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ASPECTS OF THE BIOLOGY OF THE FRESHWATER CRAYFISH  
PARANEPHROPS PLANIFRONS WHITE IN LAKE ROTOITI.

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A dissertation submitted towards the degree  
of Bachelor of Philosophy

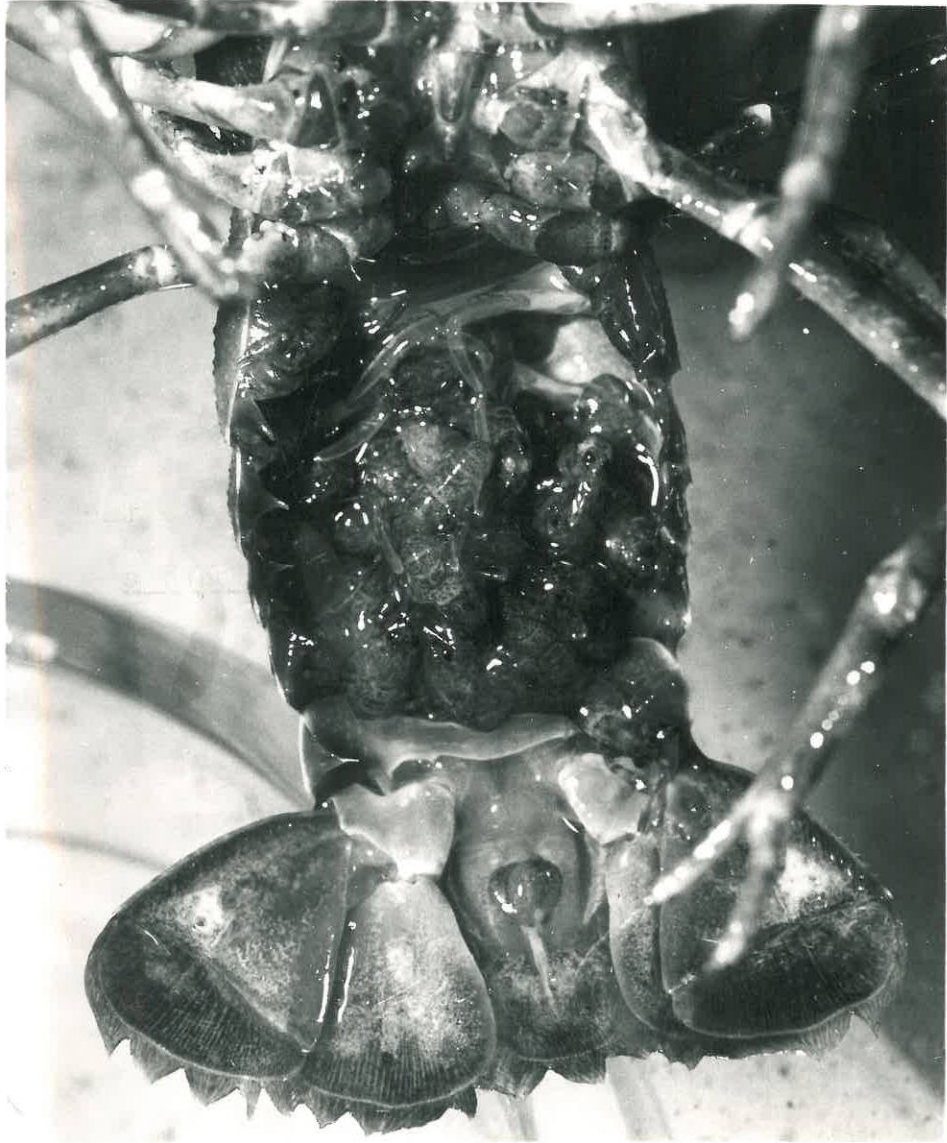
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Biological Sciences

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February 1974

Frontispiece: Cluster of newly hatched young attached to  
the abdomen of female Paranephrops plani-  
frons White.



## ABSTRACT

Aspects of the biology of Paranephrops planifrons White in Lake Rotoiti were studied and comparisons made with P. planifrons inhabiting neighbouring Lakes Okataina and Rotorua. Two migrations upwards occurred, in spring and summer, the first thought to be associated with temperature and egg-hatching, the second due to hypolimnetic deoxygenation. Hence in late summer and early autumn crayfish were concentrated above and within the thermocline. Movement downwards occurred in early winter, after lake turnover and this was thought to be associated with gonad maturation, induced by low temperatures and shorter photoperiod. During winter crayfish distributed evenly over the lake floor. There were two breeding seasons, in late autumn and winter (the larger of the two) and late spring and summer. Lake Okataina P. planifrons bred annually, during late autumn and winter, and showed no apparent seasonal movement patterns. Moulting occurred during the warmer months.

Average densities of 0.030, 0.014 and 0.003 adult crayfish/m.<sup>2</sup> were calculated for Lakes Rotoiti, Okataina and Rotorua respectively. In these populations a broad inverse relationship was found between density and mean population size, for individual sizes were small in Wright's Bay, Rotoiti, compared to those in Lakes Okataina and Rotorua and other parts of Rotoiti. Sizes of males and females were not significantly different and mean size was constant throughout all depths. Sex ratios of 1.9:1 and 2.3:1 in favour of males were found in Lakes Rotoiti and

Okataina respectively. Stomach content analyses revealed that the diet was mainly detritus, but also included animal remains and vascular plant material. Sediment analyses showed that food quality was essentially the same at all depths. Feeding was continuous at depths greater than 20m. but in shallower water it took place only at night. It appeared that P. planifrons does not display homing and the home range is extensive. Observations revealed that territorial behaviour occurred and males were not dominant over females, although larger crayfish were dominant over smaller animals.

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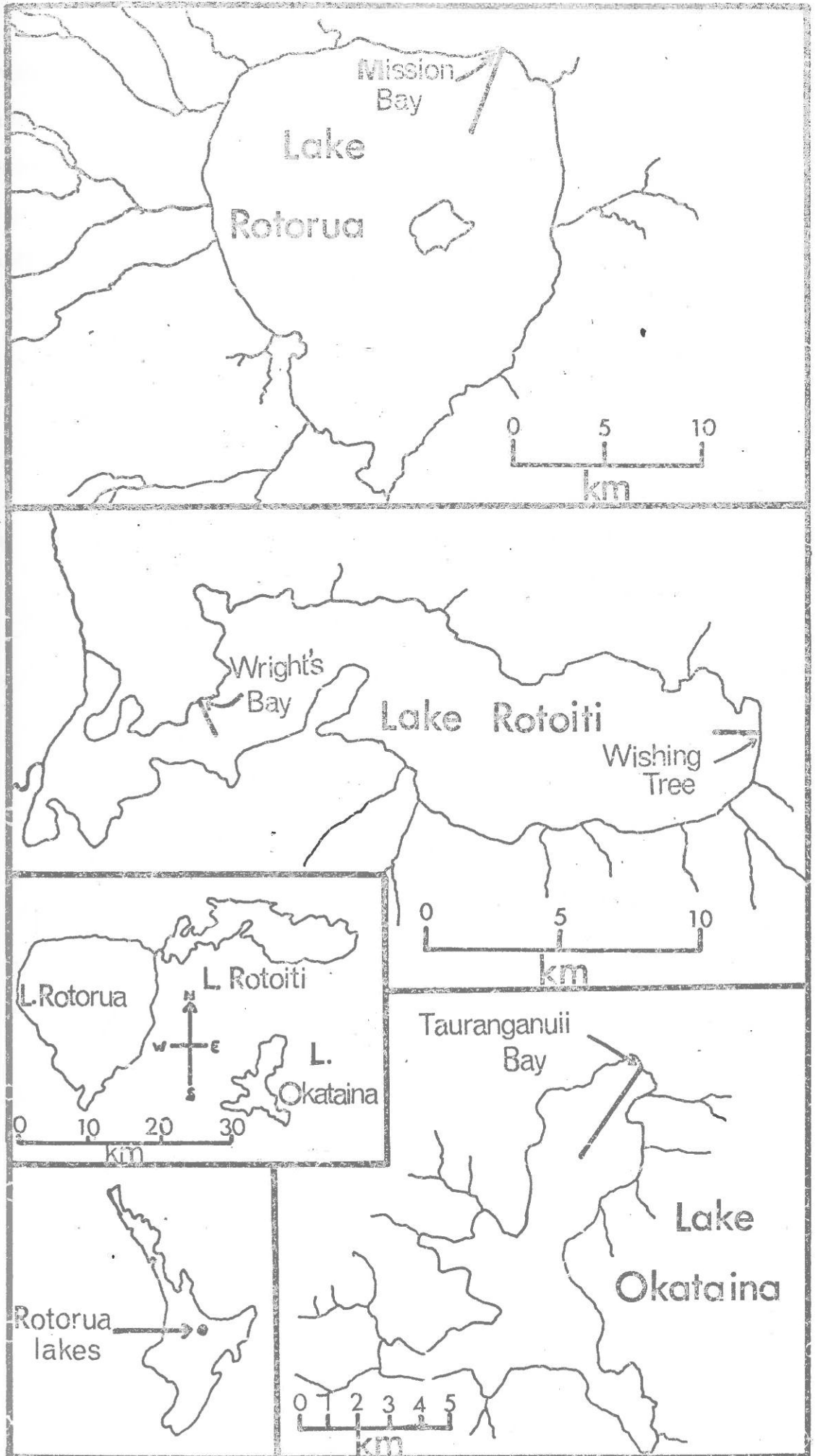
## INTRODUCTION

Although very little is known about the role played by crayfish in lakes, studies by Momot (1967a; 1967b) and Moshiri and Goldman (1969) indicate that they are intimately associated in the food relationships of lentic benthic systems. In a trophic sense crayfish are important because they may be one of the chief energy transformers between various links in lake food webs (Momot 1967a; M.S.). They are able to utilize detrital material, primary, intermediate and terminal production and hence can attain high levels of production. Coupled with this their use as food by predators (Momot 1967b; Potts 1972) makes them one of the most important groups of animals inhabiting lake ecosystems.

The New Zealand freshwater crayfish Paranephrops planifrons White, which inhabits lakes and streams of the North Island and north-western region of the South Island, has received surprisingly little attention. It was first named and described by White (1842) and since then a full taxonomic study has been documented (Chilton 1889; 1900, Archey 1915, Hopkins 1970 and Riek 1972). Nothing is known of its habits in lakes but aspects of its biology have been studied by Hopkins (1966; 1967a; 1967b), who examined growth rates and the breeding cycle of stream populations in the Wellington and Wairarapa districts.

The aim of this study was to investigate the ecology of P. planifrons in Lake Rotoiti, a moderately large mesotrophic lake in the Central North Island (Fig. 1). Aspects of its biology including spatial distribution,

Fig. 1: The locations of Lakes Rotoiti, Rotorua and Okataina studied in the Rotorua district. Regions in each lake where trapping and other research was carried out are shown.



breeding and population structure were studied between March 1973 and January 1974. As well a few comparative observations were made on this species in neighbouring oligotrophic Lake Okataina and adjacent Lake Rotorua which is strongly mesotrophic.

## METHODS

Three methods were used to collect crayfish during this study; SCUBA diving, trapping and dip-netting in the shallows at night.

### 1. DIVING.

SCUBA diving was used in two ways to assess crayfish distribution; in studies using a transect laid on the lake floor and in horizontal dives. The main problem encountered when endeavouring to obtain accurate quantitative assessments with this method was disturbance of the muddy substrate of these lakes. However, this was almost totally averted by keeping movements on and near the bottom to a minimum.

#### (a) Transect.

The transect consisted of two parallel nylon lines running from the shoreline out into the lake for a distance of 220m. (Plate 1). These lines were separated at 10m. intervals by a connecting line 5m. in length, giving the transect a ladder appearance. Thus there were 22 sectors of equal area ( $10\text{m.} \times 5\text{m.} = 50\text{m.}^2$ ). At 10m. intervals the lines were staked so that they were some 20cm. above the lake floor making the transect easily identifiable, as visibility was often as low as 2m. A cross-section of the transect and the depth at each sector is shown in Fig. 2.

There were a number of ways in which the transect was incorporated into the study. The principal purpose was to ascertain whether crayfish underwent a seasonal migration. In order to investigate the seasonal migration pattern quantitatively, 16oz. beer cans with one end open were

Plate 1. The transect, marked by buoys and extending out  
from the shoreline at Wright's Bay.

