COMMONWEALTH OF AUSTRALIA
DEPARTMENT OF SUPPLY

AUSTRALIAN NATIONAL ANTARCTIC RESEARCH EXPEDITIONS

ANARE SCIENTIFIC REPORTS

SERIES B (II) ZOOLOGY

PUBLICATION No. 110

SOME ASPECTS OF THE ECOLOGY OF A CALANOID COPEPOD, *PSEUDOBOECKELLA BREVICAUDATA* BRADY 1875, ON A SUBANTARCTIC ISLAND

by

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ISSUED BY THE ANTARCTIC DIVISION
DEPARTMENT OF SUPPLY, MELBOURNE
1970

Registered at the G.P.O. Melbourne
for transmission by post as a book

Printed in Australia by
Brown Prior Anderson Pty Ltd 5 Evans Street Burwood Victoria

CONTENTS

page

ABSTRACT 1

0. INTRODUCTION 3

0.1 GEOGRAPHY AND CLIMATE OF MACQUARIE ISLAND 3

1. METHODS 7

1.1 FIELD METHODS 7

1.1.1. Morphometry 7
1.1.2. Hydrology samples 7
1.1.3. Physical determinations 7
1.1.4. Plankton samples 7

1.2. LABORATORY METHODS 8

1.2.1. Chemical determinations 8
1.2.2. Plankton counts 11
1.2.3. Egg desiccation 11
1.2.4. Hatching 12
1.2.5. Effect of food on size and growth rate 13

2. RESULTS 14

2.1 CHARACTERISTICS OF THE ENVIRONMENT 14

2.1.1. General description and morphometry 14
2.1.1.1. Prion Lake 14
2.1.1.2. "23U" Pond 17
2.1.1.3. "S" Pond 18
2.1.1.4. Duck Lagoon and "F_5" Pond 22
2.1.1.5. Kerguelen Islands 23
2.1.2. Physical characteristics 23
2.1.2.1. Colour and transparency 23
2.1.2.2. Temperature 25
2.1.3. Chemical characteristics 27
2.1.3.1. Major ions, total (dissolved) solids and conductivity 27
2.1.3.2. Hydrogen ion concentration 33
2.1.3.3. Phosphate (soluble) 34

page
2.1.3.4. Ammoniacal nitrogen, nitrite and nitrate 34
2.1.3.5. Organic nitrogen and oxygen absorbed 36
2.1.3.6. Colloidal silica, iron and aluminium oxide and dissolved iron 38
2.1.3.7. Oxygen (dissolved) 41
2.1.3.8. Chlorophyll *a* 41
2.1.3.9. Factors affecting the primary productivity of Macquarie Island inland waters 41

2.2. POST-EMBRYONIC DEVELOPMENTAL STAGES 43

2.2.1. Adult stages 43
2.2.2. Immature stages 48
2.2.2.1. Egg and hatching 48
2.2.2.2. Nauplius stages 49
2.2.2.3. Copepodid stages 51

2.3. SYSTEMATICS AND DISTRIBUTION 53

2.3.1. The genus Pseudoboeckella Mrazek 1901 54
2.3.2. Pseudoboeckella brevicaudata Brady 1875 56
2.3.3. Distribution and dispersal 57

2.4. SEASONAL ACTIVITY AND ABUNDANCE 59

2.4.1. Distribution on Macquarie Island 59
2.4.2. Behaviour and dispersion 60
2.4.3. Seasonal abundance 63
2.4.4. Length variation 67
2.4.5. Egg production, sex ratio, reproductive activity and clutch size 73
2.4.6. Hatching 77
2.4.7. Food and growth 82
2.4.7.1. Food 82
2.4.7.2. Growth 84
2.4.8. Morphology 84

3. DISCUSSION 88

4. ACKNOWLEDGMENTS 93

5. REFERENCES 94

APPENDIX I 98

LIST OF PLATES

Plate No. page

0.1. AERIAL VIEW OF PLATEAU AND COASTAL TERRACE 5

1.1. "K" SAMPLER FOR USE IN SMALL PONDS 10

2.1.1. OBLIQUE AERIAL VIEW OF PRION LAKE 15

2.1.2. "23U" POND, VIEWED FROM SOUTH-WEST 18

2.1.3. "S" POND IN SUMMER 19

2.1.4. "S" POND IN WINTER 19

2.1.5. MARGINAL FILAMENTOUS ALGAL MAT ZONE 21

2.1.6. DUCK LAGOON 21

2.1.7. "F_5" POND 22

2.2.1. HATCHING OF EGG 49

LIST OF FIGURES

Fig. No. page

0.1. MAP OF MACQUARIE ISLAND 4

2.1.1. BATHYMETRIC MAP OF PRION LAKE 16

2.1.2. SCHEMATIC PLAN OF "23U" POND 17

2.1.3. BATHYMETRIC MAP OF "S" POND 20

2.1.4. BATHYMETRIC MAP OF DUCK LAGOON 20

2.1.5. MEAN WATER COLUMN TEMPERATURES 24

2.1.6. RATIO Na TO Cl IN MACQUARIE ISLAND INLAND WATERS 27

2.1.7. EFFECT OF DISTANCE FROM SEA ON TOTAL SOLIDS AND O.O.F. 28

2.1.8. SEASONAL VARIATION OF TRANSPARENCY, WATER LEVEL, PRECIPITATION AND CONDUCTIVITY 31

2.1.9. SEASONAL DISTRIBUTION OF CHLOROPHYLL *a*, PHOSPHATE AND SILICA 39

2.2.1. MORPHOLOGY OF COPEPODID AND ADULT 44

2.2.2. MOUTHPARTS OF ADULT 46

2.2.3. SWIMMING LEGS OF ADULT 47

2.2.4. NAUPLIUS STAGES 50

2.2.5. FIFTH PAIR OF LEGS IN COPEPODID AND ADULT 52

2.3.1. FIFTH LEGS OF ADULT MALES FROM DIFFERENT LOCALITIES 55

2.3.2. DISTRIBUTION OF GENERA *Pseudoboeckella, Parabroetus* AND SUBANTARCTIC *Boeckella* SPP. 58

2.4.1. SCHEMATIC SECTION THROUGH "S" POND 62

2.4.2. SEASONAL ABUNDANCE IN "23U" POND AND PRION LAKE 64

2.4.3. SEASONAL ABUNDANCE IN "F_5" POND, DUCK LAGOON AND "S" POND . . 65

2.4.4. SEASONAL MEAN LENGTH VARIATION 68

2.4.5. FREQUENCY DISTRIBUTIONS OF LENGTH FOR ADULT FEMALES 70

2.4.6. SEASONAL VARIATION IN EGG PRODUCTION 72

2.4.7. FREQUENCY DISTRIBUTION OF NUMBER OF SETAE ON 4TH PAIR SWIMMING LEGS 85

3.1. ANNUAL TEMPERATURE CYCLES FOR STATIONS IN SUBANTARCTIC AND ANTARCTIC ZONES 89

LIST OF TABLES

Table No. page

1.1. WATER COLUMN DENSITIES OF *P. brevicaudata* 9

1.2. TEMPERATURES OF "S" POND AND OPTIMAL CONDITIONS 9

1.2.3. RESISTANCE OF EGGS TO DESICCATION 12

2.1.1. MICRO-GRADIENTS OF TEMPERATURE, "S" POND 23

2.1.2. FREQUENCY OF DAYS WITH MEAN TEMPERATURE $\geq 10°C$ 25

2.1.3. COMPARISON OF IONIC COMPOSITION OF SURFACE WATERS 26

2.1.4. Ca/Cl AND Cl/SO_4 RATIOS FOR MACQUARIE ISLAND INLAND WATERS 29

2.1.5. pH, CONDUCTIVITY AND SOLUBLE PHOSPHATE OF SOME SURFACE WATERS 30

2.1.6. pH, CONDUCTIVITY AND SOLUBLE PHOSPHATE OF COASTAL TERRACE SURFACE WATERS 32

2.1.7. pH OF SOME PLATEAU WATERS 33

2.1.8. AMMONIACAL NITROGEN, NITRATE AND NITRITE OF MACQUARIE ISLAND SURFACE WATERS 35

2.1.9. AMMONIACAL NITROGEN, NITRATE AND NITRITE OF SURFACE WATERS AT MACQUARIE AND KERGUELEN ISLANDS 36

2.1.10. ORGANIC NITROGEN AND OXYGEN ABSORBED OF INLAND WATERS 37

2.1.11. COLLOIDAL SILICA, IRON AND ALUMINIUM OXIDE, AND SOLUBLE IRON OF INLAND WATERS 38

2.1.12. DISSOLVED OXYGEN, PRION LAKE 40

2.2.1. SETAE, SPINES AND AESTHETES ON ANTENNULES OF MALES AND FEMALES 43

2.2.2. SETATION OF SWIMMING LEGS OF ADULT FEMALE 45

2.4.1. VERTICAL DISTRIBUTION OF INSTAR GROUPS 60

2.4.2. RELATIVE DENSITIES *P. brevicaudata* STAGES DAY AND NIGHT 61

2.4.3. DENSITY OF COPEPODIDS AND ADULTS IN DAY SAMPLES 62

2.4.4. DISTRIBUTION IN SURFACE WATERS ON "WINDY" AND "CALM" DAYS 63

2.4.5. CORRELATION OF MEAN METASOME LENGTH WITH TEMPERATURE AND CHLOROPHYLL *a* 71

2.4.6. OVIGEROUS AND SPERMATOPHORE-BEARING FEMALES, AND SEX RATIOS, PRION LAKE 74

Table No. page

2.4.7. OVIGEROUS AND SPERMATOPHORE-BEARING FEMALES, AND SEX RATIOS, "23U" POND AND DUCK LAGOON 75

2.4.8. CORRELATION COEFFICIENTS: SEX RATIO, AND OVIGEROUS AND SPERMATOPHORE-BEARING FEMALES 75

2.4.9. CORRELATION OF CLUTCH SIZE WITH LENGTH 76

2.4.10. CORRELATION OF CLUTCH SIZE, LENGTH AND TEMPERATURE .. 77

2.4.11. EFFECT OF TEMPERATURE ON HATCHING 79

2.4.12. MEAN PERCENTAGE HATCHING AND HATCHING RATES 81

2.4.13 COMPARISON OF EGG SIZES 82

2.4.14. EFFECT OF FOOD LEVELS ON SURVIVAL AND GROWTH RATE 83

2.4.15. EFFECT OF FOOD LEVEL ON LENGTH 83

SOME ASPECTS OF THE ECOLOGY OF A CALANOID COPEPOD, *PSEUDOBOECKELLA BREVICAUDATA* BRADY 1875, ON A SUBANTARCTIC ISLAND

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ABSTRACT

Although Macquarie Island is a relatively small oceanic island, freshwater ponds and lakes abound. The dominant species of the freshwater zooplankton is the calanoid copepod, *Pseudoboeckella brevicaudata* Brady 1875. This species is widely distributed throughout the subantarctic zone.

Three main types of inland water bodies occur on Macquarie Island. The seasonal changes of the main limnological elements and the life cycle activity of *P. brevicaudata* were studied in at least one example of each type of water body. The results of this investigation revealed the presence of differences in the growth rate, morphology, reproductive activity and other life cycle phenomena, between populations of *P. brevicaudata* in different water bodies. An attempt was made to examine the nature and action of those environmental factors which were associated with these differences.

INTRODUCTION

Although the land masses within the antarctic and subantarctic zones have been visited frequently by scientific expeditions, relatively little is known of the ecology of the invertebrate fauna. This is particularly true for the fauna of the freshwater biotope, for which only a single account (Holdgate 1961) has so far been published. Reports on the general limnology of this region are only slightly more common (Armitage and House 1962; Angino *et al.* 1962, 1963, 1964; Goldman *et al.* 1963; Wilson and Wellman 1962).

This report provides an account of the general ecology of the calanoid copepod *Pseudoboeckella brevicaudata* Brady 1875 on Macquarie Island. This species is one of the most widespread and abundant members of the zooplankton communities of the subantarctic freshwater biotope.

A broad study of the limnology of the island was undertaken to characterize the different types of habitats occupied by *P. brevicaudata* and, further, to investigate the influence of environmental factors on the growth and development of this species.

The field observations, upon which this report is based, were made during the period 1961-63, whilst the author was a member of an ANARE scientific party at Macquarie Island.

0.1 GEOGRAPHY AND CLIMATE OF MACQUARIE ISLAND

Macquarie Island, at latitude 54°30′S and longitude 158°57′E, is an oceanic island in the Southern Ocean (Figure 0.1). It arises from a deep submarine ridge which runs northwards to the subantarctic islands of New Zealand. The nearest land, Campbell and Auckland Islands, lies approximately 650 km to the north-east; Tasmania is 1300 km north-west, and the Antarctic Continent is 1450 km south.

The island is a narrow strip of land 34 km long by up to 5 km wide, with its major axis running approximately 10° east of north. From a narrow coastal terrace, cliffs rise steeply to the level of the plateau, which ranges in elevation from 180 m to 300 m, with the highest point 430 m (Figure 0.1, Plate 0.1).

The island is thought to have appeared during the early part of the Tertiary epoch, then subsided, reappearing in the Miocene after a period of considerable volcanic activity (Mawson 1943). This supposedly resulted in a land mass of much greater area than the present. Both marine erosion and glaciation have contributed to the reduction of the island to its present size, and a recent rise in the land has brought about the exposure of a coastal terrace along the west coast. Although the plateau shows much evidence of past glacial action, in the large expanses of glacial till, glacial valleys, terminal moraines, and scattered erratic boulders, the extent of the ice sheet during the Pleistocene is unknown. However,

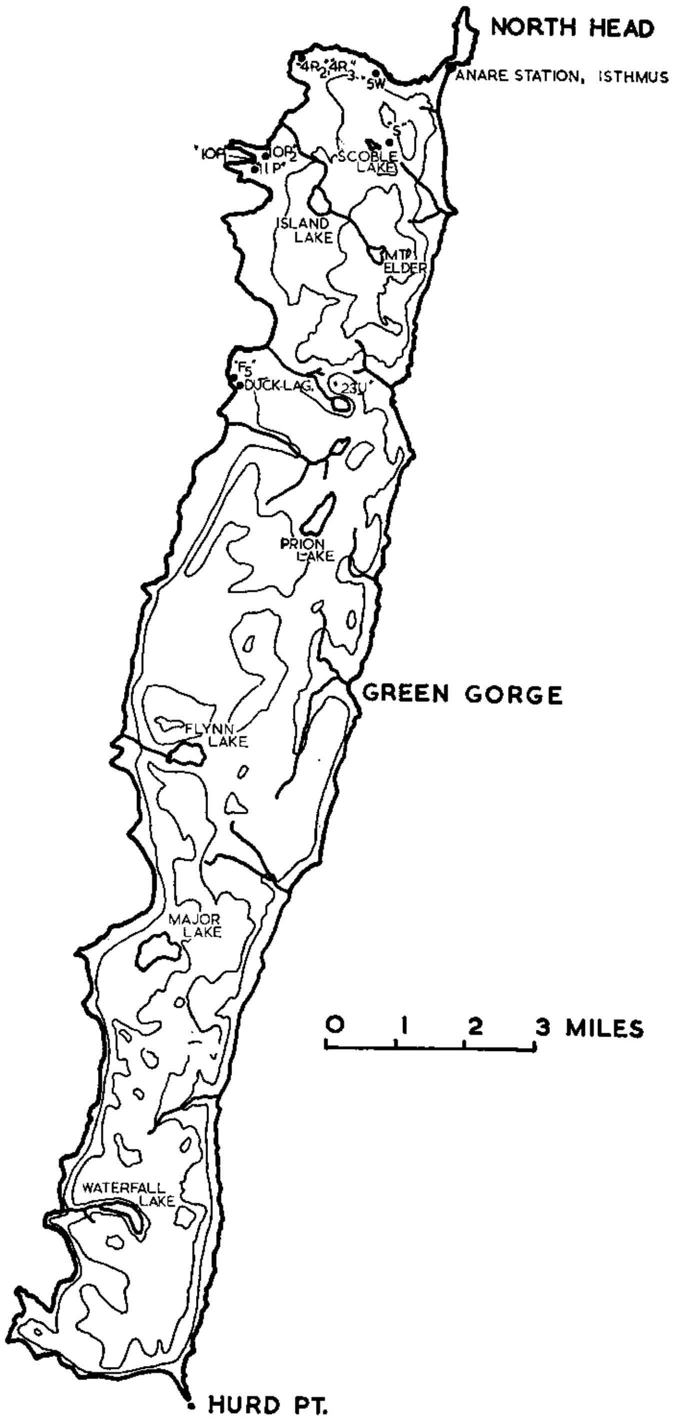


Figure 0.1. Map of Macquarie Island, showing positions of the larger lakes. Smaller water bodies referred to in this report are indicated by closed circles. Contour intervals are 400 ft.

it is unlikely that the present fauna or flora has survived from the Pleistocene ice-ages (Taylor 1955, Bunt 1956). Pollens found in the lignite beds on the island indicate the presence of a preglacial flora quite distinct from the present one (Bunt 1956).

The rocks of the island are all basic and igneous, consisting of gabbros, ultrabasics, pegmatites, dolerites, and basalts (Mawson 1943). Taylor (1955) has classified the soils into highmoor peats, fen peats, bog peats and tundra soils.

Most of the island is covered with vegetation, except for the higher, exposed areas of the plateau, where the severity of the climate has limited the further spread of the present flora. Thirty-eight species of vascular plants (3 of these recently introduced) occur in five principal formations; wet tussock grasslands, herbfield, fen, bog, and feldmark (Taylor 1955). Peat-forming mosses are common, and substantial deposits of peat are found on the plateau and coastal terrace.

ANARE photo Air photo

PLATE 0.1. Aerial view of part of the plateau and coastal terrace. The largest water body shown is Island Lake. + indicates the position of "S" Pond)

The subantarctic or cold temperate zone (in which Macquarie Island is situated) lies between the Antarctic and Subtropical Convergences, and includes the Magellanian province of South America, Falkland Islands, Gough Island, Tristan da Cunha, Crozet Islands, Marion and Prince Edward Islands, St Paul and New Amsterdam Islands, Kerguelen Islands, Auckland and Campbell Islands (Figure 2.3.2). The climate of Macquarie Island is characteristic of this zone, having high humidities, high wind velocities and a very small temperature range (both daily and annual). Rain, hail, snow and drizzle are frequent, giving an annual precipitation of 1440 mm (40·5 in.) spread over about 330 days of the year (Law and Burstall 1956). Fogs and mists are common throughout the year. The mean duration of hours of sunshine per day is 1·8 hr. Consistent high winds from the west and north-west blow with a mean annual velocity of 31 kmph (19·2 mph). The mean annual temperature is 4·5°C, with a mean annual range of 3·0°C to 6·3°C, and an extreme range of —8·3°C to 11·4°C. These values, and the mean daily temperature range of 3·2°C, indicate the marked maritime nature of the climate.

1. METHODS

1.1. FIELD METHODS

1.1.1. *Morphometry*

The method of shoreline traverses, sometimes in association with aerial photography, was used to map lake outlines. Depth contours were obtained using a sounding line. However, at Prion Lake a "Transcentury" model T100 echo-sounder was used for depth measurement.

1.1.2. *Hydrology samples*

Prion Lake samples were collected at 5 m intervals from surface to bottom using a Nansen bottle. Where larger samples were required (i.e., for chlorophyll determinations) a Van Dorn bottle was used. Anchored buoys, above water of depth 20 and 30 m respectively, marked the positions of the two hydrological stations at Prion Lake (Figure 2.1.1). Surface samples only were collected from other water bodies.

Water samples, not analysed immediately, were preserved by the addition of AR grade chloroform (Barnes 1959) and stored in a cool, dark place.

1.1.3. *Physical determinations*

Transparency was measured at both Prion Lake stations, using a 25 cm Secchi disc. Corresponding measurements could not be made in the shallower ponds.

Incident solar radiation values were obtained, using a thermopile connected to a sensitive galvanometer.

Water temperature was measured at Prion Lake, using a thermistor direct-reading thermometer, designed and built by S.T.C., Sydney. This unit could be read reliably to 0·25°C under field conditions. Since stratification never occurred, temperatures were generally taken at 5 m intervals from surface to bottom at each station. "Negretti and Zambra" (mercury in steel) thermographs were used to obtain continuous recordings of mean water column temperatures in the shallow ponds. One of these was set up permanently at "S" Pond. The other was kept at "23U" Pond from March to September, 1962, then subsequently transferred to Duck Lagoon.

To detect and measure water temperature gradients in small ponds a "Grant" thermistor recording thermograph was used. All other temperatures were obtained, using a mercury in glass thermometer.

1.1.4. *Plankton samples*

Non-quantitative plankton samples were collected, using an N70 or hand net. All nets used for *P. brevicaudata* collections (quantitative or non-quantitative) were made from No. 20 bolting silk (mesh size, 0·095 mm).

At Prion Lake, quantitative plankton samples were obtained, using a closing-type Clarke-Bumpus sampler. On each visit to the lake, weather permitting, tows were made during the day and night, at times as close as possible to 1000 and 2200 hr. Night sampling consisted of horizontal tows at depths of 0 (subsurface), 5, 10, 15, and 23 m. The system was repeated for day sampling but, in addition, an oblique and a horizontal subsurface littoral tow were made. All tows (with the exception of the littoral tow) were made along the shortest course between stations A and B (Figure 2.1.1). As only a single Clarke-Bumpus sampler was available, the time taken for a series of horizontal tows (0 to 23 m) prevented a duplicate tow being made on the same day. Therefore tows made on consecutive nights are considered to represent duplicates. Three pairs of such duplicates were obtained (Table 1.1). The Clarke-Bumpus sampler was calibrated by D. J. Tranter of CSIRO, Cronulla, N.S.W. The filtration rate was 4·38 l/count over the range of towing speeds, 1 to 3 knots, and the mean acceptance was 88·9%. Clogging of the net never occurred at Prion Lake. Approximately 350 l of water were filtered during each horizontal tow.

Quantitative sampling of the shallow ponds proved very difficult. The most successful technique developed consisted of collecting a known volume of surface water using a bucket of calibrated volume, and then filtering the water through a hand net. This method was used at "S" Pond, "23U" Pond, Duck Lagoon and "F5" Pond. All such samples were taken near the edge of the ponds in an open water region, and are termed "limnetic" samples. On each sampling visit the total volume of water filtered by this method was 60 l at "S" Pond, 30 l at "23U" Pond, 60 l at Duck Lagoon and 10 l at "F5" Pond. The volume sampled depended on the volume of the water body. Samples of equal volume were collected at each of the sampling sites in any one water body (Figures 2.1.3, 4). Only one sampling site was maintained at "23U" Pond (Figure 2.1.2) because of the difficulties of sampling peculiar to this water body arising from the widespread luxurious growths of aquatic vascular plants.

A small "K" sampler of 0·5 l capacity (Plate 1.1) was designed to obtain quantitative samples in small ponds. Samples collected adjacent to the margins of a pond, using this sampler, were termed "littoral" and those taken immediately above the bottom were termed "benthic".

Plankton samples used for counting were preserved in 5% formalin immediately after collection.

1.2. LABORATORY METHODS

1.2.1. *Chemical determinations*

Conductivity was measured with a "London Switchgear" conductivity bridge, model MC1. This instrument was compensated for temperature to give readings at 20°C.

Hydrogen ion concentration was measured with a "Lovibond Comparator". Lack of a complete range of "Lovibond Comparator" indicator solutions at the island laboratory meant that in some cases pH values could not be obtained exactly. This method of pH measurement is ineffective for waters of very low buffer capacity. Consequently it was impossible to obtain pH values from the many low buffer capacity waters on Macquarie Island.

Soluble phosphate was estimated by the standard colorimetric method (Barnes 1959), using a "Hilger Spekker" absorptiometer.

TABLE 1.1

Duplicate mean water column densities (No/m^3 × 1000) of *P. brevicaudata* from night tows (0-23 m) at Prion Lake using a Clarke-Bumpus sampler.

Developmental stage groups: N1 = Nauplius 1, N2-6 = Nauplius stage 2-6 inclusive, C = total copepodid stages; A ♂ = adult male, A ♀ = adult female, A ♀ ov = adult ovigerous female, A ♀ sp. = adult spermatophore-bearing female.

DEVELOPMENTAL STAGES

Date	N1	N2-6	C	A ♂	A ♀	A ♀ ov	A ♀ sp.
17.10.62	0·333	3·321	25·31	0·346	0·593	0·016	0·032
18.10.62	0·241	3·32	17·30	0·396	0·533	0·024	0·041
Mean	0·287	3·32	21·30	0·371	0·563	0·020	0·036
% Deviat.	16·0	0·0	18·8	6·7	5·3	20·0	13·9
15.11.62	0·203	4·23	23·38	0·105	0·372	0·089	0·038
16.11.62	0·205	3·98	21·43	0·161	0·492	0·097	0·027
Mean	0·204	4·10	22·40	0·133	0·432	0·093	0·032
% Deviat.	0·5	3·0	4·5	21·0	13·9	4·3	17·2
3.10.62	0·313	4·48	19·88	0·274	0·273		
4.10.62	0·194	3·50	15·12	0·205	0·310		
Mean	0·253	3·99	17·50	0·239	0·291		
% Deviat.	23·8	12·3	13·6	14·3	6·4		
Mean % Deviat.	13·4	5·1	12·3	14·0	8·5	12·1	15·6

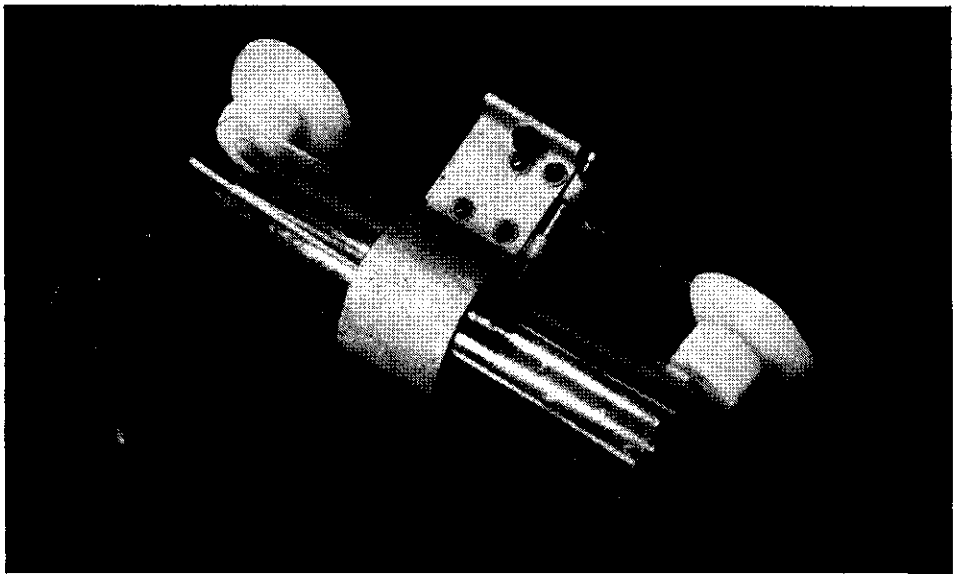
TABLE 1.2

Temperatures (°C) of "S" Pond and "optimal" conditions obtained from thermograph records, for the same dates.

Time: Hours

Date	Conditions	0000	0300	0600	0900	1200	1500	1800	2100
19.11.62	"S" Pond	2·2	1·8	2·5	6·0	8·7	9·3	7·5	4·7
,,	"Optimal"	4·5	4·5	5·0	6·5	7·0	7·3	6·5	5·5
20.11.62	"S" Pond	3·2	2·2	3·0	6·5	9·5	10·1	8·4	7·2
	"Optimal"	4·7	4·3	4·0	6·5	7·5	8·2	8·0	7·1

Chlorophyll concentrations were determined, using a method modified from Davis (1957). Water samples (0·5 to 2·0 l) were filtered through HA millipore papers, which were subsequently extracted with 90% acetone. As these papers clog readily, frequently two to three were used per sample. Extracted chlorophyll was measured, using a "Hilger Spekker" absorptiometer, with "Ilford" 608 filters.



ANARE photo A. Campbell-Drury

PLATE 1.1. "K" sampler, for use in small ponds, shown in open position. It is closed by withdrawing the brass pin (normally attached to a cable). When in use this sampler is mounted on the end of a long handle.

As spectral transmission of this filter below 6,500 A is low, this method effectively measures only chlorophyll *a*. The "Hilger Spekker" was calibrated against a standard solution of pure chlorophyll *a* (provided by Dr. G. Humphrey of CSIRO Division of Fisheries and Oceanography, Cronulla, N.S.W.) and chlorophyll solutions prepared from sea water, several freshwater samples and a culture of a marine *Nitschia* sp. The chlorophyll concentrations in all the latter were calculated, using equations supplied by Dr. G. Humphrey and Dr. S. W. Jeffrey. Calibration of the "Hilger Spekker" for chlorophyll, *a* using all these solutions, gave results that were in close agreement.

Oxygen was determined at Prion Lake, using the standard Winkler method (Barnes 1959).

Some preserved water samples were returned to Australia for a detailed analysis of their chemical composition, since facilities for such work were not available on Macquarie Island. Total solids, sodium, potassium, calcium, magnesium, iron, chloride, sulphate, nitrite, nitrate, bicarbonate, silica, iron and aluminium oxide, ammoniacal nitrogen, organic nitrogen and oxygen absorbed (from permanganate solution, in 30 min at 100°C) were determined. The methods used were those described by American Public Health Association (1955). Colorimetric methods were used for nitrite, nitrate and soluble silica. Distillation methods, with and without Kjeldahl treatment, were used for ammoniacal and organic nitrogen respectively. Other determinations were made gravimetrically.

1.2.2. *Plankton counts*

Where high densities of copepods were encountered in plankton catches, counts were made on several subsamples, obtained by using a subsampler of a type similar to that described by Kott (1953). Otherwise, whole catches were counted. The stages used for enumeration of the copepod populations were readily identified (without dissection) under a low-power dissecting microscope during counting.

Copepods are rarely randomly distributed in their environment. This is a factor which may often lead to serious errors in calculating population densities from plankton catches. A particular cause of non-random distributions are diurnal vertical migrations. The diurnal migratory activities of *P. brevicaudata* are described in a later Section (2.4.2). From these results it was apparent that all stages of this species are more uniformly distributed at night. Consequently, night catches only have been used for estimates of population densities in Prion Lake. The formula used to calculate the mean population density in the 0-23 m water column in Prion Lake is given below.

Mean Density of copepods in the 0-23 m water column

$$= \frac{1{\cdot}365\, d_1 + 1{\cdot}178\, d_2 + 1{\cdot}041\, d_3 + d_4}{4{\cdot}584},$$

where d_1 = mean of density of copepods between 0 and 5 m depth samples;
d_2 = ,, 5 ,, 10 ,, ;
d_3 = ,, 10 ,, 15 ,, ;
d_4 = ,, 15 ,, 23 ,, .

1·365:1·178:1·041:1·0 represents the ratio of the lake areas at depths of 2·5, 7·5, 12·5 and 19 m.

This formula accounted for the areal differences in the lake between the different towing depths. No tows were made below 23 m because of the probability of fouling the net on the bottom at such depths.

Population densities of the various developmental stage groups obtained from duplicate tows at Prion Lake are shown in Table 1.1. The deviations of these duplicates from their means compare favourably with previously reported values (Comita 1956; Bayly 1962). Deviations of duplicates from means for samples from other water bodies never exceeded 35%. For water bodies other than Prion Lake, population densities were estimated from samples obtained during daylight. Only on a few occasions was it possible to obtain night samples from such water bodies.

A high-power phase-contrast microscope was used to examine the finer structures of the developmental stages of *P. brevicaudata*. Length measurements were made, using a microscope with an eyepiece micrometer. For adults, metasome length was found to be a better index of size than total length, since the urosome was frequently curled up beneath the body. In younger stages, since this problem did not arise, total length measurements were made.

1.2.3. *Egg desiccation*

In all the experiments on egg desiccation, ovigerous females from "23U" Pond were used.

To determine the role of the egg sac in the resistance of eggs to desiccation, females were treated in two ways:

a. Ovigerous females were placed in small drops of water on glass slides. As the water evaporated slowly, eggs were shed from the egg sac by the fifth pair of legs (treatment "F", Table 1.2.3).

b. Ovigerous females were placed on glass slides, and dried immediately with blotting paper. The females died rapidly, and the eggs remained in the egg sac (treatment "O" in Table 1.2.3).

TABLE 1.2.3

Resistance of eggs to desiccation
O = eggs contained in ovisac; F = free eggs
a. 75% humidity

Treatment	Time	No. of females	No. eggs hatched	No. hatched per female	% survival of eggs
O	21 hrs.	16	21	1·3	9
F	21 hrs.	14	33	2·3	14
O	3 days	13	0	0·0	0
F	3 days	15	0	0·0	0
O	7 days	16	0	0·0	0
F	7 days	11	0	0·0	0

b. 92% humidity

Treatment	Time	No. of females	No. eggs hatched	No. hatched per female	% survival of eggs
O	4 days	12	62	5·2	58
F	4 days	15	41	2·7	30
O	7 days	12	26	2·2	25
F	7 days	10	49	4·9	54
O	10 days	12	7	0·6	7
F	10 days	10	18	1·8	20

Following these treatments, the slides were placed in desiccators containing atmospheres with relative humidities of 75% and 92% respectively. The desiccators were kept at temperatures between 5 to 10°C.

1.2.4. *Hatching*

For all hatching experiments, eggs were obtained from females collected from Prion Lake, "23U" Pond and Duck Lagoon. The relative scarcity of ovigerous females in "S" Pond at the time of the experiments made comparative studies of eggs from this population impossible.

