

ECOLOGY OF THE FRESH-WATER LAKES OF SIGNY ISLAND,
SOUTH ORKNEY ISLANDS:

III. BIOLOGY OF THE COPEPOD *Pseudoboeckella silvestri* Daday
(CALANOIDA, CENTROPAGIDAE)

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ABSTRACT. *Pseudoboeckella silvestri* has successfully colonized the harsh environment of most standing fresh-water bodies on Signy Island. The species is tolerant of a wide range of salinities and of low oxygen concentrations. Pool populations can also withstand high and rapidly fluctuating temperatures, and have an accelerated univoltine life cycle. Availability and perhaps type of food appear to be the main factors affecting the continuous multivoltine lake populations, controlling maturation rates, longevity, body size and fecundity. The success of colonization may be due to the ability of later copepodid stages to feed on algal felt debris.

THE purpose of this paper is to outline the cyclic activities of a fresh-water calanoid copepod in an extreme environment. General descriptions of the geomorphological, physical, chemical and biological properties of certain lakes and pools on Signy Island have already been published (Heywood, 1967a, b, 1968; Goodman, 1969).

The lakes are small and conform to a basic pattern of a steep-sided trough, 3-6 m. in depth, surrounded by a sub-lacustrine shelf of varying width. Pools are frozen solid and lakes are frozen to depths of 1-2 m. for 8-11 months of each year. Lake waters are almost anaerobic during the winter. Salinities vary considerably from one water body to another and seasonally in each water body during ice formation and melt (overall ranges recorded are: pools, 40-610 p.p.m. Cl⁻; lakes, 17-110 p.p.m. Cl⁻). These fresh-water bodies are obviously harsh environments for plant and animal life.

Algae are the dominant primary producers for, with the exception of part of the phytoplankton and submerged patches of moss (rare in the lakes), there are no other forms of vegetation. The benthic flora is generally luxuriant, particularly over the shelf areas of the lakes. However, the phytoplankton is probably poor in quantity, at least during the summer months.

Protozoa, Rotifera, Tardigrada, Nematoda and Annelida (Enchytraeidae) are to be found in the periphyton and benthos of all pools and lakes. The fauna may also include up to eight species of Crustacea:

<i>Branchinecta gaini</i> Daday	Anostraca
<i>Pseudoboeckella silvestri</i> Daday	Copepoda
<i>Parabroteas sarsi</i> (Daday)	Copepoda
<i>Macrothrix hirsuticornis</i> Norman and Brady	Cladocera
<i>Alona rectangula</i> Sars	Cladocera
<i>Ilyocryptus brevidentatus</i> Ekman	Cladocera
<i>Cypridopsis frigigena</i> H. Graf	Ostracoda
<i>Eucypris</i> sp.	Ostracoda

Pseudoboeckella silvestri occurs in most of the pools and in all of the lakes. The species has not colonized the streams on Signy Island. Its presence in running water is accidental; individuals are being continually swept out of the lakes and into the sea.

Pseudoboeckella and the closely related genera *Boeckella*, *Hemiboeckella* and *Parabroteas* are Southern Hemisphere members of the Centropagidae, which have successfully invaded fresh and brackish waters and which have a very interesting circumpolar distribution. The general consensus of opinion is that the genera originated in Antarctica and migrated northwards during the onset of glaciation. The major diversification of species occurred afterwards, there being distinctive South American and Australasian groups. *Pseudoboeckella silvestri* has previously been found in Patagonia, the Falkland Islands, South Georgia, north-eastern Antarctic Peninsula and the South Shetland Islands.

METHODS

Five lakes (lakes 2, 3, 6, 7 and 10; Fig. 1) were selected for general study but it was possible to sample only lake 2 (Fig. 2) with reasonable frequency. Comment is therefore confined mainly to the activities of *P. silvestri* within this lake and reference to populations in other lakes is only made where significant variation has been recorded.

Various methods for obtaining horizontal hauls under ice cover were tried during the 1962 winter but all were rejected on grounds of time consumption. Sampling was therefore restricted

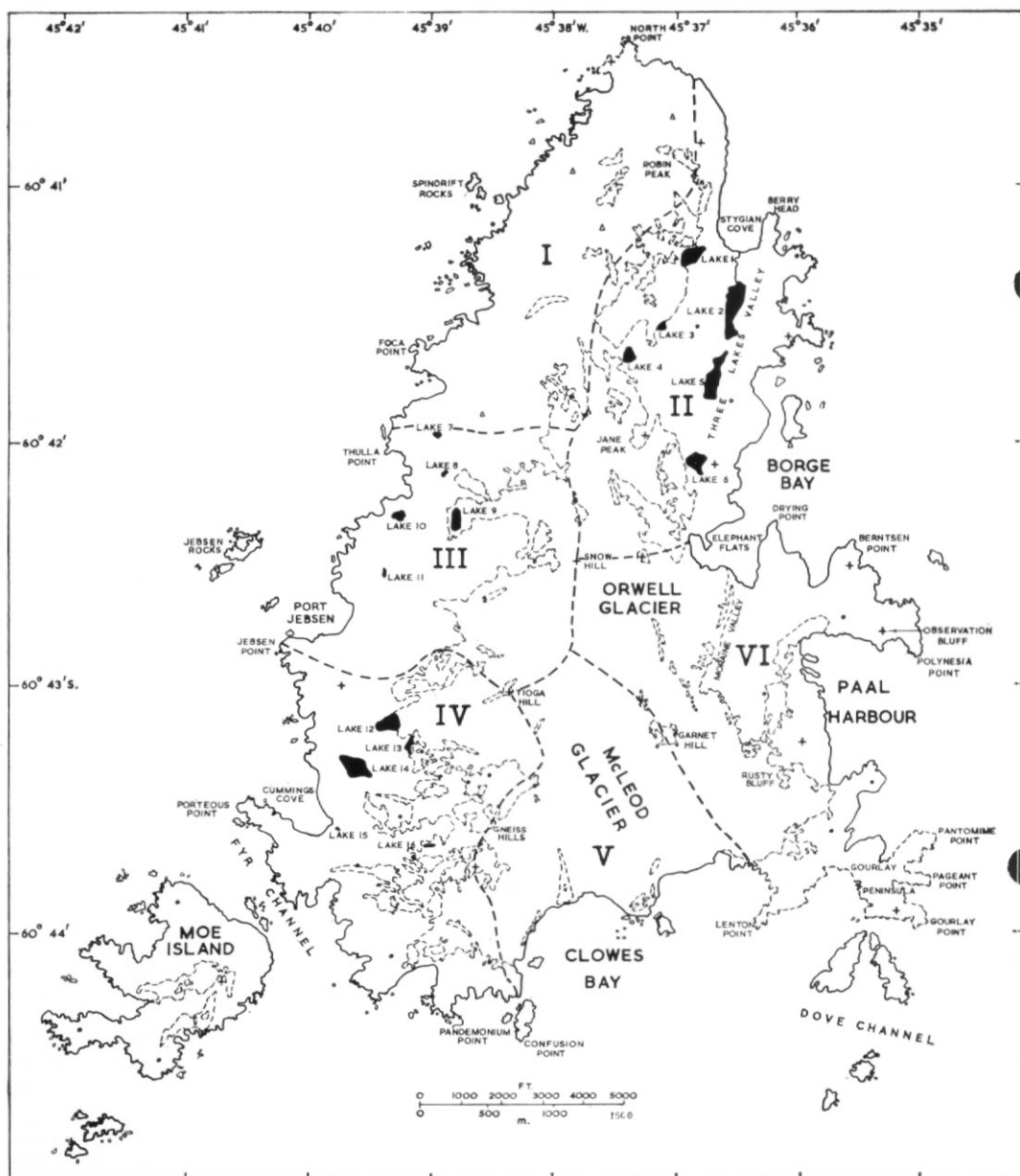


Fig. 1. Sketch map of Signy Island, South Orkney Islands, showing the limits of the six main catchment areas (I-VI) and the locations of the fresh-water lakes (1-16).

