ON THE ECOLOGY OF FLAGELLATES FROM SOME BRACKISH AND FRESH WATER ROCKPOOLS OF FINLAND.

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WITH PLATES I—XII.

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CONTENTS.

Introduction.

During the course of culture experiments on Phytoflagellates emergent from dried muds from the Tvärminne archipelago, a visit to Finland was made in order to gain a first hand insight into the ecological background of the organisms concerned. The investigation undertaken was necessarily incomplete; nevertheless, publication of the results and some of the questions raised by them may serve to draw attention to the Baltic flagellates and their special problems in ecology.

The Tvärminne archipelago forms part of the great archipelago of Finland and lies off the south coast between the port of Hangö and Ekenäs. A useful map of the district and many photographs are to be found in SUNDSTRÖM (1927).

The underlying rocks are igneous, crystalline, and worn smooth with ice. HÄYREN (1931) recognised, according to degree of exposure and vegetation, five regions in the archipelago: the Hinterland, the Coastland, the Inner Islands, the Outer Islands and the Sea Zone. Only on the last two of these do the typical rock pools occur, and it is with these that we are concerned. The islands of the Sea Zone are mostly naked rock (Plate I). On the Outer Islands, on the other hand, there are trees (Plate XI), concurrent with the presence of greater quantity of soil, though on these islands also there is much exposed rock. Apparently the important factor is the degree of exposure to the winter scouring of ice.

The sea in this part of the Baltic has a salinity of about 6 $^0/_{00}$ NaCl.

The macro-vegetation of the islands (discussed by HÄYREN in summary in 1931 and part in detail in 1914) shows successions beginning with lichen communities, through moss, moorland herb and shrub communities, finally to a rock *Pinetum.* The soil where it occurs is poor and sandy and acid, yielding a dark humic solution on alkaline extraction

The islands are studded with pools, varying in dimensions from a few centimetres across to several metres, and which, broadly speaking, follow successions parallel to those of the land vegetation. BOHLIN (1897) used three categories of algal vegetation for the Runmarö pools: Peatmoor Formation, Rainpool Formation, and Submarine Formation. However, these three main divisions lend themselves easily to subdivisions, as LEVANDER (1900) has shown. Thus, within the Submarine Formation the frequency with which sea splash is received is used as a criterion, while within the other formations permanence is considered important. This classification, which is given in detail below, being based on observation and experience, is very suitable for use on occasions, such as the present, when more precise investigation of physical conditions cannot be made.

LEVANDER's nine Pool Types are as follows:

Type I. *Intertidal Sea Water Pools,* at sea level but normally isolated from the sea and only in continuity during rough weather and times of abnormally high water.

Type II. *Permanent Rock Pools in the Normal Splash Zone,* never in continuity with the sea.

Type III. *Stagnant Brackish Pools,* above the normal splash zone receiving sea splash very rarely. Subject to drying out.

Type IV. *Seaweed Pools.* Rock pools or marsh pools at sea level in which seaweed, carried in by storms, lies rotting.

Type V. *Ephemeral Rain Pools*, above the splash zone; fresh water with no vegetation, and subject to drying out.

Type VIa. *Permanent Rain Pools*, with clear water and no vegetation.

Type VIb. *Permanent Rain Pools*, with peaty water and some vegetation in or around the pool.

Type VII. *Moss Pools*. Permanent or ephemeral pools with *Drepanocladus* spp. lining the sides and bottom, but with the water surface free.

Type VIII. *Rock Sphagneta*. Sphagnum filled hollows with no free water surface.

Type IX. *Marsh*. Large or middle size pools with a muddy bottom and vegetation.

LEVANDER's classification has been used in this paper, but with certain modifications suiting the present purpose. No alteration to the designation of the categories has been made, but intermediate types between one category and the next being frequent, in certain cases it has been found necessary to lump two categories together. This has been done with Pool Types I and II and with Pool Types VI b and IX. Type VIII was omitted from the present study.

The method of making the classifications in the field was rather empirical, depending on position, dimensions, macro-vegetation and salinity. Difficulty was most frequently met in dealing with the types intermediate between III and V, pools with a salinity of 0.4—1.5 $^0/_{00}$ NaCl. The presence of the halophilic lichen *Verrucaria maura* (the dark rim around the pool in Plate VI) was found to be an unreliable guide as its salt requirements apparently are lower than the upper limit of tolerance of the type organism of Type V pools, *Haematococcus pluvialis*. For instance, when the pool on Plate VI (Ostspiken No. 53) was photographed it was red with motile *Haematococcus* and had a salinity of 0.13 $^0/_{00}$ NaCl. In general, pools with a salinity over 1.0 $^0/_{00}$ NaCl were classified as Type III, and those below as Types V or VIa, as the case may be. Similarly, the boundary between V and VIa was decided by depth and area, and, it must be confessed, an indefinable, character which differentiated between the two.

During the month of July 1951 thirteen visits to the islands were made, and 147 pools were sampled. The 'Outer Islands' visited were Brännskär, Väst Rovholmen, Långskär, and islands in the 'Sea Zone' Ostspiken, Storsundsharun and Segelskär. Records were made of rough dimensions, positions, salinities, classification and, in some cases, pH and temperatures. Weather and other relevant facts were also noted, also macro-vegetation and some animals. Of the micro-flora only the most frequently occurring non-motile types were recorded generically, and of the motile types, which were recorded specifically, again only the most frequent or abundant types were taken into account. The method of collecting and examination was such that samples

were taken in 25 ml. bottles by dipping, and these were left to stand over-night uncorked by a north window and examined the following day. Muds from the same pools were dried and filed for future examination. Extensive use has been made of Contingency Tables in the presentation of results and, with one exception, actual numbers of records (not percentages) are given; e.g. in Table 1, out of a total of 141 records, 40 were of Type V pools, and out of those 40, 17 had a depth of between 5 and 10 cm.

Table 1. Depth of pools.

Distribution of records according to depth of water and Pool Type.

Actual numbers of records shown.

Pool Type

Depth (cm)	I	III	IV	V	VIa	VIb	VII	Total
0 — 2.5	1	6	—	5	—	—	—	12
2.5 — 5.0	—	11	—	11	2	1	6	31
5.0 — 10	—	18	—	17	4	4	4	47
10 — 20	—	9	—	5	10	4	2	30
20 — 40	6	1	2	2	5	2	—	18
40 —	—	1	—	—	1	1	—	3
Total	7	46	2	40	22	12	12	141

Table 2. Areas of pools.

Distribution of records according to area of pool and Pool Type.

Actual numbers of records shown.

Pool Type

Pool area (m²)	I	III	IV	V	VIa	VIb	VII	Total
0— 0.01	—	1	—	1	—	—	—	2
0.01— 0.03	—	3	—	—	—	—	—	3
0.03— 0.10	—	7	—	9	2	1	1	20
0.10— 0.30	—	15	—	10	5	1	3	34
0.30— 1.00	7	12	—	13	7	4	5	48
1.00— 3.00	—	6	1	6	4	3	2	22
3.00—10.00	2	2	1	1	4	4	—	14
10.00—30.00	—	—	—	—	—	1	—	1
Total	9	46	2	40	22	14	11	144

Table 3. Salinity of pools.

Distribution of records according to salinity and Pool Type.

Actual number of records shown. Salinity as Cl expressed in $^0/_{00}$ NaCl.

Pool Type

Salinity	I	III	IV	V	VIa	VIb	VII	Total
0 — 0.1	—	—	—	7	3	6	6	22
0.1 — 0.4	—	3	1	17	5	2	3	31
0.4 — 1.6	—	13	—	8	5	3	1	30
1.6 — 6.4	4	9	—	—	—	—	—	13
6.4 — 25	5	16	1	—	—	—	—	22
25 —	—	4	—	—	—	—	—	4
Total	9	45	2	32	13	11	10	122

Analysis of Records.

Physical characteristics of the Pool Types.

Depths and areas, recorded by rough measurements, are given in Tables 1 and 2, and salinities in Table 3. These measurements do not take into account the degree to which the pools concerned may have dried up; nevertheless, they will serve as a guide to the range found.

Type I (intertidal sea water pools and permanent rock pools in the splash zone, including also LEVANDER's Type II) could usually be distinguished from other types by the presence of *Cladophora* and *Enteromorpha*. However, this feature was not universal, and so did not form a criterion of the Pool Type. Some of these pools are shown on Plate II. Most of them lie within half a metre of sea level, but exceptions are frequent where the normal splash zone is extended (on exposed islands, for example, or where the peculiarities of rock formation, such as deep fissures leading to the sea have resulted in a unidirectional extension of the zone by a type of »spout» action). In salt content these pools for the most part did not differ much from that of the sea. Most had a salinity of between 6 and 8 $^0/_{00}$ NaCl; the value slightly higher than that of the sea being in accord with expectation, as evaporation should be demonstrable during the summer months. The pools are mostly large, with an area between 0.3 and 1.0 sq.m. and a depth between 20 and 40 cm. They have clear water and a sandy bottom.

The Type III pools (brackish pools above the normal splash zone) form the great majority of the salt pools. Some examples of them are shown on Plates II and III. On the inner islands they are mostly peripheral, but are

not so limited on exposed islands. Their dimensions vary very much, as do their salinities; the greater number have a depth between 5 and 10 cm. and an area between 0.03 and 1.0 sq.m. The highest salinities recorded were over 60 $^0/_{00}$ NaCl, and a continuous series was found between pools with this high figure and entirely fresh water pools. These pools are without vegetation. They have a dark coloured debris, rather gritty and with lichen fragments present.

The Type V pools (ephemeral rain pools above the normal splash zone, shown on Plates IV, V, VI) include all the smaller fresh water rock pools without vegetation. With respect to dimensions, colour of water and absence of humus they resemble the Type III pools. In point of fact, an arbitrary boundary between these two types was set at the salinity of 1.0 $^0/_{00}$ NaCl.

In the category VIa are included all permanent and semipermanent pools of low salinity without vegetation and with colourless (not peaty) water, illustrated by Plates VII and VIII. These pools differ from Types III and V in that they are larger and therefore less given to drying out. The maximum depth encountered was more than 40 cm., while most lay between 10 and 20 cm. In area they are mostly bigger than 0.1 sq.m., the biggest being 10 sq.m. They merge into the larger of the Brackish pools, as do the Type V pools into the smaller.

Type VIb pools are permanent, or semi-permanent, pools with vegetation and more or less peaty water (Plates X and XI). In this category are probably also included the Type IX pools of LEVANDER, as no satisfactory character could be found to differentiate between the two types except in the extreme forms of either. The vegetation in and around the pools may consist of a few clumps of grass in crevices only, and then the bottom is rocky with no more substratum than is found in the ephemeral pools; or, at the other extreme, it may consist of *Juncus*, *Scirpus* or *Sparganium* growing in the muddy bottom of the pool. The water is straw coloured and is often quite dark. Iron Bacteria are sometimes present. In this and the next type to be considered instances of salinity over 0.1 $^0/_{00}$ NaCl were rare, so the habitat can be considered entirely a fresh water one. VIb pools cover the same size range as do the VIa pools.

The 'Moss Pools' (Type VII) are small, quite fresh and in wet weather have a free water surface (Plate XII). The bottom is rocky but covered with a mat of *Drepanocladus* spp. It is a well defined type, but does merge on one side into the 'Minature *Sphagnetum*' (LEVANDER's Type VIII). Typically, they are small rock hollows fed by water seeping through crevices, and may be ephemeral or semi-permanent according to size (though in July 1951 most of them were full). The water is coloured. The majority have a depth within the limits of 2.5 and 10 cm. and an area between 0.1 and 1.0 sq.m.

Number of species.

In attempting to assess the comparative number of species of flagellates associated with each Pool Type, the assumption was made that species number increases exponentially with the number of pools examined, approaching finally a steady value given by E in the exponential equation

$$\text{Log} \left(\frac{E - a}{E} \right) = \frac{-t}{T}$$

where T is a constant, and a is the number of species obtained on examination of t pools.

Table 4. Species yield.

Mean number of species recorded (a) per t pools. The Errors indicated are 'Standard Error of the Mean'. At $t = \infty$, $a = E$. The calculated limits of E in each case, as set by the Standard Errors, are given in the last columns.

