OBSERVATIONS ON THE DIET AND DEVELOPMENT OF
Pseudoboeckella poppei (CALANOIDA, CENTROPAGIDAE)
FROM AN ANTARCTIC LAKE

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ABSTRACT. Analyses of the gut contents of *P. poppei* have shown that all the copepodid stages are unselective particle feeders in the plankton and that stages III to VI also feed unselectively in the benthos. The single annual recruitment to the population of Sombre Lake was synchronized by limited survival of nauplii in the latter half of the winter, probably as a result of food scarcity. Egg development took approximately 12 days. Animals developed from copepodid stage I to stage VI (adult) in 18 weeks. Fecundity was low. All this was in marked contrast to nearby Heywood Lake, where the phytoplankton was richer, nauplii developed throughout the year and the generations were less well defined.

Development and body size appear to be governed by the food available as are respiration rate and dry weight/wet weight ratio, which both increase when food is plentiful.

THIS paper describes the diet and life history of *Pseudoboeckella poppei* (Daday) in Sombre Lake (lat. 60°41'20"S., long. 45°36'50"W.), Signy Island, South Orkney Islands. Comparisons are made with populations which occur in nearby lakes and which have been mistakenly reported as *P. silvestri* (Heywood, 1970*a*, *b*, 1977).

Sombre Lake lies 4 m. above mean sea-level in Paternoster Valley (Fig. 1). The lake has a surface area of approximately 27,600 m.² and a maximum depth of 11·2 m.

METHODS

Field work

The work was carried out at three stations (Fig. 2). Station A, the deepest point of the lake, was used for all water sampling. Station B, a SCUBA diving site, lay 20 m. to the south-west of station A. To minimize disturbance at station A, all diving was carried out in a sector south of station B. Station C covered several square metres of shallow water (about 20 cm. deep) near the south-east shore of the lake.

Observations were made of *P. poppei* and its environment at intervals of a month or less during the period 21 March 1973–25 March 1974. Temperature and dissolved oxygen were measured using a probe after the design of Mackereth (1964). Water samples were taken from 1, 4 and 9 m. depths using a "Whale Gusher 10" bilge pump (Munster and Simms Engineering Ltd., Old Belfast Road, Bangor, Northern Ireland) and a flexible polythene pipe. The pump could be operated satisfactorily at air temperatures as low as −20° C, if taken into the field when completely dry and then used continuously.

Animals were removed from the water by filtration and transported to the laboratory in plastic containers immersed in a methanol–snow (1/1) freezing mixture at approximately −40° C for gut-content analysis. The animal-free water was retained for phytoplankton cell enumeration and chlorophyll$_a$ determination.

The benthos was sampled by diving. Animals, plants and substrate were scooped into plastic clip-top bottles which had bottoms of fine mesh (50 threads/cm.). The mesh prevented the bottles from being crushed during descent by allowing water to flow in. During ascent the mesh allowed very little of the sample to escape. Six containers were filled on each dive and each container was sealed in a polythene bag and immersed in methanol–snow (1/1) freezing mixture for transport to the laboratory. Samples of the benthos were taken at station C using the same containers but on this site some of the algae had to be scraped off the rocks with the lip of the container.

Further samples of *P. poppei* were obtained by vertical hauls with a zooplankton net for life-history studies, wet- and dry-weight determinations, respiration studies and for determination of clutch size. They were transported to the laboratory alive in large vacuum flasks.

CONTOUR INTERVAL 20m.

⌒ STREAMS

---- STREAMS RUNNING UNDER ICE

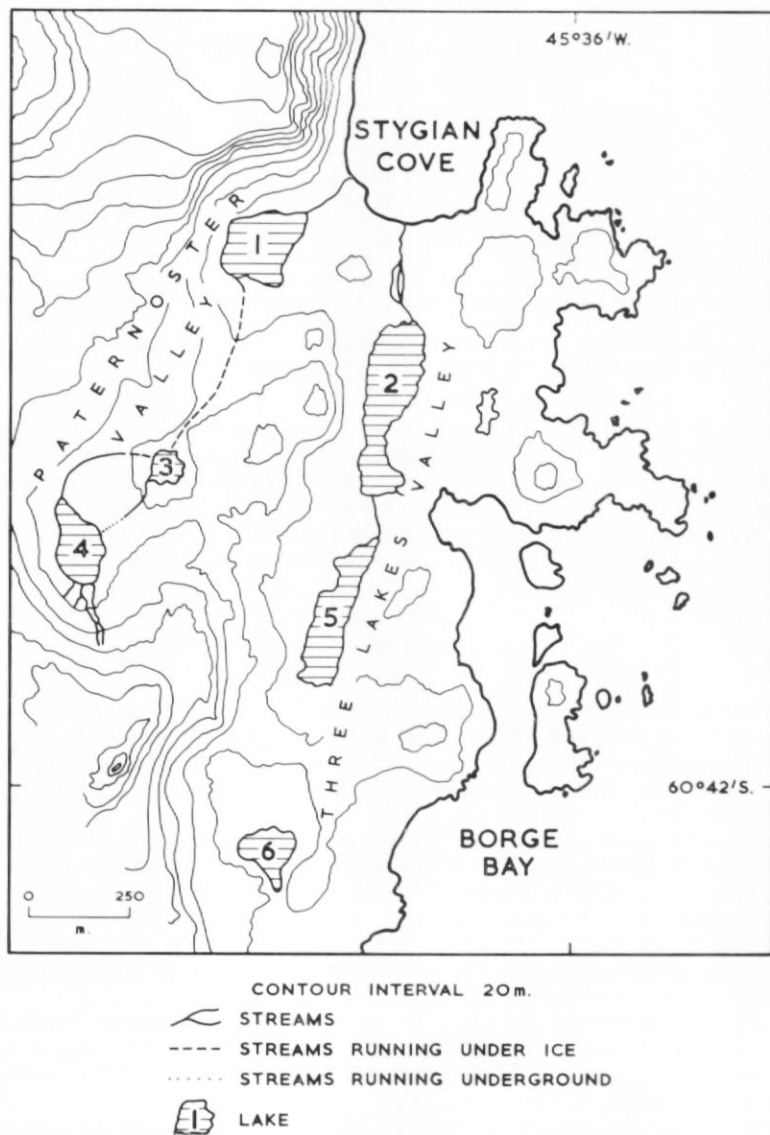······ STREAMS RUNNING UNDERGROUND

▣ LAKE

Fig. 1. The lakes of north-east Signy Island (from D.O.S. sheet 210). Additional information from Light (1976). (Several lakes on Signy Island have recently been named by the Antarctic Place-Names Committee. The old lake numbers have been used in this figure for the sake of clarity. The numbers and names of the lakes are as follows:

Lake 1   Sombre Lake; Lake 2   Heywood Lake; Lake 3   Changing Lake;
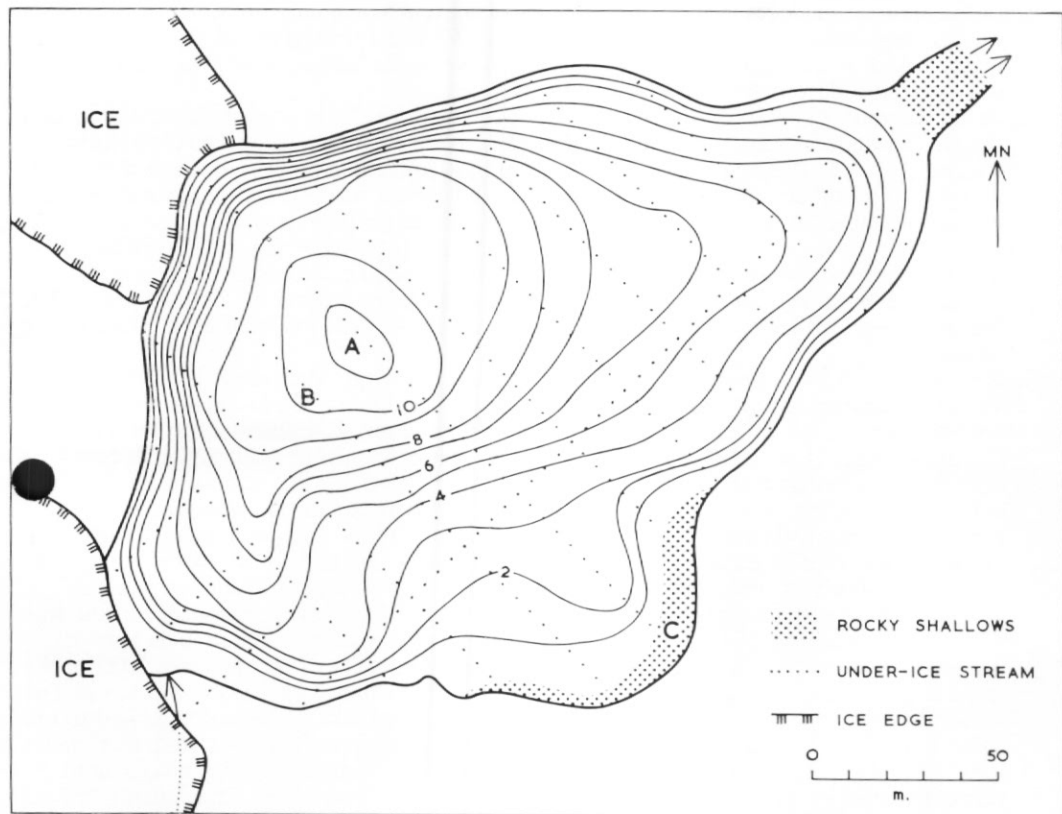Lake 4   Moss Lake; Lake 5   Knob Lake; Lake 6   Pumphouse Lake.

Fig. 2. Outline of Sombre Lake showing bathymetric contours in metres. A, B and C mark the sampling stations.

Laboratory work

Samples were treated as follows:

i. Chlorophyll$_a$ content was determined by the standard spectrophotometric method of Richards and Thompson (1952) within 3–4 hr. of collection. 1 l. sub-samples were used.

ii. Algal cells were sedimented from 500 ml. sub-samples using Lugol's iodine. Five replicate counts were made on an inverted microscope (Lund and others, 1958). In abundant species up to 700 cells were counted.

iii. Benthos and substrates were examined under the microscope and described qualitatively.

iv. Animals for gut-content analysis were kept frozen until immediately prior to dissection. Freezing was found to be the best method of preservation. Chemical preservatives tended to decolourize the gut contents and caused the animals to void their guts as they died, giving an incorrect number for animals with empty guts at the time of capture.

The guts of animals were removed with mounted needles on to microscope slides. The contents were teased out and smears made. Whenever possible, the contents of the fore and hind guts were examined separately. However, in most cases it was only possible to dissect out either the fore or hind gut, not both. The removal of one part of the gut usually resulted in the loss of the contents from the other. In each case a note was made of which part of the gut was being examined in an attempt to gain information on digestion.

An estimate was made of the percentage volume of various organisms and of uniden-tifiable material present. The estimate was inexact but it gave some idea of abundance

rather than of just presence or absence. Algae were provisionally identified with the aid of drawings made by Dr. H. Belcher (Culture Centre for Algae and Protozoa, Cambridge) and J. J. Light (British Antarctic Survey). Reference was also made to the drawings and descriptions of Fritsch (1912).

v. In the life-history study, animals were divided into life stages, counted, measured and sexed. The animals were measured with a microscope eye-piece scale. The cephalothorax was measured to the nearest eye-piece division (40μm. intervals for copepodid stages V and VI). The other errors in the method caused by positioning of the animal did not exceed the limits of accuracy imposed by the eye-piece scale. *P. poppei*, in common with most other calanoid copepods, passes through 13 life stages—egg, six naupliar stages and six copepodid stages, of which the last is the adult. In the text, naupliar stages are designated by arabic numerals 1 to 6, copepodid stages by roman numerals I to VI. Nauplii were neither counted nor measured but a note was made of their presence or absence.