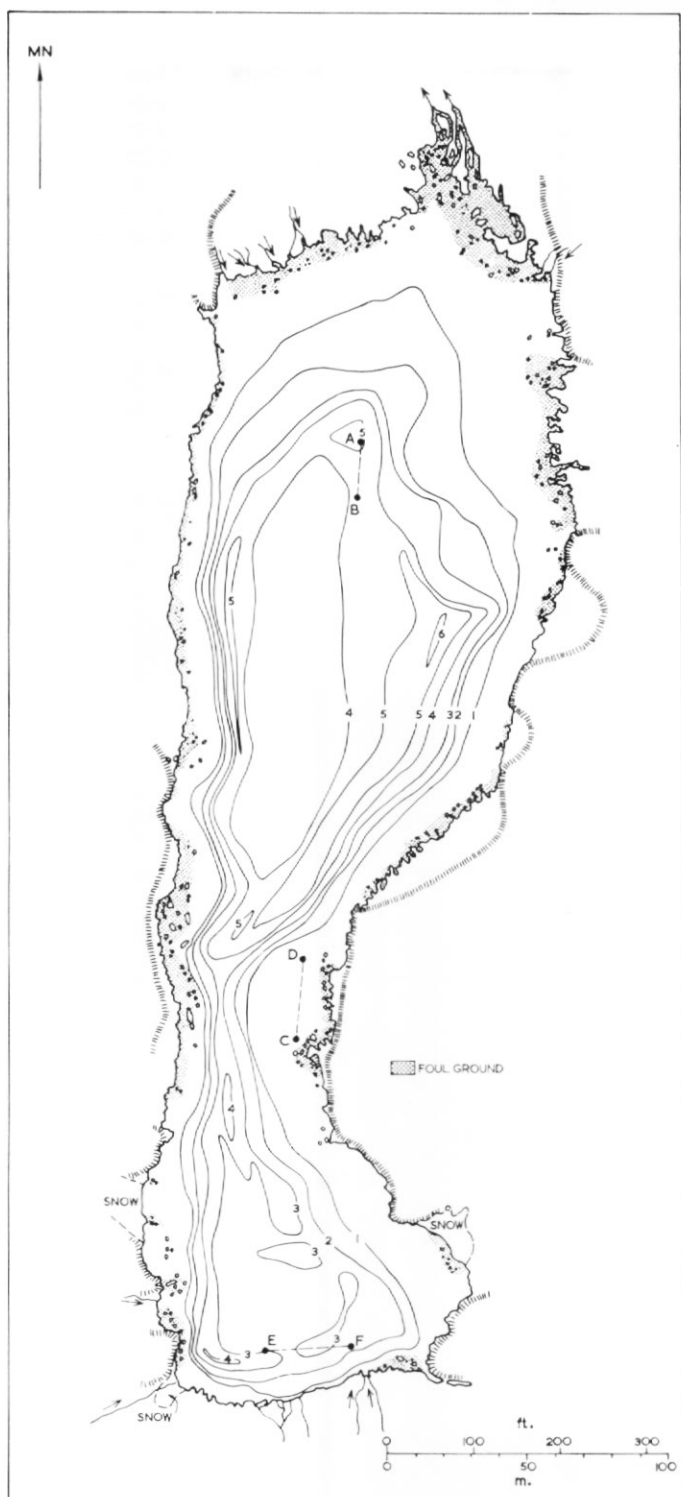


Fig. 2. Outline of lake 2 in Three Lakes Valley, showing the bathymetric contours in metres. A, B, C, D, E and F mark the sampling stations. (From a plane-table survey by M. W. Holdgate.)

to vertical hauls taken at stations A, C and E. Station C was eventually abandoned as unworkable. The bedrock of the shelf area is quartz-mica-schist, which has been split by freeze-thaw action into sharp tightly jammed flakes. Normal techniques for sampling the benthos of stony substrates (Macan, 1958) could not be applied and the problem could not be solved under field conditions.

Stations A and E were sampled with a closing net designed and built during the 1962 winter (Fig. 3). Design was limited by climatic conditions and available raw materials. String throttles

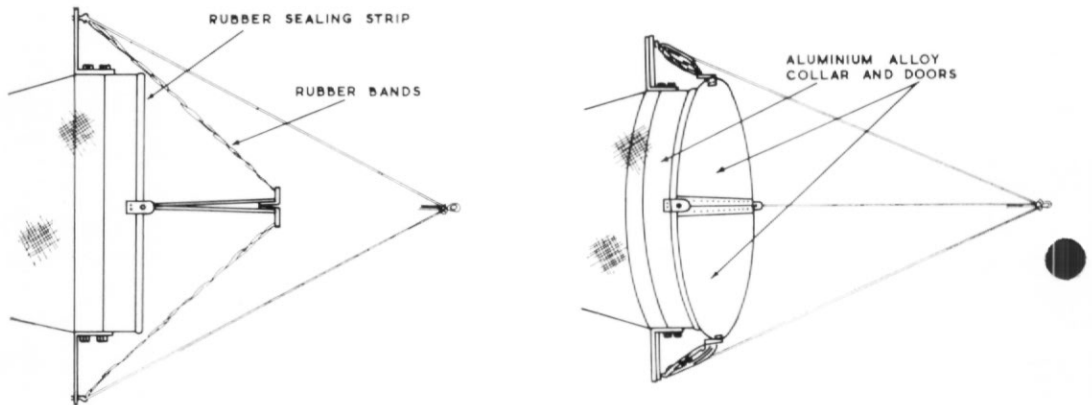


Fig. 3. Closing net mechanism.

could not be used because the net was subject to freezing conditions even during the summer. Rubber for closing the doors had to be very elastic because of the considerable extension in length required. Ordinary "office" rubber bands were found to be ideal when used in bundles of four, holding the doors firmly against the rubber seal on closure. Unfortunately, they perished rapidly and had to be changed between individual hauls. The netting was 0.07 mm.^2 mesh bolting silk and the effective net aperture was 29 cm. in diameter. The presence of the closing mechanism had no significant effect on the catching power of the net (Fig. 4).

