells/ml. The test animals, whose guts were full of inert material were of two classes; young adults, 2-4 mm long and fully mature individuals 10-12 mm long. All trials were carried out at a temperature of 26°C and a salinity of 150 ppt. The test containers were kept in dim light to reduce cell division of the food alga, Dunaliella euchlora over the experimental period.

Ten Artemia of the 10-12 mm size range were placed in separate experimental containers (250 ml pyrex beakers) at each food density and allowed to feed undisturbed for six hours. At the end of the six hours they were removed and replaced in the inorganic suspension. Cell density in the beakers was remeasured to estimate uptake of cells, and after 24 hours in the inorganic suspension all faecal pellets produced were collected and wet combusted in potassium dichromate/sulphuric acid oxidising solution, (Marshall and Orr 1955). There was now available an absolute measure of cell uptake and a measure of the undigested organic material in the faeces. This provided the opportunity to calculate the efficiency of digestion for different size classes and at different food densities.

RESULTS

Results are presented in table 3.8 which shows the energy equivalent of the algal cells expressed in joules, as determined by wet combustion. The efficiency of assimilation of ingested food was lower as ingestion rate increased. In adult animals the amount of algae assimilated varied only slightly at different algal concentrations but the proportion of the total intake that passed through undigested steadily

Initial cell density cells/cm^3	Size class mm	No.	Final cell density cells/cm^3	Energy assimilated (Joules)	Energy in faeces (Joules)	Percent assimilated	Percent rejected	Amt. assimilated per animal (Joules)
4000	10-12	10	2280	7.48	6.02	57	43	0.75
4000	2-4	100	2624	5.79	4.94	54	46	0.058
6000	10-12	10	4030	7.53	7.83	49	51	0.75
6000	2-4	100	4434	6.35	5.86	52	48	0.064
8000	10-12	10	5554	8.77	10.29	46	54	0.88
8000	2-4	100	6046	7.77	7.47	51	49	0.078
10000	10-12	10	7320	8.78	12.12	42	58	0.88
10000	2-4	100	7870	7.81	8.81	47	53	0.078

Table 3.8 Feeding Efficiency of Adult and Juvenile Artemia salina in various densities of Dunaliella euchlora culture.

increased as the alga concentration was increased. This effect was seen in both large and small Artemia.

At the lowest experimental density (4000 cells/ml) of algal cells larger Artemia were more efficient feeders than small but in the next highest density (6000 cells/ml) the order was reversed with smaller animals assimilating more of the ingested food. This was also found at the two highest cell densities.

It would appear that the rate of ingestion of cells was nearly maximal at the lowest cell density because the numbers ingested rose by only 56% and 54% for large and small Artemia respectively, when the food concentration was increased by 250%. The hypothesis that the ingesting and digesting processes were working to near capacity was reinforced by the very small increase in the amount of algal energy assimilated throughout the range of feeding situations tested. There was a larger increase in percent assimilation by smaller Artemia but in both size classes the increase was only in the three lower cell concentrations.

Artemia is a very active animal which rarely stops swimming. The cost of this activity in terms of food energy uptake has been estimated by Bertalanffy and Krywienczyk (1953) and shows that at 26^{o}C the oxygen uptake for 10-12 mm Artemia was 0.5 ml/hr. For ten Artemia over a six hour period this amounts to 0.3 ml of oxygen. Employing an oxycalorific coefficient of 4.86 (Khmeleva 1969), the energy consumption over the feeding period would be 1.62 calories or 6.78 J. The total algal food energy intake was, for the lowest cell concentration, 7.48 J. The balance remaining after respiration losses are deducted is 0.7 J, and represents the amount of energy converted from algae to Artemia biomass neglecting

ammonia excretion. The conversion efficiency (algae to biomass) in this case was about 9.3%. At the 6 000, 8 000 and 10 000 cell/ml food densities, conversion efficiencies were 10.0%, 22.6% and 22.7% respectively. No calculations, other than the percentage of ingested algal cells assimilated, were made for the 2-4 mm Artemia because errors in estimation of the metabolic rate of this size class were too high.

DISCUSSION

Gibor, (1957) working with Artemia from Great Salt Lake, Utah, found that the efficiency of assimilation of Dunaliella viridis varied widely depending on the age of the Artemia and the density of the alga but that the conversion efficiency to biomass could approach 53%. This figure is much higher than any obtained in the present experiments but was obtained as Gibor stated "under ideal conditions".

The lowest cell density could be expected to be the most efficiently assimilated since the animals are less likely to be overloaded with fresh food before the previously ingested material has been thoroughly processed. However, this could also be expected to be the least effectively converted to Artemia body material as more energy is required for obtaining food. In the present experiments, at the lowest cell density, Artemia just covered its feeding energy costs with a 9.9% excess of income over expenditure but at the highest density there was a 22% excess.

The effect of feeding Artemia on dense suspensions of Dunaliella tertiolecta, (almost identical to D. euchlora), was investigated by Mason (1963) who found that at densities ranging from 12,000 to 400,000 cells/ml the efficiency of conversion varied from 12% to 22%. The animals used in Mason's study originated from Mono Lake, California, and were considered in

Mason (1967) to be a physiologically distinct race of Artemia that could not interbreed with Artemia from San Francisco or Great Salt Lake. Because of this it is difficult to directly compare their performance in algal conversion with those from Lake Grassmere. The Mono Lake results also showed that large Artemia performed better than small Artemia at lower cell densities, probably reflecting the effect of the larger volumes of water filtered by adult animals. Provasoli and Shiraishi (1959) concluded that the 5th, 6th and 8th instars (length range 2 to 7 mm) were the developmental stages most affected by quantity of food supply. In these instars growth is at its maximum and a deficit between uptake and requirements for metabolism and tissue building has drastic consequences with mass death.

Artemia is an "automatic" feeder, passing a certain volume of water through its feeding setae per unit time. The rate is temperature dependent but no evidence has yet been produced for a variable filtering mechanism. In the absence of such evidence it may be assumed that the rate of passage of food through the gut is influenced by the input from feeding. A visual impression of declining efficiency of digestion by animals feeding in dense algal cultures may be gained by the change of colour of the faeces. The faecal pellets, normally grey/black, become increasingly green as the food density is increased and the undigested plant material in the faeces increases.

3.6 LIPID CONTENT OF ARTEMIA

INTRODUCTION

The fat and oil component of Artemia represents a very high energy food source for a potential consumer. As it is

principally a food storage product, the amount present may vary widely over the year. It seems reasonable to assume that the quantity of stored lipids would follow the abundance of algal food in the ponds if this were related to ingestion rate and assimilation (cf. section 3.5). Lipids are present in all green algae, comprising up to 20% by dry weight of the cell contents, mainly as unsaturated fatty acids ranging from C12 to C24. The common straight chain saturated fatty acids of animals and higher plants are also generally present (Miller 1962).

METHODS

Adult Artemia were selected at random from each set of samples and dried at 50°C for 24 hours. The low temperature minimised losses due to volatilisation of oils when heated. When constant weight had been achieved the animals were placed in a micro-soxhlet apparatus and extracted with petroleum ether for three hours. This time was more than sufficient to extract all of the available soluble lipid. The loss in weight after extraction was regarded as the loss due to lipids present in Artemia, and was expressed as a percentage of the original dry weight.

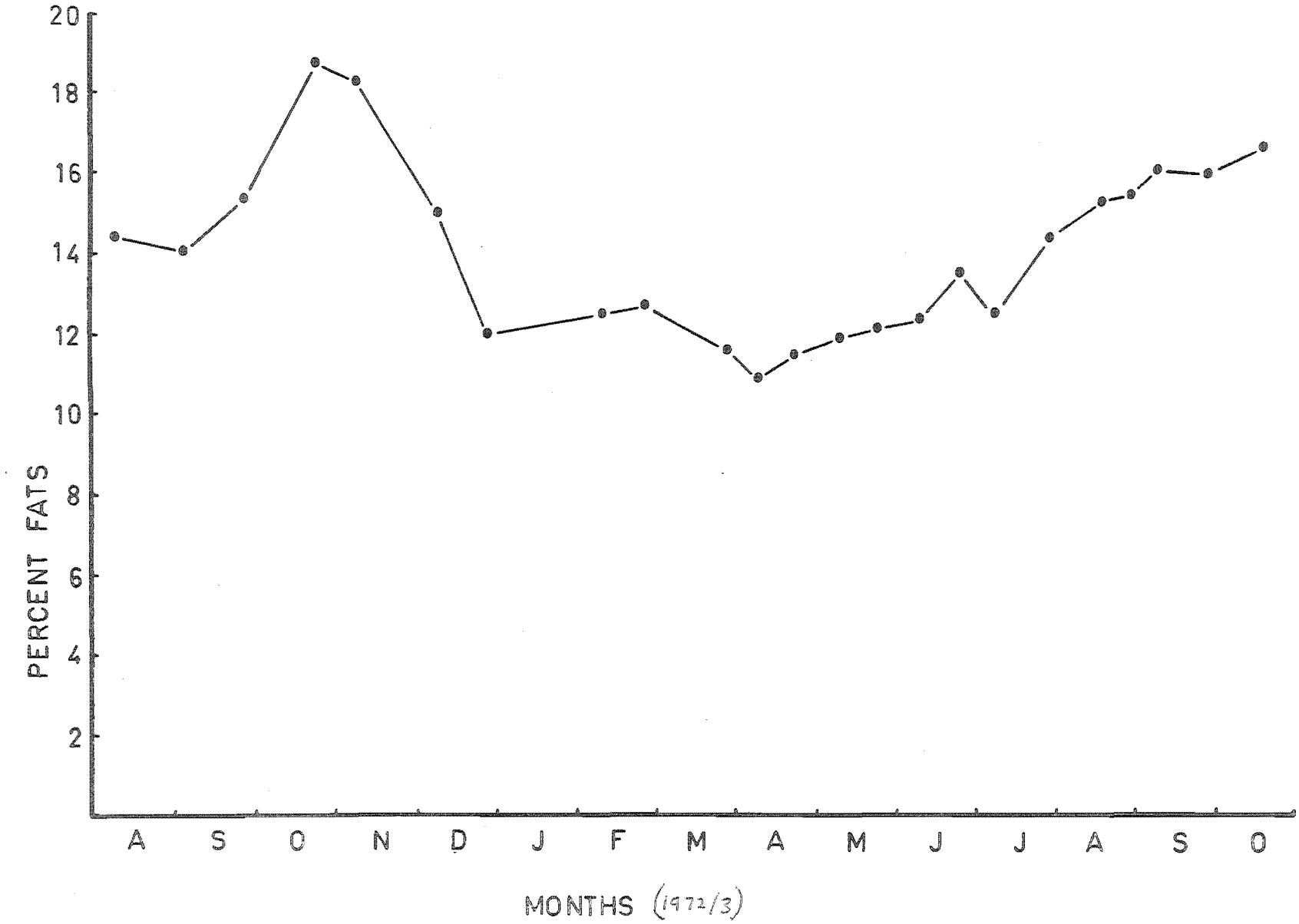
Before drying the Artemia were examined for the presence of fat globules in the tissues. At some times of the year, notably mid to late spring, very large amber coloured globules were observed at the bases of the swimming pleopods and around the mid-gut. Other smaller droplets were irregularly dispersed throughout the body.

RESULTS

The percentage of lipids present was quite high at all times of the year but as Fig 3.5 shows, a peak of 18.3% occurred in October, 1972, and a similar although lower peak, 17.2% was

FIGURE 3.5

Lipid content expressed as percentage of dry weight measured over the sampling period


20
18
16
14
12
10
8
6
4
2
PERCENT FATS
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
MONTHS (1972/3)

found in 1973. The build-up to the peaks coincided with the spring blooms of algae, and the fall in lipid values came when the algal growth was declining. The minimum level in April came after a slight increase brought about by the faint autumn bloom of algae. Throughout the winter, levels remained fairly constant although there was some evidence of a slight rise just before the spring rise became apparent in mid July. The petroleum ether extraction is not a particularly accurate method of analysis since lipids and fatty acids differ in their solubilities and it may have been more successful if a chloroform-methanol solvent was used.

Evidence that the animals responded directly to an increase in food supply was provided qualitatively by rearing a culture of Artemia on a minimal diet of algae. These grew to adult size but on examination showed no lipid droplets anywhere in the body. The diet was next supplemented by adding extra algal suspension and within six days small droplets of lipid were visible around the gut. The diet was further enhanced by daily feeding with yeast. Within another two weeks, inaddition to the droplets around the gut, large globules of lipid had been deposited at the bases of the pleopods and along the limbs. A return to low food conditions caused the disappearance of droplets within 18 days.

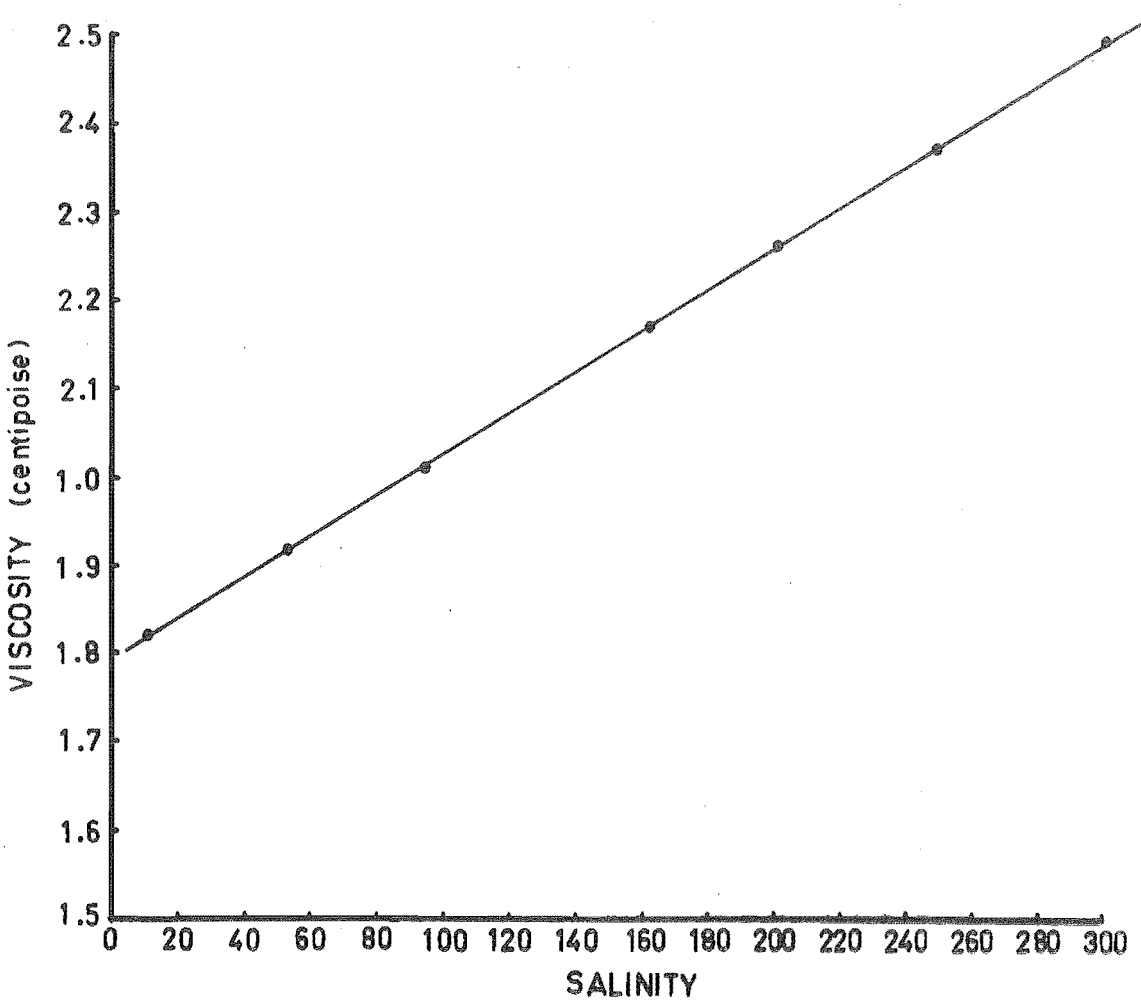
There was no close relationship between lipid content and egg production.

3.7 VISCOSITY OF THE BRINES

In seawater, viscosity is in the form of internal fluid friction or forces of drag that the molecular and ionic components exert on one another. As the seawater is evaporated to brine the viscosity increases in a linear fashion (Fig. 3.6).

FIGURE 3.6

The viscosity of seawater brine related to its salinity


VISCOSITY (centipoise)
2.5
2.4
2.3
2.2
2.1
1.0
1.9
1.8
1.7
1.6
1.5
0
20
40
60
80
100
120
140
160
180
200
220
240
260
280
300
SALINITY

The more ionic components present the more water molecules are restricted and the more viscous the solution becomes. The density of the solution is also greatly affected by a temperature increase widening the inter molecular distance and reducing the incidence of organized hydrogen bonding between molecules.

THE EFFECT OF VISCOSITY CHANGE ON SWIMMING OF ARTEMIA

It was shown in Fig. 3.6 that between the salinities of normal seawater, about 35 ppt, and the maximum salinity reached in the Grassmere ponds, about 300 ppt, there is a 34% increase in viscosity of the solution. Since Artemia survive in the ponds over all of this range it is possible that there may be some noticable effect on the swimming ability of the animals.

METHOD

Ten adult Artemia were selected at random from a culture of 140 ppt salinity kept at 25°C. For five, ten second periods the number of swimming strokes made by an animal was counted and the distance travelled calculated by drawing the swimming path on a grid pattern that corresponded to a similar grid directly under the transparent base of the culture vessel. This was done for each test subject independently. The mean number of limb strokes and distance travelled was calculated. The same procedure was then carried out at three further salinities, 60 ppt, 220 ppt and 300 ppt. Artemia were introduced and allowed 60 seconds to settle into their swimming rhythm before the above measurements were made. Artemia are remarkably unperturbed by drastic changes in the environmental salinity but as a check that factors other than the viscosity were not affecting them, the same ten Artemia

were acclimated to 330 ppt salinity for 48 hours and then put through the same set of tests. Throughout the tests the temperature was maintained at 25°C.

If the rate of progress was impeded by increased viscosity there arose the possibility that feeding may also become less efficient at high salinities as the volume of water filtered becomes less. Therefore, suspensions of 10 000 cells/ml of Dunaliella euchlora were prepared in the salinities used above, (60 ppt, 140 ppt, 220 ppt and 300 ppt) at 25°C. Ten mature adults, 10-11 mm long were placed in containers of each salinity without regulated food supplies and allowed to acclimate for 24 hours. After this period they were transferred to the cultures containing measured cell densities and allowed to feed for 6 hours. They were then removed and the algal density remeasured. Four similar trials were run.

RESULTS

Table 3.9 shows the summarised results for the swimming rates at the four salinities. An analysis of variance test indicated no significant difference in the number of limb strokes per period at any salinity. When a similar test, (Table 3.9.1) was applied to the distances covered, however, there was a highly significant variation in the means at the 1% level implying that increased viscosity of the solution definitely slowed locomotion. The ratio, lm/d, (number of limb strokes divided by distance covered) is a measure of the effort expended relative to the distance covered, and it increased by 33.7% from the 60 ppt solution to the 300 ppt solution.

Artemia that had been acclimated to 300 ppt salinity were found to be swimming at a similar rate to those that had been suddenly introduced.

	60		140		220		300	
	lm	d	lm	d	lm	d	lm	d
Animal 1	34	39	37	33	31	31	28	28
number 2	31	38	33	34	32	27	33	25
3	42	41	39	40	40	36	36	24
4	36	40	33	36	37	35	32	29
5	33	44	38	39	34	32	36	31
6	35	32	31	28	36	31	33	27
7	34	33	32	32	32	29	37	30
8	29	31	35	36	31	27	24	19
9	38	42	32	33	36	32	35	27
10	44	49	46	48	40	39	42	34
$\bar{X}$	35.6	38.9	35.6	35.9	34.9	31.9	33.6	37.4
ratio lm/d	0.92		0.99		1.09		1.23	

Table 3.9 Limb movements (lm) and distance travelled (d) in a tensecond period at four different brine visconsities. (lm) and (d) are the means of five determinations.

	Sum of S.	D.F.	Var.	F.	F0.01
BSS	764.9	3	248.9	10.41**	4.3
WSS	860.1	36	23.89		
Total	1625	39			

Table 3.9.1 Analysis of variance test applied to the means of the distance covered in ten seconds in brine of four viscosities.

Salinity (ppt)	60		140		220		300	
	do	di	do	di	do	di	do	di
Trail No. 1	10000	7500	10000	7300	10000	7500	10000	7920
2	10000	7320	10000	7600	10000	7700	10000	7800
3	10000	7400	10000	7500	10000	7850	10000	7800
4	10000	7300	10000	7700	10000	7800	10000	7850
$\bar{X}$		7380		7525		7712		7842
% consumed		26.2		24.7		22.9		21.6

Table 3.10 Food uptake at four brine viscosities: do and di are the cell densities at the beginning and end of the experimental period respectively expressed as cells/cm^3.

	Sum of S.	D.F.	Var.	F.	F0.01
BSS	497052	3	165684	10.2**	6.0
WSS	194148	15	16179		
Total	691200	18			

Table 3.10.1 Analysis of variance test applied to the mean number of algal cells unconsumed after an experimental feeding period at four beine viscosities.

Results of the feeding trials, shown in Table 3.10, were also subjected to an analysis of variance between the means, (Table 3.10.1). A significant difference was found at the 1% level reinforcing the hypothesis that the viscosity of the solution has an effect on the efficiency of the feeding. The percentage of the available food consumed was calculated and a decrease of 17.6% was found between the 60 ppt and 300 ppt solutions.

DISCUSSION

The combination of increased effort required to move through the denser solution and the reduced food intake at higher viscosities may be one of the major factors accounting for the slower increase in Artemia numbers at highest salinities. Once Artemia is fully grown, very little food energy is channelled into body maintenance or new exoskeleton manufacture. The vast bulk is used in egg production and respiration. Egg production is the process most likely to be reduced as the energy intake in food diminishes. It was shown in section 3.2 that the number of eggs carried by mature females at a given time decreased rapidly as the salinity rose over 200 ppt. The inference that may be drawn from the graph is that up to a salinity of 200 ppt the uptake rate of food was sufficient to supply energy for body maintenance and respiration and to maintain the optimal egg production rate. But since both maintenance and respiration are essential and fixed expenditures, and the effort per unit of food obtained was rising as the salinity rose, the point arrived at 200 ppt where the intake was insufficient to satisfy all demands and egg production was cut back. This ideal situation would only hold where the food supply was relatively constant throughout the salinity series and is certainly not clear cut in the

Grassmere ponds where the crop of algae is variable and tends to decrease with increasing salinity.

3.8 POPULATION BUILDUP UNDER CONTROLLED CONDITIONS OF SALINITY, ALGAL GROWTH, TEMPERATURE AND SUPPLEMENTARY FEEDING.

INTRODUCTION

Although in many cases it is not valid to apply the results of aquarium studies to large bodies of water, the value of this type of situation lies in the ease with which known conditions can be maintained. Such parameters as temperature, illumination or food intake may be absolutely controlled or one varied relative to the rest to gauge its contribution to the maintenance of equilibrium of the population. In the following set of experiments two of the most important environmental factors in Lake Grassmere, salinity and food availability, were manipulated.

METHODS

Two 11 litre aquaria were filled; the first with Lake Grassmere water adjusted with distilled water to a salinity of 75 ppt and the second to 150 ppt. Both were inoculated with Dunaliella euchlora and left until a bloom developed. Analysis of the water showed that the initial concentration of soluble phosphate was 0.120 g/m^3 and that of reactive nitrate 0.39 g/m^3. In both aquaria temperature was maintained at 26°C. Illumination was provided by two 65 watt cool white fluorescent tubes.