vi. Respiration measurements were made on copepodid stage V animals in preference to adults to minimize the risk of using moribund specimens. Eight replicates and two controls were used in each experiment. The respiration chambers were 5 ml. hypodermic syringes (Ewer, 1942; Gilchrist, 1958). A short length of tubing, which could be sealed with a bung, was fitted on to each nozzle. Two $1 \cdot 74$ ml. sub-samples of water could be extracted, without aeration, from each experimental chamber with a syringe pipette for "micro-Winkler" oxygen determinations (Fox and Wingfield, 1938). The animals were kept in glass-fibre (GF/C) filtered lake water at $5°$ C until their guts were empty. Six females and four males were pipetted into each respiration vessel. Ten animals were used in each vessel so that the reduction in oxygen concentration was within the sensitivity of the method. The ratio of six females to four males was determined by the availability of animals from the lake. The animals were left in the respiration vessels for $2\frac{1}{2}$ hr. to recover from the disturbance caused by pipetting. The vessels were then very carefully re-filled with fresh filtered lake water and returned to the water bath for 5–6 hr. at $5° \pm 0 \cdot 01°$ C. Duplicate oxygen determinations were then made for experimental and control vessels. For each group of animals the oxygen consumption was calculated by subtracting the final oxygen concentration in the experimental vessel (the mean of two determinations) from the mean of eight determinations, four initial and four final, in the control vessels.

vii. Wet weight/dry weight ratios were determined for copepodid stage V animals also. The animals were kept in glass-fibre filtered lake water until their guts appeared empty and then blotted and weighed on a micro-balance in groups of ten individuals of the same sex. The animals were then dried at about $60°$ C until a constant dry weight was obtained.

RESULTS AND DISCUSSION

The lake flora and the diet of P. poppei

The flora can be described in terms of four distinct habitats:

i. *Plankton.* From April 1973 to March 1974 recorded chlorophyll$_a$ levels never exceeded $5 \cdot 96 \mu$g./l. in Sombre Lake (Fig. 3a), whereas recorded maxima in Amos Lake (a lake on the west coast of Signy Island, formerly lake 10 (Heywood, 1967)) and Heywood Lake were $19 \cdot 5$ and $94 \cdot 6 \mu$g./l., respectively. The phytoplankton could be relatively sparse for several reasons. Sombre Lake receives most of its water directly, or indirectly via Changing Lake, from an ice field which extends to its western shore. The streams connecting all three lakes in Paternoster Valley run under the ice field for practically all their lengths (Heywood, 1967; Light, 1976). Furthermore, steep cliffs, which rise to a height of 170 m. within 200 m. of the lake shore, restrict periods when sunlight falls directly on the lake. Shading of the lake surface and the low temperature of the inflowing water result in persistent ice cover in the spring, which further reduces the light available to the algae. (In 1969–70 the surface of the lake remained frozen throughout the
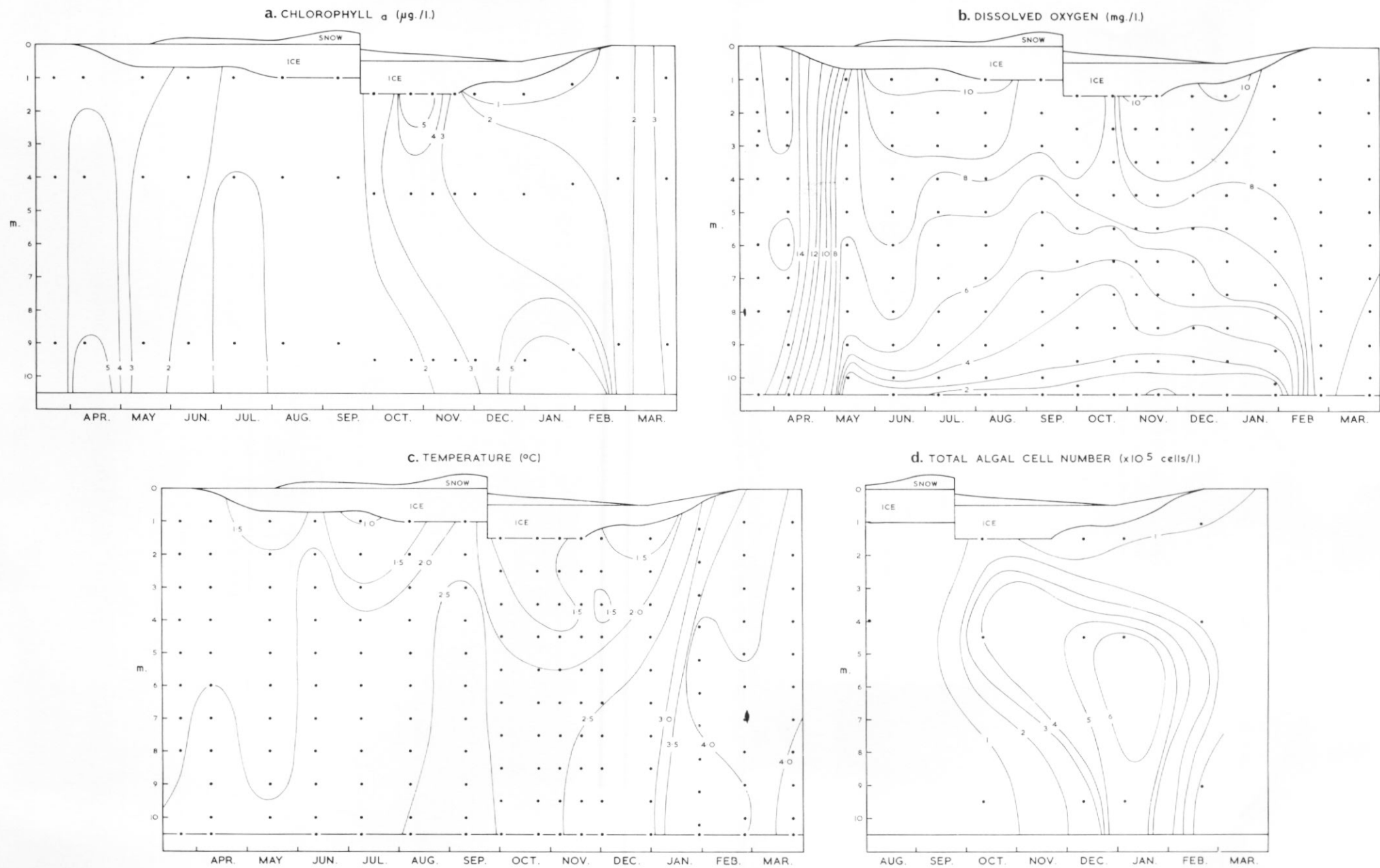
a. CHLOROPHYLL $_a$ (µg./l.)

b. DISSOLVED OXYGEN (mg./l.)

c. TEMPERATURE (°C)

d. TOTAL ALGAL CELL NUMBER (x10^5 cells/l.)