For some experimental groups, eggs were collected from large numbers of females (40 on 27.6.62; 60 on 18.12.62; 200 on 31.12.62) kept together in 0·5 l of pond water. Under these conditions females normally shed their eggs within two days of capture. The eggs were released when the egg sac was torn open by the action of the sharp inward-pointing spines on the second segment of the exopods on the fifth pair of legs (Figure 2.2.5/7). As the eggs were shed, they were transferred with a pipette into phials containing filtered pond water. For other groups, one to five females were placed directly into phials of pond water. These females were removed immediately their eggs were shed. All phials contained 30 ml of millipore (HA) filtered water obtained from the same water body as the eggs it contained.

Hatching rates were obtained by recording the daily appearance of nauplii. Eggs were incubated in constant temperature (±0·4°C) water baths. Since constant temperature conditions were not available with natural illumination, these experiments were carried out in darkness.

Field conditions of small ponds were simulated by keeping phials in a naturally illuminated indoor area. These conditions were termed "optimal", since they most closely resembled field conditions and provided the highest per cent hatching (Sect. 2.4.6). The daily temperature variations of the "optimal" conditions were less than those for "S" Pond, but were always in excess of 2·0°C (Table 1.2).

1.2.5. *Effect of food on size and growth rate*

To test the effect of food upon size and growth rate, 10 nauplii, or fewer, were placed in glass jars containing 0·5 l of either Prion Lake or "23U" Pond water. This water was collected immediately prior to the commencement of the experiment, and the food level was estimated as chlorophyll *a* concentration. Macroscopic fauna was removed from the water during a thorough inspection, after it had been filtered through a coarse net. Jars containing the nauplii were set up under "optimal" conditions (as for "hatching", in previous section). A continuous record of temperature was kept, using a thermograph.

Nauplii were hatched from eggs obtained from large numbers of females (greater than 100). This ensured that the nauplii were representative of the populations from which they had been obtained. Nauplii were transferred to experimental jars when less than 24 hours old. The jars were inspected several times a week, when dead animals were removed and their stages recorded. At the end of the experiment all the copepods were dissected, identified and measured.

2. RESULTS

2.1. CHARACTERISTICS OF THE ENVIRONMENT

This section contains a general account of the limnology of Macquarie Island inland waters. Inland waters are defined as those surface waters which occur above the region of the highest tides. Welch's (1935) terminology for lentic water bodies has been used throughout this work.

On Macquarie Island, ponds and lakes are common, representing approximately 1/50th of the island's total area. Continuous rainfall and high humidities have caused even small depressions to be almost permanently filled with water. Consequently, perennial water bodies range in area from several square metres to 46 hectares (Major Lake). Streams, cascades and waterfalls are numerous, and ponds along the coastal terrace are common.

2.1.1. *General descriptions and morphometry*

There are three main types of lentic, inland water bodies on Macquarie Island:

type "a": ponds occurring on fen and bog peat beds on the coastal terrace;
type "b": ponds occurring on fen and highmoor peat beds on the plateau;
type "c": lakes and ponds occurring on tundra soils and glacial till material, on the plateau, the larger lakes occupying glacial valleys or moraine-dammed depressions.

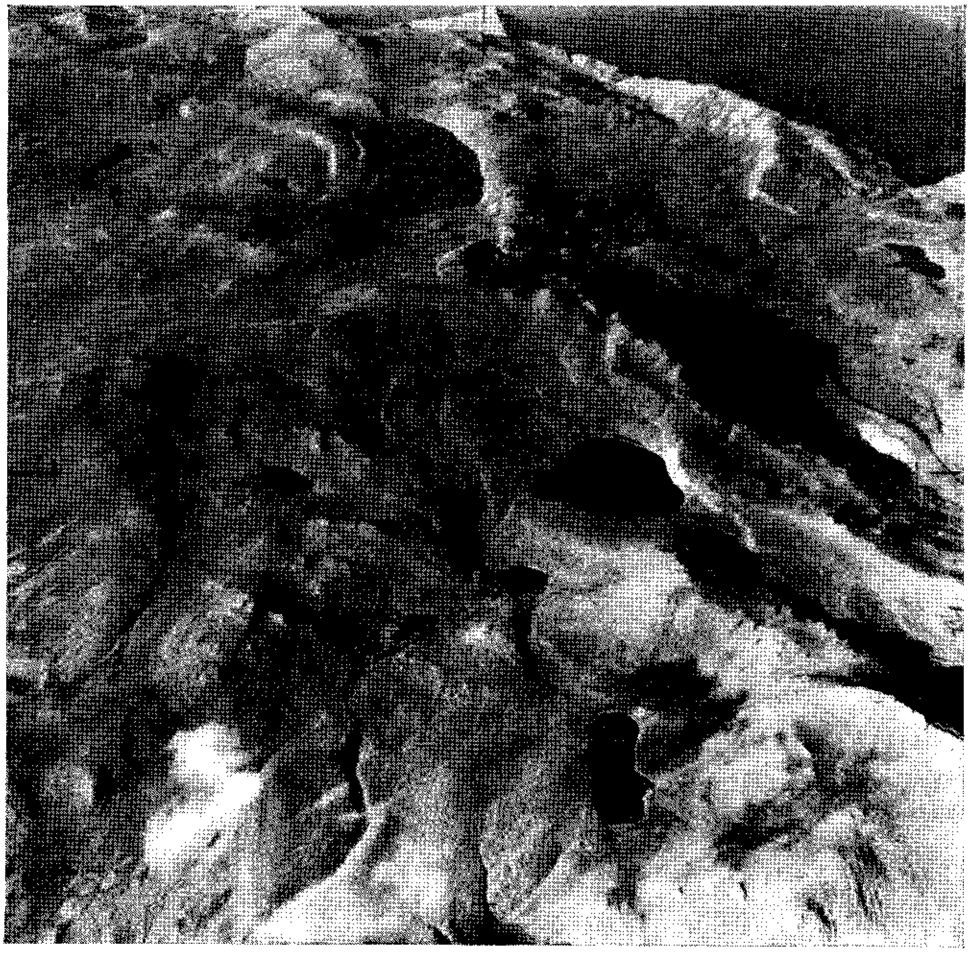
On the coastal terrace, ponds close to the sea are frequently made saline when seawater is swept inland during storms. Coastal terrace ponds are also subject to pollution by effluents from seal wallows and penguin rookeries, and subsequently become colonized by vigorous growths of red (Rhodobacterineae) and filamentous white (*Thiothrix* sp.) sulphur bacteria (Bunt 1954). Consequently, smaller ponds of the type "a" are regarded as temporary freshwater habitats.

P. brevicaudata was collected from all types of lentic freshwater habitats, ranging from large lakes to small ponds (volume less than 0·1 m^3). Five water bodies, including the three main types encountered on this island, selected for regular sampling of *P. brevicaudata,* were:

a plateau lake, Prion Lake (type "c");
plateau ponds "23U" Pond (type "b"), and "S" Pond (type "b");
coastal terrace ponds Duck Lagoon (type "a"), and "F_5" Pond (type "a").

2.1.1.1. Prion Lake (Figure 2.1.1, Plate 2.1.1)

There are four major plateau lakes on Macquarie Island. These are Flynn, Prion, Major and Waterfall Lakes (Figure 0.1). Only Prion Lake (altitude 170 m)



ANARE photo Air photo

PLATE 2.1.1. Oblique aerial view of Prion Lake (indicated by cross). "23U" Pond (triangle) is shown in left background.

was accessible and within reasonable range of the main station on the Isthmus (Figure 0.1).

This lake occupies a steep-sided glacial valley (Plate 2.1.1). Wave-cut shingle and sand beaches occur around the perimeter, except for the eastern shore which is strewn with small boulders, and broken by occasional headlands of bedrock.

The main morphometric parameters are listed below:

area = 36·3 ha;
total volume = 6·35 by 10^6 m^3;
maximum depth = 32·2 m;
mean depth = 17·5 m;
maximum length = 1150 m;
shoreline length = 2755 m;

shoreline development = 1·29;
mean depth: maximum depth ($\bar{z}:z_m$) = 0·54;
areas at towing depths (metres): A_{31} = 1·28 ha; A_{30} =5·60 ha; A_{23} = 12·52 ha; A_{20} = 15·00 ha; A_{15} = 21·35 ha; A_{10} = 27·11 ha; A_5 = 30·85 ha.

The ratio of the areas at the towing depths are:

$A_0:A_5:A_{10}:A_{15}:A_{23}$ = 2·88:2·45:2·15:1·69:1·00.

The lake basin is steep-sided along the east, west and northern margins. This feature is reflected in the high $\bar{z}:z_m$ value (i.e., greater than 0·5) which is characteristic of the values obtained for glacially overdeepened valleys (Hutchinson 1957). The form of the basin is that of a rectangular-section trench increasing in depth northwards, at which end the floor rises steeply against a barrier of bedrock. The low shoreline development index (shoreline development is the ratio of the length of the shoreline to the circumference of a circle of equal area of the lake) of 1·29 reflects the simple and regular form of the shoreline. The lake has a continuous wave-cut littoral shelf of varying width, and depth of 1 to 2 m. There are no inlet or outlet streams. Water drains from the lake by seepage at the northern end.

The floor of the lake is covered with glacial till material upon which occur mats of the mosses *Brachythecum salebrosum, Drepanocladus aduncus, Bryum* sp. and several species of hepatics. These plant associations occur at all depths. Rare patches of the aquatic vascular plant *Myriophyllum elatinoides* grow in an attenuated form in the shallower regions.

The slopes surrounding the lake are relatively well covered with plants of the herbfield and feldmark associations.

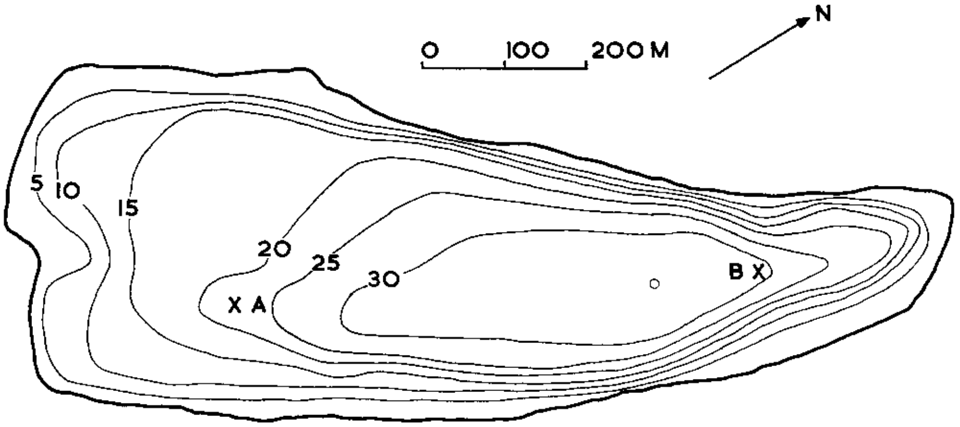


FIGURE 2.1.1. Bathymetric map of Prion Lake (depth in metres). Crosses indicate the positions of the sampling stations A and B, and the open circle the position of the greatest depth (32·2 m).

2.1.1.2 "23U" Pond = Stoney Creek Lake (Figure 2.1.2, Plates 2.1.1, 2)

"23U" Pond (altitude 99 m, Figure 0.1) occupies a shallow depression and is nowhere deeper than 60 cm. The mean depth is approximately 30 cm. Covering the floor is a relatively deep layer of loosely packed silty peat material. This pond appears to provide a very favourable environment for the growth of the vascular aquatic, *Myriophyllum elatinoides,* which forms dense stands throughout. The filamentous green alga *Rhizoclonium* sp. floats above the *M. elatinoides,* forming almost continuous surface mats (Figure 2.1.2, Plate 2.1.2). Only the more exposed eastern end of the pond is free of the algal mats. A semi-aquatic vascular plant *Callitriche antarctica* has colonized areas where the peat bed rises almost to the surface ("C" in Figure 2.1.2). This plant also grows inwards from the margins in association with mosses *Breutelia pendula,* and *Drepanocladus aduncus.* "23U" Pond appeared to be an incipient fen area, in which fen association plants were

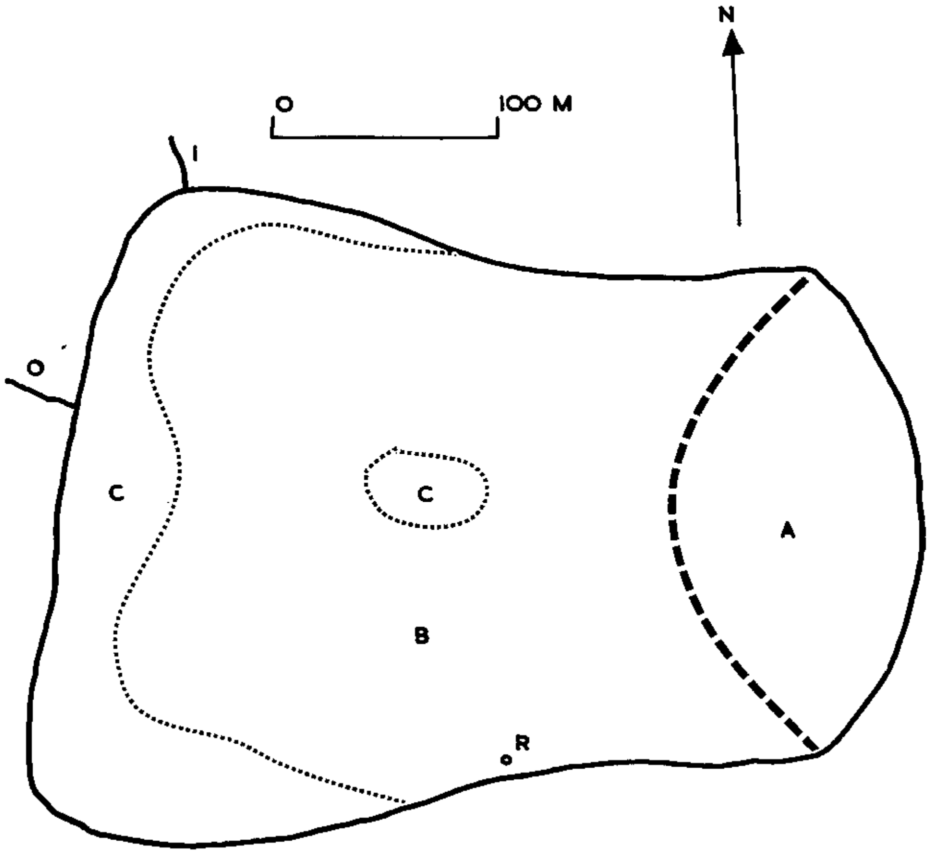


FIGURE 2.1.2. Schematic plan of "23U" Pond. A represents the area of open water, B the area covered by floating filamentous algal mats (*Rhizoclonium* sp. dominant) and C the areas of emergent vascular flora. R indicates position of thermograph and site of sampling (depth 10 cm). O and I are outlet and inlet streams respectively.

ANARE photo A. J. Evans

PLATE 2.1.2. "23U" Pond, viewed from the south-west. Snow can be seen lying upon the areas of the rooted aquatic plants and floating algal mats.

rapidly colonizing the more highly silted margins. There is a swift flowing outlet stream at the western end draining into Stoney Creek through a narrow cutting in a ridge, indicating that the level of the water has been somewhat higher in the past. A small inlet stream flows into the north-western corner.

Plants of the feldmark and herbfield associations grow on the slopes surrounding this water body.

2.1.1.3. "S" Pond (Figure 2.1.3, Plates 0.1, 2.1.3 to 5)

"S" Pond lies in a shallow depression in a rich fen peat bed on the plateau at an altitude of 220 m (Figure 0.1). It has an average depth of 20 cm, a maximum depth of 40 cm, and an average volume of 6·8 m^3. There is an outlet stream on its south-western end draining towards Scoble Lake.

A single vascular plant, the semi-aquatic *Ranunculus biternatus*, grows in the shallower water adjacent to the margins of the pond (Figure 2.1.3, Plate 2.1.3). The floor is otherwise bare of vegetation. A filamentous green alga *Rhizoclonium* sp. forms thick marginal mats (Plate 2.1.5).

The surrounding terrestial plant associations consist of subglacial herbfield and feldmark communities.

ANARE photo A. J. Evans

PLATE 2.1.3. "S" Pond, summer. See Figure 2.1.3 for general description.

ANARE photo A. J. Evans

PLATE 2.1.4. "S" Pond, winter. Thermograph is to right of pack.

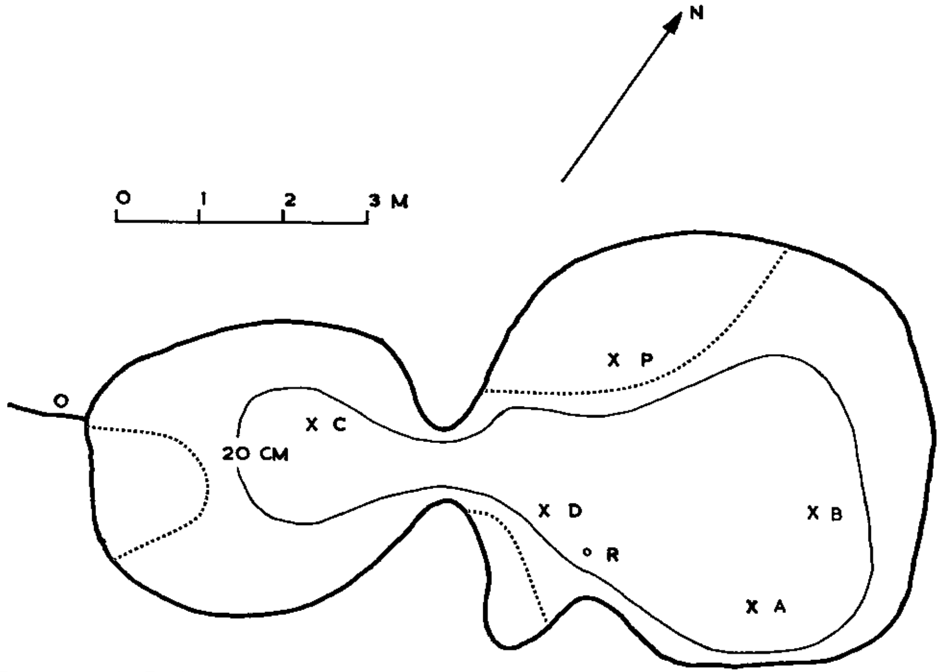


FIGURE 2.1.3. Bathymetric map of "S" Pond. Areas of the semi-aquatic plant *Ranunculus biternatus* (an emergent growth from the margins) are indicated by broken lines. Points A, B, C, D, and P represent sampling sites. R indicates position of the bulb of the thermograph and O the outlet stream.

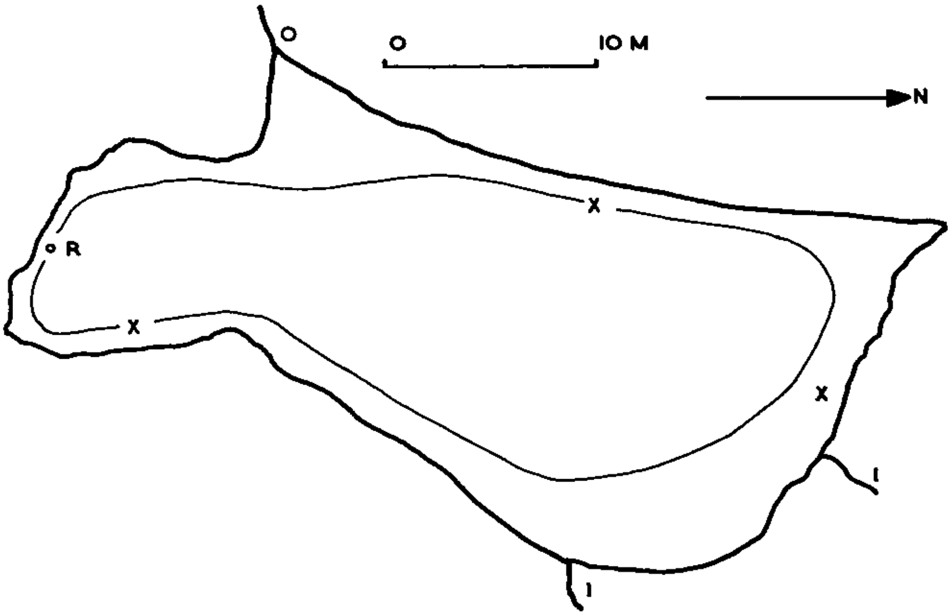


FIGURE 2.1.4. Bathymetric map of Duck Lagoon (contour line, 1 m). Crosses indicate sampling sites; R, position of the bulb of the thermograph; I and O, the inlet and outlet streams respectively.

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PLATE 2.1.5. Marginal filamentous algal mat zone, "S" Pond. *Rhizoclonium* sp. is the dominant form. *Spirogyra* sp. and filamentous blue-green algae are also present.

ANARE photo A. J. Evans

PLATE 2.1.6. Duck Lagoon. Many of the smaller ponds surrounding Duck Lagoon support populations of *P. brevicaudata*.

2.1.1.4. Duck Lagoon and "F_5" Pond (Figure 2.1.4, Plates 2.1.6 and 7)

These water bodies are situated on the western coastal terrace, in fen peat beds. Both are less than 100 m from the sea and have an altitude of less than 5 m. Sea spray and sea water are often carried directly into these ponds by the prevailing westerly winds.

Duck Lagoon has a mean depth of approximately 1·25 m, with a maximum depth of 2 m and a total volume of approximately 375 m³ (Figure 2.1.4). "F_5" Pond is much scaller, with an average depth of approximately 25 cm and a total volume of less than 1 m³ (Plate 2.1.7). "F_5" Pond, because of its small volume and proximity to the sea, was regarded as a "temporary" freshwater habitat. Duck Lagoon, being of larger volume, was less affected by marine influences.

ANARE photo A. J. Evans

PLATE 2.1.7. "F_5" Pond.

Duck Lagoon flows into the sea by an outlet stream on the western side and is fed by two inlet streams on the north-eastern corner (Figure 2.1.4, Plate 2.1.6). The floor is covered with fen peat material and studded with boulders. Dense stands of *Myriophyllum elatinoides* and filamentous algal mats of *Rhizoclonium* sp. are common. Surface algal mats are less extensive than in "23U" Pond and occur mainly about the margins. The most common terrestial vascular plants occurring around the edges are characteristic of the maritime grassland community (Taylor 1955). "F_5" Pond occupies a small depression in the fen peat between stools of *Poa foliosa,* and cushions of *Colobanthus muscoides,* and *Cotula plumosa.* Partly submerged boulders project into the pool.

2.1.1.5. Kerguelen Islands

During March 1963, members of ANARE made some collections from freshwater ponds and lakes on the Kerguelen Islands. Collections were made from: a pond on fen peat, altitude 18 m; Studer Lake 1, a large lake on glacial till, altitude 310 m; a small pond adjoining Studer Lake 1, on glacial till; and a small pond on glacial till, altitude 61 m.

A list of the most common species of aquatic fauna and flora found in the water bodies on Macquarie Island is given in Appendix I.

2.1.2. *Physical characteristics*

2.1.2.1. Colour and transparency

The larger plateau lakes of Macquarie Island receive much of their water by drainage from tundra soils and consequently the water is colourless and of low turbidity. In contrast, the waters draining from peat beds are brown in colour due to the presence of soluble or colloidal organic matter.

Prion Lake had an annual mean Secchi disc transparency of 12·6 m. There was no difference between values obtained for stations A and B. The overall range was 10·5 to 16·0 m, summer values being generally lower than winter values (Figure 2.1.8). These high values are typical for those of oligotrophic alpine and subalpine lakes of Europe and Canada (Hutchinson 1957, Rawson 1960).

TABLE 2.1.1

Micro-gradients of temperature (°C), "S" Pond

(a) Variation of temperature (°C) with depth

Date	Time hrs.	Site*	Surface temp.	Midway surface to bottom temp.	Bottom temp.	Surface soil temp.
26.2.62	1550	A	9·2	9·2	8·9	7·1
,,	,,	B	9·2		8·4	7·1
24.12.62		A	9·4		8·8	

(b) Variation of temperature (°C) with position in relation to margins

Date	Time hrs.	Site*	Open water, temp.	Algal marginal zone, temp.
6.1.62	1000	A	6·4	6·6
,,	,,	B	6·3	6·4
,,	,,	C	6·7	7·0
29.1.62	1200	A	5·1	5·0
,,	2200	A	6·0	6·0
26.2.62	1550	A	9·2	9·9
,,	,,	C	9·2	9·0

* See Figure 2.1.3

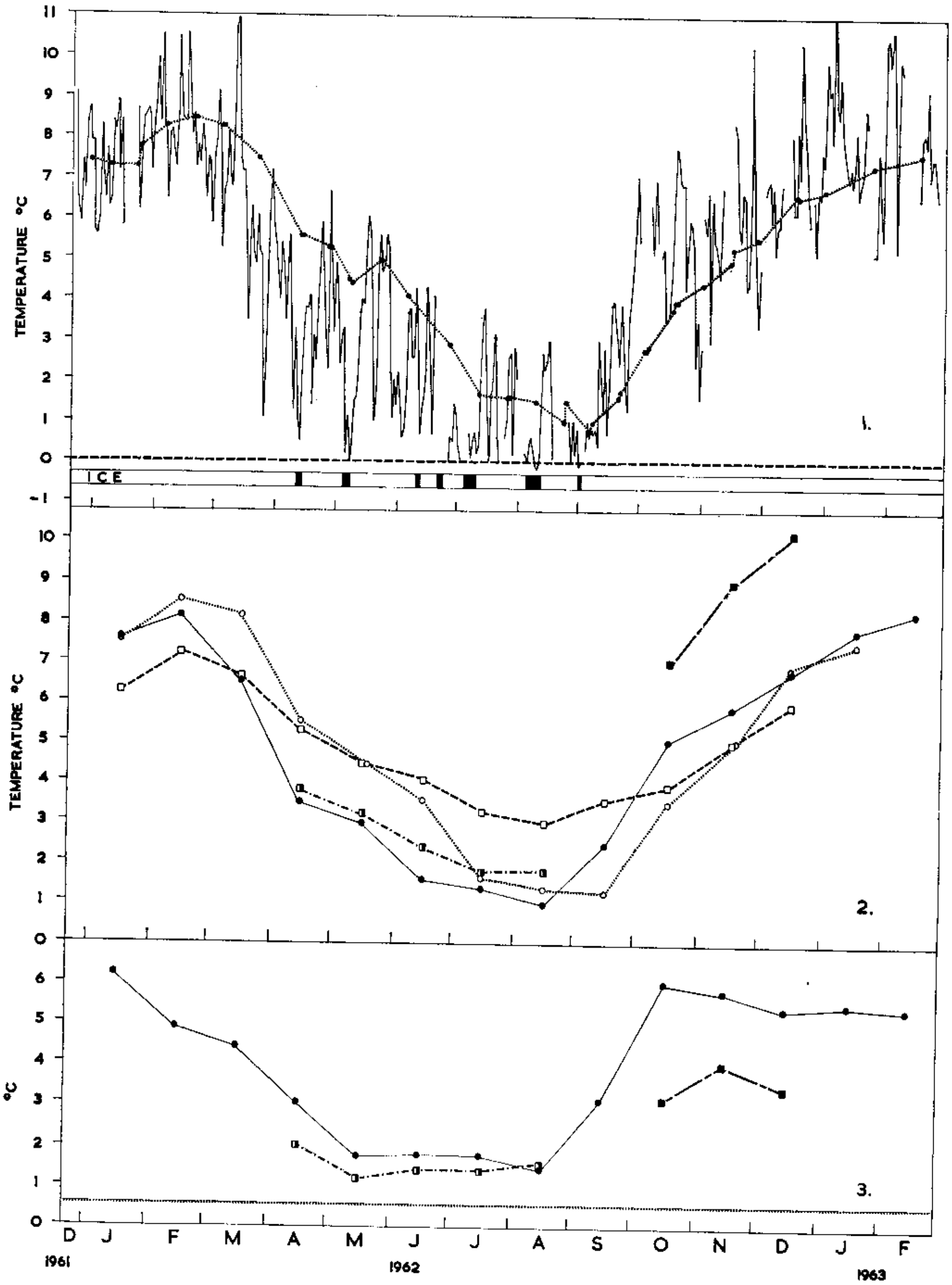


FIGURE 2.1.5. Mean water column temperatures for various water bodies: (1) mean daily temperature (incidence of surface ice refers to "S" Pond only); (2) monthly mean temperature; (3) monthly mean daily temperature variation (maximum value only shown for Prion Lake).

.... Prion Lake	— — — — Duck Lagoon
———— "S" Pond	—·—·—·— "23U" Pond

— — — — — air temperature, Isthmus

2.1.2.2. Temperature

The annual range of temperature occurring in Prion Lake was 8·75°C to 0·8°C (Figure 2.1.5). Thermal stratification never occurred nor was there ever any difference in temperature between the water columns at stations A and B (Evans 1965). The greatest temperature difference measured in the water column between the surface and 25 m depth was 0·7°C. The mean annual difference between surface and bottom temperatures, for both stations, was 0·05°C. Daily temperature variation was never greater than 0·5°C. No ice cover formed during the period of observation.

Prion Lake is a polymictic, third-class lake in terms of Hutchinson's (1957, p. 535) system for thermal classification. Both the slow rate of warming during the cool summers, and the continuous exposure to high winds, keep the water permanently in complete circulation, and prevent the establishment of a thermocline.

The results obtained from thermograph records for "S" Pond, "23U" Pond and Duck Lagoon are shown in Figure 2.1.5. Since "S" Pond was both small and shallow the daily temperature variations were greater than recorded elsewhere (Figure 2.1.5, Graph 3). Consequently, although the annual range for the monthly mean temperatures was 8·3 to 0·8°C, the extreme annual range was 16·3 to —0·2°C. Sudden temperature changes were caused by falls of snow or rain. During the winter, snow drifts commonly filled the small depression occupied by "S" Pond. However, this usually occurred without complete freezing, and therefore free water was always present. Melting of the snow was rapid and normally completed within a few days. Freezing of surface waters occurred occasionally during the winter. The thickest ice crust encountered was 10 cm thick, but more usually it was less than 4 cm. Such an ice cover rarely lasted longer than a week.

On several occasions measurements were taken to investigate the nature of the temperature micro-gradients in "S" Pond. Only small variations with depth and position were observed (Table 2.1.1).

At the lower altitude of Duck Lagoon freezing was very rare during the winter, and snow drifts uncommon. Daily temperature variation was slightly less than that occurring in "S" Pond.

TABLE 2.1.2

Frequency of days for which mean temperature ≥ 10°C. (Suitable data were only available from "S" Pond, Prion Lake and Duck Lagoon.)

Month	Year	Prion Lake	"S" Pond	Duck Lagoon
Feb.	1962	0	3	
Mar.	,,	0	2	
Oct.	,,	0	0	2
Nov.	,,	0	1	5
Dec.	,,	0	1	11
Jan.	1963	0	3	3*
Feb.	,,	0		6*

* Incomplete data for this month

TABLE 2.1.3

Comparison of the relative ionic compositions of some natural surface waters. Where more than one determination of ionic composition has been made for any water body, annual mean values are used N.D. = none detectable; O.O.F. = oceanic origin factor.

Location	Ionic proportions m equiv./1% of total cations or anions							Total solids mg/1	Total major cations m equiv./1	Total major anions m equiv./1	Dist. from sea, west coast m	Type	O.O.F.
	Na	K	Ca	Mg	Cl	SO_4	HCO_3						
"S" Pond	71	6	5·0	18·0	90	9	1	113	1·94	1·83	2,750	b	98·0
"23U" Pond	57	2	20·5	20·5	65	7	28	184	2·81	2·76	2,400	b	71·6
Prion Lake	73	5	5·0	17·0	86	9	5	93	1·53	1·51	3,000	c	94·8
Duck Lagoon	81	3	5·0	11·0	74	9	17	582	9·37	8·97	175	a	81·6
Duck Lagoon (post storm)	75	4	4·0	17·0	89	9	2	5,824	98·51	98·95	175	a	98·1
"11P" Pond	69	8	4·0	19·0	92	6	2	507	8·54	8·43	50	a	99·9
"10P$_1$" Pond	74	4	3·0	19·0	90	8	2	5,904	100·96	100·23	18	a	99·7
"10P$_2$" Pond	63	6	11·0	20·0	89	4	7	657	11·04	10·91	45	a	98·0
"4R$_2$" Pond	74	5	4·0	17·0	90	7	3	2,850	48·63	47·94	140	a	99·9
"5W" Pond	50	6	20·0	24·0	73	2	25	266	4·15	4·09	370	a	80·7
"4R$_3$" Pond	73	5	4·0	18·0	94	4	2	2,505	43·56	42·88	140	a	99·9
North Head (north) Pond	68	7	5·0	20·0	91	2	7	663	10·42	9·91	200	b	99·9
North Head (south) Pond	73	3	6·0	18·0	93	5	2	491	8·31	8·45	200	b	99·9
Scobles Lake	63	7	8·0	22·0	82	9	9	143	2·36	2·24	2,200	b/c	90·9
Scobles Lake Pond	74	4	3·0	19·0	88	12	—	172	3·01	2·96	2,200	b	99·9
Elder Lake (north)	66	5	6·0	23·0	82	9	9	109	1·82	1·72	3,200	c	90·6
Kerguelen water	55	14	10·0	21·0	68	14	18	56	0·86	0·83		a/c	72·3
Falkland Islands bog waters (Gorham and Cragg 1960)	72	2	5·0	19·0	88	12	N.D.		2·35				
World average freshwater (Conway 1942)	16	3	64·0	17·0	10	16	73						
Precipitation Isthmus	73	6	4·0	17·0	90	9	1	3,575	61·66	59·44	35		99·2
Precipitation Prion Lake	66	9	5·0	20·0	86	12	2	74	1·11	1·23	3,000		99·2
Sea water, Macquarie Island, 12.3.62	76	2	4·0	18·0	90	9	1	34,912	608·00	600·00			
Sea water average (Lyman and Fleming 1940)	77	2	3·0	18·0	90	9	1	34,482	597·00	605·00			

Differences in temperature between the water bodies on the island were mainly determined by their altitude, mean depth and total volume. Hence the highest temperature (17·6°C) was recorded from Duck Lagoon (alt. less than 7m), and the lowest (—0·2°C) from "S" Pond (alt. 220 m). Duck Lagoon temperatures were consistently several degrees centigrade higher than those for Prion Lake or "S" Pond (Figure 2.1.5). This difference is further exemplified in Table 2.1.2. Both volume and mean depth are factors which affect the nature of the seasonal temperature cycle and the rate of gain or loss of heat. Hence the daily temperature variation occurring in Prion Lake was always small (never greater than 0·5°C), and its rate of heating slow, as indicated by an annual temperature cycle which lagged approximately one month behind that for "S" Pond (Figure 2.1.5).