The salinities, temperatures and illumination were kept constant throughout the entire series of experiments but after the first five weeks the nutrient levels in the tanks were adjusted to phosphate 0.8 $g.m^3$ and nitrate 1.0 g/m^3. After a second five week period this nutrient combination was main-

tained and 300 mg of pasteurised yeast suspension was added daily to each aquarium.

The Artemia populations were initiated by introducing ten adult males, ten adult egg-bearing females and approximately 200 eggs to each aquarium. Each population was allowed to develop for five weeks and the numbers of Artemia were assessed twice a week by taking 100 ml subsamples from the aquaria after thorough aqitation. The total present was calculated from the means of 10 such subsamples. After the first five weeks in the unsupplemented lake water the populations were removed, the solution modified as detailed above and the population restarted in an identical manner. A similar procedure was followed after the second modification. Difficulty was experienced in maintaining the nutrient levels because of high bacterial growth, particularly immediately after the modifications, but the problem diminished as the system settled down. Routine additions of phosphate and nitrate were made when the Artemia were sampled. Salinity was maintained by additions of distilled water and checked with an inductive salinometer.

RESULTS

The build up in number of Artemia in the unmodified lake water at salinities of 75 and 150 ppt is shown in Fig. 3.7. By the end of the first week most of the eggs introduced had hatched and approximately 150 Artemia were present. Egg bearing females were shedding eggs continually and by the end of the second week the population was approaching 300. A fairly rapid linear increase occurred until the end of the fourth week when numbers began to stabilise at approximately 2000. In the higher salinity aquarium hatching of eggs was much more protracted and little increase in numbers was evident

FIGURE 3.7

The build up in numbers of two populations of *Artemia* in unmodified Lake Grassmere water at salinities of (a) 75 ppt and (b) 150 ppt

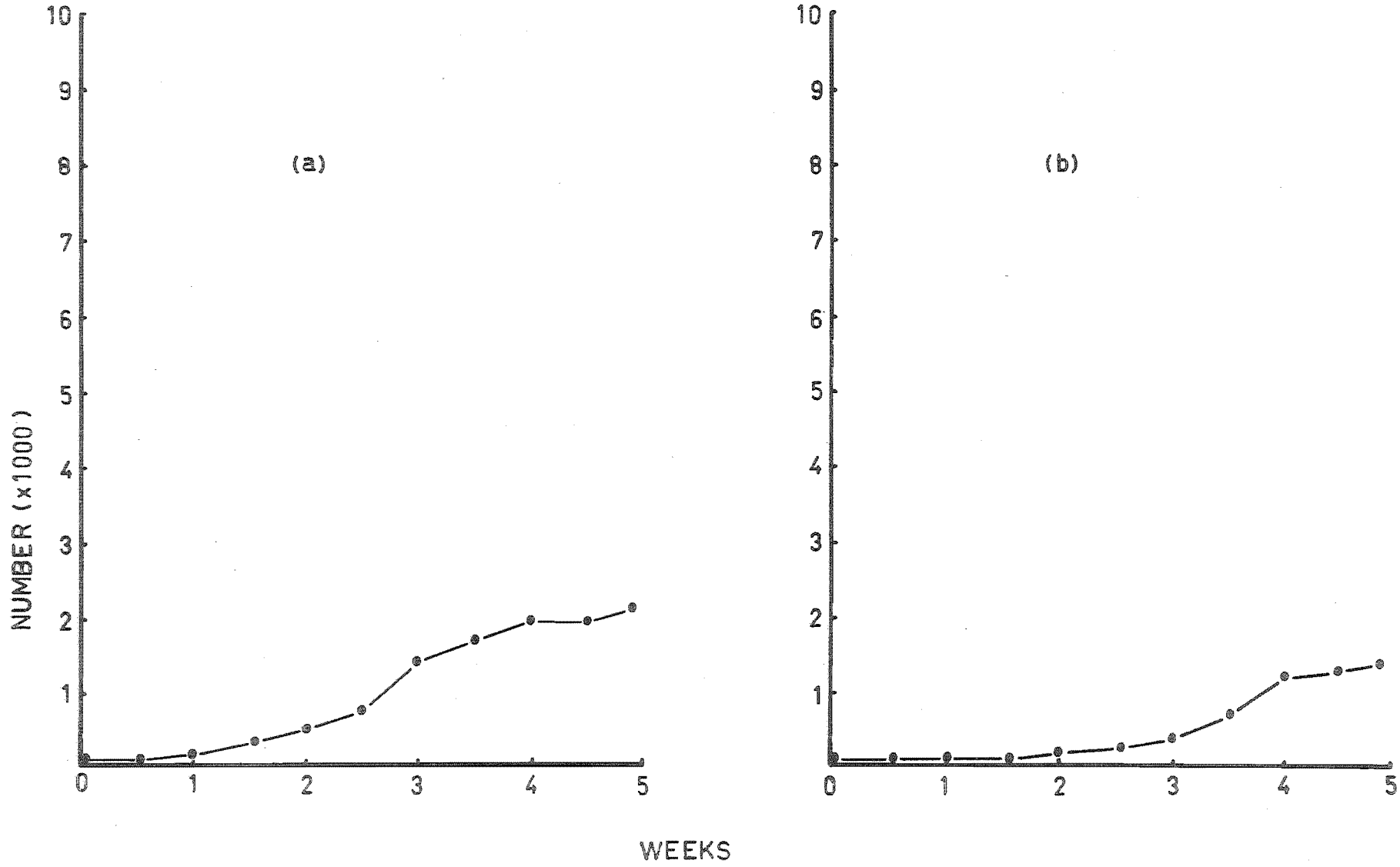

(a)
(b)
NUMBER (x1000)
WEEKS
0
1
2
3
4
5
6
7
8
9
10

FIGURE 3.8

The build up in numbers of two populations of Artemia in nutrient enriched lake water at salinities of (a) 75 ppt and (b) 150 ppt

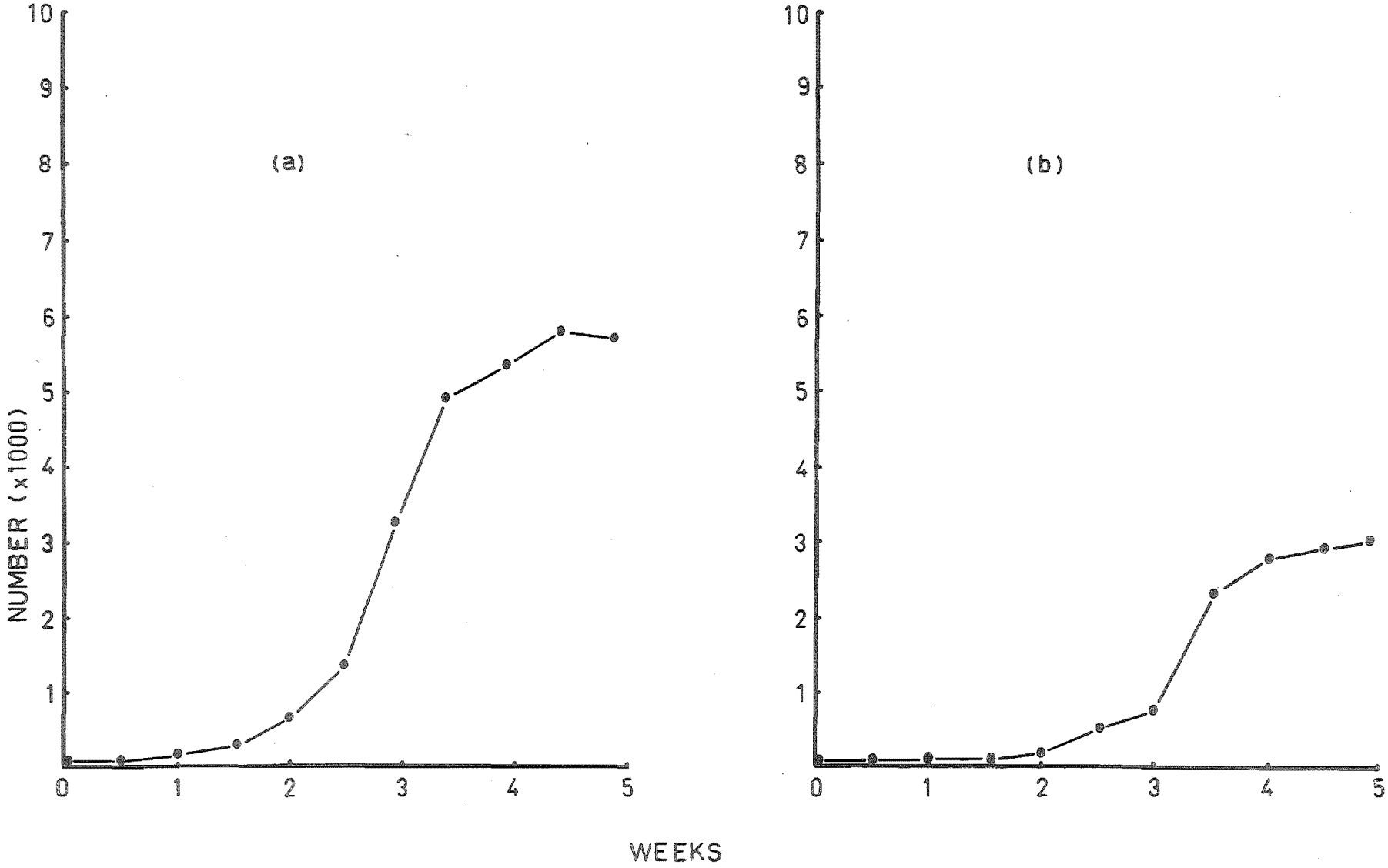
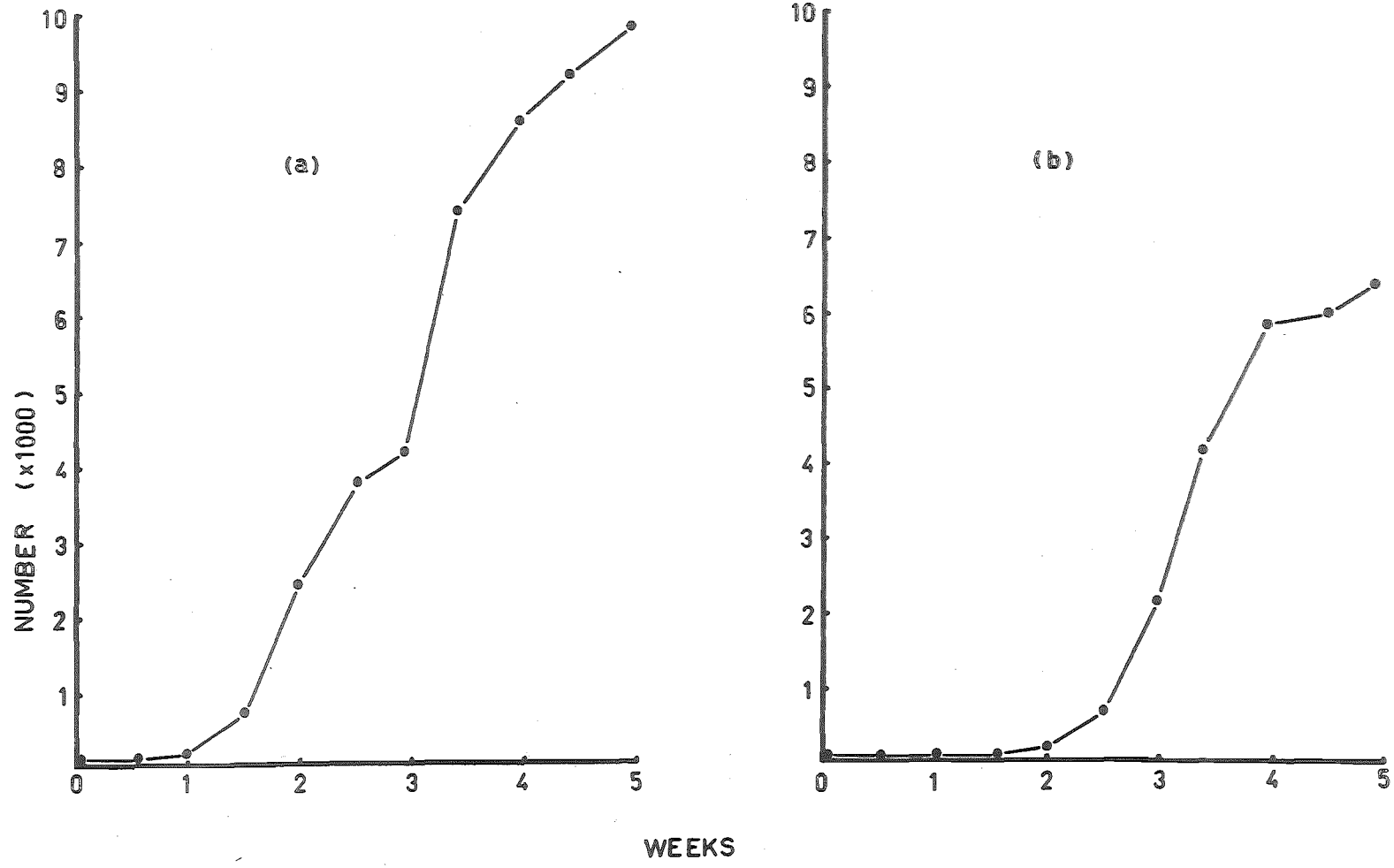

(a)
(b)
NUMBER (x1000)
WEEKS
0
1
2
3
4
5
1
2
3
4
5
6
7
8
9
10

FIGURE 3.9

The build up in numbers of two populations of Artemia in nutrient enriched lake water and with supplementary feeding at salinities of (a) 75 ppt and (b) 150 ppt


(a)
(b)
NUMBER (x1000)
WEEKS
0
1
2
3
4
5
1
2
3
4
5
6
7
8
9
10

until midway through the third week. A similar rise to that found at 75 ppt took place but it occurred less rapidly and the population reached a maximum of about 1 500 animals. In each of the aquaria the density of Dunaliella cells at the beginning of the experimental period was approximately 1 100 cells/ml.

The second populations, Fig. 3.8, were set up in a similar fashion in nutrient enriched solutions which initially contained 5,400 Dunaliella cells/ml. After an initial lag period during which eggs hatched the increase in numbers was much more rapid than in unmodified seawater. By the end of the fourth week there were about 5,600 Artemia present at 75 ppt salinity whereas at 150 ppt salinity a considerably lower number (2600), was found. A peak of 6,000 was reached by the middle of the fifth week in the lower salinity and in the higher salinity the total had risen very slowly to approximately 2,900.

The third populations (Fig. 3.9), established in similarly enriched media, but fed supplementary yeast, increased in numbers at an extremely rapid rate after the normal lag phase. At the lower salinity a peak density of 9,600 was achieved during the fifth week. After a slow start the rate of increase in numbers in the 150 ppt medium approximately equalled that in the less concentrated solution but after reaching a population size of 5,700 the rate of increase fell drastically. At the end of five weeks a slow rise was still in progress but the population still numbered only 6,100.

DISCUSSION

In unmodified lake water the buildup of numbers was slow at both salinities and the lag period was very long,

particularly in the 150 ppt salinity. However, the final number of Artemia was not vastly different : 2200 and 1600 respectively. This illustrates one of the chief salinity effects, that of increasing the hatching time of eggs (cf. section 3.3). This variation in lag time was shown throughout this set of experiments. The salinity effect is also manifest in a reduced production of eggs or ovoviviparous nauplii per female (cf. section 3.2.2), leading to a slightly slower build-up from progeny of the egg bearing females introduced. Growth rate of Artemia was not greatly affected, any retardation being masked by the overall limiting effect of the available food supply. In both unmodified lake water media the Dunaliella cell count was low throughout the period.

When the water was fertilized, great differences, reflecting the greater amount of food available, were seen. As in the first set of experiments, the rate of increase during the most rapid part of the buildup was about equal at both salinities but the rate slowed after a short time as food became limiting at the higher salinity. An almost identical situation existed when supplementary feeding was introduced except that the maximum population sizes attained were larger.

It seems, therefore, that high salinity acts on the food supply to limit Artemia numbers as well as directly on the animals to limit their rate of increase.

While food production is adequate there was very little difference in the breeding and growth rates of populations kept at different salinities except for increasing egg hatching time with increasing salinity. When the yeast cells were added in suspension the new source of food energy allowed a further increase in the growth rate of the population. A new equilibrium consistent with the food supply was established but

the level still reflected the effect of higher salinity with reduced numbers.

The density of Artemia did not seem to affect its rate of increase up to at least 9,600 in 11 litres of brine. This density translated to numbers per m^3 is approximately 860,000, a number which was maintained for six months with no apparent decrease in quality or vitality of the population. This is vastly more than in Lake Grassmere where numbers more than 25,000/m^3 are exceptional and 7 000 - 8 000 is normal for a good growing period.

3.9 POPULATION DENSITY AND PRODUCTION OF ARTEMIA IN THE CONCENTRATING PONDS

When managing a population it is essential to have detailed information on its rate of growth and change in numbers at all periods of the year. This is particularly important where a regular harvest is required. In Lake Grassmere Artemia is a fast growing species with the potential for a rapid turnover. This situation allows exploitation by repeated, closely spaced nettings. The fast turnover, however, may produce great fluctuations in numbers and production of Artemia as environmental conditions and food supplies change. The food supply in the ponds has been shown to be mainly two closely related species of Dunaliella that to a large extent are spatially isolated in the series of ponds by the salinity. Both co-exist only at the highest salinities. In this situation there is none of the compensating effect that a wide variety of algae might create by providing alternative food cources.

METHOD - POPULATION DENSITY

Sampling of Artemia in the ponds was done with a box

sampler that enclosed a known volume of water which was filtered through a plankton net. The sampler consisted of a square perspex box 30 cm X 30 cm X 30 cm. The top was open and the bottom was a sliding panel. The sliding panel supported a conical net that terminated in a 250 ml glass bottle. In use the bottom panel was slid open and the box lowered until completely full. While still full the panel was slid back. As the box was raised out of the water the contents were filtered through the net (0.2 mm mesh), and any particulate material, including all stages of Artemia were retained and flushed into the bottle.

Three samples were taken from each concentrating pond at each visit by walking out into the ponds at the points marked 'S' in Fig. 1.2. It was mentioned in section 1 that the wind had a drastic effect on the distribution of Artemia in the concentrating ponds. It was found to be impossible to compensate for the extreme sampling bias caused by the water movement so sampling was performed only during periods of negligible winds. During the first two visits to the ponds five random samples were taken from each pond at surface, midwater and bottom. Variations in the numbers of Artemia caught was slight (20% or less). This small variation is probably brought about, at least in part, by the constant depth, consistently fine sediment, even illumination and absence of any large attached vegetation in the made-made pools. The validity of Point 'S' in each pond as a representative sample was tested on several occasions by taking other random samples around the pond. In each case, provided conditions were as stated above, the distribution of Artemia was found to be very even throughout the ponds. The Artemia adults and nauplii were normally counted in total for every sample, but where

extremely large numbers of nauplii were present subsampling was performed by shaking the nauplii in one litre of water and taking five 100 ml subsamples. The numbers in the net sample were converted to numbers per cubic metre by multiplying by 37 since the volume of the sampler was 27 litres.

RESULTS

Numbers of juveniles (up to 2 mm), and adults (over 2 mm), present on each sampling day are shown in Table 3.10. The reason for separating animals into age classes was because one of the objectives of the project was to assess the long term possibility of harvesting Artemia.

At the beginning of the sampling period, 10 August 1972, numbers of adults were low in all concentrating ponds although they tended to be more abundant in the less saline ponds. This trend was more pronounced when juveniles were considered. There was practically no hatching of eggs in ponds P9 - F5 exept for an unexplained outbreak in F2. This situation prevailed until the end of September (21.9.72), when hatching began to accelerate in all ponds (although almost all females had been carrying eggs for some time prior to this) (Fig. 3.1). The higher salinity ponds that had been showing the effects of egg hatching lag, possibly caused by high salinities and low temperatures, (cf. section 3.3), were now beginning to show numbers comparable to lower salinity ponds.

Maximum numbers, both juvenile and adults, were found in the 26.10.72 sample when 20,856 adults/m^3 were recorded in P4 and 10, 710 adults/m^3 in F2. During December a fall in numbers occurred in all ponds and breeding stopped in the now very saline and very hot (30^{o}C), F series ponds. Breeding in the F series began to recover in late January but throughout late summer numbers were highest in P3 - P8 and lower in the F

series ponds. Breeding of Artemia was briefly interrupted in ponds P3 - P8 in late March when large water transfers were in progress sweeping much of the population up the concentrating series as fresh seawater was drawn in from the body of the lake. The movement of water up the concentrating chain, and the lower autumn temperatures appeared to stabilise the population density and numbers of adult and juvenile Artemia were not greatly different throughout the system. Numbers were not high, however, and tended to decrease as winter advanced.

During August 1973, the spring rise in numbers became evident again and the population built up to a higher level than during the same period in 1972. Breeding and naupliar nubmers were much higher in the F series ponds also, and there was no period of total juvenile absence as in 1972. Between August and November the effect of salinity and reduced food availability were indicated by the decrease in numbers up the concentrating series.

The largest populations were found consistently in the lower P series of ponds, P4 - P8. P3 lagged behind P4 at the beginning of each phase of population increase, although comparable numbers were achieved during the most productive periods.

METHOD - PRODUCTION

The data that were available for measuring production of the Artemia population were: numbers of juveniles and adults per cubic metre, the proportion of mature females, the percentage of females carrying eggs, the rate of hatching of eggs and the growth rate. Total production of the Artemia population is given by the sum of the increase in weight of each individual in the population plus the total weight of

eggs produced during the period concerned and the growth of new animals hatching from the eggs. Artemia reproduces more or less continuously throughout its life span and as a result cohorts cannot be recognised. The production calculation for every time period, therefore, had to contain an expression for recruitment.

The first phase of analysis used a computer program written by R.L. Hunt of the Lawrence Creek Research Station, Wisconson. This produced estimates of percent mortality, and instantaneous rates of increase, (Appendix 2), over the interval between samples but it did not give a very satisfactory production estimate. The estimate was not satisfactory because the program was designed for work on fish and included an expression for increase in weight of the animals over a growth season. The growth pattern of an arthropod cannot be well compared to that of a fish and could not be applied to the program. Attempts to modify the program to delete the expression and insert an expression for turnover rate of the Artemia population were not successful.

The production estimate was derived from the equation used by Pechen and Shushkina (1964) and Winberg, Pechen and Shushkina (1965), for calculating production of copepods. In their studies the copepod production was divided into three phases; egg production, production due to growth of nauplii from hatching to copepodid stage, and production by growth from copepodid to adult copepod. The analagous stages in Artemia life history are egg, nauplius, metanauplius and adult. The metanauplius stage in Artemia lasts until all limbs are present, usually 10th instar and 1.8 - 2.2 mm length.

$$P = \frac{Ne \quad We}{Te} + \frac{Nn \quad Wn}{Tn} + \frac{Nc \quad Wc}{Tc}$$

P is production per day, Ne is the number of eggs produced per female per day, Nn is the number of nauplii and metanauplii up to 2 mm long, and Nc is the number of adults present. The weight of an egg is represented by We, Wn is the change in weight between an egg and a 2 mm Artemia and Wc is the change in weight between a 2 mm and a fully grown individual. Te is the hatching time of the egg, Tn is the growth period between hatching and 2 mm and Tc is the time taken to grow from 2 mm to full size.