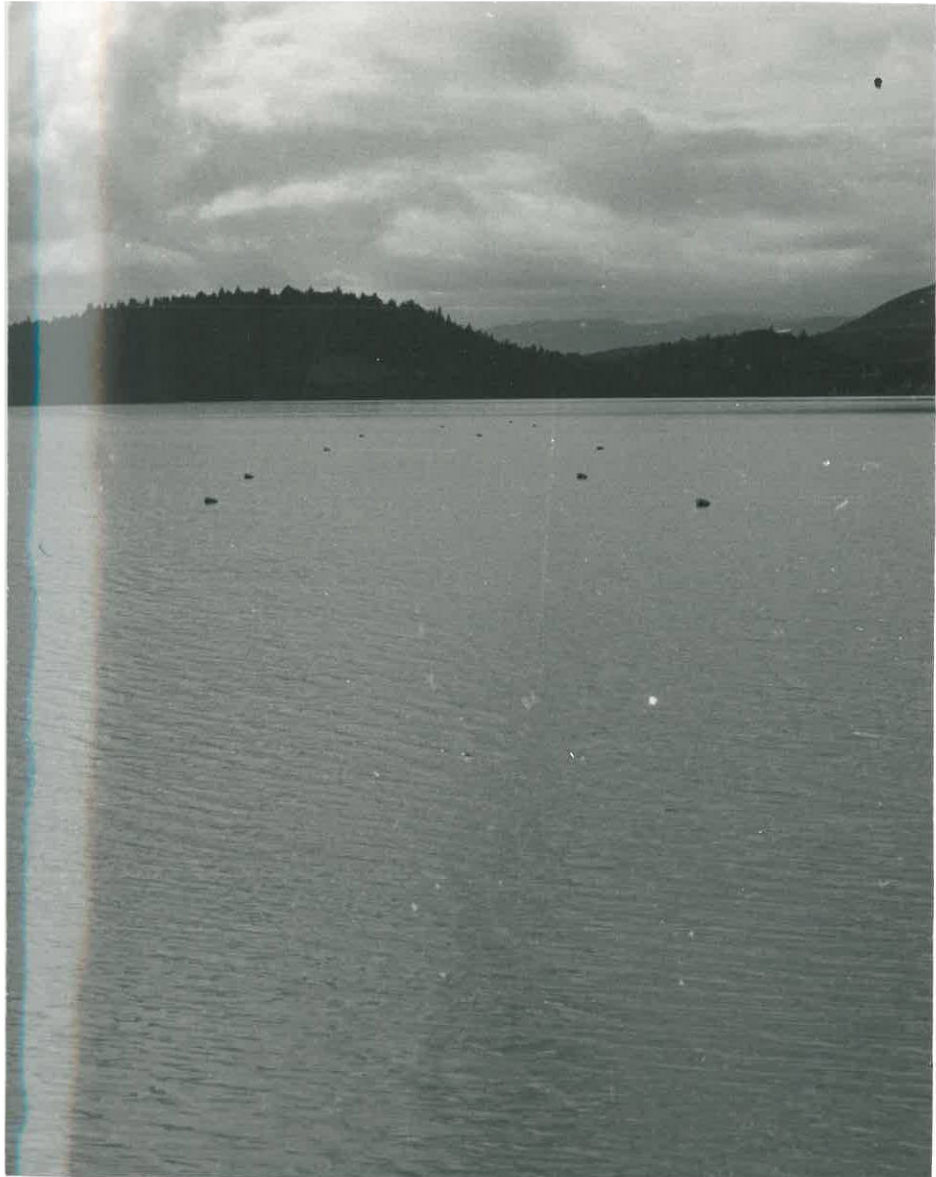
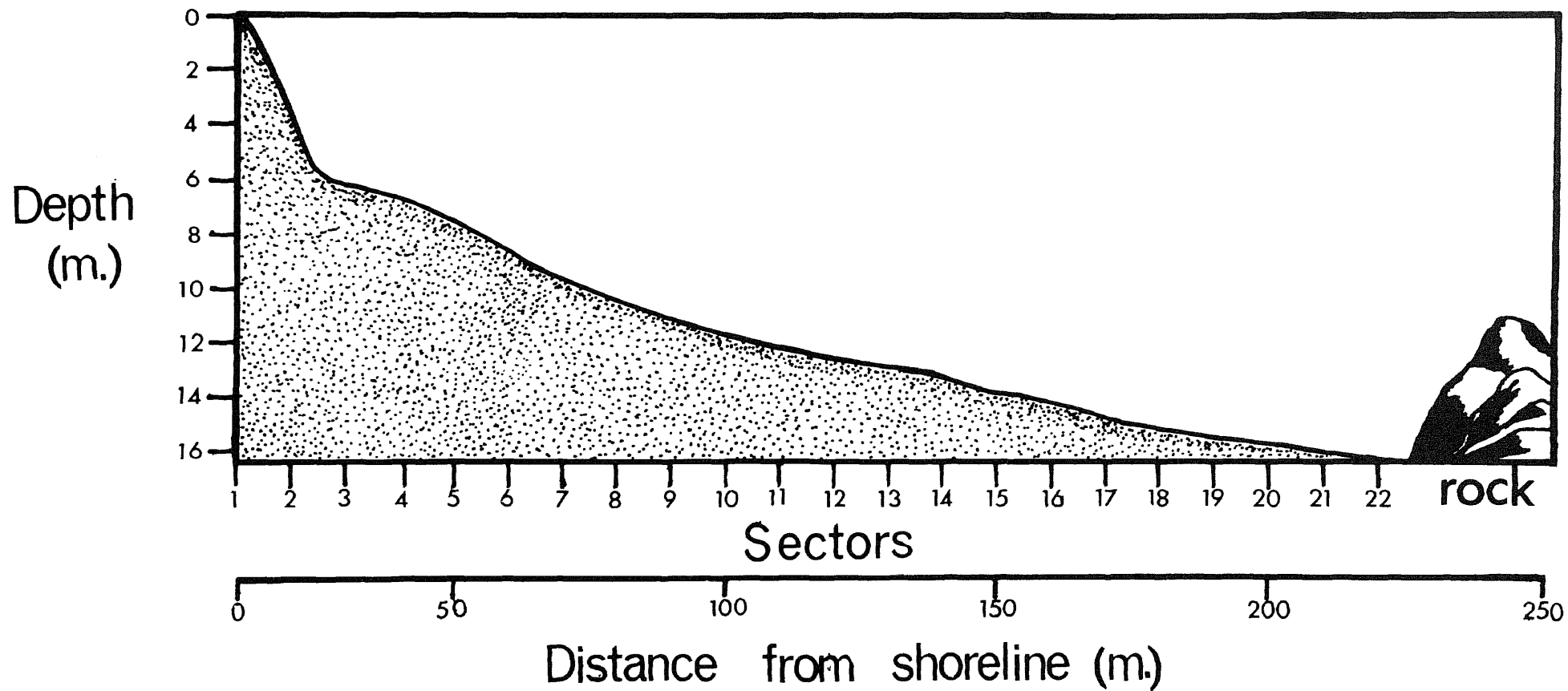


Fig. 2: Cross-section of the transect at Wright's Bay  
showing depths of each sector.



placed in two parallel rows throughout the transect. About 10 were put in each sector. These were found to offer suitable homes, one crayfish being the occupant of a single can. Cans in sectors 1 and 2 were subjected to silting up due to wave action on the mud substrate and were subsequently lost but as no crayfish were ever found above sector 4 (see later) this part of the transect was left with only a few cans. At sector 22 the transect intersected a large rock estimated to be 30m. long by 6m. wide by 5m. high. It was highly dissected with cracks which crayfish inhabited. Similar rocks were seen during other dives in the lake. Estimations of the total on the rock, by diving for a certain period, were also used to give an indication of the migratory pattern.

Dives were made at approximately monthly intervals from April 1973 to January 1974, and the total number of crayfish encountered in the transect was recorded. These were sexed and the presence or absence of eggs and the pleopod state of females noted.

During these dives the numbers found in the transect were also used to determine population densities between depths of 7 and 16.3m. i.e. from sectors 4 - 22. Crayfish were never found in cans within the first 3 sectors and it seemed that Lagarosiphon weed beds and small rocks down to 5m. offered more suitable homes, at least during the hours of daylight.

The transect was also used in a homing and home range experiment described in the section on trapping, and to determine whether Paranephrops planifrons displayed territoriality in the field.

(b) Horizontal dive.

Another method employed to obtain information on concentration and the depth distribution, although used only once was that of Endean (1969) for estimating population density of the Crown-of-Thorns starfish, Acanthaster planci. At 5m. intervals horizontal dives were made for 7 minute periods and the number of crayfish observed was recorded. However, this method was not used again as the crayfish tended to hide under sunken logs and debris at the dive location (the eastern end of the lake) and because visibility became progressively less with increasing depth, the field of vision being reduced from ca 5m. at the surface to ca 2m. at 27m. depth. Since the visual area covered was not equal at all depths quantitative assessment was thus made very inaccurate. However, in open-bottomed oligotrophic lakes this method could be quite successful.

2. TRAPPING.

(a) Trap design.

Previous workers have used various trap designs to capture crayfish. Most of these traps were modified from minnow, eel and other fish traps (Camougis and Hichar 1959, Aiken 1965, Moriarty 1971, Moshiri et al 1971, Momot and Gowing 1972 and Fast and Momot 1973). Momot (1967a) and Momot and Gall (1971) found that the traps they used were size selective, for crayfish below a certain length (24mm. cephalothoracic length) were never caught. Bearing this in mind traps were designed to make entry as easy and as uncomplicated as possible.

6 traps were constructed each consisting of a square aluminium frame of 62cm., by 32cm. in height and covered by galvanized steel mesh (mesh size 2 x 2mm.) (Plate 2). Positioned in the centre of each side was a vertically sliding sprung gate (15 x 15cm.) which opened flush with the substrate so that the crayfish could gain easy entry. Each gate was held open by a cord connecting it to a release mechanism which was triggered by a 2lb. lead messenger. This design allowed trappings to be made for specific periods of time, and also ensured that no crayfish escaped when they were being pulled to the surface. The interiors of the traps were partitioned into 4 feeding bays which were added to reduce the chances of escape when the messenger was sliding the rope, for the slight vibration produced may have triggered the escape reaction of entrapped crayfish. Traps were baited in each corner with beef liver (Moriarty 1971) which was found to be very successful.

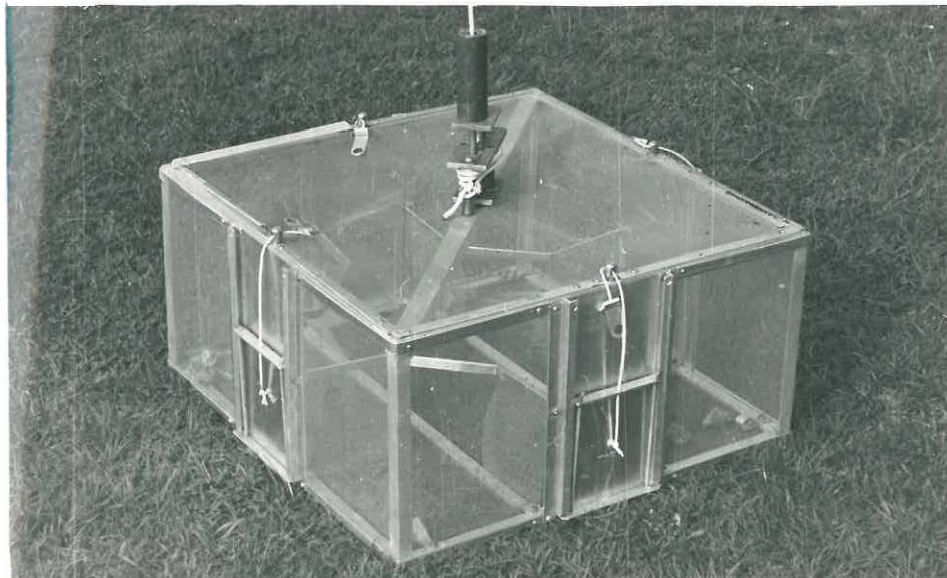
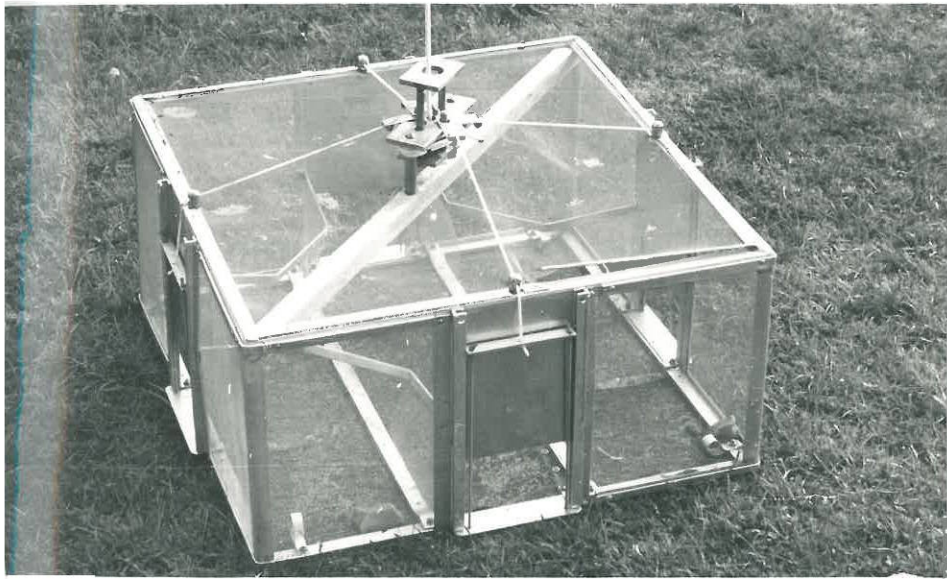
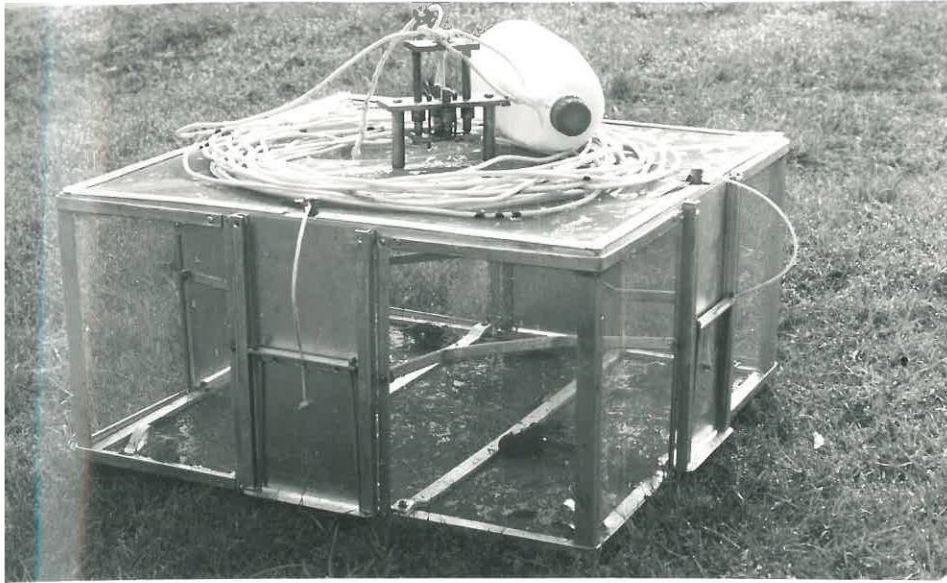
However, the trap design did not overcome the problem of size selection, as no crayfish of less than 23.0mm. cephalothoracic length were captured. On one occasion 2 very small juveniles were found in a trap but it was thought that they had become detached from their entrapped mother. This phenomenon of size selection was unexplained, for in the laboratory it was found that immature P. planifrons readily consumed beef liver. It could be, however, that in the field young crayfish have a preference for vegetable matter, as Tack (1941) found for Cambarus immunis.

Plate 2.

Above : Crayfish trap showing buoy, graduated rope, re-  
lease mechanism, feeding bays and a few  
captured crayfish.

Centre: Trap baited and in 'set' position.

Below: Trap triggered. Note messenger used to trigger  
release mechanism.



(b) Trapping method.

Trapping commenced in September 1973 and was used to trace the spatial distribution pattern until January 1974. These results and those obtained from the transect were used to obtain an overall pattern of movement. Each time samples were taken light and temperature readings were obtained down to 30m. using a thermistor thermometer/ photometer (Bell 1962). At about one monthly intervals 5 traps were arranged at depths of 1, 10, 20, 30 and 50m. Traps were usually set in the late afternoon, raised and emptied every 2 - 3 hours until about 2 a.m., then left until the following morning. Over a trapping period the total caught at each depth was recorded and the cephalothoracic length of each animal was measured with Vernier calipers accurate to within 0.1mm., from the tip of the rostrum to the mid-dorsal posterior border of the carapace. Its sex was also noted. Females were checked for presence of eggs, cement glands and state of pleopods, while males were examined for sperm extrusion (see section on breeding).

Abrahamsson (1971) reported that gravid females of Pacifastacus leniusculus occurred less frequently in traps than did males and non-gravid females. Tack (1941) states that egg-bearing C. immunis females remain in the seclusion of burrows and under stones and do not feed. There was no evidence of this occurring for Paranephrops planifrons as the relative numbers observed while diving were comparable to those caught in traps.