Four hauls were taken from each metre stratum. This number was determined by the small *Parabroteas sarsi* population because the hauls were for use in a general study of the zooplankton. The hauls were taken in pairs. 5 min. separated the hauls of each pair and each "run" of pairs was separated by 30 min. The net was operated by two men and the release string was kept taut during hauling so that the doors could be closed immediately the net had swept the metre stratum. Hauling rate was governed by counting and was therefore subjective. Some constancy was achieved by using the same operators throughout the study period. It was assumed that the shortness of each haul abrogated the need for a flow meter. The coefficient of variation for replicate hauls, taken by this method throughout 1963, varied from 26 to 52 per cent. This compares favourably with similar coefficients obtained by other authors (Bayly, 1962). Approximately 1.5 per cent of each catch was swept into the net during descent and by the closing action of the doors.

Each catch was washed out of the net into 96 per cent alcohol. The resulting fixative strength was approximately 25 per cent. On return to the station, the contents were concentrated by filtration and preserved in 70 per cent alcohol. Formalin was rejected as a fixative/preservative because it polymerized in the field even during the summer.

Only the contents of large catches were sub-sampled before examination and enumeration under a stereomicroscope.

Diurnal variation in distribution patterns was not investigated. The possible effects of diurnal variation were avoided by sampling the lake stations at approximately the same time on each occasion.

Mean body lengths for the study on variation in body size were based on measurements

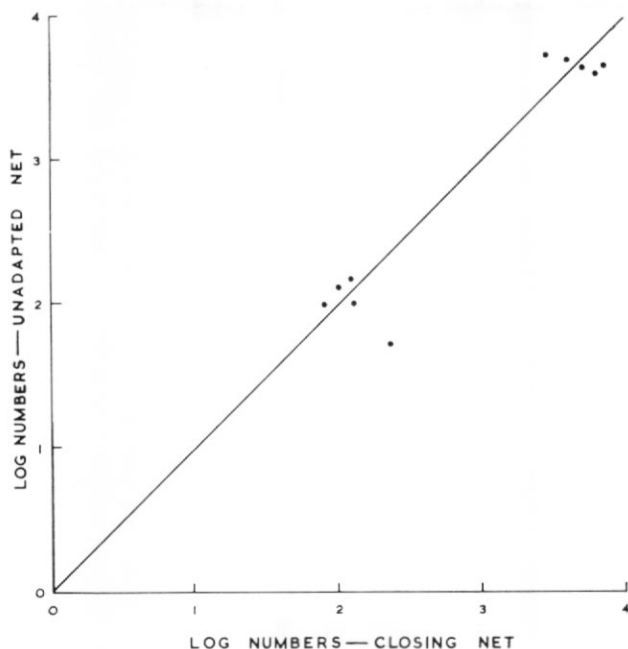


Fig. 4. Comparison of vertical hauls taken from 2 to 0 m. using an unadapted net and the closing net alternately.

from 50 to 100 individuals. The parameter "cephalothorax length" was chosen and, for convenience, the values are given in ocular units. Mean clutch sizes were calculated from the eggs of 50 individuals or, if this number was not available, the eggs of all ovigerous females present.

Information on pool populations has been obtained mainly from casual observation and discussion with B. J. A. Goodman.

RESULTS AND DISCUSSION

Life history

P. silvestri, in common with most other calanoids, passes through 13 stages during its life span—egg, six naupliar and six copepodid stages, the last copepodid stage being the adult. The species forms almost continually breeding populations in the lakes of Signy Island. It was not possible to define the length of each life stage, mortality rates and individual longevity from the enumeration of samples for several reasons. Although there are peaks of sexual activity, the peaks of numbers for the various life stages were not recorded because of the long inter-sample period. There was also a sampling bias against the later copepodid stages. The mouth parts of *P. silvestri* are basically those of a filter feeder which becomes modified for detritus feeding on ecdysis through the third and fourth copepodid stages (Heywood, 1970). Consequently, copepodid stages IV to VI are nektobenthic and, during the summer months, they swarm over the algae-covered shelf areas. As mentioned above (p. 4), sampling over this substrate could not be undertaken with the apparatus available. The effect of the bias is clearly shown in Table I. Direct observation showed that the peak in adult numbers occurred during February/March. The April/May peak in the samples was produced by the nektobenthos being forced off the shelf area by encroaching ice. It must be assumed that the sampling bias remained even in winter for large numbers of these nektobenthic stages were probably still attracted to areas likely to collect algal debris—the inner fringes of the shelf, and sides and floor of the trough. Information on population dynamics gained from studying the change in mean cephalothorax lengths (a method similar to that used by Tonolli (1961) on *Eudiaptomus*

TABLE I. SEASONAL VARIATION* IN *Pseudoboeckella silvestri* NUMBERS (PER M.⁻³); LAKE 2, SIGNY ISLAND

Date	Nauplii 1-6	Copepodids					
		I	II	III	IV	V	VI
<i>Station A</i>							
1963							
7 January	14,100	7,900	17,900	8,700	1,750	640	130
30 January	3,500	2,800	2,400	800	850	420	120
17 February	500	640	900	650	540	160	30
21 March	100	70	260	170	600	380	50
27 May	130	2	4	25	150	900	600
6 July	250	1	10	50	150	580	400
29 July	570	1	1	8	55	380	490
23 August	670	1	0	10	60	320	360
3 October	2,380	380	20	4	100	750	330
23 October	2,400	300	600	80	25	270	850
17 November	1,900	370	570	700	450	280	750
1964							
5 January	850	200	330	350	180	600	230
<i>Station E</i>							
1963							
7 January	8,800	4,300	5,850	1,270	440	290	40
30 January	4,050	2,000	4,150	1,450	1,670	450	70
17 February	460	610	590	340	530	200	36
21 March	50	110	90	130	270	190	150
25 April	0	10	10	80	700	3,570	1,060
24 May	30	20	50	80	840	5,220	1,600
6 July	320	7	14	60	240	1,000	550
30 July	1,450	5	5	20	70	270	170
22 August	380	5	5	10	60	300	400
27 September	300	225	30	10	40	250	170
25 October	1,300	950	2,200	100	100	400	200
19 November	5,100	1,120	1,460	1,300	450	100	120
1964							
5 January	2,340	180	310	430	280	650	230

* The variation shown reflects biological activity only, the ice factor being ignored in the density calculations.

vulgaris) was limited by the long inter-sample interval and the possibility of ambiguity caused by the complex inter-reaction of intraspecific competition and change in diet.

Peaks of sexual activity occur while the lakes are ice-covered (Fig. 5) and probably coincide with periods of high phytoplankton activity. Some species of Antarctic photo-autotrophic phytoplankton are known to be adapted to low light intensities and to be inhibited or injured at levels of higher illumination (Goldman and others, 1963). If the species present in the Signy Island lakes are similarly adapted, the following assumptions may be made:

- i. Productivity is low in summer because the phytoplankters cannot remain in the optimum light zone under turbulent conditions.
- ii. "Blooms" are likely to occur in April/May and October/November; periods of reasonable day length when the ice-covered lakes are snow-free (Heywood, 1968) and the phytoplankters are able to maintain station at any level where light conditions are good.