The first part of the equation estimated egg production, the second naupliar and metanaupliar production, and the third part the production of the adults. The main reason for using this equation was that it was very flexible and could easily take into account changing hatching times and growth rates that depend to a degree on the prevailing combination of temperature and salinity measured in the ponds when they were sampled.

RESULTS

Production is shown as (g/m^3)/day in Table 3.12. As expected, production followed population density fairly closely, (Table 3.11). Production was extremely low in the more saline F series ponds between August and October 1972, ranging between 0.002 and 0.08 (g/m^3)/day until egg hatching boosted the population during October/November. There was a pronounced difference between production in the lower P series, where a maximum of 0.996 (g/m^3)/day was recorded in P4 on 26 October 1972, and F4 and F5 when at the same time 0.243 and 0.242 (g/m^3)/day were produced. Productivity was high in P3 during the spring of 1972, rivalling and at times surpassing, that of P4, P5 and P6. However, the influx of

new water and the breakup of the calcium sulphate crust in mid 1973 drastically reduced production. This is shown clearly by the total production figures for *Artemia* in each pond, P3 lagging well behind P4 (Table 3.11). P4, which had the lowest salinity apart from P3 and the most permanently stable substrate, was the most productive pond in the series. Production declined as the average salinity of ponds rose except in F1 when there seemed to have been a more rapid build-up of numbers of *Artemia* during spring 1973 than occurred in either P10 or F2.

SECTION 4

ENERGY FLOW

4.1 INTRODUCTION

The first law of thermodynamics states that "energy may be converted from one form to another but it is never created or destroyed". This statement covers such ecologically important conversions as light energy into the latent energy of chemical compounds and subsequent conversion of chemical energy into mechanical, electrical and heat energy.

The second law of thermodynamics, probably the more important in a system of inter-related conversions, may be written as "no process involving an energy transformation will spontaneously occur unless there is a degradation of the energy from a concentrated from into a dispersed form" (Odum 1959). Because some of the energy is changed into unusable forms such as heat, no spontaneous conversion is 100 percent efficient.

In a food chain these laws apply such that there is a loss of potential energy at each food transfer and although there is a definite relationship between the amount of energy being put into the chain and that emerging, only a small proportion fixed by the plants at the head of the chain emerges after passage through several links in the chain.

Losses vary with the animals comprising the chain and may be high as found by McVey (1972) when raising hawksbill turtles. In two enclosures 30.5% and 29.2% of the food fed to the animals was recovered as turtle biomass. In shrimp pond culture the recovery of food energy varied widely according to stocking conditions between 8% and 30% (Broom 1968). The balance of the energy is lost in respiration,

faeces and urine.

Where several food chains interlink, the resulting food web may be extremely complicated and difficult to express accurately and quantatively. In the Lake Grassmere ponds, however, there is only one major food species and only one major consumer. Thus it should be possible to estimate with a high degree of accuracy the flow of energy between Dunaliella and Artemia and the amount incorporated into the Artemia population. The ratio between energy entering a link in a food chain and that emerging represents the ecological efficiency. Typical ecological efficiencies for primary aquatic consumers (herbivores) are 13.3% calculated by Lindeman (1941) for Cedar Bog Lake, Minnesota and 16% found by Odum (1957) in Silver Springs, Florida. These are values for mixed populations of invertebrates, but for pure cultures of Artemia from some Russian Lakes, (Sivash, Voznesenovskoye Lake, and Sasyk Lake) and an estuarine lagoon (Kuyal'nik near Odessa), a value of 18% was calculated by Khmeleva (1969). This is an attractive result since in the experience of Slobodkin (1960), ecological efficiencies vary between 5 and 15% for invertebrates in natural systems. From the point of view of cultivation for harvesting high ecological efficiencies are most desirable.

In the following section, the energy taken in by the Artemia population, the energy lost by excretion with faeces, the energy lost by respiration, and the energy used in egg production will be considered and compared with the energy fixed by the green algae and the standing crop of Artemia. The method used has been to divide the population into size classes and estimate the above energy values separately for each, since animal size has a definite bearing on feeding,

excretory, and respiratory rates. The sum of the values for the size classes provide a population value. The values determined from these calculations are set out in Table 4.4 for ready comparison between ponds and between periods of the year.

4.2 ENERGY CONTAINED IN STANDING CROP OF ARTEMIA

There are several methods of estimating the energy contained in organic material. Early workers converted the biomass of a standing crop to energy equivalents by comparing the mass present with that of a known equivalent (MacFadyen 1948), and fairly inflexible and arbitrary values were assigned to certain groups of plankton.

A more accurate method that was subsequently evolved was that of estimating the amounts of carbon, nitrogen, oxygen and hydrogen and converting the sum of these to an energy equivalent using standard biochemical values for material containing these components, (Spoehr and Milner 1949; Vinogradov 1952).

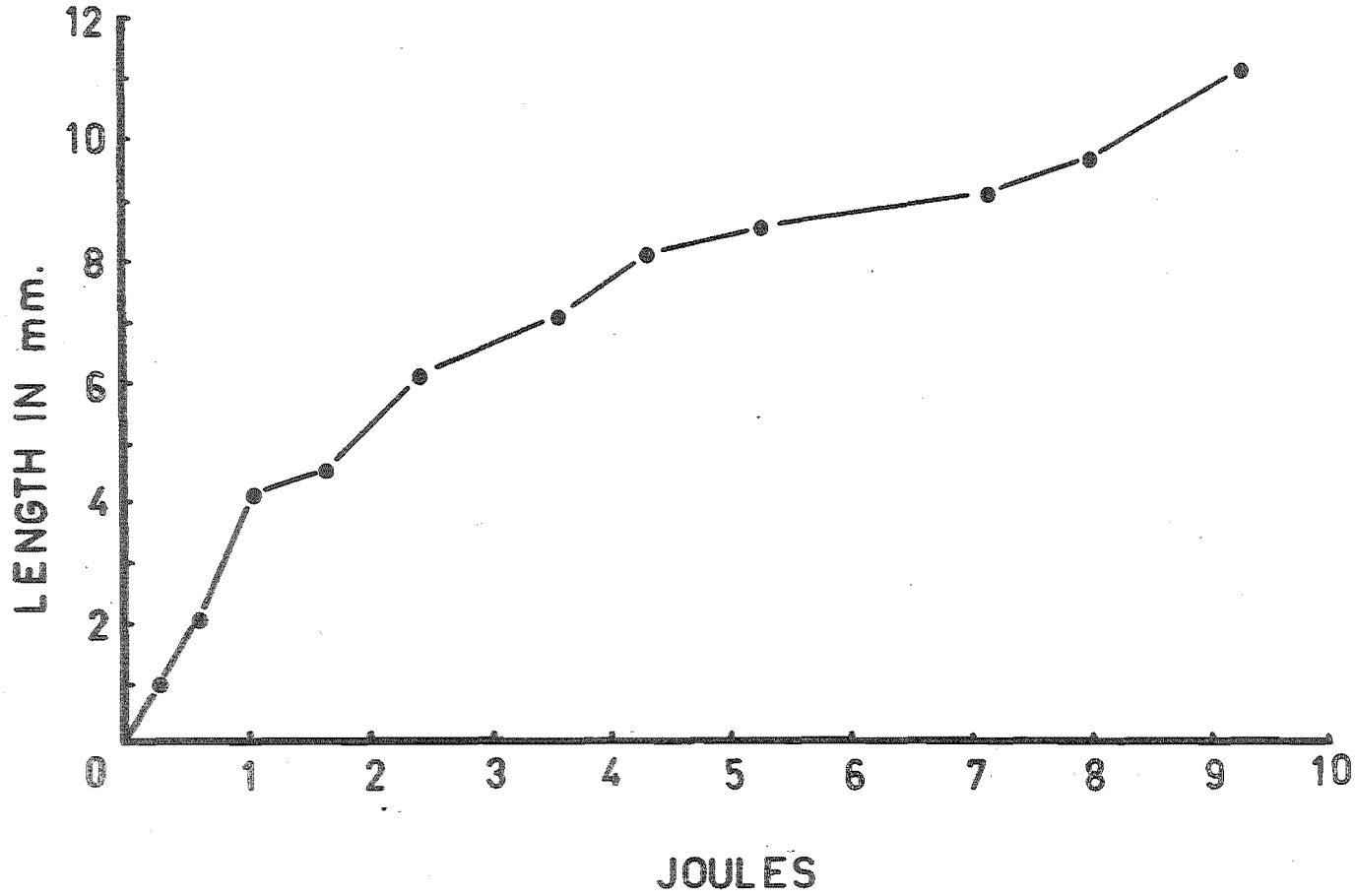
Two direct methods that have been perfected are bomb calorimetery where organic material is burned in an atmosphere of oxygen, and wet combustion where a strong oxidising agent attacks the organic material in solution and is itself reduced. The oxidising agent normally used changes colour in proportion to the extent of its reduction. The degree of reduction is directly proportional to the amount of carbonaceous material present and may be converted to an energy equivalent.

METHOD

Wet combustion as described by Strickland and Parsons (1968) was used. Freshly killed Artemia from a mixed

FIGURE 4.1

Energy content of *Artemia* related to body length as determined by wet combustion


LENGTH IN MM.
12
10
8
6
4
2
0
1
2
3
4
5
6
7
8
9
10
JOULES

population were sorted into the following length classes; 1 mm, 2 mm, 4 mm, 4.5 mm, 6 mm, 7 mm, 8 mm, 8.5 mm, 9 mm and 11 mm. Sufficient were grouped to provide a minimum weight of 20 mg, the smallest mass that can be reliably processed by the wet combustion process that was used.

The results for each size class were expressed as mg of organic carbon and converted to Joules by multiplying by 38.9.

RESULTS

The energy content of Artemia of 11 length classes is shown in Fig. 4.1. The increase in contained energy forms a curve analagous to a length/weight relationship. The values were applied to field populations by estimating the numbers of each size class on each sampling date and multiplying through by values derived from the curve. The grand total for all size classes was used as a standing crop value for each pond in the energy budget, Table 4.4.

RESPIRATION OF ARTEMIA

4.3 INTRODUCTION

One of the major expenditures of energy in an active animal such as Artemia is that used in metabolism, i.e., the conversion of the potential energy in consumed food into the mechanical electrical and heat energy of a living organism. This can be determined by measuring the uptake of oxygen from the water that the animal is living in. Artemia rarely stop swimming and swim at a normal rate in a very small volume of water. The advantage of this is that respiratory values obtained experimentally should bear a good relationship to those of an animal swimming freely in unlimited water, (i.e., a lake).

METHOD

Determinations of respiratory rate were made at 15°C and 30°C in Millipore filtered brine of 140 ppt salinity. The numbers of animals used in each individual trial ranged from 200 nauplii of 0.05 mg ± 0.01 mg to four adults of 0.4 ± 0.1 mg. The test *Artemia* were enclosed in 20 mm lengths of heavy walled polythene hose whose ends were plugged with small rubber bungs. The respiration chambers were suspended in water for four hours. Measurement of oxygen tensions was by a micro-Winkler technique as described by Fox and Wingfield (1938). The sample for analysis was taken by forcing the needle of the micro-Winkler syringe through the wall of the polythene tube and drawing out a sample without the entry of any atmospheric oxygen. Three measurements were made for each size of *Artemia* (at each temperature) and the mean plotted. Control chambers without *Artemia* were tested for oxygen depletion due to bacterial activity.

Further tests made under the same conditions were run to determine the effects of varying salinity. The brines used were 100 ppt, 150 ppt and 200 ppt.

RESULTS AND DISCUSSION

Oxygen consumption in µl/hr is plotted against animal size in Fig. 4.2, (B and E), and compared with the determination of Conover (1960), (A); Khmeleva (1969), (C); Altman and Dittmer (1971), (D); and Bertalanffy and Krywienczyk (1963), (F).

The determination from 5°C to 30°C (E) form an almost geometric series with the data for respiration of Lake Grassmere *Artemia* being very similar to those of Conover, Khmeleva, and Altman and Dittmer. For unknown reasons the values found by Bertalanffy and Krywienczyk are far higher

than those for Grassmere specimens. As they did not state where their animals originated from they may have been a "physiological variant" of Artemia, or their animals may have been more active than mine.

At 5°C Artemia move very little and normally survive for only a few days. This lack of activity is indicated by the very slow increase in oxygen uptake as size increases, Fig. 4.2. It is not normally until 20°C that a marked increase in activity is seen but between 20°C and 30°C a rapid increase in swimming rate is found. Many authors have proposed an optimal water temperature for Artemia cultivation of about 25 - 30°C based on growth rates. This appears to be confirmed by the respiration rates shown in Fig. 4.2.

Results of the respiration experiments at different salinities showed that there was no detectable change over the range tested at any given temperature. This confirms the findings of Gilchrist (1956) and Khmeleva (1969) but differs from those of Kuenen (1939) who found an increase of 1.5 times when salinity was raised from 29 ppt to 116 ppt. By contrast Eliassen (1952) found a decrease in metabolism with an increase in salinity.

The oxygen used in respiration may be directly related to other forms of energy using the oxycalorific coefficient of 4.86 (Khmeleva 1969). The oxycalorific value in calories was converted to Joules by multiplying by 4.19. The sizes of the Artemia were expressed in milligrams for the sake of comparison with other work. Using the number of each size class calculated as in Section 4.2, estimates were made of the energy in Joules respired by the pond populations of Artemia. These are included in the energy budget (Table 4.4).

FIGURE 4.2

Oxygen consumption of Artemia at five temperatures and over a range in size from metanauplius to adult

A: Conover (1960)

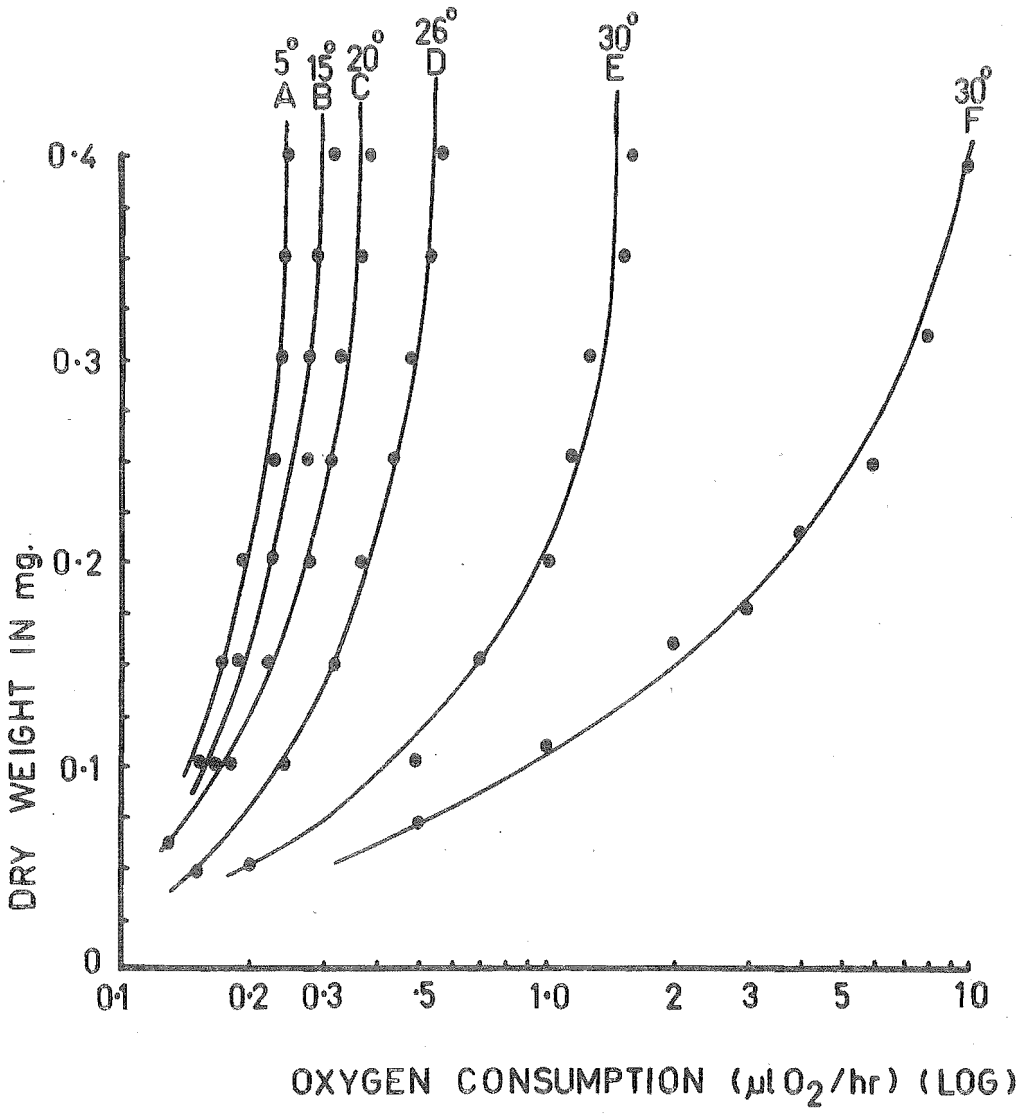
B: Personal result

C: Khmeleva (1969)

D: Altman and Dittmer (1971) (From Gilchrist 1956)

E: Personal result

F: Bertalanffy and Krywienczyk (1953)


5° A
15° B
20° C
26° D
30° E
30° F
0·4
0·3
0·2
0·1
0
DRY WEIGHT IN mg.
0·1
0·2
0·3
·5
1·0
2
3
5
10
OXYGEN CONSUMPTION (µl O_2/hr) (LOG)

4.4 ENERGY CONTAINED IN ARTEMIA EGGS

In adult Artemia, moulting is far less frequent than in the naupliar and metanaupliar stages. Energy loss via this avenue is accordingly greatly diminished and the main energy expenditures are in metabolism and reproduction. Artemia is a prolific breeder, producing eggs more or less continually throughout adulthood (for up to 100 days). The continual output of eggs, either laid unhatched or represented by ovoviviparous nauplii, allows a more accurate estimate of energy content to be made than if egg production was spasmodic.

METHOD

Three 1,000 egg samples were taken of both 'summer' and 'winter' eggs. Winter eggs were identified by their more robust, more darkly pigmented coat and were mainly obtained from ponds substrates at the beginning of winter where they were submerged and in a diapause-like state.

The analytical method used to determine their energy content was wet combustion with a sulphuric acid/potassium dichromate mixture. Samples were prepared for analysis in two ways. Two of the three summer and winter egg samples were combusted with no pretreatment whereas the others were carefully ground up with a mortar and pestle.

RESULTS

The mean weight of 1,000 'summer' eggs was 3.7 mg and of 1,000 'winter' eggs, 4.1 mg. The energy content calculated for the 'summer' eggs sample were 22.2 kJ/g and 21 kJ/g respectively and for 'winter' eggs, 22.6 kJ/g and 22.4 kJ/g respectively. Those for pulverised summer and winter eggs were 22.3 kJ/g and 22.6 kJ/g respectively. It was concluded that there was no difference in energy contents between summer and winter eggs, and that the shells presented

no resistance to the wet combustion oxidant.

The contribution of eggs to the energy budgets of the ponds was assessed as follows. Reference to section 3.2.2 gave mean daily egg productions at salinities ranging from 50 - 250 ppt, the percentage of Artemia larger than the minimum egg-laying size (about 7 mm) was obtained from sample data. The actual number of Artemia capable of reproducing was found from Table 3.11 and the proportion of females carrying eggs was obtained from section 3.2.1. A sex ratio of 1 : 1 was assumed. The daily egg production in grams for each pond on each sampling day was converted to production in Joules by multiplying by 22.5×10^3, and tabulated in the energy budget, Table 4.4.

4.5 ENERGY CONTAINED IN FAECES

It was shown in section 3.5 that the amount of ingested material that was not assimilated varied considerably with the density of the food supply. The results of that section were expressed as percentage ingestion and egestion and the energy equivalents of each for very small and very large Artemia. In this section that work is expanded and applied to the lake populations.

METHOD

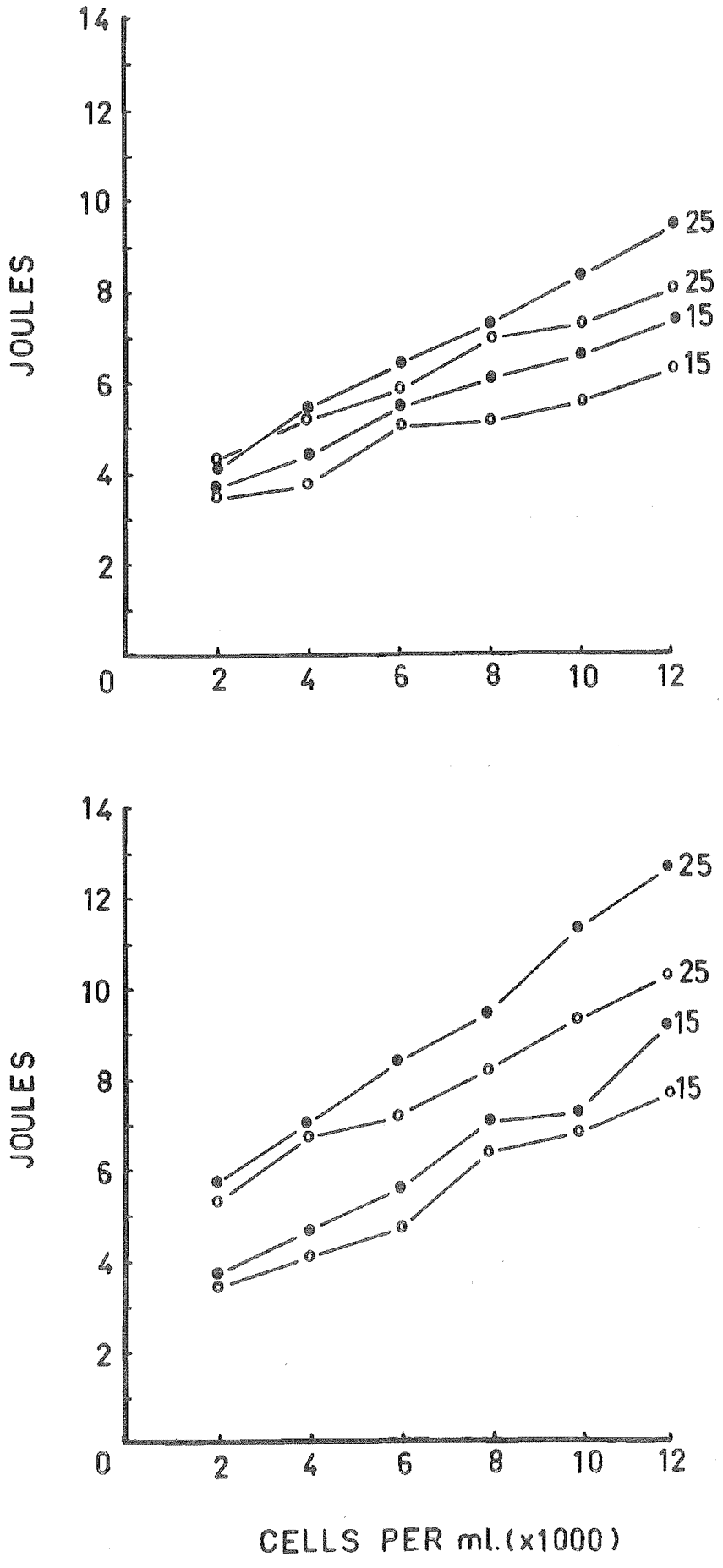
Standard cultures of Dunaliella euchlora were prepared containing 2,000, 4,000, 6,000, 8,000, 10,000 and 12,000 cells/ml. Five 250 ml beakers of each dilution were set up. Artemia were divided into the following size classes, 2 - 3.9 mm (100 animals), 4 - 5.9 mm (50 animals), 6 - 7.9 mm (25 animals), 8 - 9.9 mm (12 animals) and 10 - 11.9 mm (8 animals). Numbers were chosen so that biomass was approximately the same for each size class. Each of the five beakers at each