It should be noted that the total number caught at

each depth did not give a true indication of the number which could be potentially captured, especially in waters shallower than 20m. Below this depth crayfish were caught at all hours but in shallower water crayfish fed only at night. It seemed possible that light of similar intensity to that at about 20m. was the critical factor affecting activity. So in order to produce a more realistic total the number of crayfish caught relative to their feeding times at each depth was calculated. This was expressed as relative number of crayfish caught per hour per trap per specific depth (R):

$$R = \frac{N}{T \cdot t}$$

where T = hours of catchable time  
 t = fraction of catchable time to total time traps laid  
 N = total number caught at specific depth

The relative percentage catch at each depth (P) was calculated as:

$$P = \frac{N \cdot 100}{A \cdot t}$$

where A =  $\sum$  total caught at all depths

(c) Effective trapping radius.

The effective capture range of a trap was estimated in two ways. On two occasions 3 sectors in the transect were randomly selected and the numbers of crayfish present in each was obtained by diving. At 8p.m. a baited trap was laid in each sector and, after 2 hours, raised and the crayfish counted.

Knowing the area of each sector ( $50\text{m.}^2$ ) and the average number of crayfish in the 3 sectors as well as the average number caught, it was possible to calculate the effective catching area per trap per hour and hence the effective catching radius of a trap (see Table 1). These transect counts were made in the late afternoon and the estimation of the effective trapping radius would have been more accurate had counting been done immediately prior to trapping when crayfish at these depths are active and feeding. However, problems with underwater lighting made night diving impracticable.

Date	Sector	Number present	Number captured	Average number in each sector	Average number caught	Effective trapping area ( $\text{m.}^2$ )	Effective trapping radius (m.)
30/12/73	7	1	10	4.3	7.7	44.2	3.8
	13	7	7				
	20	5	6				
	Total 13		23				
20/ 1/74	10	4	12	6.7	9.7	36.2	3.4
	17	9	14				
	21	7	3				
	Total 20		29				

Table 1. Calculated effective trapping area and effective trapping radius.

The effective trapping radius was also calculated from knowledge of the relative number of crayfish caught per trap per hour (3.72) at 10m. during the January trapping programme (20/1/74) and the number present (75) in the whole transect on that date. The trapping radius

calculated by this method (3.8m.) was similar to the other estimates.

(d) Homing and home range.

Trapping was also employed to obtain an indication of home range and homing and to estimate distances travelled during a given time period. Crayfish in cans were individually identified by punching combinations of holes through the uropods and telson with ticket punches. Altogether 22 were tagged and their relative positions and those of unoccupied cans were noted (Fig. 3). 4 traps were placed on the same evening in the positions indicated in Fig. 3 and raised after  $2\frac{1}{2}$  hours. All crayfish captured were recorded and, if tagged, the distance they had travelled was calculated.

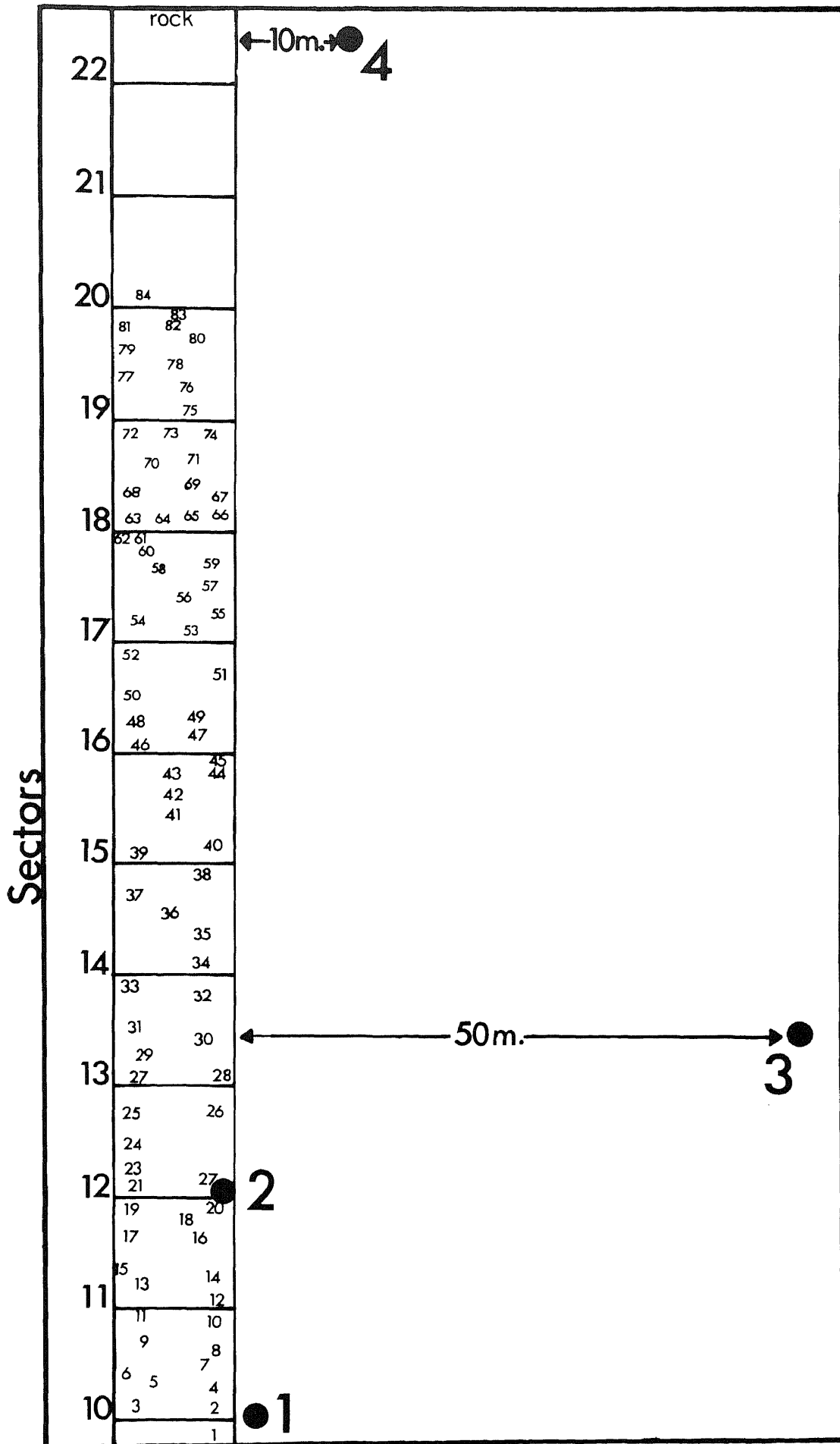
(e) 24 hour activity pattern.

A series of trappings over 24 hours was made to ascertain periods of feeding, which also determined crayfish activity patterns. 5 traps were laid at the same depths used in the monthly trapping programme. They were set at 2 p.m. and for the following 24 hours were raised every 3 hours. The numbers caught at each interval were used as a measure of the intensity of the activity of the crayfish.

### 3. DIP-NETTING.

By dip-netting at night in the shallows of Wright's Bay specimens whose gut contents did not contain liver could be obtained for stomach analyses. This method of capture was also employed to a small extent to complement results of shallow water trappings in this area, as well as for obtaining specimens in November to help determine

Fig. 3: Diagram of transect showing the exact location of each can within sectors 10 - 20. The positions of 4 traps are shown. View Fig. 3 in conjunction with Table 9.



● trap

the population structure.

#### 4. ANALYSIS OF SEDIMENTS AND STOMACH CONTENTS.

Sediments were collected from the 3 lakes as follows. On most occasions it was obtained at all depths by an Ekman grab. The top 3 - 4mm., within which crayfish probably obtain nourishment, was scraped off using a knife. On one occasion sediment from a depth of 15m. was collected by SCUBA. An open ended plastic container was pushed horizontally along the substrate for about 10m. to collect the upper few millimetres. The sediments were sieved to extract particles of the same order of size as those contained in the stomach contents.

Crayfish used for gut contents analysis were collected by dip-net in the shallows at night when feeding was maximal and by SCUBA to depths of 13m. in Lake Rotoiti only. Those in deeper water were obtained by trapping but with these animals it was necessary to remove consumed liver from the gut contents. Immediately after capture the gut cavities were injected with about 2mls. of 10% formalin in order to preserve gut contents for subsequent analysis. Material in the gut was found to range in size from 125  $\mu$ m to 1.0mm., most being approximately 500  $\mu$ m in diameter. Wherever stomach contents were obtained for analysis of percentage organic content and calorific value, sediments were also recovered from the same locality so that a direct comparison could be made.

Both sediments and stomach contents were ground to uniform composition using a mortar and pestle and then

dried to constant weight at 60°C. Percentage organic composition was then determined by ashing for 4 hours at 530°C. (Winberg 1971). Approximate determinations of the calorific content of similar samples were made by acid-dichromate oxidation, using the semi-micro method of Maciolek (1962). Because this method only oxidises about 90% of the organic matter present (Winberg loc. cit.) the results have been corrected by 10%.

DISTRIBUTION

Some species of crayfish have a distinct seasonal migration in which they move into deep water during the winter and return to the shallows during summer. However, very little work has been done on such migrational patterns. Apart from an intensive study by Momot (1967a), Momot and Gowing (1972) and Fast and Momot (1973) on Orconectes virilis in marl lakes of Michigan, and work by Abrahamsson and Goldman (1970) on the distribution of Pacifastacus leniusculus in Lake Tahoe, no other studies seem to have been published. The only other observations have been those made on the movement of crayfish in streams and ditches (Henry 1951, Camougis and Hichar 1959, Black 1963, Momot 1966, Mobberly and Pfrimmer 1967, Aiken 1968 and Merkle 1969), but these studies were not of sufficient duration to discern seasonal patterns of movement.

By combining the results obtained from the transect, which are presented in Figs. 4, 5 and 6, with those from the trapping experiments (Fig. 7) it was possible to determine the seasonal spatial distribution of Paranephrops planifrons in Lake Rotoiti. Results from the transect gave information on movements of crayfish in shallow water from April 1973 to January 1974. These values are probably reasonably typical of the whole lake as the bottom at similar depths elsewhere was found to be strewn with broken bottles and cans which offered habitats similar to those provided in the transect. Trappings, which began in September show movement patterns in deeper waters as well as complementing transect results in the shallows.

Fig. 4: Total numbers of crayfish and numbers of males, females and gravid females within the transect. Numbers found on the rock at the end of the transect are also shown.

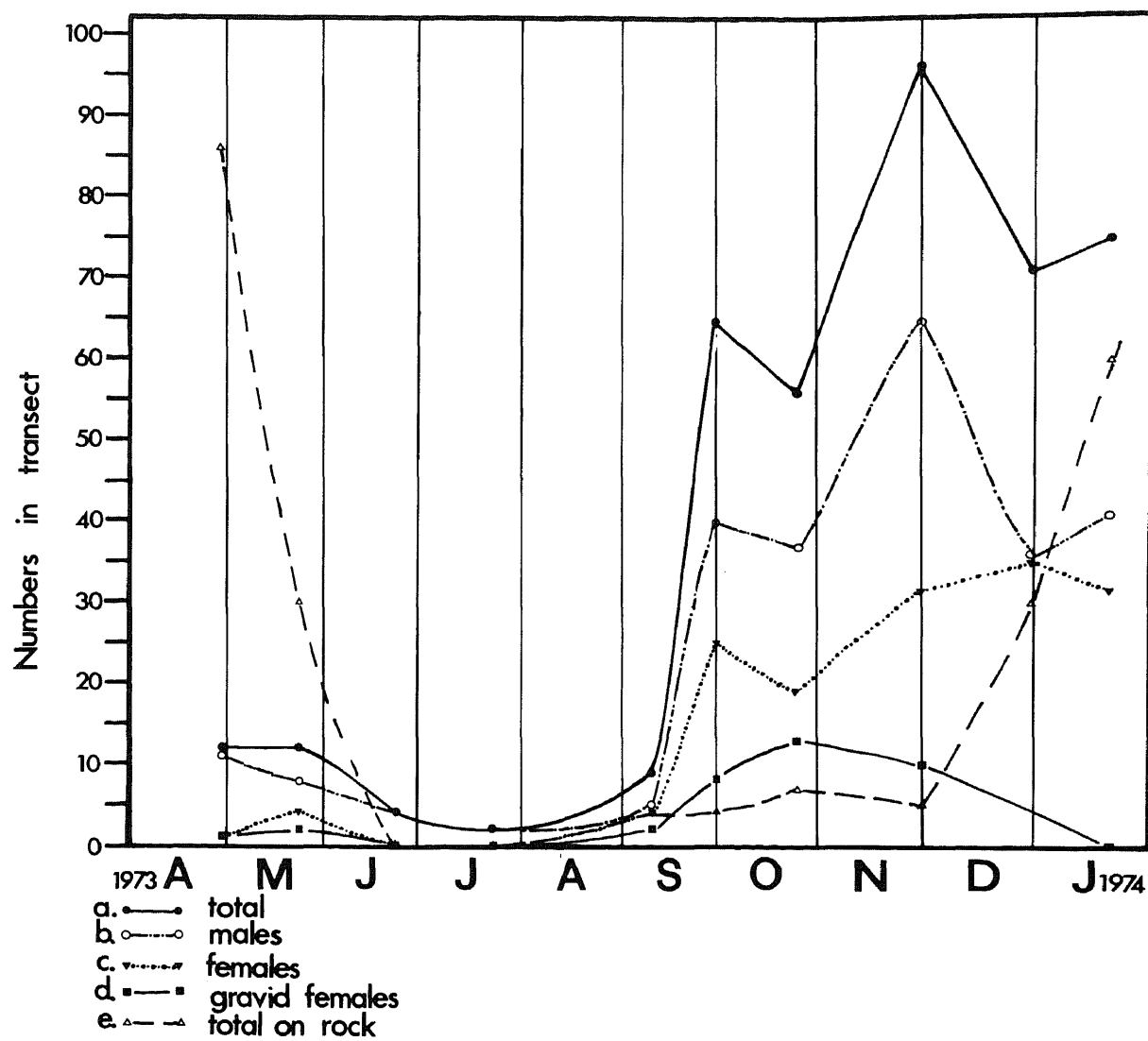


Fig. 5: Seasonal depth distribution of total population, males, females and gravid females (blank) within the transect, expressed as a percentage of the total number caught. Total numbers caught are shown above each diagram.