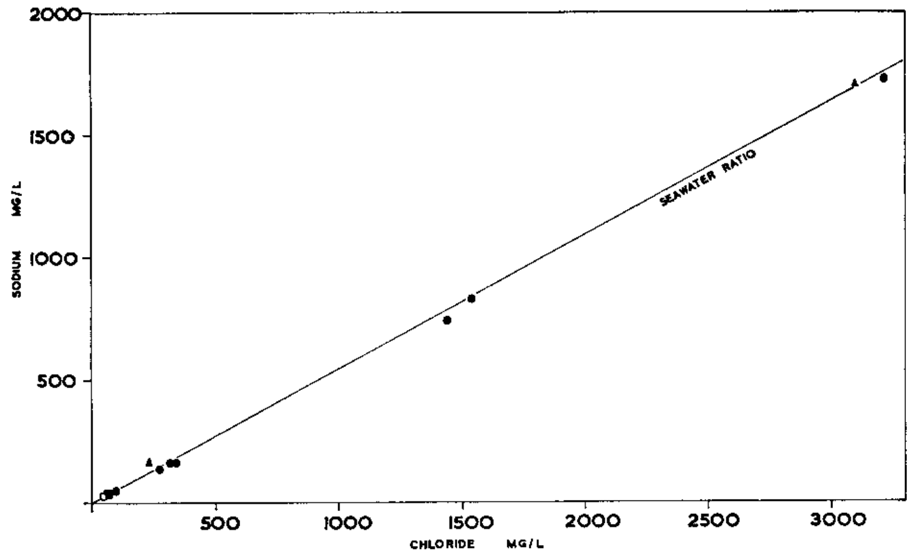


FIGURE 2.1.6. Ratio of Na to Cl in Macquarie Island inland water, compared to seawater ratio. ○ Prion Lake; ■ "S" Pond; ▲ Duck Lagoon; ● Coastal terrace pools.

2.1.3. *Chemical characteristics*

2.1.3.1. Major ions, total (dissolved) solids and conductivity

Although Ca and HCO_3 are characteristically the major ions in freshwater (Conway 1942), Na and Cl were found to be the most common ions in Macquarie Island inland waters. This suggested that much of the dissolved solids in these waters was probably of marine origin. Table 2.1.3 shows that Macquarie Island inland waters were strikingly similar in ionic composition to "average" or Macquarie Island sea water. Further, the Na/Cl ratios in Macquarie Island inland waters were identical to those for sea water (Figure 2.1.6).

Anderson (1941) devised a formula to estimate the proportion of major ions that were of marine origin in an inland water. This is given below:

$$\text{Oceanic origin factor (\%)} \atop \text{(O.O.F.)} = \frac{\text{(Cl milli. equiv. per litre) by } 1\cdot107 \text{ by } 100}{\text{(Total anions, milli. equiv. per litre)}}.$$

O.O.F. values obtained for the inland waters of Macquarie Island ranged from 67·2% to 99·9% (mean 92·2%, Table 2.1.3). The lowest values of 67·2%, 80·7% and 81·5% were from "23U" Pond, "5W" Pond and Duck Lagoon respectively. These waters contained higher proportions of Ca and HCO_3 than sea water. Although the amount of total solids in the inland waters is mainly dependent upon their distance from the sea (in the direction of the prevailing wind), there is no similar relationship between this distance and the O.O.F. of the waters (Figure 2.1.7).

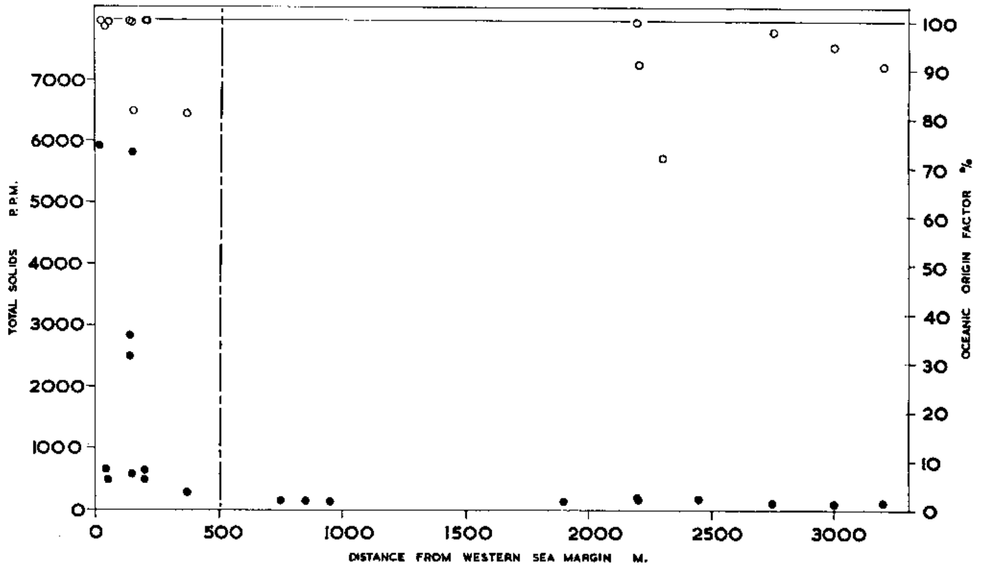


FIGURE 2.1.7. Effect of distance from sea on total solids (closed circles) and O.O.F. (open circles) for Macquarie Island inland waters. Broken vertical line represents the division between coastal terrace (left) and plateau waters (right).

Analysis of atmospheric precipitation samples, collected at Prion Lake and the Isthmus (Table 2.1.3), indicates that they are strikingly similar in ionic composition to both inland freshwater and offshore sea water of Macquarie Island. It is again evident from such results that most of the soluble material in the inland waters is derived from the sea, being carried inland in the form of windborne spray or some other type of precipitation.

Ca/Cl values were generally close to the range of 0·033 to 0·058 obtained for sea water and atmospheric precipitation samples (Table 2.1.4). This ratio for "world average freshwater" is 6·4, due to the higher and lower relative amounts of Ca and Cl respectively. However, the value of 0·057 for bog waters of Falkland Islands (Gorham and Cragg 1960) agrees well with those from Macquarie Island inland waters. At Macquarie Island and the Falkland Islands, water drainage and run off occurs from peat beds or glacial till, both of which are known to contribute little Ca to natural waters (Gorham 1961).

Notably higher Ca/Cl values were obtained for "23U" Pond, "5W" Pond, "$10P_2$" Pond and Scoble's Lake (Table 2.1.4). In these water bodies, therefore, Ca other than that of marine origin was present. Plateau waters were deficient in Ca (mean concentration 3·9 mg/l, cf. Williams 1964c), whereas waters of the coastal terrace are, in comparison, well supplied (mean concentration 27·6 mg/l).

Most Cl/SO_4 values occurred within the range of 10·0 to 7·2 obtained from precipitation and sea water values (Table 2.1.4). Higher than sea water, Cl/SO_4 values obtained by Gorham and Cragg (1960) for permanently waterlogged ponds were also obtained for permanent coastal terrace ponds of Macquarie Island (Table 2.1.4). This may be partly accounted for by the known decreases of SO_4, in small ponds, which occur during summer, caused by bacterial reduction (Mann 1958). High Cl/SO_4 values obtained for the North Head ponds were probably the result of contamination by sheep.

Where the ionic composition of water shows little seasonal variation, conductivity can be used as a reliable measure of the total dissolved solids. For the range 0 to 1,000 μmhos (for Macquarie Island inland waters) the relationship between total dissolved solids (ppm) and conductivity (μhmos) was linear, with a regression coefficient = 0·68. Williams (1964b) found this value to be 0·58 for the sodium-

TABLE 2.1.4

Ca/Cl and Cl/SO_4 ratios for some Macquarie Island inland waters

Location	Cl mg/l	Ca/Cl m equiv.	Cl/SO_4 m equiv.	Type of water body
"S" Pond	58·4	0·056	10·0	b
"23U" Pond	64·0	0·315	9·3	b
Prion Lake	46·1	0·058	9·6	c
Duck Lagoon	235·0	0·068	8·2	a
Duck Lagoon (after storm)	3,120·0	0·045	9·9	a
"11P" Pond	274·5	0·044	15·3	a
"10P" Pond	3,220·0	0·033	11·2	a
"$10P_2$" Pond	345·0	0·124	22·1	a
"$4R_2$" Pond	154·0	0·045	12·8	a
"5W" Pond	105·5	0·274	36·8	a
"$4R_3$" Pond	1,445.5	0·043	23·6	a
North Head Pond (north)	320·0	0·055	46·0	b
North Head Pond (south)	280·0	0·065	18·6	b
Scobles Lake	65·5	0·097	9·1	b/c
Scobles Lake Pond	92·0	0·034	7·3	b
Elder Lake (north)	50·0	0·073	9·1	c
Kerguelen Islands	19·9	0·147	4·9	a/c
World average freshwater (Conway 1942)		6·400	0·63	
Falkland Islands bog waters (Gorham and Cragg 1960)	72·0	0·057	7·3	
Precipitation Prion Lake	37·5	0·045	10·0	
Precipitation Isthmus	1,890·0	0·058	7·2	
Sea water Macquarie Island	19,170·0	0·044	10·0	
Sea water (Lyman and Fleming 1940)		0·033	10·0	

and chloride-dominated Victorian and South Australian inland waters. This author gives 0·61 to 1·21 (at 18°C) as the range previously obtained by other workers for inland waters. With higher values for total dissolved solids the relationship with conductivity (for inland waters of Macquarie Island) is no longer linear, and the regression coefficient approaches the value of 1·0.

TABLE 2.1.5

pH, conductivity and soluble phosphate of surface waters of some plateau lakes and ponds (N.D. = not detected; N.M. = no measurement, because of low buffering)

Location	Date	pH	Condy μmhos 20°C	Sol. PO_4 mg/m^3
Ainsworth Lake	9.4.62	6·6	221	N.D.
Waterfall Lake	10.4.62	7·0	216	N.D.
North Head Pool	10.6.62	>6·8, <7·6	690	N.D.
"14Z" Pond	9.7.62	>6·8, <7·6	260	
Scobles Lake	23.7.62		268	
Scobles Lake	28.7.62	6·4	197	N.D.
Ainsworth Lake	27.7.62	<5·4	190	N.D.
Major Lake	28.7.62	6·6	213	N.D.
Island Lake	7.8.62	>6·8, <7·6	186	
Waterfall Lake	8.8.62	>6·8, <7·6	204	N.D.
Pyramid Peak Lake	1.8.62	N.M.	141	N.D.
"33P" Pond	11.8.62	N.M.	170	Trace
"35Q" Pond	11.8.62	N.M.	202	N.D.
Island Lake	16.8.62	>6·8, <7·6	194	Trace
North Head Pond	17.8.62	>6·8, <7·6	780	N.D.
North Head Pond (a)	16.1.63	6·8	740	N.D.
,, (b)	16.1.63	7·3	1,000	N.D.
,, (c)	16.1.63	8·6	880	N.D.
,, (d)	16.1.63	7·5	1,000	N.D.
,, (e)	16.1.63	7·8	920	N.D.
"9U" Pond	30.1.63	6·6	430	
North Head Pond	1.2.63	6·7	840	
Scobles Lake	9.3.63	7·0	237	

Conductivities of Macquarie Island inland waters are listed in Tables 2.1.5 and 6. The water bodies of the coastal terrace range from brackish ponds of conductivity 14,200 μmhos to freshwater ponds of conductivity 420 μmhos (brackish water is defined as water containing 3,000 or more ppm of dissolved solids, Williams 1964a). Conductivities of the plateau waters were lower, ranging from 130 to 430 μmhos (North Head ponds excluded).

Seasonal variation in the conductivity of the plateau waters was usually small (Table 2.1.5, Figure 2.1.8). No significant seasonal changes were observed in Prion Lake water (Figure 2.1.8), even though a 12 cm rise in water level occurred during the winter. Nor was there any variation in conductivity between samples taken at different depths or stations in this lake. The overall mean of 157 μmhos for Prion Lake fell within the range given for alpine lakes (Ruttner 1953).

"23U" Pond, with a mean conductivity of 282 μhmos, also showed little seasonal variation (Figure 2.1.8). A substantial increase in water level, resulting from an increase in precipitation occurring during June and July, had no effect on conductivity in this pond.

Melting snow drifts caused a considerable decrease in conductivity, during the winter, in "S" Pond (Figure 2.1.8). The small volume of this pond largely

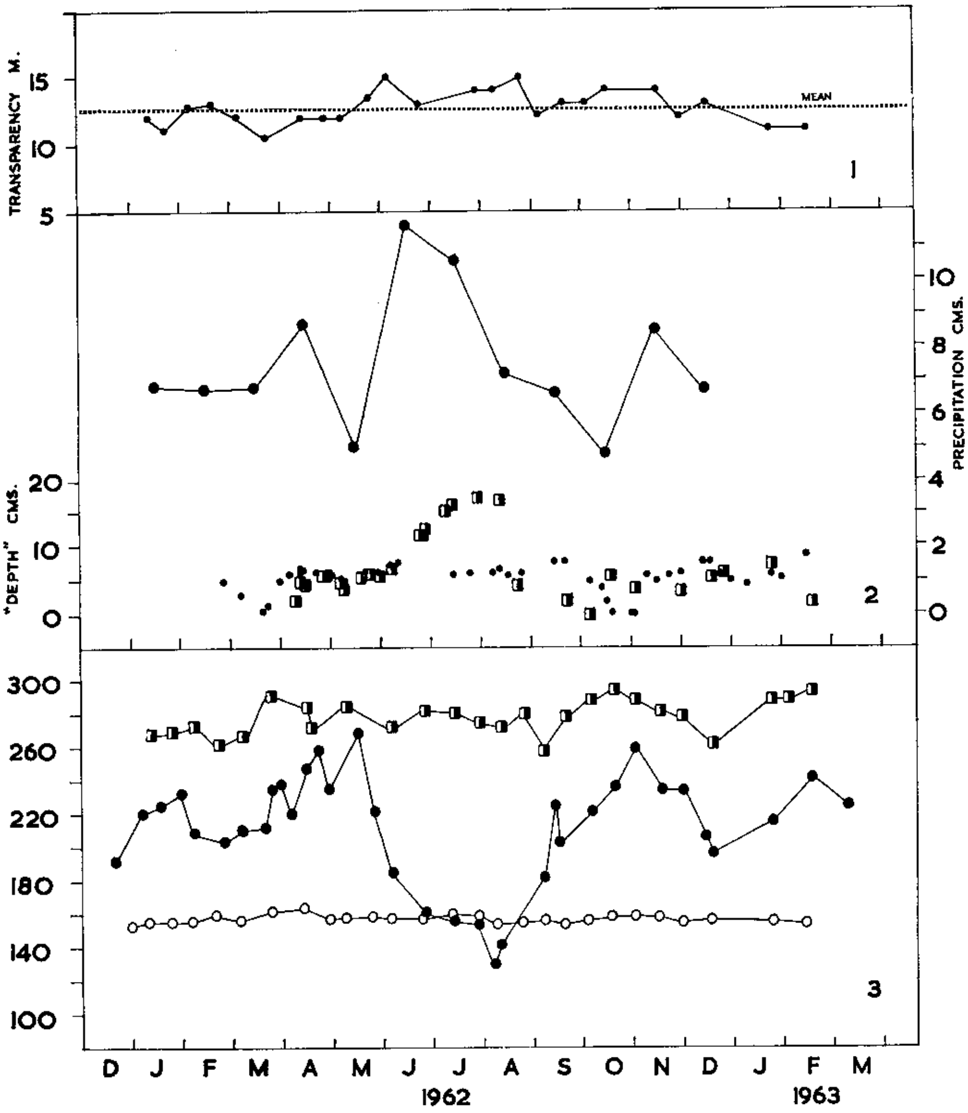


FIGURE 2.1.8. Seasonal variation of (1) transparency (Prion Lake); (2) water level and precipitation; (3) conductivity (at 20°C). "Depth" was a measure of the variation in the water level from the lowest level. Precipitation refers to atmospheric precipitation measured at the meteorological station on the Isthmus.

Legend for 2:
● Precipitation
◧ "23U" Pond
• "S" Pond

Legend for 3:
○ Prion Lake
◧ "23U" Pond
● "S" Pond

TABLE 2.1.6

pH, conductivity, soluble phosphate of coastal terrace surface waters (including Duck Lagoon and “F_5”)

Location	Date	pH	Condy µmhos 20°C	Sol. PO_4 mg/m^3
“9Q” Pond	19.2.62	<7·6	645	
Green Gorge Lagoon	20.2.62	>6·8, <7·6	235	
“F_3” Pond	13.4.62	7·25	600	
Duck Lagoon	13.4.62	6·6	850	
“F_5” Pond	13.4.62	6·9	3,010	
Green Gorge Lagoon	10.7.62	>6·8, <7·6	194	
Fen Pond, Aurora Point	30.7.62	6·4	820	37·3
Fen Pond near Duck Lagoon	30.7.62	>6·8, <7·6	800	55·0
Duck Lagoon	30.7.62	>6·8, <7·6	795	56·3
“F_5” Pond	30.7.62	>6·8, <7·6	1,000	109·3
“14Z” Pond	7.8.62	>6·8, <7·6	255	48·3
“4V” Pond	14.8.62	>6·8, <7·6	455	61·0
“$4T_1$” Pond	14.8.62	≤5·2	565	75·4
“$4T_2$” Pond	14.8.62	>6·8, <7·6	565	38·0
“8Q” Pond	14.8.62	>6·8, <7·6	600	141·8
“21O” Pond	16.8.62	≤5·2	6,600	153·3
“$21O_2$” Pond	16.8.62	>6·8, <7·6	1,680	259·6
Duck Lagoon	16.8.62	>6·8, <7·6	740	62·0
“14Z” Pond	22.8.62		263	15·8
Duck Lagoon	18.9.62	>6·8, <7·6	840	34·0
“F_5” Pond	18.9.62	>6·8, <7·6	1,580	64·0
“F_{10}” Pond	18.9.62	>6·8, <7·6	14,200	96·0
Langdon Point Pond	23.9.62	>6·8, <7·6	570	221·3
“F_5” Pond	27.9.62	>6·8, <7·6	1,500	89.0
“F_{10}” Pond	27.9.62	>6·8, <7·6	3,820	43·7
Duck Lagoon	27.9.62	>6·8, <7·6	850	29·3
Duck Lagoon	11.10.62	7·8	900	31·0
“F_5” Pond	11.10.62	>6·8, <7·6	1,520	156·3
“F_{10}” Pond	11.10.62	8·2	6,900	7·3
Duck Lagoon	25.10.62	>6·8, <7·6	870	11·6
“F_5” Pond	25.10.62	>6·8, <7·6	1,290	139·1
“F_{10}” Pond	25.10.62	>6·8, <7·6	3,880	1·6
“F_{10}” Pond	8.11.62	7·8	2,720	3·3
“F_5” Pond	8.11.62	>6·8, <7·6	1,350	110·3
Duck Lagoon	8.11.62	>6·8, <7·6	880	30·0
Duck Lagoon	23.11.62	7·8	895	48·1
“F_{10}” Pond	23.11.62	7·8	6,810	8·1
“F_5” Pond	23.11.62	>6·8, <7·6	1,520	109·0
Duck Lagoon	13.12.62	7·2	850	122·3
“F_5” Pond	13.12.62	7·0	1,580	125·7
Duck Lagoon	24.12.62	8·2	840	114·0
“F_5” Pond	24.12.62	7·0	1,450	187·0
“$4R_1$” Pond	14.1.63	6·7	4,700	
“$4R_2$” Pond	14.1.63	6·6	3,600	
“$4R_3$” Pond	14.1.63	6·4	3,500	
“$5S_1$” Pond	14.1.63	≦5·2	1,000	
“5W” Pond	14.1.63	7·0	420	
“10O” Pond	30.1.63	8·7	14,200	
“11Q” Pond	30.1.63	6·8	475	
“$10P_2$” Pond	30.1.63	6·4	1,000	
“11P” Pond	30.1.63	5·7	860	
“$10P_1$” Pond	30.1.63	6·6	6,100	
“F_5” Pond	7.3.63	6·8	7,700	50·0
Duck Lagoon	7.3.63	7·6	6,350	120·0

accounted for the relatively great effect of rather minor environmental changes on conductivity. Such was also the case for "F_5" Pond (Table 2.1.6). Duck Lagoon and "F_5" Pond underwent a seven-fold increase in conductivity on 7.3.63. This was due to an inflow of sea water, swept inland by westerly gales. Large masses of fronds of the marine giant kelp *Durvillea antarctica* were also deposited in these and other ponds on the coastal terrace during the storm. Past weather records indicate that such storms are not rare events. Prior to the storm the mean conductivity of Duck Lagoon was 840 μmhos, whereas subsequently the conductivity rose to 6,350 μmhos (Table 2.1.6). The conductivity of "F_5" Pond was more variable, ranging from 1,580 to 3,010 μmhos before the storm, and rising afterwards to 7,700 μmhos (Table 2.1.6).

The conductivity of atmospheric precipitation ranged from 72 to 190 μmhos at Prior Lake to 133 to 1,120 μmhos at the meteorological station on the Isthmus.

The inland waters of the Kerguelen Islands contained low concentrations of dissolved solids (range 50-83 mg/l). The mean O.O.F. value of 52·8% was also much lower than values obtained for Macquarie Island inland waters.

2.1.3.2. Hydrogen ion concentration (pH)

Measurement of the pH of water from Prion Lake was frequently impossible because of its low buffer capacity. The few values obtained ranged from 6·3 to

TABLE 2.1.7

pH of some plateau waters
(N.M. = no measurement because of low buffering)

Date	Prion Lake	"23U" Pond	"S" Pond
30.12.62	7·3		
10.1.62	7·1	7·9	6·4
23.1.62	6·4	7·25	6·4
6.2.62	N.M.	10·25	5·9
20.2.62	6·7	>6·8, <7·6	5·6
5.3.62	N.M.		
23.3.62	6·3	7·6	5·7
13.4.62	N.M.	7·25	5·9
28.4.62	”		5·6
8.5.62	”	>6·8, <7·6	N.M.
23.5.62	”	>6·8, <7·6	N.M.
5.6.62	”	>6·8, <7·6	5·4
25.6.62	”	>6·8, <7·6	≤5·2
12.7.62	”	>6·8, <7·6	≤5·2
28.7.62	”	>6·8, <7·6	≤5·2
9.8.62	”		N.M.
24.8.62	”	8·2	
7.9.62	”	>6·8, <7·6	N.M.
20.9.62	”	>6·8, <7·6	≤5·2
3.10.62	”	>9·2	
17.10.62	”	>9·2	≤5·2
1.11.62	”	>9·2	≤5·2
15.11.62	”	>6·8, <7·6	≤5·2
17.12.62	”	8·4	6·4
23.1.63	”	7·0	
15.2.63	6·4	79·2	5·7

7·3. "S" Pond water was always acid (Table 2.1.7), while "23U" Pond water was either alkaline or neutral (Table 2.1.7). Duck Lagoon and "F_5" Pond were usually weakly alkaline, varying from pH 6·6 to 8·2 (Table 2.1.6). There was little difference between the pH of the coastal terrace (<5·2-8·7, Table 2.1.6) and plateau waters (<5·2-8·6, Tables 2.1.4 and 6, excluding data from "23U" Pond). Peat waters are generally acid (Gorham and Cragg 1960) as a result of cation exchange processes.

However the alkalinity of "23U" Pond is no doubt a product of the higher HCO_3 concentrations in this water associated with higher levels of Ca. The pH of atmospheric precipitation varied from 6·0 to 6·9.

2.1.3.3. Phosphate (soluble)

PO_4 was never detected in Prion Lake or in "S" Pond, and it occurred only rarely in other plateau waters (Table 2.1.5). In contrast, high concentrations of phosphate were measured in ponds on the coastal terrace (Table 2.1.6, Figure 2.1.9) and in "23U" Pond (Figure 2.1.9). In these instances, summer values were generally higher than winter values, and there appeared to be a spring decrease associated with an increase in chlorophyll (Figure 2.1.9).

Peat water and soils are usually poor in phosphate (Gorham 1956). Notable exceptions to this were many of the coastal terrace ponds and the plateau water body "23U" Pond. This latter water body was atypical of the plateau lakes but resembled the coastal terrace ponds in that it supported luxuriant stands of the rooted aquatic plant *Myriophyllum elatinoides*. This plant, where it is abundant, probably plays an important role in the phosphorus cycle. The very high phosphate concentrations of some coastal terrace ponds are most probably due largely to effluents from adjacent seal wallows and pits of decomposing giant kelp.

2.1.3.4. Ammoniacal nitrogen, nitrite and nitrate

The absence of NO_3 in most waters may be due to its reduction to NO_2, during storage of the preserved samples, since NO_3 determinations were only made on the preserved samples after their return to Australia. High ammoniacal nitrogen concentrations may also partly arise from the effects of prolonged storage.

Ammoniacal nitrogen values for coastal terrace waters ranged from 80 to 900 mg/m³, which were higher than those for plateau waters, 6 to 220 mg/m³. The single unexpectedly high value for Prion Lake of 170 mg/m³ cannot be explained. Hutchinson (1957) records values of up to 250 mg/m³ for unpolluted natural waters. The presence of large populations of heterotrophic bacteria in the organically rich waters of the coastal terrace (see Section 2.1.3.5) may account for high ammoniacal nitrogen values measured in these.

NO_2 had a distribution similar to ammoniacal nitrogen (Tables 2.1.8 and 9). It is rare in plateau waters (2-23 mg/m³) but was present in high concentrations in coastal terrace waters (10 to 130 mg/m³).

NO_3, in contrast, appeared to be absent from most waters (Tables 2.1.8 and 9). Even if NO_2 concentrations are considered to represent oxidized nitrate, plateau waters would only contain 20 mg/m³ or less. NO_3 concentrations are generally low in peat waters. Gorham (1956) has found NO_3 concentrations in some English bog waters to lie within the range of less than 20 mg/m³ to 70 mg/m³. Unlike

TABLE 2.1.8

Ammoniacal nitrogen, nitrate and nitrite of Prion Lake, "S" Pond, "23U" Pond and Duck Lagoon (mg/m^3)

Date	Prion Lake			"S" Pond			"23U" Pond			Duck Lagoon		
	Ammon. N	NO_3	NO_2	Ammon. N	NO_3	NO_2	Ammon. N	NO_3	NO_2	Ammon. N	NO_3	NO_2
22.2.62		—	2					—	3			
26.2.62					—	20						
28.4.62		—	10					900	20			
1.5.62					—	6						
26.6.62								2,700	23			
27.6.62		—	16									
5.7.62					—	20						
27.7.62		—	16									
28.7.62								2,700	16			
7.8.62					—	13						
24.8.62		—	13									
2.9.62					—	13						
21.10.62					—	10						
1.11.62	170	—	16									
23.11.62				220	—	10				180	—	13
30.11.62							180	900	20			
24.12.62				Trace	—	20				300	—	70
11.3.63				25	—	Trace				110	—	Trace

other plateau waters, "23U" Pond was well supplied with NO_3 (Table 2.1.8), values ranging from 900 to 2,700 mg/m^3. Similar levels of NO_3 were measured in two coastal terrace ponds (Table 2.1.9).

NO_3 and NO_2 were absent from Kerguelen Island inland waters, and ammoniacal nitrogen was present in relatively low amounts (6 to 32 mg/m^3, Table 2.1.9).

2.1.3.5. Organic nitrogen and oxygen absorbed

Organic nitrogen and oxygen absorbed are both a measure of suspended and dissolved organic material.

The highest values for these determinations were obtained for the coastal terrace waters (excluding a single high and atypical value for "S" Pond on 10.1.62) for which the range 1·16 to 3·55 mg/l and 20·8 to 74·0 mg/l were obtained for organic nitrogen and oxygen absorbed respectively (Table 2.1.10). Slightly lower values were measured in plateau waters, where organic nitrogen content varied from 0·42 to 2·29 mg/l and oxygen absorbed from 4·8 to 20·6 mg/l (Table 2.1.10). As expected for waters in peat beds (or those that receive their water by drainage through peaty soils), all were well supplied with organic material. Some of the organic material, however, may have been supplied from atmospheric precipitation. Values of 1·35 to 2·15 mg/l and 3·5 to 17·8 mg/l were measured for organic nitrogen and oxygen absorbed respectively in the precipitation samples. Values obtained for Kerguelen Islands inland waters were similar to those for plateau waters of Macquarie Island (Table 2.1.10).

TABLE 2.1.9

Ammoniacal nitrogen, nitrate and nitrite of coastal terrace and plateau surface waters, Macquarie Island and some surface waters, Kerguelen Islands (mg/m^3)

Location	Date	Ammon. N.	NO_3	NO_2
	Coastal terrace waters, Macquarie Island			
"11P" Pond	30.1.63	410	—	10
"10P$_1$" Pond	30.1.63	170	600	90
"10P$_2$" Pond	30.1.63	900	1,200	130
"4R$_2$" Pond	14.1.63	840	—	80
"5W" Pond	14.1.63	80	—	30
"4R$_3$" Pond	14.1.63	780	—	130
"F$_5$" Pond	7.3.63	200	—	Trace
Precipitation Isthmus		360	—	—
	Plateau waters, Macquarie Island			
Scobles Lake		10	—	Trace
Scobles Lake Pond		30	—	Trace
Elder Lake (north)		6	—	—
North Head Pond		280–1,000	—	30–60
Precipitation Prion Lake		60	—	—
	Kerguelen Islands waters			
Fen Pond 18 m altitude	11.3.63	15	—	—
Small pond, Studer Lake I	11.3.63	30	—	—
Studer Lake I	11.3.63	32	—	—
Pond on scree	11.3.63	6	—	—

TABLE 2.1.10

Organic nitrogen and oxygen absorbed (mg/l) of inland waters, Macquarie and Kerguelen Islands

	Plateau			Coastal Terrace			Kerguelen	
Location	Org. N	O_2 abs.	Location	Org. N	O_2 abs.	Location	Org. N	O_2 abs.
Prion Lake	1·34	4·8	Duck Lagoon	1·16–2·38	2·08–26·0	1	1·14	6·2
“S” Pond	0·42–2·24	14·1–20·6	“11P” Pond	2·45	69·0	2–3	1·06	5·8
“23U” Pond	2·29	5·5	“$10P_1$” Pond	2·05	50·0	4	0·59	1·7
Scobles Lake	0·64	9·2	“$10P_2$” Pond	2·94	74·0	5	0·59	4·9
Scobles Lake Pond	0·44	12·8	“$4R_2$” Pond	3·55	43·0			
Elder Lake (north)	0·51	14·5	“5W” Pond	1·62	22·0			
North Head Pond	1·76–2·67	22·6–31·7	“$4R_3$” Pond	1·55	36·0			
Precipitation Isthmus	2·15	17·8	“F_5” Pond	1·90	22·6			
Precipitation Prion Lake	1·35	3·5						

TABLE 2.1.11

Colloidal silica, iron and aluminium oxide, and soluble iron (mg/l) of inland waters, Macquarie and Kerguelen Islands

Location	Colloidal silica	Al. and iron oxides	Sol. Fe
Plateau waters, Macquarie Island			
Prion Lake mean	1·7	0·20	0–0·06 (?)
"S" Pond mean	1·9	0·40	Trace–0·08
"23U" Pond	6·5	0·20	Trace–0·08
Scobles Lake	3·7	0·70	Trace
Scobles Lake Pond	1·6	0·12	Trace
Elder Lake (north)	2·5	1·00	Trace
North Head Ponds	1·6–40·6	2·60–51·90	Trace
Prion rainwaters	2·7	1·10	Trace
Coastal terrace waters, Macquarie Island			
Duck Lagoon (before storm)	5·4	0·50	0·06
Duck Lagoon (after storm)	3·8	0·70	Trace
"11P" Pond	6·6	0·70	Trace
"10P$_1$" Pond	9·8	3·00	Trace
"10P$_2$" Pond	3·5	1·00	Trace
"4R$_2$" Pond	8·7	1·60	Trace
"5W" Pond	6·3	1·00	Trace
"4R$_3$" Pond	2·9	1·40	Trace
"F$_5$" Pond	7·0	8·60	Trace
Isthmus rainwater	50·6	20·00	Trace
Kerguelen Islands waters			
1	14·1	2·80	—
2–3	1·6	0·50	Trace
4	2·4	0·50	—
5	1·6	0·80	—

2.1.3.6. Colloidal silica, iron and aluminium oxide and dissolved iron

Plateau waters generally contained lower concentrations of silica than coastal terrace waters (Table 2.1.11). In both cases the silica present could be accounted for by the amounts supplied from atmospheric precipitation. The mean concentrations of silica in "23U" Pond and Duck Lagoon of 6·5 and 5·4 mg/l respectively were higher than those for "S" Pond and Prion Lake of 1·9 and 1·7 mg/l respectively. No obvious pattern of seasonal variation is apparent from the few measurements available (Figure 2.1.9/3).