FIGURE 4.3

The algal energy assimilated, (dots), and the energy contained in faeces, (circles), recorded in Joules for populations at 15°C and 25°C for the size range 2 - 3.9 mm, (100 Artemia)

FIGURE 4.4

The algal energy assimilated, (dots), and energy contained in faeces, (circles), recorded in Joules for populations at 15°C and 25°C for the size range 4 - 5.9 mm, (50 Artemia)


JOULES
14
12
10
8
6
4
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0
2
4
6
8
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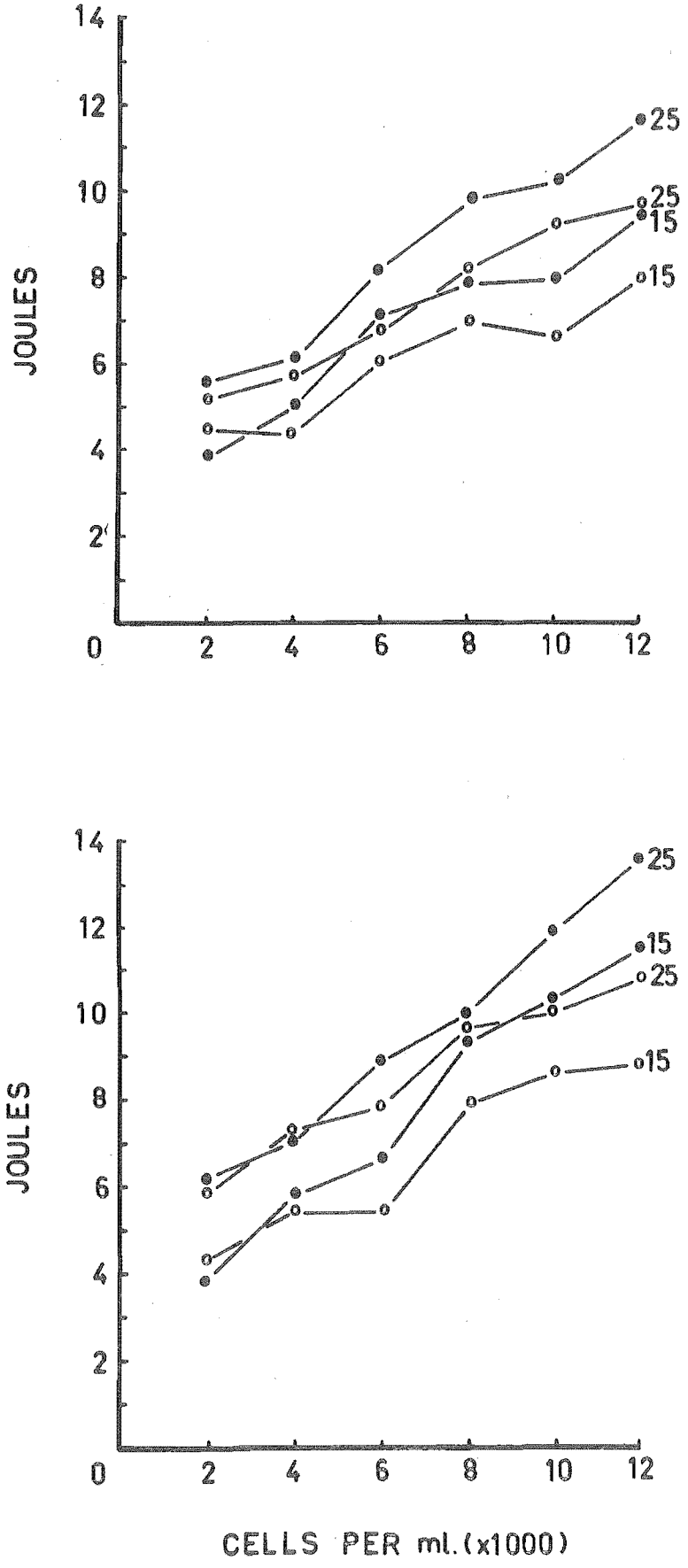
12
25
25
15
15
JOULES
14
12
10
8
6
4
2
0
2
4
6
8
10
12
25
25
15
15
CELLS PER ml.(x1000)

FIGURE 4.5

The algal energy assimilated, (dots), and energy contained in faeces, (circles), recorded in Joules for populations at 15°C and 25°C for the size range 6 - 7.9 mm, (25 Artemia)

FIGURE 4.6

The algal energy assimilated, (dots), and energy contained in faeces, (circles), recorded in Joules for populations at 15°C and 25°C for the size range 8 - 9.9 mm, (12 Artemia)


JOULES
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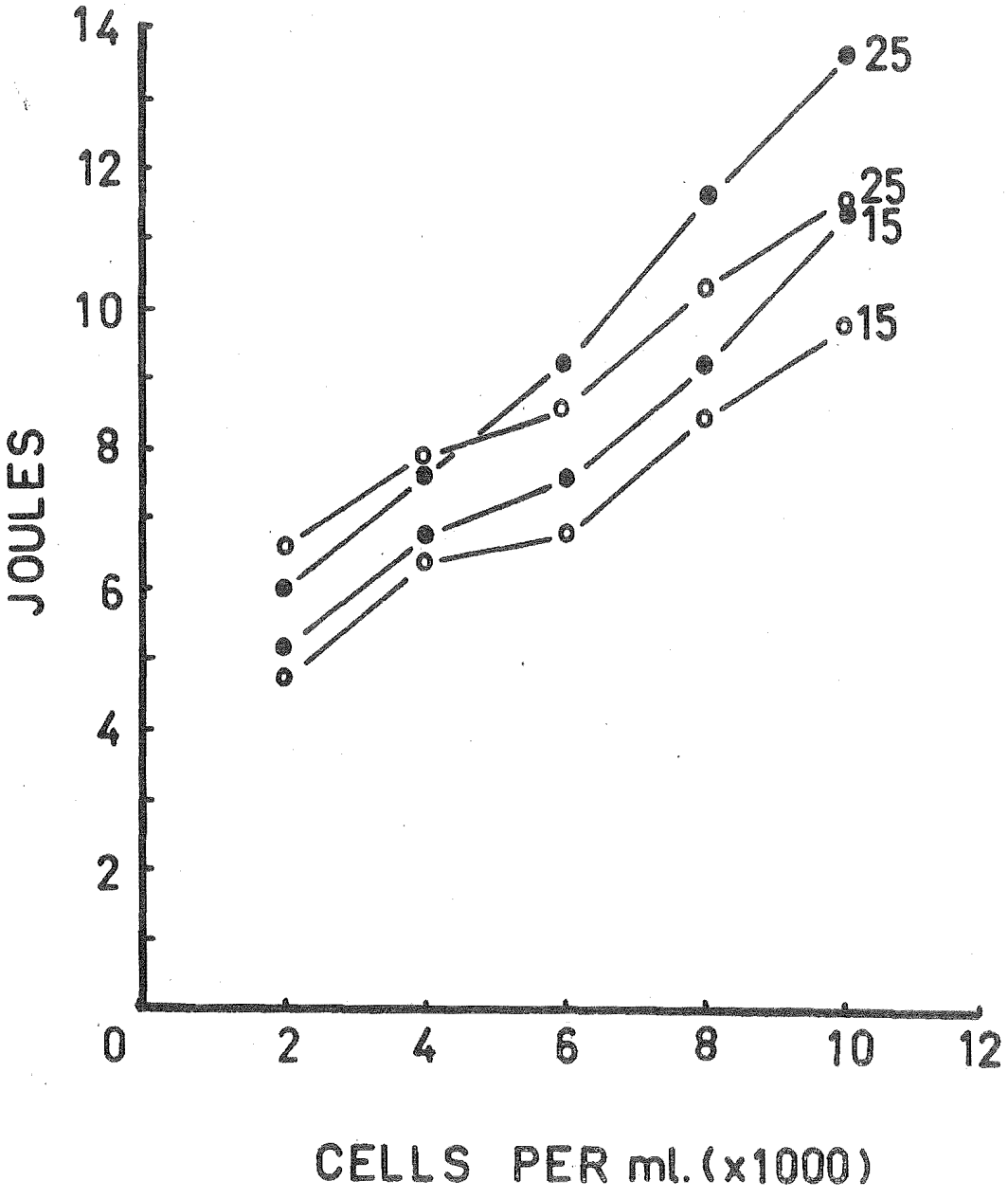
15
JOULES
14
12
10
8
6
4
2
0
2
4
6
8
10
12
25
15
25
15
CELLS PER ml.(x1000)

FIGURE 4.7

The algal energy assimilated, (dots), and energy contained in faeces, (circles), recorded in Joules for populations at 15°C and 25°C for the size range 10 - 11.9 mm, (8 Artemia)


14
12
10
8
6
4
2
0
JOULES
2
4
6
8
10
12
CELLS PER ml. (x1000)
25
25
15
15

cell density had one of the size class groups of Artemia added. Conditions were similar to those described in section 3.5. The animals were allowed to feed undistrubed for 24 hours, after which they were removed and their faecal pellets were collected. The experiment was performed at two temperatures, 15°C and 25°C and at a salinity of 175 ppt.

The decrease in algal cell density in the cultures was recorded after the feeding period and assimilation of algae calculated as in section 3.5. Energy content of faecal pellets was determined by wet combustion in sulphuric acid/ potassium dichromate oxidising solution.

RESULTS

The results are expressed as a series of graphs; (Figs. 4.3, 4.4, 4.5, 4.6 and 4.7), which show energy assimilated and the energy remaining in the faecal pellets for each size class at 15°C and 25°C. As algal cell density increased the amount of energy assimilated also increased but at the same time the relative amount lost in the faeces increased. The over all pattern was similar to that found in section 3.5.

CALCULATION OF FAECAL ENERGY LOSSES FOR THE POND POPULATIONS

The density of D. euchlora in the ponds was measured in milligrams of organic carbon/m^3 of water. To relate this to the artificially cultured cell suspensions that were fed to Artemia to determine cell ingestion and egestion, wet combustion experiments were performed to obtain an organic carbon equivalent. It was found that 1000 cells/ml represented 300 (mg/C)/m^3.

The total number of Artemia per cubic metre is known from section 3 and the percentage of animals in each size class was calculated by subsampling. This allowed the numbers

in each size class present to be calculated.

For each size class in turn the appropriate graph was consulted at the cell density existing in the pond. The energy in the faeces produced by each class was summed and the grand total used in the energy budget for the pond on the sampling day, Table 4.4.

4.6 ARTEMIA PRODUCTION IN KILOJOULES PER DAY

Production of Artemia as determined from the formula in section 3.9 is expressed in grams/m^3. To convert this value to kJ for inclusion in the energy budget for the ponds it had to be multiplied by a factor representing the energy equivalent of the weight of Artemia body material. Depending on the lipid content of the Artemia the conversion factor ranged from 20.1 to 22.0 kJ/g. It was decided to adopt a mean value for lipids throughout the year and use a conversion factor of 20.5 kJ/g. Table 4.1 shows the production of Artemia expressed as (kJ/day)/m^3.

4.7 ALGAL PRODUCTION IN KILOJOULES PER SIX HOUR PERIOD

As with Artemia production, it was necessary to convert photosynthetic production of Dunaliella intially expressed as mgC/m^3, into energy equivalents. The energy equivalent of Dunaliella was determined by wet combustion of pure cultures of both D. euchlora and D. salina. The results showed no difference between them in terms of energy per unit dry weight. The value used as a conversion factor from grams to kilojoules was 22.7 kJ/g. Table 4.2 shows the production of algae expressed as (kJ/6h)/m^3.

ERRORS INHERENT IN THE METHODS

The major sources of errors in converting from biomass to energy equivalents are;

	P3	P4	P5	P6	P7	P8	P9	P10	F1	F2	F3	F4	F5
10/8/72	.191	4.00	.703	.542	2.79	3.88	.703	.563	1.35	.603	.040	.140	.140
25/8/72	.279	4.37	5.69	.513	4.09	4.21	.636	.575	1.72	1.06	.103	.082	.205
5/9/72	.250	4.49	7.31	.390	4.35	5.03	.800	.472	1.66	2.09	.143	.123	.205
21/9/72	8.35	8.82	1.50	4.65	6.11	6.34	4.62	1.75	11.04	1.74	.042	.879	2.36
9/10/72	14.93	15.57	16.86	8.48	7.62	5.62	1.47	4.87	6.96	1.45	.576	.321	3.89
26/10/72	13.97	22.12	12.01	9.43	11.77	10.71	5.26	7.88	11.50	3.15	3.64	5.39	5.37
11/11/72	9.53	6.89	10.52	9.82	9.72	8.02	3.37	6.18	7.31	5.99	.879	1.26	.796
7/12/72	2.61	3.02	3.41	6.04	4.66	7.64	2.77	3.74	5.46	1.13	.800	1.11	.780
30/12/72	2.19	2.78	1.23	4.99	2.23	2.71	1.41	.925	2.51	.744	.463	1.06	.221
10/1/73	2.47	3.36	3.28	3.86	5.06	5.49	.442	.885	2.65	.704	.241	.382	.100
29/1/73	4.99	5.73	6.59	6.44	7.17	9.15	5.65	3.70	2.78	1.87	.905	.964	.060
15/2/73	2.95	3.52	5.17	4.29	3.54	5.26	4.88	2.53	2.62	.566	.963	.984	.377
23/3/73	.965	1.56	4.59	2.19	2.09	2.96	2.50	2.28	3.45	1.11	1.39	1.27	.841
29/3/73	.099	.121	1.02	.181	.463	.865	.844	2.47	3.26	1.89	1.67	1.38	1.01
12/4/73	N O S A M P L E												
26/4/73	.543	2.83	3.03	.643	.724	1.13	1.95	2.07	2.39	.865	1.75	1.41	.925
10/5/73	.821	6.51	6.24	6.24	.800	1.47	2.59	1.72	1.52	.760	1.33	.760	.575
25/5/73	1.11	5.07	5.78	7.22	1.46	1.83	3.79	1.54	1.09	.657	.944	.883	.657
14/6/73	2.01	6.12	3.20	3.74	.842	.903	2.85	.246	.452	.164	.780	.164	.308
28/6/73	3.59	4.94	4.42	4.56	1.23	.925	2.86	.865	.201	.160	.282	.282	.101
12/7/73	3.32	7.07	5.67	4.85	4.46	2.23	5.75	1.69	.463	.442	.402	.422	.322
27/7/73	N O S A M P L E												
9/8/73	2.75	14.45	9.51	6.98	9.05	5.09	6.92	4.23	4.31	2.22	2.69	.760	.657
13/9/73	5.30	14.97	14.73	11.73	9.47	7.42	9.97	5.91	10.05	5.89	1.84	1.86	1.46
28/9/73	11.49	24.87	10.92	15.88	14.82	12.80	13.59	10.47	17.03	8.21	5.00	2.65	2.48
18/10/73	14.57	33.34	19.74	17.11	22.59	14.38	15.75	13.38	19.74	13.36	5.88	5.05	3.98
1/11/73	N O S A M P L E												

Table 4.1 Artemia Production expressed as kilojoules per day per cubic metre.

	P3	.4	P5	P6	P7	P8	P9	P10	F1	F2	F3	F4	F5
10/8/72	21.1	25.7	23.6	22.0	27.9	31.6	23.6	19.3	14.1	16.3	6.8	8.6	5.2
25/8/72	22.2	34.3	30.4	25.9	32.5	44.3	22.5	24.7	17.3	19.9	9.5	11.6	9.9
5/9/72	39.3	41.9	28.6	21.6	37.7	37.2	21.1	23.2	17.9	22.9	23.2	16.1	7.3
21/9/72	33.8	40.6	39.5	44.5	42.9	19.5	26.3	29.1	27.7	24.7	27.7	22.2	21.1
9/10/72	37.2	52.2	56.5	43.4	51.1	14.5	16.8	22.2	22.9	22.9	16.9	23.6	24.7
26/10/72	34.7	56.5	44.3	38.8	33.6	9.5	15.2	14.1	10.7	14.1	12.7	14.1	39.2
11/11/72	46.3	61.1	48.6	24.7	30.4	5.0	11.1	5.2	5.9	6.8	11.4	12.0	18.8
7/12/72	25.2	48.4	26.3	17.5	15.4	3.6	3.2	7.0	8.4	2.7	8.4	14.5	6.8
30/12/72	22.2	23.2	15.6	11.8	9.3	6.1	2.5	5.2	3.6	3.2	9.5	18.8	24.1
10/1/73	14.3	16.7	24.2	9.3	7.3	9.5	8.4	6.4	4.8	3.6	8.4	23.6	38.4
29/1/73	24.2	20.2	32.9	15.6	6.8	6.4	7.3	5.7	3.9	5.2	5.2	14.1	14.5
15/2/73	6.4	15.4	16.8	5.9	4.8	4.8	3.9	4.8	3.2	3.9	6.8	6.8	11.1
23/2/73	4.3	9.5	14.2	6.8	7.5	5.2	3.6	6.8	2.0	3.2	5.9	3.2	4.8
29/3/73	2.5	8.6	11.1	4.5	5.7	5.9	4.8	8.6	4.9	8.4	8.4	16.3	19.1
12/4/73	2.0	2.5	3.9	3.2	4.8	8.6	9.5	11.6	15.6	23.2	29.1	24.7	42.9
26/4/73	2.7	5.9	8.6	10.6	15.0	17.9	6.8	9.5	12.3	18.8	17.3	13.4	47.2
10/5/73	3.6	4.5	15.4	7.3	4.3	6.6	4.3	6.4	5.9	9.5	6.4	3.2	23.6
25/5/73	5.9	9.5	17.5	8.6	6.4	3.2	1.6	2.5	2.5	3.6	4.8	6.1	14.5
14/6/73	3.2	14.8	19.1	14.5	37.2	3.2	2.5	4.3	5.7	4.3	5.7	8.4	4.8
28/6/73	7.5	18.8	22.2	20.2	28.1	6.4	9.5	14.1	8.1	7.5	3.2	9.5	2.3
12/7/73	5.9	25.7	18.8	18.8	32.1	24.1	15.2	17.3	7.7	10.4	6.8	8.6	3.6
27/7/73	9.5	37.7	29.3	25.2	38.8	29.2	29.2	37.2	37.5	14.5	12.3	10.7	5.2
9/8/73	14.3	43.6	60.8	48.1	46.7	44.0	45.9	47.4	66.3	38.4	21.1	15.2	7.3
13/9/73	17.5	46.8	52.2	64.5	60.4	55.2	50.4	52.7	65/1	41.3	27.9	17.3	5.2
28/9/73	33.1	48.4	46.3	49.7	45.9	52.7	45.6	53.1	44.5	32.5	23.2	21.1	10.7
18/10/73	39.5	45.8	53.1	46.1	39.9	39.0	33.6	44.5	28.6	26.3	23.2	33.4	14.5
1/11/73	52.6	37.9	45.6	47.2	38.4	33.8	21.1	20.2	23.6	15.7	19.1	13.8	25.2
TOTAL	542.1	797.3	802.2	721.7	696.5	527.2	446.7	502.8	467.9	402.2	337.8	367.7	452.0
MEAN	20.1	29.5	29.7	26.7	25.8	19.5	16.4	18.6	17.3	14.9	12.3	13.9	16.7

Table 4.2 Algal production expressed as kilojoules per cubic metre per 6 hour incubator period

(1) in the wet combustions. Most methods have a variation of about $\pm$ 10%.

(2) in the assumption of a standard conversion factor from Artemia and algal biomass to energy equivalents while there is a slight variation occurring all the time.

(3) in the collection of faecal pellets that are difficult to handle and are subject to leaching by the water.

(4) in the neglect of soluble excretary products of Artemia and algae.

All of these are very difficult to accord quantitative values, but the overall error may be high.

4.8 ENERGY BUDGETS

The block diagram comrising Table 4.3 is an attempt to isolate portions of the Lake Grassmere community, namely the benthic algae, pelagic algae, and Artemia salina population, and examine their contributions of processed energy and their energy conversions. Isolating the components in this fashion is an artivicial solution since these cannot be regarded as "black boxes" where energy is poured in and having been converted, emerges according to pre-determined rules. Many interactions and alternative pathways exist to the commonly depicted diagrams.

The diagram assumes consumption of the algae directly by the Artemia and makes no allowance for the possible consumption of the algal cells by protozoa that exist in variable numbers in the Grassmere ponds and subsequent capture of the protozoa with the ingested algal energy. Similarly, no provision has been made for ingestion of detrital material along with the algae or portions of cast Artemia exoskeleton that were found densely covered with Dunaliella euchlora cells.

The importance of these two sources varied enormously throughout the sampling period and could not be reliably quantitatively expressed.

What is left is a basic scheme showing the algal energy available to the community at a number of points throughout the year and the amountof energy passing through the system and emerging as Artemia biomass. The intermediate losses are estimated on the basis of laboratory experiments under simulated pond conditions.

As far as harvesting of Artemia is concerned the direct losses of energy are as respiration and infaeces. Egg production is counted as a loss in that Artemia body materials are going into the manufacture of the eggs, but this expenditure also represents a store of potential energy in a concentrated form that will subsequently be transformed into new Artemia, (with further losses), on hatching.

Table 4.4 contains the results of calculations described in sections 4.2 to 4.6 and is presented as a summary of energy flow over the ponds P3 - F5 for each sampling day.