Pool Type	Mean number of species recorded (a) per t pools		Limits of E calculated
I	t 2	7	8.3 — 20 +
	a 1.93 ($\pm$ 0.186)	5.40 ($\pm$ 0.16)	
III	t 5	20	13.8 — 16.8
	a 6.21 ($\pm$ 0.43)	13.30 ($\pm$ 0.60)	
V	t 5	20	19.1 — 30 +
	a 6.83 ($\pm$ 0.69)	17.60 ($\pm$ 1.05)	
VIa	t 2	10	27.4 — 100 +
	a 3.65 ($\pm$ 0.27)	14.78 ($\pm$ 1.14)	
VIb	t 2	7	16.2 — 60 +
	a 4.07 ($\pm$ 0.37)	11.70 ($\pm$ 0.78)	
VII	t 2	7	15.6 — 25.5
	a 4.83 ($\pm$ 0.30)	12.13 ($\pm$ 0.51)	

For each Pool Type, values of a obtained from the records for corresponding values of t, together with the values of E calculated from them, are shown in Table 4. It is seen that the Standard Errors of the Means are of a high order, causing knowledge of E to be set between very wide limits. E, of course, only represents the number of species that is *likely* to be recorded under the particular collecting and recording conditions in operation were an infinite number of pools to be examined.

It can be inferred with moderate certainty from these values of E in Table 4 that pools of Type III will yield fewer species than will those of Types V, VIa and VIb. Further comparisons are not justified, but it is possible that by far the greatest number of species would be obtained from Type VIa and VIb pools, and the least from Type I.

The low species yield of the salt pools leads one to expect some sort of correlation between species number and salinity. Of 45 species recorded from 84 pools of Types III, V and VIa, 22 species were found in the 21 pools of salinity below 0.15 $^o/_{oo}$ NaCl, and only 15 species in each of the three groups of 21 pools between 0.15—0.5, 0.5—6.0 and above 6.0 $^o/_{oo}$ NaCl respectively. Therefore, if any correlation exists between species yield and salinity it is that pools of very low salinity have about half as many more species than pools of moderate and higher salinity. This appears to be due to the presence of inland fresh water species (usually in small numbers of individuals) in the pools that are very nearly fresh, and their absence from pools that are even slightly brackish.

Abundance of individuals.

A very rough quantitative estimate was attached to each record. Pools of Type I proved to be poorest in number of individuals of both flagellates and non-motile planktonic algae, while Types III and VII were the richest. In Type VIa pools non-motile forms tended to be more often in quantity than did flagellates (Tables 5 and 6).

Table 5. Abundance of flagellates.

Distribution of records according to quantity of flagellates and Pool Type.

Actual number of records shown.

'A b s e n t': no flagellates in sample; 'P r e s e n t': flagellates present in small numbers; 'A b u n d a n t': present in large numbers, but not in quantity enough to colour the water to the naked eye; 'V e r y   a b u n d a n t': present in quantity enough to colour the water to the naked eye.

Pool Type

	I	III	V	VIa	VIb	VII	Total
Absent	4	5	6	4	4	1	24
Present	3	8	10	5	4	1	31
Abundant	3	17	15	8	5	8	56
Very abundant	—	16	9	5	2	2	34
Total	10	46	40	22	15	12	145

Table 6. Abundance of non-motile planktonic algae.

Distribution of records according to quantity of non-motile plankton and Pool Type.
Actual number of records shown. Convention as in previous Table.

Pool Type

	I	III	V	VIa	VIb	VII	Total
Absent	9	33	30	10	8	5	95
Present.................	1	6	4	6	3	2	22
Abundant	—	2	3	3	2	4	14
Very abundant	—	5	3	3	2	1	14
Total	10	46	40	22	15	12	145

Table 7. Pool depth and abundance.

Distribution of records according to depth of pool and abundance of individuals,
expressed as a percentage of the records in each depth group.
Convention as in previous Tables.

Depth (cm)

	0—2.5	2.5—5.0	5—10	10—20	20—40	40—
Absent	18	5	10	15	11	20
Present.................	45	9	12	15	28	40
Abundant	27	46	42	39	39	20
Very abundant	9	40	36	30	22	20
Total records	11	32	49	26	18	5

Within the three Pool Types (III, V and VIa), which differ from each other
only in salinity or dimensions, no correlation was found between abundance
and salinity, but between abundance and depth of pool there appeared to be a
degree of correspondence. This is shown in Table 7. The correlation with
depth may account for the generally sparse populations of the VIb and VIa
pools, most of which are of comparatively large dimensions, and for the
often dense populations of the Type III pools, many of which are small.
It appears that pools between 2.5 and 10 cm. deep are most favourable for
the development of the really dense phytoplankton. It is possible that the
control of dispersal effected by the pool dimensions of both nutrients and
organisms concerned is favourable down to a certain limit of depth; below
this, extreme conditions have an overruling adverse influence.

The principal species.

The following identifications were made:

EUGLENINEAE

Entosiphon ovatum Stokes	Fresh water
Euglena gracilis Klebs	» »
E. pisciformis Klebs	» »
E. sanguinea Ehr.	» »
Peranema trichophorum Ehr.	» »
*Petalomonas spp.	Fresh and brackish
Trachelomonas hispida Perty	Fresh water

PERIDINIEAE

Amphidinium spp.	Brackish water
Glenodinium foliaceum Stein	» »
G. armatum Levander	Fresh and brackish
Gymnodinium albulum Lind.	Brackish water
Gyrodinium fissum Levander	» »
Gyrodinium sp.	» »
*Hemidinium nasutum Stein	Fresh water
*H. ochraceum Levander	» »
*Massartia spp.	Fresh and brackish
Oxyrrhis marina Dujardin	Brackish water
Peridinium volzii Lemm.	Fresh water

CRYPTOMONADINEAE

Chilomonas paramoecium Ehr.	Fresh water
*Cryptomonas spp.	Fresh and brackish

CHRYSOMONADINEAE

Chromulina minor Pascher	Fresh water
Monochrysis lutheri nov. spec.	Brackish water
*Ochromonas spp.	
Synura sp.	

PROTOMASTIGINEAE

*Bodo spp.	
*Heterochromonas globosa Skuja	Brackish water
*Monas spp.	
*Nephromonas hyalina nov. gen., nov. spec.	Fresh and brackish

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*Species obtained also from dry material.

VOLVOCALES

*Brachiomonas submarina Bohlin	Brackish water
Carteria salina Wislonch	» »
*C. globosa Pascher	Fresh water
C. micronucleata Korschikoff	» »
Chlamydomonas globosa Snow.	» »
*C. minima Korsch.	» »
C. pulsatilla Wollenweber	Brackish water
*Chlorogonium? elongatum Dangeard	Fresh water
C.? tetragamum Bohlin	» »
*Dysmorphococcus coccifer Korsch.	» »
Eudorina charkowensis (Korsch.) Pascher	Fresh water
*Gonium pectorale Müller	» »
G. sociale Dujardin	» »
Haematococcus droebakensis Woll.	» »
*H. pluvialis Flotow	» »
Paulschulzia pseudovolvox Skuja	» »
Pedinomonas upsilon nov. spec.	» »
Pyramimonas sp.	Brackish water
*Stephanosphaera pluvialis Cohn.	Fresh water

OTHER ALGAE

Botryococcus braunii Kütz.	Fresh water
B. sudeticus Lemm.	» »
Cosmarium subpalangula Elfring	» »
Nitzschia closterium forma minutissima T-form	
Nelson (syn. Phaeodactylum tricornutum Bohlin)	Brackish water

It has already been mentioned that attention was centred on the most frequently occurring and most abundant species, as these are of greatest ecological interest. Many forms had necessarily to be left unidentified and indeed undescribed, but in the main these were occasionals and rarities.

To use any of the technical ecological terms, such as »association», »society», etc. would be inappropriate in the present instance. Successions may be so rapid that it is possible for the ecological structure within a pool to become completely transformed almost over night. Until the dynamics of these successions have been worked out in considerable detail, any terms which imply sociological relationship are bound to state more than is known. For the present, then, only frequency of records has been used in defining the micro-vegetation of the Pool Types. Some facts pertinent to the question of mutual relationships and dynamics are discussed later in this paper.

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*Species obtained also from dry material.

Table 8.

Distribution of records according to species and Pool Type.

Actual number of records shown.

Pool Type

Species	I	III	V	VIa	VIb	VII	Total
Gonium pectorale	—	1	2	2	2	4	11
Peridinium volzii	—	—	—	—	3	5	8
Cosmarium subpalangula	—	—	2	1	—	2	5
Chlamydomonas globosa	—	—	2	1	3	1	7
Cryptomonas spp	—	8	1	3	3	2	17
Chlorogonium tetragamum	—	—	4	2	—	1	7
Hemidinium ochraceum	—	1	7	—	1	2	11
Scenedesmus spp	1	2	2	5	7	3	20
Stephanosphaera pluvialis	—	1	10	3	1	1	16
Haematococcus pluvialis	—	3	20	3	—	—	26
Nephromonas hyalina	—	2	—	2	1	—	5
Oocystis sp.	—	2	3	2	—	—	7
Monochrysis lutheri	1	1	2	2	1	—	7
Pyramimonas spp	1	4	2	1	—	—	8
Chlamydomonas pulsatilla	—	4	1	—	—	—	5
Glenodinium armatum	—	6	1	2	—	—	9
Massartia spp	3	5	—	2	1	—	11
Brachiomonas submarina	1	15	6	1	—	—	23
Oxyrrhis marina	1	12	—	—	—	—	13
Gyrodinium fissum	1	5	—	—	—	—	6
Number of pools	10	46	40	22	15	12	145

Table 8 shows the distribution of the records of the most important species among the Pool Types. Type I had a plankton population too sparse to be sampled adequately by the collecting method employed. Ten pools of this type were sampled and nine flagellate records were obtained, seven of which were of Dinoflagellates. The list for Type III is headed by *Brachiomonas submarina* and *Oxyrrhis marina*, with a *Cryptomonas* sp. and *Glenodinium armatum* and other Dinoflagellates less common. In Type V pools *Haematococcus pluvialis* and *Stephanosphaera pluvialis*, or *Hemidinium ochraceum* on Brännskär, were most frequent. *B. submarina* was also found there. *Peridinium volzii* and *Gonium pectorale* were most common in the Type VII pools, together with occasionally *Euglena* spp., *Trachelomonas* spp., *Draparnaldia* sp., *Cosmarium subpalangula* and other Conjugales. The typical species for the Type VIa and VIb pools could be defined less easily. *Scenedesmus* spp. were most frequently met with here, but on the whole more variety with accordingly less consistency was found in these pools than in other types, particularly among the flagellates. Of the two, VIa had the more species in common with V, and VIb had more in common with VII.

Pool Type	I 'Splash pools'	III 'Brackish pools'	V 'Ephemeral rain pools'	VIa Permanent rain pools without vegetation	VIb Permanent rain pools with vegetation	VII Moss pools
Position in respect to sea	Sea level Exposed	Above regular splash zone	Above regular splash zone	Above regular splash zone	Sheltered from sea	Sheltered from sea
Macro-vegetation	Cladophora Enteromorpha	None	None	None	Scirpus, Juncus, Grass etc.	Drepanocladus spp...
Colour of water	Colourless	Colourless	Colourless	Colourless	Straw coloured (peaty)	Straw coloured (peaty)
Character of sediment	Sand	Black	Black	Black	Mud. Iron bacteria often present	Moss. Iron bacteria often present
Salinity range $^0/_{00}$	6—8	0.4—64	0 (—1)	0 (—1)	0 (—1)	0 (—0.4)
Depth of majority (cm.)	20—40	2.5—20	2.5—10	5—40	5—40	2.5—20
Area of majority (m²)	0.3—10	0.03—1.0	0.03—1.0	0.1—10	0.3—10	0.1—3.0
Abundance of individuals	Very low	Very high	Medium	Medium	Low	High
Number of species	Low	Low	Medium high	Very high	High	Medium low
Characteristic flagellates	Dino-flagellates	Brachiomonas submarina. Oxyrrhis Marina	Haematococcus pluvialis. Stephanosphaera pluvialis. Hemidinium ochraceum	None characteristic	Peridinium volzii. Chlamydomonas globosa	Peridinium volzii. Gonium pectorale
Characteristic non-motile algae	None	Scenedesmus spp.	None	Scenedesmus spp. Oocystis sp.	Scenedesmus spp.	Scenedesmus spp. Cosmarium subpalangula

Table 9. Summary of physical and population characteristics of Levander's Pool Types.

Considerable overlap in species occurs also between I and III, and between III and V. These might be due to any of the following considerations: the sharing of certain characteristics by the Pool Types concerned, the indefiniteness of the boundary between one Type and the other, or a width of tolerance of the organism coupled with a factor of chance.