Aluminium and iron oxides were also found in higher concentrations in coastal terrace waters than in plateau waters (Table 2.1.11). Since all samples analysed were collected from surface waters, the amount of iron present was correspondingly low (Table 2.1.11). Occasional values as high as 0·08 mg/l were measured. In some small ponds large amounts of a flocculent, reddish precipitate of ferric hydroxide were observed.

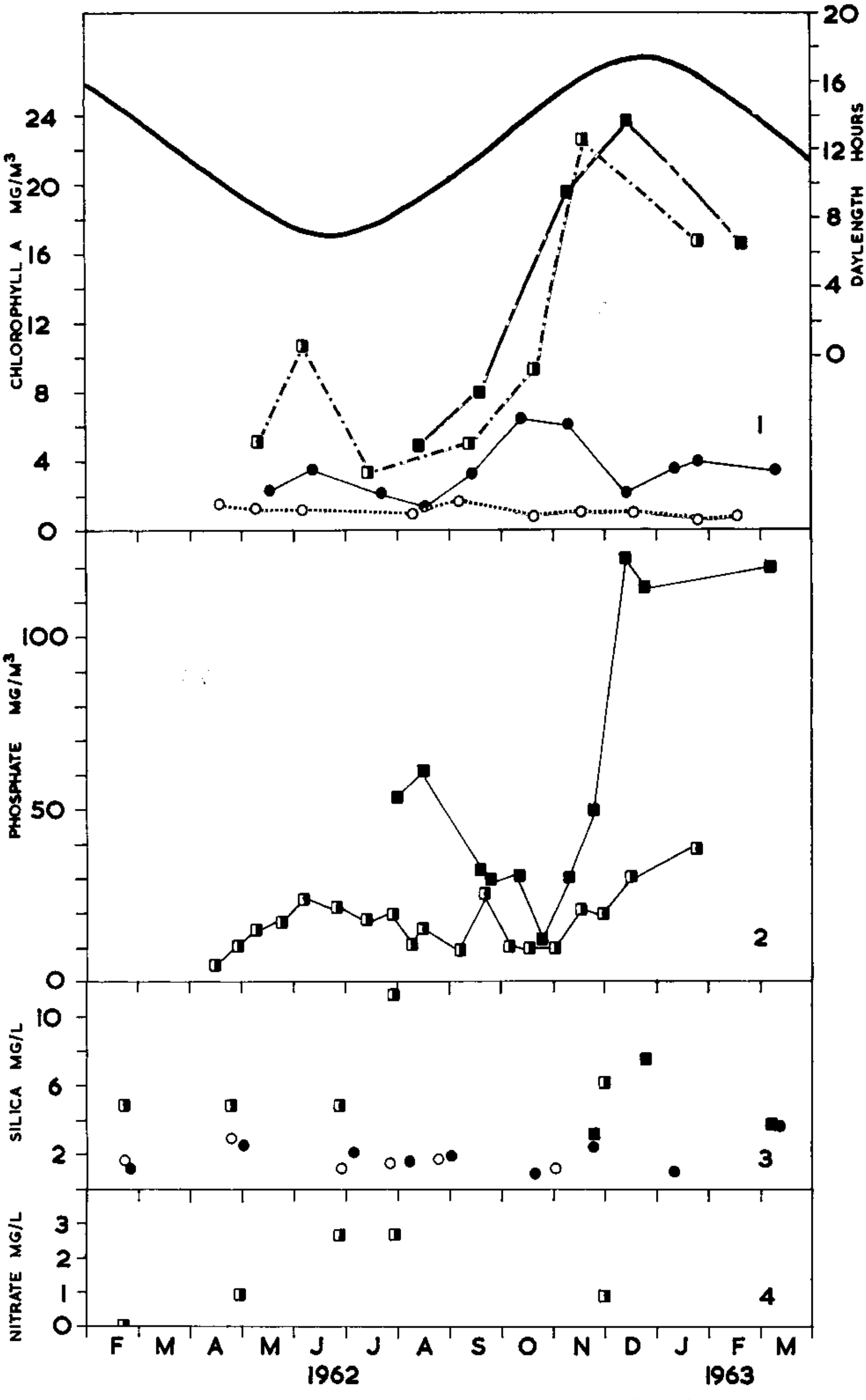


FIGURE 2.1.9. Seasonal distribution of (1) chlorophyll *a*; (2) phosphate (soluble); (3) silica. ○ Prion Lake; ● "S" Pond; ◨ "23U" Pond; ■ Duck Lagoon.

TABLE 2.1.12

Dissolved oxygen, Prion Lake

Date	Stn.	Mean temp. °C	Air press. mm Hg	O_2 mg/l Surf.	5 m	10 m	15 m	20 m	25 m	Mean O_2 mg/l
24.8.62	A	5·3	733	11·18	11·29	11·26	11·18	11·21	11·21	11·24
	B			11·26	11·32	11·32	11·26	11·18		
8.5.62	A	4·4	723	11·65	11·32	11·24	11·23	11·17	11·27	11·29
	B			11·33	11·30	11·30	11·30	11·37		
23.5.62	A	5·0	748	11·78	11·74	11·78	11·74	11·72	11·70	11·73
	B			11·74	11·70	11·70	11·70	11·70		
5.6.62	A	4·1	721	11·70	11·69	11·70	11·70	11·70	11·69	11·63
	B			11·66	11·55	11·61	11·55	11·37		
25.6.62	A	2·8	732	11·73	11·61	11·60	11·57	11·65	11·65	11·65
	B			11·73	11·67	11·62		11·70		
12.7.62	A	1·7	750	12·39	12·39	12·37	12·29	12·35	12·39	12·36
27.7.62	A	1·6	723	12·37	12·39	12·36	12·34	12·39	12·30	12·36
9.8.62	A	1·5	732	12·26	12·18	12·11	12·14	12·23	12·26	12·20
	B			12·26	12·23	12·23	12·18	12·14		
24.8.62	A	1·0	735	12·58	12·54	12·56	12·52	12·62	12·58	12·56
	B			12·58	12·54	12·54	12·54	12·54		
11.11.62	A	5·4	732	11·17	11·22	11·17	11·19	11·19	11·20	11·19
24.1.63	A	7·4	720	10·85	10·86	10·86	10·86	10·82	10·82	10·85

2.1.3.7. Oxygen (dissolved)

Determinations of dissolved oxygen were only made at Prion Lake. Here oxygen concentrations showed no variation with depth (Table 2.1.12). It is obvious, both from this result and that in Sect. 2.1.2.2, that the water of Prion Lake is in complete and continual circulation. Little seasonal change in the percentage saturation of oxygen occurred (Table 2.1.12). The mean saturation value for the period of observation (values corrected for pressure) was 94·8%. The orthograde distribution of oxygen found in Prion Lake is a characteristic feature of oligotrophic lakes (Ruttner 1953).

2.1.3.8. Chlorophyll *a*

Chlorophyll *a*, which is universally distributed in all photosynthesizing plants, was measured to obtain an estimate of the standing crop of phytoplankton. Good correlations between chlorophyll and biomass, and chlorophyll and productivity, have been obtained (Emerson *et al.* 1940; Riley 1941; Ryther and Yentsch 1957, 1958; Burkholder and Sieburth 1961).

The results of chlorophyll *a* determinations are shown in Figure 2.1.9. With the exception of Prion Lake, for which values were always below 1·62 mg/m^3, a spring increase (Sept.-Oct.) was found to occur in all the water bodies investigated. This increase coincided both with the onset of increasing daylength (Figure 2.1.9) and an increase in water temperatures (Figure 2.1.5). A December decrease in chlorophyll *a* in "S" Pond was probably due to the "flushing effect" of an increase in precipitation occurring between late November and early December (Figure 2.1.8). Summer chlorophyll *a* values for "23U" Pond and Duck Lagoon were higher than those for Prion Lake and "S" Pond (Figure 2.1.9) and reached maxima of 25·55 and 23·67 mg/m^3 respectively. A single measurement from a coastal terrace pond ($4R_3$) on 14.1.63 gave a result of 17·3 g/m^3, and on 9.3.63 a plateau lake, Scoble Lake, had a concentration of 4·25 g/m^3.

The low chlorophyll *a* concentration in Prion Lake would be expected from its high Secchi disc transparency measurements (Atkins *et al.* 1954).

2.1.3.9. Factors affecting the primary productivity of Macquarie Island inland waters

The common marine origin of the major ions occurring in the inland waters of Macquarie Island accounted for the uniformity of their chemical composition. The differences in the total concentrations of these ions can largely be attributed to the distance, in the direction of the prevailing wind, of the water body from the sea. However, it is the concentration of nutrient ions such as PO_4 and NO_3 which are more likely to influence primary productivity. The highest chlorophyll concentrations (a measure of the photoplankton standing crop) occurred in "23U" Pond and Duck Lagoon, both of which had phosphate-rich waters. In "S" Pond and Prion Lake, where no measurable amounts of soluble PO_4 were encountered, chlorophyll values were correspondingly low.

The supply of PO_4 to the surface waters mainly depends upon its rate of release from the bottom or littoral sediments (Hutchinson 1957). Under aerobic conditions (at bottom/mud-water interface) PO_4 is held in the bottom muds associated with ferric hydroxide complexes (Mortimer 1941). Since the deeper waters of Prion Lake are always well supplied with oxygen, aerobic conditions at the surface of the bottom muds would prevent the release of nutrients obtained from the surface waters in the sedimenting seston. Moreover, these aerobic conditions would inhibit the release of PO_4 from organic materials by bacterial decomposition. Anaerobic bottom conditions, by reversing the above processes, promote the release of soluble PO_4 into overlying waters. In "23U" Pond and Duck Lagoon where dense stands of *Myriophyllum* occur, it is probable that the vegetation stabilizes the water column sufficiently, to allow for the development of such anaerobic conditions in the bottom waters. Further, both Hutchinson (1957), and Hayes and Phillips (1958) using radioactive phosphorus have established the importance of the role of rooted littoral vegetation in recycling epilimnetic phosphorus. They indicated that in shallow water bodies it may well constitute the major source of PO_4.

NO_3 concentrations in Duck Lagoon, "S" Pond and Prion Lake were low, even when all the NO_2 in these waters is considered to represent reduced NO_3. Since "23U" Pond water was well supplied with NO_3 and had similar chlorophyll concentrations to Duck Lagoon (in which no NO_3 was found) the nutrient role of nitrate in these waters is not clear. The inhibition of nitrification by acid waters (Hutchinson 1957) may partly account for the absence of NO_3 in "S" Pond waters.

Although silica has been found to be a limiting factor in some natural waters, on Macquarie Island it is present in sufficient concentrations to make this situation improbable.

The effect of dissolved organic material on primary productivity is unknown. It may be important in the maintenance of PO_4 in the epilimnetic waters as a result of the activity of the associated bacterial populations (Hayes and Phillips 1958). "23U" Pond, Duck Lagoon and "S" Pond were all well supplied with organic material, whereas lower concentrations occurred in Prion Lake.

Areal productivity is frequently directly dependent on mean depth (Gorham 1958; Frey and Stahl 1958). Prion Lake, which has a mean depth of 17·5 m, would therefore be expected to be less productive than "23U" Pond, Duck Lagoon and "S" Pond, none of the latter having mean depths greater than 1·25 m.

It is apparent from both the foregoing discussion and the previous results that Prion Lake must be regarded as an oligotrophic water body. Its orthograde oxygen distribution, low nutrient and chlorophyll concentrations, high transparency and morphometric data all support this conclusion. In contrast, "23U" Pond and Duck Lagoon produced large phytoplankton standing crops and were generally rich in nutrient ions. The level of primary productivity in "S" Pond must be regarded as being intermediate between those of the latter water bodies and Prion Lake.

In conclusion, the conditions which are most likely to influence the nutrient status of the inland waters are the presence of the rooted aquatic *Myriophyllum elatinoides* and the supply of decomposition products from seal wallows and giant kelp.

2.2. POSTEMBRYONIC DEVELOPMENTAL STAGES

Pseudoboeckella brevicaudata passes through 6 naupliar and 5 copepodid stages before developing into the final adult form. In this section a brief description of the immature stages, sufficient for their identification, is given, together with a more detailed description of the adult stages. These descriptions have been made from specimens collected from Macquarie Island. No previous account of the immature stages of *P. brevicaudata* exists. Brady (1918) has briefly described the adults of this species from Macquarie Island and brief descriptions of adults from other localities have been published (Mrazek 1901; Ekman 1905; Scott 1914; Brehm 1953).

2.2.1. *Adult stages*

Female

Size. Length 1·42-2·50 mm.

Body (Figures 2.2.1/5, 7, 8).

Metasome. Consists of one cephalic and 5 thoracic segments. Lateral margins of last thoracic segment extend posteriorly in the form of two projections (metasomal wings). Right metasomal wing bilobed, and smaller than left. Left metasomal wing with small coniform bulge on inner margin.

TABLE 2.2.1

Distribution of setae, spines and aesthetes on antennules of adult males and females (not including right geniculate male antennule)
s = spines; a = aesthetes

Locality	No. obs.	Antennule segment																								
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
"23U" Pond	30	1, 1a	3, 1a	1, 1a	2	2, 1a	1	2, 1a	1, 1s	2, 1a	1	1, 1a	1, 1s, 1a	1	1, 1a	1, 1a	1, 1a	1, 1a	1	1, 1a	1	1	2	2	2	5, 1a
Duck Lagoon	30	1, 1a	3, 1a	1, 1a	2	2, 1a	1	2, 1a	1, 1s	2, 1a	1	1, 1a	1, 1a, 1s	1	1, 1a	1, 1/0a	1, 1a	1, 1a	1	1, 1a	1	1	2	2	2	5, 1a
Prion Lake	30	1, 1a	3, 1a	1, 1a	2	2/1, 1a	1	2, 1a	1, 1s	2, 1a	1	1, 1a	1, 1a, 1s	1	1, 1a	1, 1a	1, 1a	1, 1/0a	1	1, 1a	1	1	2	2	2	5, 1a

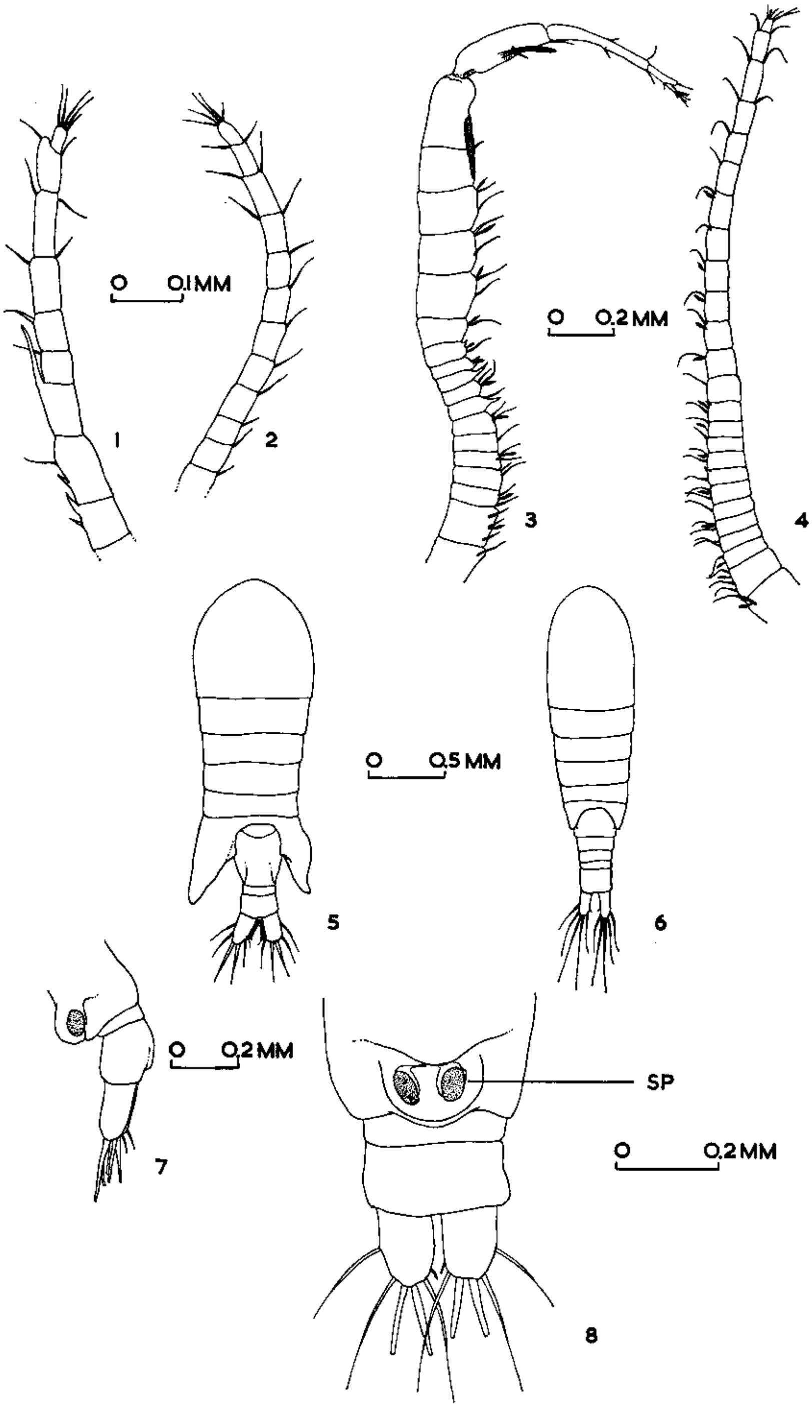


FIGURE 2.2.1. (1) Right antennule (terminal segments) of male copepodids 4 and 5; (2) left antennule (terminal segments) of male copepodids 4 and 5, and right and left antennule of female copepodids 4 and 5; (3) right antennule, male adult (showing aesthetes); (4) left antennule, male adult, and right and left antennule of female adult (showing aesthetes); (5) dorsal view of body of adult female; (6) dorsal view of body of adult male; (7) lateral view of adult female urosome; (8) ventral view of adult female urosome (SP: spermatheca).

Urosome. Three-segmented. Caudal rami lined on inner margins with fine hairs. First urosome segment with ventral hemispherical bulge containing paired spermathecae, connected by paired ducts to a chamber below the crescent-shaped genital opening. Ovigerous females carry a single egg sac attached medially to genital opening. Egg sacs contained 1-63 eggs.

Colour. Cuticle blue to colourless. Body, red to pale orange.

Antennules (Figures 2.2.1/4, Table 2.2.1).

Twenty-five-segmented. Extend to first urosome segment. Arrangement of setae and aesthetes very constant.

Antennae (Figures 2.2.2/1).

Exopod 7-segmented; second segment with 2 incomplete sutures; seta formula 1.3.1.1.1.1.4. Endopod 2-segmented; seta formula 2.16; distal segment with 11 stout and 5 smaller terminal setae.

Mandibles (Figures 2.2.2/2).

Exopod 4-segmented; seta formula 1.1.1.3. Endopod 2-segmented; seta formula 4.9; distal segment with 6 stout and 3 smaller setae. Basis with 4 setae. Masticatory process with 8 teeth and 1 spine.

Maxillules (Figures 2.2.2/3).

Exopod with 8 setae. Endopod with 13 setae and 3 incomplete sutures. Epipod with 9 stout setae. Two inner lobes with 3 and 4 setae respectively. Gnathobase with 9 or 10 stout teeth and 5 setae.

Maxillae (Figures 2.2.2/4).

Sutures incomplete. Single large spiniform tooth arising from a cylindrical lobe; a pair of denticulate margins line the inner face of this tooth.

Maxillipeds (Figures 2.2.2/5).

Seven-segmented; seta formula (including teeth) 10.3.2.2.2.3.4; segment 1 bears a curved tooth arising from a papillate process on its distal inner margin; segments 3, 4 and 5 each with a single curved tooth.

TABLE 2.2.2

Setation of swimming legs of adult female (pairs 1-4, the same as those for adult male)

Pair	Exopod segment			Endopod segment		
	1	2	3	1	2	3
1	1	2	6	1–2	0–1	4–5
2	2	2	7–8	1	1–2	5–8
3	2	2	7–8	1	1–2	6–8
4	2	2	7–8	0–1	1–3	4–8
5	1	2	7	1	1–2	5–6

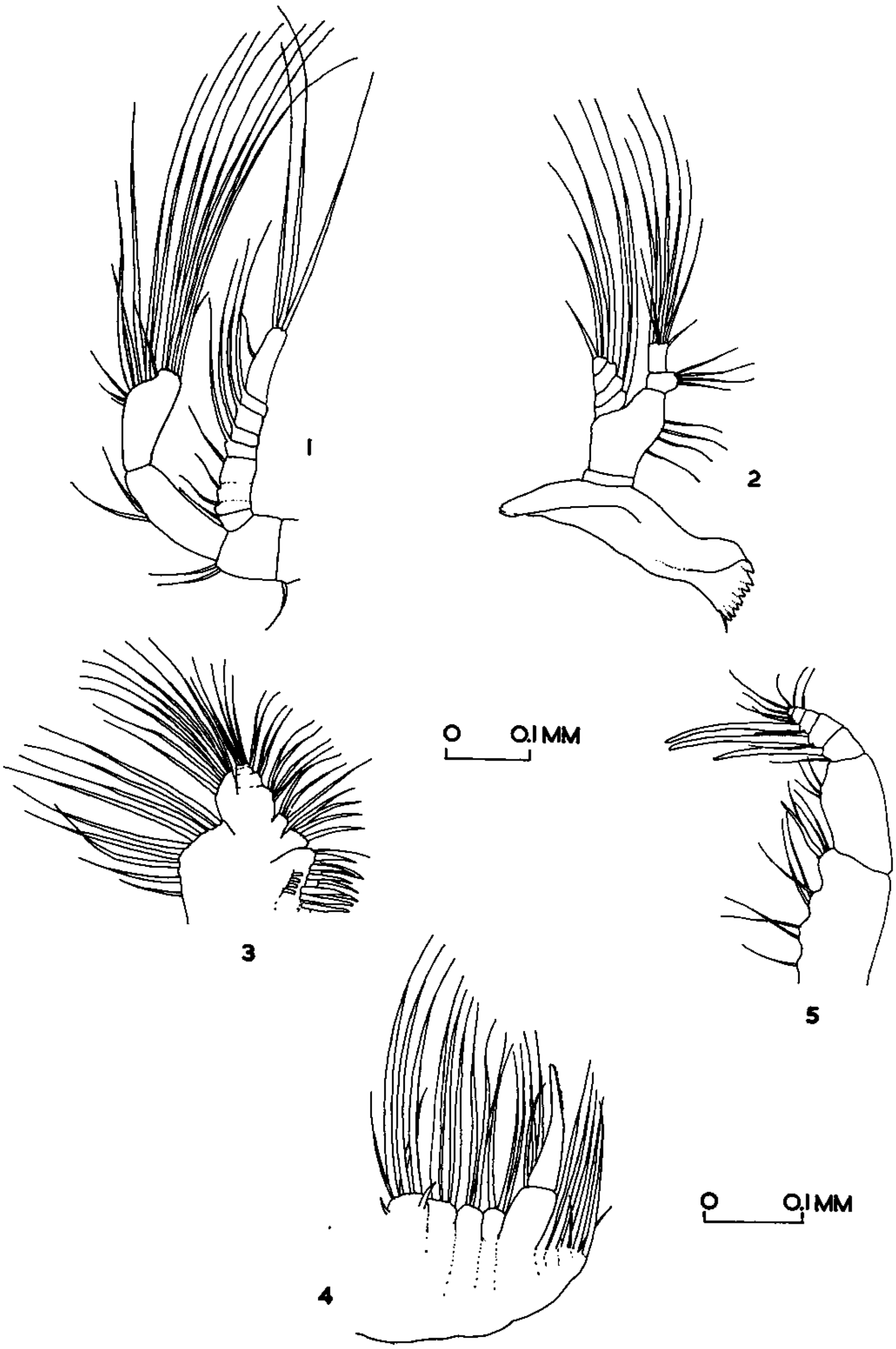


FIGURE 2.2.2. Mouthparts (adult): (*1*) antenna; (2) mandible; (3) maxillule; (4) maxilla; (5) maxilliped.

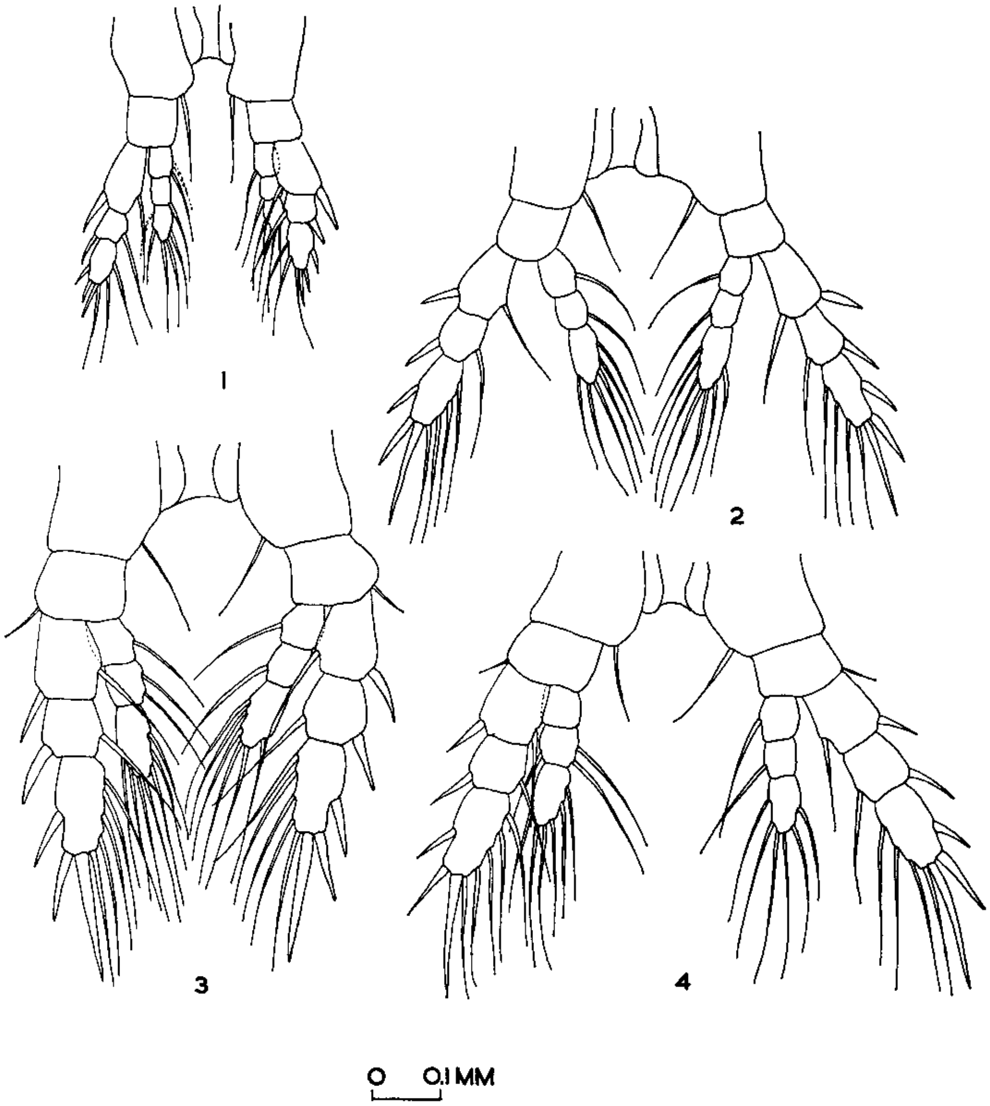


FIGURE 2.2.3. Swimming legs (adult): (1) first legs; (2) second legs; (3) third legs; (4) fourth legs.

Legs 1-4 (Figure 2.2.3, Table 2.2.2).

Exopods and endopods all 3-segmented; number and arrangement of setae variable, commonly asymmetrically distributed.

Legs 5 (Figure 2.2.5, Table 2.2.2).

Exopod and endopod 3-segmented; number and arrangement of setae show little variation; second segment of exopod with a stout, curved, spine-like process bearing a pair of denticulate margins (see Section 1.2.4).

Male

Size. Length 1·25-2·05 mm.

Body (Figures 2.2.1/6).

Narrower and smaller than female.

Metasome. As in adult female, except metasomal wings absent.

Urosome. Five-segmented; genital opening in first segment; hairs absent from inner margins of caudal rami; setae as in female.

Colour. As in adult female.

Antennules (Figures 2.2.1/3, 4).

Left antennule 25-segmented, as in female. Right antennule is a prehensile appendage (geniculate) of 22 segments, longer than left antennule; segments 8, 10 and 11 with spinous projections; an articulating joint between segments 18 and 19; segment 20 with an incomplete suture; segment 21 with a terminal cylindrical projection extending to the middle of segment 22.

Antennae, etc. These and mouth-parts as in adult female.

Legs 1-4. As in adult female.

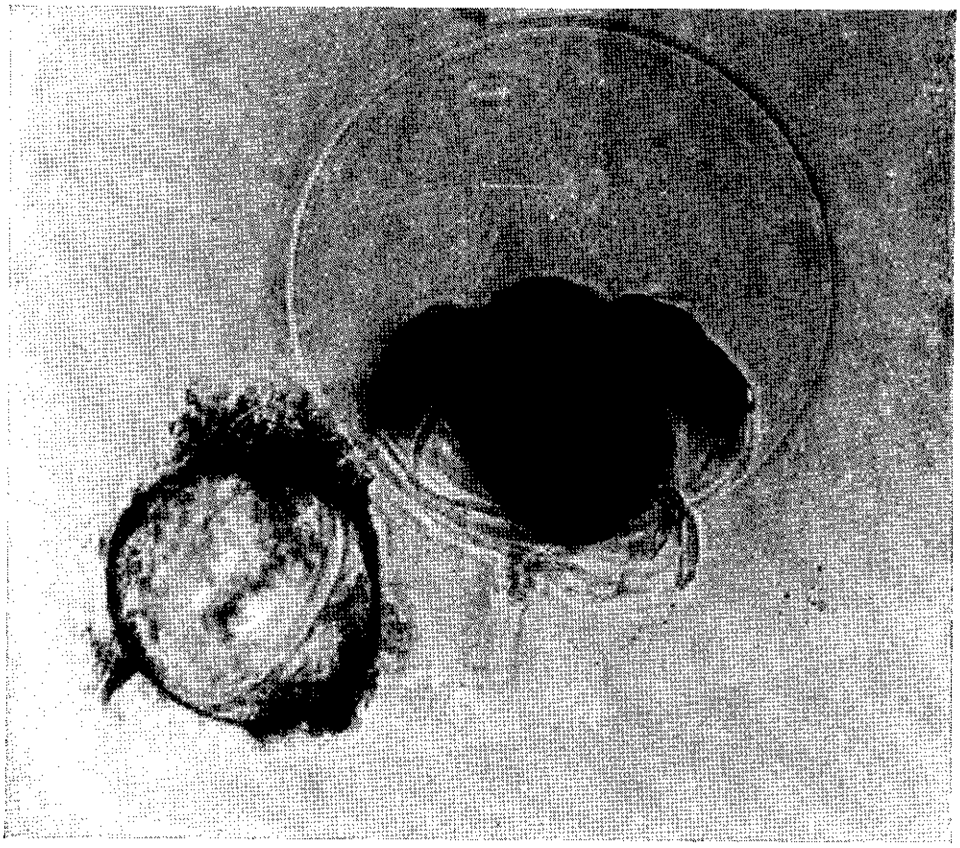
Legs 5 (Figure 2.2.5). Both exopods with a terminal claw and a single stout seta on segments 1 and 2. Right endopod 3-segmented with 1 small terminal spine and 2 terminal setae on distal segment; terminal setae unequal and variable in length; rarely an additional lateral seta on distal segment (Prion Lake and "S" Pond populations); proximal segment with a lobe-like projection on inner margin. Two processes, one cylindrical (vestigial left endopod) and another triangulate and lamellate arise from left basis near base of left exopod.

2.2.2. *Immature stages*

2.2.2.1. Egg and hatching (Plate 2.2.1)

The eggs are spherical, pale orange to deep red, and densely packed with yolk granules. The diameter varies from 0·15 to 0·22 mm. The embryo is contained within two membranes. The outer membrane or shell is transparent, colourless, inelastic and chitinous and has a fracture line along its circumference. When hatching commences, this membrane breaks along the fracture line into two equal hemispheres between which the inner membrane containing the nauplius bulges. The thin, colourless, transparent inner membrane (free of the outer shell) continues to expand until it bursts, releasing the nauplius. The time for hatching, from the rupture of the outer membrane to the rupture of the inner membrane, is 10 to 15 minutes.

Initially, swelling of the inner membrane is very rapid. Bursting occurs frequently without any associated activity of the nauplius. It is probable that both swelling and rupture of this membrane are caused by an osmotic uptake of water. Similar hatching processes have been described for other freshwater calanoid copepods (Davis 1959; Marshall and Orr 1954). Eggs of *P. brevicaudata* differ from those of other calanoids (Davis 1959; Marshall and Orr 1954) in having a thicker outer membrane or shell which has a definite fracture line.