4.9 GENERAL DISCUSSION

The Lake Grassmere community with only two major, (and phylogenetically similar), algae and a single consumer species is not stable. Reference to tables of algae and animal numbers and biomasses show some extremely violent numerical fluctuations between samples. This aspect introduces errors immediately when all calculations that are going to contribute to an annual trend are based on the numbers and biomasses recorded from a spot sample. The distance of Lake Grassmere from adequate laboratory facilities, and transport

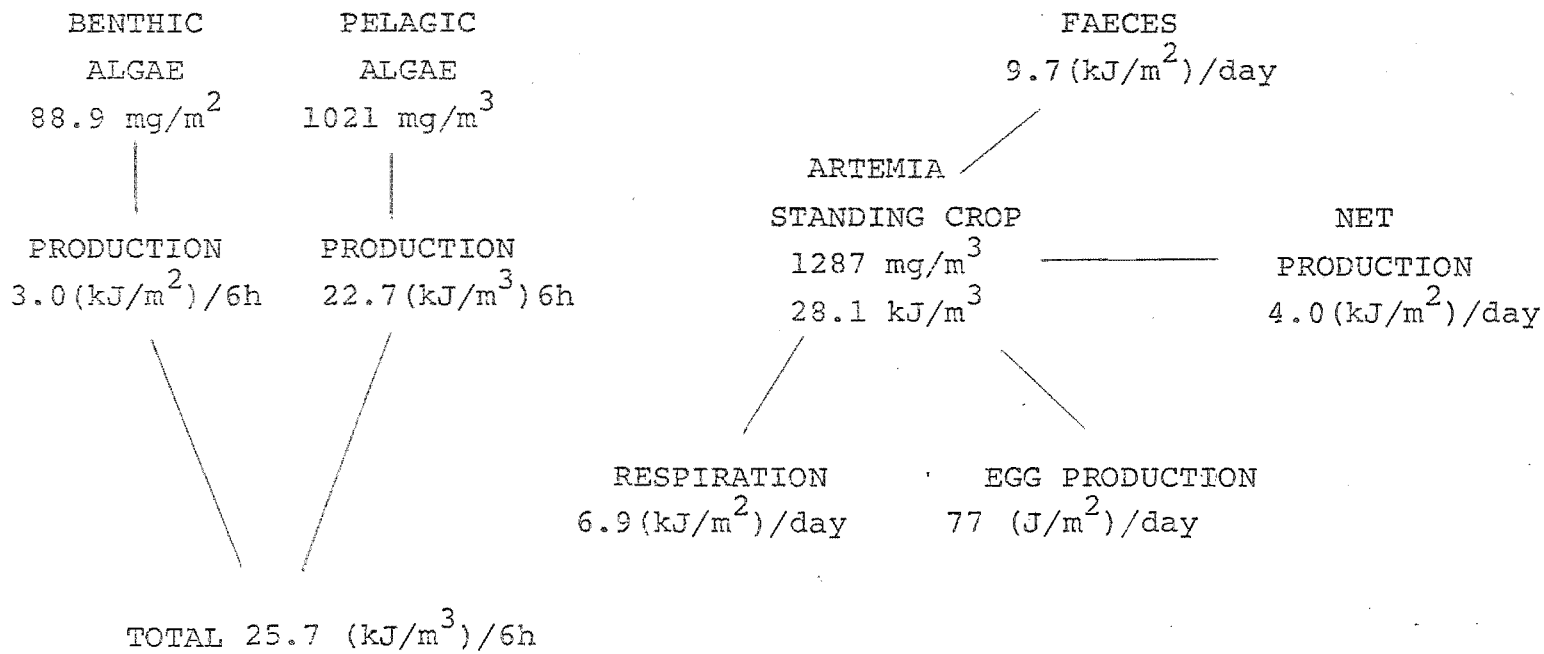


Table 4.3 Block diagram showing relationships of values expressed in the energy budget, Table 4.4. The example is P4 on 10 August, 1972.

difficulties, prevented intensive sampling to give a more detailed picture of the large and small fluctuations. The microfauna and flora numbers, (bacterial and Protozoa), were even more unstable than those of algae or Artemia. An intensive study of the microfauna is outside the scope of the present study but it was noticed that protozoa in particular, were often in evidence but with the data available no common causal factor for fluctuations could be found. The Protozoa would certainly be a substantial food item in the Artemia diet since they were seen to be taken in feeding trials. They unfortunately proved almost impossible to culture reliably.

In addition to algal cells the pond waters contained a variable suspension of organic and inorganic detritus. This material was impossible to separate from the algae and no reliable estimates of its potential food energy values were obtained. This too was taken by Artemia during feedings.

Another potential food source was from portions of cast Artemia exoskeleton, particularly the phyllopoda, covered in fine hairy processes. The surfaces had normally a dense bacterial and algal flora as well as adherent organic and inorganic particles. These were ingested and the material removed by digestion.

These examples indicate that the potential food supply at some periods may be considerably higher than that calculated solely on algal production.

Although egestion as faeces may be measured accurately, equipment was not available to calculate losses by excretion of ammonia. The ammonia and other excreted molecules contain chemical energy that may be utilised by specialised detrital feeders and as such, any not be lost to the ecosystem, but the energy is lost to the Artemia. Another loss of chemical

energy is in the moulting of Artemia. Khmeleva (1969) concluded that Artemia lost as much energy via this avenue throughout its lifetime as the amount of energy in the animal's tissues at adulthood.

The production estimates shown in Table 4.4 are those of a natural population in the absence of predators. These would not hold if the population were to be exploited by harvesting. The effects of harvesting could only validly be estimated from a pond not disturbed by salt making.

Table 4.4

Energy budgets for all ponds on each sampling day.

Key to abbreviations:

BA/Sc	-	Standing crop of benthic algae, MgC/m^2.
BA/P	-	Production of benthic algae, $kJ/m^2/6h$.
PA/Sc	-	Standing crop of pelagic algae, MgC/m^3.
PA/P	-	Production of pelagic algae, $kJ/m^3/6h$.
TOT	-	Total algal production.
ASC b/m^3	-	Artemia standing crop - grams.
ASC kJ/m^3	-	Artemia standing crop - kilojoules.
RSP	-	Respiration losses, kJ/m^3.
EGG	-	Energy used in egg manufacture, kJ/m^3.
FAC	-	Faecal losses kJ/m^3.
PRO	-	Production of Artemia neglecting mortality and losses by moulting.

P3	BA Sc	BA P	PA Sc	PA P	TOT	ASC g/m^3	ASC kJ/m^3	RSP	EGG	FAC	PRO
10/8/72	91	2.0	829	19.1	21.1	0.023	0.48	0.12	1.29	0.17	0.19
25/8/72	93	2.8	887	19.4	22.2	0.028	0.59	0.18	2.59	0.39	0.28
5/9/72	146	5.3	1544	34.0	39.3	0.033	0.69	0.16	9.20	0.87	0.25
21/9/72	129	4.8	1341	29.0	33.8	1.012	20.81	8.67	200.70	14.03	8.35
9/10/72	148	5.4	1472	31.8	37.2	1.744	35.72	6.35	132.21	17.22	14.93
26/10/72	139	5.3	1370	29.4	34.7	1.461	30.13	7.14	117.52	17.01	13.97
11/11/72	169	8.1	1850	38.2	46.3	0.752	15.44	5.31	111.16	14.60	9.53
7/12/72	148	4.2	1372	31.0	35.2	0.524	10.84	3.63	45.52	5.06	2.61
30/12/72	92	2.4	878	19.8	22.2	0.523	10.73	4.58	68.67	5.92	2.19
10/1/73	53	1.4	567	12.9	14.3	0.919	18.85	8.95	226.20	7.67	2.47
29/1/73	87	2.2	973	22.0	24.2	0.567	11.64	5.95	117.44	8.55	4.99
15/2/73	24	0.6	246	5.8	6.4	0.156	3.21	1.58	74.73	2.51	2.95
23/3/73	12	0.3	168	4.0	4.3	0.060	1.24	0.46	5.70	1.46	0.97
29/3/73	7	0.4	93	2.1	2.5	0.092	1.90	0.61	7.41	0.55	0.09
26/4/73	9	0.2	111	2.5	2.7	0.123	1.53	0.45	8.56	0.97	0.54
10/5/73	14	0.4	146	3.2	3.6	0.111	2.29	0.66	11.85	1.60	0.81
25/5/73	7	0.1	253	5.8	5.9	0.087	1.80	0.29	6.30	0.23	1.11
14/6/73	0	0.0	140	3.2	3.2	0.223	4.59	0.73	14.68	2.64	2.09
28/6/73	0	0.0	330	7.5	7.5	0.372	7.64	1.11	42.79	3.99	3.59
12/7/73	0	0.0	260	5.9	5.9	0.523	10.73	1.63	55.79	4.59	3.32
9/8/73	0	0.0	390	14.3	14.3	0.465	9.55	1.47	33.43	4.40	2.75
13/9/73	0	00.0	760	17.5	17.5	0.682	13.99	2.13	51.76	6.00	5.30
28/9/73	68	0.9	1372	32.2	33.1	1.994	40.88	6.70	163.52	16.49	11.49
18/10/73	121	4.8	1599	34.7	39.5	2.151	44.10	7.32	149.94	19.06	14.57

P4	BA Sc	BA P	PA Sc	PA P	TOT	ASC g/m^3	ASC kJ/m^3	RSP	EGG	FAC	PRO
10/8/72	88	3.0	1021	22.7	25.7	1.287	28.1	6.9	77	9.7	4.00
25/8/72	92	3.0	1018	31.3	34.3	1.364	29.8	7.4	134	10.1	4.37
5/9/72	165	3.8	1655	38.1	41.9	1.480	32.4	7.7	197	10.4	4.49
21/9/72	182	4.4	1598	36.2	40.6	1.229	26.9	11.22	269	28.07	8.82
9/10/72	239	5.4	2031	46.8	52.2	4.781	139.1	24.7	525	38.8	15.57
26/10/72	274	6.4	2195	50.1	56.5	7.080	206	30.6	798	49.8	22.12
11/11/72	202	6.8	2458	54.3	61.1	1.258	36.6	12.6	265	19.5	6.89
7/12/72	121	5.4	1968	43.0	48.4	1.010	29.4	6.9	123	8.6	3.02
30/12/72	67	2.5	933	20.7	23.2	0.964	17.1	7.3	110	8.2	2.78
10/1/73	61	1.5	659	15.2	16.7	1.045	18.5	8.8	134	10.9	3.36
29/1/73	106	3.0	774	17.2	20.2	1.966	34.8	11.5	231	14.6	5.37
15/2/73	65	1.7	615	13.7	15.4	1.143	20.2	7.5	136	9.4	3.25
23/3/73	86	2.0	324	7.5	9.5	0.386	6.8	4.9	86	5.2	1.56
29/3/73	160	4.3	220	4.3	8.6	0.220	0.4	0.37	4	0.44	0.12
26/4/73	24	0.6	236	5.3	5.9	0.494	8.7	4.3	19	4.9	2.83
10/5/73	13	0.5	177	4.0	4.5	0.428	7.6	1.5	35	1.97	1.06
25/5/73	47	0.9	373	8.6	9.5	0.580	13.1	2.1	52	2.97	1.07
14/6/73	51	1.3	589	13.5	14.8	0.646	14.6	1.94	47	3.29	1.42
28/6/73	75	2.1	745	16.7	18.8	0.791	17.9	3.99	10	6.6	2.9
12/7/73	131	3.0	279	22.7	25.7	1.054	25.4	5.3	131	8.6	3.9
9/8/73	270	8.3	2160	35.3	43.6	3.000	72.3	10.4	265	16.9	7.6
13/9/73	253	6.2	1767	40.6	46.8	3.973	95.5	14.5	357	19.7	10.6
28/9/73	191	4.9	1918	43.7	48.6	5.638	135.9	22.3	550	34.8	16.32
18/10/73	333	8.2	1666	36.6	45.8	8.600	207.3	29.1	718	49.4	21.3

P5	BA Sc	BA P	PA Sc	PA P	TOT	ASC g/m^3	ASC kJ/m^3	RSP	EGG	FAC	PRO
10/8/72	101	2.3	919	21.3	23.6	0.296	5.94	1.46	16.00	1.06	0.703
25/8/72	139	3.8	1171	26.6	30.4	0.522	10.47	3.21	46.50	8.03	5.690
5/9/72	169	3.6	1056	25.0	28.6	0.622	12.48	2.95	74.80	9.38	7.310
21/9/72	162	5.6	1558	33.9	39.5	0.131	2.62	1.09	2.65	2.55	1.500
9/10/72	211	13.0	1999	43.5	56.5	1.131	22.68	4.04	83.90	14.00	16.860
26/10/72	238	6.6	1682	37.7	44.3	1.979	39.69	9.41	154.79	19.30	12.010
11/11/72	251	8.5	1859	40.1	48.6	1.941	38.92	13.38	280.22	22.64	10.520
7/12/72	163	3.1	527	23.2	26.3	0.714	14.32	4.79	60.14	8.71	3.410
30/12/72	76	1.4	614	14.2	15.6	0.249	5.00	2.13	32.00	2.92	1.230
10/1/73	89	2.3	970	21.9	24.2	0.430	8.63	4.10	62.13	8.92	3.280
29/1/73	92	3.0	1348	29.9	32.9	0.951	19.06	9.76	125.79	14.53	6.590
15/2/73	62	1.6	658	15.2	16.8	0.701	14.05	6.92	94.14	10.77	5.170
23/3/73	33	1.4	577	12.7	14.1	0.638	12.79	4.75	161.15	9.60	4.590
29/3/73	29	1.0	451	10.1	11.1	0.115	2.31	0.74	27.72	1.14	1.020
26/4/73	24	0.7	356	7.9	8.6	0.221	4.43	1.30	8.86	3.81	3.030
10/5/73	71	1.4	619	14.0	15.4	0.332	6.67	1.93	30.68	7.49	6.240
25/5/73	77	2.1	693	15.4	17.5	0.369	7.39	1.20	28.82	6.76	5.780
14/6/73	67	1.7	760	17.4	19.1	0.213	4.29	0.68	13.70	2.52	3.200
28/6/73	76	2.0	894	20.2	22.2	0.336	6.74	0.98	37.74	4.82	4.420
12/7/73	85	2.2	735	16.6	18.8	0.447	8.98	1.36	46.69	5.29	5.670
9/8/73	164	7.5	2476	53.3	60.8	1.392	27.70	4.27	96.95	14.16	9.510
13/9/73	158	6.9	2112	45.3	52.2	1.875	37.60	5.72	139.12	18.46	14.730
28/9/73	149	6.5	1861	39.8	46.3	1.830	36.70	6.02	146.80	16.00	10.920
18/10/73	200	8.5	2110	44.6	53.1	2.649	53.11	8.82	185.89	24.39	19.740

P6	BA Sc	BA P	PA Sc	PA P	TOT	ASC g/m^3	ASC kJ/m^3	RSP	EGG	FAC	PRO
10/8/72	91	2.7	859	18.3	22.0	0.157	3.13	0.77	8.45	1.71	0.542
25/8/72	102	3.2	1018	22.7	25.9	0.112	2.25	0.72	9.90	1.69	0.513
5/9/72	96	2.8	1384	18.8	21.6	0.066	1.32	0.31	7.92	0.50	0.390
21/9/72	191	6.9	1729	37.6	44.5	0.300	6.02	2.51	60.20	6.42	4.650
9/10/72	174	6.5	1706	36.9	43,4	0.723	14.49	2.58	217.35	8.62	8.840
26/10/72	162	5.9	1528	32.9	38.8	1.686	33.80	8.01	131.82	16.41	9.430
11/11/72	102	4.4	868	20.3	24.7	1.925	38.60	13.27	277.92	19.22	9.820
7/12/72	68	2.0	702	15.5	17.5	1.621	32.51	10.89	136.54	14.67	6.040
30/12/72	43	1.2	477	10.6	11.8	1.332	26.71	11.40	170.94	14.99	4.990
10/1/73	32	1.0	358	8.3	9.3	0.782	14.59	6.93	105.04	9.41	3.860
29/1/73	61	1.5	619	14.1	15.6	1.036	20.78	10.63	137.15	16.23	6.440
15/2/73	19	0.5	241	5.4	5.9	0.531	10.65	5.26	71.35	8.11	4.290
23/3/73	23	0.6	267	6.2	6.8	0.144	2.89	1.07	36.41	2.21	2.190
29/3/73	16	0.6	174	3.9	4.5	0.053	1.07	0.34	12.84	0.18	0.181
26/4/73	42	0.9	418	9.7	10.6	0.158	3.16	0.93	6.32	0.72	0.643
10/5/73	23	0.8	287	6.5	7.3	0.279	5.60	3.62	25.76	8.49	6.240
25/5/73	36	0.9	344	7.7	8.6	0.484	9.70	6.58	37.83	13.52	7.220
14/6/73	51	0.9	569	13.6	14.5	0.259	5.20	2.82	16.64	4.96	3.740
28/6/73	69	2.1	801	18.1	20.2	0.339	6.80	2.99	38.08	6.82	4.560
12/7/73	96	3.9	994	18.8	22.7	0.439	8.80	3.34	45.76	8.31	4.850
9/8/73	182	4.8	1808	43.3	48.1	1.087	21.80	6.35	76.30	12.20	6.980
13/9/73	211	5.9	2607	48.6	64.5	2.045	41.00	16.23	151.70	25.91	11.730
28/9/73	189	6.9	1971	42.8	49.7	2.481	49.75	18.16	199.00	29.24	15.880
18/10/73	194	7.5	1906	38.6	46.1	2.933	58.80	19.76	205.80	34.61	17.110

P7	BA Sc	BA P	PA Sc	PA P	TOT	ASC g/m^3	ASC kJ/m^3	RSP	EGG	FAC	PRO
10/8/72	117	2.7	1093	25.2	27.9	0.234	4.80	1.18	3.18	3.01	2.79
25/8/72	124	4.2	1266	28.3	32,5	0.363	7.45	2.29	32.78	5.21	4.09
5/9/72	153	5.0	1467	32.7	37.7	0.461	9.45	2.24	56.70	5.08	4.35
21/9/72	179	5.8	1601	37.1	42.9	0.961	19.71	8.21	197.12	13.83	6.11
9/10/72	223	7.3	1987	43.8	51.1	1.395	28.60	12.09	105.82	16.62	7.62
26/10/72	138	5.1	1322	28.5	33.6	2.183	44.76	10.61	174.56	19.48	11.77
11/11/72	139	5.4	1171	25.0	30.4	1.869	38.33	13.18	275.97	22.72	9.72
7/12/72	72	1.6	608	13.8	15.4	0.859	17.62	5.90	74.00	8.99	4.66
30/12/72	33	1.1	367	8.2	9.3	0.472	9.68	4.13	61.95	5.06	2.23
10/1/73	27	0.8	293	6.5	7.3	0.727	14.90	6.89	107.28	10.71	5.06
29/1/73	24	0.6	276	6.2	6.8	1.104	22.63	11.58	149.35	16.68	7.17
15/2/73	16	0.5	194	4,3	4.8	0.572	11.74	5.79	78.65	8.84	3.54
23/3/73	31	0.6	309	6.9	7.5	0.428	8.78	3.26	110.63	4.38	2.09
29/3/73	21	0.5	219	5.2	5.7	0.141	2.90	0.93	34.80	0.88	0.46
26/4/73	57	1.9	613	13.7	15.6	0.170	3.49	1.03	16.05	1.02	0.72
10/5/73	16	0.4	174	3.9	4.3	0.149	3.07	0.49	11.97	0.96	0.80
25/5/73	22	0.9	248	5.5	6.4	0.118	2.42	0.70	13.55	0.89	1.46
14/6/73	83	3.7	807	33.5	37.2	0.062	1.28	0.21	6.65	0.91	0.84
28/6/73	116	2.8	1114	25.3	28.1	0.116	2.37	0.38	8.29	1.34	1.23
12/7/73	138	3.8	1249	29.3	33.1	0.703	14.41	2.09	47.68	6.01	4.46
9/8/73	191	6.3	1779	40.4	46.7	1.405	28.80	4.37	94.80	14.24	9.05
13/9/73	251	8.1	2329	52.3	60.4	1.697	34.80	5.36	128.76	13.29	9.47
28/9/73	182	6.4	1808	39.5	45.9	2.216	45.42	6.90	180.96	16.72	14.82
18/10/73	162	6.4	1578	33.5	39.9	3.273	67.10	11.00	234.85	30.66	22.59

	BA		PA			ASC	ASC				
P8	Sc	P	Sc	P	TOT	g/m^3	kJ/m^3	RSP	EGG	FAC	PRO
10/8/72	129	3.2	1241	28.4	31.6	0.372	7.62	1.87	5.05	4.62	3.88
25/8/72	187	5.5	1733	38.8	44.3	0.487	9.98	3.06	13.46	6.87	4.21
5/9/72	158	4.9	1452	32.3	37.2	0.539	11.04	2.61	66.24	6.52	5.03
21/9/72	76	2.7	784	16.8	19.5	0.380	7.80	3.25	117.00	8.19	6.34
9/10/72	61	2.2	559	12.3	14,5	0.663	13.60	4.42	50.32	8.33	5.62
26/10/72	36	1.4	384	8.1	9.5	2.439	50.00	11.85	19.50	21.28	10.71
11/11/72	21	1.1	189	3.9	5.0	1.782	36.53	12.56	263.02	19.31	8.02
7/12/72	14	0.4	146	3.2	3.6	1.761	56.10	12.09	151.62	17.87	7.64
30/12/72	26	0.4	244	5.7	6.1	0.615	12.60	5.38	80.64	7.92	2.71
10/1/73	38	1.0	382	8.5	9.5	0.745	15.28	7.26	110.01	10.11	5.49
29/1/73	26	0.6	254	5.8	6.4	1.305	26.75	13.70	176.55	22.10	9.15
15/2/73	19	0.4	191	4.4	4.8	1.011	20.73	10.24	138.89	14.98	5.26
23/3/73	21	0.5	199	4.7	5.2	0.513	10.60	3.93	133.56	5.77	2.96
29/3/73	24	0.5	236	5.4	5.9	0.222	4.56	1.47	54.72	1.48	0.87
26/4/73	81	1.7	759	16.2	17.9	0.133	2.72	0.79	5.44	1.72	1.13
10/5/73	28	0.9	252	5.7	0.6	0.106	2.17	0.63	9.98	1.61	1.47
25/5/73	11	0.2	89	2.1	2.3	0.123	2.53	0.19	9.87	1.76	1.83
14/6/73	13	0.3	127	2.9	3.2	0.056	1.14	0.18	3.64	0.97	0.903
28/6/73	26	0.6	244	5.8	6.4	0.088	1.80	0.26	10.08	1.22	0.925
12/7/73	98	2.9	942	21.2	24.1	0.244	5.01	0.76	26.05	2.69	2.23
9/8/73	191	5.4	1729	38.6	44.0	0.639	13.09	2.02	45.81	6.12	5.09
13/9/73	232	7.4	2158	47.8	55.2	1.063	21.80	3.31	76.76	9.29	7.42
28/9/73	226	7.3	2064	45.4	52.7	1.836	37.64	6.17	150.56	16.04	12.80
18/10/73	168	6.1	1522	32.9	39.0	1.976	40.50	6.72	141.75	19.14	14.38

P9	BA Sc	BA P	PA Sc	PA P	TOT	ASC g/m^3	ASC kJ/m^3	RSP	EGG	FAC	PRO
10/8/72	82	2.4	938	21.2	23.6	0.211	4.32	1.06	11.66	2.00	0.70
25/8/72	101	2.8	979	19.7	22.5	0.191	3.92	1.20	17.25	1.16	0.63
5/9/72	88	2.7	832	18.4	21.1	0.241	4.91	1.16	29.46	1.02	0.80
21/9/72	112	3.6	1028	22.7	26.3	0.304	6.24	2.60	93.60	6.44	4.62
9/10/72	78	2,4	642	14.4	16.8	0.267	5.48	1.97	20.28	2.82	1.47
26/10/72	67	2.3	593	12.9	15.2	0.707	14.50	3.44	56.55	8.31	5.36
11/11/72	46	1.9	454	9.2	11.1	1.143	23.44	8.06	168.76	9.99	3.37
7/12/72	13	0.4	127	2.8	3.2	0.824	16.90	6.66	70.98	7.01	2.77
30/12/72	10	0.4	100	2.1	2.5	0.427	8.76	3.74	56.06	4.52	1.40
10/1/73	35	0.9	325	7.5	8.4	0.139	2.84	1.35	20.44	1.29	0.44
29/1/73	29	0.9	291	6.4	7.3	0.737	15.10	7.73	99.66	12.54	5.65
15/2/73	16	0.3	164	3.6	3.9	0.727	14.90	7.36	99.83	9.28	4.88
23/3/73	15	0.3	155	3.3	3.6	0.328	6.73	2.49	84.79	4.04	2.50
29/3/73	19	0.5	191	4.3	4.8	0.154	3.16	1.02	37.92	1.62	0.84
26/4/73	25	0.6	275	6.2	6.8	0.157	3.22	0.95	6.44	2.42	1.95
10/5/73	19	0.4	171	3.9	4.3	0.142	2.91	0.84	13.39	2.97	2.59
25/5/73	7	0.2	73	1.4	1.6	0.159	3.27	0.53	12.75	3.91	3.79
14/6/73	10	0.3	100	2.2	2.5	0.205	4.20	0.67	13.40	3.11	2.85
28/6/73	36	0.8	384	8.7	9.5	0.273	5.60	0.81	31.36	3.43	2.86
12/7/73	64	1.7	596	13.5	15.2	0.459	9.41	1.43	48.93	6.82	5.75
9/8/73	193	5.5	1907	40.4	45.9	1.045	21.42	3.29	74.97	10.10	6.92
13/9/73	222	6.8	1958	43.6	50.4	1.536	31.49	4.79	116.51	13.49	9.97
28/9/73	201	6.1	1899	39.5	45.6	2.385	48.90	8.02	191.56	20.85	13.59
18/10/73	144	5.4	1316	28.2	33.6	2.673	54.80	9.10	191.80	24.22	15.75