Fig. 3. Nomograms showing chlorophyll$_a$ concentration, dissolved oxygen concentration, temperature and phytoplankton cell numbers in Sombre Lake. (On or around 23 September 1973 an avalanche deposited a large quantity of snow on the lake surface. The west side of the lake was covered by 1–3 m. of snow up to 15 m. from the shore. The ice under the snow was depressed and flooded to a depth of 30 cm. On the east and north sides of the lake the ice was raised as much as 1·3 m. and cracks were formed up to 2 m. wide. A large volume of water was ejected from the lake on to the sea ice in Stygian Cove and the depth of water at station A was reduced by 0·5 m. The loss was not fully made up until February 1974.)

TABLE I. NUTRIENT LEVELS IN THREE SIGNY ISLAND LAKES

Lake	Date	Depth (m.)	Cl' (mg./l.)	NO_2' (mg./l.)	NO_3' (mg./l.)	P (mg./l.)	SiO_3'' (mg./l.)	K^+ (mg./l.)	Na^+ (mg./l.)	Mg^{++} (mg./l.)
					WINTER					
		S	16·3	0·0077	0·410	0·060	0·190	0·65	18·2	7·2
Sombre Lake	8 June 1974	5	20·0	0·0048	0·390	0·065	0·193	0·70	21·3	9·5
		9	19·6	0·0055	0·410	0·066	0·193	0·70	21·0	9·5
		S	58·5	0·0308	1·400	0·018	0·231	0·33	17·0	3·7
Heywood Lake	4 June 1974	3	60·3	0·0331	–	0·018	0·240	0·34	17·6	5·6
		5	60·3	0·0336	1·500	0·018	0·243	0·30	16·2	5·8
		S	79·1	0·0495	10·100	0·152	0·358	3·9	72	7·9
Amos Lake	10 June 1974	1·5	79·1	0·0517	9·300	0·154	0·360	4·2	76	8·1
		3	79·1	0·0586	9·150	0·154	0·360	4·1	72	8·5
					SUMMER					
		S	19·7	0·0071	0·516	0·001	0·253	0·65	26·5	10·2
Sombre Lake	23 February 1975	5	19·3	0·0074	0·509	–	0·223	0·80	25·5	10·6
		9	19·0	0·0071	0·513	0·002	0·219	0·65	24·5	9·8
		S	32·7	0·0386	4·622	0·052	0·415	1·45	44·0	15·0
Heywood Lake	22 February 1975	3	32·7	0·0402	5·196	0·054	0·459	1·40	43·0	18·5
		5	32·3	0·0400	4·732	0·049	0·412	1·45	44·0	17·5
		S	9·6	0·0493	3·40	0·162	0·220	0·3	98	9·2
Amos Lake	18 November 1974	1·5	10·2	0·0495	3·80	0·200	0·218	0·3	92	9·6
		3	11·8	0·0502	4·10	0·213	0·223	0·3	93	9·8

S   Surface.

summer; in 1972–73 and 1973–74 the lake was ice-free for 4 and 7 weeks, respectively.) Low temperatures and light levels probably restrict plant activity.

Although no long-term data exist on nutrient levels, they are known to be relatively low. Examples of nutrient levels for summer and winter in Sombre Lake, Amos Lake and Heywood Lake are set out in Table I. Unlike some other low-lying lakes on the island, Sombre Lake is not enriched by seal faeces. However, high nutrient levels and near-anaerobic conditions have been recorded in the bottom few centimetres of the trough in winter (4·5 mg./l. SiO_3'' and 0·184 mg./l. PO_4''' on 26 October 1970. 0·15 mg./l. dissolved oxygen on 15 September 1970 (personal communication from J. J. Light)).

The phytoplankton is dominated by Chlorophyceae and Cryptophyceae. There are also considerable numbers of Bacillariophyceae (Table II).

TABLE II. OCCURRENCE OF ALGAL SPECIES IN SOMBRE LAKE, SIGNY ISLAND

		Plankton 1 m.	Plankton 4 m.	Plankton 9 m.	Trough benthos	Shallows benthos (1)	Shallows benthos (2)
Bacillariophyceae	Fragilaria capucina	+	++	+	++	++	+++
	Nitzschia fonticula	+	+	+	++	++	++
	Achnanthes kryophila	+	+		++	++	++
	Navicula sp. A	+	+	+	+	++	++
	Navicula sp. B		+		++	++	
	Gomphonema angustatum			+	+	+++	+++
	Stauroneis phoenicenteron				+		
	Pinnularia microstauron				+	+	+
	Fragilaropsis sp.				+	+	
	Navicula cuspidata						+
Chlorophyceae Chlorococcales	Chlorella sp.	++	+++	++	++	++	++
	Ankistrodesmus falcatus	+	++	+++	++		
	Lambertia gracilepes		+	+			
	Schroederia sp.	+	+	+			
Volvocales	Chlamydomonas sp.	+	+++	+++			
Cryptophyceae	Cryptomonas sp.	++	+++	++			
Chrysophyceae	Cysts			+		+	
Xanthophyceae	Tribonema sp.				+++		
Cyanophyceae	Phormidium tenue			+	+	+++	++
	Phormidium fragile					++	++
	Phormidium uncinatum				+	++	++
	Phormidium angustissimum					+	
Euglenophyceae	Euglenoid sp.	+	+				

+ Present;   ++ Common;   +++ Very common.