ANARE photo A. J. Evans

PLATE 2.2.1. Hatching of *P. brevicaudata* egg. Nauplius 1 is shown contained within the swelling inner membrane. The outer membrane (broken open into 2 hemispheres) is alongside.

2.2.2.2. Nauplius stages

Nauplii are characterized by the absence of body segmentation and swimming legs, and the possession of 3-segmented antennules. Colour of the body varies from pale orange to deep red. The shape of the body and the setation of the distal segments of the antennules were the main characters used to identify the naupliar stages.

Nauplius 1 (Figures 2.2.4/1, 7, Plate 2.2.1)

Size. Length 0·20-0·23 mm.
Body. Globose with caudal region rounded.
Antennules. Distal segment with 3 terminal setae.

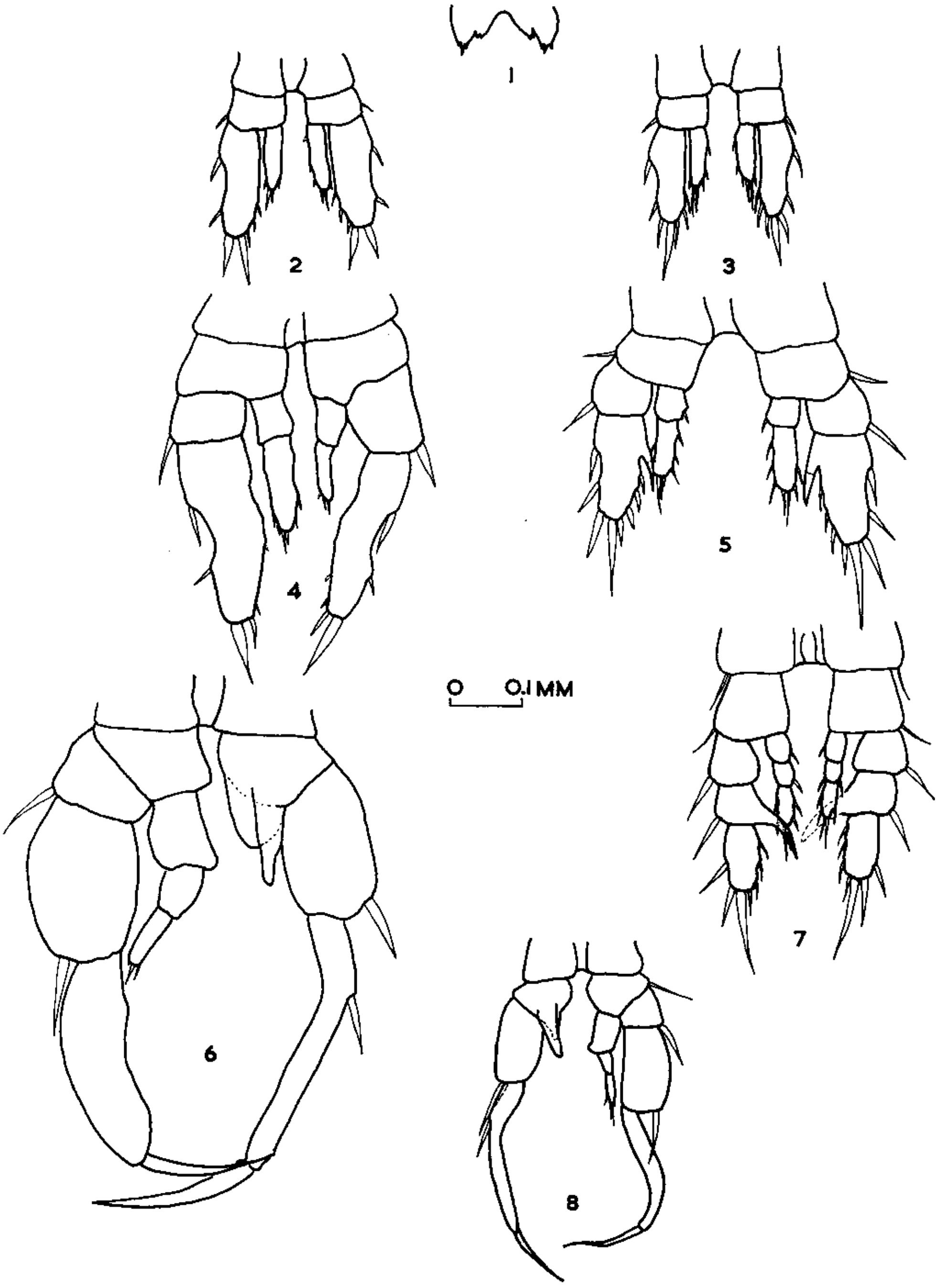
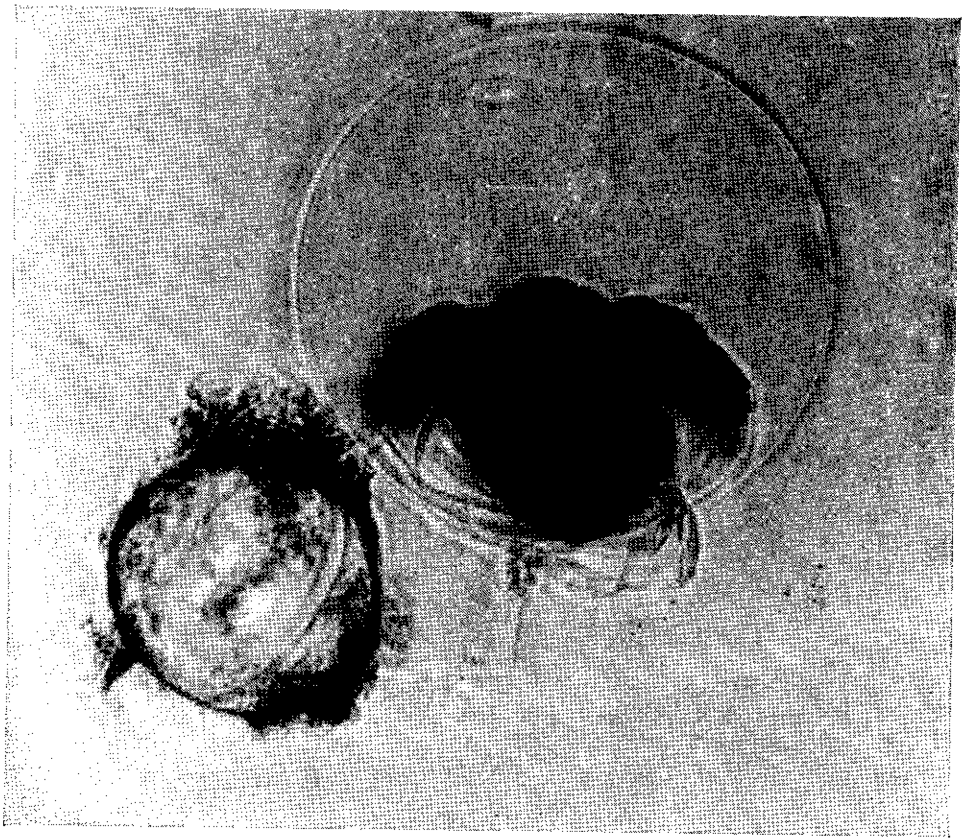


FIGURE 2.2.5. Fifth pair of legs: (1) copepodid 3, male and female; (2) copepodid 4, male; (3) copepodid 4, female; (4) copepodid 5, male; (5) copepodid 5, female; (6) adult, male; (7) adult, female; (8) adult, male (Prion Lake).

copepods (Davis 1959; Marshall and Orr 1954). Eggs of *P. brevicaudata* differ from those of other calanoids (Davis 1959; Marshall and Orr 1954) in having a thicker outer membrane or shell which has a definite fracture line.



ANARE photo A. J. Evans

PLATE 2.2.1. Hatching of *P. brevicaudata* egg. Nauplius 1 is shown contained within the swelling inner membrane. The outer membrane (broken open into 2 hemispheres) is alongside.

2.2.2.2. Nauplius stages

Nauplii are characterized by the absence of body segmentation and swimming legs, and the possession of 3-segmented antennules. Colour of the body varies from pale orange to deep red. The shape of the body and the setation of the distal segments of the antennules were the main characters used to identify the naupliar stages.

Nauplius 1 (Figures 2.2.4/1, 7, Plate 2.2.1)

Size. Length 0·20-0·23 mm.
Body. Globose with caudal region rounded.
Antennules. Distal segment with 3 terminal setae.

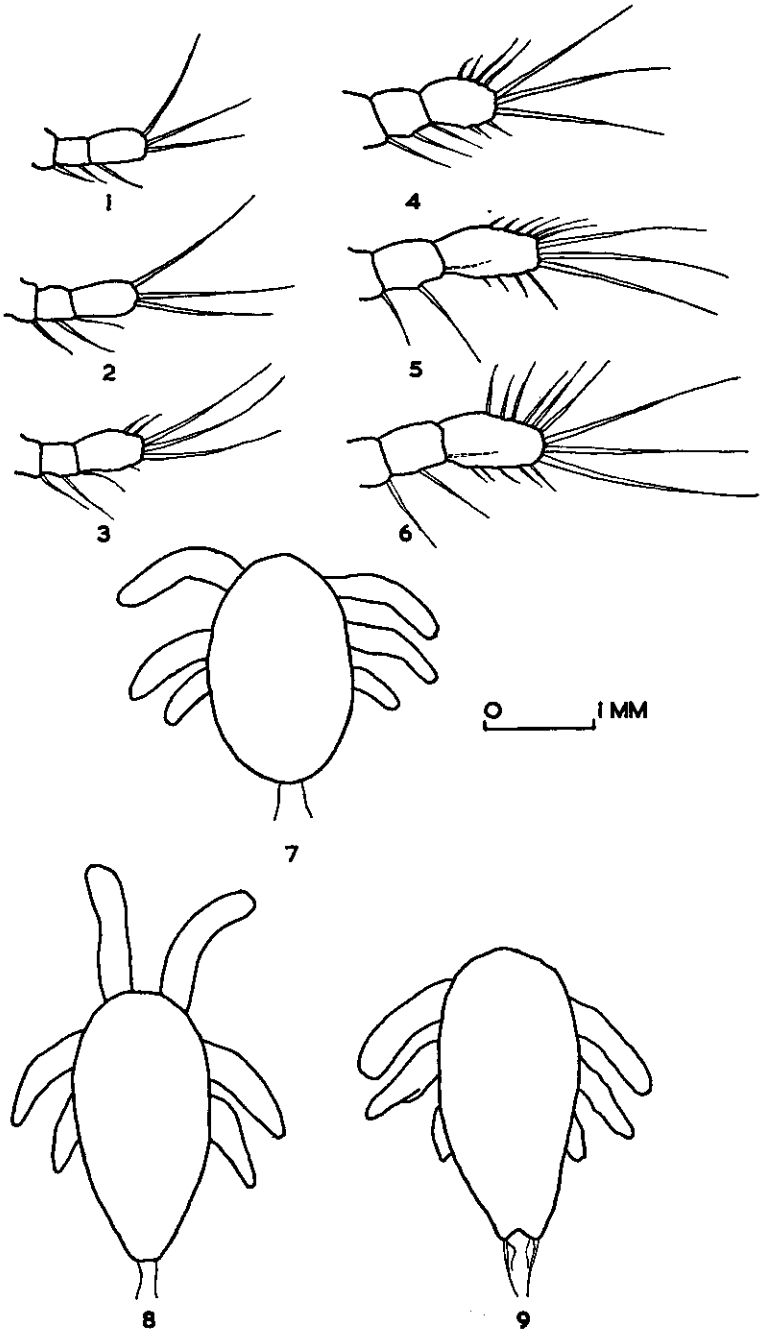


FIGURE 2.2.4. Nauplius stages: (1) antennule, nauplius 1; (2) antennule, nauplius 2; (3) antellule, nauplius 3; (4) antennule, nauplius 4; (5) antennule, nauplius 5; (6) antennule, nauplius 6; (7) dorsal view of nauplius 1; (8) dorsal view of nauplius 2; (9) dorsal view of nauplius 3.

Antennae. Exopod with 6 setae; endopod with 2 lateral and 2 terminal setae. Mandibles; exopod with 5 setae; endopod with 6 setae.

Nauplius 2 (Figures 2.2.4/2, 8)

Size. Length 0·23-0·25 mm.

Body. Elongate and tapering to a blunt end caudally.

Antennules. As in Nauplius 1.

Antennae. Exopod with 7 setae; endopod with 3 terminal and 3 lateral setae. Mandibles; exopod with 6 setae; endopod with 9 setae.

Nauplius 3 (Figures 2.2.4/3, 9)

Size. Length 0·25-0·28 mm.

Body. Elongate with cleft in caudal region separating caudal rami.

Antennules. Distal segment with 3 terminal, 1 ventral and 2 dorsal setae.

Nauplius 4 (Figures 2.2.4/4)

Size. Length 0·28-0·34 mm.

Body. As in Nauplius 3.

Antennules. Distal segment with 3 terminal, 3 ventral and 4 dorsal setae. Maxillules present; rudimentary and bilobed.

Nauplius 5 (Figures 2.2.4/5)

Size. Length 0·34-0·42 mm.

Body. As in previous stage, although caudal region more elongated.

Antennules. Distal segment with 3 terminal, 4 ventral and 6 dorsal setae. Maxillules further developed. Maxilla present; rudimentary.

Nauplius 6 (Figures 2.2.4/6)

Size. Length 0·41-0·53 mm.

Body. As in previous stage.

Antennules. Distal segment with 3 terminal, 5 ventral and 6 dorsal setae. Maxillipeds present; rudimentary. Other mouth-parts further developed. First and second pairs of legs present; rudimentary.

2.2.2.3. Copepodid stages

Copepodids have segmented bodies divided into metasome and urosome. Colour of the body varies from pale orange to red. The number of pairs of swimming legs, the segmentation and setation of the fifth pair of legs and the segmentation of the urosome were the main characters used in identifying the copepodid stages. External morphology cannot be used to distinguish between sexes until the 4th copepodid stage.

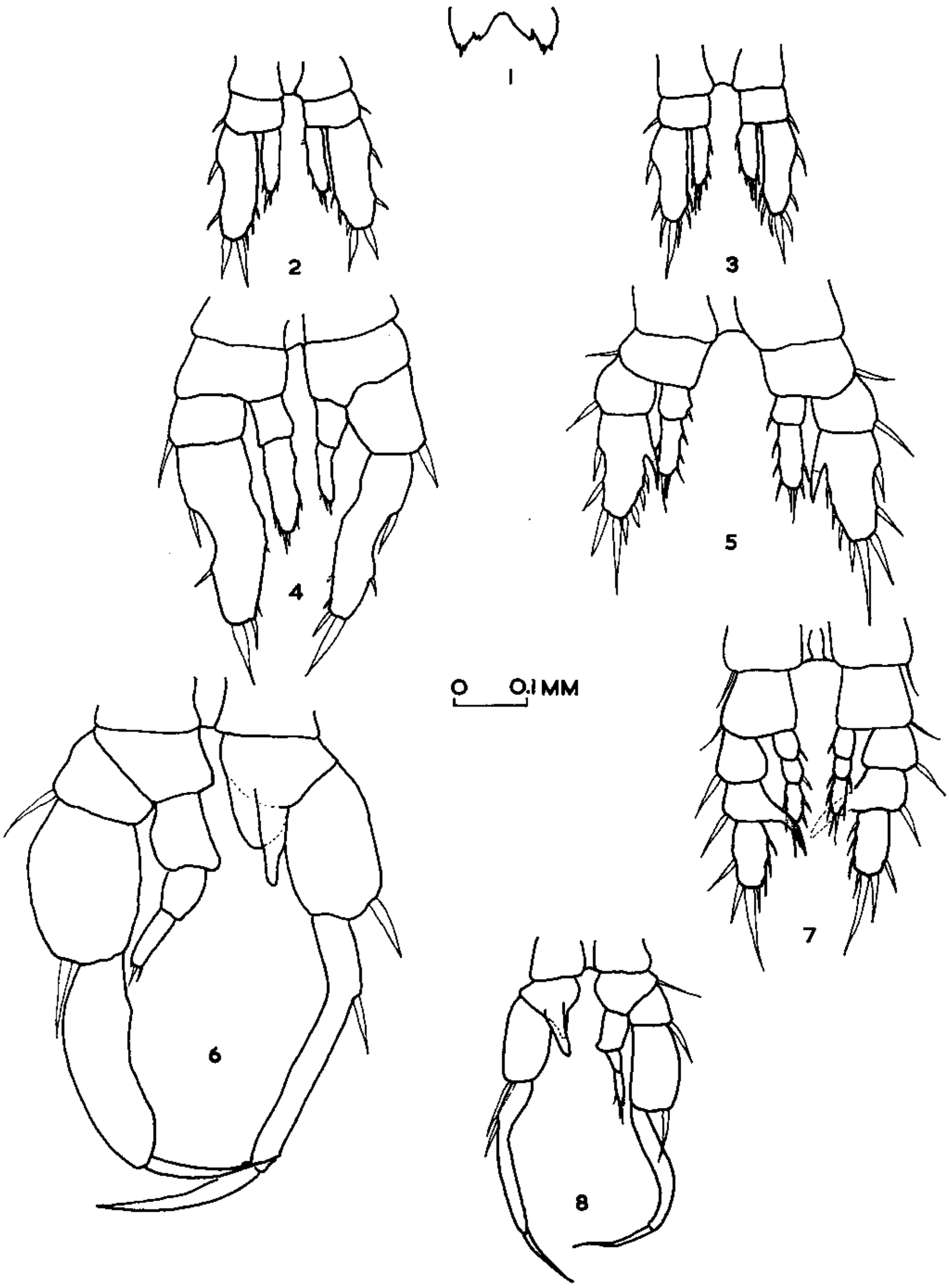


FIGURE 2.2.5. Fifth pair of legs: (1) copepodid 3, male and female; (2) copepodid 4, male; (3) copepodid 4, female; (4) copepodid 5, male; (5) copepodid 5, female; (6) adult, male; (7) adult, female; (8) adult, male (Prion Lake).

Copepodid 1

Size. Length 0·56-0·74 mm.
Urosome. One-segmented.
Legs. Three pairs; third pair rudimentary.

Copepodid 2

Size. Length 0·78-0·84 mm.
Urosome. One-segmented.
Legs. Four pairs; fourth pair rudimentary.

Copepodid 3 (Figures 2.2.5/1)

Size. Length 1·10-1·25 mm.
Urosome. Two-segmented.
Legs. Five pairs, fifth pair rudimentary.

Copepodid 4 (Figures 2.2.1/1, 2.2.5/2, 3)

Size. Length: female 1·30-1·60 mm; male 1·30-1·58 mm.
Urosome. Female: 3-segmented.
Male: 3-segmented.
Legs. Female: fifth pair symmetrical; exopod 1-segmented with 7 setae; endopod 1-segmented with 6 setae.
Male: fifth pair asymmetrical; exopods 1-segmented with 7 setae; endopods 1-segmented, right with 5-6 setae and left with 4 setae.
Antennules. Female: antennules symmetrical and 25-segmented.
Male: right antennule longer than left; both antennules 25-segmented; segments 17, 18, 19 of right antennule bearing spines, absent in left and female antennules.

Copepodid 5 (Figures 2.2.5/4, 5)

Size. Length: female 1·63-1·95 mm; male 1·63-1·78 mm.
Urosome. Female: 3-segmented.
Male: 4-segmented.
Legs. Female: fifth pair symmetrical; exopod 2-segmented with seta formula 1.8 and a stout spine arising from inner margin of distal segment; endopod 2-segmented with seta formula 1.7.
Male: fifth pair asymmetrical; right exopod larger than left, both 2-segmented, seta formula 1.5-6; endopods 2-segmented; right endopod much larger than left, seta formula 0.6; seta formula of left endopod 0.2-3.
Antennules. Female: antennules as in previous stage.
Male: antennules as in previous stage.

2.3. SYSTEMATICS AND DISTRIBUTION

Prior to the consideration of the distribution of *P. brevicaudata* and its relationship to other closely related species of the same region, some attention must be given to the taxonomic descriptions of the genus *Pseudoboeckella*. This is necessary since, at the present time, it is impossible to clearly distinguish this genus from the closely related genus *Boeckella*.

Pseudoboeckella and *Boeckella,* together with *Parabroteus,* represent the only members of the 8 freshwater genera of the family Centropagidae which occur within the subantarctic and antarctic regions.

2.3.1. *The genus Pseudoboeckella Mrazek 1901*

Mrazek (1901) created the genus *Pseudoboeckella,* distinguishing it from *Boeckella* de Guerne and Richard 1889. However, his description was inadequate and Marsh (1924) and Ringuelet (1958) subsequently used the structure of the fifth pair of legs of the male to distinguish between the genera. Unfortunately, there is disagreement between these authors and accordingly the generic descriptions of both authors are given here:

> *Boeckella* (after Marsh 1924). Endopods of male fifth pair of legs 1- to 3-segmented; if 3-segmented, without setae on terminal segment, otherwise setae may be present although rare.
>
> (After Ringuelet 1958.) Endopods of male fifth pair of legs 1- to 3-segmented, without hairs or spines. Females, relatively small with long antennules reaching to caudal rami; rarely shorter, always reach beyond first urosome segment.
>
> *Pseudoboeckella* (after Marsh 1924). Right endopod of male fifth pair of legs 3-segmented; distal segment with setae.
>
> (After Ringuelet 1958.) Right endopod of male fifth pair of legs with hairs or spines and usually 3-segmented. Left endopod reduced; usually without hairs, or occasionally 1 seta. Females, robust with relatively short atennules not extending beyond metasome; exceptionally reaching to the second urosome segment.

There is no really satisfactory classification given to distinguish between females of the genera.

If Ringuelet's classification is used, *Boeckella occidentalis* Marsh, *B. orientalis* Sars, *B. robusta* Sars and *B. geniculata* Bayly (personal communication) must be included in *Pseudoboeckella.* If Marsh's classification is used, *P. vallentini* Scott and *P. gibbosa* Brehm must be included in *Boeckella.*

It is obvious from a comparison of the foregoing descriptions that the basis for the separation of the genera *Pseudoboeckella* and *Boeckella* is a very minor one. The status of each as a separate genus is undoubtedly questionable. However, the purpose of this discussion has been to establish a consistent usage of existing taxonomy and therefore the use of these two genera is retained. Since Marsh's (1924) description alone clearly distinguishes between these genera, his classification is accepted and used here.

Pseudoboeckella, after Marsh 1924, consists of 13 species (Figure 2.3.2). However, some of these species may be synonymous. In only two cases, known to the author, have *Pseudoboeckella* spp. been collected sympatrically. Mrazek (1901) recorded *P. poppei* and *P. brevicaudata* from the same collection ("Coll. Mich 79. Sud-Patagonien, Punta Arenas, Laguna de los patos bravos; 10.X.1892"), and the author found *P. brevicaudata* and *P. volucris* together in collections from Kerguelen Islands. In both cases they are good "morphological" species.

Ringuelet (1958) has indicated the probable synonomy of *P. poppei* Mrazek with *P. entzi* Daday. *P. palustris* Harding, *P. calcaris* Harding and *P. peruviensis* Löffler all occur in the Arequipo-Puno region of Peru. There is no evidence that they occur sympatrically, and they closely resemble each other. In this paper, *P. remotissima* Brehm is regarded as a synonym of *P. brevicaudata* for reasons discussed in the next section.

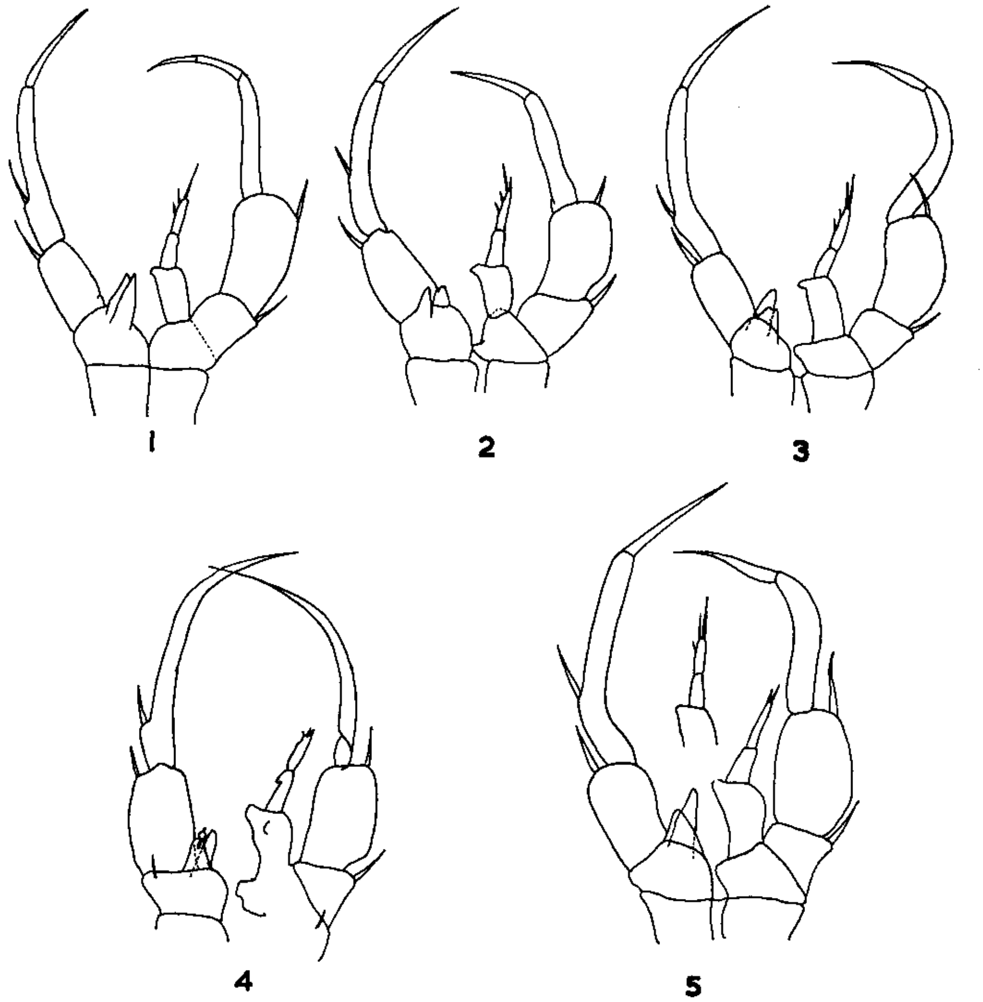


FIGURE 2.3.1. Fifth legs of adult males of *Pseudoboeckella* spp. (not drawn to scale): (1) *P. brevicaudata*, Punta Arenas (from Mrazek 1901); (2) *P. brevicaudata*, Tierra del Fuego and Falkland Islands (from Ekman 1905); (3) *P. brevicaudata*, Kerguelen Islands; (4) *P. brevicaudata*, Heard Island (from Brehm 1953); (5) *P. brevicaudata*, Macquarie Island. Separate right endopod (not to scale) represents "3-setae condition" found in adult males from Prion Lake and "S" Pond.

2.3.2. *Pseudoboeckella brevicaudata Brady 1875*

Centropages brevicaudata Brady 1875, p. 215 (Figs. 11-19).
Paraboeckella brevicaudata Mrazek 1901, pp. 1-29 (Figs. 6, 7, 12, 21, 26, 27, 29, 45, 46, 50, 52).
Boeckella vexillifera Ekman 1905, p. 16 (Figs. 7-12).
Pseudoboeckella remotissima Brehm 1953, pp. 643-650 (Figs. 1-5).

P. brevicaudata is widely distributed throughout the subantarctic zone (Figure 2.3.2), occurring at Punta Arenas (Magellanes), Tierra del Fuego, Falkland Islands, Kerguelen Islands, and Macquarie Island. In a single instance (Heard Island) it has been collected from the antarctic region.

Listed below are the variations in the taxonomic characters observed between the forms of this species occurring at different locations. Preserved specimens were examined from Kerguelen Islands and Macquarie Island only. Otherwise the descriptions were obtained from published reports. The main specific characters used for the genus *Pseudoboeckella* are the segmentation and setation of the male fifth pair of legs.

Punta Arenas (Mrazek 1901). Right endopod of male fifth leg with 1 large terminal and 2 small lateral setae on terminal segment (Figures 2.3.1/1).

Ushuaia Peninsula, Tierra del Fuego (Ekman 1905). Right endopod of male fifth leg with 2 lateral and 2 terminal setae on terminal segment (Figures 2.3.1/2).

Falkland Islands (Ekman 1905; Scott 1914). Right endopod of male fifth leg with 1 or 2 terminal setae on terminal segment.

Kerguelen Islands. Right endopod of male fifth leg with 2 lateral and 2 terminal setae on terminal segments; lateral setae variable in size; rarely only one lateral seta present (Figures 2.3.1/3).

Heard Island (= *P. remotissima* Brehm 1953). Right endopod of male fifth legs with 3 small setae on terminal segment and a "hyaline hook-like projection" on second segment (Figures 2.3.1/4). *P. remotissima* Brehm is regarded as a synonym for *P. brevicaudata* since the form of the main taxonomic character, the male fifth pairs of legs, falls within the range of variation encountered between different subantarctic populations of the latter species. However, several structures described by Brehm (1954), the "hook" on the second male endopod of fifth pair of legs and the "ball-shaped protrusion" on the right side of the female genital segment were not found in other *P. brevicaudata* forms. Nevertheless, it is considered that such differences alone do not justify the creation of a new species.

Macquarie Island. Right endopod of male fifth leg with 2 terminal setae and rarely an additionl lateral seta on the terminal segment (Figures 2.3.1/5).

The morphological differences between these forms are very small. If Scott's (1914) description of the Falkland Islands form is disregarded (on the grounds that his description disagrees with the more complete one given by Ekman 1905), then the most reduced form of the right endopod of the male fifth leg occurs in copepods taken from the most westerly populations, Heard and Macquarie Islands. Forms from Punta Arenas, Ushuaia, Falkland Islands and the Kerguelen Islands all have 3-4 well-developed setae on the right endopod of the male fifth leg. No differences were found between the females of this species occurring at the different localities, except in the case of the Heard Island form. The Heard Island form is the most divergent example, and it is obviously for this reason that Brehm (1953) classified it as a distinct species *(P. remotissima).* It is the only population of *P. brevicaudata* occurring in the antarctic zone. It may therefore represent an example of changes occurring in secondary sexual characters arising from pleiotrophic effects, associated with adaptive changes, to a more severe environment.

2.3.3. *Distribution and dispersal*

Pseudoboeckella spp. are characteristically "cold-water" animals. They occur in Antarctica, the antarctic and subantarctic islands and South America, where the distribution extends northwards to Peru along the Andes Mountains. A single example which occurs outside this range is *P. thomsoni* from Uruguay. This present distribution would indicate that the southern tip of South America and/or Antarctica were probably the original centres from which the dispersal of this genus occurred. During the Pleistocene ice ages the northward range of the distribution would have been extended, and many of the most southerly populations obliterated. The islands south of the Antarctic Convergence as well as Kerguelen Islands still possess permanent ice sheets, and Falkland, Marion, and Macquarie Islands all show signs of recent glaciation. It is unlikely, therefore, that any *Pseudoboeckella* spp. could have survived on these islands during the Pleistocene period. However, with the retreat of the Pleistocene ice sheets, relict populations could remain in the high Andes in the lower latitudes of South America, and colonization or recolonization of the antarctic and subantarctic regions could then occur.

Six pseudoboeckellid species now inhabit the subantarctic and antarctic regions *(P. braziliensis, P. brevicaudata, P. longicaudata, P. poppei, P. silvestrii* and *P. volucris).* Only two species *(P. brevicaudata* and *P. volucris),* however, are found on the islands east of the Scotia Arc (Figure 2.3.2). The colonization of these islands has undoubtedly occurred from the Falkland Islands or South America. *P. brevicaudata* occurs both in South America and the Falkland Islands and *Boeckella vallentini,* the species most closely related to *Pseudoboeckella volucris,* occurs in the Falkland Islands. It is interesting to observe that, although *P. brevicaudata* occurs at one location (Heard Island) within the antarctic zone, in the presence of congeneric species on the islands of the Scotia Arc, it is absent from this zone. This suggests that the presence of species better adapted to a colder environment has prevented the colonization by *P. brevicaudata* of the antarctic islands in this area.

The widespread range of *P. brevicaudata* was sufficiently unusual, for a freshwater calanoid copepod, to warrant an investigation into the mode and circumstances of its dispersal.