P10	BA Sc	BA P	PA Sc	PA P	TOT	ASC g/m^3	ASC kJ/m^3	RSP	EGG	FAC	PRO
10/8/72	84	2.0	746	17.3	19.3	0.166	3.40	0.84	2.27	1.12	0.56
25/8/72	101	3.1	969	21.6	24.7	0.169	3.48	1.07	15.31	1.44	0.57
5/9/72	97	3.2	903	20.1	23.2	0.152	3.12	1.22	18.72	1.51	0.47
21/9/72	122	4.1	1138	25.0	29.1	0.098	2.00	0.83	30.00	2.18	1.75
9/10/72	93	3.1	877	19.1	22.2	0.556	11.40	4.02	42.18	7.98	4.87
26/10/72	58	2.2	552	11.9	14.1	0.908	18.61	4.41	72.58	12.33	7.88
11/11/72	22	0.9	208	4.3	5.2	0.913	18.72	6.47	134.78	11.29	6.18
7/12/72	20	1.0	270	6.0	7.0	0.903	18.51	6.20	77.74	9.20	3.74
30/12/72	18	0.6	202	4.6	5.2	0.277	4.69	2.00	30.02	2.47	0.92
10/1/73	24	0.7	256	5.7	6.4	0.228	4.68	2.22	33.69	2.73	0.88
29/1/73	23	0.6	217	5.1	5.7	0.604	12.39	6.34	81.75	9.22	3.70
18/2/73	21	0.4	199	4.4	4.8	0.533	10.92	5.39	73.16	7.29	2.53
23/3/73	28	0.6	262	6.2	6.8	0.307	6.29	2.33	79.25	3.99	2.28
29/3/73	37	0.7	343	7.9	8.6	0.439	9.01	2.90	108.10	5.12	2.47
26/4/73	41	0.8	369	8.7	9.5	0.222	4.56	1.34	9.12	2.92	2.07
10/5/73	25	0.7	245	5.7	6.4	0.167	3.42	0.99	15.73	2.61	1.73
25/5/73	9	0.4	91	2.1	2.5	0.092	1.88	0.31	7.33	1.66	1.54
14/6/73	19	0.3	171	4.0	4.3	0.098	2.00	0.32	6.40	0.43	0.24
28/6/73	62	1.5	548	12.6	14.1	0.194	3.98	0.58	22.28	1.27	0.86
12/7/73	72	2.1	678	15.2	17.3	0.304	6.24	0.95	32.45	2.28	1.69
9/8/73	202	5.6	1858	41.8	47.4	0.477	9.77	1.51	34.19	5.42	4.23
13/9/73	231	7.0	2059	45.7	52.7	0.876	17.59	2.67	65.08	8.11	5.91
28/9/73	239	7.5	2071	45.6	53.1	1.415	29.00	4.76	116.00	14.79	10.47
18/10/73	193	7.3	1727	37.2	44.5	1.831	37.53	6.23	131.35	18.77	13.38

	BA		PA			ASC	ASC				
F1	Sc	P	Sc	P	TOT	g/m^3	kJ/m^3	RSP	EGG	FAC	PRO
10/8/72	54	1.5	546	12.6	14.1	0.425	8.72	2.15	23.50	3.22	1.35
25/8/72	72	2.3	668	15.0	17.3	0.500	10.26	3.27	45.14	4.86	1.72
5/9/72	76	2.3	714	15.6	17.9	0.479	9.82	2.32	58.90	3.91	1.66
21/9/72	115	4.0	1085	23.7	27.7	0.987	24.23	8.43	303.45	18.22	11.04
9/10/72	80	6.8	740	16.1	22.9	1.151	23.59	6.19	87.28	12.61	6.96
26/10/72	44	1.5	426	9.2	10.7	1.585	32.50	7.70	126.75	18.24	11.30
11/11/72	24	1.0	236	4.9	5.9	1.463	30.00	10.32	216.00	16.98	7.31
7/12/72	26	1.0	334	7.4	8.4	1.098	22.50	7.54	94.50	12.44	5.46
30/12/72	17	0.4	143	3.2	3.6	0.024	8.50	3.63	54.40	5.82	2.51
10/1/73	19	0.5	181	4.3	4.8	0.541	11.10	5.27	79.92	7.41	2.65
29/1/73	15	0.3	155	3.6	3.9	0.332	6.80	3.48	44.88	6.11	2.87
15/2/73	12	0.3	118	2.9	3.2	0.365	7.49	3.70	50.18	5.91	2.62
23/3/73	7	0.2	73	1.8	2.0	0.571	11.71	4.34	147.54	6.99	3.45
29/3/73	11	0.2	209	4.7	4.9	0.781	16.01	5.15	192.12	8.14	3.26
26/4/73	34	1.1	506	11.2	12.3	0.488	10.00	2.94	20.00	4.87	2.39
10/5/73	25	0.5	235	5.9	5.9	0.263	5.40	1.57	24.84	2.94	1.52
25/5/73	12	0.4	98	2.5	2.5	0.159	3.25	0.52	12.67	1.50	1.09
14/6/73	23	0.6	217	5.1	5.7	0.093	1.90	0.30	6.08	0.71	0.45
28/6/73	25	0.8	235	7.6	8.4	0.047	0.96	0.14	5.37	0.31	0.20
12/7/73	22	0.9	308	6.8	7.7	0.086	1.76	0.27	9.15	0.70	0.46
9/8/73	254	8.3	2356	58.2	66.5	0.296	6.06	0.93	21.21	5.18	4.31
13/9/73	271	8.7	2569	56.4	65.1	1.289	26.44	4.02	97.82	13.77	10.05
28/9/73	183	6.4	1737	38.1	44.5	2.416	49.53	8.12	198.12	24.68	17.03
18/10/73	124	4.9	1046	24.5	28.4	3.038	62.28	10.34	217.98	26.32	19.74

F2	BA Sc	BA P	PA Sc	PA P	TOT	ASC g/m^3	ASC kJ/m^3	RSP	EGG	FAC	PRO
10/8/72	69	1.5	641	14.8	16.3	0.113	2.31	0.56	6.24	1.10	0.60
25/8/72	84	2.4	786	17.5	19.9	0.113	2.32	0.71	10.21	1.21	1.06
5/9/72	92	3.1	888	19.8	22.9	0.164	3.31	0.79	20.22	2.42	2.09
21/9/72	102	3.2	978	21.5	24.7	0.165	3.38	1.41	50.70	1.96	1.74
9/10/72	93	3.4	897	19.5	22.9	0.254	5.20	2.92	19.24	3.84	1.45
26/10/72	62	2.2	558	11.9	14.1	2.858	58.58	13.88	228.46	16.20	3.15
11/11/72	28	1.2	282	5.6	6.8	1.399	28.69	9.87	206.56	13.85	5.99
7/12/72	11	0.3	109	2.4	2.7	0.336	6.88	2.30	28.89	3.16	1.13
30/12/72	10	0.4	120	2.8	3.2	0.223	4.58	1.96	29.31	2.33	0.74
10/1/73	14	0.4	146	3.2	3.6	0.168	3.45	1.64	24.84	1.98	0.70
29/1/73	17	0.5	213	4.7	5.2	0.116	2.38	1.22	15.71	2.49	1.87
15/2/73	22	0.3	152	3.6	3.9	0.156	3.20	1.58	21.44	1.74	0.56
23/3/73	12	0.3	128	2.9	3.2	0.316	6.47	1.90	81.52	1.92	1.11
29/3/73	39	0.8	331	7.6	8.4	0.574	11.77	3.41	141.24	4.62	1.89
26/4/73	72	1.8	758	17.0	18.8	0.213	4.36	0.71	23.54	1.24	0.86
10/5/73	38	0.8	362	8.7	9.5	0.110	2.26	0.36	10.39	1.20	0.76
25/5/73	15	0.3	145	3.3	3.6	0.050	1.03	0.15	4.01	0.69	0.65
14/4/73	16	0.4	164	3.9	4.3	0.026	0.53	0.08	1.69	0.18	0.16
28/6/73	32	0.6	308	6.9	7.5	0.023	0.47	0.07	1.99	0.16	0.16
12/7/73	41	1.1	399	9.3	10.4	0.061	1.26	0.19	6.71	0.47	0.44
9/8/73	163	4.4	1507	34.0	38.4	0.454	9.30	1.43	32.55	3.16	2.22
13/9/73	178	5.6	1612	35.7	41.3	0.791	16.21	2.46	59.97	7.91	5.89
28/9/73	133	4.7	1267	27.8	32.5	1.551	31.80	5.22	127.20	12.71	8.21
18/10/73	105	2.9	955	13.4	16.3	2.234	45.80	7.60	157.30	17.29	13.36

F3	BA Sc	BA P	PA Sc	PA P	TOT	ASC g/m^3	ASC kJ/m^3	RSP	EGG	FAC	PRO
10/8/72	26	0.6	264	6.2	6.8	0.008	0.18	0.04	0.49	0.05	0.04
25/8/72	37	1.1	383	8.4	9.5	0.021	0.43	0.13	1.89	0.18	0.10
5/8/72	92	3.1	908	20.1	23.2	0.035	0.71	0.17	4.26	0.29	0.14
21/9/72	124	4.0	1076	23.7	27.7	0.016	0.32	1.33	4.80	1.01	0.04
9/10/72	72	2.8	628	14.0	16.8	0.058	1.18	1.21	4.37	1.52	0.57
26/10/72	54	1.8	516	10.9	12.7	0.371	7.61	1.80	29.67	4.23	3.64
11/11/72	46	2.9	444	8.5	11.4	0.224	4.60	1.58	33.12	2.11	0.87
7/12/72	37	1.0	323	7.4	8.4	0.243	4.99	1.67	20.96	2.36	0.80
30/12/72	40	1.0	370	8.5	9.5	0.142	2.91	1.24	18.62	1.44	0.46
10/1/73	35	0.9	335	7.5	8.4	0.073	1.49	0.71	10.73	0.72	0.24
29/1/73	19	0.5	201	4.7	5.2	0.064	1.32	0.67	8.71	1.26	0.90
15/2/73	21	0.6	269	6.2	6.8	0.154	3.15	1.56	21.11	2.23	0.96
23/3/73	22	0.5	238	5.4	5.9	0.237	4.86	1.80	61.24	3.00	1.39
29/3/73	31	1.1	309	7.3	8.4	0.300	6.16	1.98	73.92	3.24	1.67
26/4/73	70	1.8	650	15.5	17.3	0.204	4.18	1.23	8.36	2.63	1.75
10/5/73	23	0.6	247	5.8	6.4	0.129	2.65	0.77	12.19	1.94	1.33
25/5/73	22	0.6	178	4.2	4.8	0.069	1.42	0.23	10.33	0.96	0.94
14/6/73	21	0.6	219	5.1	5.7	0.072	1.48	0.24	4.74	0.83	0.78
28/6/73	14	0.3	126	2.9	3.2	0.034	0.70	0.10	3.92	0.32	0.28
12/7/73	28	0.7	262	6.0	6.8	0.036	0.74	0.11	3.84	0.40	0.40
9/8/73	81	2.5	139	18.6	21.1	0.240	4.91	0.75	17.18	3.02	2.69
13/9/73	118	3.7	1102	24.2	27.9	0.312	6.40	0.97	23.68	2.26	1.84
28/9/73	94	3.3	916	19.9	23.2	0.431	8.83	1.45	35.32	5.84	5.00
18/10/73	106	3.7	894	19.5	23.2	0.975	19.99	3.32	59.96	8.22	5.88

F4	BA Sc	BA P	PA Sc	PA P	TOT	ASC g/m^3	ASC kJ/m^3	RSP	EGG	FAC	PRO
10/8/72	32	0.7	348	7.9	8.6	0.040	0.81	0.19	2.19	0.31	0.14
25/8/72	42	1.4	468	10.2	11.6	0.026	0.53	0.16	2.33	0.18	0.08
5/9/72	62	2.2	628	13.9	16.1	0.035	0.72	0.17	4.32	0.21	0.12
21/9/72	84	3.0	886	19.2	22.2	0.047	0.96	0.40	14.40	1.08	0.87
9/10/72	89	3.4	931	20.2	23.6	0.046	0.94	0.67	3.48	0.72	0.32
26/10/72	62	0.9	618	13.2	14.1	0.502	10.29	2.44	40.13	7.03	5.39
11/11/72	51	2.1	469	9.9	12.0	0.370	7.59	2.61	54.64	3.34	1.26
7/12/72	50	1.8	580	12.7	14.5	0.303	6.22	2.11	26.12	2.91	1.11
30/12/72	52	2.0	768	16.8	18.2	0.288	5.91	2.54	37.82	3.24	1.06
10/1/73	32	0.9	998	22.7	23.6	0.119	2.44	1.16	17.56	1.40	0.38
29/1/73	14	0.7	586	13.4	14.1	0.072	1.48	0.75	9.77	1.32	0.86
15/2/73	2	0.1	289	6.7	6.8	0.135	2.76	1.36	18.49	2.11	0.98
23/3/73	0.8	0.1	129	3.1	3.2	0.250	5.13	2.05	64.63	3.09	1.27
29/3/73	16	0.4	704	15.9	16.3	0.305	6.25	2.01	75.00	2.84	1.38
26/8/73	17	0.4	673	13.0	13.4	0.272	5.58	1.64	11.16	2.96	1.41
10/5/73	13	0.2	127	3.0	3.2	0.100	2.06	0.59	9.47	1.16	0.76
25/5/73	19	0.3	261	5.8	6.1	0.086	1.76	0.29	6.86	0.94	0.88
14/6/73	24	0.7	336	7.7	8.4	0.022	0.45	0.07	4.44	0.18	0.16
28/6/73	7	0.1	413	9.4	9.5	0.041	0.84	0.12	3.26	0.32	0.28
12/7/73	8	0.1	372	8.5	8.6	0.069	1.41	0.21	6.23	0.49	0.44
9/8/73	22	0.3	638	14.5	15.2	0.098	2.02	0.31	7.07	0.82	0.76
13/9/73	27	0.2	713	16.5	17.3	0.256	5.24	0.80	19.38	2.52	1.86
28/9/73	24	0.4	896	20.5	21.1	0.383	7.86	1.29	31.44	3.55	2.65
18/10/73	46	0.4	654	16.0	16.4	0.531	10.89	1.81	28.11	5.72	5.05

F5	BA Sc	BA P	PA Sc	PA P	TOT	ASC g/m^3	ASC kJ/m^3	RSP	EGG	FAC	PRO
10/8/72	3	0.1	217	5.1	5.2	0.039	0.79	0.19	2.13	0.26	0.14
25/8/72	16	0.4	414	9.5	9.9	0.064	1.32	0.41	5.81	0.48	0.20
5/9/72	7	0.3	303	7.0	7.3	0.108	2.22	0.53	13.32	0.59	0.20
21/9/72	6	0.6	914	19.7	21.1	0.166	3.40	1.42	51.00	3.44	2.36
9/10/72	49	0.8	51	23.9	24.7	0.368	7.54	2.34	27.89	5.77	3.89
26/10/72	68	2.0	1622	37.0	39.0	0.671	13.75	3.26	53.63	8.45	5.37
11/11/72	42	0.4	778	18.4	18.8	0.227	4.66	1.56	33.55	2.04	0.79
7/12/72	28	0.01	1012	6.81	6.82	0.120	2.47	1.05	10.37	1.43	0.78
30/12/72	17	0.5	1023	23.6	24.1	0.068	1.39	0.66	8.89	0.70	0.22
10/1/73	36	0.9	1634	37.5	38.4	0.026	0.54	0.28	3.88	0.26	0.10
29/1/73	29	0.8	591	13.7	14.5	0.008	0.17	0.08	1.12	0.11	0.06
15/2/73	13	0.2	467	10.7	11.1	0.063	1.30	0.48	8.71	0.63	0.37
23/3/73	16	0.4	194	4.4	4.8	0.114	2.33	0.75	29.36	1.50	0.84
29/3/73	15	0.2	815	18.9	19.1	0.199	4.08	1.19	48.96	1.89	1.01
26/4/73	30	0.8	2010	46.4	47.2	0.171	3.50	1.02	7.00	1.65	0.92
10/5/73	14	0.4	1016	23.2	23.6	0.072	1.47	0.24	6.76	0.68	0.57
25/5/73	8	0.3	612	14.2	14.5	0.068	1.40	0.22	5.46	0.69	0.65
14/6/73	16	0.4	194	4.4	4.8	0.034	0.70	0.10	2.24	0.23	0.30
28/6/73	7	0.1	103	2.2	2.3	0.016	0.33	0.05	1.84	0.06	0.10
12/7/73	16	0.4	144	3.2	3.6	0.060	1.23	0.19	4.22	0.38	0.32
9/8/73	5	0.2	315	7.1	7.3	0.067	1.38	0.21	4.83	0.53	0.65
13/9/73	29	0.3	201	4.5	5.2	0.183	3.76	0.57	13.91	1.76	1.46
21/9/73	1	0.04	459	10.72	10.76	0.313	6.41	1.05	25.64	3.12	2.48
18/10/73	2	0.05	628	14.34	14.39	0.499	10.23	1.69	31.81	5.17	3.98

With minor variations, the pattern of energy flow and conversion through all ponds was the same except for P3 which lacked benthic algae during winter as a result of dilution of brine which allowed solution of the calcium sulphate binding the sediment particules (Table 1.2). All other ponds exhibited the same seasonal trends already described when considering algal production and Artemia population fluctuations. These were a spring peak of Dunaliella production leading to a late spring/early summer Artemia production peak. The high level of energy flow attained as the algae and Artemia flourished tapered off rapidly as the summer progressed. There was no well defined autumn rise and through the winter months energy flow was uniformly low. Indications of a "spring" rise in energy flow began to show themselves as early as mid July in the lower ponds of the P series but were delayed until August/September in the F series. Total energy flow was greatest in P5 but declined gradually up the concentrating chain as salinity increased.

The ratio of benthic algal biomass to pelagic algal biomass fell as the average salinity rose. Thus the mean ratio for P5 was 0.102 whereas that for F5 was only 0.012. The principal cause of this change was the increased occurrence of the red pigmented alga D. salina which does not have a palmellate benthic stage in the higher salinity ponds. In P3 there was no benthic algal cover between 14 June and 13 September 1973. The loss of the palmellar form of D. euchlora caused an immediate fall in total algal production that was partially compensated for, however, by an increase in production of pelgaic D. euchlora cells. This may also have been stimulated by an increase in the amount of reactive phosphate present. This phosphate was formerly bound up in the sediment

and was therefore unavailable (see Table 1.4, 14.6.73).

The energy expended in egg production fluctuated seasonally in much the same manner as shown for the percentage of females carrying eggs, Fig. 3.1. A rapidly attained peak of egg production was followed by an equally rapid drop as summer arrived, but in all ponds there was a short revival of egg production in January. This was followed by a slow fall to a winter minimum. As with overall production, the energy expended in egg laying fell from a peak value in P4 and became very low in the F series where high average annual salinity inhibited egg laying. The flow of energy that is expended in respiration does not have a simple correspondence with population density. since it depends on the distribution of size classes considered as in section 4.3, and the temperature of the water. The seasonal change may be illustrated by calculation of the respiratory energy expended per gram of standing crop in P4 on 29 January 1973, (summer) and 14 June 1974, (winter). In summer, respiratory expenditure was 5.8 kJ/g or standing crop and in winter 2.9 kJ/g of standing crop. This range of respiratory energy expenditure is typical of all ponds, and represents a large loss when food supplies are becoming scarce at the conclusion of the spring algal bloom. The respiration expenditure will then be maintained at the expense of stored energy reserves within the Artemia's tissues. Exhaustion of reserves in this manner may account for mass deaths and rapid drops in standing crops over the summer.

ANNUAL AND SEASONAL PRODUCTION OF ARTEMIA

Table 4.5 gives a summary of the annual and seasonal production of Artemia from each concentrating pond. The allocation of months to seasons is as follows; spring, September

Table 4.5. ANNUAL AND SEASONAL PRODUCTION OF *ARTEMIA* EXPRESSED IN kJ/M^3. BRACKETED FIGURE IS g/m^3

Pond	Annual Prod.	SPRING	SUMMER	AUTUMN	WINTER
P3	1470.8 (71.7)	887.6 (42.8)	317.1 (15.4)	103.5 (5.1)	273.0 (13.3)
P4	1699.7 (82.9)	885.5 (43.2)	257.5 (12.6)	177.5 (8.7)	379.0 (18.5)
P5	2082.2 (101.6)	845.7 (41.3)	272.0 (13.3)	403.0 (19.7)	552.5 (26.9)
P6	1872.7 (91.3)	680.5 (33.2)	364.0 (17.8)	284.9 (13.9)	413.1 (20.2)
P7	1583.7 (77.2)	735.2 (35.9)	326.8 (15.9)	151.5 (7.4)	370.2 (18.1)
P8	1515.6 (73.9)	694.7 (33.9)	372.8 (18.2)	156.3 (7.6)	291.6 (14.2)
P9	1212.9 (59.1)	306.6 (14.9)	205.1 (10.0)	261.2 (12.7)	439.4 (21.4)
P10	911.9 (44.4)	426.8 (20.8)	159.9 (7.8)	213.7 (10.4)	111.5 (5.4)
F1	1500.2 (73.1)	739.6 (36.1)	215.5 (10.5)	255.4 (12.5)	134.9 (6.6)
F2	526.7 (25.6)	266.5 (13.0)	74.7 (3.6)	93.6 (4.6)	87.4 (4.3)
F3	279.9 (14.5)	36.6 (1.8)	44.9 (2.2)	140.3 (6.8)	75.2 (3.7)
F4	365.4 (17.8)	150.4 (7.3)	60.5 (2.9)	116.6 (5.7)	38.3 (1.9)
F5	357.1 (17.4)	226.0 (11.0)	18.6 (0.9)	76.4 (3.7)	36.1 (1.8)

October November; summer, December January February; autumn, March April May; winter, June July August. The downward trend in total annual production as the salinity increases shows well for the pond series with an overall maximum in P5. Most of the ponds showed maximum production in spring, the exceptions being P9 and F3 where maxima occurred in winter and autumn respectively. In no pond did the summer production equal or exceed the spring production, and in most ponds more Artemia was produced during winter than summer.

ECOLOGICAL EFFICIENCY

The ecological efficiencies, (the percentage of total energy input to the Artemia population from uptake of pelagic algal cells that is actually incorporated in harvestable Artemia biomass) were calculated for P4 for each sampling date. The results were as below:

Date	Percent	Date	Percent
10/8/72	19.3	23/3/73	13.3
25/8/72	19.8	29/3/73	12.8
5/9/72	19.7	26/4/73	23.4
21/9/72	18.2	10/5/73	23.5
9/10/72	19.6	25/5/73	17.2
26/10/72	21.4	14/6/73	21.2
11/11/72	21.3	28/6/73	21.4
7/12/72	16.2	12/7/73	21.7
30/12/72	15.1	9/8/73	21.6
10/1/73	14.4	13/9/73	23.4
29/1/73	16.9	28/9/73	22.0
15/2/73	16.0	18/10/73	21.2

The average for the sampling period was 19.1%, a satisfactory overall figure representing, by most biological standards, an efficient conversion of food between tropic

levels. The large range reflects the variable abundance of food, with the lower efficiencies occurring when most of the food intake was going directly into fulfilling respiratory requirements and a small proportion into new tissue growth.