ii. *The benthos of the trough.* There is a rich, predominantly bacillariophycean and xanthophycean flora. The Bacillariophyceae are found among the fine particles of mica-schist and organic matter that form the mud bottom of the trough, while the filamentous xanthophycean *Tribonema* sp. lies over a large proportion of the bottom. Small quantities of the mosses *Amblystegium* sp. and *Drepanocladus* sp. (Light and Heywood, 1973) occur on the south side of the trough, near the outflow and to the west of station

A in 5–6 m. of water. The amount of moss is very small compared with that in Moss Lake higher up Paternoster Valley.

iii. *The epilithic flora of the shallows.* This takes the form of red-brown mats of densely packed cyanophycean filaments, among which diatoms grow. In much of the material examined, the cyanophycean filaments were dead but the associated diatom population was still alive. It is not known whether dead filaments were distributed as a surface layer over the whole mat, or whether filaments were dead throughout the depth of the mat in localized areas.

iv. *The detached benthic flora of the shallows.* This has the appearance of small grey-green flakes, which litter the bottom between rocks. The flakes are apparently formed when epilithic algal mats are scoured by ice action. Almost all the Cyanophyceae are dead but the diatoms are alive, abundant and often growing in chains. In winter the flora of the shallows is frozen into the lake ice.

Bacteria, fungi and Protozoa were found in all the habitats described above.

Pseudoboeckella poppei was observed at all depths throughout the year. Large numbers of animals, mainly adults, swarmed over the trough floor and seemed to be undeterred by very low winter oxygen levels (Fig. 3b). However, numbers were always greatest in the plankton.

Most of the guts examined were from adult animals. However, many guts from copepodid ages II, III, IV and V were examined and found to have similar contents. In general, the abundance of an algal species in the guts reflected the abundance of the species in the phytoplankton at the same depth and time.

Ankistrodesmus falcatus was a good indicator because it was easy to identify even when partially digested. In December and January a small bloom was recorded at a depth of 4 m. (Table III), which showed up in the gut analyses. A bloom, which reached a peak in December at a depth of 9 m., comprised 47 per cent of the phytoplankton by cell number. Guts of associated animals contained up to 95 per cent of identifiable *A. falcatus*. This was very unusual in that most guts usually contained at least 95 per cent of unidentifiable material.

The changes in the concentration of *Chlorella* sp. cells (Table III) were closely matched by changes in abundance in the guts. Two other abundant algae, *Cryptomonas* sp. and *Chlamydomonas* sp., also provided good supporting evidence, despite the fact that they were often difficult to identify after ingestion. An anomalous situation occurred on 4 January 1974. A *Chlamydomonas* sp. bloom recorded at 4 m. was reflected in the gut contents of animals caught at that depth. The bloom was also recorded at 9 m., where it comprised 75 per cent of the phytoplankton by cell number, but the guts of animals caught at this depth contained very little *Chlamydomonas*. *Tribonema* sp. was found in some of the guts and it is possible that the animals were collected from the benthos in error and not from the plankton. There is another possible explanation. In October 1970, Light (personal communication) observed a big algal concentration in a very narrow band at a depth of 9 m. If a similar situation occurred on 4 January 1974, a distorted picture could have been obtained if the animal sample was taken from outside the algal layer. The depth interval between samples made it impossible to determine whether the bloom occurred at all depths.

The relationship between *P. poppei* and potential food species is most apparent in the three benthic communities because the algae are easier to identify. In all cases, individuals were found to have a complete range of potential food species and a variety of other particles such as mica-schist in their guts.

On the trough floor, *Tribonema* sp. filaments often comprised 50 per cent of the identifiable gut contents and the diatoms growing at the mud/water interface were also found in large numbers. In the shallow-water benthic habitats, *Phormidium* spp. occur in almost all the guts but not in the quantities one might expect from their dense growth on the rocks. This may indicate that firmly encrusted filaments are not available to *P. poppei* but that detached or loose filaments are. The diatoms in the interstices of the cyanophycean mats (mainly *Gomphonema angustatum, Fragilaria capucina* and *Nitzchia fonticula*) may be unavailable if enclosed by firmly attached filaments. However, large numbers are clearly available and they can form as much as 50 per cent of the total gut contents. Heywood (1970a) suggested that the maxillipeds of *P. poppei* are adapted for stirring up debris and making it available for filtration. This method of feeding could account for the relatively small amounts of *Phormidium* spp. in the

TABLE III. THE PHYTOPLANKTON OF SOMBRE LAKE (cells × 10^3/l.)

Date		2 August 1973	10 October 1973			31 October 1973	10 December 1973			4 January 1974			20 February 1974		
Depth		4 m.	1 m.	4 m.	9 m.	4 m.	1 m.	4 m.	9 m.	1 m.	4 m.	9 m.	1 m.	4 m.	9 m.
Bacillariophyceae	*Fragilaria capucina*		13	3	13	52		3	10	3					
	Nitzschia fonticula	1				3							13	13	5
	Achnanthes kryophila					3				16					
	Navicula sp. A				3					5	3				
	Navicula sp. B					3									
	Gomphonema angustatum				3										
Chlorophyceae Chlorococcales	*Chlorella* sp.	3	70	280	18	170	8	160	54	10	21	16	8	13	23
	Ankistrodesmus falcatus			3	16	8		3	106	3	31	65	23	21	10
	Lambertia gracilepes					3			3					3	
	Schroederia sp.										18	10	10	10	8
Volvocales	*Chlamydomonas* sp.	2	3	3	5	3		57	26	13	590	430	10	31	18
Cryptophyceae	*Cryptomonas* sp.	3	88	110	10	310	8	49	21	49	26	44		26	
Chrysophyceae	*Chrysococcus* sp.	1													
	Cyst									5					
Cyanophyceae	*Phormidium* sp.					10						8		16	
Euglenophyceae	Euglenoid sp.						3	5							
Algal total		9	173	400	67	570	18	280	220	98	690	570	72	140	65

guts. However, *P. poppei* does take in live cells, including some *Phormidium* spp. and not just debris. No animals younger than copepodid stage III were caught from the benthos of the shallows and it has been suggested (Heywood, 1970*a*) that only on ecdysis to stage III does *P. poppei* become adapted for this mode of feeding.