The eastwards dispersal of other subantarctic *Pseudoboeckella* spp. to the islands beyond the Scotia Arc may have been limited by either the absence of suitable habitats or dispersal mechanisms insufficient to bridge the considerable oceanic gaps involved. From a consideration of evidence presented elsewhere (Evans 1965) it seems unlikely that the first condition was important in this respect. It was therefore concluded that the factor of major importance involved

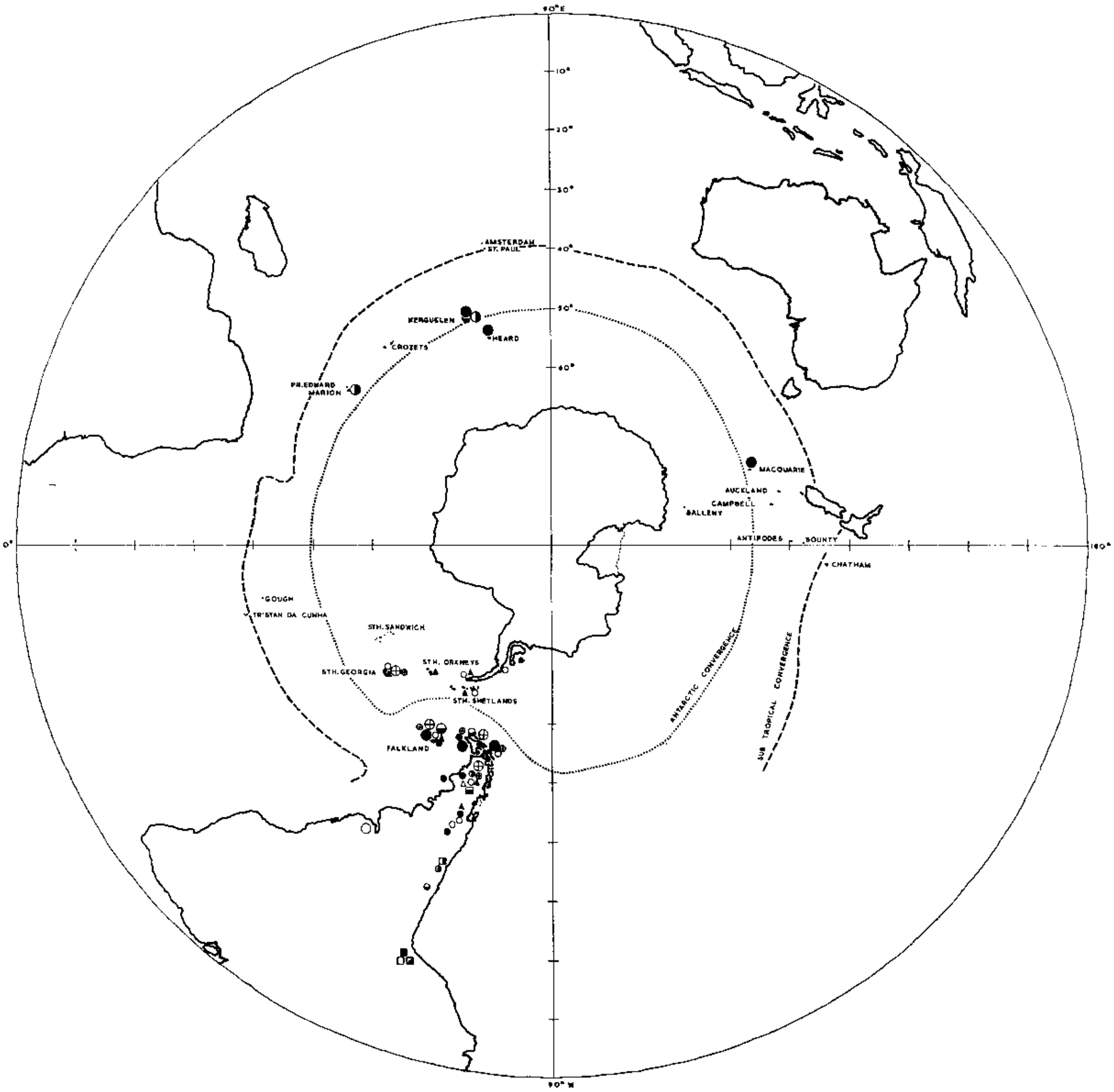


FIGURE 2.3.2. Distribution of the genera *Pseudoboeckella* and *Parabroteus* and the subantarctic-antarctic *Boeckella* spp.

- • *Pseudoboeckella braziliensis* Lubbock
- ● ,, *brevicaudata* Brady
- ■ ,, *calcaris* Harding
- ◑ ,, *dubia* Daday
- △ ,, *entzi* Daday
- ◒ ,, *erubescens* Brehm
- ⬓ ,, *longicaudata* Daday
- □ ,, *palustris* Harding
- ◪ *Pseudoboeckella peruviensis* Löffler
- o ,, *poppei* Mrazek
- ▲ ,, *silvestrii* Daday
- ○ ,, *thomsoni* Brehm
- ◑ ,, *volucris* Kieffer
- ◨ *Boeckella gibbosa* Brehm
- ⊕ ,, *michaelseni* Mrazek
- ◒ ,, *vallentini* Scott
- ⊕ *Parabroteus sarsi* Daday

in the successful colonization by *P. brevicaudata* of Kerguelen Islands, Heard Island and Macquarie Island was its mode of dispersal.

Two elements of long distance dispersal are considered. There is firstly the role played by the dispersal agent, and secondly the adaptations of the species that enable its survival under the conditions of dispersal. Since no stage of *P. brevicaudata* can survive immersion in sea water, the dispersal must be achieved completely by aerial means.

The role of birds as long distance dispersal agents is well known (Falla 1960). On Macquarie Island this form of dispersal accounts for the presence of many species of vascular plants (Taylor 1955).

Falla (1960) quotes an instance (occurring in the subantarctic zone) in which a Giant Petrel *(Macronectes giganteus)* was collected five weeks later and 7,000 miles distant from the site of banding. These birds are frequently observed swimming on freshwater bodies on Macquarie Island where they are common. Since storms frequently occur throughout the subantarctic zone, in which strong westerly winds blow continuously for many days, unbroken flights between the subantarctic islands by such birds are quite probable.

A juvenile Giant Petrel shot at Macquarie Island was found to be carrying an immature stage of *P. brevicaudata* in some filamentous algae attached to one of its feet. The bird was some distance from any water body at the time of capture.

Since ovigerous females are common in the algal mats of ponds, birds may adventitiously collect eggs along with the algae material. The egg is the only stage of *P. brevicaudata* that can survive out of water, and therefore is the most likely dispersal stage. At a relative humidity of 92% some eggs can survive for at least 10 days (Table 1.2.3). This survival seems to be independent of whether they are retained within the egg sac of the female or not (Table 1.2.3). At lower humidity the duration of survival is reduced (Table 1.2.3). It seems reasonable to assume that eggs carried in algal material close to the body may, even in flight, experience quite high humidity.

2.4. SEASONAL ACTIVITY AND ABUNDANCE

2.4.1. *Distribution on Macquarie Island*

P. brevicaudata occurs in water bodies ranging in size from the larger lakes (Figure 0.1) to small, shallow ponds with volumes less than $0 \cdot 1 m^3$. However, it is absent from shallow ponds (mean depth less than 1 m) which lack rooted aquatic plants or marginal zones of filamentous green algae.

Waters from which it has been collected ranged in conductivity from 130 to 6,600 μmhos. Since the upper limit for the conductivity of freshwaters is 4,000 μmhos, this means that *P. brevicaudata* occurs occasionally in slightly brackish waters.

Water temperatures on Macquarie Island ranged from —0·2°C to 17·6°C. Total freezing of water bodies was never observed. The upper lethal temperature for this species (between 25-28°C) would never normally occur at Macquarie Island.

The activities of seals and penguins, and the decomposition of giant kelp pollutes many coastal terrace ponds. These polluted water bodies support dense bacterial communities, and are not generally colonized by freshwater crustaceans. In rare cases *P. brevicaudata* does occur in the marginal free-water zones of some polluted ponds.

The three main factors limiting the distribution of *P. brevicaudata* in the lentic waters of Macquarie Island are salinity, pollution and the absence of "shelter zones" as provided by filamentous algae or rooted aquatic plants.

2.4.2. *Behaviour and dispersion*

Copepods are rarely randomly or uniformly distributed in their environment. Generally the surface waters are vacated during the day and reoccupied during darkness (Cushing 1951).

TABLE 2.4.1

The vertical distribution of various instar groups of *P. brevicaudata* in Prion Lake during daylight (1000 hrs.) and darkness (2200 hrs.). The means have been obtained from seven sets of observations. N.S. = not significant.

Depth m	Night density %* (mean ± S.E.M.)	Day density %* (mean ± S.E.M.)	t	P
		a. Nauplius 1		
0	17·1 ± 1·9	18·7 ± 3·4	0·412	N.S.
5	19·8 ± 1·8	15·8 ± 1·4	1·782	N.S.
10	21·6 ± 2·3	18·1 ± 2·2	1·084	N.S.
15	18·7 ± 2·0	20·9 ± 2·6	0·653	N.S.
23	18·1 ± 1·5	11·1 ± 2·3	2·560	>0·02, <0·05
		b. Nauplii 2-6 (inclusive)		
0	20·4 ± 1·7	19·5 ± 3·0	0·261	N.S.
5	17·9 ± 1·0	19·3 ± 1·4	0·821	N.S.
10	17·4 ± 1·3	23·4 ± 2·3	2·286	>0·02, <0·05
15	17·2 ± 0·9	23·7 ± 2·5	2·437	>0·02, <0·05
23	16·2 ± 1·1	13·2 ± 1·3	1·788	N.S.
		c. Copepodids		
0	21·0 ± 2·7	4·7 ± 1·7	5·138	<0·001
5	20·8 ± 1·3	9·7 ± 2·2	4·302	>0·001, <0.002
10	19·4 ± 1·8	18·7 ± 4·1	0·157	N.S.
15	20·1 ± 1·6	18·8 ± 4·0	0·316	N.S.
23	15·8 ± 2·8	18·5 ± 2·7	0·713	N.S.
		d. Adults		
0	22·2 ± 2·8	0·1 ± 0·1	7·839	<0·001
5	18·4 ± 1·8	2·2 ± 0·8	8·418	<0·001
10	20·6 ± 2·4	3·5 ± 1·1	6·507	<0·001
15	21·1 ± 1·2	3·2 ± 0·8	12·326	<0·001
23	19·0 ± 0·9	8·0 ± 1·3	6·920	<0·001

* Since the absolute densities of various instars varied with the season, densities at each depth are expressed as a percentage of the total of the densities from all sampling depths. This total was obtained from either the day or night samples, on the basis of whichever was the larger.

For the purpose of quantitative sampling of copepod populations it is therefore preferable to make the catches at night, whereby both larger and more representative samples of the total population can be obtained. Sampling of the population of *P. brevicaudata* in Prion Lake was therefore carried out at night. To test whether these assumptions were justified for this population, additional daylight samples were obtained on seven occasions. The mean distributions with depth obtained from those results, for day and night catches, of the various instar groups have been compared in Table 2.4.1. From these results it is apparent that only the adult and copepod stages undertake daily vertical migrations, upward at night and downward during daylight. There was no significant difference between the daylight and night vertical distributions for either of the nauplius groups. These results also indicated that all groups were more uniformly distributed with depth during the hours of darkness.

TABLE 2.4.2

Relative densities of *P. brevicaudata* stages in night and day samples from "S" Pond. These values were calculated as percentages of the maximum density for each region and stage group on each sampling date. Night and day samples were taken on the same day. The number of such pairs of samples is shown in brackets. Values shown are means ± S.E.M. N = night; D = day.

Region of sampling	Nauplii (stages 1–6)		Copepodids (stages 1–5)		Adults	
	N	D	N	D	N	D
"Limnetic"	83 ± 16	72 ± 14	96 ± 3	58 ± 14	85 ± 15	44 ± 18
	(6)		(6)		(6)	
"Littoral"			96 ± 4	68 ± 20	100 ± 0	52 ± 20
			(4)		(4)	
"Benthic"			79 ± 13	73 ± 12	69 ± 19	75 ± 15
			(5)		(4)	

The absence of diurnal migratory activity in nauplii may be due largely to their small size. As weaker swimmers their distribution would largely be due to the pattern of circulation of the lake's currents. Certainly the most marked vertical migration was that of the adult, which is the largest stage and probably the strongest swimmer. In addition, laboratory observations indicate that there are some behavioural differences between the various stages. Nauplii are strongly attracted to a bright light source whereas the later stages tend to move away from one. Obviously, a combination of factors must be taken into account to explain the differences in the migratory activity between these groups.

The distribution of various stages of *P. brevicaudata* in "S" Pond during daylight and darkness was investigated. Since it was not possible to visit this pond frequently at night, the data obtained were consequently limited (Table 2.4.2). The position of the three regions of the pond sampled, termed limnetic, littoral and benthic, are indicated in Figure 2.4.1. The high variability of these results generally precluded the possibility of observing any definite differences between the distributions of the different stage classes. There was, however, a tendency for greater numbers of all the stages to be found in all regions of the pond during darkness, a result which was slightly more marked for the later stages. This apparent paradox could only be explained by assuming that during the period of daylight there was a concentration of copepods in some "unsampled" zone, from which they migrated into the open waters during the night. Such a zone was the region along the margin of the pond occupied by mats of filamentous algae (Plate 2.1.5, Figure 2.4.1). When samples were obtained from this zone, much greater densities of the later stages were encountered than occurred in the open waters of the pond (Table 2.4.3).

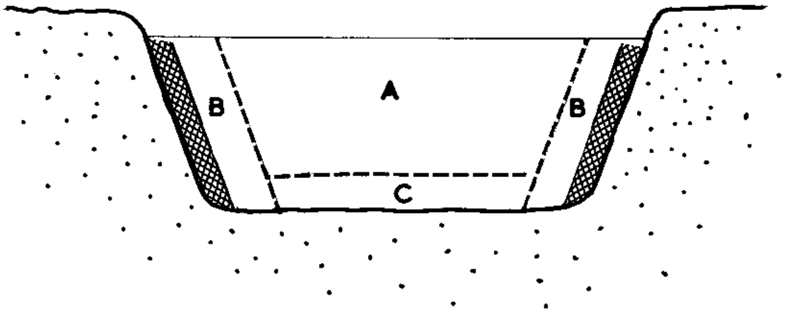


FIGURE 2.4.1. Schematic section through "S" Pond showing the position of the marginal filamentous algal mat zone (cross-hatched) and the regions of sampling. A = limnetic samples; B = littoral samples; C = benthic samples.

TABLE 2.4.3

The density (no./m^3 × 1,000) of copepodids and adults in day samples from the open waters and marginal algal mat regions, "S" Pond

Date	Limnetic sample		Marginal mat sample	
	Copepodids	Adults	Copepodids	Adults
30.3.62	1·188	0·462	864·286	221·429
16.5.62	0·022	0·022	—	4·950
29.5.62	—	0·022	—	14·850
11.6.62	—	0·066	—	29·700

The distribution of *P. brevicaudata* in small ponds may be influenced by factors other than those already mentioned. Surface swarming was observed in "23U" Pond and Duck Lagoon on calm, fine days. Collections were made on one such occasion, at Duck Lagoon. Within a swarm, densities were 20·0 and 30·0 (No./m^3 by 1,000) for copepodids and adults respectively, whereas densities outside the swarm were 4·0 and 4·5 (No./m^3 by 1,000). This phenomenon appeared similar to the swarming of *Calanus finmarchicus* described by Marshall and Orr (1955). The swarms appeared as dense patches of copepods near the surface.

On windy days copepodids and adults of *P. brevicaudata* are usually rare in the surface waters of shallow ponds (Table 2.4.4). Their absence from this region may result from an avoidance behaviour towards the turbulent water (rheotaxis).

TABLE 2.4.4

Distribution of *P. brevicaudata* in surface waters on "windy" and "calm" days. Densities are shown as no./m^3 × 1,000.

"Windy" day				"Calm" day			
Date	Nauplii	Copepodids	Adults	Date	Nauplii	Copepodids	Adults
12.4.62	3·379	0·726	3·933	15.4.62	3·829	1·232	11·788
11.7.62	1·094	0·233	0·266	13.7.62	2·733	2·516	14·952

Probably as a result of the absence of an aphotic zone in shallow ponds, the typical vertical migratory activity of the later stages has become modified. Under these conditions the equivalent behaviour of the daylight withdrawal into deeper waters is a retreat into the marginal algal zone. On Macquarie Island, *P. brevicaudata* is only found in the shallow ponds where either rooted aquatics or algal mat areas are present. It would therefore appear that shelter from light is a necessary requirement for this species. It is further interesting to observe that on Macquarie Island the more deeply pigmented forms of *P. brevicaudata* occur in the most transparent waters. Such an observation has been made for other copepod species, and it has been suggested that the increased pigment may serve as a protection against the greater solar radiation penetrating highly transparent waters (Fairbridge 1945).

Nauplii of *P. brevicaudata* never undergo the marked migrations or display the patterns of behaviour characteristic of the later developmental stages. Nauplii densities were therefore usually more reliable estimates of their population size whether obtained from night, day, pond or lake samples. In contrast, many environmental factors influence the patterns of dispersion of the copepodids and adults. Estimates of these from quantitative samples are therefore less reliable. Night samples from Prion Lake, however, can be expected to give good estimates of the relative numbers of all developmental stages, since these were all fairly uniformly distributed with depth in such collections. In contrast, it has been shown that pond day samples must underestimate true copepodid and adult densities in such water bodies.

2.4.3. *Seasonal abundance*

As a result of the limited duration of field work at Macquarie Island, no population was studied for a period exceeding 15 months. Prion Lake and "S" Pond were sampled regularly for a 12-month period; other water bodies were sampled for shorter periods.

The developmental stage-groups of *P. brevicaudata* enumerated were nauplius 1, nauplii 2-6 (inclusive), copepodids and adults. The first postembryonic stage,

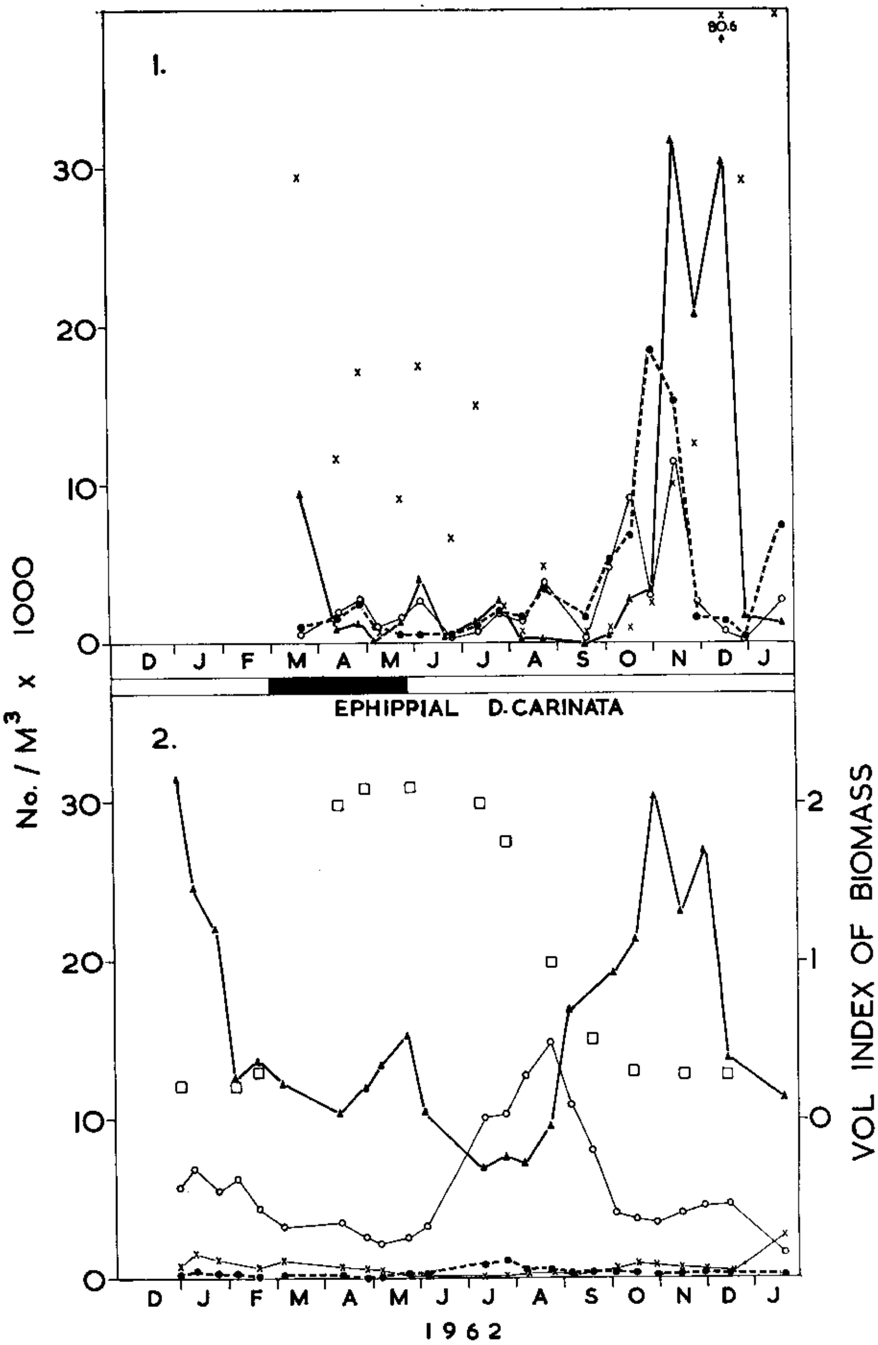


FIGURE 2.4.2. Seasonal abundance of *P. brevicaudata*: (1) "23U" Pond; (2) Prion Lake. (Volume index of biomass relates only to the data for *Daphnia carinata*.)

● Nauplius 1
○ Nauplii 2-6
▲ Copepodids
× Adults
□ *Daphnia carinata*

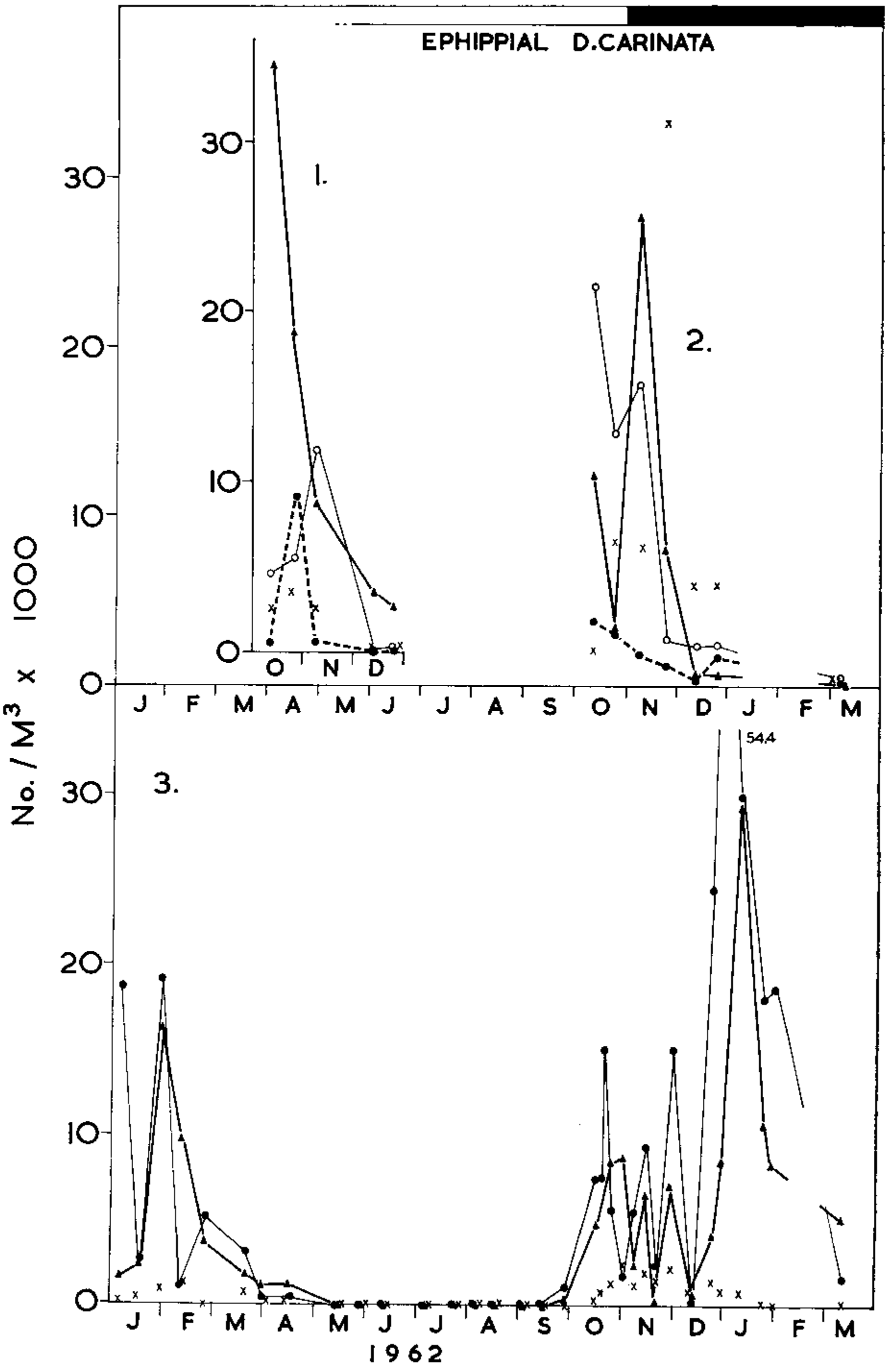


FIGURE 2.4.3. Seasonal abundance of *P. brevicaudata*: (1) "F_5" Pond; (2) Duck Lagoon; (3) "S" Pond.

● Nauplius 1, or total nauplii for "S" Pond ▲ Copepodids
○ Nauplii 2-6 × Adults

nauplius 1, is of very short duration (24-48 hours at 8°C). The frequency of this stage could therefore be used to represent the relative frequency of egg hatching on the previous day. On this basis, hatching of eggs occurred throughout the year in all populations studied (Figures 2.4.2, 3), although during winter (May to September) the frequency of hatching in "S" Pond was extremely low (Evans 1965). The hatching rate in "23U" Pond and "S" Pond increased rapidly after mid-September, concurrent with increases in daylength, temperature, daily temperature variation and chlorophyll (Sections 2.1.2, 3), and reached a maximum during summer. In contrast, the maximum frequency of hatching in Prion Lake occurred in July, 2-3 months earlier than observed in the other populations. In spite of these differences the maximum numbers of copepodids in Prion Lake and "23U" Pond occurred almost simultaneously (Figure 2.4.2). This indicated that there were differences in the developmental rates between the two populations. The time for development from nauplius 1 to copepodid was approximately 3 months in Prion Lake, and approximately 1 month in "23U" Pond (Figure 2.4.2, time intervals between respective peaks).

During the period September to December the continuous build-up of the immature stages in Prion Lake and "23U" Pond did not occur in "S" Pond. Instead, the numbers of all age groups fluctuated considerably during this period in this pond. This increased variability no doubt reflected the greater variability of the environmental conditions of this pond (Sections 2.1.2, 3). An examination of the population data from "S" Pond suggests that the developmental rates for this population are similar to those for "23U" Pond.

Higher densities of most stages occurred in "23U" Pond, "S" Pond, Duck Lagoon and "F_5" Pond than in Prion Lake. Summer densities of copepodids in Prion Lake, however, were higher than those encountered in some of the other populations (Figures 2.4.2, 3). These differences are considered in a later section.

Although relatively few samples were collected from Duck Lagoon and "F_5" Pond, it appeared that these populations reached peak densities earlier (Figure 2.4.3). This difference could arise from the higher temperatures occurring in Duck Lagoon and "F_5" Pond (Section 2.1.2). Optimal temperatures for development may therefore occur earlier. A consistent trend of decreasing frequency in hatching and decreasing numbers of all developmental stages in Duck Lagoon and "F_5" Pond populations commenced during November. The cause of this early decline is unknown. The temperatures in these water bodies at this time are certainly higher than found elsewhere and this may be one factor influencing directly or indirectly the population changes.

The cladoceran *Daphnia carinata* is the only other planktonic crustacean occurring in the lentic freshwater habitat on Macquarie Island. It was collected from all water bodies which were regularly sampled for *P. brevicaudata,* with the exception of "S" Pond. *D. carinata* performed a marked daily vertical migration and was absent from surface water during the hours of daylight. Consequently it was rarely taken in pond samples collected during the day. However, its seasonal abundance was determined in Prion Lake from night samples (Figure 2.4.2).

Although the abundance of *D. carinata* appears inversely related to that of *P. brevicaudata* in Prion Lake, there is no evidence to indicate any causal relationship between these populations. The February decrease in copepodids occurred prior to the increase in *D. carinata* during May to April. Further, the increase in nauplii and copepodids occurring later in the year, during the decline in the cladoceran population, was a product only of the increased frequency of egg-hatching occurring much earlier.

Ephippia are produced in cladoceran populations, usually associated with a decrease in the reproductive rate, a high population density or a decline in population density (Slobodkin 1954). Different seasonal distributions of ephippial females in Prion Lake and Duck Lagoon (Figures 2.4.2, 3) reflect the slight differences in seasonal cycle found between the *P. brevicaudata* populations in these same water bodies.

There are no predators of *P. brevicaudata* in Prion Lake. Freshwater fish are absent from the island. In ponds, planaria are common amongst the filamentous algal mats and these have been observed to feed on eggs and nauplii of *P. brevicaudata* in the laboratory. Slobodkin (1962) reported the feeding of *Dugesia* sp. on nauplii of *Artemia* sp. Planaria, therefore, represent a possible source of predation on *P. brevicaudata* populations in "23U" Pond, "S" Pond, Duck Lagoon and "F_5" Pond. The importance of the effect of this predation on population growth is unknown. Epizoic and epiphytic growths, including a stalked vorticellid ciliate and diatoms, are common on copepodids and adults. However, these do not appear to impair the efficiency of the host in any way.

2.4.4. *Length variation*

Seasonal variation in length is common in copepod species (Sewell 1948, Marshall and Orr 1955, Deevey 1960, and Bayly 1962). This phenomenon occurred in all the observed populations of *P. brevicaudata* on Macquarie Island.

Length measurements were made on adult females. The reason for measuring one sex only is explained in the following section. Since adult copepods do not moult, seasonal changes in the mean length of adults will arise from recruitment or mortality of different sized individuals. These implications of seasonal change in length are now considered for the various populations.

"23U" Pond. In this pond the mean length of adults was greater during winter than summer (Figure 2.4.4). The transition between summer and winter size groups was particularly rapid during March 1962. The two samples preceding this change, 5.2.62, 6.3.62 (Figure 2.4.4) had distributions significantly different from a normal distribution (tested by method of normal deviates, $P<0{\cdot}001$ for both). The February sample was clearly bimodal (Figure 2.4.5). Although this was not the case with the subsequent sample (Figure 2.4.5: 6.3.62), both modes of the previous sample were represented. After this date, adults of the shorter mode did not occur again in collections until the following summer (Figures 2.4.4, 5). This would imply that the size change in March is largely due to a mortality of adults belonging to the shorter mode. Although there are few relevant population data available (Figure 2.4.2), it seems improbable that a recruitment of large mode animals from the developing immature stages would have been responsible for this change.

During the winter, a further increase in length occurred. Since immature stages occurred throughout this period, this increase was probably due to a recruitment of large individuals into the adult population. The production of larger animals during cold periods has been frequently reported for other copepod species, and this phenomenon is discussed later in this section.

On 2.11.62 a significant decrease in mean length occurred, accompanied by a decrease in the coefficient of variation. By this time the immature stages had increased in numbers (Figure 2.4.2). Thus the decrease in mean length was probably brought about by the appearance of the first summer generation of adults. On 24.12.62 a further decline in mean length occurred which continued for the remainder of the sampling period. The presence of a large population of immature copepods during this period (Figure 2.4.2) implied that the decrease was caused by a heavy recruitment of smaller adults. The final February sample (18.2.63), like that of the previous February, was not normally distributed ($P<0{\cdot}001$). However unlike it, this was due to a leptokurtic instead of a bimodal distribution. The difference between these two samples could not be explained from the data available.

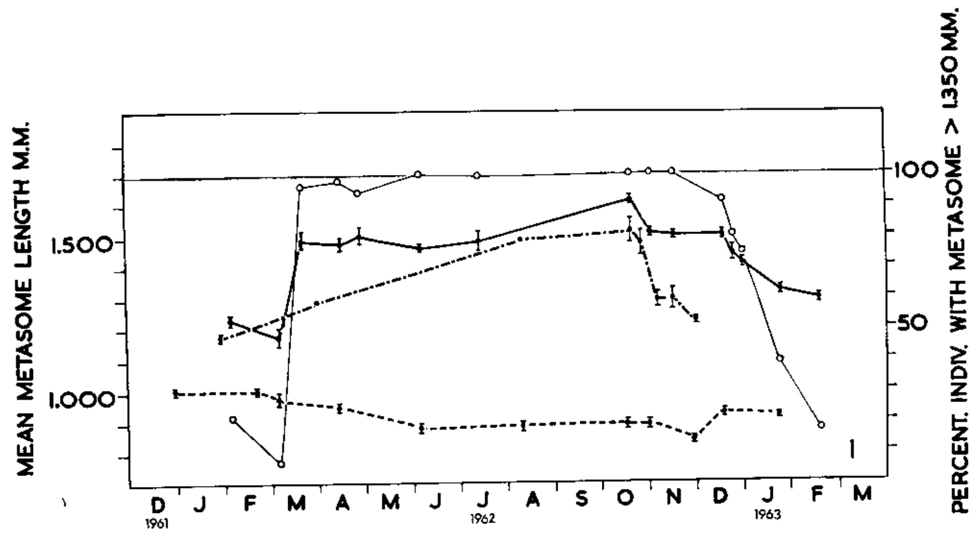


FIGURE 2.4.4. 1. Seasonal mean length variation. 95% confidence limits of means are given. Open circles indicate the percentage of adults in "23U" Pond sample with metasome length greater than 1·350 mm.

— — — — — Prion Lake; ———— "23U" Pond; —·—·— "S" Pond.

The pattern of seasonal change in mean length indicated that small summer adults were present for 4-5 months. Since this value represents only the duration of a size class, the longevity of the summer adults may be either equivalent to, or shorter than, this period. By similar reasoning the longevity of the winter adults is 7-8 months or less. Even taking into account the uncertainties in both cases, winter adults undoubtedly survive longer than their summer counterparts.