Table 9 summarises the main features of the Pool Types and their associated floras. Though LEVANDER's classification has proved useful, it has the weak point that it masks the essential difference between pools with and those without vegetation by including the larger of both as subdivisions of a single Type (VI).

Salinity.

With regard to NaCl content, the pools fall into three categories: fresh water pools, salt pools with more or less constant salt content, and salt pools whose salt content varies. Into the second group fall the Splash Pools, while into the third group fall the great majority of Brackish Pools (Type III pools).

These variable pools grade at one end of their range into fresh water pools. while at the other they may have a salinity as great as 64 $^0/_{00}$. Their salinity range will depend on many factors, amongst which may be enumerated: the frequency with which they receive sea splash (of salinity about 6 $^0/_{00}$) compared with that with which rain water is received; their capacity in comparison with the area from which drainage is received; the ratio of their surface area to capacity; and their position on the island in relation to splash, drainage, wind etc. The actual salinity of a pool at any one time will depend to a great extent on the weather. E.g. during fine spells in the summer there is a general tendency for the pools to dry up and increase in salinity as they do so.

122 of the pool samples were titrated for chloride (the results of these are expressed as grams NaCl per litre — $^0/_{00}$ — assuming that all chloride was present as NaCl), and their salinities correlated with the species present in them. In this way the 'Salt Climate' of a number of flagellates was obtained. This is shown in Table 10.

The organisms can be grouped according to the position of the maximum number of records. 1) Those which show a marked decrease in the number of records over 0.1 $^0/_{00}$. Pool Types VIb and VII provide most of the organisms, and they may be regarded as being strictly fresh water species, e.g. *Gonium pectorale* and *Peridinium volzii*. 2) Fresh water species whose maximum lies between 0.1 and 0.4 $^0/_{00}$ and which tolerate up to about 2$^0/_{00}$. These correspond with the typical Rain Pool species, e.g. *Haematococcus pluvialis* and *Stephanosphaera pluvialis*. 3) Euryhaline species with a very wide range, principally Pool Type III organisms, e.g. *Brachiomonas submarina* and *Chlamydomonas*

Table 10. Flagellates and salinity.

Distribution of records of flagellates according to salinity.

Actual number of records shown. Salinity as Cl expressed as $^0/_{00}$ NaCl.

Salinity

Organism	0—0.1	0.1—0.4	0.4—1.6	1.6—6.4	6.4—25	25—	Total
Peridinium volzii	4	1	—	—	—	—	5
Gonium pectorale	5	1	—	—	—	—	6
Hemidinium ochraceum	3	2	1	—	—	—	6
Stephanosphaera pluvialis	4	9	1	—	—	—	14
Chlamydomonas globosa	1	2	1	—	—	—	4
Chlorogonium tetragamum	2	2	2	—	—	— -	6
Haematococcus pluvialis	1	12	3	1	—	—	17
Nephromonas hyalina	—	1	1	1	—	—	3
Glenodinium armatum	1	2	3	—	3	—	9
Chlamydomonas pulsatilla	—	—	2	2	1	—	5
Massartia spp	—	3	3	2	1	1	10
Brachiomonas submarina	—	6	7	5	3	1	22
Monochrysis lutheri	—	1	2	1	2	1	7
Cryptomonas spp	3	2	—	3	4	—	12
Gyrodinium fissum	—	—	—	1	5	—	6
Pyramimonas sp	—	—	—	—	4	—	4
Oxyrrhis marina	—	—	—	1	9	3	13
Total salinity records	22	29	27	13	23	4	118

pulsatilla. 4) Euryhaline species with a comparatively narrow range (4—16 $^0/_{00}$) e.g. *Gyrodinium fissum.* 5) Euryhaline species whose lower, but not upper, boundary is marked. *Oxyrrhis marina* belongs here.

There is a degree of correspondence between the above arrangement of species and that based on the Pool Types of LEVANDER, but this may be due to factors other than salinity. For instance, group 4 above contains the species of the Splash Pools (Type I). Now this habitat may be favoured either because these pools have a narrow salinity range or because their temperature variation is not quite as extreme as in other brackish pools, or because of some other factor such as the presence of *Enteromorpha* or *Cladophora* and high pH. Again, it is probable that the first and second groups above do not separate merely on optimum salt concentration but also on the presence or absence of humic substances. Certainly, if humus is harmful, an organism would benefit if small concentrations of salt were tolerated, for these would tend to keep down the humic concentration.

Nutrients.

This most important aspect of the pool ecology was omitted owing to its complexity, in view of the short time available for the investigation. However, a few general observations may be of value.

The chemical nature of some of the Tvärminne pools has been studied by JÄRNEFELT (1940), but unfortunately this work has been inaccessable to the author.

Of the possible sources of nutrients (used in the widest sense) the following are likely to be of importance:

Mainly inorganic and humic	1)	Sea water			
	2)	Water draining from the soil			
	3)	»	»	»	rock surface and Lichens
Mainly organic	4)	Rotting seaweeds			
	5)	Insect larvae			
	6)	Gull droppings			

The nutrients from the sea affect, of course, mainly the salt pools (Types I, III, IV, and to a lesser extent V and VIa). Substances from the soil affect mostly Pool Types VIb and VII and are rich in humus. The water draining from the rock surface and lichens will be of equal importance in all Pool Types.

Seaweed products will have most effect in Type IV pools, but their influence will not be confined to these Seaweed Pools. Very often single fronds of *Fucus vesiculosus* are found in other types of pool, and a single frond of seaweed in a small pool is likely to have a marked influence on the amount of organic matter in solution.

Type III pools which have become very salt during fine weather often harbour dead insect larvae. These larvae cannot be called a source of organic material since in the first place they are products of the pool; but they can be regarded as agents by which the organic content of certain kinds of pool is conserved.

The most important and singular source of organic nitrogen, particularly on the outermost islands, is without doubt the excrement of gulls. Gull droppings are the most conspicuous feature of nesting places, causing the rocks to be whitened and the neighbourhood to stench. Such a concentration of manure becomes spread widely on these nesting islands. On other islands no such concentrations occur; nevertheless, the influence of the birds is not negligible.

On Storsundsharun and Segelskär thirteen samples were taken from pools around which there was visible excrement. One such pool is shown on Plate IX. The alga colouring the water is *Chlamydomonas pulsatilla*. All these 'Gull

Pools' were rather salt: six had a salinity between 0.4 and 1.6 °/oo NaCl, three between 1.6 and 6.4, three between 0.1 and 0.4 and one over 6.4. Thus, gull nitrogen is associated with salt.

The 'Gull Pool', whose conditions are rather extreme (and really a sub-division of the Type III pool) is the home of *Chlamydomonas pulsatilla*. Other species do occur (Table 11) but *C. pulsatilla* is confined to them and is also the most frequent species.

Table 11. Pools adjacent to visible gull excrement.

Species	Records in 'Gull Pools'	Total records of the species
1. Flagellates.		
Chlamydomonas pulsatilla	4	5
Haematococcus pluvialis	4	26
Massartia spp	2	12
Stephanosphaera pluvialis	2	16
Brachiomonas submarina	2	23
Chlorogonium spp	2	14
Pyramimonas sp	1	4
Nephromonas hyalina	1	5
Glenodinium armatum	1	9
Cryptomonas spp	1	17
2. Non-motile Planktonic Algae		
Nanochloris?	2	2
Phaeodactylum tricornutum	1	2
Oocystis sp	1	7
Scenedesmus spp	1	23

Total records of pools of this type: 13

It seems that most of the organic, and much of the inorganic, nutrient material in the Tvärminne pools is aasociated with NaCl, while the remaining inorganic nutrients are associated with high humus concentrations. It is to be expected, then, that the majority of the algae must tolerate a certain concen-tration of either one or the other of these.

Temperature.

Records were obtained of midday temperatures between 16° and 29° C. in the pools, and rock temperatures up to 32°. LEVANDER (1900) recorded temperatures up to 30° in the pools and 32° in the moss layer of a *Sphagnum* pool. No doubt, on occasions higher temperatures could be obtained. LE-

VANDER's records of temperature variation in three pools show the greater variation in the shallower of them. Less precisely, but covering a wider range of material (including records from 46 pools) a similar correlation of temperature variation with pool depth has been attempted. This is shown in Tables 12 and 13. For the sake of analysis the temperatures recorded on sunny days are kept apart from those taken on cloudy days.

Table 12. Correlation of temperature variation with depth.

Distribution of records according to depth of pool and temperature.

1) Windy and sunny, Mid-day. Spikarna and Långskär.

Pool Depth (c m)

Temperature ° C.	0—2.5	2.5—5	5—10	10—20	20—40	40—	Total
17 — 19	—	—	—	1	—	—	1
19 — 21	—	—	—	2	1	1	4
21 — 23	—	—	1	2	2	—	5
23 — 25	1	—	4	1	2	—	8
25 — 27	1	5	2	1	—	—	9
27 — 29	1	—	—	—	—	—	1
Total	3	5	7	7	5	1	28

Sea temperature at surface: 17.3
Shaded pool 15 cm. deep: 16
Rock temperature in sun: 32.5

Table 13. Correlation of temperature variation with depth.

Distribution of records according to depth of pool and temperature.

2) Windy and cloudy, Mid-day. Väst Rovholmen and Storsundsharun.

Pool Depth (c m)

Temperature ° C.	2.5—5	5—10	10—20	20—40	Total
15 — 17	—	2	1	—	3
17 — 19	—	5	2	1	8
19 — 21	3	3	1	—	7
Total	3	10	4	1	18

Sea temperature at surface: 16

Rise in temperature during the day depends on heat received at the surface, less heat lost at the surface, and on the volume of water to be heated up. Since both heat gained due to radiation and heat lost through evaporation

depend to a large extent on surface area, and volume is usually some factor of depth × surface area, the following relationship might be expected to exist:

$$\text{Heat change} = \frac{\text{Surface area}}{\text{Depth} \times \text{Surface area}} = \frac{1}{\text{Depth}}$$

This rather obvious consideration is, in fact, supported by the temperature records. The overall variation between cloudy and sunny days is evident, as is also the greater variation in the shallower pools. Pools that were obviously overshadowed were not included in the Tables, for the temperature of these was more uniform and low.

Sufficient records were not obtained for the effect of temperature on flagellate populations to be seen. Some minimum tolerances are given, however;

Haematococcus pluvialis	17	— 25.3
Stephanosphaera pluvialis	17	— 25.3
Brachiomonas submarina	16.4	— 26.3
Oxyrrhis marina	18	— 29
Glenodinium armatum	24	— 24
Monochrysis lutheri	26.7	— 29

These, of course, do not represent continuous temperatures. *O. marina* has been found not to multiply in a continuous temperature over 25°, and *B. submarina* over 28°. On the other hand, *H. pluvialis* will multiply at 34° in the laboratory.

Hydrogen-ion concentration.

The pH of soil from 33 dried-up pools was found to lie within the limits of 6 and 7, and the pH of water of 32 pools taken in the field lay between 7 and 10 (Table 14).

Table 14. Hydrogen ion concentration.
Readings of pH from various pools taken on two occasions.

Pool Type.

(i) Cloudy Day.

I	9.0,	9.0,	9.0		
III	8.9,	8.0,	7.5,	7.5,	7.5,	7.1
V	7.5,	7.5,	7.4,	7.1	
VIa	7.5,	7.0			
VIb	8.0,	7.5			
VII	7.4				

(ii) Sunny Day.

I	9.0					
III	9.0,	8.5,	8.0			
V	10.0,	9.0,	9.0,	8.5,	8.5,	8.5,	8.0
VIa	9.0,	8.5				
VIb						
VII						

No correlation was found between pH and Pool Type, with the exception possibly of Type I pools which gave high values. Readings taken on sunny days gave a higher average than did those taken on cloudy days, as would be expected. On one occasion, pools with a very dense growth of *Chlamydomonas pulsatilla* had a lower pH than neighbouring pools sparsely populated by *Haematococcus pluvialis* (8—8.₅ and 9—10, respectively), most probably an effect of the high concentration of gull excrement in the former.

KUENEN (1939) obtained pH values as low as 4.₅ in peaty pools. It appears that these pools may sometimes be very acid, but that they are not always so is suggested by two of the entries in Table 14. Coloured water may not necessarily indicate low pH.

All that can be concluded is that the 'geological' pH is low on account of the acid nature of the rock formation, and that the 'biological' pH is often higher due to the presence of autotrophic organisms.

Aestivation.