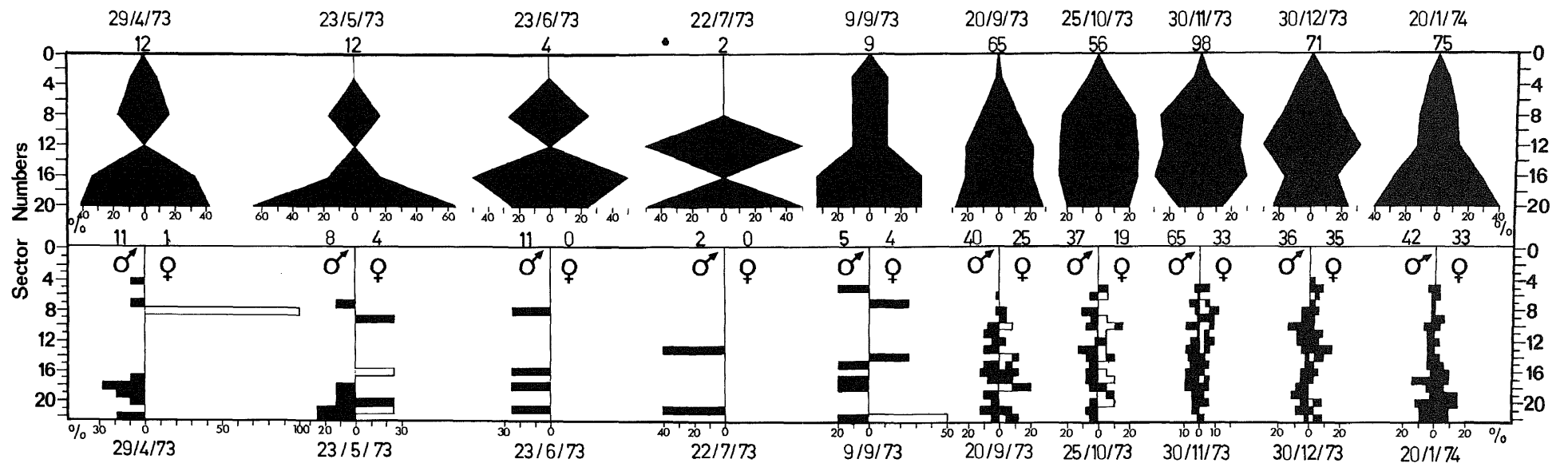


Fig. 6: Percentage of males and females present in  
sectors 4 - 13. (Depths shallower than 12m.).

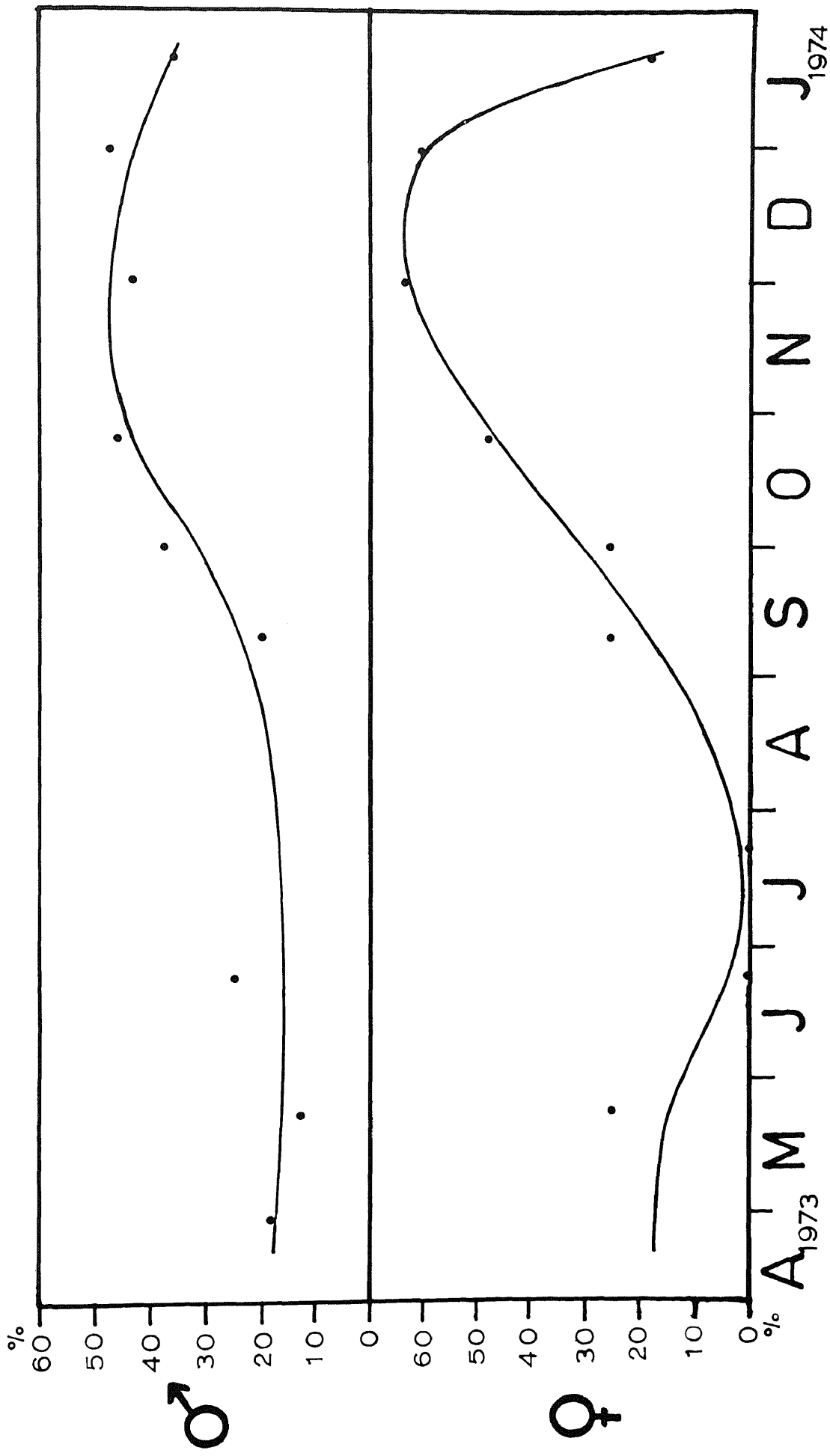
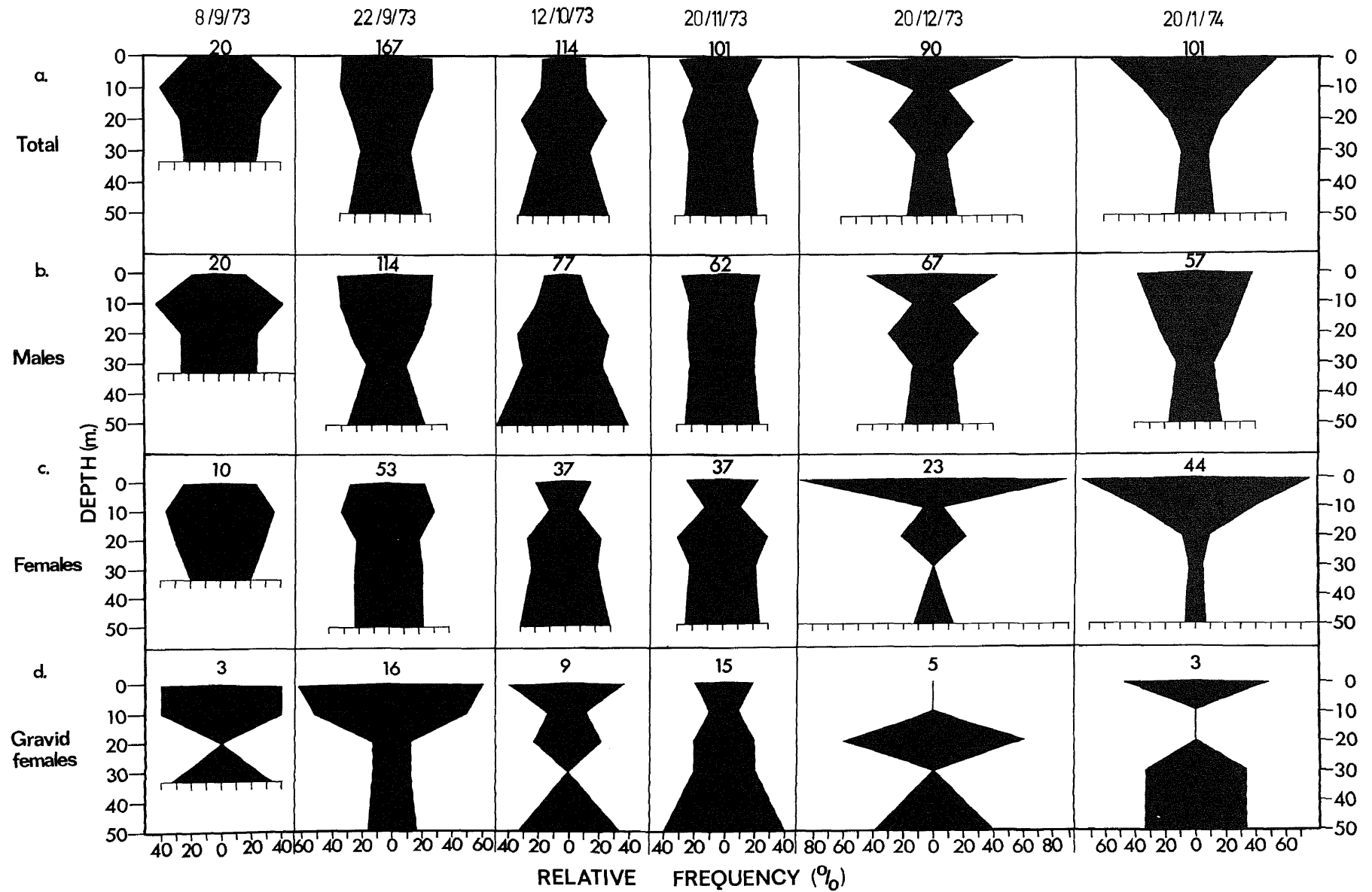


Fig. 7: Relative percentage of the total population, males, females and gravid females, trapped between 0 and 50m. from September 1973 to January 1974, in Lake Rotoiti. Total numbers caught on each date are given above each diagram.



In autumn there was a general migration out of the transect and the crayfish spent the winter months in deeper waters. Table 2 shows the result obtained from horizontal diving for 7 minute periods at 5m. depth intervals, towards the end of the winter, at the eastern end of Rotoiti. Distances covered at each depth were in the order of 80m.

Depth (m.)	Number seen in 7 minutes
5	3
10	3
15	1
20	7
27	ca 20 (1 minute)

Table 2: Number observed during horizontal dives of 7 minutes each at the depths indicated.

As noted above (p 7 ), the results obtained were not considered to be of great quantitative accuracy but they also give an indication that there were relatively fewer crayfish in shallower water (0 - 15m. depth).

From mid-September onwards there was a migration of both males and females back into shallower waters (Figs. 4 and 5). Fig. 5 shows the percentage distribution of the animals along the transect. Within the transect there was a general movement downwards during April and August followed by an influx in the shallower water in September. However, in January a concentration towards the deeper end of the transect occurred (Figs. 5 and 6). By this time the top of the thermocline had entered the lower quarter of the transect and it is possible that the crayfish preferred the cooler water there.

From December to January the numbers of females

increased relative to males until the sex ratio was close to 1:1, rather than the usual 1.9:1 (see p 49). This was the result of a definite upward movement of females between late September and December, whereas the males did not show such a pronounced movement (Fig. 5).

This pattern can be seen more clearly in Fig. 6 which shows that at the onset of summer there was a tendency for a greater percentage of females to inhabit shallower waters of the transect. Gravid females showed a similar pattern. Meanwhile the percentage of males in this region also rose but more than 50% remained in the deeper half of the transect, perhaps indicating a preference for deeper and/or colder waters, or waters of lower light intensity. It is possible that this apparent differential distribution may be related to breeding activity of the females, shallower water being preferred or required for some reason (see later). It should be noted, however, that this pattern broke down during January.

The depth distribution of all mature crayfish to a depth of 50m. between September and January, as determined by trap sampling, is shown in Fig. 7. From September to November the crayfish appeared to be fairly evenly distributed with depth, but from November onwards there was a general shrinking of numbers in deeper waters and an increase in density in shallower waters (Fig. 7a).

Lowered oxygen concentrations in the hypolimnion may supply the stimulus for this upward movement since Whittle (1973) has shown that beginning at 5 ppm  $O_2$  P. planifrons shows increasing oxygen consumption and activity as

oxygen tensions decline. Oxygen concentrations of 5 ppm occurred at 50m. depth in early December (Fish pers. comm. Fig. 8b) at which time movement upwards had begun, so ca 5 ppm  $O_2$  in the hypolimnion may supply the cue for the commencement of migratory behaviour. In Whittle's experiments crayfish survived in oxygen levels as low as 1 ppm, so it was not surprising to find a few remaining at 50m. at the end of the sampling period, in January, when oxygen concentration at this depth was 2 ppm (Fig. 7a).

The depth distribution of males, females and gravid females obtained from the trap samples are shown in Figs. 7b, 7c and 7d respectively. Numbers of males tended to be relatively constant at all depths throughout the trapping period (Fig. 7b), the upward movement beginning in November, but females had shown a relatively greater increase in shallower water by December (Figs. 7c and 7d), which indicated that the relative movement of the sexes was not the same. It may be that females have a lower tolerance of decreased oxygen levels than males, or possibly breeding habits may play a vital role in this differential movement.

Thus, in summary, it appears that in autumn there is a general movement of mature crayfish out into the deeper waters of Lake Rotoiti. Here they spend the winter and probably distribute evenly over the floor of the lake. In September there is a rapid mass migration of both males and females into the shallows, although a large proportion of the population remains in deeper waters, With the

onset of summer and progressive deoxygenation of the hypolimnion there is a second general movement upwards of both sexes, females moving up at a slightly faster rate, leading to concentration in the shallows. Although research was not carried out over late summer and early autumn, it was surmised that during this period when the hypolimnion was totally deoxygenated (Fish, unpublished data), the population was forced into the epilimnion and thermocline, and, after lake turnover in autumn, crayfish were free to disperse to greater depths.

Momot (1967a), Momot and Gowing (1972) and Fast and Momot (1973) record that O. virilis in marl lakes of Michigan underwent seasonal migrations. The pattern was similar to that of P. planifrons in Lake Rotoiti in that there was movement down to deeper waters in autumn after lake destratification, followed by a migration upwards in spring, the population as a whole then spending the summer period in the shallows. But there were some major differences between the relative positions and movements of males and females of these two species at various times of the year. O. virilis had only a single upwards movement during spring, for the purposes of egg-hatching, and because it had a preference for warmer waters. P. planifrons also migrated upward at this time (September) possibly for purposes of egg-hatching, but it is difficult to find a reason why males migrated upwards also. Surface temperatures were still within 1°C. of those at 50m. during September (see Fig. 8a), hence it was unlikely that temperature was a governing factor. There is evidence that P. planifrons, unlike O. virilis has a prefer-

ence for cooler water. A more likely explanation based on photoperiod and temperature regulating hormonal levels and consequent timing of breeding seasons (see later), is given on p 62). Another, but more gradual migration of P. planifrons that had remained in the deeper waters occurred as summer advanced but as noted above was probably due to progressive deoxygenation of the hypolimnion.

Momot (1967a) reported that males of O. virilis were largely confined to shallower waters and the females to deeper, colder waters. Aiken (1968) postulated that this difference in depth distribution of females came about because the combination of photoperiod and temperature required to induce their sexual maturation was only found in deeper water. He found that maturation occurred only when crayfish were kept in total darkness at temperatures below 10°C. for a minimum of 4 months. However, Fast and Momot (1973) disagreed and considered that O. virilis prefers warmer waters (20 - 24°C.) and believe that aggressive behaviour of adult males forces the females out into the cooler waters.