The time for development, from nauplius 1 to adult during the summer increase in the population, was estimated as the interval between the onset of the summer increase in nauplius 1 (mid-September, Figure 2.4.2) and the appearance of the first summer generation of adults. The latter was indicated by a sharp decline in mean length of adults in early November (Figure 2.4.4). An accompanying decrease in the coefficient of variation at this time further indicated the production of a pulse of uniform-sized adults. Developmental time estimated in this way was approximately 2 months. Consequently, if maturation of the gonads occurred soon after the final moult, then two generations could be produced during the summer period.

"S" Pond. Seasonal changes in the mean length of adults in "S" Pond were similar to those occurring in "23U" Pond (Figure 2.4.4). There was, however, a more gradual increase in mean length during the winter. As the numbers of immature copepods were low during this period (Figure 2.4.3) the expected rate of recruitment of adults would be very low.

The onset of hatching (mid-September, Figures 2.4.2, 3) and the first observed decline in mean length following the winter increase (late October, Figure 2.4.4) occurred simultaneously in "S" Pond and "23U" Pond populations. This indicated that the developmental rates in these two populations were similar.

Prion Lake. The pattern of seasonal change in length of adults in Prion Lake differed from those observed for "S" Pond and "23U" Pond (Figure 2.4.4). Adult length decreased during winter and increased during summer. This may be due to both or one of two factors.

a. Developmental rate. The time for development from nauplius 1 to adult in Prion Lake was approximately 6 months. This was the time between the peak numbers of nauplii and adults (Figure 2.4.2). Since this developmental rate was considerably slower than those for *P. brevicaudata* in "23U" Pond and "S" Pond, the environmental conditions which determine the size of adults would have operated earlier on adults occurring in Prion Lake simultaneously with adults from the other two populations.

b. Relative abundance of food. The final size of crustaceans is influenced by their food supply (Richman 1958; Mason 1963). The low chlorophyll values measured in Prion Lake are indicative of the small phytoplankton standing crop which may be limiting the growth of the copepod throughout the year. The decrease in mean length during the winter, in contrast to the increase observed in other populations, would indicate that during winter the food shortage became more critical. Mean length values of adults from Prion Lake were always considerably lower than those obtained from other populations, although some overlap in the length of individuals occurred (Figure 2.4.5).

Data on seasonal variation of length was not available from Duck Lagoon or "F_5" Pond. The few measurements obtained indicate that adults from these populations, like those from "S" Pond and "23U" Pond, are much larger than adults from Prion Lake.

To investigate the possible origins of seasonal length variation, correlations between length and temperature, and length and chlorophyll, were calculated (Table 2.4.5). Significant negative correlations (at the 5% level) were found between length and temperature of the water, at the time of sampling, for "23U" Pond and

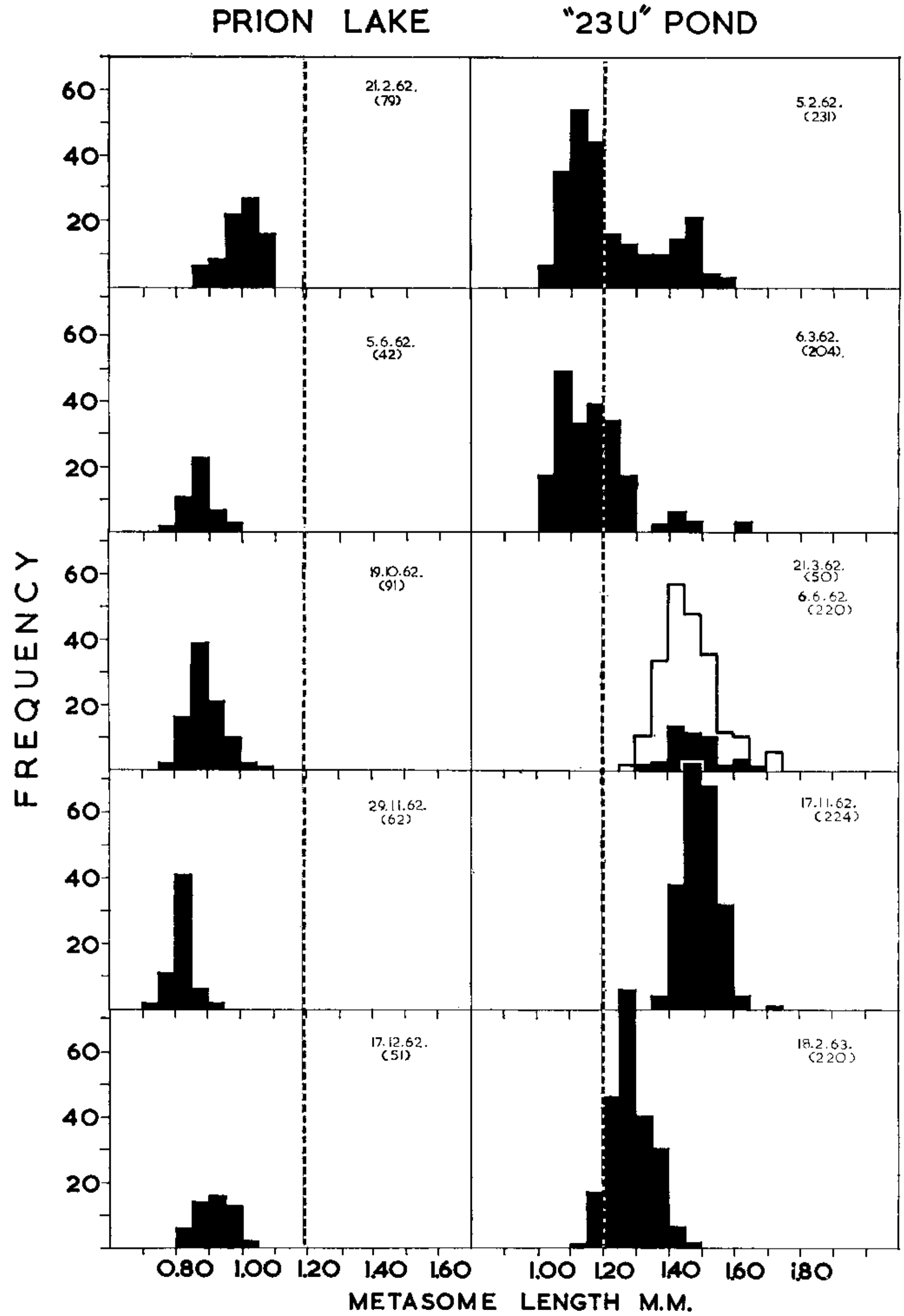


FIGURE 2.4.5. Frequency distributions of length for adult females from Prion Lake and "23U" Pond. Sample size in brackets. Distribution for 6.6.62, superimposed on distribution for 21.3.62.

"S" Pond samples. In contrast, a significant positive correlation between these values (at the 5% level) was obtained for Prion Lake adults (Table 2.4.5).

If temperature influences final size, it would be expected to operate throughout the life of the animal. Where temperature varied throughout the year, the best correlation between length and temperature would be expected for temperatures taken from some mean point in the growth period rather than at the time of collection of the sample. Correlations were therefore also calculated between length and temperature occurring at a time, half the duration of the developmental period, prior to the sample data (Table 2.4.5). These data gave higher negative correlations for "23U" Pond and "S" Pond populations. The absence of any significant correlations between length and temperature for Prion Lake samples when calculated on this basis (Table 2.4.5) suggest that the significant positive value previously obtained is probably spurious.

TABLE 2.4.5

Correlation coefficients for mean metasome length with temperature and chlorophyll *a*
x = length; y = temperature; z = chlorophyll *a*
P. shown in brackets; N.S. = not significant

Locality	Temp.	No. of pairs	r_{xy}	No. of pairs	r_{xz}
"23U" Pond	Day of sampling	15	—0·575 (·05)	9	—0·262 (N.S.)
,,	1 month previous	15	—0·682 (·01)	9	—0·722 (·05)
"S" Pond	Day of sampling	8	—0·722 (·05)		
,,	1 month previous	8	—0·875 (·01)		
Prion Lake	Day of sampling	11	0·711 (·02)		
,,	3 months previous	11	0·375 (N.S.)		

Significant negative correlations between length and water temperature in natural copepod populations have been previously reported by Marshall and Orr (1955), Deevey (1960), El-Maghraby (1961), Bayly (1962) and McLaren (1964). Experimental confirmation of this relationship was obtained by Coker (1933). No significant positive correlations between length and water temperature have been obtained for copepods. Deevey (1960) found that the highest correlations between length and temperature were obtained if temperatures one month prior to sampling were used. A similar result was obtained by McLaren (1964). This author showed that the relationship between length and temperature for the calanoid *Pseudocalarus minutus* was unusually linear, if mean temperatures were calculated from values obtained throughout the life of the copepod.

A significant negative correlation (at 5% level) between chlorophyll and length was obtained for adults from "23U" Pond (Table 2.4.5). However, the partial correlation coefficient for the same data ($r_{xz.y} = 0{\cdot}335$; n.s. for 6 d.f., see Table 2.4.5 for terminology) indicated that this is a consequence of the high correlation that occurs between chlorophyll and temperature ($r_{zy} = 0{\cdot}890$). There were insufficient data to calculate a similar correlation for "S" Pond population.

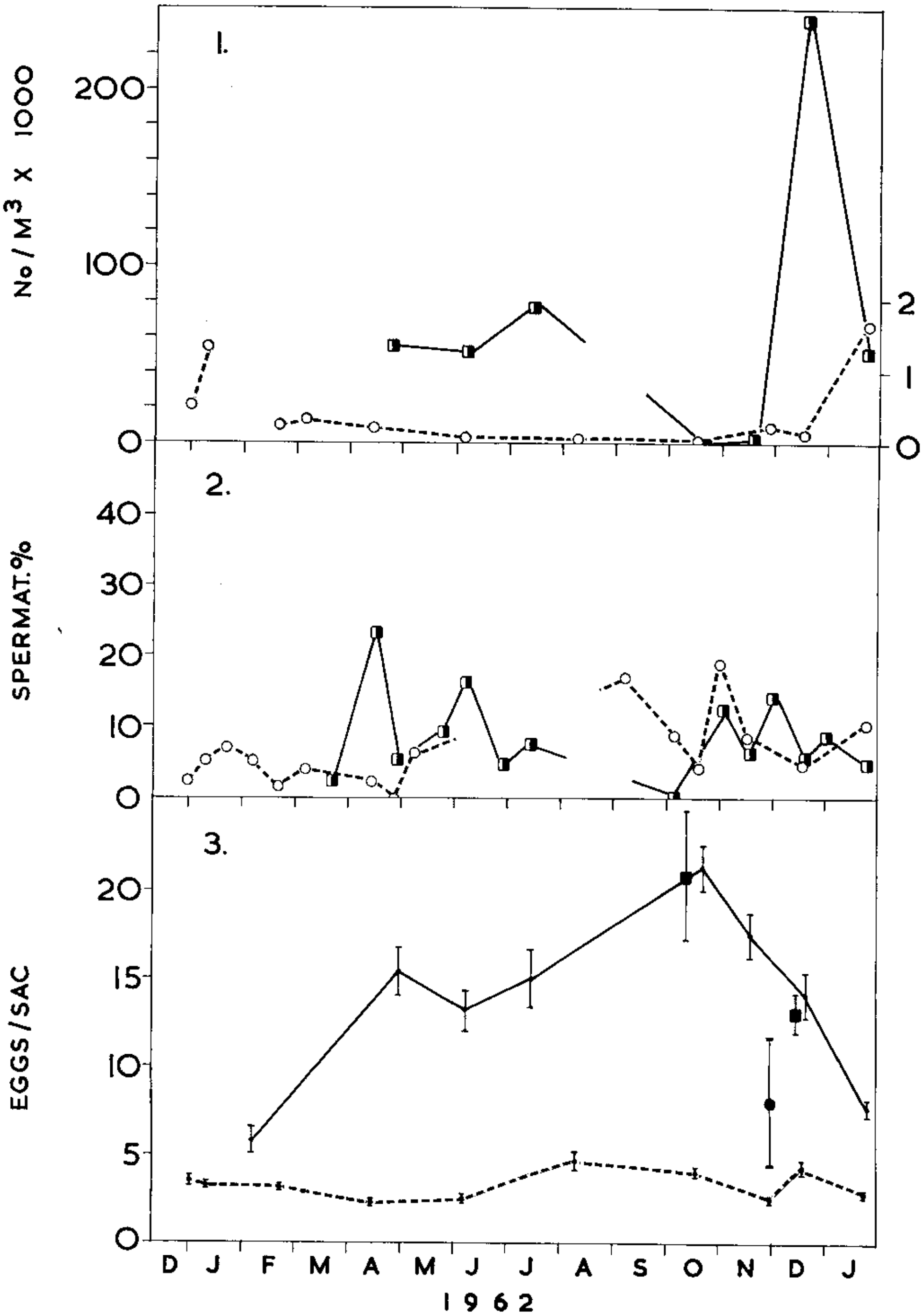


FIGURE 2.4.6. (1) Seasonal variation in egg production. Egg production = mean clutch size × density of ovigerous females (number/m^3 × 1,000). Left abscissa, number of eggs/m^3 × 1,000 in "23U" Pond; right abscissa, number of eggs/m^3 × 1,000 for Prion Lake. (2) Seasonal variation in percentage of spermatophore-bearing females. (3) Seasonal variation in mean clutch size (egg/sac) 95% confidence limits are given with each value.

(Broken lines, Prion Lake; continuous lines, "23U" Pond.)

■ Duck Lagoon ● "S" Pond ◨ 23U" Pond ○ Prion Lake

2.4.5. *Egg production, sex ratio, reproductive activity and clutch size*

Egg production

Females carry their eggs for a number of days in a sac attached to the abdomen. Laboratory observations indicated that hatching of eggs occurs 7 or more days after release of the eggs from the egg sac. The mechanism for the release of eggs is described in Section 1.2.4.

The eggs of *P. brevicaudata* are denser than water. For this reason counts of free eggs in net samples do not provide any useful information. The egg production of populations was therefore obtained by multiplying mean clutch size (clutch size = number of eggs per sac) by the density of ovigerous (egg sac-bearing) females. Seasonal variation in the duration for which egg sacs remain attached to females may constitute a source of error in these results.

Egg production for Prion Lake and "23U" Pond both showed summer maxima (Figure 2.4.6./1). Since the effect of the error mentioned above will cause egg production to be overestimated during the winter and underestimated during the summer, as egg-bearing time was longer in winter than summer (Evans 1965), these results can be considered valid.

The summer maximum in egg production may arise from:

a. An increase in reproductive activity. This term refers to sexual activity, rate of production of eggs per female and the percentage of ovigerous females in a population.

b. An increase in the total number of adult females. These considerations are examined in subsequent sections.

It is obvious that the production of eggs per m^3 in "23U" Pond was much greater than that in Prior Lake (Figure 2.4.6/1). This difference was reflected in the densities of nauplii 1 occurring in these water bodies (Figure 2.4.2).

Sex ratio and sexual activity

The sex ratio was determined for samples containing 100 or more adults. It was usually greater than 1·0 for all the populations examined (Tables 2.4.6, 7). Although considerable variation in this value occurred, no seasonal trends were apparent. Annual means of the sex ratio for Prion Lake and "23U" Pond populations were not significantly different (using a "t" test, at 5% level).

Sex ratios greater than 1·0 have been recorded for other calanoid copepod populations (Comita and Anderson 1959, and Lindquist 1961). Mednikov (*op. cit.* Bayly 1962) has suggested that high sex ratios are an adaptive response to a shortage of food. This was not the case in *P. brevicaudata* as sex ratios greater than 1·0 were obtained for both the eutrophic "23U" Pond and the oligotrophic Prion Lake.

These observed departures in the sex ratio from the expected value of 1·0 are most probably due to the greater longevity of females. Jacobs (1961) found that the males of *Pseudodiaptomus coronatus* grow more rapidly than the females when kept at identical conditions, which suggests that they are probably more short-lived.

A measure of sexual activity was obtained by determining the percentage of females bearing spermatophores. In using these results it was assumed that the duration of the attachment of the spermatophores was not influenced by season. Seasonal variation in the incidence of spermatophore-bearing females is shown in Figures 2.4.6/2. It is apparent from these results that the values for "23U" Pond and Prion Lake show no obvious seasonal trends.

These observations were in contrast to the distinct seasonal changes reported in two calanoid copepod populations by Comita (1956) and Comita and Anderson (1959). In both studies far greater frequencies of spermatophore-bearing females were observed than in *P. brevicaudata* populations. In one study (Comita and Anderson 1959) the greatest incidence of spermatophore-bearing females occurred during a period when males predominated. If (as appeared in this example) the number of spermatophore-bearing females is related to the relative density of males, a negative correlation between sex ratio and frequency of the spermatophore-bearing females would be expected. However, no significant correlation (at the 5% level) between these variables was obtained for the "23U" Pond population, although a positive correlation just significant at the 5% level was obtained for the Prion Lake population (Table 2.4.8). It is therefore unlikely that there is

TABLE 2.4.6

The percentage of ovigerous females, the densities of ovigerous and spermatophore-bearing females and the sex ratio from Prion Lake samples. Densities are expressed as number of individuals per m^3 × 1,000.

Date	No. of ♀♀ examined	Percentage* ovig. ♀♀	Density ovig. ♀♀	Density sperm. ♀♀	Sex ratio ♀♀/♂♂
31.12.62	345	25·8	0·146	0·014	1·74
9.1.62	300	35·1	0·415	0·121	2·85
23.1.62	360	36·7	0·282	0·055	2·06
6.2.62	204	14·1	0·046	0·020	1·34
20.2.62	141	23·9	0·073	0·005	0·84
5.3.62	294	21·4	0·123	0·023	1·10
13.4.62	255	24·4	0·096	0·009	1·12
27.4.62	171	26·0	0·096	—	1·83
7.5.62	189	20·5	0·073	0·023	2·60
23.5.62	48		0·105	0·032	
5.6.62	30		0·039	—	
12.7.62	51		0·023	0·005	
9.8.62	69		0·018	0·005	
24.8.62	84		0·014	0·018	
6.9.62	120	22·6	0·055	0·041	2·52
3.10.62	351	3·4	0·014	0·025	1·32
17.10.62	273	2·3	0·014	0·032	1·67
18.10.62	273	5·4	0·027	0·036	1·34
31.10.62	357	6·8	0·052	0·052	2·40
15.11.62	221	23·9	0·097	0·041	3·52
16.11.62	315	19.8	0·092	0·037	2·89
29.11.62	90		0·105	0·023	
17.12.62	117	14·0	0·025	0·009	0·81
23.1.63	241	34·6	0·615	0·183	2·04

* Only calculated from samples containing more than 100 females

TABLE 2.4.7

The percentage of ovigerous females, the densities of ovigerous and spermatophore-bearing females and the sex ratio from "23U" Pond and Duck Lagoon samples. Densities expressed as numbers of individuals per m³ × 1,000.

Date	No. of ♀♀ examined	Percentage* ovig. ♀♀	Density ovig. ♀♀	Density sperm. ♀♀	Sex ratio ♀♀/♂♂
		a. "23U" Pond			
9.3.62	134	37·2			3·36
21.3.62	318	26·7	5·661	0·466	2·53
15.4.62	141	5·0	0·233	1·099	0·65
28.4.62	293	36·0	3·563	0·500	1·28
9.5.62	18		0·233	0·099	
24.5.62	311	26·8	1·838	0·639	3·02
6.6.62	484	38·5	3·896	1·320	1·50
27.6.62	148	51·3	2·531	0·233	2·64
13.7.62	304	50·5	5·095	0·766	2·08
26.7.62	40		0·462	0·066	
25.8.62	33		0·0528	0·166	
5.10.62	19		—	0·166	
19.10.62	14		—	0·033	
2.11.62	72		0·132	0·300	
17.11.62	223	2·2	0·166	0·462	2·90
30.11.62	256	16·4	1·399	1·199	2·13
18.12.62	639	39·9	16·983	2·531	1·12
31.12.62	236	27·6	4·329	1·320	1·33
24.1.63	303	32·6	6·593	0·999	0·99
		b. Duck Lagoon			
11.10.62	72	2·8	0·066	0·066	0·91
25.10.62	165	24·4	0·660	0·528	0·47
8.11.62	164	39·0	2·131		2·16
23.11.62	363	45·8	5·528		0·57
24.12.62	264	29·2	1·265		2·60

* Only calculated for samples containing more than 100 females

TABLE 2.4.8

Correlation coefficients for sex ratio, percentage spermatophore-bearing females and percentage ovigerous females from samples collected between December 1961 and January 1963. Only samples containing more than 100 females have been used.

x = sex ratio; y = percentage spermatophore-bearing females; z = percentage ovigerous females. P. values in brackets; N.S. = not significant.

Locality	No. of pairs	r_{xy}	r_{xz}	r_{yz}
Prion Lake	19	0·450 (0·05)	0·341 (N.S.)	—0·058 (N.S.)
"23U" Pond	13	—0·406 (N.S.)	—0·076 (N.S.)	—0·327 (N.S.)

ever a shortage of males limiting sexual activity in either population. For this reason, when examining the population implications of seasonal size change in adults in the previous section, it was only necessary to use results for females.

The relatively low incidence of spermatophore-bearing females may result from a shorter duration of attachment of the spermatophore or the lower rate of fertilization of the females. The latter condition would be characteristic of a population, in which more eggs can be produced with fewer matings. Spermathecae of *P. brevicaudata* were large and these may store sufficient sperm for the fertilization of several clutches of eggs. Prolonged sperm storage in spermathecae has been recorded for other calanoid copepods (Marshall and Orr 1955, and Jacob 1961).

No marked seasonal trends in the percentage of females which are ovigerous occurred in either Prion Lake or "23U" Pond populations (Tables 2.4.6, 7), although higher values tended to coincide with the periods of maximum densities of the adults in Prion Lake. There was no significant correlation (at 5% level) between the percentage of ovigerous females and sex ratio, or between the percentage of ovigerous females and the percentage of spermatophore-bearing females (Table 2.4.8). Neither the incidence of spermatophores or the sex ratio appear to influence the numbers of the ovigerous females. This indicated that the reproductive activity of the females may vary little throughout the year.

Clutch size

Clutch size is the number of eggs per egg sac.

The seasonal variations in clutch size for Prion Lake and "23U" Pond populations are shown in Figures 2.4.6/3. The few values plotted for Duck Lagoon samples were similar to those from "23U" Pond. A single value from "S" Pond. (Figures 2.4.6/3) fell between those obtained for Prion Lake and "23U" Pond. When correlation coefficients were calculated between length and clutch size within each sample (Table 2.4.9.), extremely variable results were obtained. Variation in

TABLE 2.4.9

Correlation coefficients of clutch size with length, within samples. x = clutch size; y = length; N.S. = not significant.

Locality	Date	No. of pairs	r_{xy}	P.
"23U" Pond	5.2.62	43	0·596	0·001
„	28.4.62	48	0·187	N.S.
„	6.6.62	49	0·266	0·10
„	13.7.62	26	0·607	0·01
„	19.10.62	49	0·592	0·001
„	17.11.62	47	0·150	N.S.
„	24.1.63	50	0·158	N.S.
Prion Lake	21.2 62	53	0·451	0·001
„	13.4.62	49	0·408	0·01
„	5.6.62	33	—0·101	N.S.
„	17.10.62	40	0·007	N.S.
„	29.11.62	51	—0·047	N.S.
„	17.12.62	39	0·644	0·001
„	23.1.62	57	0·076	N.S.

the age structure of the breeding adult population is one possible source of this variation between samples. However, when correlations were calculated between seasonal changes in clutch size and length, clutch size in "23U" Pond was strongly correlated with mean length of females (Table 2.4.10), but in Prion Lake no significant correlation was observed (Table 2.4.10). No significant correlation was obtained between clutch size and water temperature for either water body (Table 2.4.10).

TABLE 2.4.10

Correlation coefficients of mean clutch size with mean length and temperature, for the period December 1961 to February 1963.

x = mean clutch size; y = mean length; z = temperature of water at time of sampling. P. values are shown in brackets; N.S. = not significant.

Locality	No. of pairs	r_{xy}	r_{xz}
"23U" Pond	10	0·940 (0·001)	−0·262 (N.S.)
Prion Lake	10	0·006 (N.S.)	−0·326 (N.S.)

Marshall and Orr (1955) have shown (in *Calanus finmarchicus*) that the rate and number of eggs laid is strongly influenced by abundance of food. Starved *Daphnia obtusa* produce eggs at a much slower rate than well-fed animals (Slobodkin 1954). The marked differences in clutch size between the Prion Lake and "23U" Pond populations can be most satisfactorily explained in terms of different food levels. Within both populations, however, there was no obvious relationship between clutch size and cholorophyll.

Seasonal and interpopulation variation of clutch size has been observed in many species of copepods (Hutchinson 1951, Roen 1957). Significant positive correlations between length and clutch size have been obtained by many authors (Margalef 1955, Bayly 1962, Marshall 1949, Ravera and Tonolli 1956). However, Davis (1961) found considerable variation in the correlation coefficient between clutch size and length in the seasonal samples of 5 species of *Diaptomus* in Lake Erie (as was found for *P. brevicaudata*). It is obvious that clutch size is influenced by many factors. Size of females, food level, and the age of the females are probably the most important.

In neither Prion Lake nor "23U" Pond did the incidence of maximum clutch size coincide with the period of the greatest egg production. Examination of the seasonal distribution of percentage ovigerous, and spermatophore-bearing females, indicated an absence of any period of increased reproductive activity. The summer increase in egg production in Prion Lake and "23U" Pond arose solely from the increases in the numbers of females that occurred during this period.

2.4.6. *Hatching*

Hatching occurred throughout the year in all water bodies studied. This was indicated from the seasonal distributions of first stage nauplii. On this basis the hatching rate in "23U" Pond and "S" Pond increased markedly in the spring, although the maximum hatching rate in Prion Lake occurred in mid-winter (Figures 2.4.2, 3). In "23U" Pond and Prion Lake, for which seasonal distributions of egg production have been estimated, the time of maximum egg-hatching occurred 9 and 6 months respectively after the period of maximum egg production (Figures 2.4.2, 3).

A series of experiments were therefore carried out in an attempt to determine the nature of these differences and to investigate some factors which might influence the hatching rate of eggs.

Seasonal changes in hatching

The long delay occurring between the peak of egg production and the maximum rate of hatching, observed in Prion Lake and "23U" Pond populations, indicated that these eggs undergo a period of arrested development. This condition of the eggs must arise from either a state of diapause or quiescence.

These states are defined by Andrewartha (1952) and Lees (1955). Since hatching occurs throughout the year in these populations, it is clear that, whichever condition exists, its operation is imperfect. That hatching can occur throughout the year was confirmed by laboratory observations. Table 2.4.11 lists the highest percentage hatchings obtained under experimental conditions of eggs collected at several different times during the year. In every case the eggs were obtained from live ovigerous females collected from the water bodies on the dates shown in the table. With the exception of two examples (31.12.62, "23U"; 31.12.62, Prion Lake), for which the total numbers of eggs hatching were obtained for a shorter period, the proportion of eggs which hatched from any sample was always greater than 50% (Table 2.4.11). However, no seasonal trend in the percentage hatching was apparent in either Prion Lake or "23U" Pond. The high coefficients of variation were due to the high inter-clutch variability, although hatching was observed in all clutches studied.

Brewer (1964) hatched an average of 91% of the eggs of the calanoid *Diaptomus stagnalis* in a series of laboratory experiments. The lower value of 70% for Prion Lake and "23U" Pond eggs suggests that a small number of these eggs may enter a state of diapause or quiescence. However, a major proportion of the egg population was obviously not subject to a state of obligatory diapause at any time of the year. The winter periods of arrested development must therefore be due to states of facultative diapause or quiescence.

Effect of temperature on egg hatching

Preliminary experiments showed that highest hatchings occurred in samples which were exposed to natural daylight and temperatures. This treatment was termed "optimal" (see Section 1.2.4). Some groups were incubated under these conditions, and other groups were kept at constant temperatures in darkness (Section 1.2.4). The temperature given for "optimal" conditions represents the mean for the whole period of incubation (Table 2.4.11).

The results from these temperature experiments are shown in Table 2.4.11. Under conditions of constant temperature a significantly greater proportion of "23U" Pond eggs hatched at 2·5°C than at 8·5°C.

TABLE 2.4.11

Effect of temperature on hatching
"Percentage hatched" represents the percentage of eggs hatching within 30 days of release from egg sac.

Group no.	Mean Temp. °C	Treatment	Date coll. ovig.	Total no. eggs	No. replicates	Percentage hatched	S.D.	Coeff. variat.	Mean time* to hatch days	S.D.	Coeff. variat.
			a. "23" Pond								
1	0·0	Constant T., darkness	27.6.62	120	6	0					
	(5·6)	Optimal	„ ‡	„	„	(73)†	(9·9)	(13·4)			
2	2·5	Constant T., darkness	26.8.62	301	10	69†	20·73	30·0	20·2	2·39	11·8
3	5·5	„	26.8.62	267	9	53	27·45	51·7	13·6	2·91	21·4
4	5·5	„	19.10.62	635	5	45	14·78	32·8	12·6	3·84	30·4
5	5·6	Optimal	27.6.62	120	6	73	9·88	13·4	12·7	1·87	14·7
6	7·0	„	19.10.62	706	5	66†	8·80	13·4	11·6	5·55	47·7
7	8·5	Constant T., darkness	26.8.62	212	10	35	20·90	59·9	10·0	1·76	17·4
8	8·5	Constant T., darkness	19.10.62	702	5	35	10·31	29·4	14·2	13·20	93·0
9	9·0	Optimal	24.1.62	39	4	72†	23·75	33·0	11·0	—	—
	8·0	„	31.12.62§	243	—	44					

b. Prion Lake

10	2·5	Constant T., darkness	26.8.62	41	9	56†	38·40	68·6	27·0	2·56	9·5
11	5·5	,,	18.10.62	74	5	56	12·55	25·6	26·1	19·40	73·5
12	7·0	Optimal	18.10.62	63	5	99†	3·52	3·6	24·4	9·94	40·7
13	7·0	Optimal dark	18.10.62	67	5	61	35·60	56·5	20·1	3·49	17·4
14	8·5	Constant T., darkness	26.8.62	41	9	48	36·40	76·0	14·7	1·75	11·9
15	8·5	,,	18.10.62	58	5	41	16·21	39·6	17·7	3·36	19·0
—	8·0	,,	18.12.62	250	—	79†					
—	8·0	,,	31.12.62	310	—	45†					
—	9·0	,,	23.1.63	27	4	57†	25·60	45·0			

"t" tests between groups at different temperatures

Groups	"t"	d.f.	P
a. "23U" Pond, percentage hatching			
2 (2·5°C), 7 (8·5°C)	3·67	18	0·002
2 (2·5°C), 8 (8·5°C)	3·43	13	0·01
3 (5·5°C), 5 (5·6°C)	1·69	13	N.S.
4 (5·5°C), 5 (5·6°C)	3·84	9	0·01
3 (5·5°C), 4 (5·5°C)	0·63	12	N.S.
6 (7·0°C), 7 (8·5°C)	3·15	13	0·01
6 (7·0°C), 8 (8·5°C)	5·29	8	0·001
b. Prion Lake, percentage hatching			
10 (2·5°C), 14 (8·5°C)	0·47	16	N.S.
10 (2·5°C), 15 (8·5°C)	0·89	12	N.S.

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* Taken from the time the eggs were released from the egg sac.

† Maxima percentage hatching for each date.

‡ Results for group 1 eggs removed from 0°C conditions and transferred to "optimal" conditions.

§ Percentage hatching within 15 days of release of eggs from egg sac.

N.S. = not significant.

When eggs from "23U" Pond were kept at 0°C (i.e., in the presence of melting ice) no hatching occurred within 30 days. However, when these eggs were transferred to "optimal" conditions at the end of this period a maximum cumulative hatch of 51% occurred within 5 days.

Similar results to those described above for "23U" Pond eggs were also obtained using Prion Lake eggs. However, in the latter case, since much smaller numbers of eggs were used, the differences between treatments were rarely significant (Table 2.4.11).

In all experiments, Prion Lake eggs took longer to hatch than "23U" Pond eggs (Table 2.4.11). This was the only consistent difference found between the eggs of the two copepod populations. However, this difference was inadequate to explain the disparity in hatching times between the two populations, under natural conditions.

The maximum rate of hatching in Prion Lake occurred in mid-winter, 2 to 3 months earlier than the onset of spring hatching in "23U" or "S" Ponds. During this period the temperature in Prion Lake gradually decreased from 3°C to 1°C. Daily temperature variation of the lake was always less than 0·5°C. In contrast, during the period of spring and summer hatching in "23U" and "S" Ponds, the mean temperature was increasing from 4°C to 8°C and daily temperature variation during this time was within the range 3°C to 6°C. Optimal (varying) temperature treatment (Table 1.2) therefore approximates the conditions encountered in "23U" and "S" Ponds, whereas the constant temperature treatment represents the conditions in Prion Lake. When hatching rates were calculated for constant and variable temperature conditions, using the data from "23U" Pond eggs, it was apparent that the higher hatching rate occurred at lower temperatures when the eggs are kept under constant or "Prion Lake"-type conditions. It was also shown that, under variable temperature or "23U" and "S" Pond-type conditions, the greatest hatching rate occurred at higher temperatures (Table 2.4.12).