Two collections of dried material were made from the Tvärminne pools, one by E. G. PRINGSHEIM in 1950, the other by the author in 1951. A similar range of species was obtained from both (Table 15). Whereas the 1950 samples were re-soakings of material taken from dry pools, the 1951 collection consisted of debris artificially dried taken from pools containing water. The contents of these pools were examined at the time of collection, so a direct comparison between the 'wet' sample and the 'dry' of the 1951 collection is possible. Table 15 includes only species of which they are three or more records. Information concerning others is given with the species list on p. 12.

It appears that a fairly sharp line can be drawn between species able and those unable to survive drying out. Those which do survive were generally encountered more frequently in the sample taken and dried than they were in the pool itself. Unfavourable conditions at the time of collection probably account for this. Though the resting stages of these species are comparatively widespread, it is evident that not even those of *Haematococcus pluvialis* are ubiquitous in debris of pools. But the difficulty of germinating resting cells of some species, e.g. *Hemidinium ochraceum*, and the possible mortality of others have to be kept in mind when making interpretations.

Concerning the viability of resting cells, only samples containing *Chlorogonium elongatum* have shown a decreased yield with the passage of time. These were good after six weeks and extremely poor after three months. Other species listed in the Table have shown no decrease in eighteen months.

Where known, the nature of the resting stage is indicated in the Table. If the only cell is the zygote and the species is dioecious, obviously both 'sexes'

Table 15. Aestivation.

Comparison of records obtained from wet and dry samples.

Species	1950 Samples 43 dry samples examined after 6—10 weeks	1951 Samples Collections examined fresh, and dried debris from the same 38 pools examined after 4—9 months			Total	Type of resting cell
		Present only in dry sample	Present in both fresh and dry sample	Present only in sample examined fresh		
Haematococcus pluvialis ...	14	15	11	2	28	Aplanospore (and zygote)
Stephanosphaera pluvialis	8	3	3	2	8	Zygote
Nephromonas hyalina	11	5	0	3	8	Cyst
Chlorogonium elongatum ...	14**	2	0	0	2	Zygote?
C. tetragamum	0	0	0	4	4	
Brachiomonas submarina ...	4	6	3	2	11	Zygote
Chlamydomonas minima ...	8	5	0	2	7	Zygote
Dysmorphococcus coccifer	8	3	0	0*	3	Aplanospore
Hemidinium ochraceum ...	11	3	1	4	8	Aplanospore
Massartia spp...................	2	5	0	2	7	
Gonium pectorale	3	1	2	2	5	
Cryptomonas spp.............	7	1	0	7	8	
Gyrodinium fissum	0	0	0	3	3	
Oxyrrhis marina	0	0	0	3	3	
Petalomonas sp................	0	1	0	3	4	
Chlamydomonas globosa ...	0	0	0	3	3	

must be present for aestivation to be possible. *Haematococcus droebakensis*, for example, was found in a pool on Storsundsharun in good quantity, but dried mud from this pool yielded no *H. droebakensis* on re-soaking. Experiments have shown that heterothallism exists among the strains of this species, and that, moreover, clones of the Storsundsharun strain do not form resting cells in culture, although gametogenesis takes place normally. Apparently only one 'sex' was present in the Storsundsharun pool.

Evidence of change.

The field-work on which the present paper is based was done in July and the first week of August 1951, that is during a single month of a summer which was by no means typical in its weather. It was colder and rather wetter than normal for the time of year, and this abnormality might well be reflected in some degree by the pool populations.

The lists of LEVANDER (1900) differ considerably from those given here. *Oxyrrhis marina* and *Chlamydomonas pulsatilla*, to mention only two important species, are not included by LEVANDER, and many species listed by him have

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* This alga was not found in any pool during July 1951.

** *C. elongatum* was absent when the same samples were soaked again after four months.

not been encountered by the present writer. These differences may partly be accounted for by the fact that LEVANDER worked some 70 km. east of Tvärminne, but may, on the other hand, be due to periodic fluctuations.

Euglena sanguinea was seen only once in July 1951, and then in a deep pool of Type VIb on Långskär, while in August 1950 it had been observed to be very frequent and widespread. Possibly *E. sanguinea* becomes most abundant in the late summer, or again, the difference may reflect a periodic rather than a seasonal change.

Certain species common in dried samples taken both in 1950 and 1951 were never seen in the pools in July 1951, even though most of the dried samples were obtained from those same pools. One example will suffice: *Dysmorphococcus coccifer*, which was usually associated with *Haematococcus pluvialis* and *Stephanosphaera pluvialis* in samples from Ephemeral Rain Pools (Type V). By August 1950 most of the sepools were dry, while at the beginning of July 1951 most of them were with water. In culture some individuals of *D. coccifer* form aplanospores after a month or two, but in general the motile phase is prolonged, unlike that of *H. pluvialis* or *Hemidinium ochraceum;* so if *D.*

Table 16.

Some changes in pool population accompanying changes in salinity in certain pools which were visited on two occasions.

Salinity change	Interval	Change in population
0.54 — 0.90	7 days	*Chlorogonium tetragamum* replaced by *Chlamydomonas pulsatilla*
0.26 — 0.40	7 »	*Stephanosphaera pluvialis* replaced by *Haematococcus pluvialis* and *Massartia* sp
0.52 — 1.00	3 »	*H. pluvialis* encysted
0.03 — 0.09	14 »	*Chlamydomonas globosa* replaced by *Pedinomonas upsilon*
10.1 — 23.7	17 »	*Brachiomonas submarina* and *Heterochromonas globosa* replaced by *Oxyrrhis marina, Glenodinium armatum* and *Massartia* sp
7.0 — 15.9	17 »	*B. submarina* replaced by *O. marina*
2.6 — 7.38*	10 »	*B. submarina* very much reduced
7.38 — 11.6**	7 »	*B. submarina* replaced by *O. marina*

* This pool had increased in depth also. Wave action.
** Same pool as previous entry.

coccifer were 'in season' and abundant one would expect to find it when sampling the pools. It is therefore very probable that it is motile very much more early in the season than July. Confirmation of this would be most interesting.

Some changes which took place during the month of July were observed. These all were cases of drying or partial drying-out of pools in question accompanied by a rise in salinity, and in most cases a change in flagellate population. These are shown in Table 16. While all the changes mentioned need not necessarily be due to an increase in salinity, it is apparent that increased salinity does account for the extinction of *Brachiomonas submarina* in the presence of *Oxyrrhis marina* (see also under *Oxyrrhis marina*). In this connection it is also significant that the majority of the records of *O. marina* were got in the latter half of the month. In *B. submarina* and *O. marina*, then, there is evidence of a seasonal periodicity connected with the drying-out of the pools.

Taxonomic and ecological notes

Brachiomonas submarina Bohlin. (Fig. 1—11).

In the paper containing the original diagnosis of the genus *Brachiomonas*, BOHLIN (1897) describes two species, *B. submarina* and *B. gracilis*, which differed from each other in the length of the arms; both are figured as possessing a papilla. A third species, *B. westiana*, was added by PASCHER; this was based on figures by WEST which differed from those of BOHLIN in having no papilla shown (WEST, 1908; PASCHER, 1927). A further species, without lateral arms, *B. simplex*, and *B. submarina* forma *obtusa*, a form with blunt arms, were described by HAZEN (1922).

Forms resembling *B. submarina*, *B. submarina* forma *obtusa*, *B. westiana* and *B. gracilis* are common at Tvärminne. *B. simplex* was not seen, and the following discussion will not include it. Some thirty clone isolations were made from Tvärminne and Öregrund material, embracing between them the complete morphological range, and it has been found impossible to distinguish between the various forms in culture.

Individuals both with and without the papilla co-exist in the same clone culture (Text Figures 1 and 2). A few cases have been seen in which it lies anterior to the points of exit of the flagella; but these are exceptional, mostly when present the papilla lies behind them, merely forming an anterior snout as figured by BOHLIN. The papilla is too small to be seen under the dissecting microscope, so isolation of individuals definitely possessing or not possessing it has not been carried out. Nevertheless, it is evident that this structure is not a constant feature, and therefore does not afford a good basis for species separation. It is suggested that *B. westiana* PASCHER be discontinued.
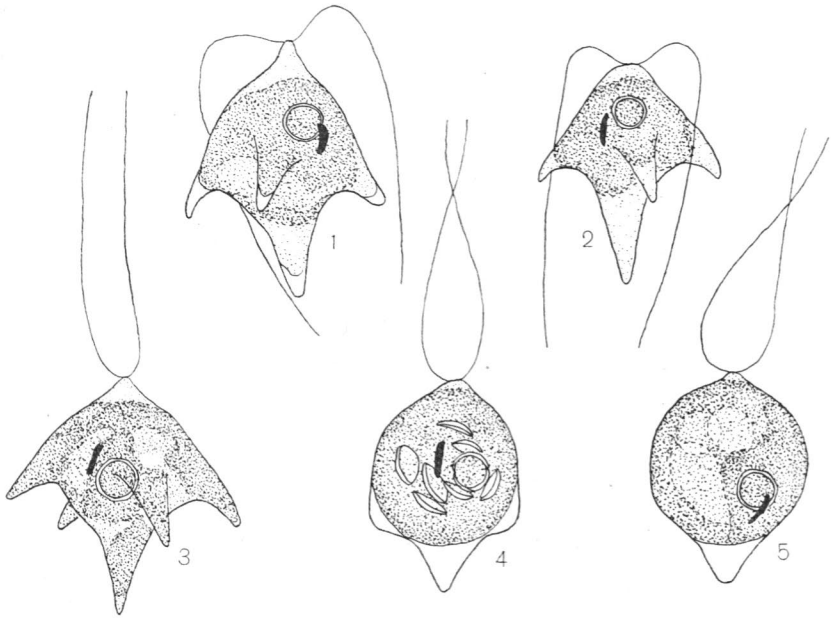
Fig. 1. × 2000. Clone 'Submarina 6', with snout-like papilla.
Chromatophore wholly, cytoplasm partly contracted from arms.

Fig. 2. × 2000. Clone 'Submarina 6', without papilla.
Cytoplasm, but not chromatophore, fills arms.

Fig. 3. × 1000. Clone 'Submarina 6', mature cell, chromatophore fills arms.

Fig. 4. × 1000. Clone 'Submarina 6', mature cell, cytoplasm contracted, arms very short.
Plate-like starch grains.

Fig. 5. × 1000. Clone 'Submarina 6', mature cell lacking arms.

As far as the length of the arms is concerned, there is very great variation from culture to culture of the same clone, the culture medium and age having a marked effect (Text Figures 1—7). In nature intermediates are found which are hard to place, though very often one form will be found to predominate in a pool. Ten 'gracilis' individuals were isolated. Typical examples are illustrated in Text Figures 8 and 9. They are more slender than any figured by BOHLIN as *B. gracilis*, and yet in culture they could not be distinguished from the clones of *B. submarina*. On morphological grounds, then, it is suggested that *B. gracilis* and *B. submarina* are one and the same species.

All the *Brachiomonas* isolations (including the 'gracilis' ones) were heterothallic. All tested fell into one of two sexual types: those capable of producing zygotes when mixed with strain 'Submarina 7', and those capable with strain 'Submarina 12' (Table 17). The significance of this is that none of the *Brachiomonas* yet tested has been found to be genetically isolated.
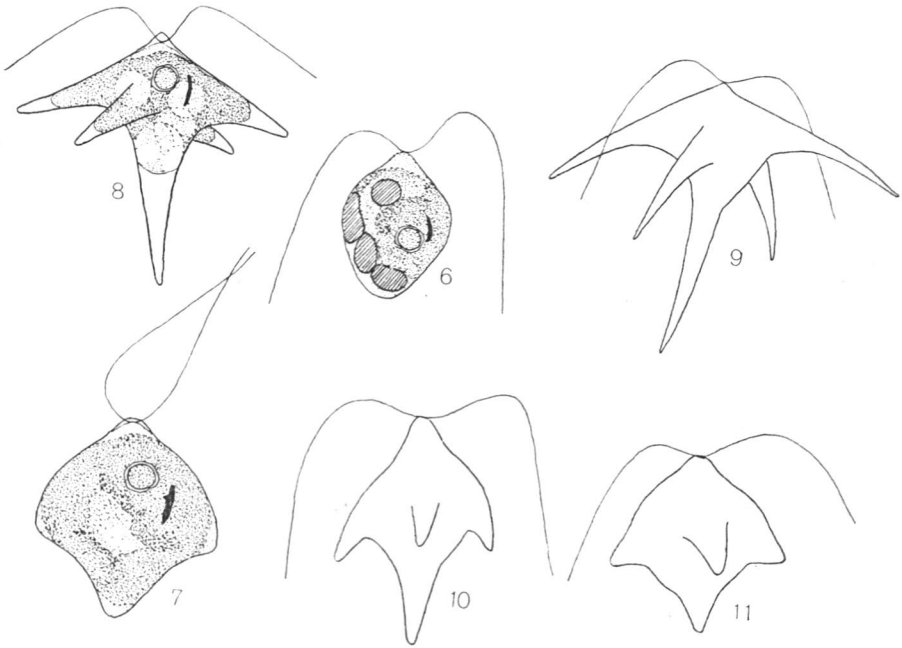
Fig. 6. × 2000. One of four cells from a recently germinated zygote (clones 'Submarina 6'
× 'Submarina 12'). The oil bodies contain an orange pigment.