Resting eggs can be produced because *P. silvestri* is able to colonize small rocky pools which freeze solid, and lake 10, the waters of which are heavily polluted by effluent from seal wallows and become too toxic to support active crustacean life during the winter months. However, there is no evidence that such eggs are produced in the other lakes examined where females carry the eggs until they hatch. Study of the changes in body size (p. 9) showed that the time for maturation could vary considerably. The majority of small-mode adults present in May

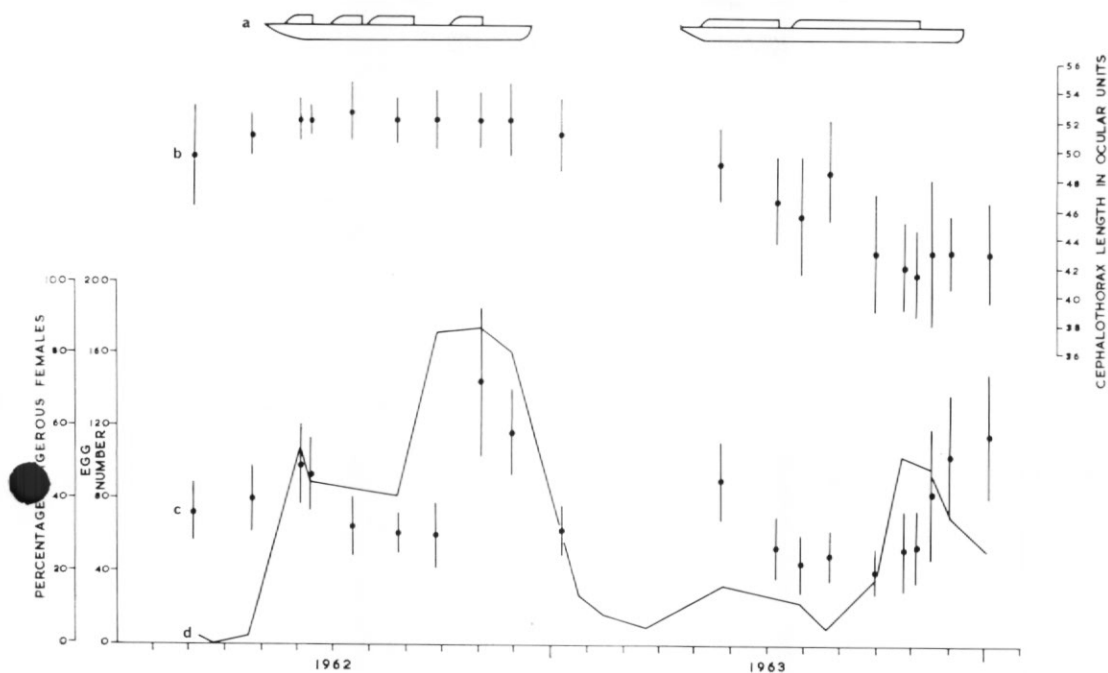


Fig. 5. Seasonal variation in lake 2 of:

- Snow and ice cover.
- Mean and standard deviation of ovigerous female cephalothorax length.
- Mean and standard deviation of clutch size.
- Percentage of ovigerous females in copepodid VI female population.

took approximately 6 months to develop from the egg stage, whereas the large-mode adults of January 1964 took approximately 3 months (Fig. 6). There were probably similar differences in the times required for sexual maturity. The variation appears to reflect the amount and perhaps type of food available to the larval stages and not the temperature of the development periods. Temperature may, however, be the major agent in determining the maturation rate of *P. silvestri* in the Signy Island pools, where temperatures of 17° C have been recorded. The entire life cycle of these individuals is considerably accelerated, from egg through to egg taking only 3 months (the pools are frozen solid for 9 months in most years). In lake 10, where maximum temperatures are unlikely to exceed 5° C, the period when conditions are favourable for *P. silvestri* probably extends over 5 months (from melt-water flush until ice formation in depth).

Attempts to culture *P. silvestri* from lake populations in the station laboratory met with little success. Cold-room facilities were not available and temperatures in aquaria fluctuated between 4° and 12° C. No individual survived from egg to adult. Some success in determining the duration of life stages was obtained by putting the various stages into separate containers. Most individuals survived two moults and therefore gave information on the duration of one life stage (Table II). From hatching to adult (not sexually mature) took 60 days on average. It must be stressed, however, that the cultures were subjected to high temperatures and rates of temperature change, and that food supplies were probably limiting; conditions were more similar to the pool than the lake environment.

Sex ratio

The numbers of copepodid stage V and VI males were significantly greater than the numbers of females on all but two occasions (C V, $d = 6$, $p = >0.001$; C VI, $d = 35$, $p = >0.001$).

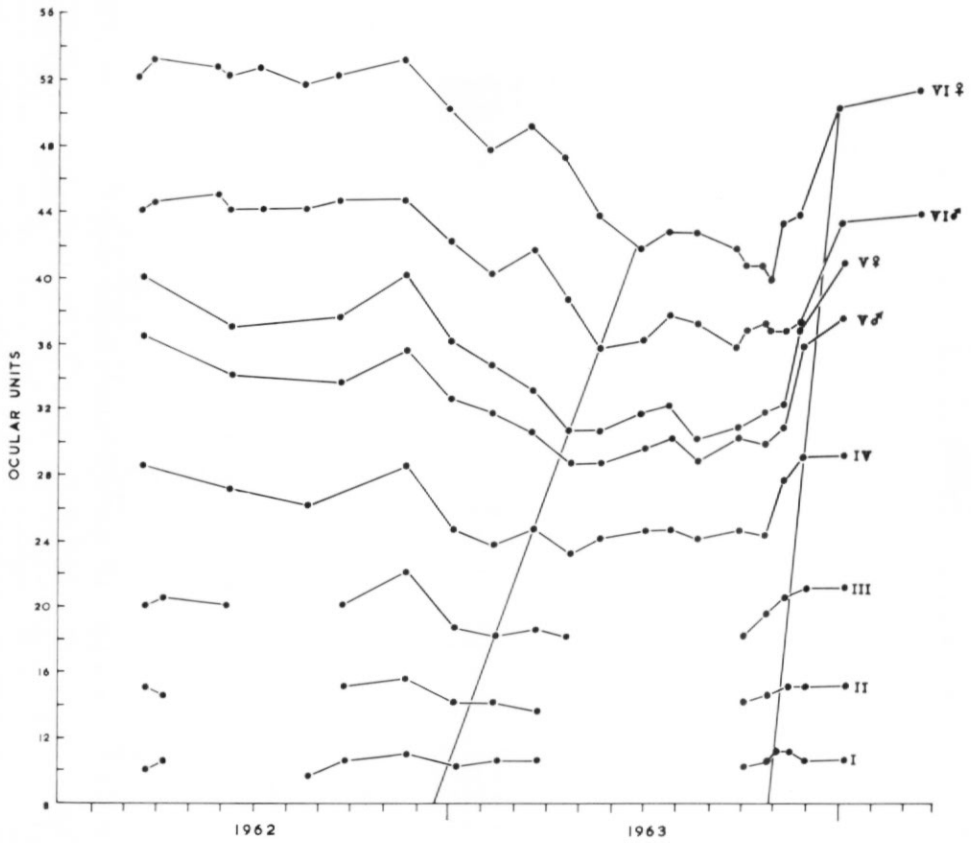


Fig. 6. Seasonal variation in mean cephalothorax length of all copepodid stages in lake 2. The oblique lines indicate the probable maturation periods of two generations.