There was no evidence to suggest that there was a significant differential depth distribution of the sexes of P. planifrons. In general, males did not appear to be dominant or more aggressive towards females, although this may not be true of very large males (see section on sex ratio p 50). In contrast to O. virilis there was some evidence from January transect records (Figs. 5 and 6) that P. planifrons preferred cooler water (15 - 18°C.).

Although there is apparently a seasonal migration of P. planifrons in lake Rotoiti, there was no evidence to

suggest that such a movement occurred in Lake Okataina. Observations from two dives down to 22m. in Lake Okataina during May and August 1973, and a trapping series to 70m. in January 1974, showed that the depth distribution and concentration of P. planifrons in this lake had not altered during this period. In May and August none were seen in the upper weed beds which extended down to 16m. but within the lower extremities of these beds, and below, where the bottom was open and muddy, crayfish were present in relatively high densities. Similar results were found in January (refer to Table 3) when numbers were greatest at 20m. depth, and crayfish were caught down to 70m. indicating that they distribute to all depths in the lake.

Depth (m.)	Numbers trapped
1	1
10	1
20	7
70	1

Table 3: Numbers trapped in L. Okataina on 21/1/74 between 7.30 and 11.30 p.m.

Lake Okataina is oligotrophic and its hypolimnion does not deoxygenate in summer. It is therefore not necessary for the crayfish to migrate from this zone. There was no evidence of an upward movement in spring of P. planifrons in Lake Okataina although information was minimal. There did not appear to be a differential movement of the sexes either, since it was noticed while diving that the ratio of males to females and proportion

of gravid females remained relatively constant down to at least 22m. Also, during January, a group of Maoris was seen to catch large numbers of crayfish in the shallows, the ratio of males to females being approximately equal to the calculated 2.3:1 ratio (see sex ratio p 49). Hence there did not appear to be any differential concentration of either sex in the shallows.

The distribution pattern displayed by P. planifrons in Lake Okataina is similar to that of Pacifastacus leniusculus which inhabits oligotrophic Lake Tahoe, in California. Abrahamsson and Goldman (1970) found that the maximum density was at 10 - 20m., with 90% of the population occurring between 0 and 40m., although some were captured as deep as 200m. They state that wave action and light appeared to limit crayfish density above 10m. and water temperature below 40m. However, they make no mention as to whether such a pattern of distribution was constant throughout the year. No mention was made of seasonal migrations, so presumably as seemed to be the case in Lake Okataina, there was none.

It may be that light levels affect the behaviour of Paranephrops planifrons too, for at the 10 and 17m. contours in Lakes Rotoiti and Okataina respectively, where light intensities are similar (ca 300 lux), crayfish were found in the open and active. In contrast, those seen while diving in shallower waters were always under cover, indicating that above a critical light level, locomotory and feeding activities are curtailed.

BREEDING

## 1. THE BREEDING CYCLE.

The breeding activity of Paranephrops planifrons in Lake Rotoiti was determined by following changes in the percentage of gravid females throughout the year, sperm production of males, state of egg development, female pleopod condition, and the presence of cement glands in females.

During autumn the percentage of females bearing eggs was determined only from transect samples and dip-netting. Unfortunately little information is available for winter because the crayfish distributed deeper into the lake, none were found in the transect and traps were not available at this time. However, in spring and summer (from September to January), the percentage of gravid females was determined from both transect and trap sampling.

Periods of sperm production were determined from the presence of males having a white toothpaste-like exudate from their gonopores. Johnson (1960) notes that such a whitish exudate is produced by the columnar epithelial cells lining the vasa deferentia of Cambarus longulus longulus. He states that this accompanies the presence of mature sperm. When observed microscopically the exudate of P. planifrons was found to contain small spherical bodies (ca 5  $\mu$ m. diameter) which were of similar diameter to spermatozoa of Procambarus clarkii (Moses 1961a). These bodies were taken to be non-flagellate spermatozoa, which are a unique feature of decapods (Moses 1961b). Black (1966) reports that mature spermatozoa of Cambarellus

shufeldti and C. puer are of a non-motile, flattened, spheroid structure.

Hopkins (1967a) has described the broad features of the different developmental stages of the eggs of P. planifrons. Newly hatched eggs are brown and similar in colour to mature oocytes in the ovary. As development proceeds the eggs become cherry-red and at later stages the structure of the developing embryo can be clearly seen.

The state of the female pleopods can be used as a useful indicator of whether a female's eggs have recently hatched and the young dispersed. The pleopods of such females still retain the old egg attachments and are not cast off till the moult into the non-reproductive stage, which generally occurs about 4 - 6 weeks after the release of young (see p 33).

Cement glands, a mass of whitish calcareous material between the bases of the last three pairs of walking legs of the females, are produced by crayfish during egg-laying and apparently provide the cement which attaches the eggs to the pleopods (Stephens 1953). In this study the presence of such cement glands in F. planifrons was used as an indicator of periods of egg-laying by the females.

The proportion of gravid females throughout the sampling period is shown in Fig. 8d. The percentage gravid increased gradually for about 6 weeks during the autumn, which indicates a period of egg-laying. At this time females were also found with cement glands (15/3/73). Throughout the winter period it was not possible to accurately determine the percentage of gravid females, and possible values extrapolated from the few animals caught

during this period are shown by the dashed line in Fig. 8d. However, in spring there were increases in the percentage bearing eggs, followed by a decline. At first sight, this would seem to indicate the production of eggs in the spring followed by a period of hatching. However, there were considerable differences between the changes in percentage of gravid females, and other features of breeding also, in deep and shallow water during the spring (Fig. 8e), which indicate that such a simple interpretation is probably not the correct one.

In shallow water the percentage of gravid females fluctuated from September to October, then gradually decreased during November, December and January. All these eggs were in a late stage of development and hatching of them occurred from September onwards. Thus, in the transect egg-hatching and dispersion of the young from winter gravid females took place between late October and December for depths down to at least 16m. (Fig. 4d). Also, females with post-hatching pleopods were found increasingly commonly from mid-October onward. It seems most likely that these were eggs which had been laid in autumn and carried over the winter. The apparent increases in percentage of females bearing eggs that took place in spring in shallow water were thus probably associated with the migration of egg-bearing females from deeper water which occurred at this time (see above), rather than with new production of eggs (Fig. 8e). Fig. 7d is interesting in this respect for it indicates that from September onwards females with winter broods tended to concentrate in the shallows where hatching took place.

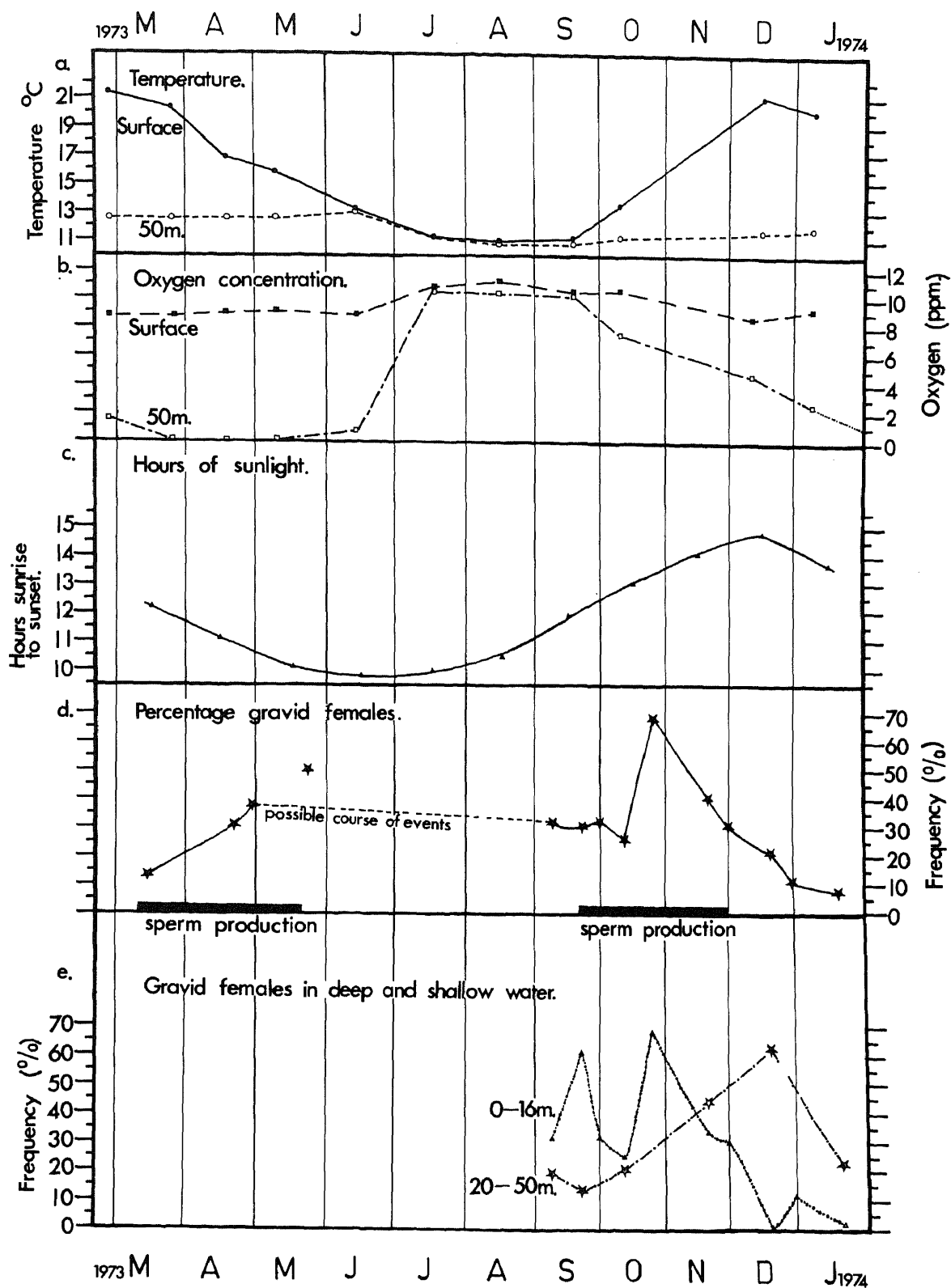
Fig. 8a: Changes in temperatures at surface and at 50m. in Lake Rotoiti.

Fig. 8b: Changes in oxygen concentrations at surface and at 50m.

Fig. 8c: Changes in daylength during the sampling period.

Fig. 8d: Seasonal changes in percentage of gravid females, and estimated periods of sperm production.

Fig. 8e: Comparison of percentage of gravid females in deep and shallow water.



However, in the deeper waters (Fig. 8e) there was a gradual increase in the percentage of gravid females over a 13 week period extending from late September to December, although numbers here were much lower than in the shallows (Fig. 7d). These eggs were newly laid and females with cement glands were found in the deeper water at these times (20/11/73, 20/12/73). Hatchings of the eggs borne by the females in deeper waters occurred from December onwards when the percentage of gravid females declined.

With increasing deoxygenation of the hypolimnion a general movement upwards of the deepwater egg-bearing females could be traced and by January one female with newly laid eggs was caught in the shallows. The possibility that summer eggs were produced in the shallows as well as in the deeper waters cannot be dismissed, but as crayfish are known to distribute randomly (as Camougis and Hichar (1959) demonstrated for Orconectes virilis in a pond), and are rather mobile (Momot and Gowing (1972) noted that one animal of the same species travelled a minimum distance of 124m. in 24 hours), it was quite possible for this female to have moved up from deeper waters. It is not known whether the females with winter broods in deep water also underwent a second breeding season immediately after release of young, or whether the summer gravid females had not bred during winter.

In an attempt to determine whether females that had borne eggs in winter also produced a summer batch of eggs, 6 females that had shed their winter young and whose pleopods were still in the reproductive state were placed in

a trough with 4 males. All the females died when attempting to moult presumably into the non-reproductive state, but in an adjacent trough 2 isolated females in a similar state were found to have moulted into the non-reproductive form during late spring, some 4 - 6 weeks after their young were released. This could indicate that these winter gravid females do not produce a summer brood.

Corresponding to the two egg-laying periods in autumn and spring there were two periods of sperm production by the males (Fig. 8d). Each of these periods of sperm production lasted for about 8 weeks. Sperm was observed exuding from the gonopores of males collected down to 15m. in the autumn and also from a number of males obtained at all depths during spring. Based on the observation by Abrahamsson (1971), that egg-laying of Pacifastacus leniusculus took place approximately 10 days after mating, it may be that the timing of sperm production and subsequent egg-laying of Paranephrops planifrons followed a similar pattern (see Fig. 8d). A similar lag period was mentioned by Moriarty (1971) for Astacus pallipes. No information was available on survival rate of discharged spermatozoa but because of the similar timing of sperm production and egg-laying, and the absence of continuous egg production, it seems unlikely that prolonged storage of spermatozoa by females occurs.

The breeding activity of crayfish is known to be affected by photoperiod and temperature. The temperatures of surface waters and those at 50m. depth and day-lengths during the sampling periods are shown in Figs. 8a and 8c

respectively. In Lake Rotoiti deoxygenation of the hypolimnion will also be important, since during the summer the crayfish are forced into shallower water of higher temperature and greater light intensity. Oxygen concentration at 0 and 50m. are shown in Fig. 8b (Fish unpublished data).

Autumn egg production could only take place in relatively shallow water for at this time the hypolimnion was totally deoxygenated (Fig. 8b). Aiken (1969a) found that egg-laying of Orconectes virilis was induced by warm water and that a temperature threshold of about 10 - 11°C. was required. Abrahamsson and Goldman (1970) found a similar situation for Pacifastacus leniusculus. However, it seems unlikely that temperature would have been a triggering factor for Paranephrops planifrons. Although it is not known if there is such a temperature requirement for egg production in P. planifrons, temperatures in autumn were quite high, varying from 20.5°C. to 13°C. during the autumn lay, and it seems unlikely that temperature would be limiting egg production at any time in the summer.

Photoperiod is also known to affect gonadal development (Stephens 1952, Lowe 1961, Aiken 1968 and Armitage et al 1973). The seasonal variation in photoperiod expressed as monthly mean number of hours from sunrise to sunset is shown in Fig. 8c. Lowe (1961) found for Cambarellus shufeldti that a combination of cooler temperatures and shorter photoperiods induced increased ovarian maturation. These 2 requirements are met for P. planifrons during winter (see Figs. 8a and 8c) and it is possible that they

may contribute to ovarian development and induce egg-laying in spring.

As mentioned above, egg-laying in spring took place only in deep water. These females had spent the winter under extremely low light intensities and temperatures as low as 10.8°C. Aiken (1969a) has found that O. virilis required 4 - 5 months of low temperatures and constant darkness for complete ovarian maturation, while Armitage et al (1973) reported that short-day photoperiods accelerated ovarian growth of O. nais. Stephens (1952) noted a similar requirement for ovarian maturation of Cambarus sp. So it is possible that the gonads of female P. planifrons at such depths reach maximum development in October having been stimulated by cold temperatures and low light intensities throughout winter and as a result eggs are produced.