Fig. 7. × 2000. Simple form, two days after germination of a zygote from dried material.
Clone 'Submarina 6' originated from such an individual.

Fig. 8. × 750. 'Gracilis' form from a wild collection. This cell gave rise to clone 'Gracilis 2'.
Note insertion of flagella where cytoplasm has receded at anterior.

Fig. 9. × 750. 'Gracilis' form from a wild collection.

Fig. 10. × 2000. Clone 'Gracilis 2', young cell.

Fig. 11. × 1000. Clone 'Gracilis 2', mature cell.

Since between the members of this group of »species» there is neither
ecological nor geographical nor genetical separation, and the morphological
distinguishing features between them are not constant, the conclusion is
inevitable that the group falls within the domain of a single species. It is
proposed to retain the name of the species first described.

Brachiomonas submarina (BOHLIN) revised (including *B. submarina* BOHLIN,
B. gracilis BOHLIN, and *B. westiana* PASCHER). Anterior papilla present or
absent; expression of lateral arms variable, from being more than the body
diameter in length and acute to being blunt and very short, normally, but
not always, directed backwards: posterior process likewise variable; stigma
situated between two arms, elongate; flagella 1 to 1 $^1/_2$ body's length; pyrenoid
central, lying normally slightly towards the stigma; protoplast filling arms
or contracted, sometimes vacuolated; no contractile vacuoles; chromatophore
ill-defined, sometimes reticulate; mature cells 15 to 40 μ in length (including

Table 17. Sex reaction of Brachiomonas clones.

Clone		Clone													
		'Submarina'						'Gracilis'							
		1	6	7	12	13	19	1	2	3	4	5	6	7	8
'Submarina'	1	0													
»	6	0	0												
»	7	0	0	0											
»	12	Z	Z	Z	0										
»	13	Z	Z	Z	0	0									
»	19	0	0	0	Z	Z	0								
'Gracilis'	1	•	•	0	Z	•	•	0							
»	2	•	•	Z	0	•	•	•	0						
»	3	•	•	Z	0	•	•	•	•	0					
»	4	•	•	0	Z	•	•	•	•	•	0				
»	5	•	•	0	Z	•	•	•	•	•	•	0			
»	6	•	•	0	Z	•	•	•	•	•	•	•	0		
»	7	•	•	0	Z	•	•	•	•	•	•	•	•	0	
»	8	•	•	Z	0	•	•	•	•	•	•	•	•	•	0

Z Zygotes produced on mixing.
0 No zygotes produced.
• Not tested.

arms), normal maximum 18 μ; diameter often a little less. Heterothallic, isogamous; gametes without cell wall, pyriform to spherical, 4 to 8 μ long; zygotes pyriform, at first 4-flagellate, negatively phototactic, afterwards spherical smooth walled cysts containing a brown oil, 8 to 15 μ in diameter.

Brachiomonas submarina has been recorded also from Britain, France and America. In Britain it appears to be common in rock pools above high tide and is quite widespread. In the Baltic area it is the type alga of Brackish Pools of low salinity. 23 records were obtained at Tvärminne with the following distribution among the Pool Types: Type III, 15; Type V, 6; Type I, 1; Type VIa, 1. Table 10 shows the salinity range and distribution. Pools of low salinity are favoured, for apparently in those of above 4 $^0/_{00}$ NaCl it is liable to be replaced by *Oxyrrhis marina*.

Laboratory experiments have been carried out vith *B. submarina* regarding its biological relation to the environment. The results of these will be discussed at a later date. At present it is sufficient to note that its distribution in corre-lation with salinity (Table 10) can be explained in terms of three points: 1) the slower growth rate at higher salinities; 2) the greater amount of gamete formation at the lowest salinities, which causes the net growth rate to be reduced; and 3) the liability to be preyed upon by *Oxyrrhis* at higher salinities.

B. submarina seldom forms a surface community in pools, for it is always found as a cloud near the bottom, seen also in culture tubes, a fact which often enables 'Brachiomonas Pools' to be recognised immediately. Of the 23 records, it was abundant in 14, and present in small quantity in 9. The maximum densities far exceed those of *Haematococcus* and *Stephanosphaera*.

Chlamydomonas pulsatilla, Wollenweber.

A number of rather asymmetric, medium sized *Chlamydomonas* forms are to be found in pools in the neighbourhood of the perches of sea birds. The chromatophore is of the eu-chlamydomonas type but broken up into longitudinally running ribbons; the cell wall is moderately thick, the anterior papilla more or less pronounced. Of these *C. pulsatilla* Woll. is the only species described and is characterised by its four contractile vacuoles (PASCHER, 1927). Another member of the group, not yet described, found in 'Gull Pools' on Puffin Island and other localities around Anglesey, differs from *C. pulsatilla* in having no contractile vacuoles. The Tvärminne form is slightly smaller than WOLLENWEBER's species, being 10—19 μ long, as opposed to the 15—23 μ of the latter, but in other respects the descriptions fit.

At Tvärminne *C. pulsatilla* was found in pools at the west end of Storsundsharun where there was much gull excrement. These were Type III pools with salinities ranging from 0.5 to 7.5 $^0/_{00}$ NaCl. In culture good growth occurs in salinities between 0 and 32 $^0/_{00}$. Aplanospores are formed in some quantity in old cultures. A '*C. pulsatilla* pool' is shown on Plate IX. Growth was extremely dense and gave the pools an opaque, dark green appearance.

Chlorogonium spp.

Taxonomy in this genus is incomplete and confused. Two species were tentatively identified, principally on dimensions and number of pyrenoids, as *C. elongatum* Dangeard and *C. tetragamum* Bohlin. Other forms mostly of small dimensions (16 μ) with single pyrenoid were encountered occasionally.

C. tetragamum was the species most frequently seen in the pools. Of it there were seven records, 4 from Type V pools, 2 from VIa and 1 from VII. It was found in salinities up to 0.6 $^0/_{00}$ NaCl. In two of the pools where heavy growth had taken place copulating gametes were seen.

C. elongatum has been found on wetting dry material, derived principally from pools of Type VIb. Two records only were obtained from wet pools, both from VIb pools.

The rather meagre evidence suggests that these *Chlorogonia* occupy different niches at Tvärminne; the former the pool without, the latter the pool with vegetation.

Haematococcus pluvialis Flotow.

This conspicuous alga has received attention from many botanists in the past, and yet its very name is still a matter of controversy (WILLE, 1903; WOLLENWEBER, 1908; GROVES, 1912) and little is even yet known about its life history and physiology.

Some facts, though, are well established. The two major phases in the life history are asexual: a short swarming period during which multiplication takes place and a resting encysted stage of indefinite duration which will withstand desiccation. In point of fact, two types of cyst exist (HAZEN, 1899): the so-called 'haematocysts' and 'palmellae'. The former become thick walled, enlarged and completely red, while the latter remain small, thin walled and contain no more haematochrome than the swarmers. It is clear that the haematocysts are resting cysts, while the palmellae, which can undergo multiplication, are of a temporary nature. However, no hard and sharp line can be drawn between the two; both are technically 'aplanospores'. The swarmers in nature normally have a central mass of haematochrome, but this is nearly absent under most culture conditions and becomes conspicuous only at the onset of encystment. The conditions which control encystment and haematochrome formation are obscure.

Sexual reproduction is apparently rare and is most easily observed when dry collections containing haematocysts are soaked. According to PEEBLES (1909) gamete formation occurs on encystment after adverse conditions have been endured. The gametes are small and thin walled, and give rise to a zygote which becomes enlarged and thick walled like the haematocyst.

It has been found that the strain prevalent in the Baltic pools differs in some physiological details from several strains originating elsewhere; the most conspicuous difference being that the period of motility preceding the onset of encystment in culture is always much shorter in the Baltic strain than in the others and growth is correspondingly poorer, particularly in inorganic media. The existence of these 'physiological strains' emphasises the necessity for caution in comparing ecological data of *H. pluvialis* gleaned from different parts of the world.

H. pluvialis is the most abundant flagellate of the islands, and indeed, if cysts are taken into account, is nearly ubiquitous. It is typical of the Ephemeral Rain Pools (Type V), not only because it is the most frequently encountered species in these pools, but also because this type of pool supplies by far the majority of records of the species *in the motile state*. It is a well

known phenomenon that the rain pools are often coloured red with a deposit of haematocysts. Indeed, these have earned them the familiar name of 'Haematococcus Pools'. Out of the 26 records of *H. pluvialis* 20 were in Type V, 3 in Type III, and 3 in Type VIa. Grouping the Types V and VIa as pools without vegetation and the Types VIb and VII and those with, the figures quoted afford a significant correlation between the presence of *H. pluvialis* in the motile condition and lack of vegetation in and around the pool. In this connection, no culture medium with pH below 6.8 has been found to support growth of this alga; nevertheless it is doubtful whether pH is the only factor concerned in the distribution, particularly since pools of Types VIb and VII do not all have pH below 6.8.

An attempt was made to correlate the presence of *Haematococcus* with depth, which may be taken as a measure of the frequency of drying out, but this was unsuccessful when only records from Type V pools were used. No correlation could be found between pools under and pools over 5 cm. depth, but, since V and VIa pools separate out to considerable extent on depth, there is a correlation between pools over and under 10 cm. deep if both V and VIa data be taken into account.

The salinity range for swarming *Haematococcus* was found to be from 0.0 to 2.0 $^0/_{00}$ NaCl (Table 10). The very great maximum between 0.1 and 0.4 $^0/_{00}$ is probably due to the fact that the majority of records of salinity below 0.1 $^0/_{00}$ came from VIb and VII pools which were not favourable to *Haematococcus* for other reasons. In culture up to 2.5 $^0/_{00}$ is tolerated and up to 1.5 $^0/_{00}$ salt has no effect on the growth rate.

A rather interesting fact in the distribution of *Haematococcus* appeared in the analysis of the records. This was that on the two most sheltered islands collected from, Brännskär and Väst Rovholmen, *Haematococcus* was almost entirely replaced by *Hemidinium ochraceum*. The distribution of records of *Haematococcus* in Type V pools among the islands is shown on Tables 18 and 19. The reason for this distribution is not clear, but three possibilities come to mind. The first and the most obvious is the influence of gulls; Storsundsharun, Spikarna and Segelskär are nesting islands, while Långskär, Brännskär and Väst Rovholmen, are not. But in this connection it should be noted that no significant correlation either way is obtained between the presence of visible gull excrement around the pool and the presence of *Haematococcus*. Secondly, the absence of trees in the first group and their presence in the second together with a greater amount of humus and soil, may be the cause. And thirdly, the greater number of pools with small quantities of salt in the outer islands may favour *Haematococcus* there. Whether these factors are operating on *Hemidinium* or on *Haematococcus* it is impossible to say. Certainly the two species appear to be mutually excluding.

Table 18. Presence of motile *Haematococcus pluvialis.*

Distribution of records according to position of island.
Data from Type V pools only.

	H. pluvialis present	H. pluvialis absent	Total
Brännskär .... * Väst Rovholmen .... Långskär	4	13	17
Spikarna .... ** Storsundsharun .... Segelskär	17	8	25
Total	21	21	42

Table 19. Presence of *Hemidinium ochraceum.*

Distribution of records according to position of island.
Data from Type V pools only.

	H. ochraceum present	H. ochraceum absent	Total
Brännskär .... Väst Rovholmen .... Långskär	8	9	17
Spikarna .... Storsundsharun .... Segelskär	0	25	25
Total	8	34	42

The *Haematococcus,* motile, seldom reached a concentration enough to colour the water; more often it was only moderately abundant. In spite of this, *H. pluvialis* was very often dominant in the pools where it occurred. The possibility of the operation of a self-inhibiting factor in this case is being investigated.