The 2-year mean female to male ratios of these life stages ($CV = 0.85$; $CV VI = 0.64$) also differed significantly ($d = 16$, $p = >0.001$) and indicated that the sex ratio was the product of environmental and not genetic factors. There is insufficient information to determine what these environmental factors are. The seasonal variations in the sex ratio presumably reflect differing

TABLE II. DURATION OF *Pseudoboeckella silvestri* STAGES IN CULTURE

Stage	Duration (days)
Egg	6-10
Nauplii: 1-6	20-24
Copepodid:	
I	3
II	3-4
III	5-6
IV	7-9
V	9-10
VI	?

and duration (Heywood, 1968). In the South Orkney Islands precipitation during early winter is frequently associated with high winds which prevent accumulation. As winter proceeds, however, lighter winds allow the rate of snow accumulation to increase. Subject therefore to the complex interactions of wind, temperature and weather, the snow cover and therefore primary production varies considerably from year to year.

Over 1.3 m. of ice and 10 cm. of hard-packed snow covered most lakes in early December 1961 and the ice cover persisted until the end of the month. The thickness and duration of the ice cover indicated that the snow-free early winter period had been long and heat loss from the lakes consequently high, producing a very thick ice cover which was afterwards protected by snow until the delayed spring thaw. As the snow-free period coincides with the period of minimum solar radiation (winter solstice), there can have been little photosynthetic activity until the thaw cleared the snow 3 weeks before the ice melted. The mortality rate of *P. silvestri* was probably high in every life stage because the greater thickness of ice even limited access to plant debris. Consequently, only a relatively small number of nauplii would be produced at the end of winter and, although the phytoplankton bloom was probably of short duration (productivity decreasing as soon as the ice melted) the amount of food per individual copepod would be high. The adults produced were of the large-modal class. Conditions during the following winter (1962) were very different. Prolonged periods (24–72 hr.) of thaw cleared the ice cover of snow every month. Unusually high air temperatures limited ice formation and maximum thickness (75–100 cm.) was not maintained for long. The amount of underwater irradiance must have been considerable compared with the previous year. Conditions after mid-winter were probably optimum for photosynthesis and the mortality rate of *P. silvestri* was consequently low. The over-wintering population increased in numbers with the result that, during the main phytoplankton bloom, the amount of food per individual copepod was actually lower than it had been in 1961. Consequently, adult *P. silvestri* produced by the main period of sexual activity were of the small-modal class. The only thaw during the 1963 winter was a 72 hr. period in July. Conditions in the lake were presumably similar to the 1961 conditions. Adult *P. silvestri* produced by the main period of sexual activity this year were of the large-modal class.

There is some direct evidence to support the suggested variation between the 1962 and 1963 winter population sizes. Bottom to surface vertical hauls were taken from the same station of lake 2 on 2 November of each year, using the same apparatus and technique. The mean values for the hauls were 590 adult *P. silvestri* in 1962 but only 20 in 1963. The variation in numbers of nauplii subsequently produced is indicated in Table I. A similar variation in population numbers was also noted for the anostracan *Branchinecta gaini*, which is also phytophagous.

Deevey (1960) has shown for marine copepods that as the annual temperature range falls below 14 deg. the effect of temperature on length progressively decreases and the effect of available food progressively increases. It thus follows, as Deevey anticipated, that where the annual temperature range is small (approximately 5 deg. in the Signy Island lakes), and food is sometimes minimal for copepod growth, food supply will be the main factor controlling body size.

The effect on *P. silvestri* of competition with *B. gaini* during periods of limited food supply is clearly shown when the seasonal variation in mean cephalothorax lengths of individuals from lake 2 (*B. gaini* present) and lake 6 (*B. gaini* absent) are compared (Fig. 7). The variation between the two populations during 1962 and 1964 (summer) presumably reflects differing general levels of productivity.

Comita (1956) has suggested that intraspecific competition for a limited food supply can produce bimodal variation in size. He found that the first individuals entering any of the later copepodid stages (IV to VI) of *Limnocalanus johanseni* were also the largest. He assumed that this was because early individuals had a trophic advantage in each stage. The trophic advantage would obviously increase with size differential. Intraspecific competition was probably a minor agent in producing the two size classes of *P. silvestri*, being particularly responsible for the small number of large-mode individuals always present in the predominantly small-mode population of 1963. It is more feasible to assume that the large-mode females breeding in early winter (1963) were of the same generation as their small-mode contemporaries rather than that they were a few of the previous generation breeding for a second time, although the latter



Fig. 7. Seasonal variation in mean cephalothorax length of adult populations in lakes 2 and 6.

possibility cannot be excluded on available evidence. Intraspecific competition of a slightly different kind could be responsible for the mean size of the adult male more readily reflecting the effect of decreasing food supply than that of the adult female (and conversely the mean size of the female more readily reflecting the effect of increasing food supply) (Fig. 6). The female is always larger than the male and therefore it always has the trophic advantage. The relative size reduction in the female is eventually greater (25 per cent) than the male (20 per cent) presumably because of their greater demand for food resulting from size and egg production.

Growth factors

The overall mean growth factor for copepodid stages II to VI is 1.31. A significant change in the recorded individual growth factors occurs between copepodid stages III and IV (Table IV), coinciding with the change in feeding habit. Since the availability of food is not reflected in the growth factors (cf. columns 2 and 3 in Table IV), the decrease in growth may result from the change of diet. (There is also evidence indicating that fecundity is affected by diet (p. 12).)

The increase in growth factor at the female copepodid VI stage is more apparent than real, reflecting the allometric growth of the cephalothoracic wings.

TABLE IV. GROWTH FACTORS OF *Pseudoboeckella silvestri*; LAKE 2, SIGNY ISLAND

Stages	1	2	3	4
C II/C I	1.37	1.37	1.38	1.44
C III/C II	1.45	1.42	1.45	1.33
C IV/C III	1.22	1.27	1.35	1.39
C V/C IV	1.28	1.27	1.30	1.31
♂ C VI/C V	1.16	1.17	1.18	1.23
♀ C VI/C V	1.27	1.30	1.32	1.29

The growth factor is the ratio of the lengths of two succeeding instars:

1. Based on shortest lengths measured.
2. Based on means of small-modal class.
3. Based on means of large-modal class.
4. Based on longest lengths measured.