Bacteria, fungi and Protozoa are taken into the gut along with the algae but it is impossible to make an estimate of their nutritional value.

It should be noted that for a large part of the year animals cannot feed in the shallows which freeze solid.

Gut-content analyses on animals fed on algal cultures in the laboratory showed that they can break up and digest: *Fragilaria capucina* (30 μm. by 5 μm.), *Chlorella* sp. (5 μm. sphere), the cyanophycean *Oscillatoria* sp. (filament) and the chlorophycean *Stichococcus bacilaris* (10 μm. by 4 μm.). These observations confirm that *P. poppei* can feed on algae of the size range and type that it encounters in the lake. Examination of the contents of fore and hind guts of animals caught in the lake revealed broken and unbroken cells in both parts. Broken cells were probably ingested along with live ones, so little information was gained on digestive efficiency.

Life history

The changing structure of the *P. poppei* population indicated that there was a single, synchronized annual recruitment (Fig. 4). The long inter-sample period made precise estimates of development times impossible. However, very approximate times can be given for the copepodid stages (Table IV; Fig. 4).

TABLE IV. DEVELOPMENT TIMES OF *Pseudoboeckella poppei* COPEPODID STAGES

Copepodid stages from	to	Approximate time (weeks)
I	II	1–2
II	III	4
III	IV	2
IV	V	4–5
V	VI	5–6
I	VI	18

Development times for eggs and nauplii were more difficult to estimate. Some observations were made on 29 gravid females kept at $3 \cdot 5$–$4 \cdot 0°$ C in the laboratory. Individuals were kept in vials containing 15 ml. of raw lake water. The water was changed on alternate days for fresh aerated water. Times of egg hatching were noted. Using the method of Edmonsdon (1960, 1965) for Rotifera, adapted for cyclopoid copepods by Taube (1966) and Burgis (1970), it was possible to extrapolate an egg-development time of approximately 12 days for *P. poppei* (Fig. 5). However, when eggs were developing in the lake, the water temperature was 1–2° C lower than the experimental temperature (Fig. 3c). Therefore, egg development may have taken a longer period.

Factors controlling the survival of nauplii may synchronize recruitment. Eggs were produced and hatched over a period of 5 months between June and October. Gravid females were present in the population for a further 4 months but in very small numbers. Despite this extended production of nauplii, copepodid stage I animals did not appear until 6 November and succeeding stages remained in the population for very short periods (Fig. 4). It seems
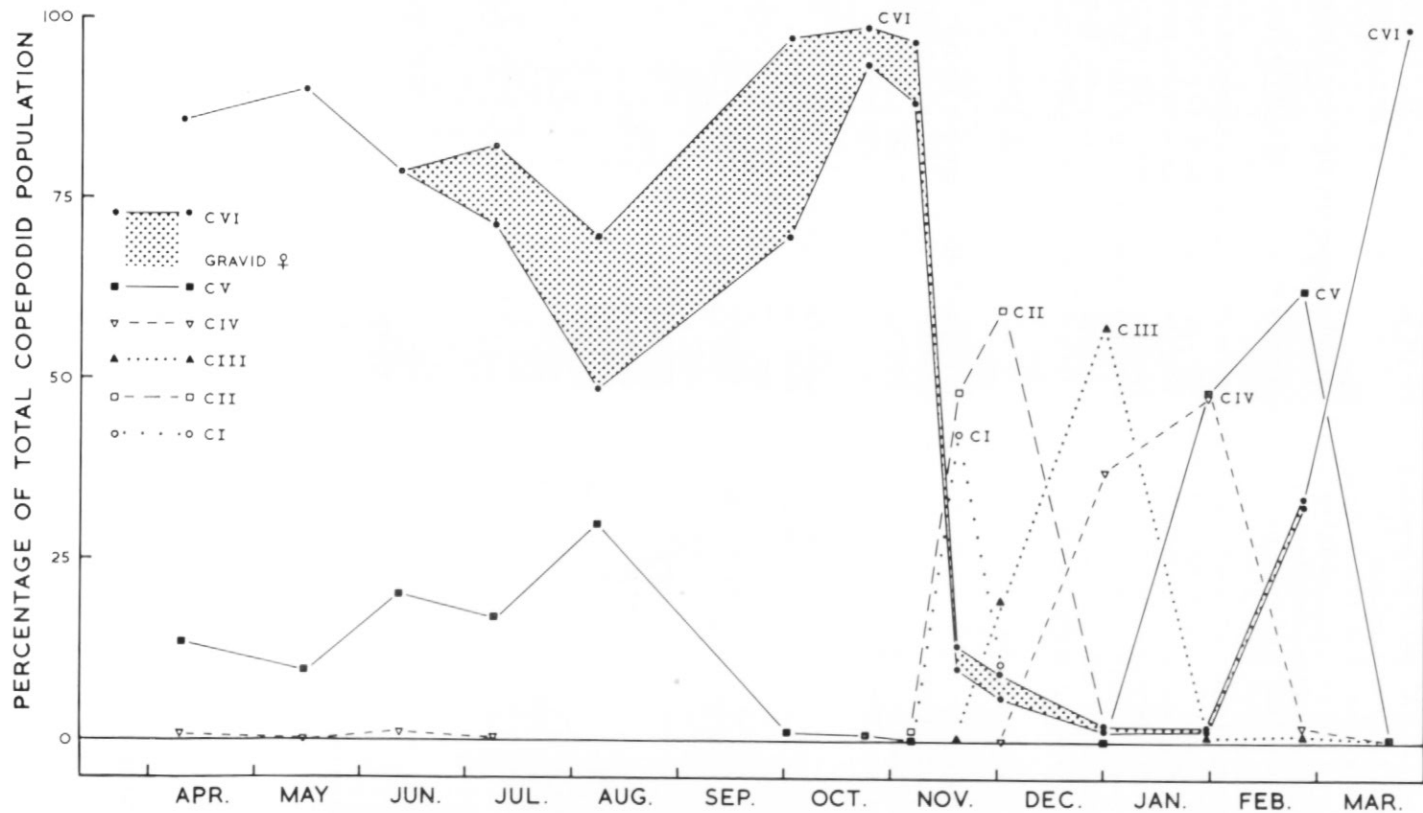
Fig. 4.   Percentage frequency of *Pseudoboeckella poppei* copepodid stages in Sombre Lake. The actual values
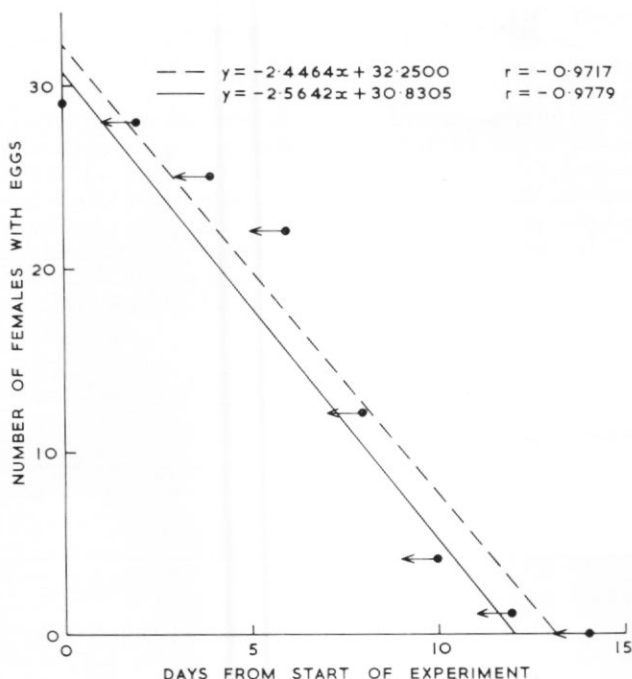are recorded in the Appendix.