To sum up, the distribution and occurrence of *Haematococcus pluvialis* is thought to be due to 1) its tolerance of small quantities of salt which allows it to colonise the large number of pools within reach of occasional sea splash; 2) its inability to survive in more permanent and peaty pools, and 3) its ability to survive frequent drying out.

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* Islands in the Tree Zone, corresponding in position to the »Äusseren Schären» of Häyren. Gulls do not nest.

** Islands in Häyren's »Meereszone», without threes. These are nesting islands.

Hemidinium ochraceum Levander. (Figs 12—13).

Little more is known about this species than what is contained in the original description (LEVANDER, 1900), and yet locally it is very abundant and very distinctive. The most outstanding feature of it is the copious formation of cysts which give the rocks in the pools where it grows a yellow-rust colour. Possibly multiplication takes place in the encysted state, the swarmers having a comparatively short existence. The author has never found swarmers in great numbers. Repeated attempts to culture the organism have failed, although encysted material can be kept alive dry for months and will release swarmers on wetting.

LEVANDER's description gives no detail of the chromatophore. This is stellate with the ends of the arms frequently flattened against the cell wall (Text figs. 12 and 13).
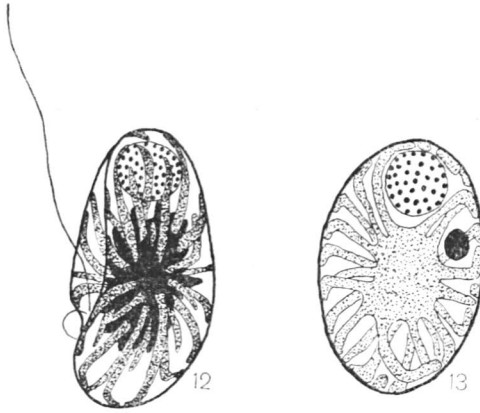
Hemidinium ochraceum.
× 1200. Semi-diagrammatic. Orange pigmented oil black in the figures.
Fig. 12, side view. *Fig. 13*, optical section of another individual.

The typical habitat is the Ephemeral Rain Pool (Type V) but there is some overlap into the Pool Types with vegetation. Out of the 11 records, 7 were from Type V pools, 2 from Type VII, 1 from Type VI and 1 from Type III. All but one of the records came from the islands of Brännskär and Väst Rovholmen.

The distribution of *Haematococcus pluvialis* in relation to that of *Hemidinium ochraceum* has been discussed under the former species. The explanations suggested there apply equally well to *Hemidinium* if they are reversed. Moreover, on the one hand the distribution according to Pool Type of *Hemidinium* does suggest that it is not so sensitive to the presence of humic substances as is *Haematococcus;* on the other, the expectation that it might be more sensitive to small quantities of NaCl is obtained from the Salinity Distribution

(Table 10). Extreme caution, though, has to be used in drawing conclusions from so few records.

Massartia spp.

The *Massartia* spp. referred to in this paper constitute a range of stigma bearing colourless forms, the smaller of which resembled *M. vorticella* (Stein) Schiller and the larger *M. stigmatica* Lind. However, the many intermediate forms made identifications very uncertain. Salinity was of no help either; both the extremes, the *M. vorticella* and *M. stigmatica* forms were found in salinities ranging from 0.1 to 25 $^o/_{oo}$ NaCl and were evenly distributed throughout the Pool Types with the exception of Type VII. None ever was found in great quantity, but they were abundant in some of the samples. They can survive drying out.

Monochrysis lutheri nov. spec. [1])   (Figs 14—16).

Cells scarcely metabolic, flattened, more or less triangular or square, often curved, 6—10 μ in diameter and 2 —3 μ thick. Flagellum $\times 1$ to $\times 1^1/_2$ body diameter in length, inserted in the middle of the concave side (i.e. ventral depression), curved when at rest. Chromatophores olive-yellow, simple, two or three. Stigma large, pale, oblong, associated with one of the chromatophores on the concave side. Protoplasm clear with two or three very conspicuous refractive reserve bodies.

A small Chrysophycean clearly referable to *Monochrysis* Skuja (1948), this form combined some of the characters of *M. vesiculifera* Skuja and *M. major* Skuja. It differs from the former in being much more flattened, and from the latter in being smaller. *M. aphanaster* Skuja has a stellate, not simple chromatophore.
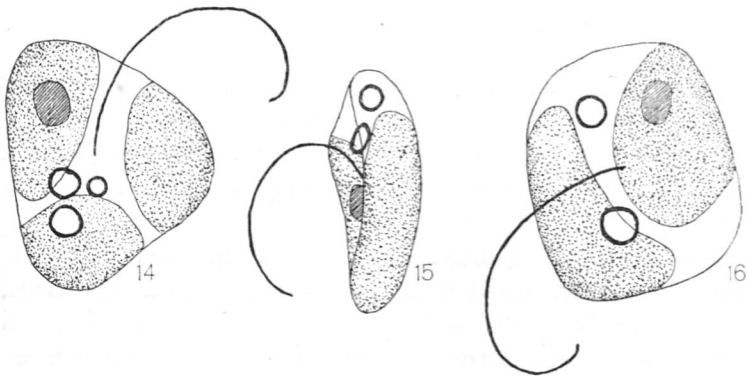
Monochrysis lutheri. $\times$ 3800.

Eight records of *M. lutheri* were obtained at Tvärminne, and three from Gåsstens Viten in the Öregrund archipelago, Sweden. Of the eight Tvärminne records, four were from Type III pools. The limits of the salinity range in which it was found are great (Table 10), but salt pools were favoured. In five of the records it was abundant and was extremely dense, colouring the water brown in two of them. These two were small pools 3 cm. deep and on the verge of drying up, with salinities of 9 and 33 $^o/_{oo}$ respectively.

Nephromonas hyalina nov. gen., nov. spec. (figs 17—24)

Body bean-shaped, asymmetric with ventral depression, non-metabolic, 10—13 μ long, 3—6 μ broad. Pellicle thin. Flagella two, one long and trailing, the other shorter and directed forwards; both inserted ventrally towards the middle of the body. Nutrition phagotrophic. Encystment takes place.
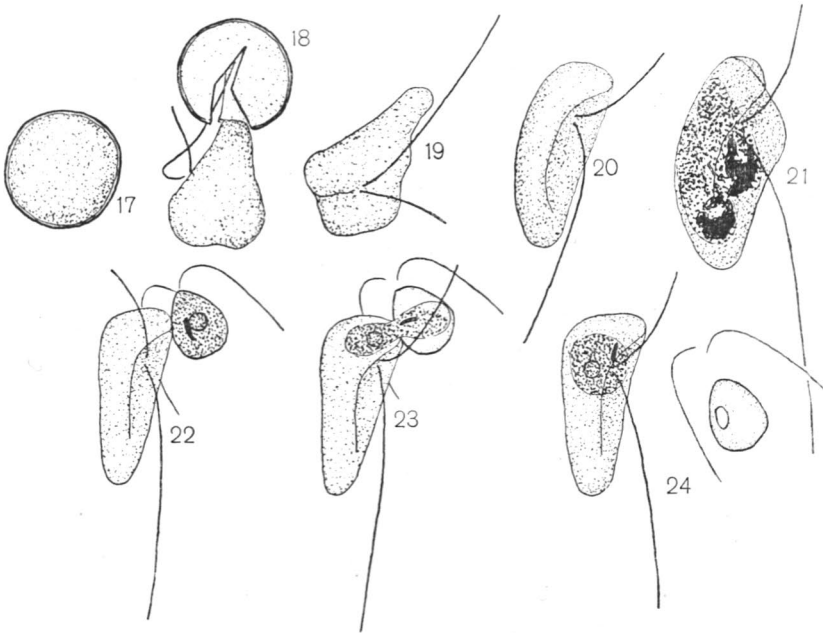
Nephromonas hyalina. × 2000.
Figs. 17—20. Emerging from a cyst.
Fig. 21 Cell after ingesting two gametes of *Haematococcus pluvialis.*
Figs. 22—24. Ingestion of *Brachiomonas submarina.*

Movement is active with a characteristic busy wriggling motion when in contact with the substratum, and when free with a motion turning on the trailing flagellum. This flagellate has been seen most frequently on soaking dry material from Tvärminne, and was rare in wet samples. Emergence

from cysts has been observed on several occasions (Text figs. 17—20). A single individual with flagella already formed emerges from each cyst. It is at first amoeboid, but characteristic shape and motility are attained within two minutes. No cytostome could be seen, and yet organisms nearly as big as the *Nephromonas* can be ingested. The method of attack was observed with *Brachiomonas* as prey (Text figs. 22—24). The prey becomes attached to the anterior end of the flagellate, and a hole is dissolved in the cell wall at the point of attachment. The contents are then sucked slowly, though visibly, through into the body of the flagellate, until only the empty cell wall is left. All the time that the *Nephromonas* is in contact with the prey it moves little, but as soon as contact is severed it resumes its quick motion.

Judging from the 11 records, the habitat appears to be Ephemeral Rain Pools (Type V) or Brackish Pools (Type III) of salinity not higher than $2.5\,^0/_{00}$.

The systematic position of *Nephromonas* is probably near *Bodo*, from which it has been separated on account of the lateral insertion of the flagella, but the method of ingesting food is reminiscent of *Peranema* (CHEN, 1950).

Oxyrrhis marina Dujardin.

This flagellate is widespread in brackish pools of the Baltic, of Britain and other parts of Europe and the U.S.A. It has also been recorded from inshore waters of the English Channel.

At Tvärminne it was found to be the dominant organism in pools of the highest salinity (Table 10) and was confined to Type III pools. Culture experiments have shown that its fastest growth rate occurs at about $16\,^0/_{00}$ NaCl, and that no growth takes place below $4\,^0/_{00}$. This agrees well with the field data. It is phagotrophic and does not need a high concentration of dissolved organic nutrients, except insofar as these may support its food organisms. It has been shown to be able to feed on a variety of organisms, from *Saccharomyces* to *Brachiomonas*, including Diatoms. For example, one single individual of *Oxyrrhis* placed in a thriving culture of *Brachiomonas* at $8\,^0/_{00}$ NaCl was able eventually to gain ascendency. This finding is supported by field observations (see p. 24) and is elegantly explained by the comparison of the maximum rates of growth of the two organisms. *Oxyrrhis* under favourable conditions is able to double its number twice in 24 hours, while *Brachiomonas* under optimum conditions, takes twice as long as this and very much longer in the range of salinity most suitable for *Oxyrrhis*.

Pools with large quantities of *Oxyrrhis* appear to have a pinkish cloud on the bottom. It was at first thought that this colour was due to a food organism, a purple bacterium often present; but cultures of *Oxyrrhis* feeding on *Brachiomonas* also show the purple colour. It appears that it is due to a

pigment in the flagellate, contained in small plate-like reserve bodies. Similar pigments are often found in Peridinieae, particularly among the marine phagotrophic ones.

Pedinomonas upsilon nov. spec.[1]) (Figs 25—28).

Cells oval to subrectangular, flattened, 7—10 μ long, 3—4 μ broad, and 2—3 μ deep. Chromatophore green, U-shaped in the plane of flattening, with the arms of the U directed forwards. Pyrenoids two, one in each arm of the chromatophore, sometimes rather lenticular. Flagellum inserted anterior-laterally, orientated in the plane of flattening, $\times$ $^1/_2$ to $\times$ 1 as long as the cell. Stigma red, posterior and lateral on opposite side to that of flagellum insertion. Nucleus posterior. Contractile vacuole single, anterior, simple.
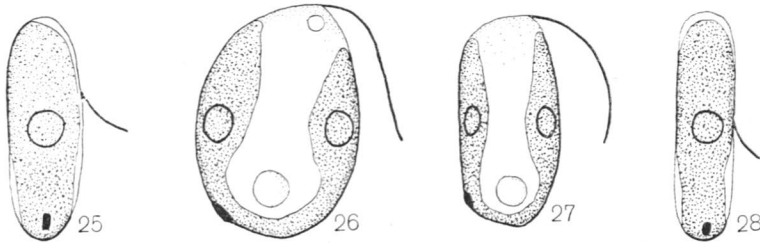
Pedinomonas upsilon. $\times$ 3800.

P. upsilon differs from other members of the genus in the shape of the cell, form of the chromatophore and number of pyrenoids. It bears a distinct resemblance to *Monomastix opisthostigma* Scherffel in general cell shape and placing of the pyrenoids and stigma, but it is about half the size, with simple contractile vacuole and without trichocysts, and the insertion of the flagellum is more tangential. SCHERFFEL placed *Monomastix* in the Polyblepharidaceae, but SKUJA (1948) transferred it to the Pyrrophyta.