Variation in clutch size

Variation in clutch size in *P. silvestri* is large (18–200 eggs) and markedly seasonal (Fig. 5). Peaks in numbers follow periods of probable high phytoplankton activity (late winter/spring and early winter; p. 6). Work on other fresh-water calanoids (reviewed by Hutchinson (1967, p. 652–59)) has also shown a clear relationship between egg number and food supply.

The low level of fecundity in *P. silvestri* recorded during summer months when there is an abundance of food in the form of algal felt debris and associated epiphyton (Heywood, 1970) may indicate that the availability of a specific type of food (some species of the phytoplankton) may be a major factor determining fecundity. The varying breeding times recorded for five sympatric diaptomids in Lake Erie by Davis (1961) may well be explained in terms of varying dominants in the phytoplankton. A dependence on differing phytoplankton species for maximum fecundity would be a major ecological distinction between zooplankters and could enable similar species to co-exist in the same environment. *P. silvestri* is probably a very suitable subject for dietetic studies. It would be particularly interesting to see if metabolic adjustment to dietary change paralleled adaptation of feeding habit and if it was as successful.

It is clear that, whereas the amount of food available throughout the whole period of growth determines the size of an individual *P. silvestri*, clutch size is determined by the amount and probably type of food available during the period the ovary is developing. Any relationship between body size and egg number is therefore circumstantial. This is clearly shown by the wide variation in egg numbers recorded for each body length (Fig. 8).

Variation in egg size

Some workers have shown that egg size increases as egg number decreases. Hutchinson (1967) has pointed out that, under conditions of low food supply, large population and high metabolic rate, the presence of an increased amount of food in the egg may be more important than a large egg production per individual female. There did not appear to be any seasonal variation in egg size in *P. silvestri*. It must be pointed out, however, that all of the material was preserved and most eggs were fixed in polyhedral shapes. Determination of true diameters was difficult and variation would have been overlooked.

Distribution within lake 2

Horizontal. The swarming of later copepodid stages over the peripheral shelf areas of the lake on the gradual adoption of nekto-benthic habits has already been described (p. 5).

*Vertical.** No significant variation in numbers with depth was recorded for the nekto-planktonic population during the summer, a period when lake waters are completely and continually stirred by strong winds (mean wind speed is normally in excess of 13 kt. (6.7 m. sec.⁻¹)).

On 28 May 1963, 1½ months after the lake surface had frozen, the population at station A was largely concentrated in the 2nd, 3rd and 4th metre strata (Fig. 9). The aggregation of nauplii in the 3rd and 4th metre zones was particularly striking (significance factor $3\bar{x}$). In July, the nauplii had migrated up to the metre immediately below the ice layer (significance factor $3\bar{x}$). The densities of the other life stages varied little and their distribution may well have been random. In October, all life stages were concentrated in the metre stratum below the ice (significance factor $2.6\bar{x}$). On 17 November 1963, the distribution of copepodids was more or less random but the nauplii were aggregated in the bottom metre stratum (significance factor $2.2\bar{x}$). The variations with depth recorded at the shallower (3 m.) station E were not

* The recorded vertical distribution patterns could not be analysed by normal statistical methods because it had been necessary to put the four hauls taken from each metre stratum into one container for transportation. Major significant departures from a random distribution could, however, be determined by the following method. Experiment had indicated that the maximum coefficient of variation was 52 per cent. Since the mean is equal to the variance in a random distribution and, since the coefficient of variation is the standard deviation expressed as a percentage of the mean, 100 per cent variation from the mean has been taken as the working limit for significance. The degree of significance has therefore been expressed in terms of multiples of the estimated mean. For example, if \bar{x} for the water column was 100 and the number recorded in a particular stratum was 300, the significance factor would be given as $3\bar{x}$.

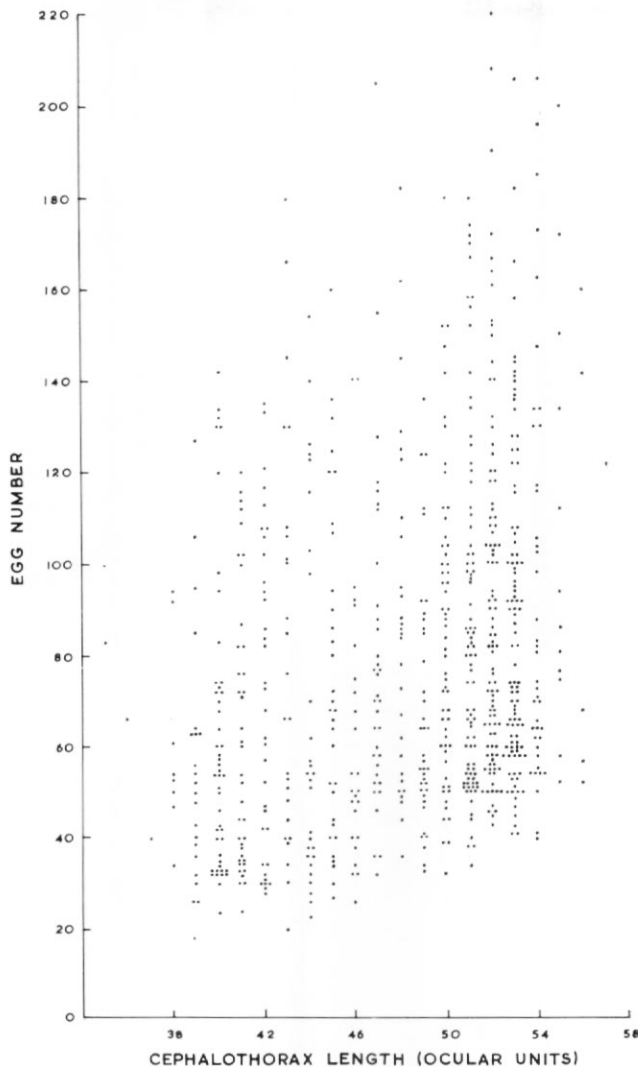


Fig. 8. Variation of clutch size with cephalothorax length.

significant under the strict application of the test used. However, the trends indicated were basically similar to the distribution patterns recorded for the deeper water.

The distribution of the whole nektoplanktonic population became random after the lake opened in mid-December.