Fig. 5. Determination of the mean development time of eggs of *P. poppei* at $3 \cdot 5$–$4 \cdot 0°$ C. The points drawn from observed data are joined with a broken regression line. Because observations were only made at 2 day intervals, a more realistic regression may be drawn by displacing all the points, except the one for day 0, 1 day to the left. This gives the continuous regression line.

likely, therefore, that the nauplii hatching out in early spring either failed to survive or developed very slowly. Direct observations of nauplii between July and October gave no indication of a big increase in numbers in the lake and it seems likely, although the lack of accurate counts makes it impossible to be certain, that they failed to survive. Nauplii may only have been able to survive as the phytoplankton increased in October (Fig. 3a and d), the discrete peaks in copepodid numbers (Fig. 4) having been preceded by discrete peaks of surviving naupliar stages.

Heywood Lake, which lies about 250 m. to the south-east of Sombre Lake (Fig. 1) and Pumphouse Lake which lies 1,500 m. due south, have *P. poppei* populations which breed continuously (Heywood, 1970b). The breeding peaks fall at the same time of year as in Sombre Lake but all naupliar and copepodid stages are always present. The phytoplankton of Heywood Lake is markedly richer than that of Sombre Lake, and it is possible that in this lake nauplii are able to survive and develop throughout the year. During the period between March 1973 and March 1974 the mean recorded chlorophyll$_a$ level in Sombre Lake was $2 \cdot 7 \mu g./l.$, whereas in Heywood Lake the mean recorded level was $12 \cdot 3 \mu g./l$. Although the minimum levels in Heywood Lake are not much higher than those in Sombre Lake ($1 \cdot 3$ and $0 \cdot 98 \mu g./l.$, respectively), the low levels persist for a much shorter time. No detailed information is available for Pumphouse Lake.

Variations in body length

Body length has been found to have a negative correlation with temperature in copepods, at least when the temperature range is high (Deevey, 1960, 1964, 1966). The temperature range in the lakes of Signy Island is relatively small and variations in body length of *P. poppei* are probably due to food availability during development (Heywood, 1970b). Deevey noted that,

at a given temperature, body length corresponded to total phytoplankton abundance in a calanoid that filtered unselectively, while in two selective filter feeders there was no such correlation. *P. poppei* is an unselective feeder and presumably its body length will be largely determined by the total potential food available during development.

In Sombre Lake, recruitment seemed to be synchronized by the survival of nauplii and all animals were exposed to similar food conditions during development. Consequently, all adults caught between April and December 1973 had a normal distribution of cephalothorax length/frequency, with the bulk of the population deviating very little from the mean (Table V; Fig. 4). During late December 1973 and January 1974 the number of adults in the lake dropped suddenly until on 29 January there were very few present. It seems that few if any of the adult population of 1973 survived to form part of the 1974 population. The new generation of adults which started to appear in February 1974 showed similar length/frequency distributions but the mean lengths were slightly shorter (Table V).

TABLE V. VARIATIONS IN CEPHALOTHORAX LENGTH (mm.) OF *Pseudoboeckella poppei* FROM HEYWOOD AND SOMBRE LAKES

Locality and date	Male			Female			Authority
	$\bar{x}$	s	n	$\bar{x}$	s	n	
Heywood Lake (2 April–26 September 1962)	2·18	0·09	300	2·57	0·11	337	Heywood, 1970b
Heywood Lake (28 May–2 December 1963)	1·79	0·15	1,355	2·08	0·19	617	Heywood, 1970b
Heywood Lake (5 January–20 March 1964)	2·12	0·14	166	2·47	0·21	101	Heywood, 1970b
Sombre Lake (9 March–31 December 1973)	2·14	0·09	492	2·49	0·10	502	Weller, this paper
Sombre Lake (26 February–25 March 1974)	2·01	0·06	73	2·31	0·06	62	Weller, this paper

In Heywood Lake, nauplii survive at all times of the year (Heywood, 1970b) and recruitment is controlled by egg production and hatching. Eggs were produced throughout the year in Heywood Lake, mainly between May and December. This is similar to Sombre Lake, where most of the eggs were produced between June and December in 1973 (Fig. 4). Individuals developing from these eggs were subject to widely differing food conditions and the resulting adults had much more variation in cephalothorax length than adults from Sombre Lake (Table V). Variation in length was increased further by the co-existence of the adults of one generation with those of the next.