The author has no hesitation in placing *P. upsilon* in the Volvocales and has thought it best to include it in *Pedinomonas*, even though this strictly necessitates a slight revision of KORSCHIKOFF's description (see PASCHER, 1927) of the genus to include species with two pyrenoids.

There were three records of *P. upsilon* at Tvärminne in 1951, two from Type VIa pools on Ostspiken and one from a Type III pool on Brännskär. In each case it was extremely abundant, giving the water a dull green colour.

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[1]) The Greek letter used to designate the specific name refers to the shape of the chromatophore.

Stephanosphaera pluvialis Cohn.

Stephanosphaera pluvialis is the colonial member of the Sphaerellaceae; it resembles *Haematococcus droebakensis* rather than *H. pluvialis*, both in structure and in life history. The sexual phase is of commoner occurrence than in *H. pluvialis*, and the zygotes which later resemble haematocysts, are the common resting stage. Since it is monoecious (HIERONYMUS, 1884; SCHULZE, 1927) it is difficult to decide whether any resting stages seen are of sexual or asexual origin, but the writer has seen no evidence to the effect that resting stages are of other than sexual origin, though such are reported in the literaure (HIERONYMUS, 1884; PASCHER, 1927). Nevertheless, whatever the part encystment plays, the period of motility is of longer duration than in *H. pluvialis* and in the normal course of events in culture is brought to an end by gamete formation. Also, cessation of a culture's motility is never complete as it is in *H. pluvialis*.

In spite of this difference in emphasis of life history, the niche occupied by the two species is very nearly identical. *Stephanosphaera* also is typical of the Ephemeral Rain Pool (Type V): out of the 16 records, 10 were from Type V pools, 3 from Type VIa and one each from Types III, VIb and VII. Here also correlation with absence of vegetation is suggested.

The range in salinity is not as wide as that of *H. pluvialis* (Table 10), and though the maximum number of records is also between 0.1 and 0.4 $^0/_{00}$ NaCl, *Stephanosphaera* has more below 0.1 $^0/_{00}$. It would seem to be less tolerant of salt.

No records of *Stephanosphaera* were obtained from Brännskär, otherwise its distribution among the islands visited is unremarkable. Though mostly present in small quantities and seldom dominant, occasionally it occurred in quantities considerably greater than the maximum of *Haematococcus*, a fact which is intelligible in the light of the difference in emphasis of the two life cycles.

Pools with much *Stephanosphaera* have an even green colour, denser neither towards the top nor bottom.

Discussion.

To the phycologist unfamiliar with the Baltic the Ephemeral Rain Pool is a new experience, and indeed comes to typify for him this land of islands. Not that temporary pools are to be found nowhere else, rather, seldom elsewhere are they associated with a catchment area free from soil and vegetation. Similarly, seldom is the *Haematococcus-Stephanosphaera* association encountered. LUND (1950) notes the occurrence of these in limestone pools in

the Pennines in England and their rarity in the non-calcarious Lakeland habitats. He tentatively suggests that this may be due (in the case of *Stephanosphaera*) to its being a calcicolous species, a hypothesis which is untenable in view of its ubiquitous occurrence in rain pools on the igneous rocks of the Baltic. The point is that in Britain hollows in naked rock are uncommon owing to the fact that agencies preventing the accumulation of soil and vegetation are lacking. But on the limestone, particularly in the dry beds of streams, 'potholes' are a common feature, and these do not receive drainage from soil. Elsewhere in Britain *H. pluvialis* is most often found in artificial places like 'bird baths', gutters, etc., which also satisfy these conditions. In contrast, on the Baltic islands whose rock surface with its bold glacial contours is kept free from the accumulation of top soil by annual scouring, very many pools receive no drainage off soil. It would be interesting to know how these pools compare with the classical and other habitats of *Stephanosphaera* in the mountains of central Europe (see PASCHER, 1927, p. 135).

Pools of Types III and VIb have their counterparts in Britain. On rocky coasts brackish pools abound, while brackish swamps and drainage ditches and other waters, are common enough behind the sea walls of lowland areas. Also the species are comparable, and in some cases, e.g. *Oxyrrhis marina*, *Brachiomonas submarina* and *Gyrodinium fissum*, they are the same. Many inland waters in Britain have floras similar to those of Pool Types VIb and VII, and on rocky coasts pools above the splash zone generally have deeply coloured water.

Consider the three cardinal flagellate communities: 1) *Haematococcus—Stephanosphaera*, 2) *Brachiomonas—Oxyrrhis* and 3) *Peridinium—Gonium*, corresponding to BOHLIN's 1) Rainwater Formation (i.e. Rain Pools, including LEVANDER's Types V and VIa), 2) Submarine Formation (i.e. Brackish Pools, including Types I, II and III), and 3) Peatmoor Formation (i.e. Peat Pools, including Types VIb and VII). The first lacks both high concentrations of humus and of sea water; the second lacks high concentrations of humus; and the third high concentrations of sea water.

Humus, pH and sodium chloride are so interdependent that in a circumscribed range of habitats such as is found at Tvärminne, it is often difficult to decide which of these factors is the primary one. Even in culture work where more control can be exercised on the environment, very great care has to be taken in the design of experiments in order to avoid confusion of secondary with primary causes.

In the case of hydrogen ion concentration, for example, there are reports of peaty pools with a very low pH (KUENEN, 1938), but at the same time there exist examples of pools with coloured water and a *Peridinium volzii—Gonium pectorale* flora having a high pH. It is doubtful whether in the present

instance the main effect of high humus concentration is to lower the pH. The capacity of humus complexes to bind metallic ions, some of which may be necessary and in short supply, may be more important. And yet *Haematococcus pluvialis*, which is not found in peaty water, also will not survive in culture if the pH is lowered below 6.5.

Where the term 'humus' has been used, the broadest meaning has been attached to it, i.e. dark coloured organic complexes present in the soil. Emphasis has been placed on the presence or absence of soil in the catchment area of the pool, as this criterion was found to be the most useful. Where much soil and vegetation were present, the fact was reflected in the colour of the water. It appears that in this soil humus accumulates faster than it is disposed of; in fact, peat forming conditions prevail and little in the way of nutrients can be expected to be set free in the soil.

When debris from a dried-up pool is soaked in fresh water a coloured solution is often obtained. This can be decolourised without altering the pH by the addition of sea water. Moreover, water of brackish pools is never coloured, even when soil and vegetation are adjacent. Thus precipitation of humus by sea water is a fact observable both in the laboratory and in the field. But the mechanism of precipitation is not clear. One would expect the addition of the electrolyte to the 'humic acid' to cause free mineral acid to be formed by base exchange and the 'humate' to be precipitated:

$$\text{H-humate} + NaCl = \text{Na-humate} + HCl$$

but the general experience is that the salt containing pools are alkaline in reaction, and this should lead to the re-solution of the 'humate'. A physical hypothesis is really more acceptable. Humus is only partly soluble in acid and neutral water, being present mostly as colloidal solutions. These can be flocculated by the addition of electrolytes (see Waksman, 1936, p. 311).

Removal of humus would then make it possible for conditions to be created in which microbial regeneration of nutrients can take place. If the argument is correct, then both Brackish and Rain Pools have the possibility of becoming rich in available nutrients, which is not the case in the Peat Pools. Whatever the origin of organic nutrients, their accessability depends in large part on the physical conditions prevailing.

One or more of the obvious secondary effects of sea water, the removal of humus and release of organic nutrients, probably accounts for the extremely low salt tolerance of the large class of Peat Pool organisms, e.g. *Perdinium volzii* and *Cosmarium subpalangula*. Similarly, the converse may be said to apply in the case of Rain Pool species, which may even benefit from the protection afforded by the salts which they tolerate in small amounts.

Haematococcus pluvialis can stand 5 $^0/_{00}$ NaCl and *Chlorogonium elongatum* double this amount. JACOBSEN (1912) obtained good growth of a strain of the former in 1 $^0/_{00}$ glucose, which indicates that in this class of organism also osmotic effects do not necessarily account for the toxicity of sodium chloride.

Osmotic effects may be of importance for salt organisms, however, and may act in one of two ways. First, a habitat such as the Brackish Pool, which changes its salinity often and comparatively rapidly, will be populated only by euryhaline species, both capable of existing in a wide range of osmotic pressures and of weathering the rapid changes. Such are *Brachiomonas* and *Oxyrrhis*, and others met in Brackish Pools. Second, a certain maximum or minimum osmotic pressure may be necessary for metabolism. *Oxyrrhis* is not found below 4 $^0/_{00}$ NaCl and cannot be grown in culture below this.

Besides the osmotic effects of the salts there are very important surface phenomena depending on correct balance of cations. How far salt flagellates are affected by these is not known. In the author's experiments *Brachiomonas* showed extreme insensitivity, but BAAS BECKING (1931) using impure material demonstrated antagonisms in *Dunaliella viridis*.

A different mechanism needs to be postulated for organisms like *Brachiomonas* which can thrive in 1.5 molar NaCl or in fresh water provided a trace of sodium is present. There may be a specific sodium requirement here.

In many euryhaline flagellates of wide range a definite region can be demonstrated in which the growth rate is greatest. Efficiency in the face of competition may therefore be expected to depend to some extent on salinity, but this has only been shown in the case of *Brachiomonas* and *Oxyrrhis*.

The term 'euryhaline' has been used in preference to 'brackish' in referring to organisms of the Type III pools. In the first place they *are* euryhaline, and they may or may not be living in brackish water. A certain amount of confusion relates to the latter term. The generally accepted meaning of 'brackish' is »having a salt content between that of fresh and oceanic water». A Baltic pelagic *Dinophysis*, for instance, is a brackish water species and is probably stenohaline, while *Oxyrrhis marina*, certainly euryhaline, existing, say, at 64 $^0/_{00}$ NaCl, could hardly be correctly labelled 'brackish water', though at other times it may be found in brackish water. Neither is *Oxyrrhis* 'marine' despite its specific name. Indeed, the designation 'marine' has often been applied to species which, though occasionally neritic, attain their greatest development in supra-littoral rock pools. Such is also probably *Nitzschia closterium* forma *minutissima* Nelson (*Phaeodactylum tricornutum* Bohlin), about which much has been written. In the classification of salt organisms the primary distinction should be between steno- and euryhaline species.

Many questions dealing with life history in relation to drying-up of the pools, dispersal, and competition remain to be investigated. At present

data are too few for adequate discussion of the dynamic problem. The role played by chance in the dispersal of organisms in small waters has been reviewed by Talling (1951), but the ponds discussed are larger and more permanent than are the majority of the Tvärminne pools. Nevertheless, the problems are likely to be analogous. The Tvärminne pools offer a unique opportunity for the study of the question, since they are very many, sufficiently uniform and small. The problem might be stated: »Is the variety in content due to selection by the particular environment from a common fund of resting stages (contained in the debris of all pools and carried around by wind and birds), or is the population of a pool dependent entirely on chance?»

Evidence from dried samples suggests that the former applies only in the case of the most common species such as *Haematococcus pluvialis*. The role of chance is more likely to be important in those habitats which are subject to the periodic cleaning out which the shallower pools get through the agency of ice, rain, sea splash, or sun and wind. In such pools after re-flooding new arrivals will at first have little or no competition. Wind-borne species, such as *H. pluvialis*, *Stephanosphaera pluvialis* and *Brachiomonas. submarina*, will of course be favoured. Much must depend on the completeness of the scouring. In pools which are less subject to complete clearance, competition might be expected in the long run to have a greater stabilising influence, and successions to have a better chance of repeating themselves in successive years. Wind-borne species will not necessarily be favoured.

Many other matters relating to the biology of particular species need answering. The effect of rainfall, for instance, on the swarming of *Haematococcus pluvialis* is as yet a matter of assumption based on very little observation. That a dry pool well stocked with haematocysts will give rise to a swarm of *H. pluvialis* on flooding there is no doubt. But does multiplication of the swarmers then take place if conditions remain favourable? There is no evidence that it does, while the fact that swarmers contain haematochrome in nature suggests that multiplication is limited in extent, for whenever multiplication has, in fact, been demonstrated in culture haematochrome has also disappeared. It is therefore necessary to postulate either multiplication in the palmelloid state or a gradual building up of a reserve of haematocysts by means of a fewfold multiplication at each swarming period. Of course, once the reserve has been built up there will always be available swarmers enough to populate the pool within a few hours as soon as conditions permit.