The number of hours of daylight (Fig. 8c) were found to be very similar at the beginning of the autumn and spring periods of sperm production. It seems possible, therefore, that photoperiod also affects cyclic male gonad development. Temperature did not appear to be a critical factor, for at times of sperm production temperatures within the lake were variable.

The only other detailed study of P. planifrons is that of Hopkins (1967a) who found that stream specimens bred annually, egg-laying occurring between April and June, and hatching taking place from mid-September to early December. This constituted a breeding period of 25 - 26 weeks. More is known of the breeding habits of crayfish in other

countries and breeding periods may differ greatly between species and even between the same species living in different localities. Those such as European Astacus spp., Pacifastacus spp. and Orconectes spp. lay eggs in autumn and subsequent development may take from 20 - 25 weeks, while species of the genus Procambarus, North American Astacidae and the Parastacidae of Australia, to which Paranephrops planifrons belongs, produce eggs in spring when maturation and hatching takes approximately 16 - 18 weeks. The genus Cambarus contains species that either produce eggs in spring or autumn. For instance, C. propinquus (Creaser 1933) and C. clarkii (Penn 1943) breed during spring, while C. longulus longulus produces eggs in autumn (Smart 1962). Lowe (1961) has found that there are 2 peak breeding seasons for Cambarellus shufeldti; those of late winter-early spring, and summer. Penn (1942; 1950) reported an almost continual period of reproduction in this species, with peak activity occurring in late winter and continuing at high levels through early summer.

Thus there appear to be two main types of cycle; in one, laying occurs in autumn and the incubation period is long, and in the other laying occurs in spring or summer and the eggs complete incubation in a relatively short time. Hopkins' (1967a) study showed breeding of Parane-phrops planifrons to follow a pattern similar to that of the former cycle but the population of P. planifrons in Lake Rotoiti showed a combination of the two cycles, a feature which has not previously been found in the one species.

P. planifrons in Lake Okataina did not appear to have a summer breeding season, although this was not proved conclusively. There was a winter breeding season, and of the 42 females observed during this period, 87% were gravid, and because of their larger size bore greater numbers of eggs (refer to Table 4). These observations thus indicate that the population is probably increasing at a greater rate than that in Rotoiti. This seems feasible for crayfish have been introduced to Lake Okataina only recently (1940's - Beamish-White pers. comm.) and the population is low, whereas the Rotoiti population in Wright's Bay is much higher and stabilization of this population, through decreased egg production may be occurring.

## 2. FECUNDITY.

A small number of female P. planifrons were examined during the study to determine the number of eggs they carried, and the results are presented in Table 4. As Hopkins (1967a) has also found for P. planifrons inhabiting streams, there was a significant positive relationship between size and egg number, and also the lake crayfish carried similar numbers of eggs to stream crayfish of the same size. This appears to be a general phenomenon displayed by crayfish (Tack 1941, Penn 1943, Prins 1968, Payne 1971 and Stypińska 1972; 1973).

Lake	Cephalothoracic length (mm.)	Egg Number
Rotoiti	36.1	98
	37.1	82
	37.8	97
	40.4	129
	41.2	118
	42.1	140
	44.3	149
	44.6	141
	51.1	192
	54.4	197
Okataina	59.2	245

Table 4: Length of gravid females and their respective egg numbers. Egg number and length are significantly correlated  $r = 0.99$ .

### 3. MOULTING.

The crustacean moulting cycle is regulated by photoperiod controlling moulting hormone levels (Aiken 1969b). Stephens (1952) for Cambarus spp. and Armitage et al (1973) for Orconectes nais found that moulting rates were significantly higher at long-day photoperiods. A number of investigators have shown that low temperatures inhibit or lower the incidence of moulting and high temperatures increase the incidence (Hess 1941, Kyer 1942 and Passano 1960). Mobberly (1963) showed this to be the case for Faxonella clypeata as did Svardson (1949) for Astacus astacus. The moulting cycle, therefore, is under hormonal and environmental control. Moulting is closely allied to seasonal sexual cycles. We have seen its relevance in some overseas male species and it has been inferred that Paranephrops planifrons must moult to the reproductive stage before

egg attachment on the pleopods can occur (Hopkins 1967a).

Hart (1956) states that adult crayfish of the genus Cambarus usually moult twice a year, once in spring and in late summer, and the young while undergoing more rapid growth, moult more often. Hopkins (1967b) found for stream-dwelling P. planifrons that moulting of males and juveniles did not occur at any specific time of the year, but in general most crayfish moulted at least once between September and December, with further moults in summer and autumn. As gravid females in winter had no opportunity to moult until early summer (Hopkins 1967a) he deduced that the main female moult occurred in summer. Because of this, mature females moulted less frequently than males and therefore their growth rates were accordingly less. Abrahamsson and Goldman (1970) report that growth rate of female Pacifastacus leniusculus was less than that of males.

In Lake Rotoiti peak moulting periods occurred between spring and summer when many adults of both sexes were observed to moult and it was possible that those in the shallower warmer waters may have moulted more frequently during this period. Unfortunately no juvenile crayfish were ever seen while in the field so moulting behaviour could not be studied, but moulting of young in the laboratory occurred at frequent intervals during the warmer months. No significant difference was found between lengths of mature males and females (see p 45), which conflicts with Hopkins' reports on adult growth rates. Growth increments in Crustacea occur only at times of

times of moult. It is possible, therefore, from the Rotociti evidence that mature males and females moult an equal number of times per year. It was not possible to tell whether crayfish of the same size were in fact of equal age, as there can be differential growth increments of the sexes at each moult, or the number of moults for each sex may differ annually. A similar equality of sizes was displayed by male and female P. planifrons inhabiting Lake Okataina.

A feature shown by males of Astacus spp., Cambarus spp., Cambarellus spp., Procambarus spp., Faxonius spp. and Orconectes spp. is seasonal variation of forms of reproductive appendages (Creaser 1931; 1933, Hobbs 1940, Tack 1941, Penn 1942, Smith 1953, Black 1958, Word et al 1958, Smart 1962, Momot 1967a and Prins 1968). Momot (1967a) reports that the reproductive appendages of Orconectes virilis males have 3 morphological forms.

- 1) a juvenile form present before sexual maturity,
- 2) a non-breeding adult form, termed second form, which appears each spring after the first moult of a new growing season,
- 3) a form characteristic of breeding adults, termed first form, which first appears at sexual maturity and after the second moult of the growing season, usually occurring during the summer. After yearling males become mature, the sequence of moults was always the same; they changed from reproductive to non-reproductive form in the spring while in the shallows, and from non-reproductive to reproductive form in the summer while in deep water,

where mating occurred.

Such a change of sexual form was not found to occur in mature P. planifrons throughout the project and Hopkins (1967a) makes no mention of such a phenomenon. It would appear that such a feature does not exist for this species.

POPULATION STRUCTURE

## 1. POPULATION DENSITY.

From the effective trapping area ( $47.1\text{m}^2$ ), and the relative number of crayfish caught/trap/specific depth, approximate population density of the crayfish in Lakes Rotoiti, Okataina and Rotorua have been calculated (Table 5). Using the average density of  $0.030$  crayfish/ $\text{m}^2$  (obtained from averaging densities at Wright's Bay and at Wishing Tree) and the total area of the lake ( $33.9 \times 10^6\text{m}^2$ , Irwin 1972) it was calculated that there were approximately  $1.0305 \times 10^6$  mature crayfish inhabiting Lake Rotoiti. Similarly, for Lakes Okataina ( $1089 \times 10^4\text{m}^2$ , Irwin 1972) and Rotorua ( $80.94 \times 10^6\text{m}^2$ , Irwin 1972), the even more approximate figures of  $1.5162 \times 10^5$  and  $2.064 \times 10^4$  adult crayfish respectively were calculated.

During late summer and early autumn the crayfish in Lake Rotoiti were shown to concentrate in shallow water, resulting from migration upwards in summer and it is probable that they would spend these months above the 20m. contour where oxygen concentration is about 5 ppm (see Fig. 10). During this period the density at Wright's Bay was calculated to be  $0.153$  crayfish/ $\text{m}^2$ . When diving it was noticed that crayfish tended to concentrate in the cooler waters of the thermocline, between the 12 and 20m. contours, although many still lived under weed beds and rocks in the warmer epilimnetic waters. Taking 50% as a conservative estimation of the total adult population within this 8m. band, a concentration of approximately  $0.306$  crayfish/ $\text{m}^2$  would be found here during these months.

Population Density

Lake	Dates of trapping	Total trapped	Depth range of traps(m.)	$\overline{C.L.}$ (mm)	Mean number of relative crayfish caught /trap/hour	Population density (No. crayfish /m <sup>2</sup> .)	
Rotorua	Wright's Bay	Sept. 1973 - Jan. 1974	631	1 - 50	44.2	2.23	0.049
	Wishing Tree	4/12/73	23	1 - 40	49.7	0.46	0.010
							} 0.030
Rotorua	3/12/73	2	1 - 15	55.1	0.14	0.003	
Okataina	21/ 4/73	10	1 - 70	59.2	0.67	0.014	

$\overline{C.L.}$  - mean cephalothoracic length

Effective trapping area = 47.1 m<sup>2</sup>.

Table 5. Calculated population densities of two areas in Lake Rotorua, and of Lakes Rotorua and Okataina.

Diving in March 1973 showed this estimation to be relatively accurate. It is possible that the concentration in the thermocline may be due to accumulation of detrital food particles settling out in the denser water layers. However, analyses of the surface sediments at these depths do not substantiate this idea as percentage organic matter did not differ significantly from those at other depths (see later, Table 7).

Abrahamsson and Goldman (1970) found a density of 0.9 adult Pacifastacus leniusculus/m.<sup>2</sup> in Lake Tahoe which is higher than that of Paranephrops planifrons. They state that average body length of this species was inversely related to the population density. Abrahamsson (1966) calculated a density of 2.0 crayfish/m.<sup>2</sup> for Astacus astacus in an isolated pond at Röggle (Skane, southern Sweden) and, the same author (1971) found that Pacifastacus leniusculus and A. astacus inhabiting a different pond were present in concentrations of 3.6 and 5.0 crayfish/m.<sup>2</sup> respectively.

These workers obtained density estimates using mark-recapture methods, while Abrahamsson and Goldman (loc. cit.) as well used a method based on effective trapping area similar to that used in the present study. They found that values obtained with the two methods were almost identical.

The population estimate of Lake Rotorua was based on only one sample and thus is highly tentative. However, if the calculated population density is correct the low value may result from predatory pressures from shags and trout

(Potts 1972). This is a shallow lake with a more extensive littoral zone than either Rotoiti or Okataina. It supports a high shag population which feed on crayfish inhabiting the littoral region and is stocked with trout which also eat crayfish. Only large specimens of Paranephrops planifrons were trapped. This may be expected as smaller crayfish would probably be easier prey for these predators.

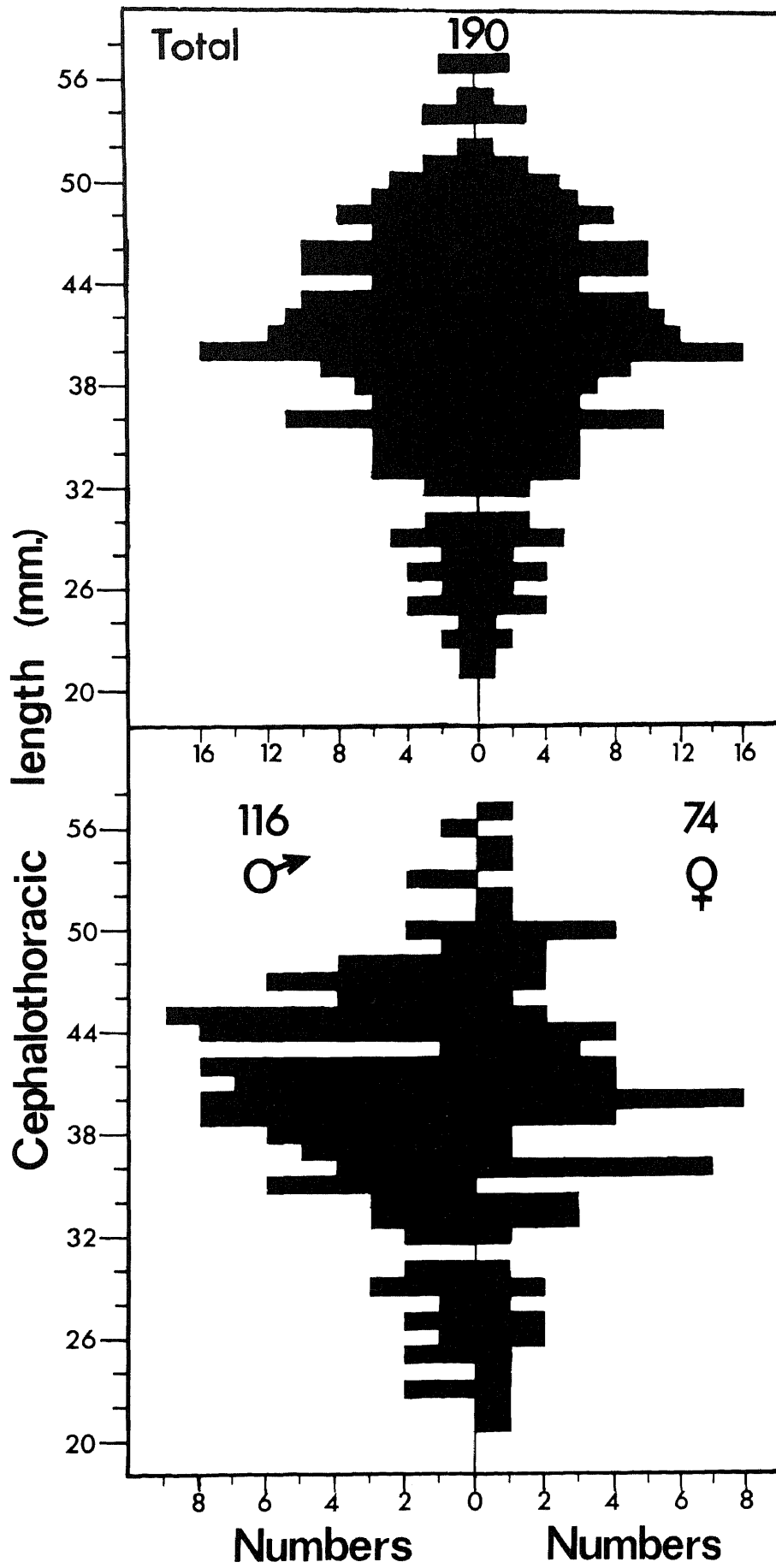
## 2. SIZE.

In order to assess the population size structure in Lake Rotoiti 180 crayfish were obtained by trapping, and by netting around the shoreline. As it was important that they did not moult during the period of capture they were obtained during a single week (13/11/73 - 20/11/73). Each crayfish was sexed and its cephalothoracic length measured.