P. silvestri nauplii are filter feeders and their aggregation and subsequent migration during the winter is probably associated with the activities of one obvious food source—the phytoplankton. The aggregations of nauplii occur in zones receiving approximately 1–10 per cent of incident radiation (Fig. 10). Several workers on low light-adapted phytoplankters have recorded maximum activity under similar conditions (Rodhe, 1962; Goldman and others, 1963; Pechlaner, 1964; Wright, 1964). Therefore, the aggregations and migrations of the various life stages of *P. silvestri* appear to provide circumstantial evidence for the assumptions made about the phytoplankton (p. 6). During suspected “bloom” periods even copepodids V and VI may be feeding mainly on phytoplankton (Fig. 9). Between June and October, however,

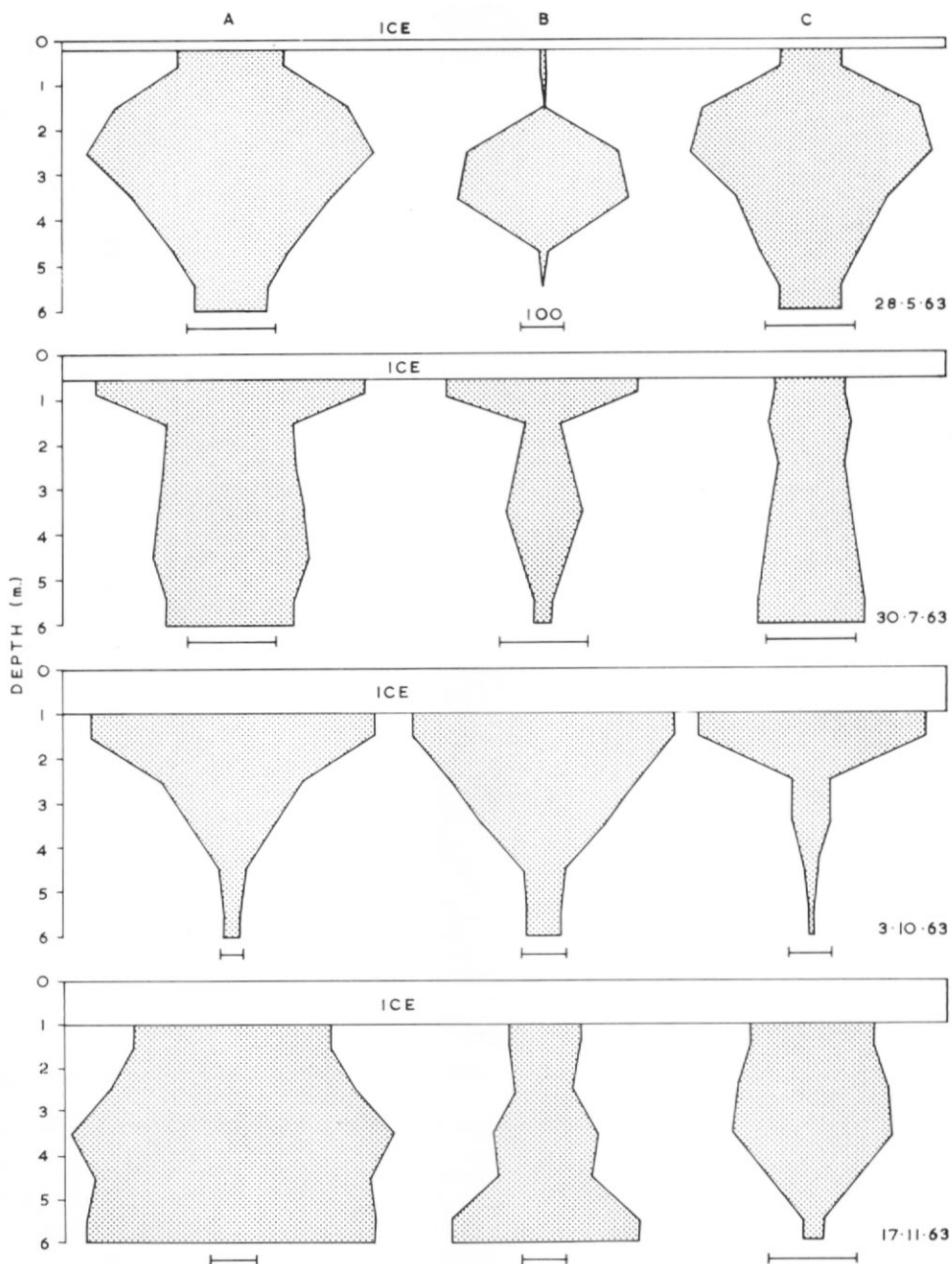


Fig. 9. Vertical distribution of *P. silvestri* in lake 2, sampling station A.
 A. Total population. B. Nauplii. C. Copepodids V and VI. Estimates of density were based on the assumption that disturbance from the up-surge of water into the ice hole did not extend beyond the immediate 1 m. stratum. Scale bars equal 1,000 individuals m^{-3} unless otherwise stated.

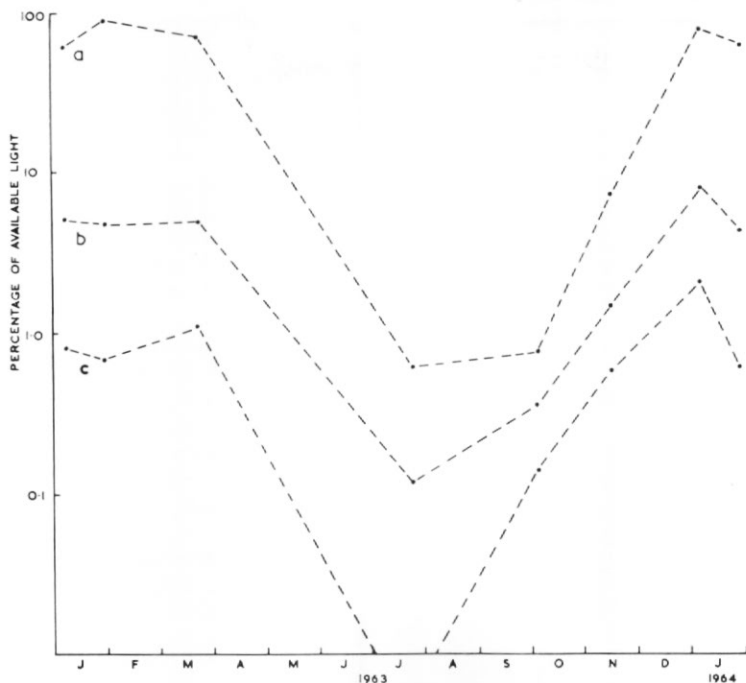


Fig. 10. Seasonal variation in the percentage of total visible light available at: a, 5 cm. depth or water-ice interface; b, 3 m. depth (mid-depth); c, lake bottom (5 m.), in lake 2; sampling station A.

when light conditions in the lake are very poor, the amount of phytoplankton appears insufficient to attract the detritus feeders.

The 17 November 1963 distribution of *P. silvestri* nauplii at station A was probably the result of at least two agencies. First, thaw conditions had removed most of the lake's snow cover and the amount of available light had increased considerably. The zone of photosynthetic activity was probably a wide one. Secondly, the uppermost metre of water contained approximately 7,000 *Parabroteas sarsi* nauplii per m.³ which feed on the *P. silvestri* nauplii (Heywood, 1970). It may be assumed, therefore, that the latter were being removed from the upper zone by the carnivores. Were this not so, the distribution of *P. silvestri* nauplii would have been more or less random, as it was at station E where the maximum density of *Parabroteas sarsi* nauplii was only 100 per m.³.

The importance of bacteria, fungi and heterotrophic phytoplankters as food sources during winter is not yet known and their effects on the distribution of *P. silvestri* cannot be assessed. More frequent sampling may well have revealed more complex density patterns.