The amount of food available to each individual is affected not only by the total food available but also by the number of individuals exploiting the food supply. Heywood (1970b)

noted that, following a winter when low light levels had severely restricted algal production and caused high mortality in all *P. poppei* life stages, few nauplii were produced. Consequently, the amount of food available to each individual in the spring was high and the adults produced were large. During the following winter mortality was lower, more nauplii were produced, the food available to each individual was less and the adults produced were small.

Respiration rates and dry weight/wet weight ratios

Few determinations were made because of the prolonged absence of copepodid stage V animals from the *P. poppei* population. Although very limited, these results are the first of their kind for an Antarctic copepod and therefore they are of value.

There was a very marked increase in respiratory rate when food was plentiful (Table VI).

TABLE VI. RESPIRATION RATES OF COPEPODID STAGE V *Pseudoboeckella poppei* EXPRESSED IN mg. O_2/g. wet weight/hr.

Date	$\bar{x}$	s	n
9 April 1973	0·22	0·14	7
14 May 1973	0·15	0·02	7
11 June 1973	0·10	0·03	8
8 July 1973	0·09	0·04	8
7 August 1973	0·14	0·04	8
29 January 1974	0·27	0·03	8
26 February 1974	0·19	0·05	8

The highest mean rate, recorded in January, was three times as great as the lowest mean rate recorded in July. The ability of copepods to tailor their respiratory requirements to the available food supply was noted by Conover (1962) in *Calanus hyperboreus*.

The dry weight/wet weight ratio decreased when food was scarce (Table VII), probably due to the utilization of storage products. A similar change was noted in *Calanus cristatus* by Omori (1970).

TABLE VII. THE DRY WEIGHT OF COPEPODID STAGE V *Pseudoboeckella poppei* EXPRESSED AS A PERCENTAGE OF THE WET WEIGHT

Date	$\bar{x}$	s	n
9 April 1973	12·5	1·7	10
8 July 1973	9·2	1·8	10
7 August 1973	7·3	0·8	10
29 January 1974	11·0	1·8	10
26 February 1974	10·9	1·6	10

Fecundity

Mean clutch sizes were small during 1973–74 (Table VIII) compared to those recorded during 1962–63 in Heywood Lake (40–140 eggs; Heywood, 1970*b*). This may have been because of limited food supply. There was a significant increase in clutch size between 23 October and 31 December 1973 ($t = 6 \cdot 72$, $P = 0 \cdot 05$) but the increase corresponded with a decrease in the number of gravid females, so the effect on the number of eggs hatched was probably not significant. There was no obvious correlation between changes in clutch size and any of the parameters monitored. Food availability was the most likely factor but on the two occasions when the algal cell numbers were highest in the phytoplankton (31 October 1973 and 4 January 1974; Table III) the clutch sizes were at their smallest and largest, respectively.

TABLE VIII. SEASONAL VARIATIONS IN CLUTCH SIZE

Date	$\bar{x}$	s	n
8 July 1973	41	6·5	20
7 August 1973	40	5·5	20
1 October 1973	38	5·2	20
23 October 1973	31	4·2	20
6 November 1973	35	5·8	20
19 November 1973	39	7·4	20
1 December 1973	42	7·9	20
31 December 1973	43	6·8	20
29 January 1974	47	12·2	8

CONCLUSIONS

P. poppei copepodid stages are unselective particle feeders in the plankton. Copepodid stages III to VI also feed unselectively in the benthos, although firmly encrusted epilithic algal species are not available to them.

Body length, respiration rate, wet weight/dry weight ratio and mortality of nauplii appear to be governed by the quantity and probably the quality of the food available.

In Sombre Lake, where the phytoplankton standing crop is relatively low, naupliar survival probably controls recruitment. Only when phytoplankton levels build up in spring do the nauplii survive. With recruitment synchronized, all individuals are subject to the same food conditions during development. This results in a population of adults of uniform body length.

In the more eutrophic Heywood Lake, higher food levels allow nauplii to develop throughout the year. Recruitment is controlled by egg production and hatching, which takes place over a period of 9 in every 12 months. Thus, developing individuals are subject to seasonal variations in food availability and attain different body lengths. The lack of synchronization of recruitment also means that one generation will co-exist with the next, giving rise to a population in which adults of very different body length may be found side by side.

The richness of the flora of a lake is controlled largely by solar radiation and nutrient levels. For any one lake, incident solar radiation will vary little from year to year but the radiation available to the lake's primary producers will be considerably affected by ice and snow thickness and duration. Variation between the nutrient levels of lakes is due almost entirely to animal pollution, mainly by elephant seals (*Mirounga leonina*), which greatly increase the nutrient levels of any lake in which they wallow. The presence or absence of seals in a lake will have a very marked effect on the biology of *P. poppei*.

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APPENDIX

COPEPODID STAGES OF *P. poppei* FROM SOMBRE LAKE AS A PERCENTAGE OF THE TOTAL COPEPODID POPULATION

Date	CI	CII	CIII	CIV	CV♂	CV♀	CVI♂	CVI♀	CVI♀ gravid	*n*
9 April 1973				0·7	5·0	8·6	59·3	26·4		140
14 May 1973					4·6	5·1	56·6	33·7		175
11 June 1973				1·0	8·8	11·4	49·2	29·5		193
8 July 1973				0·4	7·5	9·5	46·8	24·6	11·1	252
7 August 1973					13·8	16·3	26·3	22·5	21·3	80
1 October 1973	0·5		0·5		0·9	0·5	36·3	34·1	27·4	223
23 October 1973						0·7	60·9	33·3	5·1	138
6 November 1973	1·2	1·2		0·3			55·0	34·0	8·4	347
19 November 1973	37·8	48·6	0·4				6·6	3·1	3·5	484
1 December 1973	10·7	60·1	19·6				4·8	1·2	3·6	168
31 December 1973		0·6	61·1	36·2		0·5	0·6	0·6	0·6	177
29 January 1974			0·8	48·6	27·0	21·6	1·6		0·5	385
26 February 1974			0·9	2·3	30·5	32·3	24·1	9·1	0·9	220
25 March 1974						0·4	55·0	44·6		242