An attempt was made to separate these animals into size-classes in order to estimate age groups, by using probability paper analysis (Harding 1949, Cassie 1954). Hopkins (1966) using this technique described the growth history for 5 different populations of P. planifrons. He found that size frequency distributions were polymodal and was able to group these populations into 3 to 4 year class components.

In Lake Rotoiti P. planifrons showed no distinct size-classes and normal size distributions were found for the adult population as a whole and for adult males and females (Fig. 9). No significant difference was found between size of males and females (Males:  $\overline{C.L.} = 41.1\text{mm.}$ , S.D. = 7.06, N = 123; Females:  $\overline{C.L.} = 40.6\text{mm.}$ , S.D. =

Fig. 9: Size structure of adult crayfish population in  
Lake Rotoiti and of adult males and females.



8.22,  $N = 78$ .  $t = 0.47$  n.s.). Abrahamsson and Goldman (1970) found distinct size groups in a population of Pacifastacus leniusculus in Lake Tahoe, as did Abrahamsson (1971) for A. astacus and P. leniusculus in a Röggle pond. The failure to find similar groups of Paranephrops planifrons in Lake Rotoiti possibly came about because of the presence of two breeding seasons, resulting in imperceptible blending of the cohorts. Also, the crayfish measured were all adults and with increasing age physiological and environmental factors could have caused increased variation in individual growth rates.

Table 6 compares the average cephalothoracic length of males and females present at 1 and 50m. These animals were obtained by trapping between September and January. There was no significant difference in size at 1 and 50m. indicating that animal size throughout the lake was evenly distributed. This contrasts with findings of Abrahamsson and Goldman (1970) who stated that larger Pacifastacus leniusculus individuals tended to be found in deeper waters of Lake Tahoe, although here population density was low.

In this study smaller sized animals were found in areas of high crayfish density than in those with low population densities (Table 5). This was most noticeable in Lake Rotoiti. In the Wright's Bay population density was high and size small, while at the eastern end of the lake density was low and crayfish much larger. This indicates that density dependent factors may be regulating size or growth rates of these populations. Abraham-

Date	Sex	Depth (m.)	C.L. (mm.)	S.D.	N.	t.
8/ 9/73	♂	1	44.0	4.37	6	0.17
		50	44.3	1.57		
	♀	1	36.0	11.95	2	0.67
		50	42.0	3.32		
22/ 9/73	♂	1	43.7	4.97	48	0.03
		50	43.8	4.21		
	♀	1	47.2	5.49	18	2.02
		50	42.5	4.59		
12/10/73	♂	1	42.9	4.55	32	0.73
		50	44.3	5.32		
	♀	1	38.0	8.67	23	1.82
		50	42.5	3.66		
20/11/73	♂	1	41.4	5.56	24	1.84
		50	44.5	3.10		
	♀	1	42.2	5.96	13	0.18
		50	42.7	5.18		
20/12/73	♂	1	43.4	4.59	30	1.70
		50	45.9	2.60		
	♀	1	43.3	4.85	15	1.86
		50	37.9	1.70		
20/ 1/74	♂	1	46.5	3.94	23	1.28
		50	44.2	4.84		
	♀	1	44.3	6.20	24	1.32
		50	49.5	8.88		

C.L. - mean cephalothoracic length

S.D. - standard deviation

N. - total number

t. - student's t.

Table 6. Mean cephalothoracic length of crayfish trapped at 1 and 50m. during spring and summer. t-tests between mean lengths of males and also between mean lengths of females at these depths showed no significant difference at the 5% level.

sson (1966) reports slow growth rates of A. astacus at Røgle where densities were very high. Hopkins (1966) noted for Paranephrops planifrons that females first matured a year earlier in lower density populations than in those of high density. Unfortunately without sufficient data on ages and growth rates it was not possible to determine whether similar relationships existed in lake-dwelling P. planifrons.

### 3. SEX RATIO.

Of the 1,297 crayfish from Wright's Bay which were sexed and measured throughout the study, 843 were males and 454 females, giving a sex ratio of 1.9:1. In the Lake Okataina sample of 90 crayfish the ratio was 2.3:1 in favour of males. Threinen 1958, Aiken 1965, Momot and Gowing 1972 and Fast and Momot 1973 have all reported sex ratios of Orconectes virilis to be similarly in favour of males, in some cases by as much as 4:1, while Abrahamsson (1966) found that male numbers of Astacus astacus in Røgle ponds exceeded that of females.

There seem to be three possible ways in which such sex ratios might come about although it is not at all clear which is most likely to be the correct explanation.

1) There may be a preponderance of presumptive males in the eggs. Laboratory observation of newly hatched larvae showed that no external sex distinguishing characteristics were present, so it could not be verified whether this was true for P. planifrons.

2) Another possibility is that proposed by Abrahamsson (1966) who found that when Astacus astacus reached sexual

maturity, males outnumbered females but not as juveniles. This was because as males increased in size their chelipeds became accentuated with increasing age, a phenomenon not occurring in females. As the population in Røgle ponds was dense (2 crayfish/m.<sup>2</sup>), male aggression resulting from territoriality caused a greater mortality of the less well equipped females. Although not actually measured, relatively larger chelipeds were observed in very large P. planifrons males.

Abrahamsson's reasoning was based on high density of population and resulting high levels of aggression in the Røgle ponds. However, in P. planifrons the densities are much lower. The mean density of crayfish in Lake Rotoiti calculated from trapping and from counts in the transect gave values of 0.06 and 0.05 crayfish/m.<sup>2</sup> respectively. Also when density was found to be maximal in the shallows in January the density was still only 0.15 crayfish/m.<sup>2</sup>. Similarly, mean density for Lake Okataina was calculated to be only 0.02 crayfish/m.<sup>2</sup>. Thus it does not appear likely that P. planifrons males outnumber females because of density induced male dominance and loss of females during fighting. Also the population of very large males, of the order of >55.0mm. cephalothoracic length, which had greatly accentuated chelipeds and hence could be capable of such behaviour, was very low and therefore presumably would have little effect on the population as a whole.

3) Perhaps the most likely explanation is that there may be greater mortality of mature females than males at times of moulting. This suggestion is based on diving ob-

servations and on an experiment where 6 females whose pleopods were in the post-gravid reproductive state were placed in the same tank as 4 males. The season was late spring, when it appears that most animals undergo at least one moult. After a period of one month it was noted that all females had died while attempting to moult, presumably into the nonreproductive state, whereas only one male had died during the same period, the remaining 3 still surviving after 3 months. However, it was not known whether these males did in fact moult.

Of the few dead crayfish encountered while diving, nearly all were mature females. For instance, of the 8 dead crayfish found in the January transect dive 6 were females. These all appeared to have died while moulting, as also did the 2 males.

FEEDING AND DAILY ACTIVITY PATTERNS

The gut contents of 115 Paranephrops planifrons taken from Wright's Bay were examined, and the consumed food was found to consist of approximately 80% detritus, 10% animal parts (most of which was pieces of crayfish carapace) and 10% vascular plant material, some of which was allochthonous leaf material. This food composition was constant throughout all depths of the lake, although the percentage of aquatic vascular plant material was slightly higher in crayfish obtained from the shallows.

Other species of crayfish do not appear to include detritus in their diet to the same extent as P. planifrons and plant material forms a greater percentage of their diet. For example, Tack (1941) described the food habits of Orconectes immunis as 83% plant, 11% detrital and 6% animal material, while Prins (1968) states that the food of Cambarus tenebrosus is 15 - 20% filamentous algae and 25% vascular aquatics with both detrital and animal material making up 8 - 14%. Bovbjerg (1970) found that O. immunis and O. virilis eat any available food, plant or animal, living or dead.

Crayfish ingest food lying on and amongst the substrate. Table 7 shows that gut contents have a higher caloric value than that of the sediments by as much as 5 times, indicating that P. planifrons is a selective feeder and does not merely ingest the substrate "en masse". It also shows that at different depths in Lake Rotoiti there is no great variation in sediment quality. These values are noticeably higher than those found in Lakes

Lake	Date	Depth (m.)	Sediment % organic	Stomach contents % organic	Sediment calorific value cal./gm.	Stomach contents calorific value cal./gm.
Rotorua	20/4/73	1	-	75.1	-	-
	"	7	-	-	-	3508.8
	"	13	-	-	-	2867.9
	20/9/73	15	18.5	-	-	-
	"	30	14.1	-	-	-
	22/9/73	1	-	64.0	-	-
	"	50	12.1	93.1	-	-
	29/9/73	1	-	-	853.8	-
	"	3	22.9	-	-	3745.1
	"	15	-	-	685.3	-
	"	30	-	-	596.0	-
	"	50	-	-	723.2	-
	"	20	-	-	-	5050.3***
	"	30	-	-	-	2123.8*
	"	50	-	-	-	3479.0**
	12/10/73	2	8.7 $\gamma$	-	148.8 $\gamma$	-
	"	30	16.3	-	635.9	-
	"	50	-	-	-	2232.0*
	20/11/73	1	-	-	-	3678.3
Rotorua	4/12/73	1	2.4 $\gamma$	-	42.0 $\gamma$	-
	"	15	2.3 $\gamma$	-	23.2 $\gamma$	-
Okataina	20/12/73	1	2.1 $\gamma$	-	14.9 $\gamma$	-
	"	33	12.0	-	252.6	-

\* 5% unsortable liver in gut.

\*\* 5 - 10% unsortable liver in gut.

\*\*\* 10 - 20% unsortable liver in gut.

- no sample.

$\gamma$  taken from sandy substrate.

Table 7. Percentage organic matter and calorific contents of sediments and stomach contents at varying depths.

Okataina and Rotorua, but the values from the latter are most probably misleading for sediments from deeper waters were not examined.

The results of the 24 hour trapping series are presented in Table 8 and indicate that P. planifrons feeds continually in waters deeper than 20m. but in shallower water feeds only at night. Roberts (1944) states that crayfish are most active during the hours of darkness and Mr D.A. Nash (pers. comm.) has seen the marine crayfish Jasus edwardsii feeding on the open bottom at night. The main feeding period of P. planifrons appeared to be between 8 p.m. and 2 a.m., with peak activity being around 11 p.m. The last 2 trappings captured no crayfish but this was thought to be because the bait had become rotten, for other trappings at similar times captured crayfish in the deeper waters. Crayfish at 1m. fed between 8 p.m. and 5 a.m. (9 hours), while those at 10m. fed for 12 hours. It appears that light intensity governs activity patterns and it is possible that light levels at depths greater than 20m. are not sufficient to "switch off" feeding behaviour during the hours of daylight.

Time	Depth (m.)					Total
	1	10	20	30	50	
5pm.	0	0	15	0*	7	22
8pm.	2	10	9	4	6	31
11pm.	13	5	2	9	13	42
2am.	9	5	5	4	12	35
5am.	6	9	4	4	1	24
8am.	0	2	3	6	2	13
11am.	0	0	0	0	0	0
2pm.	0	0	0	0	0	0

\* trap release faulty.

Table 8: Number caught in traps at specific depths over 24 hour period on 22 - 23/9/73.

HOMING, HOME RANGE AND TERRITORIALITY

The results of the experiments to determine whether Paranephrops planifrons in Lake Rotoiti had a home range, and whether homing occurred, are given in Table 9. The tagged crayfish are listed as well as the respective cans they occupied at the time of tagging. In Fig. 3 the location of each can in the transect between sectors 10 and 20 is shown. Those cans denoted NA did not contain crayfish but when checked the following day (16/12/73) were found to be occupied, however none of the occupants were tagged. Also, many of the cans that had housed tagged crayfish were empty, although some were inhabited (e.g. cans 35, 48 and 50), but none by tagged crayfish.

These results suggest that P. planifrons does not display homing although this conclusion should be treated with caution as tagging may have upset the normal behavioural and movement patterns of the crayfish. Movements would appear to be random throughout the course of a night's foraging since there was no evidence that any of the animals returned to the home they occupied the previous day.

Although it appears that P. planifrons does not exhibit homing in Lake Rotoiti, it was noticed while diving in Lake Okataina that a few crayfish beneath the weed beds were resting in furrows (some 20cm. long, 7cm. wide and 3cm. deep) obviously scoured out of the mud. These crayfish may display homing and return to such furrows after a night's foraging. But on the other hand they may occupy furrows made by other crayfish, or, a

15/12/73			16/12/73	
Can number	Crayfish and sex	Tag combination on tail fan	Crayfish and sex	Tag combination on tail fan
1	♂	0 0	-	NA
3	♂	0	-	NA
5	-	NA	♂	NT
9	♂	0	-	NA
10	-	NA	♀	NT
13	-	NA	♂	NT
16	♀	0	-	NA
18	♂	0	-	NA
23	♂	0 0	-	NA
25	♀	X	-	NA
27	-	NA	♂	NT
32	♂	X	-	NA
34	♀	X	-	NA
35	♀	X	♂	NT
37	-	NA	♂	NT
38	-	NA	♀	NT
41	♀G	X X	-	NA
43	-	NA	♂	NT
44	-	NA	♂	NT
47	-	NA	♂	NT
48	♂	X X	♂	NT
50	♂	X X	♂	NT
54	♂	X X	-	NA
56	♀G	X X	-	NA
57	-	NA	♂	NT
60	♀	X X	-	NA
61	-	NA	♀	NT
62	♂	0 0	-	NA
65	-	NA	♂	NT
69	♀	X X X	♀G	NT
74	♀	X X X	-	NA
76	♀	0 0	♂	NT
82	♂	0 0	♀	NT
84	♀G	0 0	♂	NT

- - can empty
- NA - not applicable
- NT - no tag
- 0 - tag pattern
- X - tag pattern
- ♀G - gravid female

Table 9. Tagged crayfish in respective cans on 15/12/73 and location of crayfish present on the following day.

new furrow may be constructed each day. Goellner (1943) (cited in Momot M.S.) found that Orconectes immunis did not display homing and as far as he could determine movements were random, although Merkle (1969) reports that O. juvenalis does show homing, one crayfish often living under the same rock for up to 30 hours.

Of the 22 tagged crayfish only one was caught in the 4 traps that were laid indiscriminantly within and near to the transect (see Fig. 3). Can No. 3 housed this crayfish which was caught in Trap 1, having travelled a distance of 5m. This was similar to the calculated average trapping radius of 3.7m.

This experiment was performed to determine whether a home range existed, and its extent. But, as only one tagged crayfish was trapped and since tagging may have influenced movements, it is difficult to draw definite conclusions from the experiment. However, as none of the tagged crayfish were found in the same locality the next day, it seems likely that P. planifrons did not show a distinct home range. Camougis and Hichar (1959) found that marked Orconectes virilis moved freely about and distributed themselves evenly throughout the total population in a pond and therefore did not show a distinct home range. Other evidence that crayfish may distribute themselves randomly comes from a study by Wickliff (1940) in which a depopulated area of a stream yielded 72.1% of the original crayfish crop 2 days later. However, Black (1963) states that, in streams, both Procambarus penni and P. bivittatus have home ranges of 33m., while Merkle (1969)

showed that stream dwelling O. juvenalis display a home range of 23m. It seems, therefore, that the phenomena of home range and homing instincts are restricted to only certain species of crayfish.