SECTION 5

UTILISATION OF THE ARTEMIA CROP

5.1 PRAWN OR SHRIMP CULTURE

There is a world wide demand for shrimp and prawn that is supplied mainly from trawling operations. The increasing value of the commodity and the extent to which the value is being artificially inflated by demand is making it more and more attractive to farm the animals. Many organizations have experimented with setting up trial hatcheries and fattening ponds but only the Japanese have committed themselves to a full scale venture.

Four basic factors that must come into any decision to enter this field are

(1) a ready market must be close at hand and not require extensive transport,

(2) a suitable shrimp or prawn must be available that will grow rapidly to an acceptable size with a good conversion ratio of food into shrimp flesh,

(3) a nutritious food must be available for the adult, and

(4) most importantly, a food must be available that will feed the nauplii of the shrimps or prawns, and a supply of unpolluted seawater must be close by with room to construct large ponds.

The most difficult time in rearing any shrimp is the period of larval metamorphosis when, via a series of moults the nauplius acquires adult characteristics. This stage normally demands intensive management in a separate hatchery. The successful and rapid maturation of prawns from the end of the larval period to their becoming harvestable animals

requires a sound knowledge of the animals habits including such things as territoriality, requirement for cover, preferred light intensities and shoaling tendencies.

Several diseases have been identified in shrimps such as 'brown spot' and 'white spot' caused by chitiniverous bacteria, and 'chalky disease' caused by a sporozoan parasite, Telohania sp., (Forster and Wickens 1972). These may spread very rapidly through a population and a knowledge of the nature of the disease and control measures is vital.

Prawn culture of an elementary type has been practised for an unknown length of time. The simplest version of this method relies on the capture of juvenile prawns by flooding paddy fields with water at the season when larvae are known to be abundant. A mixed population of several species results but they grow on naturally occurring food. The average yield from this type of system is 340 kg/hectare, but in Singapore yields have reached 900 kg/ha, (Tham 1968).

Culturing methods are similar in the Philippines but somewhat more advanced in that culturalists select a single local species, Penaeus monodon, and prepare special pools for this purpose. Again most of the food consumed is that occurring naturally but rice bran is added as food and fertiliser, (Caces-Borja and Rasalan 1968). Survival to maturity tends to be as low as 20% and yields average only 280 kg/hectare.

Pond culture is also used in Japan but there it is a much more tightly controlled system. Gravid, wild females caught at sea are induced to spawn in large tanks that have been fertilised and innoculated with algae, (Hudinaga 1969). The eggs hatch as nauplii within 24 hours and moult without having fed to the protozoea stage when they begin feeding on

the algae. This sustains them until the mysis stage is reached when Artemia nauplii become their main food. This diet lasts until about seven days of age when the resulting juveniles are introduced to outdoor ponds of up to four hectares. Here they are fed a minced mixture of clam, trash fish, and shrimp or Artemia. No reliance is placed on natural food production in the ponds and yields of up to 3000 kg/ha are normal. Feeding expenses are extremely high in Japan since most of the clam used is also sold as a human food. This expenditure is offset by the price realised by prawn in Japan of up to $7.00 per kg, (Shigueno 1972).

At the present time the Japanese enterprise is the only one running profitably but others are being developed.

The next hurdle to be surmounted is that of the necessity to rely on a supply of gravid females caught at sea. This requires a knowledge of conditions necessary to bring a female into breeding condition and produce viable eggs. Intensive research has resulted in numerous successes both in egg production and the culture of larval stages with almost 100% success. Cook (1969) describes methods for Penaeus aztecus, P. duorarum, P. setiferus, Sicyonia brevirostris, Trachypenaeus similis, and Xiphopenaeus kroyeri. Liao and Huang (1970) write similarly about Penaeus japonicus, P. monodon, P. semisulcatus, P. teraoi, Metapenaeus monoceros, and M. joyneri. Production of Penaeus keranthurus has been looked into. In all of these cases production of very large numbers of juveniles provides no problems.

The expensive part of any form of shrimp farming is the growing period from juveniles to harvestable adults. Production costs here can frequently eat up any profits, especially where a slow growing form is being cultured. Most

pond systems are not highly efficient and food is lost continually. The current trends are towards intensive rearing in small controlled environment systems similar to those currently used in intensive terrestrial animal husbandry, e.g., poultry or pigs.

5.1.1 WATER TEMPERATURE AND GROWTH RATE

Without exception the fastest growing prawns are tropical species (Forster and Wickens 1972), mainly Penaeidae, although the caridean genus, Macrobrachium, also contains fast growing species. Palaemon serratus, a cool water species occurring around most of the British Isles and continental Europe has been shown to reach a commercial size of six to eight grams within one year under optimum laboratory conditions but take up to four years for the same growth in open ponds in the temperate English climate. The optimum temperature for growth was found to be 22°C but growth occurred throughout a range from 4°C to 24°C. For commercial outdoor production a range of 15°C - 24°C would allow moderate growth rates, about 5 g/year, without the necessity of supplementary heating, (Forster and Wickens 1972). The final size of the New Zealand representative of the Palaemonidae, Palaemon affinis, is smaller than the European species, and probably insufficient for commercial exploitation.

Macrobrachium rosenbergii is a large freshwater tropical prawn found widely distributed in the Indo-Pacific region. It has been widely studies because of its rapid growth rate, high food conversion ability and ready adaptation to mass culture situations. Since it is a member of the Caridea, the eggs are incubated after spawning in contrast to the Penaeidea where the eggs are simply shed into the water column. Culture must be at a temperature of 28°C or higher in fresh or brackish

water. In nature adults live in freshwater but travel to brackish estuarine areas to spawn. Consequently larval rearing units normally operate at salinities of about 15 ppt. Newly hatched larvae readily consume Artemia nauplii.

5.1.2 ECONOMICS OF SHRIMP FARMING

Production costs vary with the type of culture being employed. The three main types are:

(1) extensive or free range culture;

(2) intensive outdoor culture;

(3) intensive indoor culture.

In all of these, larval rearing facilities are necessary. The cost of this will to a large extent depend on the type of shrimps used for culture since larval lifetimes vary greatly. A secondary aspect is that of obtaining larvae. Many overseas enterprises, notably Japan and mainland South East Asia, are able to trawl for egg bearing females locally and allow them to shed their eggs in monitored tanks. It is unlikely that a local shrimp suitable for culture will be found around the New Zealand coast so larvae production will probably rely on cultivated females that have been induced to spawn either by artificially modifying the environment or allowing the natural annual cycle to take place. This is the situation in Hawaii where the giant Malaysian Prawn, Macrobrachium rosenbergii, was originally imported from the Indonesian region and a breeding stock has to be maintained. Fujimura and Okamoto (1970) described the rearing of M. rosenbergii in 19000 litre tanks and estimated the cost of production of newly metamorphosed larvae at $NZ1.60 per thousand assuming a larval life of 35 days and a survival to metamorphisis of 21%. The Japanese industry relies on wild females for breeding stock and Shigueno (1969) estimated larval

rearing costs at approximately 90 cents per thousand. Liao and Huang (1970) conducted a survey of costs of rearing six species of penaeid larvae in Taiwan and estimated average costs, assuming 25-30% survival, of $NZ1.80 per thousand. Considering these estimates, Forster and Wickens (1972), considered that in the United Kingdom a cost of $NZ2.00 per thousand metamorphosed larvae seemed a realistic target.

Larval rearing facilities, however, also necessarily involve construction of tanks, ponds, buildings to house the tanks, equipment for growing batches of algae, equipment to harvest Artemia nauplii, and pumps to circulate and transfer water, and these would involve much extra expense.

5.1.3 FOOD SUPPLIES

Although cultured shrimps will survive and mature in ponds using naturally occurring food, experience in Malaysia and the Philippines has shown that shrimp productivity is very low. Supplementary feeding, by boosting the energy available, greatly increases yield. Where intensive rearing is undertaken the density of shrimp is such that natural food production is totally inadequate and complete reliance must be placed on prepared diets. There are a great number of such foods, reviewed elsewhere, (5.1.4), that usually aim at a balance of carbohydrate protein and trace elements that can be assimilated efficiently by shrimp. The cost of any animal feed usually reflects its protein content and in this way the cost of prawn diets may be compared to foods such as trout pellets or poultry pellets that cost about 20 to 30 cents per kg in New Zealand. Efficiency of conversion of such food into shrimp or prawn is likely to be somewhere between two and three to one, but less than in fish since significant losses occur due to moulting. By this reasoning food would cost

between 40 and 90 cents per kg of shrimp produced but this assumes 100% survival, and that all of the food supplied is eaten. An operational example was quoted by Neale and Latapie (1972) concerning pond culture on Grant Terre Island, Louisiana. Ponds of 0.1 ha were stocked with juvenile brown shrimp, Penaeus aztecus at the rate of 37 050 per hectare (16 kg/ha). Feeding was with "Purina Catfish Chow", (sinking pellets), at the rate of five percent of shrimp biomass per day. Weight of the shrimp increased over an 80 day growing period to 480 kg/ha. Food provided, therefore, ranged from 0.8 (kg/ha)/d initially to 24 (kg/ha)/d immediately before harvesting. Conversion efficiency was 2.3:1 and mortality over the period was 10%. The conversion efficiency of 2.3:1 implies that 1067 kg/ha of food was supplied for a yield of 480 kg/ha of shrimp. Basing the cost of food on the estimate of 30 cents per kg, expenditure on feeding is about $356. The price being fetched for brown shrimp during this period, (1970), was $US1.44 per kg, (Anderson and Tabb 1970), giving an income from sales of the shrimp of about $US691 per ha. This profit of $235 ignores expenses for labour, plant and power supplies, and possibly supplementary heating. At the present time with world wide inflation, costs incurred in any venture are continually fluctuating and any amounts quoted can only be a rather crude guide.

5.1.4 ARTIFICIAL DIETS FOR CRUSTACEA

The development of successful crustacean diets has been slowed by the inability to find a simple binder that will keep pelletised food intact for a matter of hours in water. Normal pellets as fed to domestic stock crumble almost immediately and rapidly foul the water. Mastication by shrimps is a slow process and particles of food will be consumed over

period of hours. Materials that have been tried include agar, alginates, carageenan, guar and locust bean gums, gelatines and cellulose compounds.

Most of these work but only trial and error will determine the best. Balazs, Ross and Brooks (1973) have devised a typical set of formulae based on soybean flour fish meal, shrimp meal, brewers' yeast and ground corn. Binding was achieved by the addition of 20% high gluten wheat flour. The shrimp meal in the formulae shown in Table 5.1 could be substituted with Artemia meal and still retain the same composition.

The ingredients were blended dry and then about 40% by weight of hot water was added. The tough dough formed by kneading was extruded through a spaghetti die and chopped to form pellets. After drying at 80°C for 10 hours the pellets retained their shape for over five hours in seawater.

Table 5.1 Shrimp diet forumlae incorporating Artemia (Balazs, Ross and Brooks 1973).

Ingredient	Diet (% composition)			
	1	2	3	4
Soybean flour	30.5	8	8	8
fish meal	-	4	6	11
shrimp (Artemia) meal	-	15	24	42
brewer's yeast	-	5	5	5
ground corn	40.5	47	35.5	12.5
high gluten wheat flour	20	20	20	20
Tricalcium phosphate	3	-	-	-
Vitamins and trace minerals	1	1	1	1
Total protein (%)	25	25	30	40

Experimental feeding of Penaeus japonicus with the diet showed good growth rate that was directly proportional to the amount of protein in the diet (Table 5.2).

Table 5.2 Growth increments of P. japonicus on four diets. Weights are those of adult P. japonicus. (Balazs, Ross and Brooks (1973).)

Species	Diet	Mean weight		Percent
		initial	final	increase
P. japonicus	1	2.25	4.63	105.8
"	2	2.27	4.70	107.0
"	3	1.66	5.62	238.6
"	4	1.50	6.44	329.3

Survival for the experimental period ranged between 86 and 100%.

5.2 SHRIMPS POSSIBLY SUITABLE FOR MASS CULTURE

PALAEMON SERRATUS

This caridean shrimp is common around most of the European coast and a great deal of research has been done on it, particularly in England and Wales (Cole 1958; Forster 1951a; Forster 1959; Panikkar 1941; Parry 1954; Scheer and Scheer 1954; Reeve 1969; Forster and Wickens 1972). It is a small shrimp with a maximum weight of 12 g and takes over a year to grow to marketable size which is about six grams. It will breed freely in captivity and produces 1500 - 4000 eggs per adult. Larval life is 19 - 30 days. Its chief attraction as a potential shrimp for cultivation is that it will grow well in cool water with a temperature range of 15 - 24^{o}C. In spite of this, its slow growth rate does not really make it an

attractive proposition at present. The chief representative of the Paleomonidae in New Zealand, P. affinis, shows much the same characteristics as P. serratus, (personal observations and J. Knight pers. comm.), but it is very small and even less likely to be a practical proposition.

PANDALUS PLATYCEROS

This is also a temperate to cool water species and is widely distributed in the northern Pacific, (Butler 1970). The mature weight is much larger than Palaemon serratus at 30 g but fecundity is not good with 1400 - 3200 eggs produced per female. Growth rate is approximately 5 g in 6 months. P. platoceros grows well in captivity but as yet (1972) has not been induced to breed in captivity. Culturing experiments were carried out at Conway in Wales, (Forster and Wickens 1972), and a growth rate of from 0.4 g to 4.9 g live weight was achieved in six months. Best survival occurred between 14°C and 15°C, a mean of 50% surviving from larvae to the young adult stage. Survival tests indicated that the temperature range that could be tolerated was 0°C - 20°C.

Apart from the problem of law fecundity, P. platyceros is a protrandrous hermaphrodite and spends about two years as a male before changing sex and being capable of egg production.

MACROBRACHIUM ROSENBERGII

M. rosenbergii is a warm water relative of the previous two species that has attracted great attention in the last few years because of its remarkable growth rate and apparent ease of cultivation under suitable conditions. It is a typical species widespread around the Indonesian archipelago inhabiting fresh and brackish water. Larval life varies in length between 24 and 35 days. Egg production is

extremely high at between 10,000 and 100,000 eggs per female. Hatching and rearing in captivity is now a well documented routine process, (Fugimura 1966; Fugimura and Okamoto 1970; Fugimura 1972). Growth rates of 60 g in six months were demonstrated by Ling (1969a) and an adult weight of 100 g may be achieved within two years. Rearing trials in Hawaii (Fugimura 1972) have shown production rates of 3820 (kg/ha)/year and attempts are being made to produce a sustained yield of 335 (kg/month)/ha by culling off market sized prawns as they become available and replacing them with juveniles. Preliminary estimates suggest that to retain best growth rates a stocking of between 10 and 20 juveniles per m^2 is optimal. The most severe problem in a temperate climate would be maintaining the water temperature within the $26^{o}C$ - $30^{o}C$ range necessary for good growth. The prawn, however, will withstand temperatures as low as $17^{o}C$.

PENAEUS JAPONICUS

The warm water panaeid is probably the most successfully cultivated prawn. It is the species used in the pioneering Japanese shrimp farms (Hudinaga 1969). It is an exceptionally fertile animal producing between 100,000 and 1,200,000 eggs per female. Larval life is short, about 7 - 10 days and weight gain may be up to 20 g in six months. Its wild range includes most of the tropical and sub-tropical Indonesian region and it is particularly common around Japan. Through the Japanese interest in its culture the biology of P. japonicus is very well known, Hudinaga and Miyamura (1962), and throughout the world attempts are being made to emulate the Japanese methods. As with M. rosenbergii, P.japonicus requires warm temperatures to be successful. Normally growth occurs in

the temperature range 25°C - 28°C.

PENAEUS MONODON

This prawn, also known as sugpo or tiger prawn, is very common around the Indopacific, the Northern coasts of Australia and particularly common around the Philippines. This is a tropical species growing best between 20°C and 35°C. In the natural state the adults move in shoals and breed in estuarine conditions. It readily matures in ponds and exhibits a good growth rate of about 22 g in six months, (Forster and Wickens 1972). The larval life is short at approximately 9 - 12 days and fecundity is moderately high with an average of 300,000 eggs being produced by each female. Experimental cultivation of P. monodon in the Philippines is reviewed by Delmendo and Rabanal (1956) and Caces Borja and Raselan (1968).

PENAEUS AZTECUS, brown shrimp.

P. DUORARUM, pink shrimp.

P. SETIFERUS, white shrimp.

These three species are widely distributed throuhout the Gulf of Mexico where they support a large commercial fishery. P. aztecus and P. setiferus also extend to the Gulf of Maracaibo where another large industry is based, (Ewald 1964).

All three are similar in growth rate and ultimate size. Growth in culture averages about 30 g per year but the maximum sizes vary, with P. duorarum reaching 100 g, P. setiferus 70g, and P. aztecus over 70 g. Fecundity is particularly good with over 1 million eggs being produced per female. Of the three P. duorarum is considered the most likely for cultivation since it is the most hardy under adverse conditions and a method for artificially inducing ovarian

maturation and subsequent spawning at a pre-determined time has been developed by Idyll (1971). Pond culture experiments have also been successfully carried out using P. aztecus and P. setiferus caught as juveniles in low salinity areas and brought to maturity in ponds, (Neal and Latapie Jr. 1972). Culture temperature for these species have ranged from 20^0C - 30^oC although they will generally tolerate changes well.

PENAEUS KERANTHURUS

This shrimp is an inhabitant of the Mediterranean and has recently been investigated as a possible culture subject (Lumare, Gozzo and Blundo 1971). Locally known as Caramonte, it has the advantage of growing well at moderately low temperatures, 15^oC - 20^oC. No accurate data is yet available on pond growth rates but the maximum size is 50 g. The adults live principally in estuarine conditions but the larvae require fresh water to mature. The larval life is up to 14 days and fecundity is excellent at about 1 million eggs per female.

Around the New Zealand shores there are, unfortunately no shrimps suitable for culture, the only readily available species being Palaemon affinis and Alope spinifrons. P. affinis is too small and slow growing. A. spinifrons is large enough to be commercially attractive but seems to be extremely slow growing at normal summer sea temperatures, (ca. 18^oC), (personal observations).

5.3 OTHER USES FOR ARTEMIA

An immediately obvious use is for sale to aquarium owners as fish food. This could be a rather important aspect since the Artemia eggs from the present main source, Great Salt

Lake, Utah, have been found to be highly contaminated with DDT and its derivatives, and often either do not hatch or poison the consumers of the eggs or nauplii (J.C. Yaldwyn pers. comm.). Unfortunately the strain of Artemia present in Lake Grassmere frequently does not produce eggs as such. Normally, females are ovoviviparous and the eggs hatch in the female's uterus from which live nauplii emerge. Heavy egg production does, however, occur at restricted periods of the year, notably autumn and mid-summer or at any time when pond conditions are becoming difficult to live in.

The high energy content of Artemia could also be utilised by harvesting the brine shrimps and incorporating them into a blended food. This could be an ideal feed for raising fingerling fish, such as salmon or trout in hatcheries. A pelletised diet such as that described in Table 5.1 would be suitable for feeding a wide range of fishes and invertebrates.

CONCLUSIONS AND SUGGESTIONS

1. Physical Conditions

The shallowness of the concentrating ponds produces both advantages and drawbacks when considering Artemia culturing. The effects of solar heating are magnified and water temperatures may reach up to 30°C during sunny summer days. On the other hand, heat is equally rapidly lost and after a series of frosts the temperature may be lowered to about 3°C during winter. The wide temperature range may be expected to have a considerable affect on the growth of Artemia and the algae which forms its food. The shallowness of the ponds also makes all the water, rather than just the surface water, vulnerable to wave action. Although Artemia is an active swimmer, it cannot compete with such force and is swept around with the waves.

Extremely high salinities and high temperatures rather than stagnation, combine to produce very low dissolved oxygen levels during summer. There is no evidence indicating that Artemia is adversely affected by very low oxygen tensions (Fox and Taylor 1955), but no work has been done on the reactions of developing eggs and nauplii. There is some evidence (Broom 1968, Fujimura 1972), that high temperatures such as those which occur at Grassmere may cause mass deaths of cultivated edible shrimps in outside ponds under mass stocking conditions. A practical method of ensuring the maximum possible dissolved oxygen levels were maintained in the ponds, would be to maintain the salinity at a relatively low level (e.g. 100 ppt, Table 1.5).

The ponds were normally free of suspended sediment because of the presence of a calcium sulphate crust binding the silt substrate into a firm mass. However, when the salinity is

lowered to the level suggested above (100 ppt) the deposit of calcium sulphate begins to redissolve. This releases the cemented silt grains and turbidity develops. In any pond used for cultivation of Artemia or an edible shrimp, turbidity would become a problem unless the bottom was sealed in some way. Possibilities are a binding compound to cement the sediment into a firm mass, or some type of impervious and chemically inert film similar to polyethylene. The suspended sediment may not do any direct harm to the animals but Artemia does not appear to distinguish between algae cells and other inorganic debris when filter feeding (Personal observations, Reeve 1963a, 1963b, 1963c). The gut would probably become packed with sediment particles in addition to food algae, so reducing the efficiency of feeding and ultimately the growth rate.

Green or red colouration in the water originated from the algae population. Because of the shallowness of the ponds, it is unlikely that lack of light would cause inhibition of photosynthesis. It is possible, however, that inhibition due to over-intense light may be reducing algae production during summer. All algae have an optimum light intensity for maximum photosynthesis and when this is exceeded on the surface of a body of water the zone of maximum photosynthesis moves deeper. If the water is shallow total production falls as the algae cannot leave the high light intensity water. The presence of very high annual sunshine hours at Lake Grassmere also raises the possibility that solar energy could be utilised for heating water in a shrimp hatchery. Some form of heating would be necessary at times to maintain water temperatures at 25°C - 30°C which is necessary to promote rapid growth of tropical and subtropical species of shrimp (see

section 5).

I have shown that strong brine is viscous enough to hinder the movement and feeding of Artemia. Temperature also affects water density, and a combination of low temperature and high salinity is likely to seriously reduce Artemia production by increasing the effort expended in feeding, slowing metabolism, and retarding egg hatching. These are further arguments for keeping ponds at a low salinity for Artemia raising, and a reason for a possible lack of success if one attempts to carry out salt making and Artemia raising concurrently in the same ponds.

Finally, it was found that the crust of calcium sulphate on the sediment surface tended to take up and accumulate phosphate compounds. This is a common phenomonen in lake sediments (Syers, Harris & Armstrong 1973). The phosphate bound up in this fashion did not appear to be available to the lake water until the crust broke up in dilute seawater. Another consequence of the break up of the crust was the release of large amounts of hydrogen sulphide from the silt that had become anaerobic under the impervious layer. Hydrogen sulphide is moderately soluble in water and an Artemia appeared to be able to survive the concentrations occurring (personal obs.). However, I have no evidence as to its effects on earlier instars of Artemia or on developing eggs.

2. Algal Growth

Of the three species of algae found in the Grassmere ponds only two, Dunaliella euchlora and D. salina, were abundant and only D. euchlora was found at salinities that may be suitable for the mass culturing of Artemia salina. The optimum salinity for growth of D. salina, as determined by laboratory experiments, was found to be well above the optimum for Artemia growth. Therefore, the alga would not be suitable for culturing purposes. D. euchlora, on the other hand, is easy to grow at relatively low salinities (100 - 150 ppt), on a small scale, and there is no reason why it should be difficult to maintain suspensions on a much larger scale.