H. pluvialis typifies the case where a short swarming period is followed by facile asexual aestivation. *Hemidinium ochraceum* and *Chlamydomonas pulsatilla* follow the same pattern, the former with an even shorter swarming period and the latter with a much longer one. More general, however, is the case where the resting stage is the zygote. *Stephanosphaera pluvialis, Haemato-*

coccus droebakensis and *Brachiomonas submarina* are examples. With these algae, judging both by the extent to which they occur in dried samples and by performance in culture, the available resting stages are not as plentiful as those of asexually encysting species. In yet a third group no resting stages are found. These species never appear on soaking dried material. Dinoflagellates, other than *H. ochraceum* and the colourless *Massartia*, particularly the euryhaline ones, do not survive this way. It can only be suggested that a reserve of these remains in the inshore waters of the sea and that their reintroduction to the pools takes place during storms.

The effect of increasing salinity has been discussed as far as it concerns *Brachiomonas* and *Oxyrrhis*, but how other species react is an open question. Can fresh water organisms avoid the harmful effects of increasing salinity by encysting? *H. pluvialis* in culture seems to be able to do so.

A statement of the static ecological structure, as it was presented to an observer on a particular occasion, however detailed it may be, can never be more than a beginning. Some of the problems which arise from an attempt to explain the structure have been discussed. For their solution there would be needed both long term field studies, especially those related to seasonal and weather conditions, and detailed dynamic studies of comparatively limited scope which might be confined to frequent observation of a small range of pools over a longer or shorter period with interest centred on two or three ecologically related species. Many of the more important species are easily maintained in culture. PRINGSHEIM (1946, p. 13 et seq.) stressed the importance of taking into consideration natural conditions for successful culture work. In a sense the ecology of a species can help in the better understanding of aspects of its physiology. Conversely, many problems in ecology can only be solved with the help of culture studies, provided, of course, they are undertaken in conjunction with field work.

Summary.

1. Records were taken of 147 pools from six islands in the Tvärminne archipelago off the south coast of Finland. They included details of position, dimensions, salinity, macro- and micro-vegetation. Interest was centred on the ecological distribution of the common phytoflagellates.

2. LEVANDER's pool classification was used as a basis of the study, but the less complex system of BOHLIN was found to be more appropriate: 1) Brackish Pools, 2) Rain Pools, 3) Peat Pools.

3. Most important of the factors differentiating between the three were a) Degree of salinity; b) Colour of water indicating humus content and depending on the presence or absence of soil and vegetation in the catchment area.

Thus Brackish and Rain Pools lack the humus effects of soil and vegetation and differ from each other only in degree of salinity; while the Peat Pools are comparatively rich in humus, having more or less coloured water and extremely low salinity.

4. The pH of soil from dry pools was low; but water of most rain and brackish pools and some peat pools gave high readings. Conditions become extreme as ephemeral pools dry out. Temperature variation was found to be greatest in shallower pools. The highest salinity recorded was 66 $^{0}/_{00}$.

5. Greatest concentrations of flagellates occurred more often in pools between 2.5 and 10 cm. than in pools either deeper or shallower than this. With respect to species, brackish pools showed greatest consistency; Greatest variety was found in the larger fresh water pools.

6. Common flagellates in the Peat Pools were *Peridinium volzii* and *Gonium pectorale*, which were often associated with Euglenineae and Conjugatae. *Haematococcus pluvialis* and *Stephanosphaera pluvialis* were the most common Rain Pool species, for which the absence of soil and vegetation near the pools was found to be an essential requirement. Most frequent in Brackish Pools were *Brachiomonas submarina* and *Oxyrrhis marina*, which are euryhaline and are not confined to waters of intermediate salinity.

7. In marked contrast to the majority of Peat and Brackish Pool species, most succesful Rain Pool species were found to withstand drying up of the habitat. The resting cell was aplanospore, zygote or cyst, depending on the species.

8. Strains of *Haematococcus pluvialis* from the shores of the Baltic, though identical morphologically, differed physiologically from strains originating elsewhere. On morphological and genetical grounds *Brachiomonas gracilis* Bohlin and *B. westiana* Pascher were included in *B. submarina* Revised. The following species were newly described: *Monochrysis lutheri* (Chrysomonadineae), *Nephromonas hyalina* (Protomastigineae) and *Pedinomonas upsilon* (Polyblepharidaceae).

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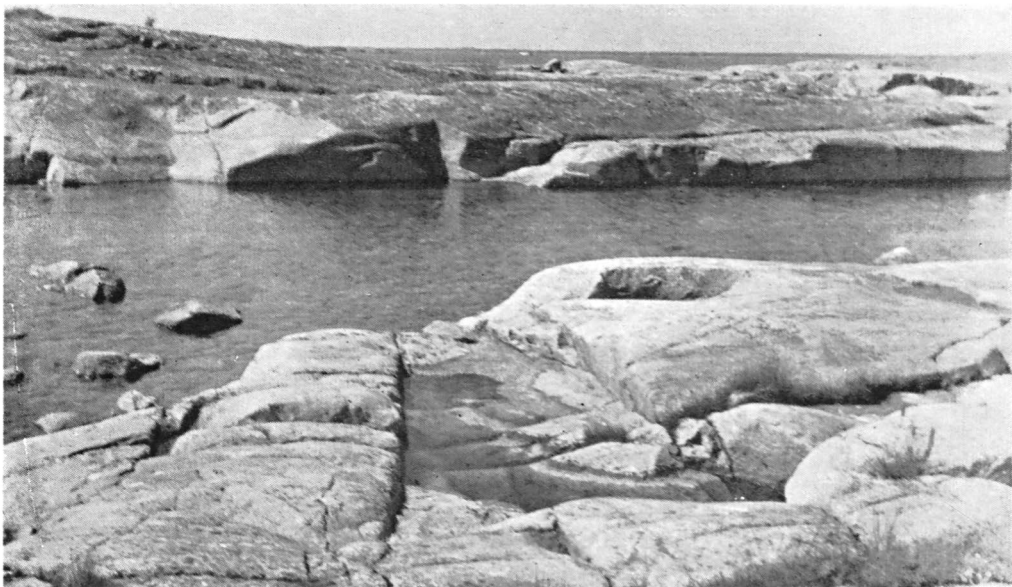## Acknowledgements.
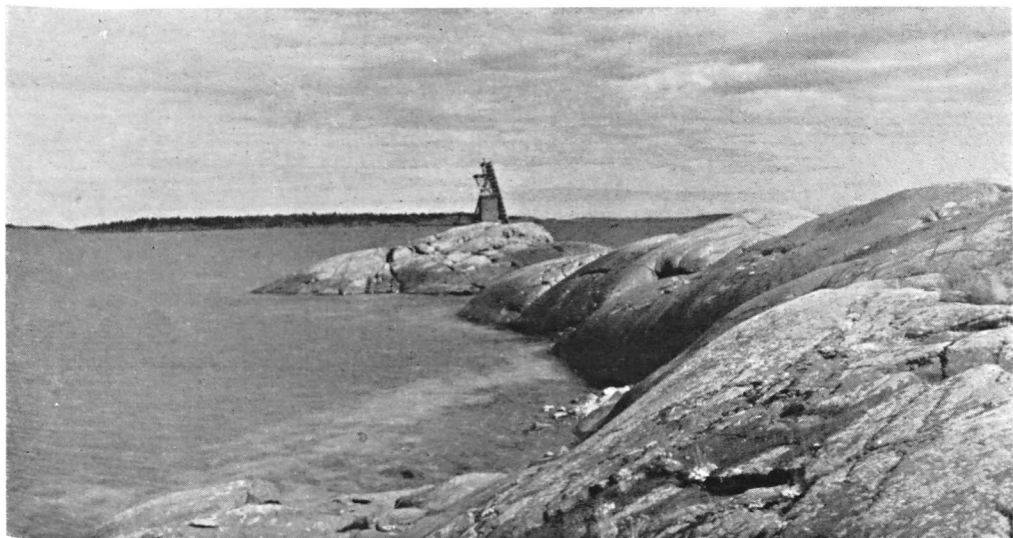
PLATE I—II.

Storsundsharun, looking East.

Långskär, Pool 317.
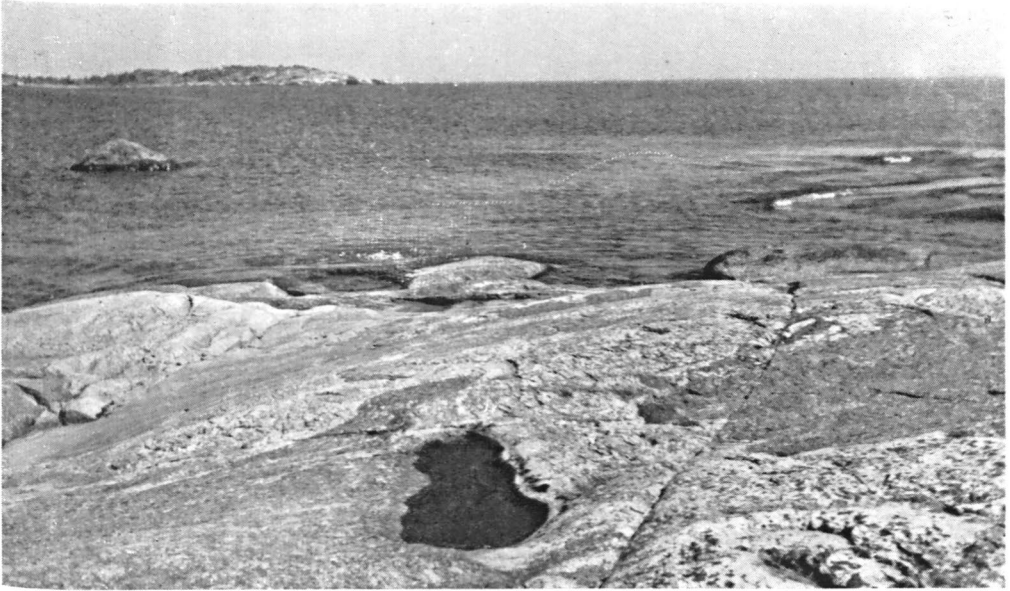A Type III pool; three Type I pools can be seen behind, at the waters's edge.

PLATE III—IV.

Ostspiken. Pool 48. A Type III pool.

Ostspiken. A small dry depression containing debris. (Classified as Type V).

PLATE V—VI.

Ostspiken. A small Type V pool. The dark colour is due to haematocysts.
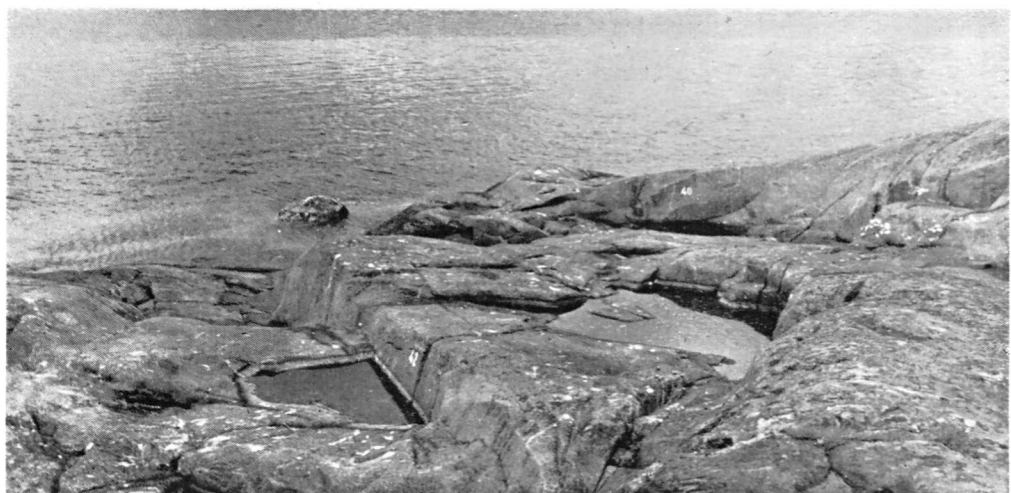

Ostspiken, Pool 53. A Type V pool. The dark rim is due to the lichen *Verrucaria maura*.

PLATE VII—VIII.

Segelskär, Type VIa pools.

Storsundsharun; three pools intermediate between Types III, V and VIa.

Storsundsharun, 'gull pools'. The dark colour in the lower of the three is due to a dense growth of *Chlamydomonas pulsatilla*. Notice the gull excrement.

PLATE XI—XII.

Långskär, Pool 193. A Type VIb pool.

Brännskär, a small pool of Type VII.