TABLE 2.4.12

Mean percentage hatching and hatching rates (per 100 eggs/day) from data for "23U" Pond eggs (Table 2.4.11)

Temp. °C	Constant temp.[1] Mean percentage hatching	Hatching rate	Variable (optimal) temp.[2] Mean percentage hatching	Hatching rate
2·5	69	3·4	70	3·4
5·5	49	3·8	70	5·3
8·5	35	2·9	70	6·0

[1] Equivalent to Prion Lake conditions
[2] Equivalent to "23U" Pond conditions

Another factor which may contribute to the difference in hatching times between Prion Lake and "23U" Pond populations is the nature of the micro-environment of the "overwintering" egg. Since the eggs of *P. brevicaudata* are denser than water they will sink toward the floor of the lake or pond. In "23U" Pond, as previously indicated, the water overlying the bottom sediments is likely to be oxygen deficient on occasions, whereas in Prion Lake the water at all depths is almost completely saturated with oxygen. Brewer (1964) showed that for eggs of *Diaptomus stagnalis* the hatching stimulus is probably a reduction of oxygen concentration caused by bacterial activity in the bottom and microenvironment where the eggs occur. Unfortunately, it was not possible to carry out experimental work to test whether similar changes might influence hatching in eggs of *P. brevicaudata*.

Two morphological differences between Prion Lake and "23U" Pond eggs have been observed. Prion Lake eggs were usually more deeply pigmented and smaller than eggs from "23U" Pond (Table 2.4.13). The extent to which these differences are responsible for the difference in developmental times between the eggs from these two populations is unknown.

TABLE 2.4.13

Comparison of egg sizes, Prion Lake and "23U" Pond (collected 12.1.63)

"23U" Pond			Prion Lake				
No. measured	Mean diam.	S.D.	No. measured	Mean diam.	S.D.	"t"	P.
36	0·175	0·014	36	0·158	0·011	24·85	<0·001

The high variability in the hatching results indicated that a varying percentage of eggs of each clutch may enter immediately into some state of arrested development. Such a condition has been described for the eggs of *Aedes aegypti* (Diptera; Culicidae) by Gillet (1955, 1959). These eggs usually entered an obligatory diapause. However, some eggs hatched soon after they were laid if conditions were suitable, and the percentage of such "pre-diapause" hatchings for any batch was shown to be under genetic control. This could create a source of considerable variation between the eggs of individuals similar to that encountered during these experiments. So far, there is not sufficient data available to determine the nature or mechanism of the arrested egg stage.

2.4.7. *Food and growth*

2.4.7.1. Food

P. brevicaudata is a filter-feeding herbivore. In "23U" Pond the food of this species, determined by dissection of the mid-gut and examination of whole sections, consisted of the following species of diatoms:

Acanthes brevipes Agardh.
Cocconeis placentulata Ehrenberg.
Fragilaria capucina Desm.
Fragilaria viriscens Ralfs.
Gomphonema intricatum Kützing.
Melosira granulata (Ehr.) Ralfs.
Navicula radiosa Kützing.
Synedra sp.

TABLE 2.4.14

The effect of different food levels on survival and growth rate

Locality	Date coll. ovig.	Duration expt. days	Water	Food level (chlorophyll *a* mgm/m^3)	Mean temp. °C	Total no. nauplii*	Mean survival		No. live stages at conclusion of expt†				
							Per cent	S.D.	N_4	N_5	N_6	C_1	C_2
Prion Lake	24.1.63	15	Prion Lake	0·51	8·0	60(6)	98·3	4·1	11	47	1		
"23U" Pond	24.1.63	15	,,	0·51	8·0	60(6)	93·3	2·4	1	39(1)	16(2)		
Prion Lake	18.12.62	28	,,	0·69	8·0	60(6)	61·6	24·0	1(3)	8(4)	12(2)	16(5)	
"23U" Pond	24.12.62	28	,,	0·69	8·0	70(7)	18·6	12·2		(9)	(9)	13(28)	
Prion Lake	24.1.63	15	"23U" Pond	19·30	8·0	48(6)	100·0	0·0	1	20	27		
"23U" Pond	24.1.63	15	,,	19·30	8·0	60(6)	90·0	24·5			2(4)	51(2)	1

* Numbers in brackets represents the number of replicates amongst which the total of eggs was distributed.
† Numbers in brackets indicates mortalities. N = nauplius stage; C = copedid stage.

TABLE 2.4.15

The effect of food level on length

Locality	Food level (chlorophyll *a* mgm/m^3)	Immature stages											
		N_4			N_5			N_6			C_1		
		No. meas.	Mean total length mm	S.D.	No. meas.	Mean total length mm	S.D.	No. meas.	Mean total length mm	S.D.	No. meas.	Mean total length mm	S.D.
Prion Lake	0·51–0·69	15	0·315	0·013	55	0·361	0·18	13	0·428	0·010	19	0·592	0·022
"23U" Pond	0·51–0·69				43	0·363	0·17	17	0·421	0·012	23	0·594	0·016
Prion Lake	19·30				20	0·406	0·012	27	0·481	0·018			
"23U" Pond	19·30										51	0·642	0·032

Many diatom frustules had been broken up to such an extent that their identification was made impossible. All the species listed above were amongst the commonest ones occurring in "23U" Pond (Appendix I), suggesting that feeding was probably non-selective.

Although many diatom species, including those in the above list, occurred in Prion Lake, they were always relatively rare (Appendix I), and none was ever found in the mid-gut of *P. brevicaudata* from this lake. This indicated that the diet of *P. brevicaudata* in Prion Lake more probably consisted of flagellate species. These were relatively more abundant than diatoms in this water body.

2.4.7.2. Growth

Interpopulation differences in growth rate and final size have already been referred to in previous Sections (2.4.3, 4). It was suggested that such differences largely arose from differences in food levels. Some evidence for quantitative and qualitative differences in diet between populations was given above.

The experiments described here were designed to test the effect of food level on size and growth rate. Newly hatched nauplii from Prion Lake and "23U" Pond populations were reared in water from both habitats. Food level in these waters was measured as chlorophyll *a*. A density of one animal to 50 ml of water was used to minimize the effect of metabolic wastes accumulating during the experiment.

Effect of food level on growth rate. The results obtained (Table 2.4.14) indicate clearly that nauplii hatched from eggs of the "23U" Pond population developed more rapidly than nauplii from eggs of the Prion Lake population. This was the case at both food levels tested. These results also showed that nauplii from both populations developed more rapidly at higher food levels.

A low growth rate accompanied by low temperatures would increase the duration of developmental stages, and consequently increase their frequency in samples. The similar densities of nauplii 2-6 and copepodid stages in Prion Lake and "23U" Pond, in contrast to the difference between the densities of the nauplius 1 stage (Figure 2.4.2), may be accounted for in this way.

Effect of food level on size. Immature stages of the same size were produced from both populations, when nauplii were reared on the same food levels (Table 2.4.15). Both populations produced significantly larger immature animals at higher food levels (Table 2.4.15).

Decreases in growth rates and size associated with low food levels have been reported in copepods by Coker (1933), and McLaren (1964).

The adaptive value of the lower growth rate of Prion Lake copepods, which was partly independent of food level, was to some extent demonstrated by their higher survival than "23U" Pond animals, when both were reared under conditions of low food level for 28 days (Table 2.4.14).

2.4.8. *Morphology*

The most variable character in the external morphology of Macquarie Island specimens of *P. brevicaudata* was the setation of the swimming legs (Section 2.2.1). Setae counts for the fourth pair of legs in the adults were made for several popula-

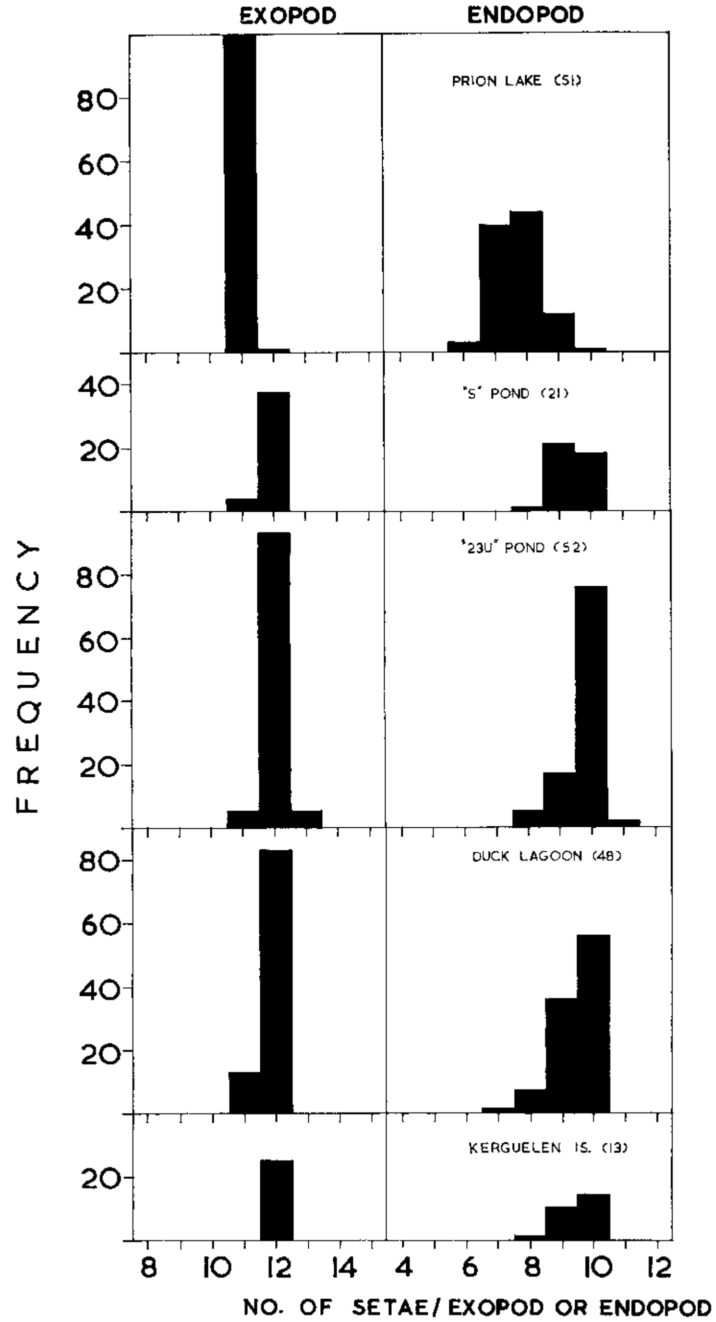

FIGURE 2.4.7. Frequency distribution of number of setae exopod or endopod on the 4th pair of swimming legs of adult *P. brevicaudata*. Numbers in brackets indicate the numbers of pairs of legs examined.

tions on Macquarie Island. These counts were made from samples collected at similar times of the year, to obviate the effect of any possible seasonal variation.

Values obtained are shown in Figure 2.4.7. Setae frequencies were obviously lower in Prion Lake copepods than animals collected elsewhere. It has been shown (Comfort 1961) that rearing animals on very low food levels not only causes a decrease in growth rate and size, but produces forms which retain many juvenile characteristics. Since the copepodid stage preceding the adult has fewer setae than the adult on the swimming legs, the low seta-count in Prion Lake adults could be regarded as a "juvenile condition". The fewer setae on Prion Lake adults might therefore be interpreted as a phenotypic response to the low food level in this lake.

The incidence of an extra seta on the right endopod of the fifth pair of legs (Figure 2.2.5) in Prion Lake adult males may represent a similar phenomenon. In the development of this appendage, fewer setae occur after the final moult than were present in the preceding stage (Figure 2.2.5). A higher frequency of setae on this appendage in the Prion Lake males could therefore be regarded as a "juvenile condition". The frequency of this extra seta (on the third endopod of the male fifth pair of legs) in 40 Prior Lake males was 33%. An extra seta was not observed in 40 males examined from "23U" Pond, although it occurred with a frequency of 17% in 30 males from "S" Pond. The latter value suggests that some of the interpopulation variation arises from causes other than that proposed.

Interpopulation variation in morphology has been observed in other species of Copepoda. Gurney (1931) described differences occurring in the structure of the geniculate antennule of *Diaptomus gracilis*; Baldi (1950) described a variation in the number of "spines" on the swimming legs of female *Mixodiaptomus laciniatus*; Bayly (1961) described variations in the segmentation and setation of the fifth pair of legs of adult *Calamoecia lucasi*. In these examples, however, there was insufficient information given about the habitats of the different populations to be able to attribute the cause of the variation to any specific factor or factors.

The eggs of *P. brevicaudata* are typically red to pale orange (see Section 2.4.6) due to the presence of a lipid soluble pigment (probably astaxanthin, Waterman 1960), uniformly distributed throughout the cellular mass. On hatching, the nauplius is a similar colour. However, during the course of normal development each successive stage becomes progressively paler, until finally the later copepodid stages are almost colourless. In the final adult stage, although the body cells are virtually colourless (with the exception of the ovary and the eggs), the cuticle is typically blue. There is no pigmentation in the cuticle of the earlier stages.

In Prion Lake the eggs and all the developmental stages of *P. brevicaudata* were deeply pigmented, particularly when compared with the same stages occurring in "23U" Pond, "S" Pond and Duck Lagoon. The adults in Prion Lake, however, lacked the blue pigmentation of the cuticle found in the other populations, although the body cells were generally uniformly pale orange in contrast to their colourless state found in adults elsewhere. This difference in pigmentation may represent another example of the "juvenile condition" of the adults in Prion Lake. If this is so, then it might also be inferred that the absence of cuticular pigmentation was indirectly caused by a shortage of food.

Interpopulation variation in colour of the type described above has been commonly observed in other freshwater species of copepods (Brehm 1953). It has been speculated that the presence of deep pigmentation may confer some protection against radiation (Fairbridge 1945) or some metabolic advantage (Pennak 1963). Deposition of pigment in eggs is a common phenomenon, and in crustaceans it has been suggested that such pigment is later used during moulting and/or in colouring of the cuticle. The deep red pigmentation encountered in the eggs and juvenile forms of *P. brevicaudata* in Prion Lake is typical of copepods occurring in the clear waters of alpine lakes (Brehm 1953). If the phytoplankton in clear waters is richer in carotenoids, then the increased pigmentation may be entirely of dietary origin. The possibility that animals living in water of low productivity may actively deposit greater amounts of pigment or lipid in the eggs, to ensure the future survival of the immature forms under these conditions, is a further attractive explanation.

3. DISCUSSION

P. brevicaudata is the only species of freshwater antarctic or subantarctic copepod which has a circumpolar range. Its spread eastward from the southernmost tip of South America, to the Falklands, Kerguelen Islands, Heard Island and Macquarie Island has, with the exception of the form found on Heard Island, been unaccompanied by any significant changes in morphology. The easternmost population, on Macquarie Island, must still be regarded in morphological terms as synonymous with the forms found elsewhere. The absence of morphological divergence suggests either that the colonization of these oceanic islands has occurred relatively recently or that the conditions occurring on each island are sufficiently similar to exert convergent forces of selection. Perhaps the latter alternative is partly supported by the observations made on the Heard Island form. Heard Island lies within the antarctic region (see Figure 2.3.2) and therefore its climate is much colder than the subantarctic islands (Figure 3.1). In the subantarctic region the climate is uniformly mild, relative to the latitudinal position, and below-freezing temperatures are relatively rare (Figure 3.1). However, at least 3 months of below-freezing conditions prevail at Heard Island (Figure 3.1). Here most of the small ponds inhabited by *P. brevicaudata* are completely frozen during the winter (Ealey, pers. comm.). Heard Island is the only instance in which *P. brevicaudata* has colonized an area outside the subantarctic region, and the form of this species occurring here is the most morphologically divergent. According to one author (Brehm 1953), the differences were considered sufficient to justify the elevation of this form to species status.

Successful colonization of oceanic islands is dependent upon a means of transport across oceanic barriers, and the assimilation of the immigrant species into the island community. Migratory seabirds must act as long distance dispersal agents for *P. brevicaudata,* since no stage of this species can survive immersion in sea water. It has been indicated that under favourable circumstances the eggs of this species could survive the passage by aerial transport from one island to another. The ability of the egg to survive out of water, which may well be a principal factor in the successful dispersal of this species, has been attributed to the presence of a robust chitinous outer shell or membrane.

Island communities are typically composed of few species. Consequently many ecological niches may remain unoccupied. This provides the opportunity for the rapid establishment of suitable immigrant species. On Macquarie Island, the colonization of the freshwater biotope by *P. brevicaudata* has been particularly successful. The species now occupies a wide range of habitats. This may have been achieved in two ways.

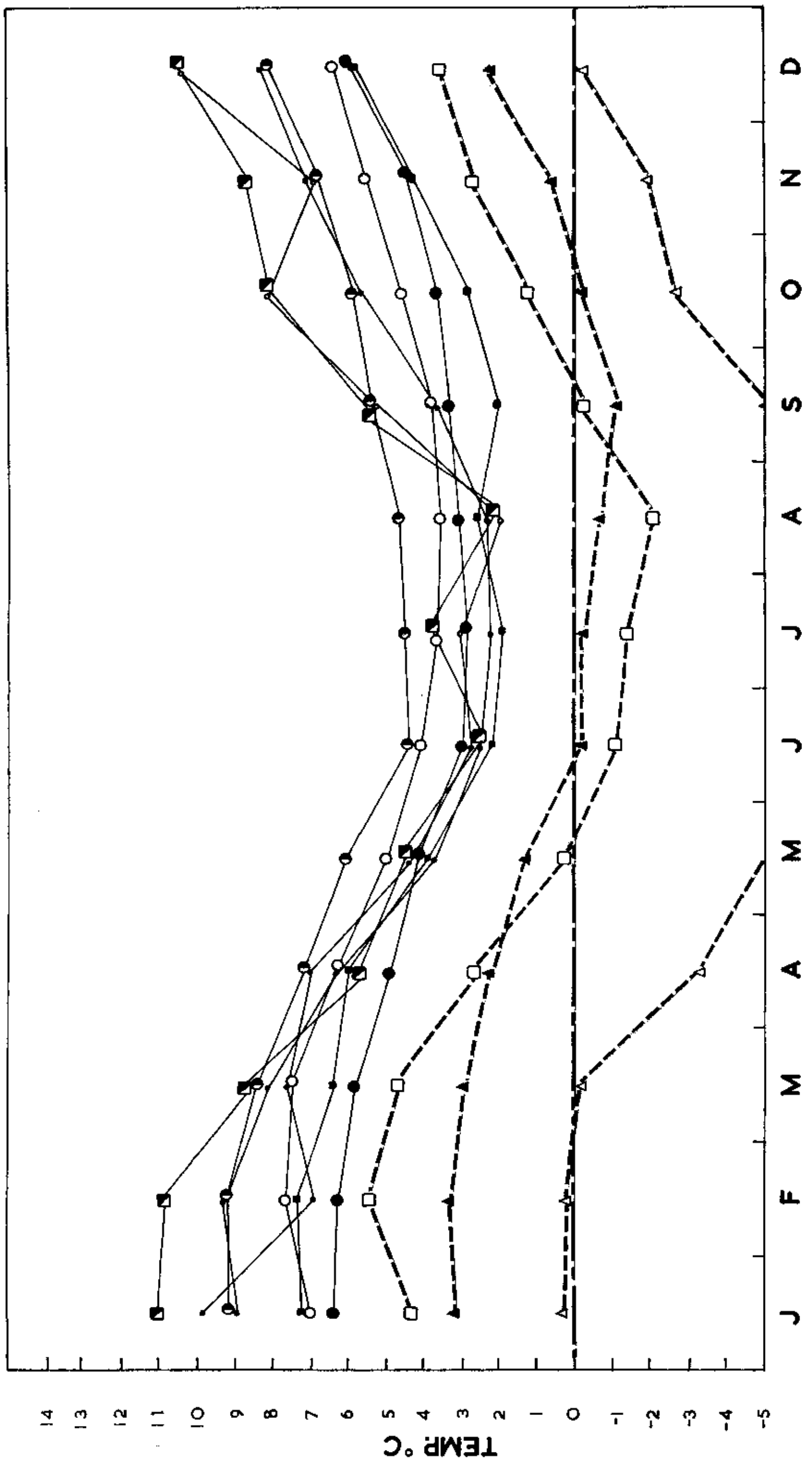

FIGURE 3.1. Annual temperature cycles for stations in subantarctic and antarctic zones (air temperatures). Broken lines represent data from antarctic stations.

◪ Punta Arenas (1.5, 53°6′ S)
o Ushuaia (6, 55° S)
◑ Campbell Island (24, 52°33′ S)
• Falkland Islands (51°42′ S)
■ Kerguelen Islands (14, 49°20′ S)
○ Marion Island (25, 46°51′ S)
● Macquarie Island (6, 54°30′ S)
□ South Georgia (54°16′ S)
▲ Heard Island (53°01′ S)
△ South Orkney Islands (61° S)

Elevation in metres, and latitude, in brackets after name of station.

1. Pre-adaptation. The gene pool of the immigrant population may contain all the genes necessary for the species to make the appropriate adaptive responses to the range of habitats available. A species which possesses a "pre-adapted" gene pool obviously has enhanced chances of successful colonization. Pre-adaptation could occur if the immigrant stock had occupied similar habitats before immigration. On Kerguelen Islands, *P. brevicaudata* occupies a range of habitats similar to those on Macquarie Island. Further westwards, at Terra del Fuego, Magallanes and the Falkland Islands, the typical habitat of this species is shallow ponds, generally close to the sea (Mrazek 1901, Ekman 1905, Scott 1914). Since this species is more likely to have been introduced from Kerguelen Islands rather than from the population further west, pre-adaptation is one probable explanation of the present occurrence of *P. brevicaudata* on Macquarie Island.

2. Selection. Expansion of the species into a wider range of habitats than that occupied by the parent stock would be possible, because of the low species pressure of the oceanic island community. This situation is well illustrated by the present distribution of the plant species on Macquarie Island (Taylor 1955). Selection would thereafter operate to improve the chances of survival of the population in its new environments.

It was beyond the scope of this study to carry out the sort of tests which might establish which of the two alternatives suggested was valid. The purpose of introducing such considerations was rather to direct attention to the processes likely to have been responsible for producing the successful exploitation by *P. brevicaudata* of the freshwater biotope on Macquarie Island.

The principal differences between the habitats of *P. brevicaudata* on Macquarie Island were in morphometry, climate and primary productivity. The effect on the general aspects of the ecology of *P. brevicaudata* attributable to these differences are described separately below.

1. *Morphometry.* The extreme examples studied on Macquarie Island were Prion Lake of mean depth 17·5 m and mean volume $6{\cdot}35 \times 10^6$ m^3, and "S" Pond of mean depth 20 cm and mean volume 6·8 m^3. In Prion Lake the later stages of *P. brevicaudata* displayed a typical daily vertical migration, withdrawing to the deeper water during the day. In "S" Pond these stages largely sought "shelter" in the marginal zones of filamentous algae during the day. Such migrations were less pronounced than in Prion Lake and occurred horizontally rather than vertically. It is possible that simple responses such as phototaxis and rheotaxis may be sufficient to account for the migratory behaviour of this species in both environments. Alternatively, however, it is also possible that some divergence in behavioural responses may have evolved in the face of such considerable differences in the physical environment.

2. *Climate.* Differences in climate between the freshwater habitats are largely due to two factors, depth and altitude. Complete freezing of water bodies was never observed on Macquarie Island. Surface freezing was usually of short duration, and the ice cover was rarely greater than 10 cm. In all water bodies, the severity of the winter conditions determined the size of the overwintering population. Consequently in "S" Pond, a shallow plateau water body of relatively high altitude, where surface freezing and snow drifts were more common than elsewhere, free-

swimming stages were rare during the winter. In contrast, all stages were well represented during the same period in two other plateau water bodies of greater depth and volume (Prion Lake and "23U" Pond).

Two other climatic effects were associated with depth or volume of the water body. Firstly, in a large deep lake such as Prion Lake the annual temperature cycle lagged approximately one month behind that of shallower water bodies. Secondly, shallow water bodies such as "S" Pond and "23U" Pond experienced considerable daily variation in temperature which did not occur in the deeper water bodies. Where temperature conditions were important in influencing developmental phenomena such as hatching and growth rate, such temperature differences as those described above might well be expected to exert considerable influences on the annual life cycle. That such was the case for *P. brevicaudata* has been shown by the observation that the peak of hatching of eggs of this species in Prion Lake occurred in mid-winter, 2-3 months earlier than in the shallower water bodies, "23U" Pond and "S" Pond.

3. *Primary Productivity.* Although no direct measurements of primary productivity were made, seasonal changes have been inferred from chlorophyll determinations. Prion Lake was shown to be an oligotrophic water body with perpetually low chlorophyll values, whereas shallow ponds such as "23U" Pond and Duck Lagoon had high summer values. The high values of the latter two water bodies were associated with the presence of dense stands of the rooted aquatic vascular plant *Myriophyllum elatinoides*. The presence of this plant appears to be the single most important factor in contributing to the high productivity of shallow water bodies. On the coastal terrace, effluents from seal wallows and pits of decomposing kelp also provided important sources of inorganic nutrients, consequently increasing productivity.

The low values of chlorophyll in Prion Lake implied that food was continually in short supply for *P. brevicaudata* in this lake. The effect of a continual relative food shortage in Prion Lake has been to produce smaller, slower-growing copepods which in turn produce smaller clutches of smaller eggs. In Section 2.4.7 it was demonstrated that the slow growth rate of Prion Lake copepods gave them an advantage in terms of survival over "23U" Pond copepods when both were reared under low food conditions. Further, there were various morphological differences between the Prion Lake forms when compared with other populations on the island. These morphological differences were considered to be most probably produced by a shortage of food. The effects of a decreased growth rate and clutch size would of course greatly decrease the final population size (Cole 1954). The decrease in the size of the adults (and other stages) implies that their energy or food requirements would be less. All of these changes can be regarded as adaptive features of a population living in the presence of a continual relative food shortage.

It is interesting to observe that, although the differences between the habitats on Macquarie Island have produced considerable differences in seasonal activity and developmental phenomena, the maximum numbers of reproductively mature adults appear at the same time in all populations of *P. brevicaudata*. This was at mid-summer when chlorophyll values were near their maximum. Chlorophyll determinations are essentially a measure of the phytoplankton standing crop. However, in the case of "23U" Pond and Duck Lagoon the increasing mid-summer chlorophyll values occurring in the presence of increased numbers of zooplankton must be indicative of an increase in primary productivity also. To the contrary, chlorophyll levels remained uniformly low throughout the year in Prion Lake. However, the presence of a greater zooplankton biomass during the spring and summer months, in the absence of any change in the accompanying chlorophyll levels in this lake, suggests that the increased zooplankton biomass must be supported by an increase in the primary productivity occurring during this period. It is therefore suggested that in all populations the maximum numbers of adults occurred during the period of highest productivity. The adaptive significance of synchronizing the maximum reproductive effort of a population with a period of highest food supply is obvious.

4. ACKNOWLEDGEMENTS

The author wishes to thank those members of the 1961-1963 ANARE party at Macquarie Island who generously assisted in field work, and in particular the Officer-in-Charge during 1962, Mr. I. Petersen, and Mr. J. Stalker of the same party. Dr. P. G. Law and Dr. F. Jacka, at that time respectively Director and Assistant Director (Scientific) of the Antarctic Division, gave valuable assistance in the planning and execution of the programme. Dr. G. Humphrey, Chief of Division of Fisheries and Oceanography, CSIRO, generously provided laboratory facilities when required, and Mr. D. Tranter also of that Division calibrated the Clarke-Bumpus sampler and gave much valuable assistance. Dr. A. A. Racek, Zoology Department, University of Sydney, gave assistance and advice during the preparation of this work. Dr. J. P. Harding, of the British Museum, gave assistance in the identification of crustacean species.

Finally, Dr. A. G. Nicholls, of the Division of Fisheries and Oceanography, CSIRO, provided helpful criticism during the later stages of the preparation of this work.

The Acting Director of the Antarctic Division, Department of Supply (Mr. D. F. Styles) authorised the publication of this report.

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APPENDIX I

Distribution of the major aquatic fauna and flora on Macquarie Island

	Prion Lake	"S" Pond	"23U" Pond	D.L.	"F$_5$" Pond
Copepoda					
Pseudoboeckella brevicaudata Brady	+	+	+	+	+
Thalastrid sp. ?	+	+	+	+	+
Cladocera					
Daphnia carinata King	+	—	+	+	+
Alona diaphana King	—	+	+	+	+
Alona quadrangularis O.F.M.	—	+	+	+	+
Macrothrix hirsuticornis Norman and Brady	—	+	+	+	+
Chydorus poppei-barroisi (group)	—	+	+	+	+
Ostracoda					
Cypretta sp.	—	+	+	+	+
Isopoda					
1 sp. (Fam.: Janiridae)*	—	—	—	—	—
Acari					
1 sp.	+	+	+	+	+
Oligochaeta†					
Microscolex macquariensis Beddard			Scobles Lake		
Marionina sp. ?			+		
Turbellaria					
? spp.		+	+	+	+
Tardigrades, nematodes, rotifers, diptera larva were also present in collections.					
Vascular Plants					
Myriophyllum elatinoides	Rare	—	+	+	—
Callitriche antarctica Englin	—	—	+	—	—
Ranunculus biternatus Smith	—	+	+	—	—
Algae					
Chlorophycae					
Rhizoclonium sp.	+	+	+	+	+
Zygnemaceae					
Spirogyra sp.	—	+	+	+	+
Staurastrum sp.	+				

* Occurs only in streams.

† Oligochaetes were collected in all these water bodies but species have not been identified.

‡ Also in sub-glacial herbfield, coastal terrace.

Letters indicate relative amounts of abundance within a water body.

A = abundant
F = frequent
O = occasional
C = common
R = rare

APPENDIX I *(continued)*

	Prion Lake	“S” Pond	“23U” Pond	D.L.	“F$_5$” Pond
Bacillarophyceae					
Acnanthes biasolettiana Grun‡	R	O	A, C	C	
A. brevipes v. *intermedia* K.‡			O	R, O	
A. subsala Paterson			R	R, O	
Amphora delicatissima Krasske	+		R		
A. ovalis K.			R	R	
Cocconeis placentula E.R.	R, O	R	R, A	O, R	
Cyclotella antiqua W. Sm.			O		
C. meneghiana Ktz.				C	
C. stelligera Cl. and Gr.	C, O		O	O	
Cymatopleura solea W.S.‡				R	
Cymbella americana A. Sch.	R		R		
C. pusilla Grun.	O			R	
Diatomella sp.			R		
D. balfouriana Grer.	+				
Diploneis smithii Breb.	R		R	R	
Epithemia sorex K.			R		
Encyonema gracile Rab.			O		
E. lunula Grun.	R		R		
Eunotia alpina K.	R	R			
E. arcus Eh.			O	R	
E. lunaris Grun.	+			R	
E. monodon Eh.					
E. pectinalis Dillwyn			R		
E. robusta Ralfs				O	
E. triodon Eh.			R		
E. trinacria Krasske‡	+				
E. zygodon Eh.	R				
Fragilaria bicapitata A. Mayer	R		R, C	O	
F. capucina Deson‡	C, O		C, O	C	
F. harrisonii (W.S.) Grun.	R		R		
F. pinnata Eh.					
F. virescens Ralfs‡	+		A	C	
Fragilariopsis antarctica Castr.	+				
Frustula minuta Rab.	+	O	R	O	
F. rhomboides (Eh.) De Toni	R	C	R		
Gomphonema intricatum K.	O		F	R	
G. parvulum K.‡	R	R	O	C	
Hantzchia amphioxys (Eh.) Grun.‡		R		R	
Mastogloia sp.		R			
M. squamosa ? Brun			R		
Melosira crenulata K.		O			
M. decipiens Grove		A	O	O	
Navicula mutica Kutz			R		
N. radiosa K.	O		C		
N. reinhardti Grun.			R		
N. rostellata Kutz	R	O	R	R	
Neidium affine (Eh.) Cleve	+				
Opephora martyi Heriband		R		R	
Pinnularia appendiculata (Ag.) Cleve‡				R, O	
P. sp.	R	R		R	
P. atwoodii Per.					
P. borealis Eh.‡					
P. brevicostata Cleve‡	R	R			
P. cardinalis (Eh.) W. Sm.‡					

APPENDIX I *(continued)*

	Prion Lake	"S" Pond	"23U" Pond	D.L.	"F_5" Pond
P. commutata Grun.	R		R		
P. divergens W. Sm.				R	
P. divergentissima (Grun.) Cleve‡		R			
P. fusciata Lagerst.					
P. interrupta W.S.				R	
P. lata W. Sm.	+	R	R		
P. macilenta Eh.	R				
P. major Grun.	O	R		R	
P. microstauron Eh.‡	R	R	R	R	
P. molaris Grun.	+	O	O	R, O	
P. nivorum ? Per.‡					
P. rupestris Hantzsch.			R		
P. viridus K.	R		R	R	
Rhopalodia gibba O. Mull.	F		R	R, O	
R. gibberula (Eh.) O.M.	R	O		O	
R. ventricosa O. Mull.			R		
Stauroneis acuta W.S.	R		R, O	R	
S. anceps var. *hyalina* Brun and Per.			R	R, O	
S. fulmen Brit.			R		
S. parvula ? (Grun.) Jen.					
S. phoenicenteron Eh.	R				
S. pygmea Kreiger			R		
Stenopterobia anceps Breb.			R		
Surirella angustata K.		R	R		
S. angustior O.M.		R			
S. bifrons K.	R	F	A		
S. engleri O.M.					
Synedra sp.	R	R	R	R	
Synedra vaucheriae (?) K.‡					
Tabellaria flocculosa Roth. K.	C	C	F, C	C	
Cyanophyceae					
Nostoc sp.			+		
Nodularia sp (?)			+		