It is possible that the algae living in the Grassmere ponds have become adapted extremely closely to their particular conditions and it is possible that the salinity optima determined by laboratory experiments could be changed by prolonged culturing at different salinities. Gibor (1956) has shown that D. euchlora may develop new strains when isolated in ponds of different salinities. This suggests that if the salinity of a pond was carefully maintained at, for example, 100 ppt, algae production would increase if a strain of D. euchlora developed that could grow with maximum efficiency in these conditions. This might be one way of reducing the fluctuations in primary productions that occur during the spring, summer and autumn periods in Grassmere as the salinity changes.

In addition to pond cultures supporting crops of Artemia, smaller bulk cultures of D. euchlora would be required if culture of an edible shrimp was to be considered. Such algae cultures would be needed to feed newly hatched shrimps which

can only ingest microscopic food. Intermediate larval stages can be fed on Artemia nauplii and other pelletised, blended food could be fed to fully metamorphosed juvenile shrimp.

Both D. salina and D. euchlora showed positive responses to additions of inorganic phosphate and nitrate in trial cultures. This indicated that fertilisation of ponds may be a possible method of stimulating production of algae over the summer months when, at present, production falls. Phosphate may be the more limiting nutrient in the ponds since levels of nitrate did not drop to the levels that caused inhibition in laboratory experiments. In the ponds, phosphate declined to levels equivalent to those which retarded growth in laboratory experiments. If additional phosphate was supplied, nitrate reserves may also become depleted, however, and the situation could arise where applications of both would be needed. Intensive culturing of this type would require a back up program of regular water analyses to determine the optimum nutrient regime and the rate of consumption of nutrients.

Sexual reproduction of D. euchlora was shown to be brought about by adverse conditions, particularly low phosphate levels and high salinities. It replaced the more usual palmellar reproduction and involved resting stages that tended to make cells unavailable to Artemia as food. To avoid this the best solution would be to maintain the salinity of the ponds below the levels where sexual reproduction occurs (approx. 200 ppt).

Production of D. euchlora taken from the concentrating ponds was determined in 6 hour light and dark bottle experiments in an incubator. Lake waters under these experimental conditions showed a spring productivity maximum followed by a fall to a summer low. The maximum primary

productivity rate recorded, 0.45 $(g/m^3)/h$, would be sufficient to support commercial crops of Artemia. However, productivity rates fell to less than 0.1 $(g/m^3)/h$ as conditions become less favourable. Mass deaths of Artemia that followed such drops indicate that the chances of sustaining commercially attractive crops in the concentrating ponds are minimal. Nevertheless, a high potential for growth has been demonstrated and it remains to be seen if this can be maintained in ponds other than those being used for the production of salt.

3. Artemia Growth

Artemia salina is capable of adapting well to its environment and many physiological varieities have been identified world wide, (Barnard 1929). This is probably made possible by the rapid breeding of Artemia and consequently considerable opportunity for genetic change within populations. If a carefully maintained set of ponds was established to raise Artemia it is likely that within a short time the population would become well adapted to a more stable environment than exists at Grassmere at present.

Egg laying is affected by temperature and food supply as shown by the observations on numbers of females carrying eggs over the sampling period. Although the proportions of egg carrying females was similar for a given period over the whole range of ponds, laboratory experiments in lake waters of different salinities showed that the number of eggs released was affected by salinity. The highest number of eggs released per animal occurred in the 100 ppt culture. The effect of salinity on egg production was also shown by sampling females from ponds ranging in salinity from 140 - 282 ppt. The number of eggs in the uterus showed a regular fall as the salinity rose.

The proportion of eggs that hatch is also affected by salinity and declines rapidly above about 180 ppt. Below 100 ppt and at temperatures of 17^{o}C and above, virtually all eggs hatch, whereas below 17^{o}C an increasing proportion (20% at 7^{o}C), will not hatch. The conclusion arrived at as a result of these experiments is that Artemia is capable of living at most salinities but breeding with difficulty at salinities in excess of 200 ppt. For maximum breeding

potential to be realised, a salinity of about 100 ppt seems to be optimal.

The natality and mortality of the population of Artemia as a whole was modelled by constructing life tables from laboratory experiments at 7°C, 17°C and 26°C. The value of rc, the potential rate of increase, showed a marked decline at successively lower temperatures. This illustrates the important role played by temperature, but at present the warmest months of the year are also some of the least productive! The reason for this seems to lie primarily with the low primary production of algae in summer. Both primary and secondary production would probably increase if the salinity of the ponds did not rise above about 100 ppt during the warm summer months.

In the life tables, the fates of single cohorts of Artemia were followed and their reproductive potential assessed by counting the numbers of eggs produced. When the progeny arising from eggs were allowed to survive (section 3.8) their numbers accumulated to levels which were able to take advantage of the food supply available. Aquarium experiments showed that there was a close correspondence between changes in food supply and changes in Artemia numbers. This suggests that Artemia is able to take advantage of temporary increases in the food supply and that use of food is very efficient. These experimental results may be extended cautiously to the concentrating ponds situation where a decline in Artemia numbers corresponded with a decrease in algae density over the summer.

The numbers of naupliar and adult Artemia in the ponds changed extremely rapidly from month to month. As for the algae there was a rapid spring build up with maximum growth in late spring and a decline in summer. At various times of the

year, but particularly in summer and autumn, mass deaths of Artemia were seen, and at these times the margins of the ponds were lined with bands of Artemia bodies up to 25 mm deep. Since these occurred during periods of falling algal production, starvation is their most likely cause, but the effect of long term changes in water chemistry and temperature cannot be entirely ruled out. It was noticed that when Artemia were underfed in aquarium cultures, deaths occurred very rapidly over a short period. Dead animals taken from the Grassmere ponds possessed no food reserves which normally are present as lipid droplets, but many females were carrying eggs suggesting that reproduction is one of the last functions to be curtailed.

Although population density gives some indication of the state of the population (i.e. increasing or declining), a knowledge of the daily production rate of Artemia is of more use in predicting when it would be best to harvest Artemia. Productivity of Artemia was highest in the lowest salinity ponds providing salinity did not drop so low that the bottom crust broke up, as happened during winter in P3. Production rate varied seasonally and it would be difficult to harvest the concentrating ponds to provide a continual supply of Artemia. The potential production, as indicated by the rate achieved during spring when over 1 (g/m^3)/day of Artemia tissue was produced, is high. It is possible that carefully maintained ponds used solely for the production of Artemia could maintain rates of this order for long periods if conditions were kept as near as possible to the optimal.

It should be noted, however, that the biomass being measured is present in the absence of predators and at any time includes large numbers of old adults that have virtually

finished growing and are simply consuming food and expending energy in metabolism and egg production. The impact of a selective predator represented by man with nets of known mesh size removing a portion of the stable population would probably be to stimulate egg and ovoviviparous naupliar production. In support of the hypothesis, aquarium experiments conducted by the author have shown that when density of Artemia rises, but food supply is not increased in proportion, egg production is inhibited and the release of eggs is slowed. However, when the population was selectively netted to remove large individuals there was normally a rapid increase of nauplii within a week. This is because the reproductive capacity of Artemia is very high and a population can recover rapidly from intense culling if adequate food supplies are available.

The overall impression gained from the study of the ponds is that production during the most facourable parts of the year is sufficient to allow harvesting. However, these periods are short lived and occur mainly in spring, leaving a long period of poor production over the summer. Since a reduction in production rate is caused by progressive changes in physical parameters which are brought about in the existing ponds during spring it would be best to set up separate ponds that are not involved in salt extraction. These would be kept for Artemia production and carefully maintained to have water characteristics like those that have been found to promote good growth in the concentrating chain. A primary factor appears to be the maintenance of the salinity at a level near to that existing at the beginning of the concentrating season, i.e. high enough to exclude oceanic fauna but not so high as to inhibit feeding and breeding of Artemia. I have already suggested that the algae flora, particularly Dunaliella

euchlora should be capable of adapting to a stable situation and reproducing satisfactorily in such conditions and would provide the basic food for brine shrimps.

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APPENDIX 1 DETERMINATION OF NITRATES

Nitrate in very strong acid solution and with controlled heating and chloride masking reacts with brucine to form a yellow complex that is determined spectrophotometrically at 410 mu. The only situation in which problems arise is where there is a high concentration of reducing agents in the water to be determined.

EQUIPMENT

Spectrophotometer; 50 ml boiling test tubes (pyrex); two 1 litre volumetric flasks; 1 100 ml burette and 2 25 ml burettes; a boiling water bath and a cold water bath.

REAGENTS

(1) 30% NaCl solution; dissolve 150 g NaCl in 500 ml of deionised water.

(2) H_2SO_4 solution; add 500 ml of analytical quality H_2SO_4 to 125 ml deionised water.

(3) Brucine-sulphanilic acid reagent; dissolve 2.0 g A.R. brucine and 0.2 g A.R. sulphanilic acid in 140 ml of deionised water. Add 6 ml of concentrated HCl.

(4) Stock nitrate solution; dissolve 0.7218 g of A.R. potassium nitrate in deionised water and make up to 1 litre in a volumetric flask.

PROCEDURE

Thaw frozen samples in a warm water bath. Set up boiling water bath and cold water bath. Prepare calibration blanks by placing 100 ml of stock nitrate into a 1 litre volumetric flask and make up with deionised water. In this dilution 1 ml = 10.0 µg N. For second blank pour 15 ml of this solution is a second 1 litre volumetric flast and again make up with deionised water. 1 ml = 0.15 µg N.

Set up boiling tubes in triplicates and into each pipette 10 ml of the following:

ABC = reagent blank, deionised water.

DEF = calibration 0.15 mg/l N.

GHI = first water sample to be determined.

JKL = second water sample to be determined.

add 2 ml NaCl to each tube, mix and place in cold water bath. Add 10 ml of H_2SO_4 and return to cold water bath. When cold again add 0.5 ml of brucine/sulphanilic acid solution and return to cold bath. Place tubes in boiling water bath for 20 minutes. After this time remove and replace in cold water bath. Place reagent blank sample into spectrophotometer and set transmittance at 100%. Read calibration blank and set up calibration curve. Determine series of unknown samples. Extinctions should agree to within 10%. If there is larger variance check procedures. Minimum level that may be reliably determined is approximately 0.009 mg/l N.

APPENDIX 2 PERCENT AND INSTANTANEOUS MORTALITIES FOR ADULT ARTEMIA (I.E. 2 mm AND LARGER).

	Population estimate at start of interval	Percent mortality	Instantaneous mortality
P3	79		
	86	-8.8607	-8.4944E-02
	112	-30.2325	-2.6419E-01
	1462	-1205.3569	-2.5691E 00
	3944	-169.7672	-9.9241E-01
	6120	-55.1724	-4.3940E-01
	4872	20.3922	2.2800E-01
	2200	54.8440	7.9494E-01
	2179	0.9546	9.5417E-03
	2250	-3.2583	-3.2112E-02
	3990	-77.3333	-5.7289E-01
	2122	46.8171	6.3134E-01
	442	79.1706	1.5686E 00
	136	69.2308	1.1785E 00
	427	-213.9703	-1.1441E 00
	294	31.1476	3.7313E-01
	347	-18.0272	-1.6579E-01
	221	36.3113	4.5109E-01
	629	-184.6152	-1.0460E 00
	1002	-59.3004	-4.6565E-01
	1841	-83.7325	-6.0834E-01
	2624	-42.5312	-3.5442E-01
	7982	-204.1919	-1.1125E 00
	8146	-2.0546	-2.0385E-02
P4	3669		
	3890	-6.0234	-5.8536E-02
	4250	-9.2544	-8.8554E-02
	2040	52.0000	7.3387E-01
	1332	34.7059	4.2619E-01
	2080	-56.1561	-4.4572E-01
	2726	-31.0576	-2.7050E-01
	2945	-8.0337	-7.7318E-02
	2820	4.2445	4.3321E-02
	2947	-4.5035	-4.4097E-02
	5729	-94.4010	-6.6478E-01
	3314	42.1540	5.4730E-01
	998	69.8854	1.2000E 00
	68	93.1864	2.6855E 00
	998	-1367.6468	-2.6862E 00
	3624	-263.1261	-1.2896E 00
	646	82.1744	1.7243E 00
	578	10.5264	1.1117E-01
	1469	-154.1521	-9.3278E-01
	1802	-22.6684	-2.0435E-01
	7036	-290.4549	-1.3622E 00
	10710	-52.2171	-4.2017E-01
	14246	-33.0158	-2.8533E-01
	23292	-63.4985	-4.9166E-01

	Population estimate at start of interval	Percent mortality	Instantaneous mortality
P5	929		
	1333	-43.4876	-3.6111E-01
	1428	-7.1267	-6.8888E-02
	306	78.5715	1.5402E 00
	4284	-1299.9998	-2.6391E 00
	6698	-56.3491	-4.4695E-01
	7650	-14.2131	-1.3294E-01
	2924	61.7778	9.6162E-01
	1008	65.5267	1.0648E 00
	1428	-41.6666	-3.4834E-01
	3325	-132.8430	-8.4522E-01
	2269	31.7594	3.8206E-01
	2210	2.6003	2.6296E-02
	340	84.6154	1.8715E 00
	379	-11.4705	-1.0863E-01
	422	-11.3456	-1.0751E-01
	476	-12.7961	-1.2046E-01
	309	35.0841	4.3200E-01
	629	-103.5597	-7.1081E-01
	892	-41.8123	-3.4937E-01
	4921	-451.6815	-1.7078E 00
	6266	-27.3318	-2.4166E-01
	7036	-12.2885	-1.1595E-01
	9299	-32.1631	-2.7890E-01
P6	694		
	467	32.7090	3.9607E-01
	238	49.0364	6.7396E-01
	442	-85.7142	-6.1907E-01
	1666	-276.9228	-1.3269E 00
	6698	-302.0406	-1.3914E 00
	7769	-15.9898	-1.4837E-01
	7038	9.4092	9.8763E-02
	5774	17.9597	1.9790E-01
	2843	50.7621	7.0841E-01
	3800	-33.6616	-2.9018E-01
	1724	54.6316	7.9025E-01
	476	72.3898	1.2868E 00
	238	50.0000	6.9305E-01
	682	-186.5544	-1.0528E 00
	599	12.1701	1.2971E-01
	714	-19.1986	-1.7566E-01
	421	41.0365	5.2817E-01
	599	-42.2802	-3.5266E-01
	1042	-73.9565	-5.5366E-01
	3989	-282.8214	-1.3424E 00
	7921	-98.5710	-6.8600E-01
	9249	-16.7655	-8.9105E-01
	11441	-23.6998	-1.2589E 00

	Population estimate at start of interval	Percent mortality	Instantaneous mortality
P7	529		
	924	-74.6691	-5.5775E-01
	1360	-47.1861	-3.8656E-01
	3672	-169.9998	-9.9327E-01
	5686	-54.8474	-4.3730E-01
	9044	-59.0573	-4.6413E-01
	7695	14.9160	1.6147E-01
	3468	54.9318	7.9688E-01
	1997	42.4164	5.5185E-01
	2633	-31.8477	-2.7651E-01
	4009	-52.2597	-4.2045E-01
	2210	44.8741	5.9546E-01
	1774	19.7285	2.1969E-01
	646	63.5852	1.0101E 00
	729	-12.8482	-1.2092E-01
	591	18.9301	2.0980E-01
	272	53.9764	7.7591E-01
	121	55.5147	8.0990E-01
	3060	-2428.9246	-3.2304E 00
	2649	13.4314	1.4418E-01
	5311	-100.4906	-6.9562E-01
	6824	-28.4880	-2.5070E-01
	8371	-22.6699	-2.5069E-01
	12292	-46.8402	-1.9181E 00
P8	1009		
	1574	-55.9960	-4.4469E-01
	1632	-3.6848	-3.6233E-02
	476	70.8334	1.2320E 00
	2210	-364.2854	-1.5353E 00
	8296	-275.3844	-1.3228E 00
	7666	7.5941	7.8925E-02
	7514	1.9828	1.9977E-02
	2634	64.9455	1.0481E 00
	2618	0.6075	6.0435E-03
	4669	-78.3422	-5.7856E-01
	4166	10.7732	1.1393E-01
	2049	50.8162	7.0950E-01
	986	51.8790	7.3135E-01
	426	56.7952	8.3910E-01
	194	54.4601	7.8647E-01
	204	-5.1546	-5.0308E-02
	69	66.1765	1.0839E 00
	182	-163.7680	-9.6992E-01
	729	-300.5493	-1.3877E 00
	2178	-198.7653	-1.0945E 00
	3924	-80.1652	-5.8873E-01
	6821	-73.8277	-5.5292E-01
	7261	-6.4506	-6.2557E-02

	Population estimate at start of interval	Percent mortality	Instantaneous mortality
P9	964		
	872	9.5436	1.0025E-01
	1088	-24.7706	-2.2135E-01
	476	56.2500	8.2657E-01
	1088	-128.5713	-8.2670E-01
	2618	-140.6249	-8.7809E-01
	3264	-24.6753	-2.2058E-01
	3770	-15.5024	-1.4416E-01
	1949	48.3024	6.5966E-01
	477	75.5260	1.4074E 00
	2522	-428.7210	-1.6653E 00
	2720	-7.8509	-7.5625E-02
	1142	58.0147	8.6773E-01
	612	46.4098	6.2371E-01
	339	44.6079	5.9064E-01
	92	72.8614	1.3040E 00
	45	51.0870	7.1503E-01
	397	-782.2220	-2.1773E 00
	686	-72.7959	-5.4697E-01
	1008	-46.9387	-3.8488E-01
	3841	-281.0513	-1.3378E 00
	5797	-50.9242	-4.1164E-01
	9624	-66.0168	-5.0695E-01
	10710	-11.2842	-1.0696E-01
P10	769		
	774	-0.6501	-6.5294E-03
	646	16.5375	1.8071E-01
	442	31.5790	3.7942E-01
	1802	-307.6921	-1.4054E 00
	3060	-69.8113	-5.2955E-01
	3420	-11.7647	-1.1127E-01
	3944	-15.3216	-1.4260E-01
	998	74.6958	1.3740E 00
	1008	-1.0020	-1.0019E-02
	2306	-128.7697	-8.2757E-01
	2250	2.4285	2.4534E-02
	1088	51.6445	7.2649E-01
	1736	-59.5588	-4.6727E-01
	682	60.7143	9.3418E-01
	471	30.9385	3.7010E-01
	374	20.5945	2.3054E-01
	429	-14.7058	-1.3724E-01
	826	-92.5407	-6.5516E-01
	1211	-46.6101	-3.8264E-01
	1496	-23.5342	-2.1139E-01
	3244	-116.8447	-7.7403E-01
	5100	-57.2133	-4.5246E-01
	6688	-31.3333	-2.7261E-01

	Population estimate at start of interval	Percent mortality	Instantaneous mortality
F1	1883		
	2344	-24.4822	-2.1903E-01
	2250	4.0103	4.0877E-02
	2720	-20.8888	-1.8974E-01
	4510	-65.8088	-5.0569E-01
	5828	-29.2239	-2.5641E-01
	6090	-4.4955	-4.4021E-02
	4556	25.1889	2.9014E-01
	1574	65.4522	1.0627E 00
	2242	-42.4396	-3.5378E-01
	1090	51.3827	7.2109E-01
	1333	-22.2935	-2.0129E-01
	2249	-68.7171	-5.2308E-01
	3400	-51.1782	-4.1332E-01
	2012	40.8236	5.2456E-01
	971	51.7396	7.2846E-01
	578	40.4738	5.1867E-01
	387	33.0450	4.0108E-01
	202	47.8037	6.5006E-01
	344	-70.2970	-5.3240E-01
	491	-42.7325	-3.5584E-01
	4723	-861.9142	-2.2638E 00
	8899	-88.4183	-6.3352E-01
	11422	-28.3514	-2.4964E-01
F2	457		
	337	26.2582	3.0453E-01
	340	-0.8902	-8.9104E-03
	442	-29.9999	-2.6240E-01
	1020	-130.7691	-8.3627E-01
	10710	-949.9998	-2.3514E 00
	6090	43.1373	5.6444E-01
	1530	74.8769	1.3812E 00
	1020	33.3334	4.0539E-01
	727	28.7255	3.3856E-01
	496	31.7745	3.8228E-01
	442	10.8871	1.1521E-01
	1428	-223.0768	-1.1727E 00
	2618	-83.3333	-6.0616E-01
	927	64.5913	1.0381E 00
	404	56.4186	8.3043E-01
	102	74.7525	1.3762E 00
	98	3.9216	3.9954E-02
	86	12.2449	1.3056E-01
	221	-156.9766	-9.4383E-01
	1889	-754.7510	-2.1456E 00
	2814	-48.9676	-3.9859E-01
	6382	-126.7944	-8.1890E-01
	8971	-40.5672	-3.4055E-01

	Population estimate at start of interval	Percent mortality	Instantaneous mortality
F3	41		
	129	-214.6339	-1.1463E 00
	170	-31.7829	-2.7602E-01
	68	60.0000	9.1617E-01
	170	-149.9999	-9.1631E-01
	1156	-579.9997	-1.9169E 00
	1009	12.7163	1.3595E-01
	1088	-7.8295	-7.5427E-02
	646	40.6250	5.2121E-01
	327	49.3808	6.8074E-01
	128	60.8563	9.3780E-01
	592	-362.4998	-1.5315E 00
	929	-56.9256	-4.5063E-01
	1190	-28.0947	-2.4764E-01
	621	47.8152	6.5028E-01
	344	44.6055	5.9060E-01
	136	60.4652	9.2786E-01
	192	-41.1764	-3.4488E-01
	112	41.6667	5.3891E-01
	89	20.5358	2.2980E-01
	621	-597.7525	-1.9427E 00
	1229	-97.9065	-6.8265E-01
	1896	-54.2717	-4.3358E-01
	3889	-105.1159	-7.1843E-01
F4	196		
	110	43.8776	5.7755E-01
	152	-38.1818	-3.2343E-01
	34	77.6316	1.4973E 00
	170	-399.9998	-1.6094E 00
	1977	-1062.9410	-2.4535E 00
	1669	15.5792	1.6930E-01
	1496	10.3655	1.0937E-01
	1462	2.2728	2.2939E-02
	521	64.3639	1.0317E 00
	166	68.1382	1.1436E 00
	484	-191.5660	-1.0701E 00
	1029	-112.6032	-7.5428E-01
	1292	-25.5587	-2.2764E-01
	1104	14.5511	1.5719E-01
	349	68.3877	1.1515E 00
	238	31.8052	3.8273E-01
	77	67.6471	1.1283E 00
	149	-93.5064	-6.6017E-01
	261	-75.1677	-5.6060E-01
	341	-30.6513	-2.6740E-01
	921	-170.0877	-9.9360E-01
	1424	-54.6145	-4.3580E-01
	1666	-16.9943	-1.5700E-01

	Population estimate at start of interval	Percent mortality	Instantaneous mortality
F5	192		
	277	-44.2708	-3.6656E-01
	476	-71.8411	-5.4143E-01
	306	35.7143	4.4176E-01
	510	-66.6666	-5.1085E-01
	1700	-233.3331	-1.2040E 00
	1060	37.6471	4.7228E-01
	578	45.4717	6.0636E-01
	306	47.0589	6.3590E-01
	132	56.8628	8.4067E-01
	33	75.0000	1.3861E 00
	248	-651.5149	-2.0169E 00
	399	-60.8870	-4.7556E-01
	816	-104.5112	-7.1548E-01
	684	16.1765	1.7640E-01
	243	64.4737	1.0348E 00
	204	16.0494	1.7488E-01
	104	49.0197	6.7363E-01
	33	68.2693	1.1477E 00
	71	-115.1514	-7.6619E-01
	199	-180.2815	-1.0306E 00
	624	-213.5677	-1.1429E 00
	1091	-74.8397	-5.5873E-01
	1742	-59.6700	-4.6797E-01