Although territoriality was not investigated on an experimental basis in this study, while diving it was often noted that some crayfish exhibited apparent territorial behaviour, making aggressive postures when approached closer than 1m. Often crayfish would travel quite quickly towards a diver from distances of about 5m., but when about 1m. away their behaviour would change to that just described. On the other hand, many crayfish were seen grouped around and under objects, such as rocks and sunken debris, in densities of up to 10 crayfish/m.<sup>2</sup>.

Territoriality is often associated with aggression resulting from dominance. Bovbjerg (1953) found that in 2 groups of male and female O. virilis there was a straight-line dominance order, and males were dominant over females. He states that in the laboratory intrinsic factors such as body size, sex and moulting may influence dominance order, while extrinsic factors such as territoriality, population density and size may be of importance in nature. Bovbjerg (1956) also found that in Procambarus alleni, size was directly related to dominance in both sexes and this was also found to be the case in Paranephrops planifrons. Laboratory observations of P. planifrons showed that large males and females were more aggressive and displayed dominance over smaller crayfish.

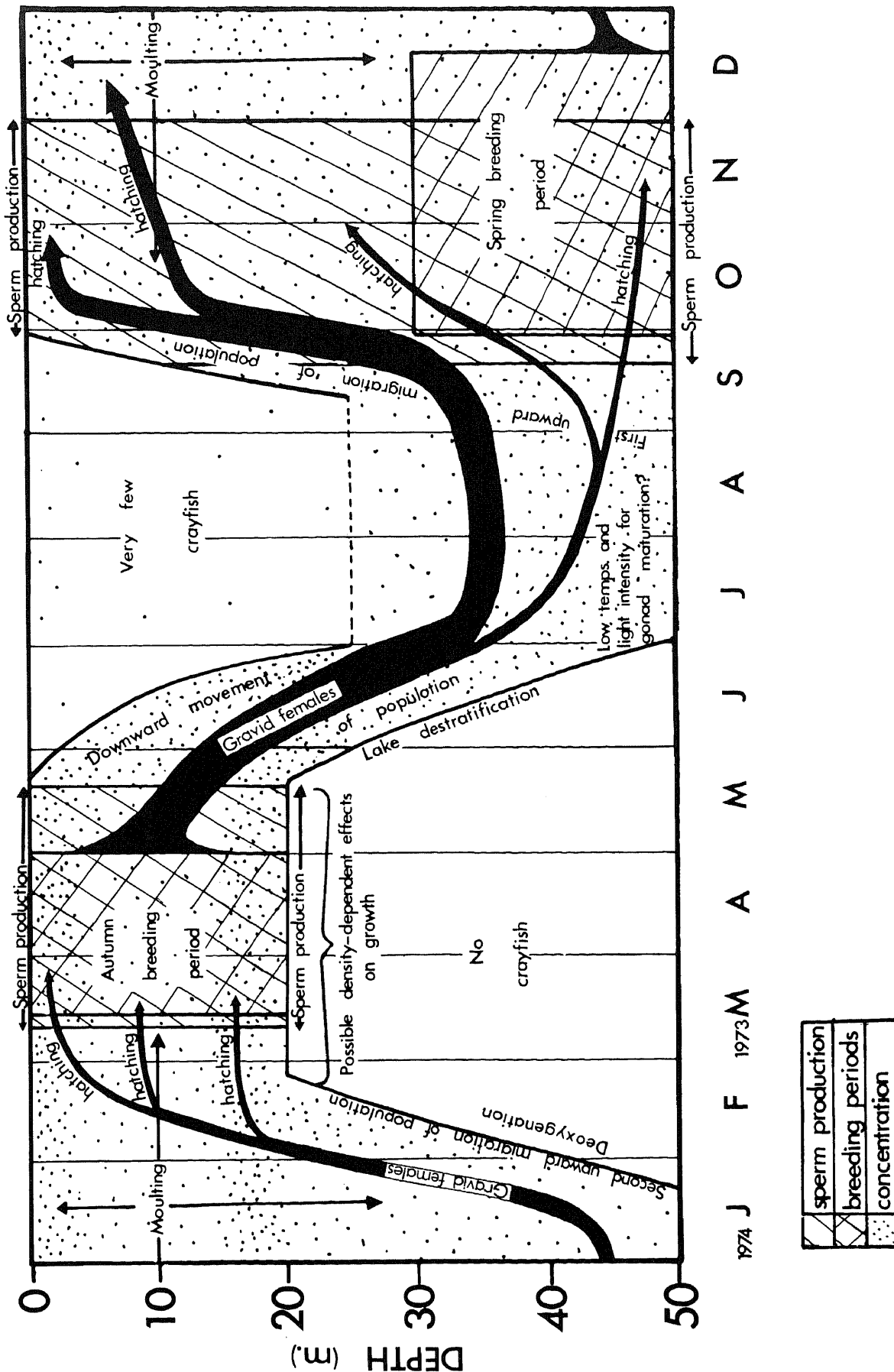
## CONCLUDING DISCUSSION

Fig. 10 summarises diagrammatically the proposed interpretations of the seasonal breeding cycle and associated distribution patterns of Paranephrops planifrons in Lake Rotoiti. It appears that during March and April 30 - 40% of the female population became gravid, which coincided with sperm production by mature males in the shallows and within the thermocline. These events began when photoperiod was about 12 hours. Thus by May the main breeding season was in progress. During May lake destratification and subsequent hypolimnetic deoxygenation permitted movement to deeper waters where the population was free to distribute over the lake floor throughout the winter months. Therefore the incubation of eggs of winter gravid females took place mainly in deeper waters.

It is not at all clear why the crayfish migrated into the deeper waters. Increased food concentration or quality with depth may have been a reason although sediment analyses did not reveal any appreciable difference in food quality at different depths. Downward movements of this type have been found to be associated with gonad maturation in Orconectes virilis (Momot 1967a, Aiken 1969a) and this may have occurred in Paranephrops planifrons as well.

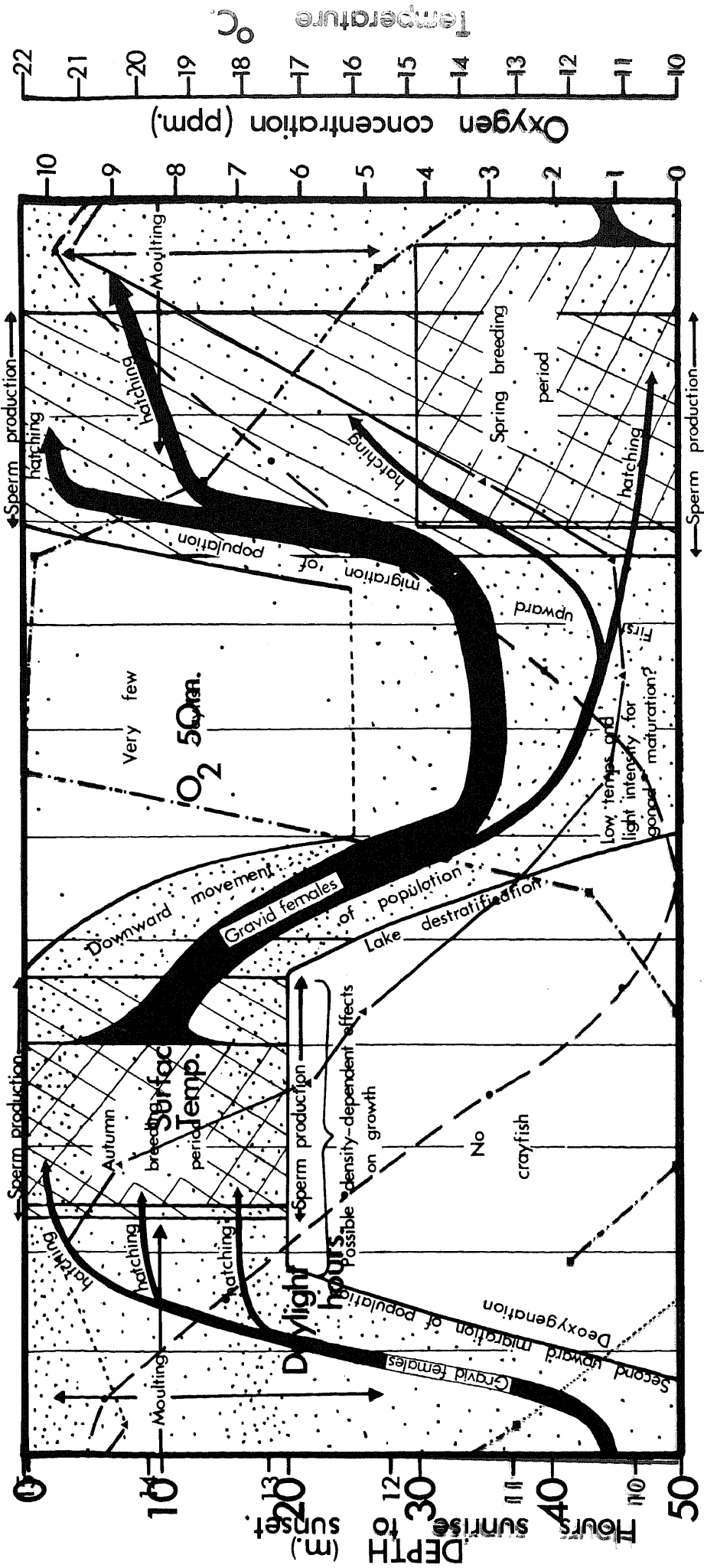
In late September there was a partial but rapid influx of both sexes into shallower water where temperatures were slightly higher and it was possible that the slight rise in temperature may have induced the migration. This movement was marked by a slight preponderance of gravid females whose eggs were beginning to hatch. Egg-

Fig. 10: Proposed seasonal breeding cycle and associated spatial distribution patterns of Paranephrops planifrons in Lake Rotoiti. Patterns of movement are depicted and factors which are thought to influence the population are indicated, and shown in the overlay. Periods of egg and sperm production, egg-hatching and moulting are given. The thickness of the arrows indicate the relative numbers of gravid females. The stippled areas show seasonal and spatial distribution and concentration of the total population.



stippled pattern	sperm production
hatched pattern	breeding periods
solid black	concentration

1974 J F 1973 M A M J J A S O N D



1974 J F 1973 M A M J J A S O N D

	sperm production
	breeding periods
	concentration

hatching continued until December. Because of this movement of females upwards most of the eggs hatched in shallow water. The reason for the migration may have been to allow egg-hatching in the shallows, since as young crayfish probably lived in the weeds (Tack 1941, Momot M.S.), it would be of adaptive value for such a migration to occur. However, this would not explain why males and non-gravid females also moved upward at this time and why some hatchings occurred in deep water. It may simply have been that the slight rise in temperatures, which had occurred during the end of September, may have been sufficient to induce the migration because of preference for the warmer water by the crayfish. A further possibility is that movement upwards is associated with gonad developmental processes taking place at the same time as hatching, and which may have been induced by the low light and temperature conditions of winter. Such conditions are known to influence the reproductive cycle of crayfish (Aiken 1969a), and movements, and events in the reproductive cycle, are often associated (Momot 1967a; M.S.).

We have seen that two breeding periods occurred and it may be that this early spring movement upwards was of animals produced only from one of these breeding periods, as timing of gonad development between successive cohorts would presumably be out of phase. If this happens to be the case one can only guess whether the crayfish involved in the September upward migration were animals from the autumn cohort or from those produced in early summer. Data on numbers were inadequate to calculate the

percentage of the population that moved up, for, if it was a majority, then it would seem logical to deduce that the movement was of autumn bred crayfish which comprise the larger breeding season.

From the beginning of October till the end of November, sperm production by males occurred at all depths and only deep water females produced eggs. About 60% of them bore eggs and egg-laying ended towards the end of December. As well, a period of increased moulting activity had begun by October which extended through summer.

The lake became fully stratified during December, after which the hypolimnion became progressively deoxygenated. It can be estimated from the rate of decline of oxygen concentrations at 50m. (Fig. 8'b) that no crayfish would be present in the hypolimnion by mid-February. It was probably the falling oxygen concentration which induced the gradual exodus of the deep water population into shallower water. Although samples were not taken after January it seems logical that hatching of the summer brood would be completed by mid-March.

Therefore, the main breeding season occurred during winter when about 30 - 40% of the females were gravid, followed by a smaller breeding season in summer when about 10% bore eggs. Hence it seems that about 40 - 50% of the female population breeds annually, and most of the egg-hatching occurs in the shallows.

It can be seen, therefore, that Paranephrops planifrons in Lake Rotoiti has a complex seasonal cycle, which does not appear to be paralleled by that of any other

species, although similarities in pattern are displayed by Orconectes virilis inhabiting marl lakes of Michigan (Momot 1967a, Momot and Gowing 1972, Fast and Momot 1973). However, this species apparently does not have a double upward migration during spring and summer of the type which occurs for P. planifrons. Also, unlike O. virilis, males of P. planifrons do not show aggression towards females and thus differential distribution of the males and females after the spring-early summer hatching period does not occur.

Evidence from Lake Okataina showed that seasonal migrations of P. planifrons probably did not occur in this oligotrophic lake and there was only one breeding season, in winter. These findings agreed with those of Hopkins (1967a) for stream-dwelling populations of P. planifrons and were similar to those of Abrahamsson and Goldman (1970) for Pacifastacus leniusculus in Lake Tahoe.

This study produced many unanswered questions. For example, in Wright's Bay population density was high and individual sizes small compared to those in other parts of Lake Rotoiti and in Lakes Okataina and Rotorua. It would thus be of interest to study growth rates of the crayfish and the factors affecting them, e.g. the effect of food concentration and population density, and their relationships, on growth. Territoriality and associated aggressive behaviour are also known to be important regulating influences in crayfish populations (e.g. Bovbjerg 1953) and a more detailed study of these aspects in Paraneohpops planifrons than made in the present study would

be desirable. Also, more must be known about density, distribution or behaviour of juvenile P. planifrons.

In this study changes in numbers of gravid females, and times of sperm production, egg-laying and egg-hatching, were used to follow breeding activity of the crayfish. However, in order to obtain a more exact understanding of breeding cycles, studies on seasonal changes of gonad state and stages of egg development are required (e.g. such as those of Stephens 1952, Armitage et al 1972; 1973).

As indicated, the reason put forward to explain why P. planifrons displayed seasonal migratory behaviour were only suggestions based on evidence from other workers such as Scudamore 1948, G.J. Stephens 1952, G.C. Stephens 1955, Lowe 1961, Momot 1967a, Aiken 1968; 1969a; 1969b, Armitage et al 1973 and Fast and Momot 1973. In order to obtain a clearer insight experiments similar to those performed by these workers on possible regulating and controlling factors, must be undertaken on P. planifrons. Studies on such factors as photoperiod and temperature which are known to control the reproductive cycle and moulting patterns of crayfish by regulating hormonal levels would be very valuable.

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