The bottom 2 m. of water are practically anaerobic from June until November (Heywood, 1968). The numbers of animals caught at this depth during July and August indicate that *P. silvestri* is not adversely affected by low oxygen concentrations. Furthermore, the main peak of sexual activity occurred when the oxygen content of the lake was still very low. It seems unlikely therefore that oxygen was a major factor determining the copepod distribution patterns of October. But the possibility that all life stages spend most of their time in the upper more oxygenated layers cannot be excluded. The ability to withstand low oxygen concentrations is not confined to Antarctic species. There are records from temperate and tropical latitudes of other copepods, mainly *Cyclops* spp., living actively under these conditions (Rylov, 1948; Beadle, 1963; Chaston, 1969).

Comparison with other *Centropagidae*

Little information on the ecology of Southern Hemisphere fresh-water *Centropagidae* is

available. Bayly (1962) studied a polycyclic population of *Boeckella propinqua* in a small, warm-monomictic eutrophic lake on Mayor Island, New Zealand. Cyclic seasonal changes in mean length and mean clutch size were inversely correlated with temperature for most of the year. Bayly made no measurements on phytoplankton but food availability is unlikely to have had any major effect on either growth or fecundity. The lake was eutrophic and the annual temperature range was approximately 14 deg. Bayly recorded a distinct bimodality in body length in November and suggested that the two modes originated from different egg sources. The larger class represented the main population reproducing in a continuous multivoltine manner, whereas the small class represented recruitment from resting eggs. Long inter-sample periods prevented observations on the development of the two modes and the explanation remains hypothetical. No information on maturation times, mortality rates or longevity was obtained.

The ecology of *Pseudoboeckella brevicaudata* on Macquarie Island is apparently similar to that of *P. silvestri* (personal communication from A. J. Evans). Winters on Macquarie Island are not very severe. Only small upland water bodies freeze over and these thaw frequently during the winter. *P. brevicaudata* breeds continuously in lakes and seasonally in pools. There was no obligatory diapause for members of lake populations. A negative correlation between body length and water temperature was established for *P. brevicaudata* in lakes having chlorophyll *a* summer values of over 6 mg./m.³ but not in lakes in which the chlorophyll *a* values never exceeded 2 mg./m.³.

The New Zealand and Signy Island lakes are widely different environments and ecological differences between closely related* species are to be expected. The probable retention of an obligatory diapause by a small proportion of the *B. propinqua* population is surprising, particularly when *P. silvestri* has not done so in a harsh lake environment.

Comita (1956) and Hutchinson (1967, p. 667-75) have reviewed the literature on the ecology of Northern Hemisphere fresh-water Centropagidae (and other fresh-water Calanoida). The Arctic and sub-Arctic species studied form univoltine populations and undergo an obligatory diapause in the egg stage.

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REFERENCES

- BAYLY, I. A. E. 1962. Ecological studies on New Zealand lacustrine zooplankton with special reference to *Boeckella propinqua* Sars (Copepoda : Calanoida). *Aust. J. mar. Freshwat. Res.*, **13**, No. 2, 143-97.
- BEADLE, L. C. 1963. Anaerobic life in a tropical crater lake. *Nature, Lond.*, **200**, No. 4912, 1223-24.
- CHASTON, I. 1969. Anaerobiosis in *Cyclops varicans*. *Limnol. Oceanogr.*, **14**, No. 2, 298-301.
- COMITA, G. W. 1956. A study of a calanoid copepod population in an Arctic lake. *Ecology*, **37**, No. 3, 576-91.
- DAVIS, C. C. 1961. Breeding of calanoid copepods in Lake Erie. *Verh. int. Verein. theor. angew. Limnol.*, **14**, No. 4, 933-43.
- DEEVEY, G. B. 1960. Relative effects of temperature and food on seasonal variations in length of marine copepods in some eastern American and western European waters. *Bull. Bingham oceanogr. Coll.*, **17**, No. 2, 54-85.
- GOLDMAN, C. R., MASON, D. T. and B. J. B. WOOD. 1963. Light injury and inhibition in Antarctic freshwater phytoplankton. *Limnol. Oceanogr.*, **8**, No. 3, 313-22.
- GOODMAN, B. J. A. 1969. A physical, chemical and biological investigation of some fresh-water pools on Signy Island, South Orkney Islands. *British Antarctic Survey Bulletin*, No. 20, 1-31.
- HEYWOOD, R. B. 1967a. The freshwater lakes of Signy Island and their fauna. (In SMITH, J. E., organizer. A discussion on the terrestrial Antarctic ecosystem. *Phil. Trans. R. Soc.*, Ser. B, **252**, No. 777, 347-62.)

* The separation of the genera *Pseudoboeckella* and *Boeckella* is taxonomically convenient rather than natural.

- . 1967b. Ecology of the fresh-water lakes of Signy Island, South Orkney Islands: I. Catchment areas, drainage systems and lake morphology. *British Antarctic Survey Bulletin*, No. 14, 25-43.
- . 1968. Ecology of the fresh-water lakes of Signy Island, South Orkney Islands: II. Physical and chemical properties of the lakes. *British Antarctic Survey Bulletin*, No. 18, 11-44.
- . 1970. The mouthparts and feeding habits of *Parabroteas sarsi* (Daday) and *Pseudoboeckella silvestri* Daday (Copepoda, Calanoida). (In HOLDGATE, M. W., ed. *Antarctic ecology*. London, Academic Press, 639-50.)
- HUTCHINSON, G. E. 1967. *A treatise on limnology. Vol. II. Introduction to lake biology and the limnoplankton*. London, John Wiley and Sons, Inc.
- MACAN, T. T. 1958. Methods of sampling the bottom fauna in stony streams. *Mitt. int. Verein. theor. angew. Limnol.*, No. 8, 21 pp.
- PECHLANER, R. 1964. Plankton production in natural lakes and hydro-electric water-basins in the alpine region of the Austrian Alps. *Verh. int. Verein. theor. angew. Limnol.*, **15**, No. 4, 375-83.
- RODHE, W. 1962. Sulla produzione di fitoplancton in laghi trasparenti di alta montagna. *Memorie Ist. ital. Idrobiol.*, **15**, 23-28.
- RYLOV, V. M. 1948. *Cyclopoida presnykh vod. Fauna U.S.S.R. N.S.*, No. 35. *Rakoobraznye*, **3**, No. 3, 314 pp. [English translation: *Freshwater Cyclopoida. Fauna of the U.S.S.R. N.S.*, No. 35. *Crustacea*, **3**, No. 3, 314 pp. (Jerusalem, Israel Program for Scientific Translations, 1963.)]
- TONOLLI, V. 1961. Studio sulla dinamica del popolamento di un copepode (*Eudiaptomus vulgaris* Schmeid.). *Memorie Ist. ital. Idrobiol.*, **13**, 179-202.
- WRIGHT, R. T. 1964. Dynamics of a phytoplankton community in an ice-covered lake. *Limnol. Oceanogr.*, **9**, No. 2, 163-78.